Oecologia (1997) 109:490–498 © Springer-Verlag 1997

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Seasonal leaf phenotypes in the canopy of a tropical dry forest: photosynthetic characteristics and associated traits

Received: 7 March 1996 / Accepted: 1 August 1996

Abstract We evaluated the hypothesis that photosynthetic traits differ between leaves produced at the beginning (May) and the end (November–December) of the rainy season in the canopy of a seasonally dry forest in Panama. Leaves produced at the end of the wet season were predicted to have higher photosynthetic capacities and higher water-use efficiencies than leaves produced during the early rainy season. Such seasonal phenotypic differentiation may be adaptive, since leaves produced immediately preceding the dry season are likely to experience greater light availability during their lifetime due to reduced cloud cover during the dry season. We used a construction crane for access to the upper canopy and sampled 1- to 2-month-old leaves marked in monthly censuses for six common tree species with various ecological habits and leaf phenologies. Photosynthetic capacity was quantified as light- and CO_2-saturated oxygen evolution rates with a leaf-disk oxygen electrode in the laboratory (O_{2max}) and as light-saturated CO_2 assimilation rates of intact leaves under ambient CO_2 (A_{max}). In four species, pre-dry season leaves had significantly higher leaf mass per unit area. In these four species, O_{2max} and A_{max} per unit area and maximum stomatal conductances were significantly greater in pre-dry season leaves than in early wet season leaves. In two species, A_{max} for a given stomatal conductance was greater in pre-dry season leaves than in early wet season leaves, suggesting a higher photosynthetic water-use efficiency in the former. Photosynthetic capacity per unit mass was not significantly different between seasons of leaf production in any species. In both early wet season and pre-dry season leaves, mean photosynthetic capacity per unit mass was positively correlated with nitrogen content per unit mass both within and among species. Seasonal phenotypic differentiation observed in canopy tree species is achieved through changes in leaf mass per unit area and increased maximum stomatal conductance rather than by changes in nitrogen allocation patterns.

Key words: Tropical canopy trees · Leaf phenology · Oxygen evolution rates · CO_2 assimilation · Phenotypic plasticity

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Introduction

The availabilities of two major plant resources often do not coincide in seasonal tropical forests (Wright and van Schaik 1994). During the rainy season, water is abundant, but greater cloud cover reduces light availability. In contrast, during the dry season, water is in limited supply but plants receive more sunlight. The opportunity for carbon gain over the lifetime of a leaf depends on the time of its production in such seasonal environments. Many trees in seasonal tropical forests, both evergreen and deciduous, flush a new cohort of leaves around the beginning of the rainy season, continue to produce leaves until late in the rainy season when they reach maximum leaf area, and then drop leaves as the dry season advances (Wright 1996). This phenological pattern may be adaptive as trees avoid drought during dry months, and have maximum leaf area during the early dry season when light availability has increased but before soil moisture drops.

Since leaves born early and late in the rainy season experience different abiotic environments during their lifetime, different phenotypes may be adaptive for early wet season leaves and pre-dry season leaves. Such seasonal phenotypic differentiation has been previously documented for an understory shrub in a seasonal moist tropical forest (Mulkey et al. 1992). Because the relative seasonal change in solar radiation and air humidity is

Table 1 List of study species, their stature, successional status, phenology of leaf production, and leaf lifespan (*All months* mean±SD for leaves born during 1–3 whole years; *EW* mean for leaves born in June–July for *Luehea*, in May–June for other species; *PD* mean for leaves born in January for *Anacardium*, November–December for other species). Significant differences in leaf lifespan between EW and PD leaves are indicated by > or < ($P<0.05$). Nomenclature follows D'Arcy (1987) and mature height and successional status are based on Croat (1978) and personal observation

Species	Family	Mature height (m)	Successional status	Leaf production	Leaf lifespan		
					All months	EW	PD
Anacardium excelsum (Bert. & Balb.) Skeels	Anacardiaceae	20–40	Early–Late	Dec–Jun	257±133	219	< 315
Luehea seemannii Tr. & Pl.	Tiliaceae	15–30	Early–Late	Jun–Dec	193±94	201	> 170
Castilla elastica Cerv.	Moraceae	10–30	Early	Apr–Oct	177±61	206	> 89
Antirrhoea trichantha Griseb. (Hemsl.)	Rubiaceae	10–15	Early	Apr–Nov	175±78	174	> 98
Urera caracasana (Jacq.) Griseb.	Urticaceae	5–10	Pioneer	Apr–Nov	91±42	113	> 60
Cecropia longipes Pitt.	Moraceae	10–15	Pioneer	Apr–Dec	87±29	85	92

greater in the upper canopy than in the understory, seasonal leaf phenotypic differentiation may have a greater adaptive potential for canopy trees than for understory plants.

The potential merit of seasonal leaf phenotypic differentiation for the carbon economy of the tree should depend on its leaf phenology and longevity. The potential adaptive value should be greater for species with shorter leaf longevity, since individual leaves experience limited environmental conditions. In contrast, seasonal phenotypic differentiation would have limited value for species with long-lived leaves that experience both wet and dry season conditions. Natural selection for the development of a pre-dry season phenotype should be strongest for species that produce significant numbers of leaves at the end of the rainy season that die by the end of the dry season.

