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DECLINE OF PHOTOSYNTHETIC CAPACITY WITH LEAF AGE IN RELATION TO LEAF LONGEVITIES FOR FIVE TROPICAL CANOPY TREE SPECIES[1]

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The effect of leaf aging on photosynthetic capacities was examined for upper canopy leaves of five tropical tree species in a seasonally dry forest in Panama. These species varied in mean leaf longevity between 174 and 315 d, and in maximum leaf life span between 304 and 679 d. The light-saturated CO_2 exchange rates of leaves produced during the primary annual leaf flush measured at 7–8 mo of age were 33–65% of the rates measured at 1–2 mo of age for species with leaf life span of < 1 yr. The negative regression slopes of photosynthetic capacity against leaf age were steeper for species with shorter maximum leaf longevity. In all species, regression slopes were less steep than the slopes predicted by assuming a linear decline toward the maximum leaf age (20–80% of the predicted decline rate). Maximum oxygen evolution rates and leaf nitrogen content declined faster with age for species with shorter leaf life spans. Statistical significance of regression slopes of oxygen evolution rates against leaf age was strongest on a leaf mass basis (r^2 = 0.49–0.87), followed by leaf nitrogen basis (r^2 = 0.48–0.77), and weakest on a leaf area basis (r^2 = 0.35–0.70).

Key words: leaf age; leaf longevity; leaf nitrogen content; photosynthetic capacities; tropical canopy trees.

Rates of photosynthesis after the full expansion of a leaf generally exhibit a monotonic decline (Sestak et al., 1985). This decline is caused by a redistribution of resources to younger leaves for optimization of the whole-shoot photosynthetic income, rather than by an uncontrolled deterioration (Field and Mooney, 1983; Hikosaka, Terashima, and Katoh, 1994). In a diverse range of plant species including tropical trees (Zotz and Winter, 1994; Ackerly and Bazzaz, 1995), it has been observed that leaf nitrogen content and photosynthetic capacity decrease linearly with leaf age. Consideration of the effect of leaf age on photosynthetic capacity is necessary in order to estimate the long-term carbon budget of a leaf and of the whole canopy. One approach to incorporate the effect of leaf age on estimation of carbon income is to repeat diel measurements of photosynthetic rates throughout the lifetime of a leaf (Zotz and Winter, 1994). Although this is perhaps the most rigorous approach for a single leaf, it is time-consuming and the results are difficult to parameterize for a population of leaves, especially when there is significant variation among leaves. Since daily net photosynthetic gain is tightly correlated with photosynthetic capacity (Zotz and Winter, 1994), if we can approximate the function of decreasing photosynthetic capacity with leaf age, it greatly facilitates modeling long-term carbon budgets for the whole canopy.

A simple approximation of this monotonic decrease with time after leaf full expansion (t) may be expressed by the following function (Kikuzawa, 1991):

$$p(t) = a\ (1 - t/b)$$

where a and b correspond to the y and x intercepts of the linear regression between photosynthetic rates and leaf age, respectively. Parameter a (y intercept of the regression) may be directly measured as the initial photosynthetic capacity at the time of leaf full expansion. In contrast, parameter b (x intercept of the regression) is statistically determined as a function of the initial photosynthetic rate (a) and the rate of its decline (a/b), and it represents the time when photosynthetic rates would reach zero in extrapolation of the regression line. The parameter b appears to approximate the actual leaf longevity when the same leaf is repeatedly measured for plants with very short life spans (e.g., Evans, 1983; Makino, Mae, and Ohira, 1984; Ackerly and Bazzaz, 1995), but correspondence of b to actual leaf longevity is unknown for trees with long-lived leaves. A link between leaf longevity with parameter b also means a correlation between leaf longevity and the rate of decline of photosynthetic rate with leaf age (a/b), which is directly measurable.

A cost–benefit analysis incorporating this function suggests that leaf longevity is expected to be short when the initial net photosynthetic rate of the leaf (a) is large and/or the decline rate (a/b) is large (Kikuzawa, 1991). A positive correlation between mean leaf longevity and initial photosynthetic capacity (model parameter a, or y intercept of regression) has been demonstrated across a variety of plant species (Reich et al., 1991; Reich, Walters, and Ellsworth, 1992; Mulkey, Kitajima, and Wright, 1995). In contrast, data for the interspecific relationship between the leaf longevity and the rate of photosynthetic decline (parameter a/b, the slope of regression) are scarce. This is so because most physiological studies on

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TABLE 1. List of study species, their leaf phenology, and leaf longevity of the primary annual flush (leaves born in the first two months of the annual leaf production); N = number of leaves in the census born during the specified birth months (% of annual leaf production), mean = mean leaf survival time (d), 90% = 90 percentile leaf survival time (d), Max. = maximum leaf survival time (d). Nomenclature follows D'Arcy (1987).

