

Leaf lifespan as a determinant of leaf structure and function among 23 amazonian tree species

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Summary. The relationships between resource availability, plant succession, and species' life history traits are often considered key to understanding variation among species and communities. Leaf lifespan is one trait important in this regard. We observed that leaf lifespan varies 30-fold among 23 species from natural and disturbed communities within a 1-km radius in the northern Amazon basin, near San Carlos de Rio Negro, Venezuela. Moreover, leaf lifespan was highly correlated with a number of important leaf structural and functional characteristics. Stomatal conductance to water vapor (g) and both mass and area-based net photosynthesis decreased with increasing leaf lifespan ($r^2 = 0.74$, 0.91 and 0.75 , respectively). Specific leaf area (SLA) also decreased with increasing leaf lifespan ($r^2 = 0.78$), while leaf toughness increased ($r^2 = 0.62$). Correlations between leaf lifespan and leaf nitrogen and phosphorus concentrations were moderate on a weight basis and not significant on an area basis. On an absolute basis, changes in SLA, net photosynthesis and leaf chemistry were large as leaf lifespan varied from 1.5 to 12 months, but such changes were small as leaf lifespan increased from 1 to 5 years. Mass-based net photosynthesis (A/mass) was highly correlated with SLA ($r^2 = 0.90$) and mass-based leaf nitrogen (N/mass) ($r^2 = 0.85$), but area-based net photosynthesis (A/area) was not well correlated with any index of leaf structure or chemistry including N/area . Overall, these results indicate that species allocate resources towards a high photosynthetic assimilation rate for a brief time, or provide resistant physical structure that results in a lower rate of carbon assimilation over a longer time, but not both.

Key words: Leaf lifespan – Amazon – Photosynthesis – Specific leaf area – Nitrogen

leaf area, (SLA)), stomatal conductance (g) and rate of photosynthesis ranges over one to two orders of magnitude. Species differences in these characteristics have been associated with biogeographical, ecological, and edaphic patterns. Extended leaf lifespan has been hypothesized to be advantageous for nutrient conservation (Monk 1966; Chapin 1980), carbon balance (Mooney and Dunn 1970; Waring and Franklin 1979), and nutrient-use efficiency (Chapin 1980; Chabot and Hicks 1982; Gray and Schlesinger 1983). Conversely, short leaf life span and/or deciduousness have been considered adaptations for rapid growth rate (Coley 1988), and drought-avoidance (Axelrod 1966) or other seasonal stresses such as cold winters. Increased leaf lifespan has also been invoked as an adaptive strategy employed by plants in the understory, in order to gain access to light during periods of overstory leaflessness (Lassoie et al. 1983; Harrington et al. 1989). Habitat resource availability has also been postulated as a driving force for the evolution of a suite of interdependent plant characteristics, including leaf lifespan (Bazzaz 1979; Chabot and Hicks 1982; Coley et al. 1985). According to these theories, resource-limited habitats favor plants with inherently slow growth; low photosynthetic rates, nutrient contents and SLA; long leaf lifetimes; and large investments in antiherbivore defenses, with the reverse more likely for resource-rich environments.

Although existing data provide general support for the above hypotheses and theories, these data are largely from studies at unrelated sites by different investigators or from studies in which leaf lifespan was at best crudely estimated (Chapin 1980; Chabot and Hicks 1982; Bazzaz 1979). As a result these data have usually not been subjected to statistical analyses. Thus, the quantitative forms of such relationships have not been determined.

Most studies which address questions related to leaf lifespan have usually examined few plant species at a time (however, see Small 1972; Kikuzawa 1983, 1984; Reich and Borchert 1984; Williams et al. 1989). Another exception is the work of Coley (1988) with a large group of species in tropical forest in Panama. She found a significant negative correlation between height growth

Variation among plant species in leaf duration, leaf nitrogen (N) content, leaf area to dry mass ratio (specific

Table 1. Species studied at San Carlos de Rio Negro

Plant community/soil	Species and family
Agricultural/oxisol	<i>Manihot esculenta</i> (Euphorbiaceae)
Secondary successional/oxisol	<i>Bellucia grossularioides</i> (Melastomataceae) <i>Cecropia ficifolia</i> (Moraceae) <i>Clidemia sericea</i> (Melastomataceae) <i>Miconia dispar</i> (Melastomataceae) <i>Solanum straminifolia</i> (Solanaceae) <i>Vismia japurensis</i> (Clusiaceae) <i>Vismia lauriformis</i> (Clusiaceae)
Species-rich tierra firme/oxisol	“ <i>Cabari</i> ” ^a (Leguminosae) <i>Licania heteromorpha</i> (Chrysobalanaceae) <i>Ocotea costulata</i> (Lauraceae) <i>Protium</i> sp. ^a (Burseraceae)
Legume-dominated tierra firme/ultisol	<i>Eperua purpurea</i> (Caesalpinaceae)
Tall caatinga/spodosol	<i>Caraipa heterocarpa</i> (Clusiaceae) <i>Eperua leucantha</i> (Caesalpinaceae) <i>Micrandra sprucei</i> (Euphorbiaceae) <i>Micropholis maguirei</i> (Sapotaceae) <i>Protium</i> sp. ^a (Burseraceae)
Bana/spodosol	<i>Aspidosperma album</i> (Apocynaceae) <i>Neea obobata</i> (Nyctaginaceae) <i>Protium</i> sp. ^a (Burseraceae) <i>Retiniphyllum truncatum</i> (Rubiaceae) <i>Rhodognaphalopsis humilis</i> (Bombacaceae)

^a Fertile material has been sent to the New York Botanical Garden for species identification

rate and mean leaf lifetime, and observed that immobile antiherbivore defenses (several fiber and tannin measures) were significantly greater in long-lived than short-lived leaves. Leaf lifetime was able to explain between 15 and 40% of the variation in these growth and leaf defensive measures, indicating that other factors were also important. Other extensive data sets of this type are minimal (Coley 1988) and even quantitative data on leaf lifespans themselves are surprisingly rare (Chabot and Hicks 1982; Nilsson et al. 1987).

We present such a data set herein comparing leaf duration and related leaf chemical, structural, and physiological properties for 23 neotropical tree species from six different plant communities found within 1 km of one another near San Carlos de Rio Negro (SCRN), in Amazonian Venezuela (Table 1). We compare leaf-level traits for these species under ambient conditions using trees growing in their natural habitats. Given the similarity in climate at all sites, these species and communities otherwise represent a diversity in soils and successional status (Cuevas and Medina 1988). Use of this sample population enabled us to answer the following questions:

- do leaf structural, chemical, and physiological traits vary in relation to increasing leaf lifespan?
- if so, what functions best describe these relationships?
- what are the physiological and ecological explanations for, and implications resulting from, these relationships?

