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Photosynthesis-nitrogen relations in Amazonian tree species

I. Patterns among species and communities

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Abstract Among species, photosynthetic capacity (A_{max}) is usually related to leaf nitrogen content (N), but variation in the species-specific relationship is not well understood. To address this issue, we studied A_{max}-N relationships in 23 species in adjacent Amazonian communities differentially limited by nitrogen (N), phosphorus (P), and/or other mineral nutrients. Five species were studied in each of three late successional forest types (Tierra Firme, Caatinga and Bana) and eight species were studied on disturbed sites (cultivated and early secondary successional Tierra Firme plots). A_{max} expressed on a mass basis (A_{mass}) was correlated ($p < 0.05$) with N_{mass} in 17 of 23 species, and A_{max} on an area basis (A_{area}) was correlated ($p < 0.05$) with N_{area} in 21 of 23 species. The slopes of A_{max}-N relationships were greater and intercepts lower for disturbance adapted early successional species than for late successional species. On a mass basis, the A_{max}-N slope averaged ≈ 15 µmol CO_2 $[g\ N]^{-1}\ s^{-1}$ for 7 early secondary successional species and ≈ 4 µmol CO_2 $[g\ N]^{-1}\ s^{-1}$ for 15 late successional species, respectively. Species from disturbed sites had shorter leaf life-span and greater specific leaf area (SLA) than late successional species. Across all 23 species, the slope of the A_{mass}-N_{mass} relationship was related ($p < 0.001$) positively to SLA ($r^2 = 0.70$) and negatively to leaf life-span ($r^2 = 0.78$) and temporal niche during secondary succession (years since cutting-and-burning, $r^2 = 0.90$). Thus, disturbance adapted early successional species display a set of traits (short leaf life-span, high SLA and A_{max} and a steep slope of A_{max}-N) conducive to resource acquisition and rapid growth in their high resource regeneration niches. The significance and form of the A_{max}-N relationship were associated with the relative nutrient limitations in the three late successional communities. At species and community levels, A_{max} was more highly dependent on N in the N-limited Caatinga than in the P- and N-limited Bana and least in the P- and Ca-limited Tierra Firme on oxisol- and differences among these three communities in their mass-based A_{max}-N slope reflects this pattern (6.0, 2.4, and 0.7 µmol CO_2 $[g\ N]^{-1}\ s^{-1}$, respectively). Among all 23 species, the estimated leaf N_{mass} needed to reach compensation (net photosynthesis $\approx$ zero) was positively related to the A_{mass}-N_{mass} slope and to dark respiration rates and negatively related to leaf life-span. Variation among species in the A_{max}-N slope was well correlated with potential photosynthetic N use efficiency, A_{max} per unit leaf N. The dependence of A_{max} on N and the form of the relationship vary among Amazonian species and communities, consistent with both relative availabilities of N, P, and other mineral nutrients, and with intrinsic ecophysiological characteristics of species adapted to habitats of varying resource availability.

Key words Amazon · Rain forests · Leaf life-span Photosynthesis · Nitrogen

Introduction

Variation in leaf N content has been widely identified as a determinant of net photosynthetic capacity (e.g., Gulmon and Chu 1981; Field and Mooney 1986). Although net photosynthetic capacity (A_{max}) and leaf N are generally related, both within and among species, ecological and species variation in this relationship are not well understood (Evans 1989). In exploring this topic, it may be useful to ask first, how much variation among species is there in this relationship, and second, are there ecologically important patterns to this variation? Field and

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Mooney (1986) found that mass-based A_{max} (A_{mass}) and leaf N (N_{mass}) (and to a lesser degree area-based expressions) were strongly correlated when data were pooled for 21 naturally growing C_3 species, suggesting a single fundamental relationship among species. Their finding was corroborated by two independent studies that found similar correlation coefficients and regression equations for the relationship of A_{mass} to N_{mass} among large numbers of species (Reich et al. 1991a, 1992). Despite the generality of this relationship across species, however, it is not clear whether the within-species form of this relationship varies systematically from species-to-species in relation to ecological patterns.

Examining the 12 studies summarized by Field and Mooney (1986, Table 1.1), it is difficult to discern any recognizable pattern of variation among species in the slope (or intercept) of the A_{mass} to N_{mass} relationship. However, the slope of the A_{mass}-N_{mass} regression was greater in open- than shade-grown individuals for *Piper* species in Mexico (Chazdon and Field 1987), and for deciduous tree species in Wisconsin (Reich et al. 1990, 1991b). Evans (1989) considered mechanistic reasons related to partitioning of N within the leaf for differences in the A_{max}-N relationships among species grown in high versus low light. His analysis also suggested that such differences might reflect differences in light habitats among species. Exceptions to the generality of the A_{max}-N relationship have also been observed (e.g., Reich and Schoettle 1988) as a result of limitations due to other nutrients such as phosphorus.

In a recent paper we examined the among species relationships between leaf life-span, leaf N, SLA and A_{max}, across 23 Amazonian species (Reich et al. 1991a). In that paper we compared young, mature leaves of each species for plants growing in their common habitat under high light conditions. In the present paper we examine the relationships between N and A_{max} within each of those species, with variation in leaf traits a result of leaf age, canopy position, genotype, habitat and other factors. We attempted to maximize the sampled range of variation in leaf N and in light levels for each species. Variation in leaf age and growth light environment were the primary sources of variation in leaf N. We also compare different communities (pooling data across species within each), to assess whether adjacent communities noted for differences in resource availability have similar or different A_{max}-N relationships.

We studied a total of 15 species in four late-successional communities: the neverflooded Tierra Firme forests on both oxisols and ultisols, and the periodically-flooded tall Caatinga and low Bana, both on white sand spodosols (Sanford et al. 1985; Saldarriaga et al. 1988). The Tierra Firme and Caatinga forests are tall with large standing biomass, while the Bana is a naturally short, scrubby forest. These species occupy relatively undisturbed communities classified as late successional primary and secondary forests in the Rio Negro region (Saldarriaga et al. 1988). For comparative purposes we will call these forests late successional. In addition, we studied 8 species in agricultural and early secondary successional communities on disturbed Tierra Firme oxisol forest sites (Uhl 1987). These different communities in the Rio Negro region appear to be constrained by different nutrient limitations.