As a part of our study of ecological variation of leaf traits in the upper canopy of seasonal tropical forest, we examined how the leaves of six canopy tree species born at different times of the year differed in photosynthetic characteristics. We quantified photosynthetic capacities, stomatal conductance, leaf mass per unit area, and nitrogen content for leaves born around the beginning and the end of the rainy season (May–June, November–December, respectively). Because leaf age had strong effects on leaf photosynthetic capacities, we standardized leaf age at time of measurement to 1–2 months of age after full expansion. We included six canopy tree species for which leaf production and survival were monitored monthly. All but one produced leaves in the rainy season but not in the dry season. These six tree species differed in leaf longevity (mean leaf lifetime between 87 and 257 days) and in the degree of deciduousness during the dry season.

Materials and methods

Site and canopy approach

The study was conducted in a seasonal dry forest in the Parque Natural Metropolitana near Panama City, Panama. Annual rainfall recorded at 1.7 km from the site averages 1740 mm, more than 90% of which occurs during the rainy season from May through December. The forest is a 75- to 150-year-old second-growth stand 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 et al. 1992). Starting in February 1994, we continuously recorded photosynthetic photon flux density (PFD), precipitation, temperature, relative humidity, and temperature with a Campbell 21X data logger (Campbell Instruments, Logan, Utah). Sensors and data logger were located 1 m from the crane tower at canopy level (20 m above ground).

Species

The six tree species used in the study are common in early successional stands, but they differ in persistence and frequency in older stands as indicated by their successional status in Table 1. Throughout this paper, the species are listed in the order of their leaf longevity, which tends to be longer for species that are more common in later successional stands (Table 1). The phenology of leaf production and leaf lifetime were determined from monthly censuses between December 1991 and August 1995 as briefly summarized here. We marked all new and (almost) fully expanded leaves with unique identification numbers in three branches per individual for at least three individuals for each species and recorded their time of birth and death. *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. *Luehea seemanii* produced leaves in two peaks, the first in June–July and the second in October–December, became gradually deciduous during the dry season, but retained approximately half of the maximum leaf area until May. *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 towards the late wet season (November), and became completely deciduous by the late dry season (March). Two pioneer species, *Urera caracasana* and *Cecropia longipes*, also had peak leaf production at the beginning of the wet season (April–May), then continued to produce smaller and relatively constant numbers of leaves throughout the wet season, and became completely deciduous by February and March, respectively. Hereafter, the species are referred to by genus only.

All leaves used in the current study were on upper canopy branches unshaded by neighboring branches or trees for most of the day. We chose to sample all leaves 1–2 months after full expansion when their photosynthetic rates were maximal. We sampled leaves from as many different branches and individuals as possible for each species. There was no particular sampling order for species or individuals. In order to distinguish seasons of leaf birth, we refer to leaves produced in November–December 1993 and sampled in January 1994 as pre-dry season leaves (PD leaves), and leaves born in May–June 1994 and sampled in June–July 1994 as early wet season leaves (EW leaves). Because *Anacardium* exchanged leaves in December unlike the other species, for *Anacar-*

dium, leaves produced in late December–January were sampled in late January–early February and are referred to as PD leaves since these are the most comparable to November–December leaves of other species.

Photosynthetic oxygen evolution rates

In January 1994 and June 1995, we sampled leaf disks (10 cm^2 each) from selected leaves of appropriate age (1–2 months after birth) marked in the monthly phenology censuses. The leaf disks were sampled just after dawn on the day of measurement and kept in the dark in aerated plastic containers lined with moist filter paper until measurements, which were completed by 2 p.m. on the same day. Photosynthetic light response curves were determined for PFDs between 0 and 1900 μmol m^{-2} s^{-1} with a leaf-disk oxygen electrode and data acquisition software (Hansatech, UK). Dark respiration rates were determined first before turning the light on. Light was provided by a Björkman-type lamp and increased in steps by combinations of neutral-density glass filters after the oxygen evolution rate reached quasi-steady state at each light level. The electrode chamber was supplied with humidified air with 10% CO_2 and maintained at around 29°C. We report photosynthetic oxygen evolution rates recorded at the highest light level as light- and CO_2-saturated oxygen evolution rates (O_{2max}). For each light curve, the apparent quantum yield was determined as the initial slope against PFD at the leaf surface between 0 and 71 μmol m^{-2} s^{-1}. Quantum yields were then corrected for PFD absorptance measured with a Li-Cor spectrophotometer and an absorption sphere (Li-Cor, Lincoln, Neb.). A non-rectangular hyperbola (Thornley 1976) was fitted to means at different light levels for each leaf season for each species:

$$O = [\alpha I + O_a - \{(\alpha I + O_a)^2 - 4\alpha I\theta O_a\}^{1/2}]/2\theta - R_d$$

where O is the oxygen evolution rate, I is the PFD at the leaf surface, α and R_d are the mean apparent quantum yield and dark respiration rate, respectively, for the appropriate season and species (fixed for individual curve fitting), and θ and O_a are fitted parameters corresponding to the convexity and the asymptotic rate, respectively, of gross oxygen evolution rates.