Species	Family	Leaf longevity of primary annual flush				
		Birth mo	N	Mean	90%	Max.
Anacardium excelsum Skeels	Anacardiaceae	Jan–Feb	864 (37%)	315	374	679
Annona spraguei Staff	Annonaceae	May–Jun	445 (62%)	221	273	304
Antirrhoea trichantha Griseb.	Rubiaceae	May–Jun	922 (39%)	174	302	306
Castilla elastica Cerv.	Moraceae	May–Jun	140 (41%)	206	273	305
Luehea seemannii Tr. & Pl.	Tiliaceae	Jun–Jul	1589 (43%)	201	364	404

the leaf age effects on photosynthetic traits do not include leaf demography data.

Here, we report the rate of the decline of photosynthetic capacity with leaf age for five tropical canopy tree species with contrasting mean and maximum leaf longevity. Based on the result of the model by Kikuzawa (1991), we predicted that the negative slopes of the regression of photosynthetic capacity against leaf age (a/b in the model) would be steeper for species with shorter leaf longevities. In order to examine a possible link between the x intercepts of the regression (parameter b) with leaf longevity, we compared x intercepts with the observed leaf longevity statistics within each species. If there is a correspondence between x intercept and leaf longevity trait of the species, it enables us to estimate the regression slope from leaf demography data. Estimation of the regression slope is of particular interest for modeling long-term carbon budgets of tropical forest canopy leaves, which contribute significantly to global primary productivity. For each species, we calculated a hypothetical regression slope assuming the x intercept to be the observed maximum (or 90th percentile of) leaf longevity, and compared this value with the observed regression slope. For a subset of these species, we examined the effects of leaf aging on light and CO_2-saturated oxygen evolution rates, leaf nitrogen content, and leaf mass per area, in order to explore the physiological and morphological correlates of the decline of photosynthetic capacities with leaf age.

METHODS

Site and canopy approach—The study was conducted in a seasonally dry forest in the Parque Natural Metropolitano near Panama City, Panama. Annual rainfall averages 1740 mm at the site, most of which occurs during the rainy season from May through December. The forest is 75–150 yr old second growth with tree heights up to 40 m. We used a 42-m tall tower crane with a 51-m jib to reach the upper canopy (Parker, Smith, and Hogan, 1992).

Species, leaf census, and sampling—Five species used in the study are common canopy trees at the site. We recorded phenology of leaf production and leaf life time in monthly censuses between December 1991 and August 1995. We marked all new and (almost) fully expanded leaves with unique identification numbers in replicate branches in each of three or more individuals for each species, and recorded their birth and death time. Leaf age (days after full expansion) was calculated as: (date of measurement) − (the date of monthly census when the leaf was first noted) + 15 d. Thus, the calculated leaf age has a potential error of ± 15 d. *Anacardium excelsum* exchanged leaves in December–January, and continued to produce leaves throughout the dry season. The rest of the species produced most leaves during the wet season. *Annona spraguei, Castilla elastica* and *Antirrhoea trichantha* produced the greatest number of leaves at the beginning of the wet season (April–May), continued to produce decreasing numbers of leaves toward the late wet season (November), and became completely deciduous by the late dry season (March). *Luehea seemannii* produced leaves in two peaks, first in June–July and second in October–December, became gradually deciduous during the dry season, but retained approximately half of the maximum leaf area until May. The complete names of the species and the longevity of the leaf cohorts sampled in the study are shown in Table 1. Hereafter, the species are referred to by genus only.