Based on differences in litterfall nutrient concentrations, ratios and annual fluxes, Cuevas and Medina (1986) suggested that Tierra Firme forests on oxisols are limited by P, Caatinga forests are limited by N, and Bana communities are limited by both N and P (Table 1). Consistent with these observations, root growth and litter decomposition studies suggest that Tierra Firme vegetation is limited by P, Ca and Mg, while both Caatinga and Bana communities are mainly N limited (Cuevas and Medina 1988, Table 1). Moreover, the ratio of P: N in foliage varies significantly among the late successional communities consistent with the notion

Table 1 Indices of nutrient dynamics in four Amazonian rain forest communities. The disturbed site represents disturbed Tierra Firme oxisol sites during the first several years of secondary succession following abandonment of cultivated *Manihot* plots

Measure	Bana	Caatinga	Tierra Firme	Disturbed	References[c]
Litterfall N (mg g^{-1})	5–7	6–7	10–16	10–15	1,4,5
Litterfall P (mg g^{-1})	0.2–0.6	0.3–0.5	0.3	0.4	1,4,5
Leaf N (mg g^{-1})	7–10	9–10	13–16	15–30	2,4,5
Leaf P (mg g^{-1})	0.4–1.0	0.8–0.9	0.6–0.8	0.8–2.0	2,4,5
Leaf P: N ratio	0.06–0.12	0.08–0.10	0.04–0.05	0.05–0.06	2,4,5
Leaf Ca (mg g^{-1})	5–7	2–4	1–2	5–10	2,4,5
Leaf Mg (mg g^{-1})	2–3	1–2	0.5–1	1–3	2,4,5
Litterfall N flux (g m^{-2} yr^{-1})	1.2	2.8–4.2	6.1–12.1	–	1
Litterfall P flux (g m^{-2} yr^{-1})	0.04	0.20–0.26	0.08–0.21	–	1
Litterfall P: N ratio	0.03–0.08	0.06–0.07	0.02–0.03	0.04	1,4,5
Root growth response[a]	N, P	N	P, Ca	–	2
Soil N mineralization[b]	–	–	14	21	3
Soil extractable P (ppm)	23	22	2	3	4

[a] Elements which induced a positive growth response are shown

[b] N mineralization rates in soil, units (mg kg^{-1} 30 $days^{-1}$)

[c] *1* Cuevas and Medina 1986; *2* Cuevas and Medina 1988; *3* Montagnini and Buschbacher 1989; *4* this study, and unpublished data; *5* Uhl 1987

that availability of P is limited for Tierra Firme species, while availability of N is limited for Caatinga and Bana species (Cuevas and Medina 1988, and Table 1). Following cutting-and-burning of Tierra Firme forest, there appears to be a greater availability of nutrients for several years than in undisturbed forest, after which levels return to pre-disturbance values (Uhl 1987; Montagnini and Buschbacher 1989; Ellsworth 1991, see Table 1). During this early secondary successional stage, limitations by P, Ca, Mg and K appear to be minimal and light availability to regeneration stage individuals is also much higher than in the late successional forests (Uhl 1987; Ellsworth 1991). Based on these collective observations (Table 1) and previous studies (see below), we formulated and tested the following hypotheses:

1) The dependence of A_{max} on leaf N is greatest in communities in which N is the most limiting nutrient (Reich and Schoettle 1988). Therefore, the strength of the A_{max}-N relationship should be related to community differences in the availability of N relative to other nutrients, with species in Caatinga forest and disturbed sites showing the strongest A_{max}-N relations and late successional Tierra Firme forest species the weakest.

2) Species adapted to higher than lower resource environments possess a suite of traits that collectively maximize assimilation and growth rate under high resource availability (Poorter et al. 1990; Reich et al. 1992). These traits include short leaf life-span and high N concentrations, SLA and A_{max}. We therefore hypothesize that species in relatively high resource agricultural and early successional sites will exhibit a strong response (steep slope) of A_{max} to N and that variation in this response will be related to other intrinsic species traits such as leaf morphology and life-span.

3) The capacity of a species to use an incremental increase in leaf N investment is dependent on the slope of the A_{max}-N relationship (Sage and Pearcy 1987). However, variation in A_{max} per unit N across species is dependent not only on the slope but also on the intercept of the A_{max}-N relationship and on N content. In this paper we explore the relationships between these different components of A_{max}-N relationships.

Materials and methods

The research site was located near San Carlos de Rio Negro, Venezuela (1°56' N, 67°03' W) at approximately 100 m elevation in the north central Amazon Basin. The climate of the region is humid equatorial, with a mean temperature of 26° C, a mean annual rainfall of 3565 mm, and a mean annual potential evaporative demand of 1900 mm (Cuevas and Medina 1986; Reich et al. 1991a). Several well differentiated communities occur in the Rio Negro region, each associated with distinct geomorphological positions and soil types (Sanford et al. 1985; Cuevas and Medina 1986). We studied species from four relatively undisturbed late successional forest communities within a 1 km distance of each other: species-rich Tierra Firme on oxisol, legume-dominated Tierra Firme on ultisol, Tall Caatinga, and Bana. Tierra Firme forests occur on the highest sites, while the Caatinga and Bana communities are at lower elevation, on periodically flooded fine-sand and coarse-sand spodosols, respectively (Sanford et al. 1985; Cuevas and Medina 1986). In addition, we studied plants in several disturbed (cultivated, early secondary successional, and treefall gap) sites on Tierra Firme oxisols. Sites were cultivated for 1–2 years following forest cutting and burning, and we studied secondary successional species that occupied recently abandoned (2–3 years after cutting and burning) Tierra Firme farms.

The agricultural community consisted largely of *Manihot esculenta*, a perennial root crop, and we also studied *Solanum straminifolia*, a pioneer species present as a weed in *Manihot* plots. The successional community included a mixture of pioneer to midsecondary successional species that occupy post-agricultural sites (Uhl 1987). One of these species, *Miconia*, is later successional than the others (Uhl 1987) and is also common in single treefall gaps in Tierra Firme forests. We studied *Miconia* in both a post-agricultural site and in a forest gap. The legume-dominated Tierra Firme community was represented only by the dominant tree species, *Eperua purpurea*, and when similar, results for this species are lumped with the species-rich Tierra Firme species. Each of the other three primary communities were represented in this study by 4 or 5 common species. To relate A_{max}-N relationships to species successional niches, data from Uhl (1987) and Saldarriaga et al. (1988) were used to estimate a time during succession when each species is most important and common in their respective community.

Leaf photosynthetic rates were measured in the field in January and February 1987 and 1988 using an open gas exchange system (Analytical Development Corporation, Hoddesdon, England). The CO_2 and water vapor sensors were calibrated against known gas standards. The following protocol was followed to ensure that near-maximum field photosynthetic rates were measured (see Reich et al. 1991a for more detail). Leaves were measured in early to mid-morning under ambient CO_2 concentrations, air temperatures, relative humidities and natural saturating irradiances (except for several leaves measured using artificial light). Under such conditions, temperatures were moderate and relative humidities high, and thus were near optimal. Measurements were made only on days following abundant rainfall during the previous five-day period. For all 23 species, photosynthetic rates were measured on a total of 14–49 leaves per species (average of 29), from about 5–15 trees. For each species, fully-expanded leaves of all ages (including old non-senescent and senescent leaves) and canopy positions were sampled, including canopy and understory microenvironments for the all forest communities. Thus, variation in leaf traits resulted from variation in leaf age, light environment and genotype. The comparison among species includes sun leaves of all species in high light microsites.