Study site and species

The research site was located near SCRN, Venezuela (1° 56' N, 67° 03' W) at approximately 100 m elevation in the north-central region of the Amazon River basin. The climate of the region is humid equatorial, with a mean annual temperature of 26° C, a mean annual rainfall of 3565 mm, and a mean annual potential evaporative demand of about 1900 mm (Jordan and Heuvelink 1981; Cuevas and Medina 1986). Mean temperature variation is slight across the year. Minimum monthly rainfall occurs in December and January, but even during these months, average rainfall (200 mm/month) (Jordan and Heuvelink 1981) still exceeds potential evapotranspiration. Thus, plant communities at SCRN, in comparison with most other ecosystems appear to be faced with slight limitations to carbon gain and growth due to low temperatures or prolonged drought. Due to the low water retention capacity of the sandy forest soils at SCRN, however, a series of dry days can lead to temporary drought (Cuevas and Medina 1983).

Vegetation and soil in the upper Río Negro region vary with small changes in elevation above the mean river level. Several well differentiated forest communities occur in the region, all associated with distinct geomorphological positions and soil types (Herrera 1977; Clark and Uhl 1987). In this report, we present data from four natural communities: species-rich Tierra Firme, legume-dominated Tierra Firme, Tall Caatinga, and the Bana. The Tierra Firme forests occur on oxisols and ultisols on the highest sites (Jordan and Uhl 1978; Jordan 1982). The Caatinga and Bana communities are at lower elevation, on periodically flooded fine-sand and coarse-sand spodosols, respectively (Klinge and Herrera 1983; Clark and Uhl 1987). In addition, we present data from a slash-and-burn agricultural community on a Tierra Firme site and a secondary successional community on a recently abandoned (2–3 years prior) Tierra Firme farm. The successional community included a mixture of pioneer species that occupy post-agricultural sites (Uhl 1987). The agricultural community consisted largely of *Manihot esculenta*, a perennial root crop, which was therefore chosen as the only species studied in this community. The legume-dominated Tierra Firme community was likewise represented by the dominant tree species, *Eperua purpurea*. Each of the other four communities were represented in this study by 4–7 common species.

The six community types differ in total biomass, standing nutrient pools, and soil chemistry (Jordan and Uhl 1978; Jordan 1982; Cuevas and Medina 1983; Klinge and Herrera 1983; Uhl and Jordan 1984; Saldarriaga 1985; Cuevas and Medina 1986; Uhl 1987) and have minimal species overlap, despite being located within 1 km of each other. The agricultural, successional and Bana communities were of short stature (mean canopy height less than 4 m) and the species studied all grow in moderate to high light microenvironments in these ecosystems (Uhl and Jordan 1984; Saldarriaga 1985; Cuevas and Medina 1986; Uhl 1987). Only sun leaves were sampled from these species. Both canopy trees (sun

leaves) and understory individuals (shade leaves) were studied for 4 of the 5 species from each of the tall forest ecosystems (Tierra Firme and Caatinga) (only understory saplings were studied in the two other species).

Methods

In order to determine leaf lifespans, tagged branches were surveyed at regular intervals from 1982 until the present (the census is ongoing). During each survey visit, the presence and position of individual new leaves on each branch is noted and dated on a drawing for that branch. The absence of each leaf is noted and dated on a subsequent survey, with leaf lifetime estimated as the time interval between the two dates. Survey intervals ranged from weekly to every three months in the different communities, with the interval scaled to approximately 10–15% of the average leaf lifespan for that community. Median leaf lifespan for each study species was estimated from data on the observed lifetimes of numerous individual leaves (total ≈ 100 –800) from numerous trees (15–50), except for two species. For these species, median leaf lifespan was estimated from data on leaf production and turnover rates for individual trees (and for one of these two, on a limited survey of lifespans of 50 individual leaves). Median leaf lifespan was used because

for species with long-lived leaves many leaves (but <50%) were still alive and mean lifespan could not be determined. In species where both mean and median lifespan were estimated, the values were similar.

At SCRN, leaf phenology is relatively aseasonal (Cuevas and Medina 1986). Since leaf lifespan varies substantially among the species studied, and leaf traits (e.g. photosynthesis, SLA) vary with leaf age as well, contrasts among species in this paper were made using leaves of a similar “physiological” age rather than a similar chronological age. Unless otherwise noted, we chose the “physiological” age of peak leaf performance as defined by maximum area- and weight-based photosynthesis and leaf nitrogen concentration. This “physiological” age corresponded in all species with the period when their median leaf lifetime was approximately 15–25% over and was therefore observed in young, fully expanded leaves (data not shown). Leaf photosynthetic rates were measured in the field in January and February 1987 and 1988 using an open gas exchange system in the differential mode (Analytical Development Corporation, Hoddesdon, England) as described by Walters and Reich (1989). Leaves were measured under ambient CO_2 concentrations, air temperatures, relative humidities, and irradiances (except for several leaves which were measured using artificial light).

Since the purpose of these observations was to measure photosynthetic rates under near optimal ambient conditions a set protocol was followed based on prior experience and on data such as photosynthetic-light response curves. Almost all measurements were made in the morning on leaves that had received direct, photosynthesis-saturating light for between 15 to 120 minutes. This protocol was used to ensure that photosynthetic light induction was

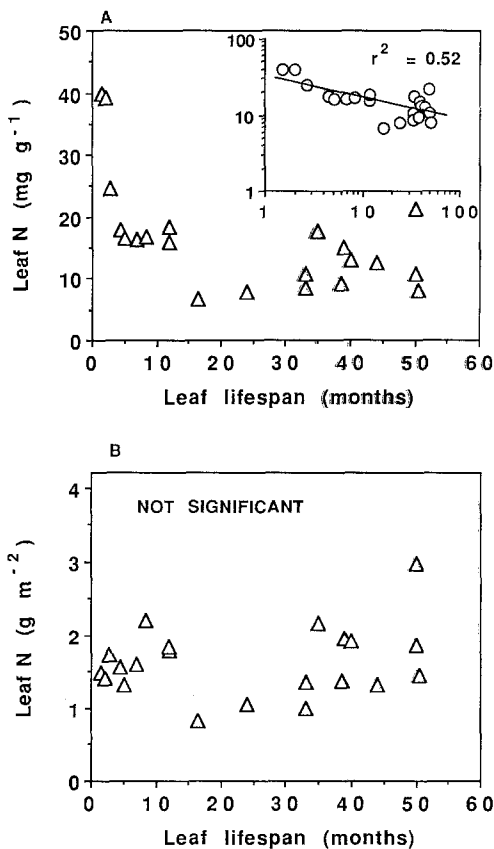


Fig. 1. A Weight-based leaf N concentration (mg g^{-1}) in relation to leaf lifespan (months), for sun leaves of 21 Amazonian tree species (no data available for sun leaves of *Eperua purpurea*, Tierra Firme or *Protium* sp., Tall Caatinga; in other Figures as well). Standard errors were on average less than 5% of the value for any given species (same for all data). The insert in A shows the same variables both on a log (base 10)-transformed scale. $\text{Log}(\text{leaf N/mass}) = 1.53 - 0.30 \log(\text{lifespan})$, $r^2 = 0.52$, $p < 0.001$. B (data as in A) presents area-based leaf N (g m^{-2}) in relation to leaf lifespan (months). This relationship was not significant ($p < 0.10$) regardless of transformation

