Photosynthetic nutrient-use efficiency in three fast-growing tropical trees with differing leaf longevities

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Summary Differences in nutrient-use efficiency have been attributed to differences in leaf habit. It has been suggested that evergreens, with their longer-lived leaves, and therefore longer nutrient retention, are more efficient than deciduous species in their use of nutrients. In tropical trees, however, leaf life span is not always a function of whole-tree deciduousness, leading to the proposal that nutrient-use efficiency is better related to leaf life span than to leaf habit. It was predicted that potential photosynthetic nutrient-use efficiency (maximum potential photosynthesis/leaf nutrient content) would decrease with increasing leaf life span, whereas cumulative photosynthetic nutrient-use efficiency (carbon assimilated over a leaf’s life span/total nutrients invested in a leaf) would increase with increasing leaf life span. Potential and cumulative photosynthetic nutrient-use efficiencies (with respect to nitrogen and phosphorus) were measured for three fast-growing tropical trees: Cedrela odorata L. (Meliaceae), Cordia alliodora (R. & P.) Cham. (Boraginaceae), and Hyeronima alchorneoides Allemão (Euphorbiaceae). Mean leaf life spans of the three species varied about threefold and ranged from 50 to 176 days. The predictions were partially supported: Cedrela odorata had the shortest-lived leaves and the highest potential nitrogen-use efficiency, whereas Hyeronima alchorneoides had the longest-lived leaves and the highest cumulative nitrogen- and phosphorus-use efficiencies. Potential phosphorus-use efficiency, however, was invariant among species. It is suggested that there are potential tradeoffs between leaf characteristics that lead to high potential and cumulative nutrient-use efficiencies. High potential nutrient-use efficiency may be beneficial in high-nutrient environments, whereas high cumulative nutrient-use efficiency may be of greater benefit to species in low-nutrient environments.

Keywords: Cedrela odorata, Cordia alliodora, Hyeronima alchorneoides, leaf life span, maximum photosynthesis, nitrogen, phosphorus.

Introduction

The efficiency with which plants use and retain nutrients can determine their relative competitive ability (Rundel 1982, Tilman et al. 1997) and dominance in a given environment (Aerts and van der Peijl 1993). Several investigators have invoked different measures of nutrient-use efficiency to characterize both spatial (Small 1972, Vitousek 1982, 1984, Gray 1983, Schlesinger et al. 1989, Silver 1994), and temporal (Chiba and Hirose 1993, Ellsworth and Reich 1996) patterns of species distribution along environmental gradients.

In the past, differences in nutrient-use efficiency among species have been attributed largely to leaf habit, i.e., whether species are deciduous or evergreen. It has been suggested that, compared with deciduous species, evergreens, by virtue of their presumed greater leaf longevity, have greater cumulative carbon gain over leaf lifetimes (Schulze et al. 1977, Chapin 1980, Chabot and Hicks 1982, DeLucia and Schlesinger 1995), accompanied by longer nutrient retention and lower rates of nutrient losses (Monk 1966, Gray 1983, Schlesinger et al. 1989, Aerts 1995). Nevertheless, leaf longevity and leaf habit may be quite unrelated, especially in tropical trees (Kikuzawa 1991, Craine and Mack 1998). A plant may be evergreen, yet have short-lived leaves. Therefore, leaf longevity, rather than leaf habit, may be a more fundamental axis along which to draw species comparisons (Reich et al. 1991, 1992, 1997, 1999).

The most widely used index of nutrient-use efficiency for individual leaves is potential photosynthetic nutrient-use efficiency (PPNUE; Field and Mooney 1986), hereafter referred to as potential PNUE. This is an instantaneous measure of nutrient-use efficiency, and is calculated as the ratio of potential maximum photosynthesis to foliar nutrient content. Although plants seldom photosynthesize at maximum rates for extended periods of time, potential PNUE is a useful index for comparing potential performance among species (Field and Mooney 1986). It is also possible to consider a more integrative measure of photosynthetic nutrient-use efficiency: the ratio of total carbon assimilation by a leaf to total nutrient investment in that leaf over its lifetime, hereafter called cumulative PNUE (cf. Small 1972, Rundel 1982).

