ECOPHYSIOLOGY

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Coordinated changes in photosynthesis, water relations and leaf nutritional traits of canopy trees along a precipitation gradient in lowland tropical forest

Abstract We investigated leaf physiological traits of dominant canopy trees in four lowland Panamanian forests with contrasting mean annual precipitation (1,800, 2,300, 3,100 and 3,500 mm). There was near complete turn-over of dominant canopy tree species among sites, resulting in greater dominance of evergreen species with long-lived leaves as precipitation increased. Mean structural and physiological traits changed along this gradient as predicted by cost–benefit theories of leaf life span. Nitrogen content per unit mass (N_{mass}) and light- and CO_2-saturated photosynthetic rates per unit mass (P_{mass}) of upper canopy leaves decreased with annual precipitation, and these changes were partially explained by increasing leaf thickness and decreasing specific leaf area (SLA). Comparison of 1,800 mm and 3,100 mm sites, where canopy access was available through the use of construction cranes, revealed an association among extended leaf longevity, greater structural defense, higher midday leaf water potential, and lower P_{mass}, N_{mass}, and SLA at wetter sites. Shorter leaf life spans and more enriched foliar $\delta^{15}N$ values in drier sites suggest greater resorption and re-metabolism of leaf N in drier forest. Greater dominance of short-lived leaves with relatively high P_{mass} in drier sites reflects a strategy to maximize photosynthesis when water is available and to minimize water loss and respiration costs during rainless periods.

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Overall, our study links coordinated change in leaf functional traits that affect productivity and nutrient cycling to seasonality in lowland tropical forests.

Introduction

Tropical forests often exhibit gradients of vegetation structure and species composition in relation to precipitation (Schimper 1903; Gentry 1988; Wright 1992). Forests on the dry side of this gradient commonly have a higher proportion of deciduous canopy species that lose their leaves during the dry season when low soil water availability may limit physiological activity. Deciduous habit reduces whole-plant transpiration and respiration during seasonal drought. Although deciduous habit means shorter leaf life span, leaves of deciduous species often have higher rates of photosynthesis per unit leaf mass (P_{mass}) than evergreen species during the growth season (Chabot and Hicks 1982; Eamus and Prior 2001). In contrast, evergreen leaves have lower P_{mass}, but exhibit a potentially longer photosynthetic season, and appear to reduce demand on soil nutrients required to replace leaves (Chabot and Hicks 1982; Vázquez and Givnish 1998; Cunningham et al. 1999). This apparent trade-off between leaf longevity and P_{mass} is predicted by cost–benefit theory of leaf longevity (Kikuzawa 1991), and is well demonstrated as a convergent evolutionary pattern across global biomes (Reich et al. 1997; Ackerly and Reich 1999). Because leaf N and specific leaf area (SLA) are positively correlated with P_{mass}, these leaf traits also decrease with leaf longevity (Reich et al. 1997). In tropical forests, growth season is defined by precipitation seasonality, but few studies have explicitly addressed the effect of precipitation regimes on leaf functional traits within the tropical latitude. Here, we focus on community-wide changes in leaf functional traits and leaf longevity of dominant tree species in relation to annual precipitation in

lowland Panama. Because leaf longevity is less coupled to leaf phenology in tropical forests (e.g., presence of evergreen species with short longevity), it is not necessarily predictable how community-wide increases in dominance of evergreen species with increasing precipitation affects leaf functional traits of common canopy trees.

Whereas a global scale comparison of precipitation tends to depict the effects of insufficient water availability (i.e., in the range of annual precipitation below 2,500 mm), several studies have demonstrated that regional precipitation gradients may affect leaf functional traits indirectly via effects on light and nutrient availability. For example, high leaf N per unit area in dry habitats in Australia may have been selected because it allows plants to photosynthesize at high rates and capitalize on higher light availability in dry habitats (Mooney et al. 1978; Cunningham et al. 1999). Leaf N of montane forest species in Hawaii decreases with increasing precipitation, probably because soil N availability decreases with increasing precipitation above 2,500 mm (Schuur and Matson 2001). Increased precipitation means accelerated rates of soil weathering and nutrient leaching. Thus, evergreenness in very wet tropical forest may be a response to relatively low nutrient availability, because increased leaf longevity is an effective nutrient conservation mechanism (Monk 1966; Aerts and Chapin 2000). Thus, on a regional scale, P_{mass} and leaf N may decrease with increased evergreen dominance and increasing precipitation, even though P_{mass} increases with increasing moisture availability for a given leaf life span in a multiple regression analysis on a global scale (Reich et al. 1999) and SLA is reported to increase with mean monthly precipitation of the three driest months (Niinemets 2001).