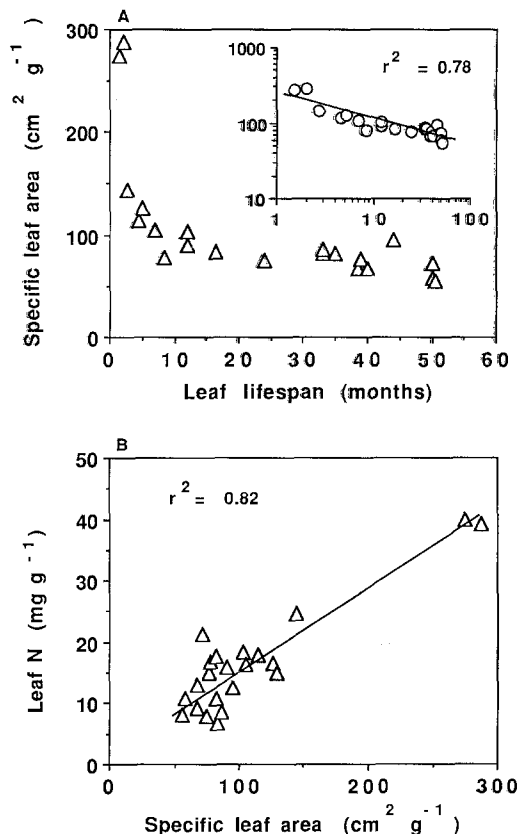


Fig. 2. A Specific leaf area ($\text{cm}^2 \text{g}^{-1}$) of sun leaves of 21 Amazonian tree species in relation to leaf lifespan (months). The insert shows the same variables both on a log (base 10)-transformed scale. $\text{Log}(\text{SLA}) = 2.37 - 0.33 \log(\text{lifespan})$, $r^2 = 0.78$, $p < 0.001$. B Leaf N/mass in relation to SLA (data as in A). $\text{Leaf N/mass} = 2.55 + 0.13(\text{SLA})$, $r^2 = 0.82$, $p < 0.001$

maximized (Pearcy et al. 1985) but that photosynthesis was not limited by midday overheating, vapor deficit stress, leaf water deficit, translocation inhibition, or other potential stresses as far as possible. Net photosynthesis measured using the above protocol closely resembles net photosynthetic capacity (90–95% as great) measured under optimal controlled conditions at ambient CO_2 concentrations (Ellsworth and Reich, unpublished data). Therefore, it will be treated synonymously with photosynthetic capacity for the purposes of comparison with other data sets. We measured photosynthetic rates of about 15–30 young, mature leaves per species, with about 2–4 leaves per individual tree. Immediately after photosynthesis measurements, each leaf was harvested, traced for subsequent leaf area determination, and oven-dried. Leaf samples were later weighed to obtain specific leaf area (SLA) ($\text{cm}^{-2} \text{g}^{-1}$). Leaf tissues were analyzed for total organic nitrogen by the University of Wisconsin Soil and Plant Analysis Laboratory using a micro-Kjeldahl assay. Leaf toughness was measured with a Chatillon penetrometer. For this analysis, twenty leaves per species were sampled (two leaves from each of 10 individuals, except for canopy foliage of tall trees in Tierra Firme and Caatinga in which four leaves were sampled from each of five individuals). Six probes were made per leaf.

Data were pooled from 1987 and 1988. Data were analyzed using analyses of variance, regression analyses, and mean separation tests (SAS 1985). Because a simple linear regression model was not generally appropriate to describe the relations between leaf lifespan and the measures of leaf structure, physiology and

chemistry, we faced two choices: either search for a more appropriate general model (or models) or transform the data so that a linear model was appropriate for the transformed data (Neter and Wasserman 1974). Although a series of more complex nonlinear models were fitted to each relationship, no single model yielded the best fit overall, and error variance was not constant in several cases. Also, there are serious difficulties in using complex nonlinear models with small data sets such as available here (R. Nordheim, personal communication; Neter and Wasserman 1974). Therefore, we chose to systematically use logarithmic transformations of the data where needed in order to linearize the regression functions and stabilize the error term variances. In addition to the statistical advantages, log transformations are often suitable for biological data, and have been previously used in relationship to leaf lifetime (e.g., Coley 1988; Williams et al. 1989). In this study, if a given relationship was not linear we first logarithmically transformed the independent variable (often leaf lifespan) and stopped at that point if an appropriate linear regression was identified (e.g., area-based net photosynthesis vs. lifespan). For other relationships (e.g. A/mass versus leaf lifespan) it was necessary to log-transform both variables to linearize the regression. In the figures, both non-transformed (main compartments) and transformed (inserts) axes are used. This enables the reader to examine both the raw data and the fit of the linear relationships between the transformed data.