Immediately after photosynthesis measurements, each leaf was harvested, traced for leaf area determination, oven-dried and weighed. Leaves were analyzed for total organic N and other mineral elements by the University of Wisconsin Soil and Plant Analysis Laboratory using a micro-Kjeldahl assay and inductively coupled plasma emission spectrometry, respectively. Median leaf life-span was estimated using a large census of individual leaves from tagged branches (see Reich et al. 1991a). Data were pooled over time and were analyzed using analyses of variance and regression analyses (SAS 1985).

Results

Contrasts among species

There was a significant linear correlation of A_{mass} with N_{mass} for all 8 species on disturbed sites and for 9 of 15 species in the 4 late successional forest communities (Table 2, Fig. 1). The correlations were stronger for species on disturbed sites (r^2 ranged from 0.47 to 0.85) than for Caatinga and Bana forest species (only 6 of 10 species had $r^2 > 0.30$), and weakest in the Tierra Firme on

Table 2 Maximum net photosynthesis-nitrogen relationships in 23 rain forest species. Sample size (n), coefficient of determination (r^2), level of significance (*P*), slope and intercept are given for regressions of the form: net photosynthesis = intercept + slope*leaf N. Abbreviations and units: A_{mass} and A_{area} (nmol g^{-1} s^{-1} and µmol m^{-2} s^{-1}, respectively); N_{mass} and N_{area} (mg g^{-1} and g m^{-2}, respectively)

Community/Species (n)	A_{mass} vs N_{mass}				A_{area} vs N_{area}			
	r^2	*P*	slope	intercept	r^2	*P*	slope	intercept
Disturbed Tierra Firme/oxisols – Cultivated and weed species								
Manihot esculenta (24)	0.68	0.001	29.9	−777	0.17	0.05	11.0	−5.2
Solanum straminifolia (14)	0.47	0.05	21.1	−455	0.39	0.05	8.8	0.7
Disturbed Tierra Firme/oxisols – Secondary successional								
Bellucia grossularioides (21)	0.79	0.001	11.2	−75	0.35	0.02	5.1	2.5
Cecropia ficifolia (45)	0.56	0.001	14.1	−120	0.49	0.001	12.7	−6.8
Clidemia sericea (17)	0.80	0.001	15.1	−129	0.74	0.001	14.5	−9.9
Vismia lauriformis (21)	0.85	0.001	20.0	−204	0.61	0.001	14.7	−9.9
Vismia japurensis (49)	0.66	0.001	12.7	−71	0.24	0.001	5.7	2.5
Disturbed Tierra Firme/oxisols – Secondary successional and gap								
Miconia dispar (17)	0.70	0.001	7.9	−40	0.60	0.001	6.7	3.2
Species-rich Tierra Firme/oxisols								
"Cabari" (37)	0.12	0.03	3.0	−23	0.40	0.001	2.4	−0.8
Licania heteromorpha (34)	0.20	0.01	5.7	−26	0.70	0.001	4.8	−1.6
Ocotea costulata (28)	0.05	0.25	2.8	8	0.29	0.005	2.1	1.5
Protium sp. (41)	0.02	0.42	1.9	37	0.33	0.001	3.8	0.5
Legume-dominated Tierra Firme/ultisols								
Eperua purpurea (23)	0.43	0.001	4.0	−7	0.43	0.001	4.8	−1.1
Tall Caatinga/spodosol								
Caraipa heterocarpa (32)	0.00	0.75	0.8	25	0.68	0.001	5.2	−1.6
Eperua leucantha (34)	0.38	0.001	7.5	−68	0.17	0.02	2.5	1.3
Micrandra sprucei (33)	0.55	0.001	7.5	−43	0.70	0.001	5.3	−2.9
Micropholis maguirei (37)	0.07	0.10	2.8	−3	0.04	0.25	−1.0	3.4
Protium sp. (23)	0.52	0.001	7.4	−44	0.20	0.05	5.4	−2.5
Bana/spodosol								
Aspidosperma album (40)	0.44	0.001	5.3	−16	0.31	0.001	2.8	1.0
Neea obovata (30)	0.36	0.001	4.5	−23	0.35	0.001	3.0	0.3
Protium sp. (21)	0.08	0.20	3.0	6	0.20	0.05	4.8	−1.0
Retiniphyllum truncatum (37)	0.62	0.001	13.1	−44	0.50	0.001	12.6	−5.0
Rhodognaphalopsis humilis (18)	0.11	0.20	5.8	−1	0.05	0.50	2.6	3.0

oxisol ($r^2 \leq 0.20$ in all four species). When expressed on an area basis, the linear correlation of A_{max}-N was also significant in most species (21 of 23 species in total, Table 2 and Fig. 2). Within each community there was substantial variation among species in the strength of area-based relations.

The slopes of the mass-based A_{max}-N relationships were greater in the planted (*Manihot*) and weed (*Solanum*) species in the cultivated plot (21–30 µmol CO_2 [g $N]^{-1}$ s^{-1}) than in the five early successional species (11–20 µmol CO_2 [g $N]^{-1}$ s^{-1}), which were in turn greater than those in 14 of the 15 late successional species (all ≤ 7.5 µmol CO_2 [g $N]^{-1}$ s^{-1}, except for *Retiniphyllum*, Table 2 and Fig. 1). The intercepts were most negative for species in the cultivated plot, followed by the early successional species, and were least negative in the late successional species (Table 2). These patterns roughly follow the rankings of A_{mass} and N_{mass} among species – both are highest in the cultivated plot (200–500 nmol g^{-1} s^{-1} and 30–40 mg g^{-1} N, respectively) and also high in the early successional species (50–300 nmol g^{-1} s^{-1} and 10–25 mg g^{-1} N, respectively). In contrast, A_{mass} and N_{mass} were low in all late successional species (0–100 nmol g^{-1} s^{-1} and 5–25 mg g^{-1} N, respectively). However, even for species with comparable leaf N values, the slope of A_{mass} to N_{mass} was greater, and the intercept more negative, for earlier than later successional species. For example, the slope was greater (11–20 µmol CO_2 [g $N]^{-1}$ s^{-1}) in *Clidemia*, *Bellucia* and the two *Vismia* sp. on an early successional oxisol site than in