Water limitation appears to be the main factor influencing community-wide changes in leaf traits on the precipitation gradient below 2,500 mm year^{-1} (Mooney et al. 1978; Werger and Morris 1991; Cunningham et al. 1999), whereas precipitation in the range of 2,500–5,000 mm year^{-1} reflects an indirect effect of precipitation through nutrient limitation on leaf phenotypes of species that span this precipitation range (Austin and Vitousek 1998; Schuur and Matson 2001). Our study fills a gap in the available data by quantifying interspecific change in leaf traits along the precipitation gradient between 1,800 mm and 3,500 mm, taking advantage of large changes in species composition over short (10–20 km) distances determined from analysis of multiple 1-ha permanent plots (Condit et al. 2002). These large changes in species composition are likely to be related to the sharp precipitation gradient across the Panamanian Isthmus, because dispersal is unlikely to be a constraint over such a short distance. One recent study of tree communities has found that climate affects species composition more than geographical distance in lowland forests in Ecuador and Peru; distant forests (>1,000 km) with similar climate shared a much larger proportion of the most common species than would be expected by chance (Pitman et al. 2001). We measured leaf physiological and structural traits to understand how patterns of resource allocation to leaves are related to climate on this regional gradient, which lies at the high end of the global precipitation range. Specifically we sought to link leaf functional traits of dominant species to shifts in community phenology and leaf longevity characteristics.

Materials and methods

Site characterization and species

Our study was conducted in lowland tropical forest along a precipitation gradient in the Panama Canal Watershed. Mean annual precipitation (MAP) across this part of the Panamanian Isthmus ranges from 1,800 mm year^{-1} on the Pacific Coast to 4,000 mm year^{-1} on the Caribbean Coast (Condit 1998). We selected four 1-ha lowland forest study plots established by the Center for Tropical Forest Science (CTFS) over a range of precipitation with minimal changes in altitude and temperature (Table 1). Dry season length (mean number of 30-day periods with <100 mm precipitation) varies between 129 days at the 1,800-mm site and 67 days near the 3,500-mm site in a long-term climate record (ACP 2002). Variation in annual precipitation during the study period (2000–2002) was within 15% of MAP at all sites. Amount and distribution of annual precipitation has the potential to influence light availability and relative humidity. Average daily light availability decreases slightly with increasing precipitation from 32.3 mol m^{-2} at the 1,800-mm site (Posada 2003); to 31.9 mol m^{-2} at Barro Colorado Island in the middle of the isthmus and to 31.4 mol m^{-2} at the 3,100-mm site (Paton and Wright 2003). Mean relative humidity is highest on the wet Caribbean coast (94.6% at the 3,100 mm site); the 1,800 mm site and Barro Colorado Island maintain values of 87.9 and 84.0%, respectively (Paton and Wright 2003).

Soils of the Panama Canal forests are well-drained clays high in Ca, Mg and N and low in K and P relative to other tropical soils (Dietrich et al. 1982; Yavitt et al. 1993; Kursar et al. 1995). Three of the study sites are on volcanic substrate whereas the 3,100-mm site lies on sedimentary substrate. However, similarities in soil characteristics between sedimentary and volcanic substrates on Barro Colorado Island (which lies in the middle of the isthmus) suggest that in this area nutrient availability is determined more by weathering and nutrient cycling by vegetation than by parent material (Yavitt 2000).

Soil water potential (Ψ_{soil}) was measured with the filter paper technique (Deka et al. 1995; Jackson et al. 2000) at six randomly selected locations in each 1-ha study plot, nine times over a 14-

Table 1 Site characteristics for 1-ha census plots in the Panama Canal Watershed. Basal area, species richness, and tree density represent species with stems ≥10 cm in diameter

Site	Mean annual precipitation (mm year^{-1})	Elevation (m)	Basal area (m^2 ha^{-1})	Species richness (no. ha^{-1})	Tree density (no. ha^{-1})
Parque Metropolitano	1,800	60	25.39	36	318
Pipeline Road	2,300	210	26.59	95	560
Fort Sherman	3,100	140	32.50	87	569
Santa Rita	3,500	282	25.74	162	497

month period (February 2001–March 2002). One 42.5-mm diameter filter paper (Whatman no. 42, batch no. 711492, Whatman, Kent, UK) was equilibrated for 6 days with a fresh soil sample taken from 15–20 cm depth. The gravimetric moisture content of the filter paper was then used to predict matric potential using a published regression equation (Deka et al. 1995). Assuming that gravitational and solute potentials are negligible, the resulting values of matric potential represent soil water potential. We also determined gravimetric soil water content on a 5-g subsample by drying at 105°C for 24 h.

At each site, we measured the eight canopy tree species representing the largest proportion of the total basal area of trees above 10-cm diameter. Species composition and phenological habit of the most common canopy trees change rapidly across this gradient, as species richness increases steeply with MAP (Table 2) (Pyke et al. 2001). Only three species spanned more than one site as one of the eight most common canopy tree species. All study plots were located in mature forest (>200 year), except the 1,800-mm site, which was a forest of mixed age (70–100 year). Measurements on the largest canopy trees at the 1,800-mm site were comparable to other sites even though this forest was younger, because canopy composition was representative of mature seasonally dry forest (Croat 1978).