After these measurements, leaves were dried at 60°C for 5 days or more before determination of dry mass per unit area and total nitrogen at the Agricultural Experimental Station of the University of Missouri Columbia.

CO_2 assimilation rates in the field

On several mornings in January–February and June–July 1994, we measured the light-saturated CO_2 assimilation rate (A_{max}) of intact 1- to 2-month-old leaves in the field with a portable infrared gas analyzer for CO_2 and water vapor (CIRAS, PP Systems, UK), under a quartz lamp providing a PFD of 1300 μmol m^{-2} s^{-1} at the leaf surface (for most samples) or comparable natural sunlight between 1100 and 1400 μmol 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 5 ppm of 350 ppm, while air humidity and leaf temperature were allowed to reflect field conditions in situ (21–31 mbar, and 29–39°C, respectively). No CO_2 assimilation data were collected for EW leaves of *Cecropia*.

Statistical analysis

Statistical analyses were done with the JMP statistical package (SAS 1994). Differences between EW leaves and PD leaves were evaluated for each species by *t*-test. We also examined the difference in A_{max} between seasons of leaf birth with analysis of covariance (ANCOVA) using stomatal conductance as the covariate.

Results

The seasonal pattern of daily total PFD and rainfall in the year of the study was characterized by an inverse relationship (Fig. 1). This was typical as shown by solar radiation and rainfall data collected at a nearby location by the Panama Canal Commission for over 30 years. The highest daily total PFD and the longest daily period of direct sun (PFD > 1000 μmol m^{-2} s^{-1}) occurred in the early dry season (January–February), and were 60% and 170% greater than wet-season values, respectively (Fig. 1A). The maximum PFD recorded for a day may be above 2300 μmol m^{-2} s^{-1} in any month. It was always above 1500 μmol m^{-2} s^{-1} from December until April and always above 1000 μmol m^{-2} s^{-1} from September through November for the year shown in Fig. 1. The early wet season was the cloudiest time and the maximum PFD was below 400 μmol m^{-2} s^{-1} on certain days in May and June.

In four species, photosynthetic capacity per unit area was higher for PD leaves than for EW leaves. Photosynthetic oxygen evolution rates of PD leaves of *Luehea*, *Antirrhoea*, *Urera*, and *Cecropia* were higher than those of EW leaves above 500 μmol m^{-2} s^{-1} (Fig. 2). In these species, PD leaves exhibited light saturation at higher light levels than EW leaves (Fig. 2), and simple regression slopes of oxygen evolution rates against PFD in the range between 750 and 1900 μmol m^{-2} s^{-1} were significantly greater for PD leaves than for EW leaves. O_{2max} determined at 1900 μmol m^{-2} s^{-1} was significantly different between EW and PD leaves in three of these species (Table 2). For *Luehea*, the sample variance was large at this highest light level, and EW and PD leaves did not differ significantly. In contrast, the light curves of *Ana-*

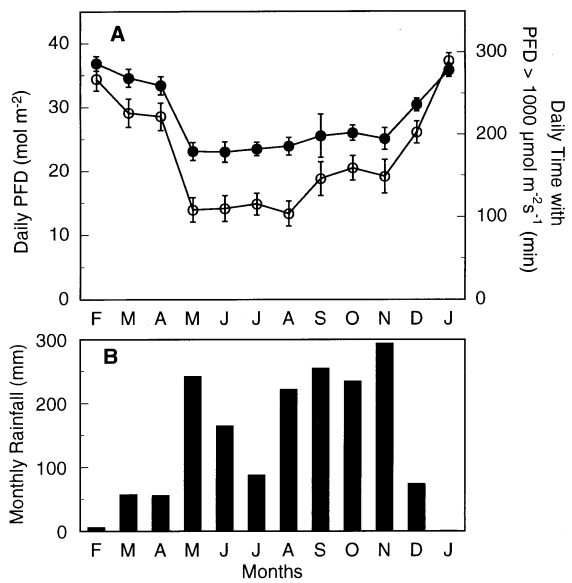

Fig. 1A, B Photosynthetic photon flux density (PFD) above the canopy and precipitation at the study site from February 1994 through January 1995. **A** Mean and SE for daily total PFD (*closed symbols*) and daily total minutes when PFD was above 1000 μmol m^{-2} s^{-1} (*open symbols*). **B** Monthly total rainfall