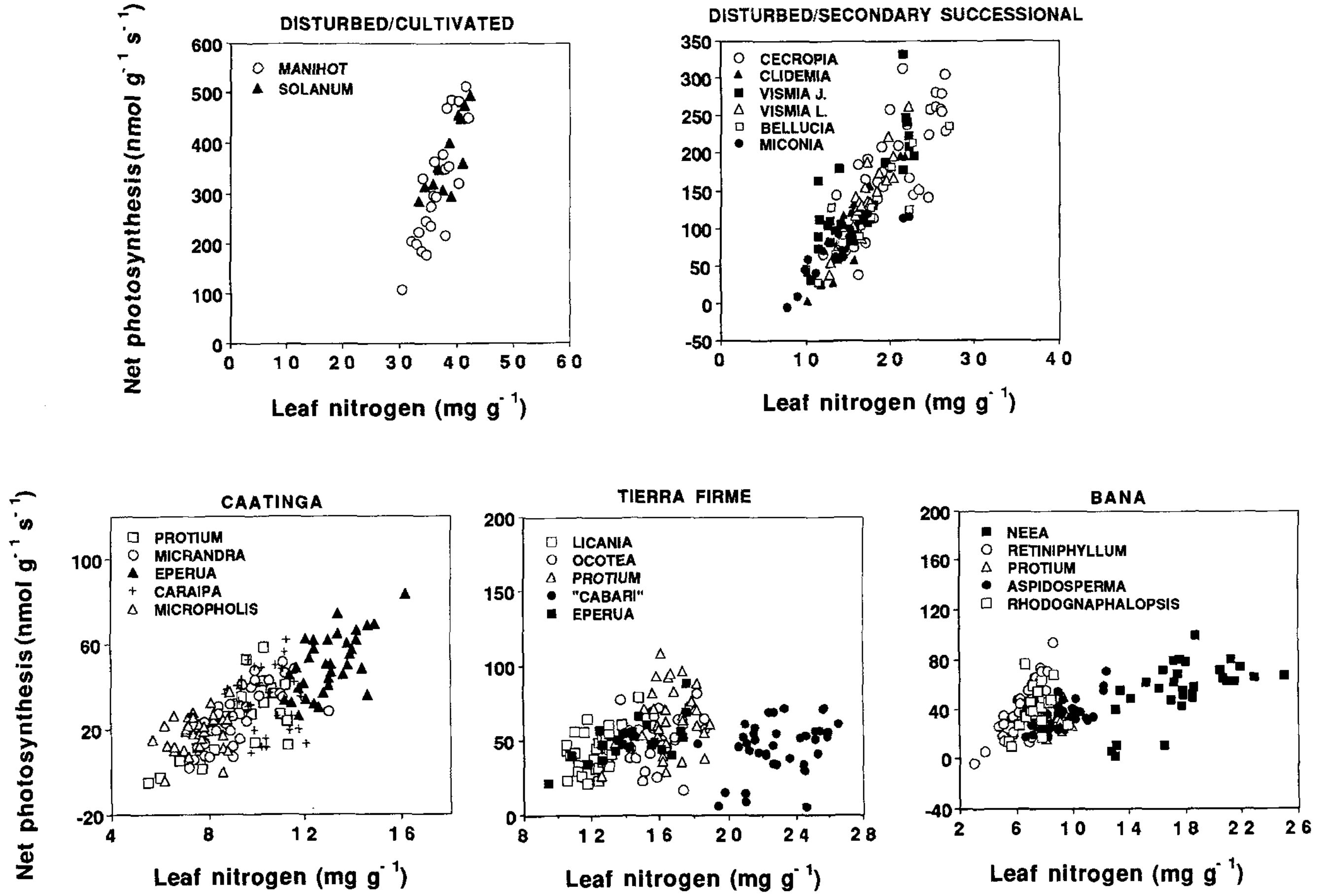

Fig. 1 Relationship between maximum mass-based net photosynthesis (nmol g^{-1} s^{-1}) and leaf nitrogen (mg g^{-1}) for species from disturbed sites (cultivated/weed and early secondary successional) and undisturbed Tierra Firme, Caatinga and Bana communities in the upper Rio Negro region of the Amazon basin. For better resolution, the scales used for each community are different, but the axes retain a common proportion so that the slopes can be visually compared. In Figures 1–3, *Eperua purpurea* from the Tierra Firme forest on ultisol is shown together with the other Tierra Firme forest species. See Tables 2 and 3 for regression equations

late successional *Ocotea*, "Cabari" (Leguminaceae), and *Protium* (2–6 μmol CO$_2$ [g N]$^{-1}$ s^{-1}, Fig. 1, Table 2), despite having similar mean leaf N$_{mass}$ (15–18 mg g^{-1} versus 16–22 mg g^{-1} for the early versus late successional species, respectively).

On average, the slope of the area-based A$_{max}$-N relationship was also higher in disturbed-site than late successional species, again except for *Retiniphyllum* (Table 2). On an area basis, however, differences among species were smaller and the total range in slope was less than on a mass basis.

Contrasts among communities

For leaves pooled within communities, A$_{mass}$ was significantly ($p < 0.001$) correlated with N$_{mass}$ in all communities except Tierra Firme ($p > 0.75$) (Table 3 and Figs. 1, 3). The slope of A$_{mass}$ versus N$_{mass}$ was greatest in the cultivated community, 28.6 μmol CO$_2$ [g N]$^{-1}$ s^{-1} (and the intercept most negative), followed in order by the early successional, Caatinga, Eperua-dominated Tierra Firme, Bana, and mixed-species Tierra Firme communities (11.8, 6.0, 4.0, 2.4, and 0.7 μmol CO$_2$ [g N]$^{-1}$ s^{-1}, respectively).

For data pooled within communities, A$_{area}$ was significantly correlated with N$_{area}$ in all communities (Table 3 and Figs. 2, 3). However, these correlations were relatively weak (r^2 ranged from 0.16 to 0.34), and at most half as strong as the mass-based A-to-N relationship in all but the Tierra Firme community. Ranking of A$_{area}$ to N$_{area}$ slopes among communities was similar as for mass-based slopes, being high in cultivated and early successional communities, intermediate in Caatinga, and lowest in Bana and Tierra Firme (Table 3, Fig. 3). When all leaves from all communities are pooled, there is a stronger relationship between A$_{mass}$ and N$_{mass}$ ($p < 0.001$, $r^2 = 0.64$) than between A$_{area}$ and N$_{area}$ ($p < 0.01$, $r^2 = 0.25$) (data not shown).

Patterns of variation in A$_{max}$-N relations among species and communities

As shown above, the strength and slope of the A$_{max}$-N relationship differs among species in communities