Photosynthesis

At the 1,800- and 3,100-mm sites, canopy sun leaves were collected using canopy cranes maintained by the Smithsonian Tropical Research Institute. The youngest fully expanded mature leaves were cut at the petiole and immediately sealed in a darkened humidified container. At the 2,300- and 3,500-mm sites, leaves were collected from the upper canopy using a shotgun and then treated in the same way. We were able to distinguish sun leaves from subcanopy leaves because sun leaves are thicker and lighter in color. Canopy trees were defined as individuals with approximately 80% of the crown exposed to full sun. All leaves were collected before 1030 hours the day after rainfall during the wet season and were transported to the laboratory within 2.5 h where photosynthesis was measured immediately.

Photosynthetic capacity was measured as the light- and CO_2-saturated rate of O_2 evolution with a Clark electrode (Model LD2, Hansatech, Norfolk, UK) (Delieu and Walker 1981) on 3–8 leaves of each of two to four individuals for a total of 15 leaves for each of the eight species per site. A 10-cm^2 leaf disk was placed in a sealed chamber containing 10% CO_2 and maintained at 29°C. Leaves were first induced with 250 and 560 µmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD) before the maximum rate of O_2 evolution at 2,000 µmol m^{-2} s^{-1} was measured. Light was provided by a quartz-halogen lamp (Björkman and Demmig 1987) with attenuation achieved by inserting neutral density filters and verified with a quantum sensor (LI-190SB, Li-Cor, Lincoln, Neb., USA). At each light level, a stable signal was usually obtained in 5–7 min. The chamber was flushed with 10% CO_2 for 2 min between changes in light intensity. Species means for maximum rates of photosynthetic O_2 evolution were correlated with light saturated CO_2 assimilation rates measured with an infrared gas analyzer (LI-6400, Li-Cor) on a subset of study species (r^2=0.82, P<0.0001, n=12).

Leaf structure and chemistry

After photosynthetic measurements, we measured leaf lamina thickness between primary and secondary veins with a digital caliper (Mitutoyo, Kawasaki, Japan). Leaf discs were dried over-night at 65°C and weighed for determination of SLA. All leaf discs from the same tree were pooled and ground to powder for chemical analysis. One composite sample from each tree was analyzed for N using an elemental analyzer (NCS 2500, Carlo Erba, Milan, Italy). A separate subsample was analyzed for δ^{15}N at the University of Georgia Institute of Ecology, Athens, Ga., USA. Leaf fiber contents

Table 2 Study species from four sites along precipitation gradient in Panamanian lowland tropical forest, including phenological classification into deciduous (losing leaves for more than a few weeks), brevi-deciduous (losing leaves once per year and immediately flushing a new set) and evergreen. Classification based on field observations and the Flora of Barro Colorado Island (Croat 1978)

Species	Family	Phenology
1,800 mm		
Anacardium excelsum	Anacardiaceae	Brevi-deciduous
Astronium graveolens	Anacardiaceae	Deciduous
Calycophyllum candidissimum	Rubiaceae	Evergreen
Chrysophyllum cainito	Sapotaceae	Evergreen
Enterolobium cyclocarpum	Fabaceae	Deciduous
Luehea seemannii	Tiliaceae	Brevi-deciduous
Pseudobombax septenatum	Bombacaeae	Deciduous
Spondias mombin	Anacardiaceae	Deciduous
2,300 mm		
Poulsenia armata	Moraceae	Brevi-deciduous
Pourouma bicolor	Moraceae	Evergreen
Sterculia apetala	Sterculiaceae	Deciduous
Tabebuia guayacan	Bignoniaceae	Deciduous
Tapirira guianensis	Anacardiaceae	Evergreen
Terminalia amazonica	Combretaceae	Brevi-deciduous
Trattinickia aspera	Burseraceae	Deciduous
Virola sebifera	Myristicaceae	Evergreen
3,100 mm		
Aspidosperma cruenta	Apocynaceae	Evergreen
Brosimum utile	Moraceae	Evergreen
Calophyllum longifolium	Clusiaceae	Evergreen
Dussia munda	Fabaceae	Evergreen
Manilkara bidentata	Sapotaceae	Evergreen
Marila laxiflora	Clusiaceae	Evergreen
P. armata	Moraceae	Brevi-deciduous
T. guianensis	Anacardiaceae	Evergreen
3,500 mm		
A. cruenta	Apocynaceae	Evergreen
Carapa guianensis	Meliaceae	Evergreen
Cassipourea eliptica	Rhizophoraceae	Evergreen
Erisma blancoa	Vochysiaceae	Evergreen
Sacaglottis trygynum	Hernandiaceae	Evergreen
Sterculia costaricana	Sterculiaceae	Brevi-deciduous
Virola koschnyi	Myrsticaceae	Evergreen
Zygia ramiflora	Fabaceae	Evergreen