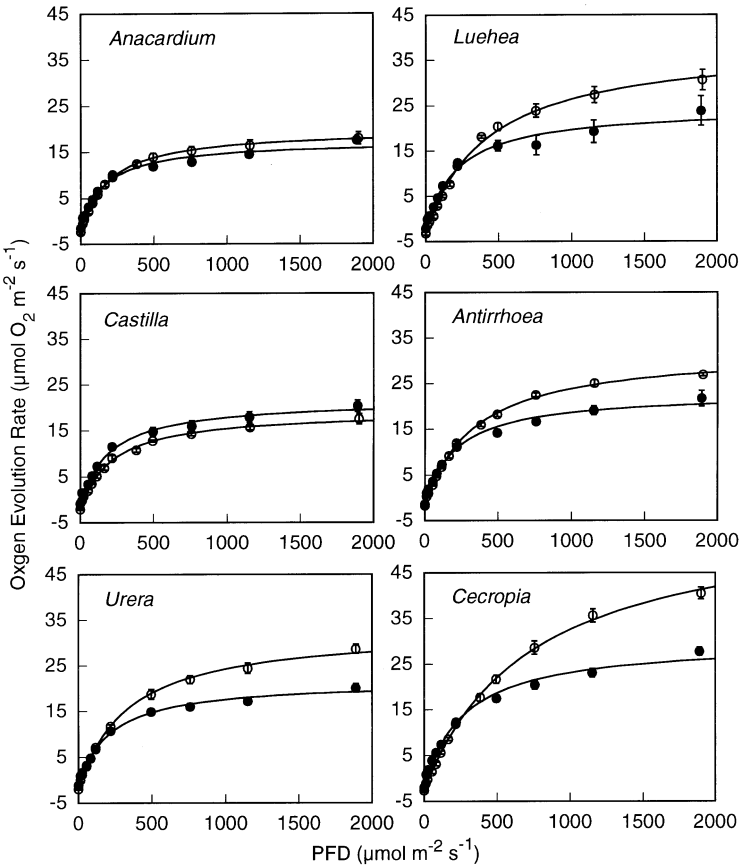

Fig. 2 Photosynthetic oxygen evolution rate plotted against PFD at the leaf surface for early wet season leaves (*closed circles*) and pre-dry season leaves (*open circles*) sampled at 1–2 months of age in the upper canopy for six tree species in a Panamanian dry forest. Mean ± SE at each light level (see Table 2 for sample sizes). Non-quadratic hyperbolas were fitted to the means at different light levels (see Materials and methods)

cardium and *Castilla* were not distinguishable between seasons of leaf birth (Fig. 2).

In contrast to area-based measurements, O_{2max} per unit leaf mass did not differ significantly between EW and PD leaves in any species (Table 2). In *Luehea*, *Antirrhoea*, *Urera*, and *Cecropia*, the four species that exhibited significantly higher O_{2max} per unit area for PD leaves than EW leaves, leaf mass per unit area was higher for PD leaves than for EW leaves (Table 2). Thus, the differences in O_{2max} per unit leaf area between seasons were attributable to differences in leaf mass per unit area. EW leaves of *Anacardium* had a greater mass per unit area than PD leaves, opposite to the trend for *Luehea*, *Antirrhoea*, *Urera*, and *Cecropia*. Neither light absorptance nor quantum yields corrected for absorptance differed significantly between EW and PD leaves in any species but *Anacardium* (Table 2, mean leaf absorptances were 0.90 and 0.86 for EW and PD leaves, respectively). EW and PD leaves did not differ in nitrogen content per unit mass or O_{2max} per unit nitrogen, except in *Urera*. O_{2max} and nitrogen content on a mass basis were strongly correlated with each other in each species (Fig. 3), and this relationship did not differ between EW and PD leaves. Species means of nitrogen content and O_{2max} on a mass basis were also highly correlated with each other ($n = 6$, $r^2 = 0.93$, $P < 0.002$).

Light-saturated CO_2 assimilation rates (A_{max}) were strongly correlated with stomatal conductance in both

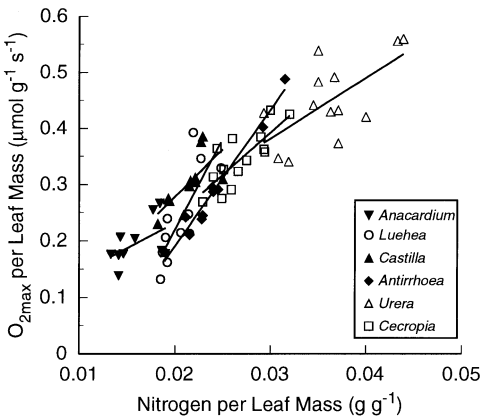

Fig. 3 Relationships between leaf nitrogen content and light- and CO_2-saturated oxygen evolution rates (O_{2max} per unit leaf mass) for 1- to 2-month-old leaves sampled in the upper canopy for six tree species. Each line indicates the regression for a species, including both early wet season and pre-dry season leaves. All regressions are statistically significant ($P < 0.05$). The regression for data pooled for all species: $y = 13.2x - 0.0183$ ($n = 78$, $r^2 = 0.77$, $P < 0.0001$)

EW and PD leaves of all species (Fig. 4). Regression slopes of A_{max} against stomatal conductance did not differ between seasons in any species (ANCOVA, $P > 0.05$). In *Luehea* and *Antirrhoea*, PD leaves had significantly higher mean and maximum A_{max} and stomatal