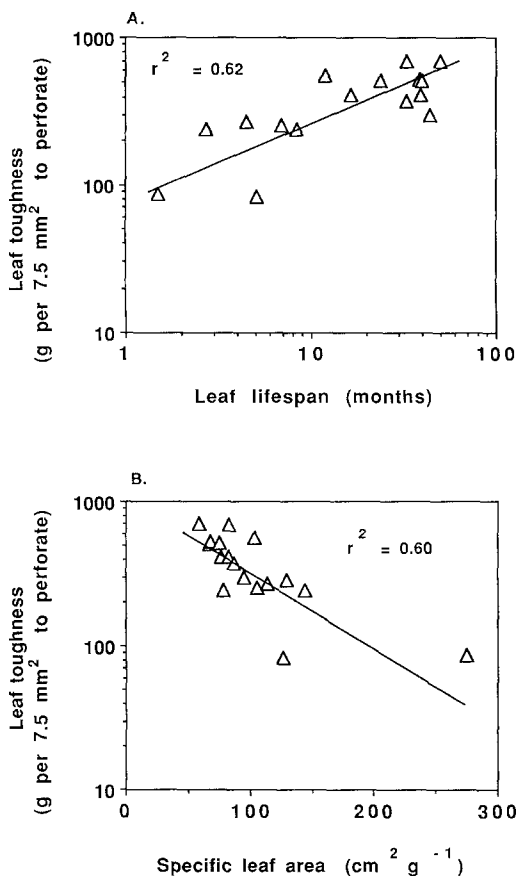


Fig. 3. **A** Leaf toughness ($\text{g per } 7.5 \text{ mm}^2 \text{ to perforate}$) of sun leaves of 16 Amazonian species in relation to leaf lifespan (months) (only shade leaves measured in the other species); $\log(\text{toughness}) = 2.0 + 0.45 * \log(\text{lifespan})$, $p < 0.001$, $r^2 = 0.62$. **B** Leaf toughness ($\text{g per } 7.5 \text{ mm}^2 \text{ to perforate}$) of Amazonian species in relation to specific leaf area ($\text{cm}^2 \text{g}^{-1}$) (data as in **A**); $\log(\text{leaf toughness}) = 2.94 - 0.0041 * \text{SLA}$, $p < 0.001$, $r^2 = 0.60$

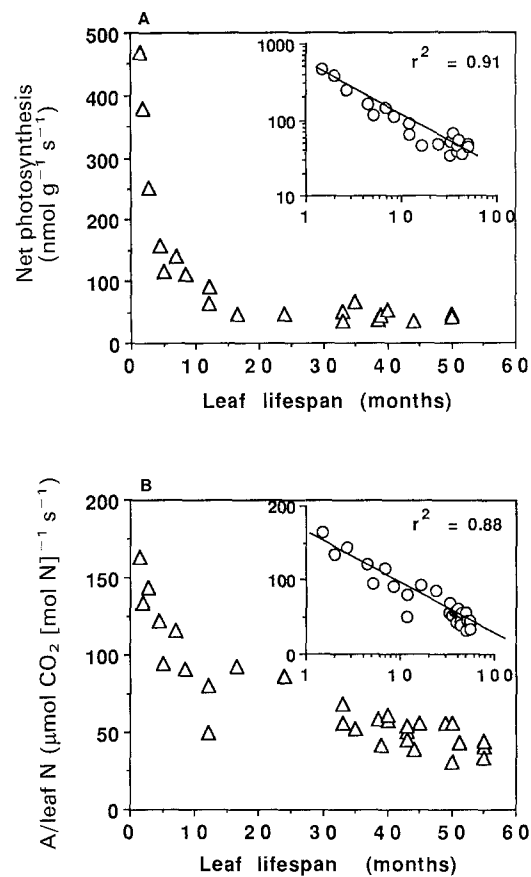


Fig. 4. **A** Weight-based net photosynthetic rate ($\text{nmol g}^{-1} \text{s}^{-1}$) in relation to leaf lifespan (months) for sun leaves of 21 Amazonian tree species. The insert shows the same variables both on a log (base 10)-transformed scale. $\log(\text{A/mass}) = 2.67 - 0.65 \log(\text{lifespan})$, $r^2 = 0.91$, $p < 0.001$. **B** Net photosynthesis per unit leaf N ($\mu\text{mol CO}_2 [\text{mol N}]^{-1} \text{s}^{-1}$) in relation to leaf lifespan (months) for sun and shade leaves of 21 and 9 species, respectively (relationship not affected by inclusion of shade leaves). The insert shows the independent variable on a log (base 10)-transformed scale. $\log(\text{A/leaf N}) = 1.624 - 0.686 \log(\text{lifespan})$, $r^2 = 0.89$, $p < 0.001$

Results

In analyzing the relationships between leaf traits and leaf duration, data from all species, sites and light environments (i.e., canopy and understory leaves) were pooled initially. Because the relationships were often different for leaves from shaded habitats (which were present only in the three tall forest communities), only data for sun leaves were used in the Figures, unless noted otherwise.

Weight-based leaf N (mg g^{-1}) decreased significantly ($r^2=0.52$, $p<0.01$ for all relationships unless mentioned otherwise) in relation to leaf lifespan (Fig. 1A). The two species with the shortest leaf lifespans had by far the greatest weight-based leaf N concentrations. No significant trends in N content per unit leaf area (leaf N/area) were found in relation to leaf lifespan, for either all data or only canopy data, regardless of transformation used (Fig. 1B). Thus, species with shorter leaf lifespans did not allocate a greater amount of N per unit leaf surface area than species with longer leaf lifespans. Trends for weight- and area-based leaf P concentration in relation to leaf lifespan (data not shown) mirrored those for leaf N concentrations.

In sun leaves SLA decreased dramatically (by 60%) among species as leaf lifespan increased from 1.5 to

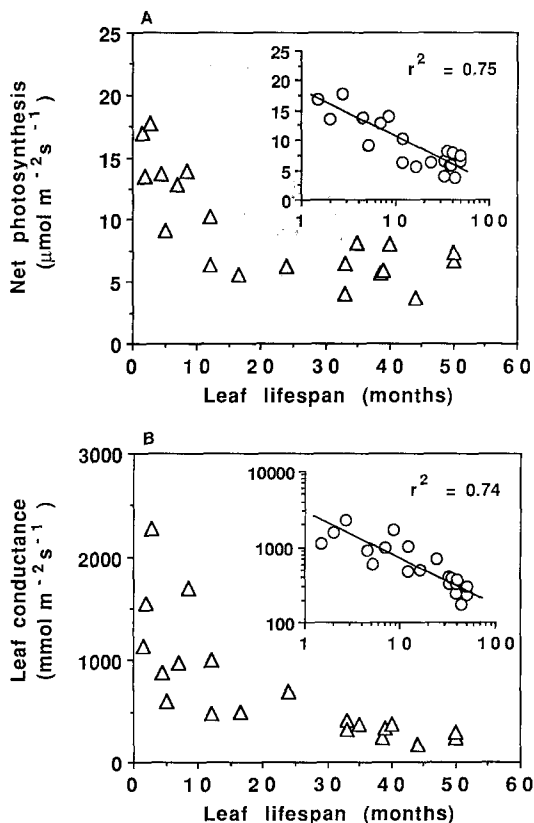


Fig. 5. **A** Area-based net photosynthetic rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$) in relation to leaf lifespan for sun leaves of 21 Amazonian tree species. The insert shows the independent variable on a log (base 10)-transformed scale. $A/\text{area} = 17.6 - 7.3 \log(\text{lifespan})$, $r^2 = 0.75$, $p < 0.001$. **B** Leaf diffusive conductance to water vapor ($\text{mmol m}^{-2} \text{s}^{-1}$) in relation to leaf lifespan (months) (data as in A). The insert shows the same variables both on a log (base-10) transformed scale. $\log(\text{leaf conductance}) = 3.38 - 0.54 \log(\text{lifespan})$, $r^2 = 0.74$, $p < 0.001$.