All leaves used in the study were produced on upper branches in exposed locations. Different sampling schemes were used for *Anacardium* with continuous dry-season leaf production and the other species with annual peak leaf production at the beginning of the rainy season. For *Anacardium,* we selected six branches from four individuals in July 1994, and sampled every third or fifth leaf in each branch from the distal end. Leaf age of *Anacardium* leaves used in the study ranged between 10 and 550 d and consisted of two groups, < 300 d and > 450 d, because this species did not produce leaves between August and November. For the rest of the species, we measured leaves born during the primary annual flush (May–June for *Annona, Antirrhoea,* and *Castilla,* June–July for *Luehea*) in June–July 1994 (1–2 mo old) and in January 1994 (6–8 mo old leaves born in the previous year). For these species, standardization of leaf production time was important since leaves born at different seasons exhibit different initial photosynthetic capacities and potential leaf life spans (longest for the leaves produced at the earliest time of the annual leaf production) (Kitajima, Mulkey, and Wright, 1997).

CO_2 exchange rates in the field—On several mornings, we measured the light-saturated CO_2 exchange rate (A) and stomatal conductance (g_s) of intact 1–2 mo old leaves in the field with a portable infrared gas analyzer (CIRAS, PP Systems, UK), under a quartz lamp providing photosynthetic photon flux density (PPFD) of 1300 μmol photons·m^{-2}·s^{-1} at the leaf surface or comparable natural sunlight between 1100 and 1400 μmol photons·m^{-2}·s^{-1} . There were no differences between measurements made with the lamp and under natural sunlight, and data were analyzed together. Measurements were taken after leaves had reached maximum stomatal conductance. The CO_2 concentration of reference air was controlled within 350 ± 5 μL/L, while air humidity and leaf temperature were allowed to reflect field conditions in situ (2.1–3.1 kPa, and 29°–39° C, respectively).

Photosynthetic oxygen evolution rates—We sampled leaf disks (10 cm^2 each) from selected leaves of contrasting ages marked in the monthly phenology censuses for *Anacardium, Antirrhoea,* and *Luehea.* These species represented three contrasting maximum leaf life spans (Table 1). The leaf disks were sampled just after dawn on the day of the measurement and kept dark in aerated plastic containers lined with moist filter paper until measurements, which were completed by 1400 on the same day. Photosynthetic light response curves were determined

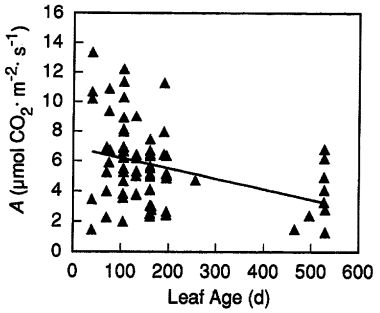

Fig. 1. Effect of leaf age on light saturated photosynthetic rates of a canopy emergent, *Anacardium excelsum* in a tropical dry forest. Each point represents a leaf. All leaves were born in January-February and measured in situ. See Table 2 for regression statistics.

for PPFD between 0 and 1900 μmol photons·m^{-2}·s^{-1} with a leaf-disk oxygen electrode and data acquisition software (Hansatech, Norfolk, UK). Light was provided by a Björkman-type lamp and increased in steps by combinations of neutral density glass filters after oxygen evolution rate reached quasi-steady state at each light level. The electrode chamber was supplied with humidified air with 10% CO_2 and cooled by circulating 28° C water. We report photosynthetic oxygen evolution rates recorded at the highest light level as light and CO_2-saturated oxygen evolution rates. After these measurements, leaves were dried at 60° C for ≥ 5 d before determination of dry mass per unit area and total nitrogen at the Agricultural Experimental Station of the University of Missouri, USA.

Statistical analysis—Statistical analyses were done with the JMP statistical package (SAS, 1994). Because sampled leaf ages consisted of two discontinuous groups in four species, the effect of leaf age on A and g_s was examined by ANOVA (comparing 1–2 mo old and 6–8 mo old leaves) as well as by regression analysis (treating age as a continuous variable). ANOVA provides a more conservative test of whether photosynthetic rates changed with chronological age. For species that exhibited significant regression slopes of A against age, x intercepts were compared to the mean, 90th, and 100th percentile points of the leaf longevity distribution determined from monthly leaf censuses. We calculated hypothetical slopes as a function of leaf longevity by assuming the initial photosynthetic rate to be the y intercept of the observed regression and a linear decline of photosynthetic rates to zero at the potential leaf span for the species, using 90th and 100th percentile points of the leaf longevity distribution. The 90th percentile point is perhaps a better estimate of typical maximum leaf longevity than the 100th percentile point, since maximum leaf longevity may be subject to sampling probability of rare events at the tail of the distribution.