Table 2 Characteriscis of early wet season (*EW*) leaves and pre-dry season (*PD*) leaves for six tree species in a Panamanian seasonal dry forest determined with leaf disks sampled for oxygen evolution measurements. Means (SD) for leaves at 1–2 months of age. Statistically significant differences between EW and PD leaves are indicated next to the PD values (* P <0.05, ** P<0.005, *** P<0.0005). *Sample size* number of leaves, O_{2max} CO_2-saturated oxygen evolution rate at 1900 µmol photons m^{-2} s^{-1} (per unit leaf area, per unit leaf mass, and per unit gram of nitrogen), *LMA* leaf mass per area, Q_y quantum yield (initial slope of O_2 against PFD corrected for absorptance), *Nitrogen* total nitrogen per unit leaf dry mass, R_d dark respiration rate per unit leaf area, *N/A* data not available due to missing absorbance values for three samples

Species	Sample Size		O_{2max}/area (µmolO_2 m^{-2} s^{-1})		LMA (g m^{-2})		O_{2max}/mass (µmol O_2 g^{-1} s^{-1})		Q_y (mol mol^{-1})		Nitrogen (mg N g^{-1})		O_{2max}/N (µmol O_2 g N^{-1} s^{-1})		R_d (µmol O_2 m^{-2} s^{-1})	
	EW	PD	EW	PD	EW	PD	EW	PD	EW	PD	EW	PD	EW	PD	EW	PD
Anacardium	5	6	17.5 (1.4)	17.4 (3.0)	102.8 (9.6)	84.1* (10.7)	0.173 (0.028)	0.209 (0.042)	0.068 (0.011)	0.087* (0.007)	14.7 (1.6)	16.6 (2.0)	11.8 (1.9)	12.6 (1.9)	−1.47 (0.51)	−2.18 (0.77)
Luehea	6	5	23.8 (8.0)	28.8 (6.2)	95.3 (15.4)	136.6** (17.3)	0.261 (0.108)	0.210 (0.032)	0.076 (0.010)	0.072 (0.007)	21.0 (2.5)	20.3 (1.3)	12.1 (4.1)	10.8 (1.2)	−2.15 (0.88)	−2.92 (0.74)
Castilla	6	4	20.4 (3.1)	17.9 (2.1)	65.3 (12.8)	77.4 (9.9)	0.325 (0.099)	0.237 (0.004)	0.066 (0.007)	0.068 N/A	25.8 (3.7)	21.3 (2.1)	12.4 (1.9)	10.8 (1.3)	−0.83 (0.61)	−2.10 (0.29)
Antirrhoea	6	4	21.9 (3.5)	26.9* (0.5)	67.3 (9.2)	93.0** (5.3)	0.328 (0.049)	0.291 (0.021)	0.071 (0.006)	0.085 (0.012)	21.7 (1.3)	20.7 (1.6)	15.1 (1.4)	14.0 (0.2)	-1.41 (0.62)	−1.70 (0.42)
Urera	5	8	20.1 (2.3)	29.5** (3.5)	45.6 (7.1)	66.9* (13.1)	0.447 (0.071)	0.450 (0.090)	0.060 (0.006)	0.078 (0.078)	32.9 (2.7)	38.3* (4.0)	13.6 (1.6)	11.7* (1.2)	−1.10 (0.73)	−1.93* (0.30)
Cecropia	7	7	27.8 (2.4)	38.9*** (3.9)	80.0 (11.2)	115.3*** (13.2)	0.353 (0.058)	0.311 (0.051)	0.076 (0.008)	0.076 (0.010)	27.8 (2.8)	26.1 (2.4)	12.7 (1.1)	13.0 (1.4)	−1.92 (0.59)	−2.50 (0.76)

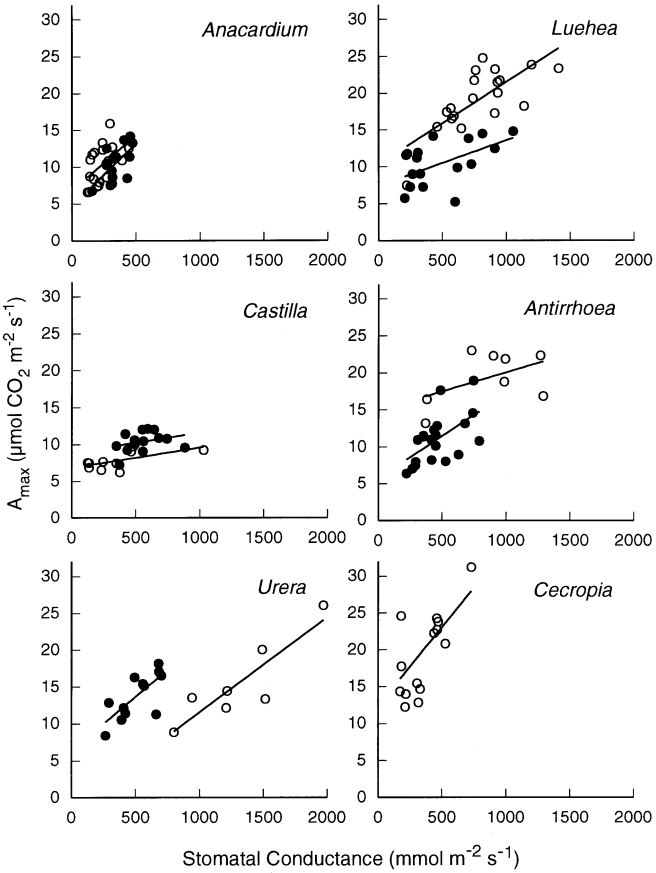

Fig. 4 Effects of stomatal conductance on light-saturated photosynthetic CO_2 assimilation rates of 1- to 2-month-old early wet season leaves (*closed circles*) and pre-dry season leaves (*open circles*) in the upper canopies of the six tree species