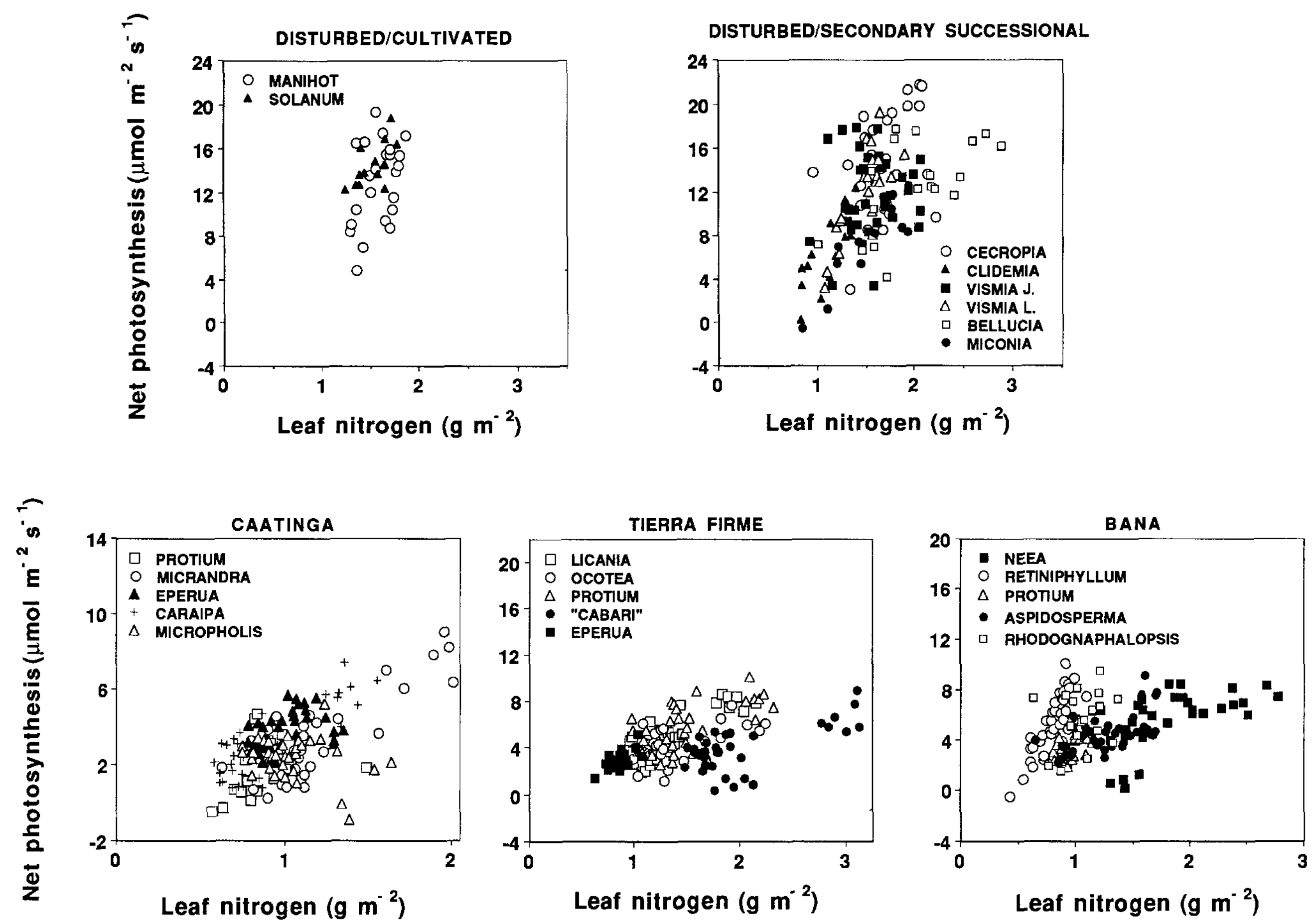

Fig. 2 Relationship between maximum area-based net photosynthesis (μmol m^{-2} s^{-1}) and leaf nitrogen (g m^{-2}) for species from disturbed sites (cultivated/weed and early secondary successional) and undisturbed Tierra Firme, Caatinga and Bana communities in the upper Rio Negro region of the Amazon basin. For better resolution, the scales used for each community are different, but the axes retain a common proportion so that the slopes can be visually compared. See Tables 2 and 3 for regression equations

marked by different resource availabilities and among species common at different stages during succession. How can we explain such patterns?

The slope of the A_{max}-N relationship decreases significantly during succession at San Carlos, as agricultural, pioneer, early successional and late successional species replace each other over time on Tierra Firme oxisol sites (Fig. 4). The slopes of the A_{mass} to N_{mass} regressions are highly correlated with temporal position during succession ($r^2 = 0.90$) and the relation is similar with or without ($r^2 = 0.84$) *Manihot* and *Solanum* in the data set (since these two species on cultivated plots have by far the highest values of many measures, evaluation of trends without their inclusion serves to check for their undue influence on observed patterns). Also, the relationship of the A_{mass} to N_{mass} slope to time of successional site occupancy is similar even if species from other soil types are included in the data set ($p < 0.001$, $r^2 = 0.75$;

Table 3 Correlations between maximum net photosynthesis and leaf N for data pooled among species in several Amazonian communities. Sample size (n), coefficient of determination (r^2), level of significance (*P*), slope and intercept are given for linear regressions. Abbreviations and units: A_{mass} and A_{area} (nmol g^{-1} s^{-1} and μmol m^{-2} s^{-1}, respectively); N_{mass} and N_{area} (mg g^{-1} and g m^{-2}, respectively)

Community (n)	A_{mass} vs N_{mass}				A_{area} vs N_{area}			
	r^2	*P*	slope	intercept	r^2	*P*	slope	intercept
Disturbed/Cultivated (38)	0.68	0.001	28.6	−750	0.16	0.05	7.8	1.4
Disturbed/Successional (170)	0.63	0.001	11.8	−73	0.32	0.001	6.8	1.2
Disturbed/All (208)	0.76	0.001	12.0	−78	0.24	0.001	6.1	2.3
Tierra firme (163)	0.01	0.75	0.7	4	0.18	0.01	2.2	1.7
Tall Caatinga (159)	0.58	0.001	6.0	−28	0.34	0.001	3.5	−0.6
Bana (152)	0.32	0.001	2.4	17	0.17	0.001	1.9	2.7

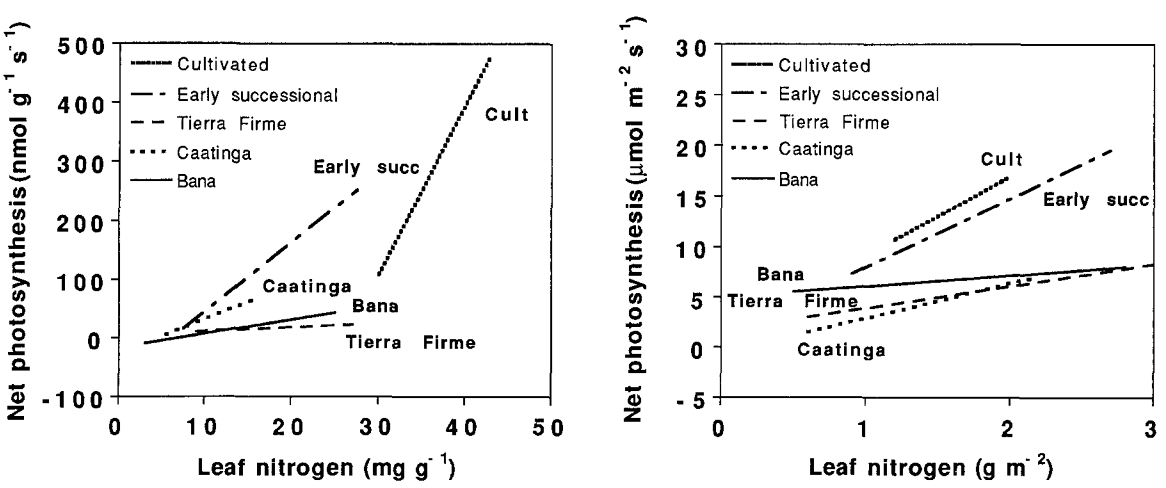

Fig. 3 Comparison of the mass- and area-based net photosynthesis to leaf nitrogen relationships for species from five communities (cultivated/weed, early secondary successional, undisturbed Tierra Firme, Caatinga and Bana) in the upper Rio Negro region of the Amazon basin. Relationships shown are the community level regressions (see Table 3) across the range of leaf N observed in each community. The axes have similar proportions so the slopes can be visually compared