RESULTS

Light-saturated photosynthetic rates (A) declined significantly with leaf age in *Anacardium, Annona, Antirrhoea,* and *Castilla* (Figs. 1, 2, Table 2). Regression slopes of A against leaf age ranged between −0.007 and −0.032 μmol CO_2·m^{-2}·s^{-1}·d^{-1} among these species. In *Anacardium,* the negative slope of A against leaf age was still significant when the analysis was restricted to leaves < 1 yr old (Fig. 1; −0.018, N = 64, r^2 = 0.10, P < 0.02). In *Luehea,* which had a maximum leaf longevity of 404 d, there was no significant decline of A in the age range examined (up to 220 d: Fig. 2, Table 2).

The observed slope for *Anacardium* was much less steep than the observed slopes of *Annona, Antirrhoea,* and *Castilla* with much shorter leaf life spans (Tables 1, 2). In all species, x intercepts (Table 2) were 20% (*Castilla*) to 85% (*Antirrhoea*) greater than the maximum leaf life spans observed (x intercepts in Table 2 compared to maximum life span in Table 1). In other words, in all species the observed slopes were much less steep than the slopes predicted by assuming linear decline towards zero A at the maximum leaf age possible (Table 2). For species with significant slopes, the observed slopes were 39% (*Anacardium*) to 76% (*Castilla*) of the predicted slopes assuming the x intercept to be at the 90th percentile point of leaf longevity (Table 2).

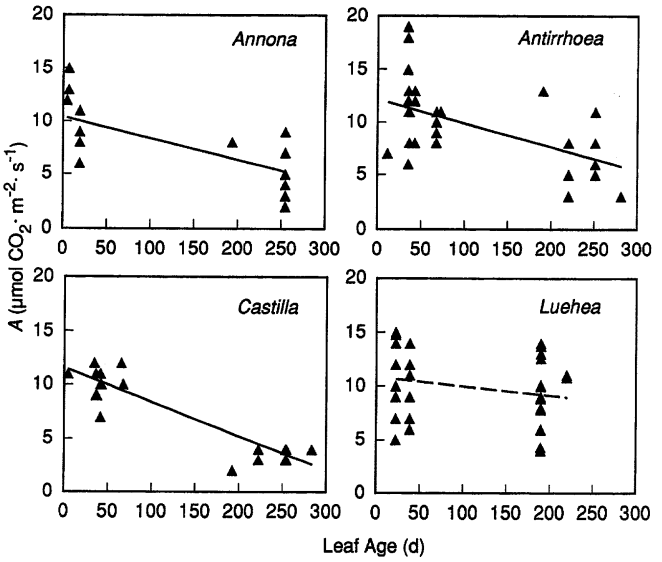

Fig. 2. Effect of leaf age on light saturated photosynthetic rates for four canopy tree species in a tropical dry forest. Each point represents a leaf. All leaves were born in the early rainy season (May-June) and measured in situ. See Table 2 for regression statistics. Significant and nonsignificant regression lines are indicated by solid and broken lines, respectively.

In three species with maximum leaf life spans of 304–306 d (*Annona, Antirrhoea,* and *Castilla*), 6–8 mo old leaves had only 33–65% of A for 1–2 mo old leaves (Table 3). Mean stomatal conductances (g_s) of 6–8 mo old leaves were also significantly lower than the means of 1–2 mo old leaves in *Antirrhoea* and *Castilla* (Table 3). In contrast, there was no significant difference in A nor g_s between 1–2 mo old leaves and 6–8 mo old leaves

TABLE 2. Intercepts (y intercepts, x intercepts) and slopes of regressions between leaf age and A for five tropical tree species (Figs. 1, 2), compared to the predicted regression slopes calculated from the observed y intercepts and the 90 and 100 percentile points of leaf longevity distribution as x intercepts (Table 1). Significant differences of slopes from zero are indicated following r^2 values (** P < 0.005, *** P < 0.0005).