about 12 months and then SLA decreased gradually (by 30%) as lifespan increased from 1 to 4 years (Fig. 2A, $r^2=0.78$). Total variation in SLA with leaf lifespan was about three-fold from lowest to highest. Leaves from understory saplings were significantly thinner (higher SLA) on average than canopy leaves from the same species and thus were examined separately. A significant negative linear relationship ($r^2=0.60$) was observed between SLA and leaf lifespan for understory individuals (data not shown). Leaf N/mass was highly linearly correlated ($r^2=0.82$) with SLA among the SCRN species (Fig. 2B).

Leaf toughness (defined as force required to perforate leaf) increased significantly ($r^2=0.62$) with increas-

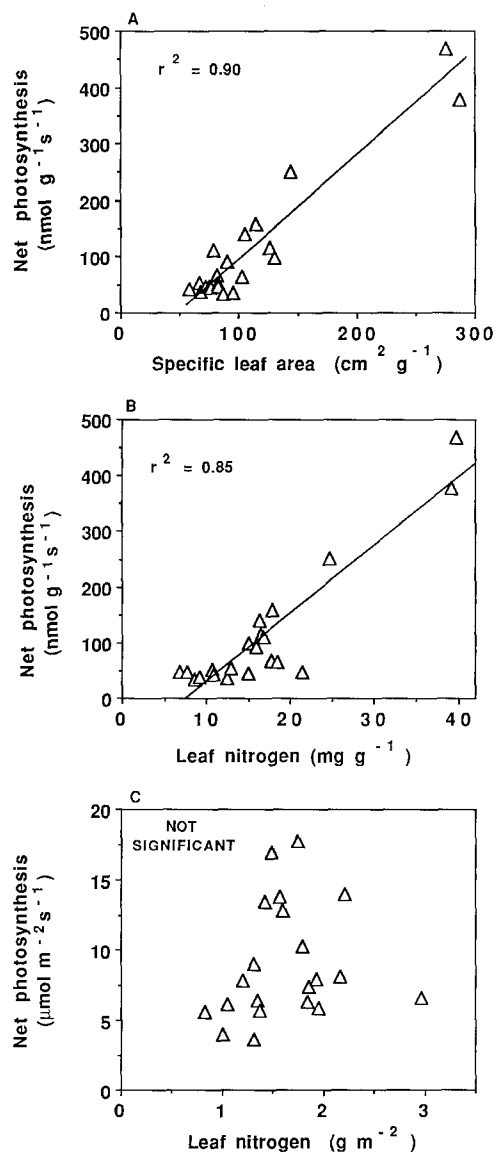


Fig. 6. **A** Weight-based net photosynthetic rate ($\text{nmol g}^{-1} \text{s}^{-1}$) in relation to specific leaf area ($\text{cm}^2 \text{g}^{-1}$) for sun leaves of 21 Amazonian tree species. $A/\text{mass} = -83.2 + 1.80(\text{SLA})$, $r^2 = 0.90$, $p < 0.001$. **B** Relationship between net photosynthesis and leaf N concentration (mg g^{-1}) on a weight basis (data as in A). $A/\text{mass} = -92.5 + 12.2(\text{N}/\text{mass})$, $r^2 = 0.85$, $p < 0.001$. **C** Relationship between area-based net photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and leaf N (g m^{-2}) (data as in A). Not significant

Table 2. Estimated impact on leaf traits of a 1-year increase in lifespan of leaves for short vs long lifetimes. Based on regression equations from Figs. 2, 4 and 5

Leaf lifespan	SLA ($\text{cm}^2 \text{g}^{-1}$)	g ($\text{mmol m}^{-2} \text{s}^{-1}$)	A/area ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	A/mass ($\text{nmol g}^{-1} \text{s}^{-1}$)	A/unit leaf N ($\mu\text{mol} [\text{mol N}]^{-1} \text{s}^{-1}$)
1.5 months	221	1927	16.0	355	150
13.5 months	92	589	9.3	84	85
Absolute change	130	1338	6.7	271	65
Proportional (%) change	(-59%)	(-69%)	(-42%)	(-76%)	(-44%)
2 years	79	432	7.5	58	68
3 years	73	347	6.2	45	56
Absolute change	7	85	1.3	13	12
Proportional (%) change	(-9%)	(-20%)	(-17%)	(-23%)	(-18%)
3 years	73	347	6.2	45	56
4 years	68	296	5.3	37	47
Absolute change	4	51	0.9	8	9
Proportional (%) change	(-6%)	(-15%)	(-15%)	(-17%)	(-15%)

ing leaf lifetime for leaves from exposed canopy positions (Fig. 3A), in agreement with the results of Coley (1988) for a tropical forest in Panama. Moreover, leaf toughness was significantly negatively correlated ($r^2 = 0.60$) with SLA among the SCRNs species (Fig. 3B).

Net photosynthesis on a dry mass basis (A/mass) decreased significantly ($r^2 = 0.91$) in relation to leaf lifespan (Fig. 4A), and the relationship was no different using data for only canopy leaves or canopy plus understory foliage. The shape of this response surface was similar as for SLA versus leaf lifespan, but even more dramatic. Differences in weight-based photosynthesis were about 10-fold for leaf lifespans ranging from 1.5 to about 15 months and then slight among species with leaf lifespan between 15 and 50 months. Photosynthesis on a leaf N basis (A/leaf N) also decreased with increasing leaf lifespan ($r^2 = 0.88$), with a three-fold range in this measure among species (Fig. 4B). Area-based photosynthesis (A/area) decreased significantly ($r^2 = 0.75$) with increasing leaf lifespan (Fig. 5A), but the decline was more gradual and the total range was three-fold rather than the ten-fold range found for mass based photosynthesis. Area-based photosynthesis was significantly lower in understory than canopy leaves (within and across species) even for similar leaf lifetimes (data not shown).

Stomatal conductance (g) varied by an order of magnitude among species and also declined significantly ($r^2 = 0.74$) with increasing leaf lifespan (Fig. 5B). Similar to photosynthesis, leaf N, and SLA, the largest absolute differences in g were noted among species with shorter leaf lifetimes. g was highly correlated with A/area ($r^2 = 0.76$) among all species.