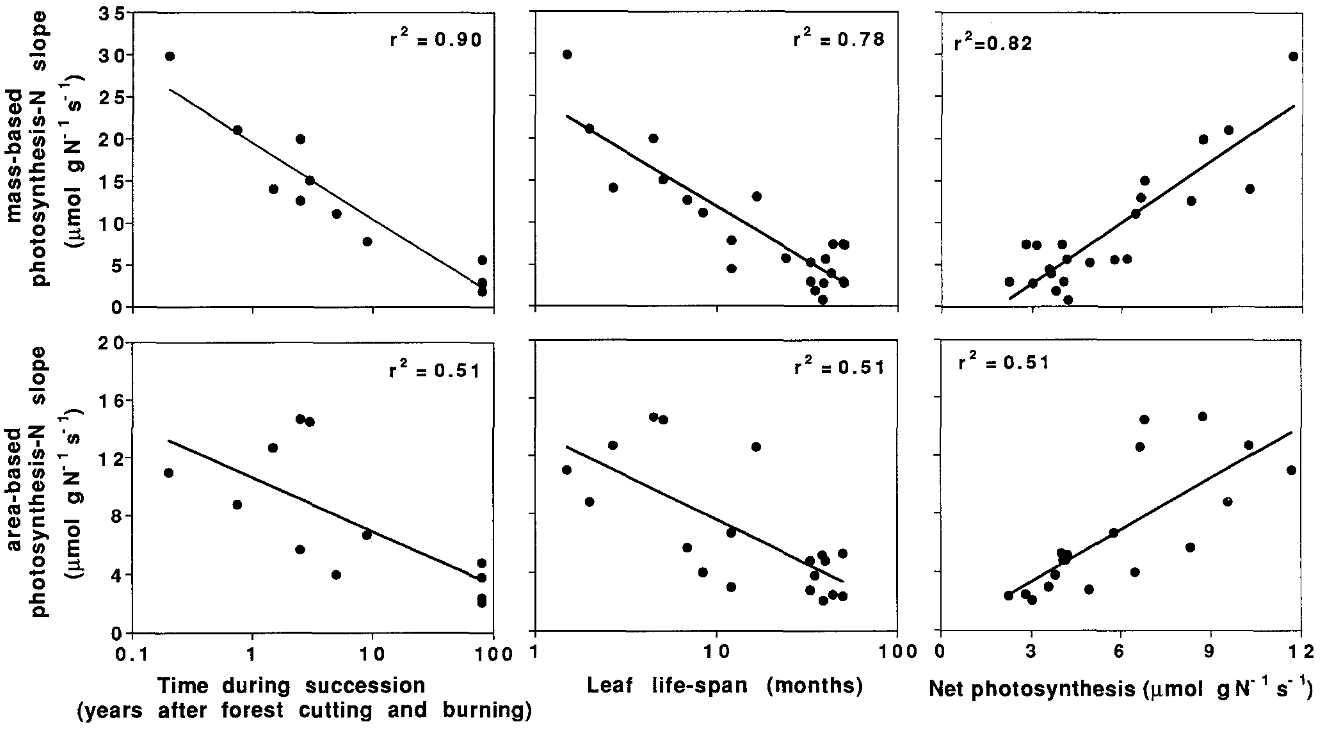

Fig. 4 Relationship of the A_{max}-N slope (μmol CO_2 [g N]$^{-1}$ s^{-1}) on both mass and area bases to temporal niche (time) during secondary succession, leaf life-span (months) and potential photosynthetic N use efficiency (A_{max}/leaf N, μmol CO_2 [g N]$^{-1}$ s^{-1}) for 23 species at San Carlos de Rio Negro, Venezuela. Each data point represents a single species within a single community. Relationship versus time during succession is shown only for species found on Tierra Firme oxisol sites. Regression equations ($p < 0.001$; all species included in analyses unless mentioned otherwise): A_{mass} to N_{mass} slope = 19.42−9.08*log (years after cutting and burning), $r^2 = 0.90$, all species on Tierra Firme oxisols (slope = 17.5−7.5*log (years after cutting and burning), $r^2 = 0.84$ without *Manihot* and *Solanum*); A_{area} to N_{area} slope = 10.7−3.7*log (years after cutting and burning), $r^2 = 0.51$; A_{mass} to N_{mass} slope = 24.85−12.91*log (leaf life-span), $r^2 = 0.78$; (slope = 21.1−10.3*log (leaf life-span), $r^2 = 0.66$, without *Manihot* and *Solanum*); A_{area} to N_{area} slope = 13.65−6.0*log (leaf life-span), $r^2 = 0.51$; A_{mass} to N_{mass} slope = −4.53+2.44* (PPNUE), $r^2 = 0.82$; A_{area} to N_{area} slope = −0.18+1.18* (PPNUE), $r^2 = 0.58$

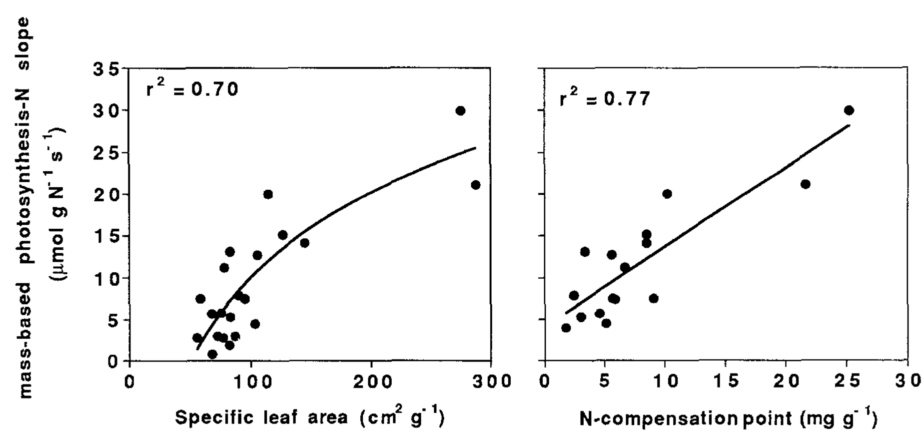

Fig. 5 Relationship of the mass-based A_{max}-N slope (µmol CO_2 [g $N]^{-1}$ s^{-1}) to specific leaf area and the N-compensation point (mg g^{-1} N at A_{mass} = zero). Each data point represents a single species within a single community. Regression equations ($p < 0.001$ unless mentioned otherwise): slope = −57.7 + 33.8*log (SLA), $r^2 = 0.70$ for all species (slope = −54.9 + 32.4*log (SLA), $r^2 = 0.43$ without *Manihot* and *Solanum*); slope = 4.11 + 0.95* (N-compensation point), $r^2 = 0.77$, all species (slope = 2.19 + 1.28* (N-compensation point, $r^2 = 0.48$, without *Manihot* and *Solanum*)

slope = 20.3 − 8.3 *log [years after cutting and burning], data not shown). The slope of the A_{area} versus N_{area} relationship also is higher in early than late succession ($r^2 = 0.51$, Fig. 4), but the magnitude of the change and the strength of the relationship are less than on a mass basis.