	Observed regression					Predicted slope (%)	
Species	N	r^2	y int.	x int.	Slope	90	100
Anacardium	74	0.12**	6.9	985	−0.007	−0.018	−0.010
Annona	18	0.51***	10.6	482	−0.022	−0.036	−0.036
Antirrhoea	29	0.29**	12.1	550	−0.022	−0.043	−0.039
Castilla	23	0.81***	11.7	365	−0.032	−0.042	−0.038
Luehea	41	0.04	10.8	1200	−0.009	−0.030	−0.025

TABLE 3. Mean (SE) of light-saturated photosynthetic rates and stomatal conductance of leaves of contrasting age categories for five tree speices in a tropical dry forest. See text for leaf sampling schemes. Sample size = number of leaves, A = light-saturated CO_2 exchange rates, g_s = stomatal conductance. Significant differences between age classes by t test are indicated next to 6–8 mo values (* $P < 0.05$, ** $P < 0.005$, *** $P < 0.0005$).

Species	Sample size		A (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$)		g_s (mol $H_2O \cdot m^{-2} \cdot s^{-1}$)	
	1–2 mo	6–8 mo	1–2 mo	6–8 mo	1–2 mo	6–8 mo
Anacardium	13	10	7.0	5.5	0.16	0.15
			(1.0)	(1.1)	(0.03)	(0.03)
Annona	9	10	10.5	5.3**	0.37	0.28
			(0.9)	(0.8)	(0.05)	(0.05)
Antirrhoea	20	9	11.0	7.1*	0.47	0.29*
			(0.7)	(1.1)	(0.04)	(0.07)
Castilla	14	9	10.4	3.4***	0.56	0.21***
			(0.3)	(0.4)	(0.03)	(0.04)
Luehea	32	9	10.5	9.1	0.42	0.42
			(0.5)	(1.0)	(0.05)	(0.09)

in the two species with maximum leaf life span > 1 yr (*Anacardium* and *Luehea*).

There was a strong correlation between A and g_s in all species. Multiple regressions of A against leaf age and g_s explained greater proportions of variance in A (R^2 = 0.38–0.90) than did simple regressions of A against leaf age (r^2 = 0.04–0.81, Table 2). The ratio of A to g_s was significantly higher for 1–2 mo old leaves than for 6–8 mo old leaves in *Annona* and *Anacardium* ($P < 0.04$ and $P < 0.001$, respectively), but no other species showed significant changes in the ratio A/g_s with leaf age.

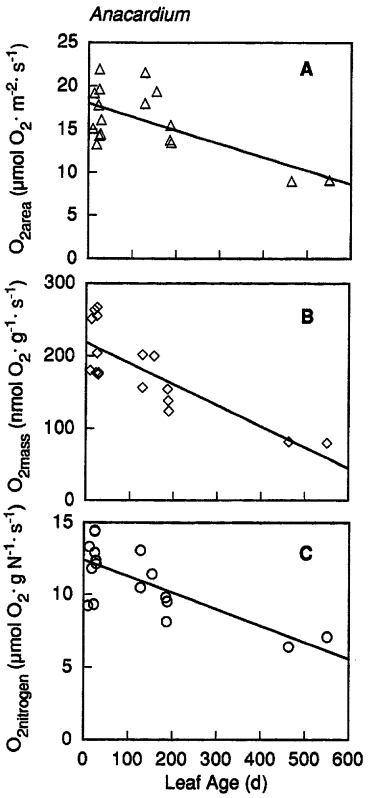

Fig. 3. Effect of leaf age on light and CO_2-saturated oxygen evolution rates per unit leaf area (A), per unit leaf mass (B), and per gram nitrogen (C) of *Anacardium excelsum*. See Table 4 for regression statistics.