conductance than EW leaves (Fig. 4, Table 3). In these species, photosynthetic rates were also higher for a given stomatal conductance in PD leaves than in EW leaves (Fig. 4). In *Urera*, stomatal conductance was so much higher in PD leaves than in EW leaves that their ranges did not overlap (Fig. 4). In contrast, PD leaves of *Castilla* had lower A_{max}, stomatal conductance, and photosynthetic rates for a given stomatal conductance than EW leaves (Fig. 4, Table 3). Stomatal conductance, but not A_{max}, of *Anacardium* was also significantly lower in PD leaves than in EW leaves.

Discussion

Seasonal leaf phenotypes

The predicted leaf phenotypic differences were observed in four of the six study species. PD leaves of *Luehea*, *Antirrhoea*, *Urera*, and *Cecropia* had higher photosynthetic capacities than EW leaves (Fig. 2, Tables 2, 3). These higher photosynthetic capacities per unit leaf area of PD leaves were completely attributable to their greater leaf mass per unit area, since oxygen evolution rates per unit

Table 3 CO_2 exchange characteristics of early wet season (*EW*) leaves and pre-dry season (*PD*) leaves for six tree species in a Panamanian seasonal dry forest under saturating light and ambient CO_2. Means (SD) for 1- to 2-month-old leaves born in each season. *Sample size* number of leaves measured, A_{max} light-saturated CO_2 assimilation rate, g_s stomatal conductance for water, C_i calculated leaf internal CO_2 concentration. Significant differences between EW and *PD* leaves are indicated after PD values (* $P<0.05$, ** $P<0.005$, *** $P<0.0005$)

Species	Sample size		A_{max} (µmol CO_2 m^{-2} s^{-1})		g_s (mmol m^{-2} s^{-1})		C_i (ppm)	
	EW	PD	EW	PD	EW	PD	EW	PD
Anacardium	15	21	10.5 (2.3)	10.5 (2.6)	345.3 (85.8)	249.1** (98.7)	259.4 (15.3)	241.7* (24.7)
Luehea	16	16	10.5 (3.1)	18.5*** (4.4)	505.8 (272.9)	782.2* (334.4)	270.7 (22.8)	248.9*** (12.9)
Castilla	14	10	10.4 (1.4)	7.8*** (1.2)	555.2 (147.8)	357.8* (270.6)	287.7 (11.9)	273.0 (28.2)
Antirrhoea	20	8	11.0 (3.3)	19.3*** (3.6)	466.8 (170.6)	865.8*** (353.0)	268.4 (18.8)	259.6 (19.2)
Urera	12	7	13.8 (3.1)	15.5 (5.7)	510.7 (154.5)	1306.6*** (392.3)	261.7 (9.2)	278.1* (20.4)
Cecropia	–	13	– –	19.9 (5.6)	–	361.9 (170.5)	– –	199.1 (39.8)

mass did not differ between leaf birth seasons (Table 2). Photosynthetic light saturation of these canopy leaves occurred at very high light levels, especially for PD leaves (Fig. 2). A similarly high PFD for light saturation has been reported for upper canopy leaves of other tropical trees (Pearcy 1987; Tuohy et al. 1991; Hogan et al. 1995). Significantly greater regression slopes of oxygen evolution rates against incident light between 750 and 1900 µmol m^{-2} s^{-1} for PD leaves than for EW leaves also indicate their potential for exploitation of higher dry season light availability (Fig. 1).

The phenotypic differentiation described here was probably not a typical acclimation response during leaf development cued by a change in light availability (Pearcy and Sims 1994; Chazdon et al. 1996). These PD leaves were fully expanded by mid-December, when light was still limited by cloud cover (Fig. 1A). Furthermore, the higher photosynthetic capacity of PD leaves probably did not result from acclimation of fully expanded leaves, which are likely to be constrained morphologically (Sims and Pearcy 1992; but see Kamaluddin and Grace 1992). The greater leaf mass per area in PD leaves than in EW leaves indicates proportionally more mesophyll tissue per unit leaf area, because nitrogen content per unit mass and oxygen evolution rates per unit mass did not differ. The observed higher maximum stomatal conductance and water-use efficiency of PD leaves probably also resulted from morphological differences, such as higher ratios of mesophyll surface area to leaf area. We are not able to exclude light as a cue for the observed seasonal phenotypic differentiation, but other studies provide evidence that leaf phenological traits are regulated by endogenous rhythms entrained by other factors in the environment (Mulkey et al. 1992; Reich 1995). The development of PD leaves preceded development of dry season conditions, like many plant phenological events which often precede the occurrence of optimal environmental conditions, and for which day length or temperature drop may be used as cues (Wright 1996).