Mass- and area-based net photosynthesis were better correlated with leaf lifespan than were determinants of photosynthesis such as leaf N (or P). The question then arises as to whether leaf N or other possible determi-

nants of photosynthesis were correlated with net photosynthesis among the SCRNs species sample. The single best correlate of net photosynthesis was SLA, which accounted for 90% of the variation among species in A/mass ($r^2 = 0.90$, Fig. 6A). Leaf N/mass was also highly correlated with variation among species in A/mass ($r^2 = 0.85$, Fig. 6B). SLA was moderately well correlated with A/area ($r^2 = 0.48$, data not shown) and leaf N/area was not significantly correlated with A/area ($p > 0.05$) (Fig. 6C).

All measured traits changed more among short rather than long-lived leaves, but the forms of the relationships between leaf traits and leaf lifespan were variable. Net photosynthesis per unit leaf area and per unit leaf N changed linearly in response to the log of leaf lifespan, and thus, the absolute differences in leaf traits between leaves with lifetimes of 1.5 (shortest observed lifetime) versus 13.5 months were 5–7 fold larger than such differences between leaves with lifetimes of 2 versus 3 or 3 versus 4 years (Table 2). The proportional change per yearly increase in lifespan in these measures was also much larger for short-lived rather than long-lived leaves. Decreases in A/mass, SLA, or leaf conductance with increasing leaf lifespan were even more abrupt. A/mass and SLA are estimated to change from $355 \text{ nmol g}^{-1} \text{ s}^{-1}$ and $221 \text{ cm}^2 \text{ g}^{-1}$ for a lifetime of 1.5 months to $84 \text{ nmol g}^{-1} \text{ s}^{-1}$ and $92 \text{ cm}^2 \text{ g}^{-1}$ respectively, if lifetime is one year longer (Table 2), which are more than 20 times as great an absolute change as occurs for increases in lifetime from 2 to 3 years or 3 to 4 years.

Discussion

Ecological considerations

Strong correlations between leaf lifespan and leaf N/mass, SLA, A/mass, A/area and A/leaf N were observed

for the SCRn data. Leaf N/area does not appear to be dependent on leaf lifespan. This is probably the result of offsetting influences on N/area of SLA and N/mass as they change with leaf lifetime: parallel decreases in SLA (which increases leaf mass/area) and N/mass result in no net change in N/area on average.

These data indicate that species with short leaf lifespans generally have thin (high SLA), fragile leaves with high weight-based nutrient concentrations and photosynthetic rates, with the reverse true for species with long-lived leaves. Absolute changes in leaf characteristics with increasing lifespan were greatest among species with the shortest lifespans, and least among species with lifespans greater than 1–2 years. This suggests that small absolute differences in leaf duration for species with short leaf lifespans may have important physiological and ecological ramifications. The converse, that large differences in leaf duration for leaves with long lifespans are relatively unimportant, is not necessarily true. Although instantaneous physiological performance of leaves could be similar or only slightly different, differences in leaf lifespan might have important impacts on ecosystem nutrient cycling, long-term individual tree nutrient use efficiency, and both net carbon gain and nutrient use efficiency over the leaf lifespan.

The general trends observed among the SCRn data set for SLA, N/mass, A/mass, A/area and g as a function of leaf lifespan and each other were more or less in keeping with observations and hypotheses from the literature (e.g. Chabot and Hicks 1982; Field and Mooney 1986). Exceptions (or modifications) include a) the lack of relationship between leaf N/area and leaf lifespan; b) the lack of relationship between leaf N/area and A/area, and c) the implications of the forms of the relationships between leaf traits and lifespan.

Why don't all species construct thin leaves with high nutrient concentrations and high photosynthetic capacity? Resource economic and growth-rate based theories suggest that this strategy will be successful only if light and nutrients are available in sufficient amounts to support high enough photosynthetic rates to pay off combined construction, maintenance, and defensive costs before leaves are either overtopped by other leaves, damaged or lost to herbivores or mechanical damage (e.g., falling detritus or wind), or otherwise become unproductive (Coley et al. 1985). Amazonian species adapted to low nutrient availability (Cuevas and Medina 1986; Reich et al., unpublished data) and/or shaded conditions during regeneration do tend to produce thick, tough long-lived leaves (Reich et al., manuscript in preparation). Leaf toughness and thickness increase (SLA decreases) with increasing leaf duration (Figs. 2 and 3), perhaps because extended leaf survival requires protection, and in nutrient- or light-poor environments metabolically undemanding structural defenses are most available (Coley et al. 1985). Leaf toughness was found to be the single most important correlate of herbivore damage (among species) to leaves of a number of tropical tree species in Panama (Coley 1983). Different species from diverse Amazonian communities therefore do appear to exhibit variation in adaptive "offensive and de-

fensive" leaf-level traits, including SLA, nutrient concentration, photosynthetic capacity, and leaf toughness and lifespan, which are associated with habitat resource availability and stability.

Nutrient allocation, conservation and use efficiency are also important considerations with respect to variation in leaf duration, and to the ways in which leaf physiology changes during the aging process. Amazonian species with short-lived foliage are fast-growing and occupy relatively resource-rich environments (Uhl 1987). In order to grow taller as quickly as possible, rapid uptake of readily available nutrients from the soil plus the reallocation of nutrients, especially N, from older leaves (Field and Mooney 1983) may be required. Amazonian species with long-lived leaves tend to be slow-growing and occupy resource-poor undisturbed sites (Uhl 1987 and Reich et al., unpublished data). Light-saturated photosynthetic rates are never particularly high in these species, but they remain relatively stable, declining little among leaves 0.5–5 years old (Reich et al., unpublished data). It is logical that species which are adapted to habitats with low nutrient availability have intrinsically nutrient-poor leaves, low photosynthetic and growth rates, a predominance of carbon-based structural defenses (such as leaf toughness), and low rates of tissue turnover (Grime 1977; Chapin 1980; Coley et al. 1985).

Physiological considerations

Why are weight- and area-based photosynthesis, and photosynthesis per unit leaf N, well correlated with leaf lifespan among a relatively diverse group of species? And why are leaf N/mass and SLA well correlated with A/mass across species, while A/area is not correlated with N/area? Consideration of variation in total leaf N, in N partitioning within leaves, and of other constraints upon photosynthesis (Field and Mooney 1986; Reich and Schoettle 1988; Evans 1989) can help explain these trends. Although they are clearly interrelated (by variation in SLA), for clarity we will first discuss weight-based relations and then those on an area basis.