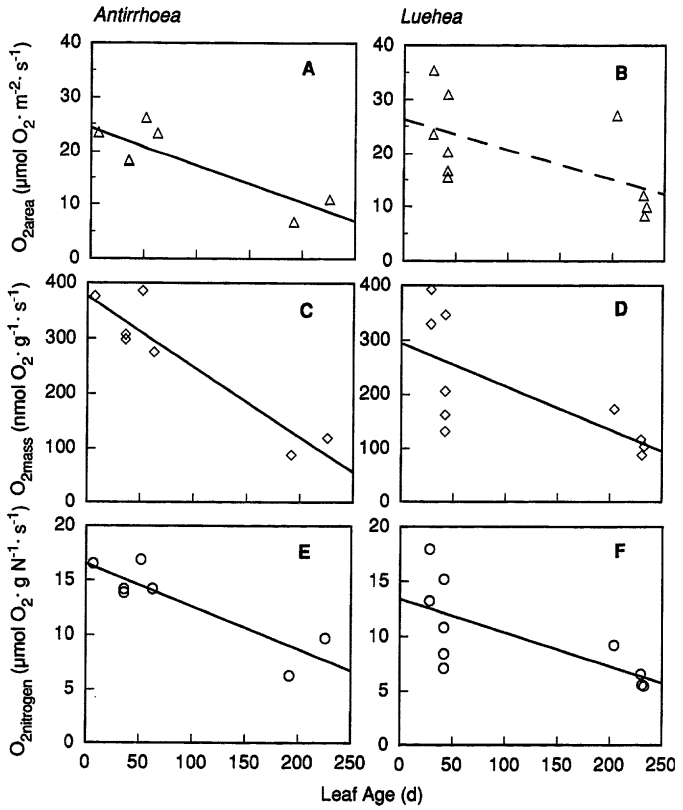

Fig. 4. Effect of leaf age on light and CO_2-saturated oxygen evolution rates per unit leaf area (A, B), per unit leaf mass (C, D), and per gram nitrogen (E, F) of *Antirrhoea trichantha* (left, A, C, E) and *Luehea seemannii* (right, B, D, F). Each point represents a leaf. See Table 4 for regression statistics. Significant and nonsignificant regression lines are indicated by solid and broken lines, respectively.

Photosynthetic capacity determined by an oxygen electrode and expressed on area, mass, and nitrogen basis all declined with leaf age (Figs. 3, 4), except for *Luehea* on an area basis (Fig. 4B, $P < 0.07$). In each species, correlation coefficients (r^2) were greatest on a mass basis (O_{2mass}), intermediate on a nitrogen basis ($O_{2nitrogen}$), and least on an area basis (Table 4). These differences in strength of the relationships observed among expressions of photosynthetic capacity reflected how leaf mass per area (LMA) and nitrogen per unit mass changed with leaf age (Table 4). In *Anacardium* and *Antirrhoea,* LMA increased significantly with leaf age. Nitrogen content per unit mass declined significantly in all species. In all species, there was a strong correlation between O_{2mass} and nitrogen content per mass (r^2 = 0.62, 0.94, and 0.77 for *Anacardium, Antirrhoea,* and *Luehea,* respectively; $P <$ 0.001 for all). There was no effect of leaf age on leaf absorptance (means for *Anacardium, Antirrhoea,* and *Luehea* were 0.89, 0.87, and 0.90, respectively) or quantum yield (the initial slope of oxygen evolution rates against incident PPFD between 0 and 71 μmol photons$\cdot m^{-2} \cdot s^{-1}$ corrected for leaf absorptance, means for *Anacardium, Antirrhoea,* and *Luehea* were 0.075, 0.069, and 0.079, respectively).

TABLE 4. Effects of age (d) on light-saturated oxygen evolution rates (area, mass, and nitrogen basis, data shown on Figs. 3, 4), leaf mass per area (LMA), and nitrogen content. * $P < 0.05$, ** $P < 0.005$, *** $P < 0.0005$.

			O_{2area} (μmol $O_2 \cdot m^{-2} \cdot s^{-1}$)		O_{2mass} (nmol $O_2 \cdot g^{-1} \cdot s^{-1}$)		$O_{2nitrogen}$ (μmol $O_2 \cdot g\ N^{-1} \cdot s^{-1}$)		LMA (g/m^2)		Nitrogen (mg/g)	
Species	N	Range (d)	Slope	r^2	Slope	r^2	Slope	r^2	Slope	r^2	Slope	r^2
Anacardium	17	10–551	−0.016	0.43**	−0.29	0.65***	−0.011	0.55**	0.07	0.42*	−0.012	0.49**
Antirrhoea	7	7–226	−0.070	0.70*	−1.28	0.87**	−0.039	0.77*	0.11	0.60*	−0.050	0.96***
Luehea	10	28–233	−0.056	0.35	−0.80	0.49*	−0.031	0.48*	0.08	0.13	−0.018	0.45*