were quantified on a single composite sample per species using a fiber analyzer (Model 200, Ankom, Macedon, N.Y., USA). Neutral detergent fiber (NDF) is what remains after removal of extractable components with detergent solution, and includes cell wall constituents not immediately nutritionally available including hemicellulose, cellulose and lignin. Acid detergent fiber (ADF) represents the total of lignin and cellulose that are not soluble in weak acid detergent, whereas lignin is defined as residual tissue after digestion with 72% H_2SO_4. Leaf toughness was measured in the field on fresh leaves as resistance of the leaf lamina to puncture with a 1.9-mm rod attached to a modified spring scale for 300 g range (Pesola, Switzerland). Such measurements are not equivalent to the material property of fracture toughness, which is a more relevant measure of toughness against herbivore action. However, leaf

toughness was correlated with fracture toughness of leaf lamina for species at the 1,800-mm site (r^2=0.88, P<0.006, n=7; K. Kitajima, unpublished data) and 3,100-mm site (r^2=0.70, P<0.0001, n=21; S. J. Wright, unpublished data).

Leaf life span and leaf water potential

Leaf life span and leaf water potential were quantified only at 1,800- and 3,100-mm sites where canopy crane access was available. Leaf water potentials (Ψ_{leaf}) were measured at predawn (0600 hours) and midday (1200 hours) for study species at the 1,800- and 3,100-mm sites using a pressure chamber (PMS Instruments, Corvallis, Ore., USA). At each site, three terminal shoots from two individuals per species were collected from the upper canopy in July 2001 (early wet season), October 2001 (late wet season), and February 2002 (dry season). Leaf life span was determined for marked leaves on upper canopy shoots that were censused every 4–6 weeks for 2–5 years as part of a larger study on canopy leaf dynamics (S.J. Wright, unpublished data). We used the median value of longevity for 66–144 leaves per species for comparison of leaf life spans.

Data analysis

Analyses of the statistical effect of climate on community mean leaf traits were conducted with one-way general linear models using annual precipitation as an independent continuous variable. We used ANCOVA to test whether the functional relationships between P_{mass} (dependent variable) and leaf traits (leaf N, SLA, and leaf life span; covariates) differ between sites (grouping variable). None of the covariates showed a significant interaction with the grouping variable (P>0.05), so the interaction term was dropped from the model. Mean Ψ_{leaf} was compared between sites by repeated measure analysis of variance using site as the between-subject factor and measurement date as a within-subject factor (von Ende 1993). Separate analyses were performed for predawn and midday Ψ_{leaf}. All analyses were conducted using SAS version 6.12 (SAS 1985).

Results

Soil water potential

Soil water potential reflected patterns of monthly precipitation, demonstrating that the main difference between sites is length and intensity of the dry season and not differences during the wet season (Fig. 1A). The two wetter sites had much higher gravimetric soil water content, not only during the dry season when sites differed in Ψ_{soil}, but also during the wet season when all four sites had a similar water potential of ~0 MPa (Fig. 1B). Maximum gravimetric soil moisture, an index of soil water-holding capacity, increased with annual precipitation from 49.4% to 89.1% of dry soil mass from the driest to wettest site (Fig. 1B).

Photosynthesis

Area-based photosynthetic capacity (P_{area}) decreased slightly with MAP, which explained 13% of the variation in P_{area} among the 32 study species (Fig. 2A). Mass-based photosynthetic capacity (P_{mass}) exhibited a more pronounced decrease with MAP, which explained 42% of the
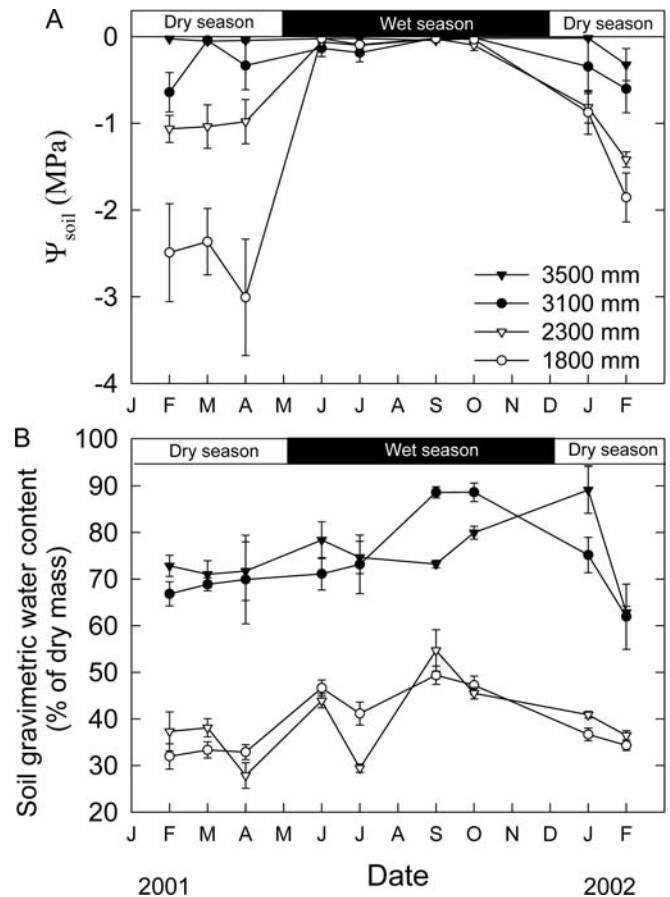