First, several correlates of A/mass, such as SLA, leaf N/mass and leaf P/mass were also negatively correlated with leaf lifespan. A/mass has been well correlated with leaf N/mass in and among a wide variety of species (Field and Mooney 1986), including those used in this study (Fig. 6 and Reich et al., unpublished data). Thus, since leaf N/mass decreased with increasing leaf lifespan (Fig. 1), a proportion of the decline in A/mass with increasing leaf lifespan may directly result from this pattern. However, A/mass was more highly correlated with leaf lifespan than was leaf N/mass itself.

Although Field and Mooney (1986) considered the idea that photosynthesis and leaf lifespan tend to be inversely related, they proposed several hypotheses to explain low A per mass and per leaf N in sclerophylls (which tend to have low SLA and longer leaf lifetimes) which did not *require* assumptions about the prerequisites for leaf longevity. First, because some minimum

N level greater than zero is required for positive net photosynthesis, the algebraic formulation of the linear A/mass vs leaf N relation results in increasing A/leaf N with increasing leaf N (Hypothesis 1). Thus, low A/leaf N may result directly from low leaf N.

Second, species with low SLA's may invest a relatively high proportion of leaf tissue (including N) to non-photosynthetic function and thus the proportion of N required for reactions not related to photosynthesis may scale negatively with SLA (Hypothesis 2). To the extent that this is true, low A/leaf N and low SLA are functionally related, because the proportion of the total leaf N invested in photosynthetic machinery decreases as SLA decreases (and thus A/mass for a given N/mass would decline). Indirect support for this idea is provided by a) the better correlation of A/leaf N with SLA ($r^2=0.62$, $p<0.001$) than with either N/mass ($r^2=0.39$, $p<0.001$) or N/area ($r^2=0.03$, $p<0.47$); and b) the fact that for species with similar N/mass, those with higher SLA have higher A/mass (data not shown); as also mentioned by Field and Mooney (1986).

A third hypothesis suggests that the partitioning of N among photosynthetic compounds and/or the activity of rate-limiting enzymes involved in photosynthesis varies among species in relation to certain ecological traits, such that A/leaf N is variable among species (Evans 1989). Shade-adapted plants tend to invest larger quantities of N in light-harvesting pigments and proteins, but make smaller investments in Calvin cycle enzymes (Bjorkman 1981, Evans 1989). Evans (1989) pointed out that within-species partitioning of N into thylakoids versus Calvin cycle compounds differs when examining variation in nutrition versus variation in irradiance during growth. At present, little is known about such partitioning among plant species adapted to different nutrient availabilities, which is the case for the SCRN species.

The first two above hypothesis in combination (with or without the third hypothesis) can adequately explain why A/mass and A/leaf N decline continuously with increasing leaf lifetime: leaf N/mass and SLA tend to decrease with leaf lifetime, and together may result in lesser total allocation of leaf N to photosynthesis, with the integrated result that A/mass declines continuously with increasing lifespan. Other possible (and potentially interacting) explanations also exist. For example, lowland tropical rainforests often have low availability of P (and other nutrients) (Cuevas and Medina 1986), and limitations of A/leaf N due to low P/N ratios may occur (Reich and Schoettle 1988, Reich et al., unpublished data). Plants with leaves of high SLA could also be less limited photosynthetically by diffusive conductance of CO_2 than those with low SLA foliage, although this possibility has not been adequately examined. Despite the fact that the above hypotheses provide physiological explanations of why sclerophylls (low SLA) have low A/leaf N without requiring consideration of differences in leaf longevity (Field and Mooney 1986), SLA and A/leaf N *do* decrease with leaf lifespan, leaving us with questions about the ecological implications of such trends (see Ecological Considerations above).

When leaf N contents and net photosynthetic rates

are expressed on area rather than weight bases, some different implications emerge. The decline in photosynthesis per leaf area with increasing leaf lifespan (Fig. 5A) cannot be explained as due to lower leaf N per unit leaf area, since N per leaf area was not a function of leaf longevity (Fig. 1B), and area-based net photosynthesis was not significantly correlated with area-based N contents (Fig. 6C). Instead, the decline in area-based photosynthesis with leaf lifespan appears to be related to decreases in A/leaf N with increasing leaf lifespan. Why do species with short leaf lifespans have higher A/leaf N than those with longer lifespans, even when leaf N/area is the same? We pointed out previously that species with short leaf lifespans have thinner (high SLA) leaves with high leaf N/mass. A/leaf N is correlated with SLA but not with leaf N/area. Thus, if two species have similar area-based leaf N but vary in SLA (and as a result, in N/mass), the species with greater SLA (and N/mass) will likely have greater A/leaf N and hence greater area-based photosynthesis.

Previous studies have found that variation in area-based net photosynthesis among species was significantly but poorly correlated with variation in area-based leaf N (Field and Mooney 1986). Among SCRN species this relationship did not hold true. Due to the relationships between either SLA or N/mass and A/mass, covariation in SLA and N/mass can result in significant A/area to N/area relationships (e.g., Chazdon and Field 1987), if variation in SLA and N/mass among leaves affect N/area in parallel: e.g., SLA decreases (or increases) while N/mass increases (or decreases) as can occur across light gradients, or during leaf development or aging. A/area can also be well correlated with N/area when N/area varies with variation in either SLA or N/mass, while the other remains relatively stable. However, relationships among diverse Amazonian species with wide variation in leaf lifespan do not fit either of these patterns, since SLA and N/mass decrease with increasing lifespan, driving N/area in opposite directions.

In conclusion, the data and analyses in this study suggest that there is a strong interdependency between leaf lifespan, A/mass, A/area, N/mass, SLA, and leaf toughness, which may result from the necessity for allocational trade-offs that enhance either productivity, nutrient conservation or defense. Apparently a plant can allocate resources towards a high photosynthetic assimilation rate for a brief time, or can provide resistant physical structure that results in a lower rate of carbon assimilation over a longer period of time, but not both. This trade-off has important ecological ramifications as it suggests that differences between species in leaf lifespan and associated traits should reflect their differences in habitat or niche. It also raises the possibility that species with great plasticity in modifying leaf lifespan and related traits may be able to grow in habitats with a wide range of resource availability, while species without plasticity in this regard will occupy a narrower range of habitats. These data also suggest that for species adapted to different nutrient availabilities, variation among species in leaf N/area is not related to variation in leaf lifespan and is not a direct cause of variation in A/area.