The slope of A_{mass}-N_{mass} decreases significantly with increasing leaf life-span (Fig. 4), with ($r^2 = 0.78$) or without *Manihot* and *Solanum* ($r^2 = 0.66$) in the data set. Variation in the slope of A_{area}-N_{area} among species was correlated with leaf life-span as well ($r^2 = 0.51$). Across species, there were positive relationships between both the A_{mass}-N_{mass} and A_{area}-N_{area} slopes and PPNUE ($r^2 = 0.82$ and 0.58, respectively, Fig. 4). Early successional species have high N-compensation points (and low y-intercepts), yet have higher A (and thus PPNUE) at similar N_{mass} than late successional species because of their higher slopes (Fig. 3).

The slope of A_{mass} to N_{mass} was also correlated with SLA (Fig. 5), with ($r^2 = 0.70$) or without ($r^2 = 0.43$) *Manihot* and *Solanum* in the data set. The A_{area} to N_{area} slope was significantly, but weakly, correlated with SLA using all data ($r^2 = 0.28$) or without *Manihot* and *Solanum* in the data set ($r^2 = 0.37$) (data not shown). Species with high SLA thus have greater gains in A_{mass} or A_{area} per incremental increase in N_{mass} or N_{area}, respectively, than those with low SLA.

The slope of A_{mass}-N_{mass} was significantly correlated with variation in N_{mass} itself (data not shown), but the correlation was only moderately strong ($r^2 = 0.53$) and highly dependent on *Manihot* and *Solanum*. With these species omitted, there was no significant relationship between the A_{max}-N slope and N_{mass} ($p > 0.25$, $r^2 = 0.09$). The slope of the A_{area}-N_{area} relationship was also not significantly related to N_{area} (data not shown). These results suggest that the A_{max}-N slope is more closely associated with variation in other leaf traits (such as leaf life-span and SLA) than with their N contents per se.

For species with short leaf life-spans, A_{mass}-N_{mass} regressions had high slopes and low y-intercepts (Table 2). We also present data for the x-intercept (leaf N_{mass} at which $A_{mass} = 0$, that we define as the "N-compensation point") for the following reasons. First, the y-intercept far exceeds the limits of the data set, while the x-intercept is nearer the border of the data. Second, observation of a leaf with low enough N that gross photosynthesis equals respiration is biologically feasible (e.g., Reich et al. 1991b), while a leaf with no N is not. Using data for significant relationships only, the slope of the A_{mass}-N_{mass} relationship among species was positively related with the N-compensation point (Fig. 5), with ($r^2 = 0.77$) or without *Manihot* and *Solanum* ($r^2 = 0.48$) in the data set. The x-intercept (N-compensation point) was also negatively related to leaf life-span and positively related to leaf dark respiration rate ($p < 0.01$, $r^2 = 0.52$ and 0.67, respectively, data not shown). Species with high capacity to increase A_{mass} per given increase in N_{mass} also require high N_{mass} to have positive rates of A_{mass}. Since several significant A_{area} versus N_{area} relationships have positive y-intercepts, the notion of an "N-compensation" point cannot be applied on an area basis.

Discussion

The strength and form of A_{max}-N relations varied substantially among Amazonian species and communities. Many studies of trees and other vegetation have reported strong correlations between A_{max}-N and leaf N (e.g., Gulmon and Chu 1981; Field et al. 1983; Chazdon and Field 1987). Few papers have reported a lack of such correlation, either because it is a rare phenomena or because of the tendency not to publish negative results, or both. In *Pinus strobus* grown in five forest soils, A_{mass} was not correlated with N_{mass} in three soils where plants had low foliar P : N ratios (or in comparing data from all five soils pooled), but A_{mass} was related to N_{mass} in two soils primarily limited by N rather than P (Reich and Schoettle 1988). Different communities in the Rio Negro region are differentially limited by N, P and/or other nutrients (Cuevas and Medina 1986, 1988; Uhl 1987, Table 1), thus enabling us to test the hypothesis that plants in communities limited by nutrients other than N would display weak or nonsignificant A_{max}-N relationships with small slopes, relative to N-limited communities. The data presented in this paper offer general support for this hypothesis.

Bana forest is limited by both N and P (Cuevas and Medina 1986, 1988; Medina and Cuevas 1990) and A_{max}-N relationships (within species and for the community pooled) were significant, but with relatively small slopes. An exception was the species *Retiniphyllum truncatum*, which had the highest A_{max}-N correlation coefficients of any Bana species, and by far the greatest slopes of any late successional species, despite very low leaf N concentrations (3 to 9 mg/g). It is interesting that this species also had the shortest leaf life-span (12 months) of this latter group of species, and a high A_{max}-N slope is consistent with a short leaf life-span (see Fig. 4).

Caatinga species are primarily N limited (Cuevas and Medina 1986, 1988; Medina and Cuevas 1990) and in this community the A_{mass}-N_{mass} correlation was strong using all data pooled (Table 3). The Caatinga had a greater slope of A_{max}-N on both mass and area bases than did the other late successional (Tierra Firme and Bana) communities. Mixed species Tierra Firme forest on oxisol is categorized as P- (and Ca, Mg, and K)-limited based on green leaf and litterfall nutrient concentrations, annual litter P flux, litter decomposition and root growth responses (Cuevas and Medina 1986, 1988; Medina and Cuevas 1990, see Table 1). All four species from this community had weak A_{mass}-N_{mass} relations ($r^2 \leq 0.20$). At the community level, no significant A_{mass}-N_{mass} relationship was observed using data pooled for these four species, and a significant but weak area-based relationship existed, with a low slope compared to other communities. Overall, the results from the mixed-species Tierra Firme forest (and the contrasting Caatinga forest of similar stature, LAI and vertical light gradients) support the hypothesis that in sites primarily limited by nutrients other than N, relationships between leaf N and photosynthesis will be weak (Reich and Schoettle 1988). However, deficiency of Ca, rather than P, may be a primary limit to A_{mass} in the late successional Tierra Firme species. In this community, A_{mass} was very weakly correlated with leaf P and better correlated with leaf Ca concentration (Reich et al., unpublished data).