The conditions that select for high potential PNUE may differ from those that select for high cumulative PNUE. There is an inverse relationship between rates of maximum photosynthesis and leaf life span (Reich et al. 1992). In addition,
longer-lived leaves may have greater proportional allocation of nutrients to non-photosynthetic functions than leaves with shorter life spans (Field and Mooney 1986). I predicted that potential PNUE increases with decreasing leaf longevity. Long-lived leaves, on the other hand, may have low rates of photosynthesis, but their greater longevity may be a result of selection for maximum carbon gain per unit of nutrient invested in leaves over their life span. Therefore, I also predicted that cumulative PNUE increases with increasing leaf longevity.

Potential and cumulative PNUE with respect to nitrogen (N) and phosphorus (P) were measured in three species of tropical trees: *Hyeronima alchorneoides* Allemão (Euphorbiaceae), *Cedrela odorata* L. (Meliaceae) and *Cordia alliodora* (R. & P.) Cham. (Boraginaceae). *Cedrela odorata* and *Cordia alliodora* have rapid leaf turnover and are similar to other, early successional tropical tree species; *Hyeronima alchorneoides* has slower leaf turnover, and is more similar to species that occur later in succession (Shukla and Ramakrishnan 1984, Haggar and Ewel 1995). I predicted that *Cedrela odorata* and *Cordia alliodora* would have high potential PNUE, whereas *Hyeronima alchorneoides* would have high cumulative PNUE.

**Methods**

**Study site and species**

The species were grown in experimental plantations at La Selva Biological Station in the Atlantic lowlands of Costa Rica. Mean annual temperature at La Selva is 25.8 °C and mean annual rainfall is approximately 4 m, with a brief dry season from February to April (Sanford et al. 1994). Soil at the site is relatively rich in extractable N (13.7 µg g⁻¹), soil depth 0–10 cm, potassium chloride extraction) and P (14.4 µg g⁻¹, soil depth 0–10 cm, acid ammonium fluoride extraction). Trees were planted in 1991, in plots of 30 × 40 m, in a randomized block design with three replicates (Haggar and Ewel 1994, 1995, 1997). The uniform conditions under which the species were grown ensured that any variation in PNUE observed could be attributed to inherent differences in leaf characteristics, rather than to phenotypic responses to differing environments.

The study species—*Cedrela odorata*, *Cordia alliodora*, and *Hyeronima alchorneoides* (hereafter, *Cedrela*, *Cordia* and *Hyeronima*, respectively)—are all fast-growing tropical hardwoods native to Costa Rica. They represent an array of foliar characteristics. *Cedrela* has large, pinnately compound leaves that can be up to a meter long, with 10–20 pairs of leaflets, each about 40 cm², and tends to be deciduous during the dry season. *Cordia* 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); during the juvenile phase it maintains its foliage year-round, although it is partially deciduous during the dry season. *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.

**Photosynthesis**

Potential PNUE was calculated as the rate of maximum potential photosynthesis (Pmax) divided by foliar nutrient content (L), Maximum potential photosynthetic rates were measured on well-lit, young, fully expanded leaves in the canopy, from a 14-m movable scaffold tower, in two of the three blocks of the experiment, during June–July 1997. Permanent tower bases in each plot enabled access to between three and five trees at a time. Maximum photosynthesis was measured on 10 leaves selected at random, not more than five leaves being selected from any one tree. Photosynthesis was measured at ambient CO₂ concentration with an LI-6200 portable photosynthesis system (LI-Cor, Inc., Lincoln, NE), with an artificial light source (Mini-Cool AC/DC lamp, Model LK 2050, Cool-Lux, Camarillo, CA) to ensure that light was saturating (> 1600 µmol m⁻² s⁻¹). Measurements were made at a relative humidity of 60–90% and leaf temperature of 30–37 °C. The same leaves were then sampled for determination of leaf mass per area (LMA) and foliar N and P.