Fig. 1 Seasonal variation in **A** soil water potential (Ψ_{soil}) and **B** gravimetric water content determined between 15–20 cm depth in four 1-ha lowland tropical forest study plots in Panama. *Points* represent mean (±1SE) (n=6)

variation (Fig. 2B). Leaf N per unit area did not differ with MAP (r^2=0.00, P=0.95). However, MAP explained 21% of the variation in leaf N per unit mass and 34% of the variation in δ^{15}N, both of which decreased significantly with increasing precipitation (Fig. 3). Leaf thickness increased (Fig. 4A), whereas SLA decreased with increasing MAP (Fig. 4B). These leaf structural changes were responsible for the stronger correlation of MAP with photosynthetic capacity and leaf N on a mass basis than on an area basis.

The relationship between P_{mass} and leaf life span or between P_{mass} and leaf N did not differ significantly between sites (P>0.1 for test of heterogeneity of means around regression slopes in ANCOVA), whereas the relationship between P_{mass} and SLA only marginally differed between sites (F=2.95, P=0.05). Therefore, species from all sites fell onto the same functional relationship between leaf traits, although species from different sites tended to occupy different ranges of the relationship (Fig. 5). P_{mass} was positively correlated with leaf N across all species and sites. This predictive relationship improved from an r^2 of 0.56–0.78 by removing the statistical outlier from the family Fabaceae (Fig. 5A). P_{mass} and SLA were positively correlated across all species and sites and were
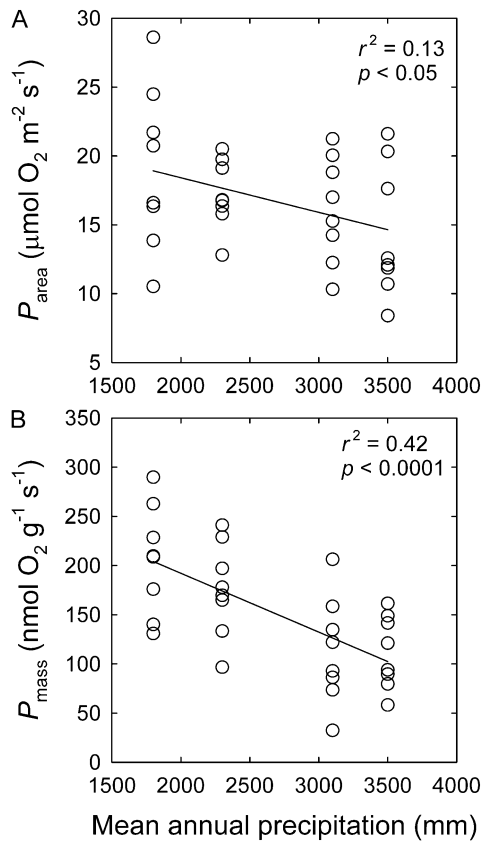
Fig. 2 Relationship between mean annual precipitation and maximum photosynthetic oxygen evolution rate **A** per unit area (P_{area}) and **B** per unit mass (P_{mass}) for the eight most common canopy species at four sites along a precipitation gradient in lowland Panamanian forest
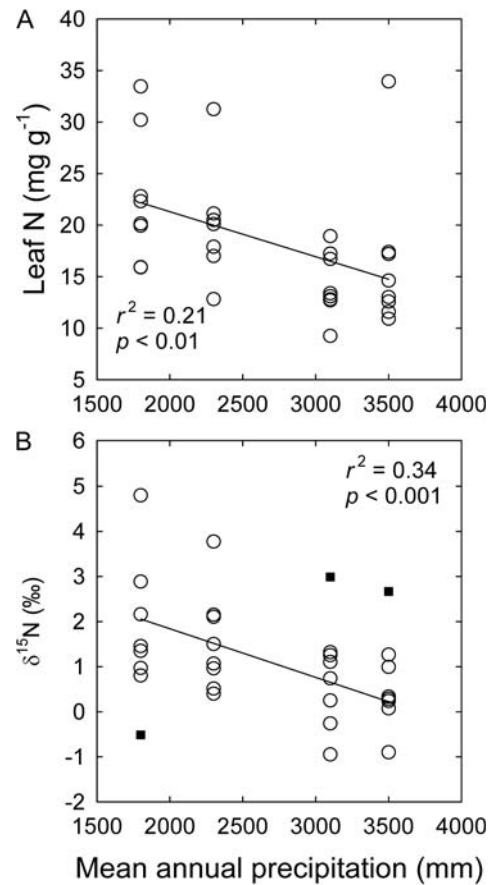