Relationship to leaf phenology and longevity

As we predicted, whether or not seasonal leaf differences were observed in a species depended on its leaf longevity and phenology. Species with shorter leaf life spans are more likely to exhibit seasonal leaf phenotypes since individual leaves experience a relatively limited range of environmental conditions. The two pioneer species with a very short leaf life span, *Cecropia* and *Urera*, both showed increased leaf mass per area and photosynthetic capacities in PD leaves. Of the three species with a leaf lifetime between 175 and 193 days, *Luehea* and *Antirrhoea* produced PD leaves with higher photosynthetic capacities than EW leaves (Fig. 2, 3).*Castilla* had minimal leaf production in November and December and did not exhibit seasonal phenotypes. *Luehea* and *Antirrhoea* were close to their maximum standing leaf crop in January, while *Castilla* was already 60–80% deciduous in January. Thus, it was perhaps not surprising not to find leaves adaptive to the dry season in *Castilla*. In fact, PD leaves sampled in the study might have been physiologically senescing at 1–2 months of age despite their nonsenescent appearance, which may explain their reduced A_{max} relative to EW leaves, a trend opposite to that of the other species (Table 3).

Anacardium, the species with the longest leaf life span, had leaves of identical photosynthetic capacities for different birth seasons (Fig. 2). The leaf production phenology of *Anacardium* (starting in December and ending in June) is the opposite to the other species (starting in May and ending in December). *Anacardium* leaves referred to as “PD” leaves were actually produced in early January and exposed to greater PFD availability during their expansion than PD leaves of other species. However, these January leaves become rapidly shaded by younger leaves, as successively emerging leaves are arranged in spirals around vertically oriented branches in *Anacardium*. Thus, high resource investment for increased photosynthetic capacity may not be optimal later in life for these January leaves with a long mean life span of 315 days. In contrast, EW leaves produced in May would not be shaded by additional leaves. In fact,

there were indications that EW leaves were exposed to greater solar radiation than PD leaves in this species, with a significantly greater leaf mass per area and a lower quantum yield, which may indicate a significant degree of chronic photoinhibition in EW leaves (Table 2). These results for *Anacardium* suggest that phenology of leaf production, patterns of leaf arrangement, and leaf longevity may override the influence of the seasonality of external environmental conditions on the development of seasonal leaf phenotypes.

Stomatal conductance

In two species (*Luehea* and *Antirrhoea*), light-saturated CO_2 assimilation rates for a given stomatal conductance were higher for PD leaves than for EW leaves (Fig. 4). Consistent with this, calculated leaf internal CO_2 concentrations were lower in PD leaves of *Luehea*. This higher instantaneous water-use efficiency in PD leaves than in EW leaves may be adaptive during the dry season. Leaf mass per unit area is perhaps a key to explain this difference, since higher leaf mass per area indicates a greater ratio of mesophyll surface area to leaf area (Nobel 1980). In addition, maximum and mean stomatal conductances were greater in PD leaves than in EW leaves. All light-saturated CO_2 assimilation rates and stomatal conductances were taken in the morning. In repeated measurements of leaves under ambient conditions throughout the day, stomatal conductances declined continuously with time of day as vapor-pressure deficit and water stress developed, and this decline was more severe during the dry season than in the rainy season (K. Kitajima, S.S. Mulkey, S.J. Wright, unpublished data). Later in the dry season, stomatal conductance and photosynthetic rates are much more restricted (Hogan et al. 1995). The high potential stomatal conductance in PD leaves of *Luehea* and *Antirrhoea* would help these species to achieve high carbon fixation rates during early mornings during the early dry season, which may be important for compensating for losses in potential photosynthetic productivity due to stomatal closure during the dry season.

The unusually high stomatal conductances found in PD leaves of *Urera* merit explanation. One possibility is that stomatal conductance was overestimated for *Urera*, as the effective surface area for transpiration was perhaps greater than the projected leaf area because of the convoluted topography of the leaf surface of this species, a common feature in Urticaceous leaves. A second possibility was that a high stomatal conductance was an adaptive trait to maximize carbon income for the very short lived PD leaves of this species. PD leaves of *Urera* had a mean life span of only 60 days, much shorter than the 113 days for EW leaves (Table 1).

Seasonal leaf phenotypes in the canopy versus the understory

Seasonal leaf phenotypes found in these canopy tree species contrast to those previously found for an understory shrub, *Psychotria marginata* (Mulkey et al. 1992). The leaf production phenology of *P. marginata* is similar to that of *Luehea*, with peaks at the beginning and the end of the wet season; however, *P. marginata* leaves generally live longer than 2 years, much longer than in any of the canopy species studied here. Similar results in both *P. marginata* and the canopy tree species include (1) leaves with phenotypic traits adaptive to dry season environments produced before the end of the rainy season, (2) higher leaf mass per area for PD leaves, and (3) higher water-use efficiency in PD leaves. In both cases, development of seasonal leaf phenotypes was probably not cued by the changes in water or light availability, but was likely regulated by internal factors, such as endogenous rhythms governing phenology (Mulkey et al. 1992; Reich 1995). However, in *P. marginata*, the light-saturated photosynthetic rates per unit area did not differ between PD and EW leaves. The light response curves of canopy tree leaves in this study had much higher saturation light intensities and higher photosynthetic capacities than shrub leaves, including those developed in light gaps (Pearcy 1987; Mulkey et al. 1992, 1993; Chazdon et al. 1996). Perhaps selection for PD leaves to become adapted to higher light availability is not strong in understory shrubs, since the relative change in PFD availabilities between seasons is small in the understory where most of the incident light is diffuse.