Cumulative PNUE was calculated as:

\[
\text{Cumulative PNUE} = \frac{\int_{t_{0}}^{t_{L}} P_s dt}{L(t) (1 - \text{Resorption})},
\]

where the numerator is daily photosynthetic carbon gain integrated over the leaf’s life. The denominator is the amount of nutrients invested in a leaf over its life span and then lost from the plant, i.e., the product of foliar nutrient content and the fraction of nutrients not resorbed before leaf abscission. Nutrient resorption was calculated as the difference in nutrient content of living leaves and of freshly fallen litter, expressed as a proportion of nutrient content of living leaves (A.J. Hiremath and J.J. Ewel, unpublished data).

Photosynthesis as a function of light availability was measured with an LI-6200 photosynthesis system with a Li-Cor dual red-blue light (Q-Beam 6205 BD, Quantum Devices Inc., Barneveld, WI) as the light source. Photosynthesis was measured while decreasing photosynthetically active radiation (PAR) step-wise from a starting value of ~1800 µmol m⁻² s⁻¹. All measurements were made at a chamber CO₂ concentration of 330–340 ppm, relative humidity of 60–80% and leaf temperature of 25–37 °C. Photosynthesis was measured in June 1998, from a scaffold tower in one block of the experiment only. Measurements were made on five branches selected at random from at least three trees.

Non-rectangular hyperbolas (Thornley 1976) were fitted to the photosynthesis–light response curves by the non-linear regression procedure in SigmaPlot (SPSS Inc. 1997). The hyperbolae were of the form:

\[
P = \frac{[(\alpha I + P_{\text{max}}) - \sqrt{(\alpha I + P_{\text{max}})^2 + 4\alpha I P_{\text{max}}}]}{2\alpha},
\]

where \(P\) is photosynthetic rate, \(I\) is photon flux density, \(P_{\text{max}}\) is
light-saturated photosynthetic rate, $\alpha$ is quantum yield (i.e., the initial slope of the photosynthesis–light response curve), and $\theta$ is a term that denotes curvature ($\theta$ was constrained between 0.5 and 0.8, and $\alpha$ was given a value of 0.05 µmol CO$_2$ µmol$^{-1}$ photons) (Valladares et al. 1997).

Cumulative photosynthesis was calculated by integrating mean daily photosynthesis over leaf life spans based on a decreasing linear function as follows:

$$\int_{\text{Lifespan}} P_s = \int_{\text{Lifespan}} f(t) dt$$

(3)

where

$$f(t) = \frac{(P_{S,\text{old}} - P_{S,\text{young}})}{(\text{Age}_{\text{old}} - \text{Age}_{\text{young}})} t + P_{S,\text{young}},$$

(4)

and where $P_{S,\text{young}}$ and $P_{S,\text{old}}$ denote mean daily photosynthesis by young and old leaves, respectively, $\text{Age}_{\text{old}} - \text{Age}_{\text{young}}$ denotes the age difference between young and old leaves in days, and $t$ denotes time in days. The assumption of a linear decline in photosynthesis with leaf age was based on observations of other fast-growing tropical trees (Zotz and Winter 1994, Ackerley and Bazzaz 1995).

Mean daily net carbon assimilation (mmol m$^{-2}$ day$^{-1}$) by young and old leaves was calculated from the light response curves and previously measured PAR data (Bigelow 1998). Leaf position was used as a surrogate for leaf age, assuming that rates of leaf production are constant. This assumption was based on observations of continuous leaf flushing year-round (except in the case of Cedrela during the dry season, when it is deciduous). A “young” leaf was defined as the youngest, fully expanded leaf closest to the growing tip on each branch. “Old” leaves were proximal to young leaves and were selected to represent approximately two thirds of the leaf life span. For example, if, on average, there were 10 fully expanded leaves per branch, then the sixth leaf from the growing tip was selected to be an “old” leaf. The age of older leaves was estimated as the fraction (60% in this example) of total leaf life span that they represented. The rate of decline in photosynthesis was calculated as the difference in mean daily carbon assimilation by young and old leaves, divided by the length of time over which the decline occurred (Equation 4).

Photosynthetically active radiation was logged at 30-min intervals by sensors mounted above the canopy. The data used were the means of the measurements taken every 30 min on six consecutive days in June 1995 (Bigelow 1998). Light incident on leaves was adjusted for percent transmission, which was calculated by simultaneous measurements of PAR above the canopy and at leaf surfaces. Simultaneous light measurements were made on five pairs of young and old Hyeronima and Cedrela leaves, and four pairs of young and old Cordia leaves; PAR was measured every 10 s and logged at 1-min intervals during 1 h on a day in October 1998.