Fig. 3 Relationship between mean annual precipitation and **A** leaf N concentration per unit mass and **B** leaf N isotopic composition ($\delta^{15}N$) for the most common canopy species at four sites along a precipitation gradient in Panama. Species from the family Fabaceae (*closed squares*) were not included in regression analysis

expressed as a log-linear function (Fig. 5B). Median leaf life spans were longer at the 3,100-mm site than they were at the 1,800-mm site ($t=-6.25$, $P=0.003$, $df=4$) and were negatively correlated with P_{mass} (Fig. 5C).

Midday leaf water potential (Ψ_{leaf}) was lower at the 1,800-mm site than at the 3,100-mm site during the early [$F_{(1,14)}=6.11$, $P<0.05$] and late wet season [$F_{(1,14)}=3.17$, $P<0.1$; Fig. 6], but not during the dry season. There were no significant differences in predawn Ψ_{leaf} among sites during any measurement period.

Leaf structure and chemistry

Leaf toughness of the eight most common species significantly increased with MAP and lamina thickness (Table 3). Fiber (NDF but not ADF or lignin) and cellulose contents per unit mass were positively related to lamina thickness; thus the proportional representation of cell wall in leaf tissue increases as leaves increase in thickness, but not directly with increasing precipitation. With increasing precipitation, nutritional content of leaves decreased (higher fiber to N ratio) and leaf toughness increased

Table 3 Correlation coefficients between leaf defensive characteristics and mean annual precipitation and lamina thickness for 32 species of lowland tropical forest canopy trees at four levels of mean annual precipitation

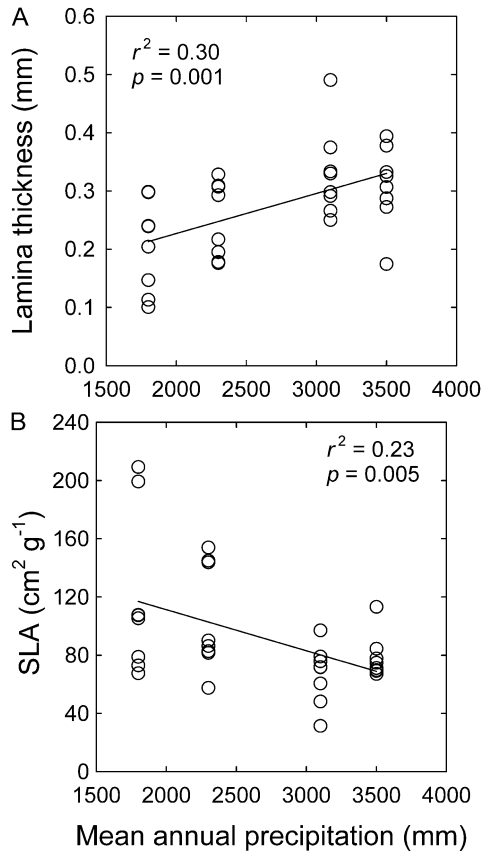|	Mean annual precipitation (mm year^{-1})		Lamina thickness (mm)	
	r	P	r	P
Toughness (kg)	0.535[a]	0.0016[a]	0.843[a]	<0.0001[a]
Fiber–NDF (% dry mass)	0.127	0.490	0.356[a]	0.0454[a]
Fiber–ADF (% dry mass)	0.124	0.500	0.276	0.1270
Lignin (% dry mass)	0.077	0.674	0.091	0.6223
Cellulose (% dry mass)	0.168	0.358	0.434[a]	0.0130[a]
NDF:N	0.470[a]	0.0067[a]	0.674[a]	<0.0001[a]
ADF:N	0.438[a]	0.0121[a]	0.600[a]	0.0003[a]
Lignin:N	0.376[a]	0.0339[a]	0.442[a]	0.0113[a]

[a]Significant correlation

Fig. 4 Relationship between mean annual precipitation and **A** lamina thickness and **B** specific leaf area (*SLA*) for the eight most common canopy species at four sites along a precipitation gradient in Panama

(Table 3). Thus, canopy leaves at higher precipitation sites must be less palatable to herbivores.