Disturbed Tierra Firme sites have a temporary period of enhanced nutrient availability following cutting and burning (Uhl 1987, Montagnini and Buschbacher 1989). Disturbed-site vegetation had the highest nutrient concentrations and SLA (Uhl 1987; Medina and Cuevas 1990, also see Figures), and the strongest A_{mass} to N_{mass} relationships with the largest slopes. Thus, data from this community also supports the idea that A_{max}-N relationships will be stronger under conditions where P, Ca or other (non-N) nutrients are not limiting.

The relative strengths of area versus mass-based expressions of A_{max}-N varied greatly among species, but were generally stronger on mass than area bases. We leave detailed exploration of the reasons for differences in mass versus area based A_{max}-N relations and slopes (i.e., how they are modified by covariation in SLA and N_{mass}) to a companion paper devoted to that topic (Reich and Walters 1994). However, we note several aspects of differences in mass versus area expressions that are relevant in the ecological context of this paper. First, in all 8 disturbed-site species, A_{max} was more poorly correlated with N on an area than mass basis, while in all 5 Tierra Firme species this relationship was either better or equal on an area than mass basis. However, there was substantial variation among species in this regard – several species had strong correlations on both area and mass bases (e.g., *Clidemia*, *Micrandra*), while other species had poor relations using either basis (e.g., *Micropholis*, *Rhodognaphalopsis*). Second, although A_{max} and N in individual species may be equally well or better correlated on either mass or area bases (this study, Field et al. 1983; Chazdon and Field 1987; Reich et al. 1990; Reich et al. 1991b; Ellsworth and Reich 1992), when data were pooled for a community or for all communities, A_{max}-N correlations were greater on mass than area bases. This is consistent with prior analyses of multiple species (Field and Mooney 1986, Reich et al. 1992).

Stronger area- than mass-based A_{max}-N correlations, as seen in the Tierra Firme, occur within species that are more plastic with respect to SLA than to N_{mass} and/or under conditions that result in large variation in SLA (Chazdon and Field 1987; DeJong et al. 1989; Reich et al. 1991b). In *Acer saccharum* along a vertical canopy gradient, Ellsworth and Reich (1993) found a strong A_{area}-N_{area} relationship, despite little variation in N_{mass}, that resulted largely from increasing SLA at more shaded canopy positions. The same patterns occur for the Tierra Firme species. Only by combining upper canopy and understory data did a significant A_{area}-N_{area} correlation exist – within each microhabitat no relationship was observed ($p > 0.50$). Upper canopy and understory leaves have similar N_{mass} and A/leaf N ($p > 0.50$), but canopy leaves have greater A_{area} and N_{area} as a result of lower SLA, and thus A_{area} and N_{area} are correlated across a light gradient due to this scaling.

A_{max}-N relationship also appear dependent on leaf structure and/or other species-level traits, that may be partially independent of nutrient availability or leaf nutrient concentration. The slopes of both A_{mass} vs. N_{mass} and A_{area} vs. N_{area} were greater in the faster growing, disturbance specialist species with high A_{mass}, N_{mass} and SLA and short leaf life-span. Moreover, early successional species with higher SLA, shorter leaf life-span and higher photosynthetic rates, but similar leaf N_{mass}, had greater slopes than late successional species. These results suggest that species traits other than leaf N concentration play an important role in the response of A_{max} to variation in leaf N. Possibilities include high internal diffusive resistances to gas exchange in thick (low SLA) leaves (Vitousek et al. 1990; Lloyd et al. 1992) and variation in investment of N among different photosynthetic and non-photosynthetic compounds (Field and Mooney 1986; Evans 1989). These results are also consistent with the idea that a linked group of leaf-level traits (including high A_{mass}, SLA, and N_{mass}, and short leaf life-span) together enable plants to have high assimilative capacity and are found only in plants adapted to high resource environments (Chapin 1980; Field and Mooney 1986; Reich et al. 1992) and suggest that species differences in photosynthetic N utilization depend on just such a set of traits, rather than on any one trait alone.

The strong correlation between the slope of the A-to-N relationship and PPNUE (maximum A per unit N) suggests that PPNUE is not merely a function of high leaf N, as would be the case if all species followed a universal A_{max}-N relationship (with identical slope and intercept). Since the N content, slope and intercept vary considerably among species, it would be possible for the slope of A_{max}-N and PPNUE to be unrelated (e.g., a sufficiently large negative intercept could offset the gain from a high slope and high leaf N). The positive correlation between the A_{max}-N slope and PPNUE suggests that species with high PPNUE employ similar means of achieving it, in short, with high investment of N to photosynthetic processes that results in higher respiratory costs and high N compensation points (x-intercept), but allows sharp gains in A_{max} per increase in unit N and thus high A_{max} when leaf N is maximal. Thus, the heavy investment in photosynthetic structures and enzymes needed to achieve a high A_{max}-N slope will be advantageous only when leaf N is sufficiently high enough to result in a high A/leaf N and when other resources, such as light, are also sufficiently available that high achieved net photosynthetic rates per unit leaf N can occur. This strategy should therefore be disadvantageous under low N availability and/or low light conditions, and in fact, we do not see these traits in species adapted to low resource regeneration niches at San Carlos de Rio Negro.

Species that occupy Amazonian sites at later stages during succession (regardless of soil type or community) show a lower capacity to use N photosynthetically than disturbed sites specialists, based on either PPNUE or the slope of A_{mass} to N_{mass} relationship. Disturbed sites are characterized not only by greater nutrient availability than primary sites, but light availability to regeneration habitats is also higher in disturbed sites and decreases with time after disturbance (Ellsworth 1991). Species at Rio Negro that characteristically occupy sites with high resource availability tend to be fast growing with short-lived foliage and with a suite of linked traits, such as high leaf N_{mass}, A_{mass}, and SLA, that collectively enable high photosynthetic productivity under high resource conditions, while species adapted to low resource habitats have the opposite traits (Uhl 1987; Reich et al. 1991a). It thus appears that species adapted to higher resource regeneration niches (sensu Grubb 1977) show a greater capacity to use N for photosynthesis than other species. These results also suggest that the slopes and intercepts of A_{max}-N relationships will vary in systematic and predictable ways among species arrayed along leaf life-span, successional and/or resource gradients, and may be an ecologically important species-level trait.

In summary, these results support the idea that the relationship between A_{max} and leaf N is variable among species (Evans 1989), and varies in ecologically patterned ways. The relationship will be generally strongest, and slopes steepest, on high resource disturbed sites, in fast growing species (with adaptations to high resource environments such as short leaf life-span, high SLA and high leaf N_{mass}), when growing on sites where N is a primary limitation. In later successional and more sclerophyllous vegetation, A_{max} may still be strongly dependent on N (e.g., species in the Caatinga), if N is the primary limiting nutrient. On sites with low availability of nutrients other than N (e.g., Tierra Firme on oxisol), species may show little to no A_{max}-N relationship.

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