DISCUSSION

Link between leaf age effects on photosynthetic capacity and leaf longevity—As we predicted, species with longer leaf life span had less steep slopes and greater x intercepts in the regressions between photosynthetic capacity and chronological leaf age. The slopes ranged between −0.032 and −0.007 μmol $CO_2 \cdot m^{-2} \cdot s^{-1} \cdot d^{-1}$ among the study species with mean leaf longevity between 183 and 343 d. A similar slope of −0.031 μmol $CO_2 \cdot m^{-2} \cdot s^{-1} \cdot d^{-1}$ was reported for a tropical evergreen tree, *Morisonia americana,* for which leaf life span is reported to be ≈ 1 yr (Sobrado, 1992). These slopes were much less steep than the slopes between −0.57 and −1.32 μmol $CO_2 \cdot m^{-2} \cdot s^{-1} \cdot d^{-1}$ for a tropical pioneer tree *Heliocarpus appendiculatus,* which had a mean leaf longevity between 28 and 37 d depending on the light and nutrient treatments (Ackerly and Bazzaz, 1995). In *H. appendiculatus,* the estimated x intercepts (29–37 d) approximate the mean leaf longevity. In contrast, the x intercepts for the five species in this study (between 365 and 985 d for significant regressions) were much greater than the mean and maximum leaf longevities of these species. As a result, in all species, the observed rate of decline was 30–60% smaller than that expected from an assumption of a linear decline toward zero at the 90th percentile point of leaf age distribution. The x intercepts for photosynthetic rates per unit leaf mass would be somewhat smaller than those on a leaf area basis. For example, x intercepts were 299, 370, and 754 d for the O_{2mass} data in Table 4 and Figs. 3, 4, for *Antirrhoea, Luehea,* and *Anacardium,* respectively. Nevertheless, these x intercepts were still much greater than the mean leaf longevities. These discrepancies between the x intercepts and the mean and maximum leaf longevities may be caused by a nonlinear decline of photosynthetic capacity with leaf age.

Our results suggest that slopes calculated by assuming y and x intercepts to be the initial photosynthetic capacity and maximum leaf life span may overestimate the negative effect of leaf age on photosynthetic capacity by 30–60%. Although photosynthetic capacity in many plant species declines linearly with leaf age after leaf full expansion (Evans, 1983; Witkowski et al., 1992; Hikosaka, Terashima, and Katoh, 1994; Zotz and Winter, 1994; Ackerly and Bazzaz, 1995), it may stay relatively constant until it starts to decline at a faster rate during the final senescent phase (Kramer and Kowslowsky, 1979; Reich et al., 1991; Schaffer, Whiley, and Kohli, 1991). If the decline in photosynthetic capacity with leaf age is caused primarily by redistribution of resources to newer leaves, then the linearity of decline is likely to be more pronounced in species with continuous leaf production, such as crop species and early successional species, than in species with a single annual leaf flush as is typical in many temperate tree species. The tree species in this study exhibited an intermediate type of leaf production as they produced 37–62 % of annual leaf cohort within the first 2 mo and the rest during the additional 6–7 mo (Table 1). It is reasonable to expect that leaves of these species exhibit a slow decline of photosynthetic capacity during most of their lifetime until they enter the final senescence phase. A simple linear regression still provides the most reasonable function to describe this decrease of photosynthetic capacity for a cohort of leaves, given the great variability of photosynthetic capacities for a given age (Figs. 1–4). Empirical estimates of photosynthetic rates as a function of leaf age are needed for a variety of plant species in order to estimate the photosynthetic income over the lifetime of a leaf and for a population of leaves (Kikuzawa, 1991; Zotz and Winter, 1994; Mulkey, Kitajima, and Wright, 1996).

Effects of season and leaf age—The photosynthetic capacity of an individual leaf at a given time is a function of both when it is born and how old it is. In *Antirrhoea, Castilla,* and *Luehea,* we found that leaves born during the early rainy season have lower photosynthetic capacities at the time of full expansion than leaves born at the end of the rainy season (Mulkey Kitajima, and Wright, 1995; Kitajima, Mulkey, and Wright, 1997). Thus, when photosynthetic rates measured during the early dry season were compared for leaves born at different times of the year (and hence of different ages at the time of measurement), the effect of leaf age on photosynthetic capacity became exaggerated, yielding steeper regression slopes than reported here (author, unpublished data). Very few studies have examined how effects of leaf age on photosynthetic capacities may differ among leaves born at different seasons. In Kiwi fruit vine (*Actinida deliciosa*), leaves emerging at 1, 2, 3, and 4 mo after the initial bud break require different times to reach full photosynthetic capacities, all reaching the peak at about 4 mo after bud break, after which photosynthetic capacities declined rather similarly (Buwalda, Meekings, and Smith, 1991). Contrasting patterns may exist in the tropical tree species studied here. Because leaves born late in the season have shorter mean longevities than leaves born early in these species (Kitajima, Mulkey, and Wright, 1997), the rate of decline of photosynthetic capacity may be steeper for the former. Time of the year and leaf age may be treated synonymously for temperate trees with a single annual flush (Reich et al., 1991). However, for tropical trees with less synchronous leaf production, a clear distinction between time of year and leaf age is essential. The whole-

canopy photosynthetic capacity is determined by a complex function that integrates leaf age effects on photosynthetic capacity for each seasonal cohort with the relative abundance of different seasonal cohorts in the canopy.