Ecological variation in photosynthetic capacities

If such seasonal leaf phenotypic differentiation is common in the upper canopies of tropical forests, there is no single value that represents the photosynthetic capacity of a canopy tree species for a whole year. For example, EW leaves and PD leaves of *Cecropia* had O_{2max} of 28 and 39 μmol m^{-2} s^{-1}, respectively. Such a degree of intraspecific variance may be easily greater than interspecific differences observed in this and other studies. In a broad comparison, photosynthetic capacities found in this study were within the range observed for tropical canopy trees in other studies (light-saturated oxygen evolution rates between 10 and 45 μmol m^{-2} s^{-1}, light-saturated CO_2 assimilation rates between 6 and 33 μmol m^{-2} s^{-1}) (Koyama 1981; Pearcy 1987; Tan et al. 1994; Zotz and Winter 1994; Hogan et al. 1995; Königer et al. 1995; Zotz et al. 1995; Chazdon et al. 1996). In these studies, the season of leaf production was not taken into account. Conclusions from interspecific comparisons might be significantly affected by the season of leaf sampling. For estimating the annual photosynthetic production of the canopy, consideration of seasonal leaf phenotypes is as important as that of leaf age (Zotz et al. 1995).

Leaf life span is considered to be a correlate of many ecological and functional traits of a species, including leaf photosynthetic capacities and nitrogen content (Kikuzawa 1991; Reich et al. 1991; Mulkey et al. 1995). Mean photosynthetic capacities and nitrogen contents per unit mass were lowest for *Anacardium* with long leaf lifespan and highest for the two pioneer species with the shortest leaf life span. Thus, interspecifically, there was a negative correlation between leaf life span and leaf nitrogen content ($r = -0.88$ and -0.81 for EW and PD leaves, respectively), as found in other comparative studies (Reich and Walters 1994; Reich et al. 1994). In all species studied here, the leaf survival time was related to leaf birth time, such that EW leaves had longer maximum and average survivorships than PD leaves, except for *Anacardium* which had an opposite seasonality (Table 1). In *Luehea*, *Antirrhoea*, and *Urera*, PD leaves with a shorter leaf life span had greater photosynthetic capacities than EW leaves with a longer leaf life span. Thus, the results of this study parallel the negative associations between photosynthetic capacity and leaf longevity identified in the interspecific comparative studies mentioned above.

Although nitrogen allocation patterns have been frequently linked to adaptation to light availability (Field and Mooney 1986; Evans 1989; Reich and Walters 1994; Hikosaka and Terashima 1995), the apparent adaptation of PD leaves to high PFD availability was not associated with a change in nitrogen allocation on a leaf mass basis. Maximum oxygen evolution rates per unit mass varied independently of the seasons of leaf birth but were strongly correlated with nitrogen content per unit leaf mass (Fig. 3). A strong relationship between photosynthetic capacity and leaf nitrogen content on a mass basis held across leaf birth seasons and species. Frequently, increased leaf mass per area is associated with decreased nitrogen content per unit mass (Reich and Walters 1994). However, PD leaves with greater mass per unit area did not have less nitrogen per unit mass than EW leaves.

Contribution of seasonal leaf phenotypes to leaf display strategy in time

The adaptive significance of leaf production in the late wet season is perhaps threefold, even though these leaves are likely to die within a relatively short time (Wright and van Schaik 1994). First, it allows some species to have the maximum canopy leaf area in the early dry season, the time of greatest solar radiation and relatively mild water stress. Secondly, it provides an opportunity for the tree to develop leaves with different phenotypes and acclimate to the dry season conditions at the whole-plant level. Our study is the first to demonstrate the existence of seasonal leaf phenotypes in canopy tree species. An alternative strategy would be acclimation of existing old leaves, which are physiologically and morphologically constrained. Finally, leaf production in the late wet season is necessary to replace senescing leaves, especially in species with a short leaf life span. A quantitative assessment of the functional characteristics of leaves produced at different times of the year provides a better understanding of the carbon economies associated with various leaf display strategies in time.

Acknowledgements The current research was supported by the Smithsonian Scholarly Studies Program, the Andrew W. Mellon Foundation, and the National Science Foundation (IBN-9220759 and BIR-9419994 to SSIII). We thank the Smithsonian Tropical Research Institute for the use of the canopy crane and for logistical support. Mirna Samaniego and Milton Garcia provided indispensable assistance in data collection. We appreciate constructive comments from R. Pearcy.

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