Leaf life span

Leaf life spans were measured over 9 months in two of the three blocks of the experiment, starting in July 1994. Successive cohorts of leaves were tethered and a census taken periodically until all tethered leaves had abscised, to calculate a mean leaf life span per cohort. Leaves were reached by means of the scaffold tower. Thirty newly emerged leaves (leafletlets, in the case of Cedrela) per cohort were tethered, and not more than 10 leaves were selected from any one individual. A census of previously marked cohorts was taken each time a new cohort was tethered, which was every 3 weeks for Cedrela, and every 6 weeks for Cordia and Hyeronima.

Foliar nutrient content and leaf mass per area

Foliar nutrients and LMA were determined on leaves used for measuring maximum potential photosynthesis. Leaf lamina disks, 0.25 cm$^2$ in area, were punched out from between veins to avoid fibrous tissue (Medina 1984). Disks were dried to constant weight at 70 °C and weighed. Leaf mass per area was calculated as the ratio of disk mass to disk area. The disks were then digested following a Kjeldahl protocol, and total N and P were analyzed on an autoanalyzer by standard colorimetry (Alpkem 1986). These foliar nutrient concentrations were used to calculate both potential and cumulative PNUE.

Rates of photosynthesis, foliar nutrient concentrations, and photosynthetic nutrient-use efficiency were analyzed by one-way analysis of variance, with species as the main effect. Analyses were performed with the GLM procedure using the SAS statistical software suite (SAS Institute Inc., Cary, NC). Interspecific differences in mean photosynthetic rates, foliar nutrient concentrations and nutrient-use efficiencies were tested by contrasts within the GLM procedure.

Results

Potential photosynthetic nutrient-use efficiency

Maximum potential photosynthesis on a leaf area basis ranged from about 8 to 12 µmol m$^{-2}$ s$^{-1}$ and followed a pattern of Cordia > Cedrela > Hyeronima (Table 1), with a significant difference in photosynthetic rate between Cordia and Hyeronima ($P = 0.0302$). Maximum photosynthesis expressed on a leaf mass basis also differed significantly among species ($P = 0.0038$), and followed a pattern of Cedrela > Cordia > Hyeronima.

Foliar N concentrations on a mass basis ranged from about 3 to 4% (Table 1). Hyeronima had a lower foliar N concentration than the other two species ($P = 0.015$), and there was no difference in foliar N concentration between Cedrela and Cordia. On the other hand, N concentration per unit leaf area was significantly higher in Cordia than in the other two species ($P = 0.023$) and is a reflection of differences in leaf mass per area among species. The thick leaves of Cordia had more foliar N per unit leaf area than the thinner leaves of Cedrela and Hyeronima.

Foliar P concentrations on a mass basis were between about 0.20 and 0.35% (Table 1). Cedrela had a higher foliar P concentration than the other two species ($P = 0.015$), but there was no difference in foliar P concentration between Hyeronima and Cordia. On an area basis, interspecific differences in foliar
Table 1. Leaf mass per area (LMA), mass- and area-based maximum photosynthetic rates, and foliar nitrogen and phosphorus concentrations of the three species. Values are means (standard errors) of two blocks, each comprising measurements on 10 leaves. Different letters indicate significant differences at $P < 0.05$.