Discussion

As precipitation increases across the Isthmus of Panama, there is a gradual change in representative leaf traits of canopy trees from short-lived leaves with high P_{mass} in seasonally dry forest, to relatively long-lived leaves with lower P_{mass} in wet forest. Lower P_{mass} is accompanied by lower nutritional value (fiber to N ratio) and increased structural toughness of leaves. Relatively short leaf life spans in seasonally dry forests reflect a strategy to maximize photosynthesis when water is available and to minimize water loss and respiration costs during rainless periods. Longer leaf life spans exhibited by evergreen trees in wetter forests are accompanied by low P_{mass}, either because of greater nutrient limitation in wetter forest, or because of greater need for defense. Overall, our data are in line with reports of decreasing canopy leaf N and productivity with increasing precipitation above 2,500 mm in tropical forest (Schuur and Matson 2001; Schuur 2003). Thus, our results corroborate the observation in Hawaii that there is a shift from a relatively nutrient rich system to a relatively carbon rich system as precipitation increases in
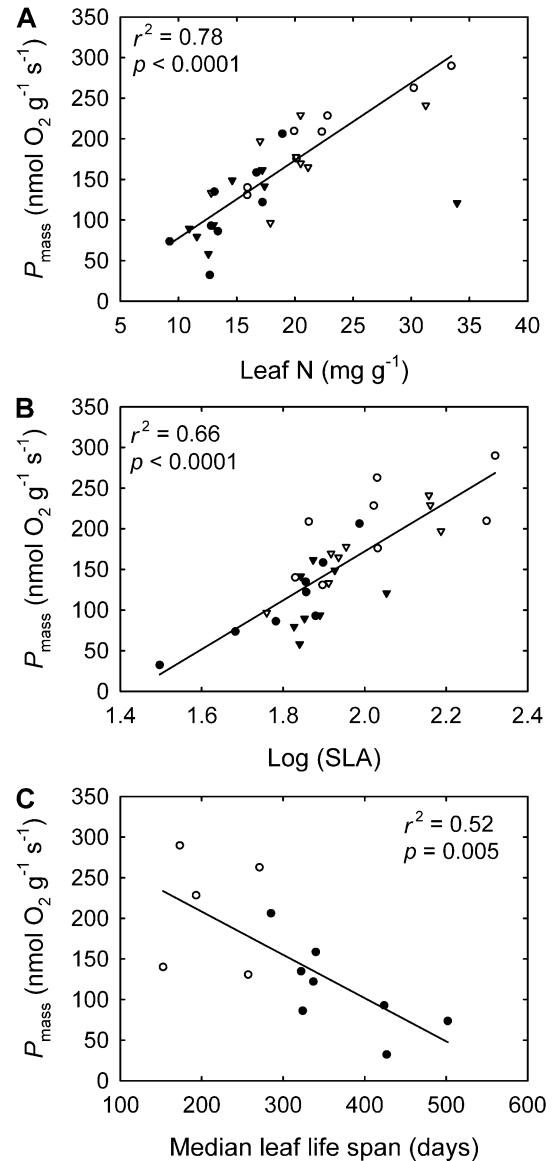

Fig. 5A–C Maximum photosynthetic O_2 evolution rate (P_{mass}) as a function of other leaf traits from study species at the 1,800-mm (*open circles*), 2,300-mm (*open triangles*), 3,100-mm (*closed circles*), and 3,500-mm (*closed triangles*) sites. P_{mass} as a function of leaf N; P_{mass}=95.56·(leaf N)–17.81 (**A**). The outlier, *Zygia ramiflora* (Fabaceae) was not included in the regression. P_{mass} as a function of log-transformed SLA; P_{mass}=301·log (SLA)−429.7 (**B**). P_{mass} as a function of median leaf life span for study species at the 1,800-mm (*open circles*) and 3,100-mm (*closed circles*) canopy crane sites P_{mass}=−0.53·(leaf life span)+314.93 (**C**)

tropical forest (Austin and Vitousek 1998). Our results are also consistent with cost–benefit theories of leaf life span that predict dry season deciduous canopy species in seasonally dry tropical forests and evergreen canopy species in wet aseasonal forests (Kikuzawa 1991; Givnish 2002).

Different precipitation regimes among study sites affected Ψ_{soil} during the dry season, but not in the wet season (Fig. 1). However, the effect of soil physical properties cannot be ignored. For a given Ψ_{soil}, the two
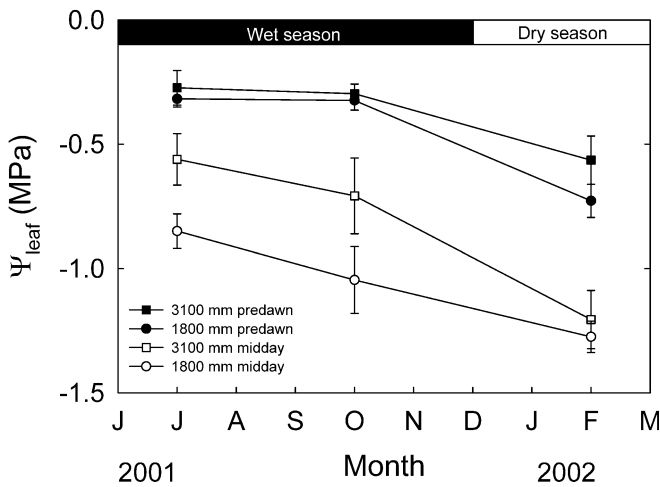
Fig. 6 Seasonal variation in leaf water potential (Ψ_{leaf}) for canopy trees at two sites with contrasting precipitation in lowland Panama. Each *point* represents the mean ($\pm 1SE$) of two individuals from six to eight species at each site