Leaf age, nitrogen reallocation, and photosynthetic capacity—The observed decline in photosynthetic rates with leaf age in our study likely resulted in part from nitrogen reallocation to newer leaves. The cohort of leaves produced during the initial leaf flush for the year and used in the study represented 37–62 % of total annual leaf production (Table 1), and all species continued to produce leaves for 6–7 more months. None of the 6–8 mo or older leaves in our study exhibited signs of physiological deterioration such as a lower light absorptance or quantum yield. Theories of optimal resource allocation among leaves predict the decline of photosynthetic rates with leaf aging long before the time of leaf death because nitrogen should be reallocated from older (often shaded) leaves to younger (unshaded) leaves, especially when nitrogen supply is limited (Field and Mooney, 1983; Makino, Mae, and Ohira, 1984; Hirose and Werger, 1987a; Ackerly, 1992; Hikosaka, Terashima, and Katoh, 1994; Ackerly and Bazzaz, 1995). Moreover, the rate at which nitrogen is reallocated from a leaf should depend on many factors, including the rate of change in its relative position within a branch, branch architecture, and shading by other branches (Kikuzawa, 1995; Ackerly, 1996). Accordingly, slopes and x intercepts of the regression of photosynthetic capacity against leaf age may vary greatly among individual leaves, which in turn results in a large variance in leaf longevity within a leaf population as observed here (Table 1).

In our study, both nitrogen content per unit mass and photosynthetic capacity per unit nitrogen (nitrogen-use efficiency) decreased with leaf age, both of which contributed to the decline of photosynthetic capacity per unit leaf mass. The decline in nitrogen content per unit mass was partially due to a dilution effect caused by the increase in leaf mass per area with leaf age in *Anacardium* and *Ahtirrhoea* (Table 4). In a study of nutrient composition of leaves sampled monthly throughout a year for seven tree species including the five reported here, nitrogen per unit leaf mass declined with leaf age (in all species), while leaf mass per area (in all species but *Luehea*) and mineral ash content per leaf mass (in all species) increased with leaf age (author unpublished data). Although a few studies did not find a change in nitrogen-use efficiency with leaf age (Mooney et al., 1981; Field and Mooney, 1983), decreasing nitrogen-use efficiency with leaf age may be a general phenomenon. When leaf photosynthetic capacities were plotted against leaf nitrogen contents of leaves of various ages for a given species, both young and old leaves fall onto a simple linear regression line with a positive x intercept, which suggests lower nitrogen-use efficiency for older leaves plotted at the lower left part of the regression (Hirose and Werger, 1987b; Reich et al., 1991, 1994; Sobrado, 1992; Witkowski et al., 1992). Perhaps this is because the ratio of RuBP carboxylase to total nitrogen decreases with the decrease in nitrogen content with leaf age (Makino, Mae, and Ohira, 1984). The decline in mesophyll conductance with leaf age (Loreto et al., 1994) may be another reason for lowered nitrogen-use efficiency. Lower maximum stomatal conductance (g_s) and water-use efficiency (or ratio of A to g_s) are often, but not always, observed with leaf aging (Field and Mooney, 1983; Grandjean Grimm and Fuhrer, 1992; Sobrado, 1992; Witkowski et al., 1992; Dawson and Bliss, 1993).

In summary, this study suggests that photosynthetic capacity of leaves at a given age may be approximated for the population of the leaves composing a canopy from leaf demographic data. By knowing the distribution of leaf age in a canopy, the overall photosynthetic performance of the canopy may be estimated. Since photosynthetic capacity and leaf nitrogen content change concomitantly, identification of ecological factors that affect leaf nitrogen allocation within a canopy, such as irradiance, phenology of leaf production, and total leaf area, may further clarify the effects of leaf age on photosynthetic performance.

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