<table>
<thead>
<tr>
<th>Species</th>
<th>LMA ($\text{g m}^{-2}$)</th>
<th>Photosynthesis $\mu\text{mol m}^{-2} \text{s}^{-1}$</th>
<th>N Concentration $\text{mmol m}^{-2}$</th>
<th>% (w/w)</th>
<th>P Concentration $\text{mmol m}^{-2}$</th>
<th>% (w/w)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hyeronima</td>
<td>79.85 ab</td>
<td>8.07 a</td>
<td>100.75 a</td>
<td>164.0 b</td>
<td>2.8 b</td>
<td>5.2 a</td>
</tr>
<tr>
<td></td>
<td>(4.5)</td>
<td>(0.71)</td>
<td>(3.05)</td>
<td>(9.3)</td>
<td>(0.0)</td>
<td>(0.5)</td>
</tr>
<tr>
<td>Cedrela</td>
<td>56.60 b</td>
<td>10.10 ab</td>
<td>180.20 b</td>
<td>150.2 b</td>
<td>3.7 a</td>
<td>6.1 a</td>
</tr>
<tr>
<td></td>
<td>(5.7)</td>
<td>(0.48)</td>
<td>(11.50)</td>
<td>(23.5)</td>
<td>(0.2)</td>
<td>(0.2)</td>
</tr>
<tr>
<td>Cordia</td>
<td>92.26 a</td>
<td>12.12 b</td>
<td>133.15 c</td>
<td>268.8 a</td>
<td>4.1 a</td>
<td>7.3 a</td>
</tr>
<tr>
<td></td>
<td>(6.3)</td>
<td>(0.95)</td>
<td>(0.15)</td>
<td>(10.1)</td>
<td>(0.1)</td>
<td>(0.8)</td>
</tr>
</tbody>
</table>

P disappeared ($P = 0.17$), because of differences in leaf mass per area among species. A high concentration of P on a mass basis was spread over a larger area in the thin leaves of Cedrela than in the thicker leaves of Cordia and Hyeronima.

Potential photosynthetic N-use efficiency ranged from 45 to 68 $\mu\text{mol CO}_2$ (mol N)$^{-1}$ s$^{-1}$, and differed significantly among species. Potential photosynthetic N-use efficiency of Cedrela was higher than that of both Hyeronima ($P = 0.0540$) and Cordia ($P = 0.0344$; Figure 1a). Potential photosynthetic P-use efficiency varied from about 1600 to 1700 $\mu\text{mol CO}_2$ (mol P)$^{-1}$ s$^{-1}$, but did not differ among species ($P = 0.1380$; Figure 1b), despite considerable interspecific variation in both foliar P and photosynthesis (Table 1).

**Cumulative photosynthetic nutrient-use efficiency**

Photosynthesis–light response curves (Figure 2) and half-hourly PAR data (adjusted for differences in percent transmis-

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**Figure 1.** Instantaneous photosynthetic nutrient-use efficiency of *Hyeronima alchorneoides*, *Cedrela odorata* and *Cordia alliodora*, with respect to (a) nitrogen, and (b) phosphorus. Labels on bars (L) indicate leaf life spans in days. Values are means of two blocks, each comprising measurements on 10 leaves. Error bars indicate standard errors (SE, $n = 2$); different letters indicate significant differences at $P < 0.05$.

**Figure 2.** Response of photosynthesis to changing light for five young and five old leaves of (a) *Hyeronima alchorneoides*, (b) *Cedrela odorata* and (c) *Cordia alliodora*. The solid lines denote non-rectangular hyperbolas fitted to the data (see Equation 2); open symbols are measured values; closed symbols are fitted values.
sion to young and old leaves (data not shown)) were used to plot daily courses of photosynthesis for young and old leaves (Figure 3). Mean daily carbon gain, calculated by summing photosynthesis over a 24-h period, ranged from about 154 mmol m\(^{-2}\) day\(^{-1}\) for older Hyeronima leaves to 332 mmol m\(^{-2}\) day\(^{-1}\) for young Cordia leaves (Table 2).

Leaf life spans of the three species were 50, 99 and 176 days for Cedrela, Cordia and Hyeronima, respectively, and are at the low end of leaf life spans reported for a range of tropical tree species (between 60 days and 4 years; Reich et al. 1991). Leaf life spans calculated from turnover rates based on leaf standing crop and annual litterfall were correlated with, but not exactly equal to, the low end of leaf life spans reported for a range of tropical tree species (between 60 days and 4 years; Reich et al. 1991).