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References

- Axelrod DI (1966) Origin of deciduous and evergreen habits in temperate forests. *Evolution* 20:1–15
- Bazzaz FA (1979) The physiological ecology of plant succession. *Ann Rev Ecol Syst* 10:351–371
- Björkman O (1981) Responses to different quantum flux densities. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds), *Physiological Plant Ecology*, I. vol. 12A, Encyclopedia of Plant Physiology, new series, Springer, Berlin, Heidelberg, New York, pp. 57–107
- Chabot BF, Hicks DJ (1982) The ecology of leaf life spans. *Ann Rev Ecol Syst* 13:229–259
- Chapin FS III (1980) The mineral nutrition of wild plants. *Ann Rev Ecol Syst* 11:233–260
- Chazdon RL, Field CB (1987) Determinants of photosynthetic capacity in six rainforest Piper species. *Oecologia* 73:222–230
- Clark K, Uhl C (1987) Farming, fishing, and fire in the history of the upper Rio Negro region of Venezuela. *Human Ecology* 15:1–26
- Coley PD (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol Monogr* 53:209–233
- Coley PD (1988) Effects of plant growth rate and leaf lifetime on the amount and type of antiherbivore defense. *Oecologia* (Berlin) 74:531–536
- Coley PD, Bryant JP, Chapin FS III (1985) Resource availability and plant anti-herbivore defense. *Science* 230:895–899
- Cuevas E, Medina E (1983) Root production and organic matter decomposition in a Tierra Firme forest of the upper Rio Negro basin. In: *Wurzelökologie und Ihre Nutzenwendung*. Int Symp Gumpenstein 1982, pp 653–666
- Cuevas E, Medina E (1986) Nutrient dynamics within amazonian forest ecosystems. I. Nutrient flux in fine litter fall and efficiency of nutrient utilization. *Oecologia* 68:466–472
- Cuevas E, Medina E (1988) Nutrient dynamics within amazonian forests. II. Fine root growth, nutrient availability and leaf litter decomposition. *Oecologia* 76:222–235
- Evans JR (1989) Photosynthesis and nitrogen relationships in leaves of C₃ plants. *Oecologia* 78:9–19
- Field C, Mooney HA (1983) Leaf age and seasonal effects on light, water, and nitrogen use efficiency in a California shrub. *Oecologia* 56:348–355
- Field C, Mooney HA (1986) The photosynthesis-nitrogen relationship in wild plants. In: *On the economy of plant form and function* (ed T. Givnish), Cambridge University Press, pp 25–55
- Gray JT, Schlesinger WH (1983) Nutrient use by evergreen and deciduous shrubs in southern California. II. Experimental investigations of the relationships between growth, nitrogen uptake, and nitrogen availability. *J Ecol* 71:43–56
- Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am Nat* 111:1169–1194
- Harrington RA, Brown JB, Reich PB (1989) Ecophysiology of exotic and native shrubs in Southern Wisconsin. I. Relationship of leaf characteristics, resource availability, and phenology to seasonal patterns of carbon gain. *Oecologia* 80:356–367
- Herrera R (1977) Soil and terrain conditions in the International Amazon Project at San Carlos de Rio Negro, Venezuela. Correlation with vegetation types. In: (ed EF Bruni; Hamburg-Reinbeck), *Transactions of the International MAB-IUFRO Workshop on Tropical Rainforest Ecosystems Research*, pp 132–188
- Jordan CF (1982) The nutrient balance of an amazonian rain forest. *Ecology* 61:14–18
- Jordan CF, Heuvelink J (1981) The water budget of an amazonian rain forest. *Acta Amazonica* 11:87–92
- Jordan CF, Uhl C (1978) Biomass of a “tierra firme” forest of the Amazon basin. *Oecol Plant* 13:387–400
- Kikuzawa K (1983) Leaf survival of woody plants in deciduous broad-leaved forests. 1. Tall trees. *Can J Bot* 61:2133–2139
- Kikuzawa K (1984) Leaf survival of woody plants in deciduous broad-leaved forests. 2. Small trees and shrubs. *Can J Bot* 62:2551–2556
- Klinge H, Herrera R (1983) Phytomass structure of natural plant communities on spodosols in southern Venezuela: the Tall Amazon Caatinga forest. *Vegetatio* 53:65–84
- Lassoie JP, Dougherty PM, Reich PB, Hinckley TM, Metcalf CM, Dina SJ (1983) Ecophysiological investigations of understory eastern redcedar in central Missouri. *Ecology* 64:1355–1366
- Monk CD (1966) An ecological significance of evergreenness. *Ecology* 47:504–505
- Mooney HA, Dunn EL (1970) Photosynthetic systems of Mediterranean-climate shrubs and trees of California and Chile. *Am Nat* 104:447–453
- Neter J, Wasserman W (1974) *Applied linear statistical models*. Richard D. Irwin, Inc. Homewood, Illinois, p 842
- Nilsen ET, Sharifi MR, Rundel PW (1987) Leaf dynamics in an evergreen and a deciduous species with even-aged leaf cohorts, from different environments. *Am Midl Nat* 118:46–55
- Pearcy RW, Osteryoung K, Calkin HW (1985) Photosynthetic responses to dynamic light environments by Hawaiian trees: the time course of CO₂ uptake and carbon gain during sunflecks. *Plant Physiol* 79:896–902
- Reich PB, Borchert R (1984) Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *J Ecol* 72:61–74
- Reich PB, Schoettle AW (1988) Role of phosphorus and nitrogen in photosynthetic and whole plant carbon gain and nutrient-use efficiency in eastern white pine. *Oecologia* 77:25–33
- Saldarriaga JG (1985) Forest succession in the upper Rio Negro of Colombia and Venezuela. Ph.D. Dissertation, University of Tennessee
- SAS (1985) *SAS User's Guide: Statistics*, Version 5, ed, S.P. Joyner, SAS Institute, Inc., Cary, NC
- Small E (1972) Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. *Can J Bot* 50:2227–2233
- Uhl C (1987) Factors controlling succession following slash-and-burn agriculture in Amazonia. *J Ecol* 75:377–407
- Uhl C, Jordan CF (1984) Vegetation and nutrient dynamics during the first five years of succession following forest cutting and burning in the Rio Negro region of Amazonia. *Ecology* 65:1476–1490
- Walters MB, Reich PB (1989) Response of *Ulmus americana* seedlings to varying nitrogen and water status. I. Photosynthesis and growth. *Tree Physiol* 5:159–172
- Waring RH, Franklin JF (1979) Evergreen coniferous forests of the Pacific Northwest. *Science* 204:1380–1386
- Williams K, Field CB, Mooney HA (1989) Relationships among leaf construction cost, leaf longevity, and light environment in rain-forest plants of the genus Piper. *Am Nat* 133:198–211