Leaf life spans were based on the assumption that photosynthetic rates were inversely related to leaf life span, because longer-lived leaves tend to have proportionally more carbon-rich protective tissue (Coley 1988, Turner 1994) at the expense of photosynthetic tissue (Coley 1988, Turner 1994). Photosynthetic rates expressed on a leaf tissue basis declined with increasing leaf life span (Table 1); nevertheless, area-based maximum photosynthetic rates were higher for leaves of the three species (45–68 µmol CO\(_2\) (mol N)\(^{-1}\) s\(^{-1}\)) are comparable with potential PNUE for tropical deciduous species with leaf life spans of 6–10 months (50–80 µmol CO\(_2\) (mol N)\(^{-1}\) s\(^{-1}\)) and higher than values reported for tropical evergreen species with leaf life spans of 11–12 months (25–30 µmol CO\(_2\) (mol N)\(^{-1}\) s\(^{-1}\); Sobrado 1991). Compared with potential PNUE measured for tropical early successional species (about 11 mol m\(^{-2}\) (Cedrela) to 30 mol m\(^{-2}\) (Hieronima) (Table 2), potential PNUE of the study species was quite low. This difference is probably associated with the method of calculation of potential PNUE. Potential PNUE based on leaf lamina nutrient contents (this study) are lower than values based on whole-leaf nutrient contents (other studies), because nutrients are inversely related to leaf life span, because longer-lived leaves, was no different from that of Cordia, which is contrary to the initial prediction. Potential PNUE with respect to P was invariant across species. The initial predictions relating potential PNUE to leaf life span were based on the assumption that photosynthetic rates are inversely related to leaf life span, because longer-lived leaves tend to have proportionally more carbon-rich protective tissue (Coley 1988, Turner 1994) at the expense of photosynthetic tissue (Coley 1988, Turner 1994). Photosynthetic rates expressed on a leaf tissue basis declined with increasing leaf life span (Table 1); nevertheless, area-based maximum photosynthetic rates were unrelated to leaf life span. Cordia, with intermediate leaf life span, but higher foliar N concentrations, had the highest area-based maximum photosynthetic rates, in keeping with the pattern of the photosynthesis–foliar N relationship described by Field and Mooney (1986) for a broad range of species. The values of potential PNUE measured for the study species (45–68 µmol CO\(_2\) (mol N)\(^{-1}\) s\(^{-1}\)) are comparable with potential PNUE measured for tropical deciduous species with leaf life spans of 6–10 months (50–80 µmol CO\(_2\) (mol N)\(^{-1}\) s\(^{-1}\)), and higher than values reported for tropical evergreen species with leaf life spans of 11–12 months (25–30 µmol CO\(_2\) (mol N)\(^{-1}\) s\(^{-1}\); Sobrado 1991). Compared with potential PNUE reported for tropical early successional species (about 61–144 µmol CO\(_2\) (mol N)\(^{-1}\) s\(^{-1}\); Ellsworth and Reich 1996), potential PNUE of the study species was quite low. This difference is probably associated with the method of calculation of potential PNUE. 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are diluted by the presence of carbon-rich vein tissue. When potential PNUE of the study species was calculated on the basis of whole-leaf nutrient contents, values (71–107 µmol CO₂ (mol N)⁻¹ s⁻¹) were more comparable with values reported by Ellsworth and Reich (1996).

Cumulative photosynthetic nutrient-use efficiency

Cumulative PNUE, with respect to both N and P, varied two-fold among species. Differences in cumulative PNUE were strongly influenced by leaf life span: *Hyeronima* had the longest-lived leaves and the highest cumulative PNUE, as predicted. However, cumulative PNUE of *Cordia* did not differ from that of *Cedrela*, even though its leaves were twice as long-lived as those of *Cedrela*. It is likely that the greater nutrient resorption and higher photosynthetic rate per unit of leaf nutrients in *Cedrela* compensates for the effect of greater leaf longevity in *Cordia*. These findings are consistent with Small’s (1972) calculations of a closely related index, “potential photosynthate.” Bog evergreens, with leaf life spans of two to three seasons, had a greater carbon gain per unit leaf N than non-bog deciduous species; furthermore, deciduous bog species, which resorbed a larger proportion of foliar N than deciduous non-bog species, had a greater carbon gain per unit leaf N than non-bog species.

The primary reason for predicting that cumulative PNUE would increase with increasing leaf life span was that cumulative carbon gain is proposed to be greater in longer-lived leaves (Schulze et al. 1977, Chapin 1980). However, cumulative carbon gain also depends on a leaf’s photosynthetic capacity (i.e., its capacity for daily carbon gain) and the rate at which this capacity declines as the leaf ages.

Mean daily carbon gain calculated from the light response curves and PAR data (292–391 mmol m⁻² day⁻¹ for young leaves of the three species) was comparable with the maximum values (370 mmol m⁻² day⁻¹) obtained by direct measurement of 24-h carbon gain in *Ceiba pentandra* (L.) Gaertn. (Bombacaceae), another fast-growing tropical tree (Zotz and Winter 1993). Mean carbon gain values calculated for the study species are higher than those measured by Zotz and Winter (1993), because my calculations are based on PAR measured on clear days in June, when insolation is high (mean daily photon flux density was 42.9 mol m⁻² day⁻¹ compared with maximum photon flux densities of 6.9 to 46.1 mol m⁻² day⁻¹ measured at La Selva between March and November; Oberbauer et al. 1989). Furthermore, my calculations of mean daily carbon gain do not take into account midday depression in photosynthesis caused by stomatal limitation. Midday stomatal closure has been measured for at least one (*Hyeronima*) of the three study species by Bigelow (1998).

All three species showed a decline in photosynthetic capacity with increasing leaf age. This decline was steepest for

![Figure 4. Cumulative photosynthetic nutrient-use efficiency, i.e., the ratio of cumulative leaf carbon gain to nutrients invested in leaves over leaf lifetimes (see Equation 1), with respect to (a) nitrogen and (b) phosphorus, for *Hyeronima alchorneoides*, *Cedrela odorata* and *Cordia alliodora*. Labels on bars (L) indicate leaf life spans in days. Values are means; error bars indicate standard errors (SE, n = 2); different letters indicate significant differences at P < 0.05.](image-url)
Cedrela and most gradual for Hyeronima. This matches predictions (Kikuzawa 1991) and results (Kitajima et al. 1997) suggesting that rate of decline in photosynthesis with leaf age is inversely related to leaf longevity.

Ecological implications

Reich et al. (1991) suggested that there are tradeoffs between leaves with high photosynthetic rates and leaves that are long-lived. By extension, there may be tradeoffs in the selection for traits leading to high potential PNUE and those leading to high cumulative PNUE. It is likely that a high potential PNUE would be advantageous in environments where nutrients are less constraining and rapid tissue and nutrient turnover do not, therefore, jeopardize nutrient supply; high cumulative PNUE is likely to be advantageous in environments where nutrients are more limiting.

These predictions are partially borne out by two of the study species, Cedrela and Hyeronima. Thus, Cedrela had the shortest-lived leaves and the highest potential PNUE (for N), whereas Hyeronima had the longest-lived leaves and the highest cumulative PNUE (for N and P). Furthermore, Cedrela tends to occur in forests on fertile soils (e.g., along rivers), whereas Hyeronima, although it also occurs on fertile soils, persists in closed forest environments that are likely to be more competitive (Clark and Clark 1992).

The third species, Cordia, exhibited neither high potential PNUE nor high cumulative PNUE, although it had the highest foliar nutrient concentration and photosynthetic rate of the three species. Cordia is likely to have the highest productivity of the three species, provided that nutrients are amply available (cf. Haggar and Ewel 1995). Cordia is also likely to be the first of the three species to experience nutrient deficiency and the effects of belowground competition for resources when nutrients become limiting (cf. Haggar and Ewel 1997). These predictions are supported by the observations that Cordia readily colonizes old fields on fertile soils, but grows slowly when planted on less fertile soils (Butterfield 1994).

By analogy with Berendse and Aerts’ (1987) discussion of nutrient-use efficiency at the whole-plant level, differences in PNUE might impart different competitive abilities on species, depending on the environment. A high potential PNUE would likely be advantageous to species in fertile, high-light environments, where growing large quickly is the key to resource capture (Tilman 1988) and there is no likely added benefit to be derived from conservative use of resources. On the other hand, a greater cumulative PNUE would likely be advantageous to species in resource-poor environments, where nutrient conservation, rather than rapid growth, is the key to persistence and fitness.

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