wetter sites had much higher soil water contents than the two drier sites. This is most likely a result of differences in particle size distribution of clay and silt. However, greater precipitation may have affected the soil structure and increased water holding capacity, as observed in response to experimental irrigation on nearby Barro Colorado Island (Kursar et al. 1995). Midday Ψ_{leaf} was lower at the 1,800-mm site than at the 3,100-mm site during the wet season but not during the dry season, despite strong differences in Ψ_{soil} in the dry season, indicating that differences in atmospheric water content and stomatal function can affect Ψ_{leaf} independent of Ψ_{soil}. Lack of a significant difference in predawn leaf water potential despite strong differences in Ψ_{soil} during the dry season suggests high water-storage capacity (Goldstein et al. 1998) or deep roots in dry forest species.

The community-wide increase in leaf life span with increasing precipitation may be an indirect result of decreased soil N availability with precipitation. Several studies have addressed the effects of precipitation on N availability as a factor governing the expression of leaf traits at the community scale (Austin and Vitousek 1998; Schuur and Matson 2001; Givnish 2002). Evergreen vegetation tends to dominate nutrient-poor habitats (Monk 1966). Dominance of evergreen species in wet forest is consistent with the hypothesis of reduced nutrient availability at very high precipitation ($>2,500$ mm $year^{-1}$). In addition, decomposition rate of leaf litter is significantly slower for wet forest species than for dry forest species (Santiago 2003) based on higher fiber: N ratios in leaves of the former (Table 3), suggesting slower nutrient turnover rates in wetter forest. Decreases in foliar and soil $\delta^{15}N$ with increasing precipitation have been interpreted as signifying increasing N-limited conditions (Austin and Vitousek 1998; Schuur and Matson 2001). However, bulk soil $\delta^{15}N$ from the four sites along this precipitation gradient did not match this pattern (Santiago 2003). Thus decreasing foliar $\delta^{15}N$ with increasing precipitation in lowland Panamanian canopy trees may indicate that species with shorter leaf life spans retranslocate leaf N more frequently than evergreen species, because $\delta^{15}N$

becomes enriched during reassimilation of nitrate and leaf N re-metabolism (Evans 2001).

Decreasing P_{mass} and leaf N with increasing precipitation may also reflect diminishing returns for N allocation to canopy leaves if the decrease in light availability with increasing precipitation is sufficiently strong to drive such a pattern. One species at the 1,800-mm site, *Luehea seemannii*, increased rates of CO_2 assimilation, branch growth, and fruit production in response to experimental light enrichment, supporting the notion that photosynthetic productivity of canopy trees of lowland forest is limited by reduced light availability due to cloud cover (Graham et al. 2003). However, it is not clear whether a difference of 0.9 mol m^{-2} for average daily light availability across this precipitation gradient contributes sufficiently to patterns of N allocation and P_{mass} of canopy leaves. Global relationships between leaf traits and climate suggest that higher light availability is related to thicker leaves with a low SLA (Niinemets 2001). In contrast, our data show thinner leaves with high SLA in sites with slightly higher light availability. Thus, it is more likely that leaf traits along this gradient reflect constraints in growth season length due to seasonality in water availability, or effects of soil nutrient availability in relation to precipitation. Nonetheless, if leaf area index increases and light availability decreases with increasing precipitation, species in wetter forest may develop under lower light conditions and may therefore be adapted to lower light availability. Further studies on variation in understory light availability along precipitation gradients are likely to broaden our understanding of how light availability during development affects canopy leaf traits.

Evergreen species are distributed bimodally on the latitudinal gradient with broad-leaved evergreens in equatorial aseasonal rainforest, replaced by broad-leaved deciduous species in subtropical seasonal dry forest and needle-leaved evergreen species in temperate and boreal forests (Chabot and Hicks 1982). The precipitation gradient across the Panamanian lowlands is on the side of the bimodal distribution of evergreen species where canopy leaf longevity increases with precipitation. Greater dominance of short-lived leaves at drier sites is consistent with the prediction that deciduous species should be dominant when seasonal differences in carbon assimilation are large, and the cost of replacing leaves relative to potential carbon income is small (Givnish 2002). More data is needed to determine whether evergreen or deciduous leaves produce a higher total net carbon income per unit leaf mass through the lifetime of the leaf. Perhaps, the trade-off relationship between leaf longevity and photosynthetic capacity may be such that total net carbon income through the leaf lifetime may be independent of leaf longevity (Mediavilla and Escudero 2003). Many dry-forest species in our study are found on the wetter side of the Panamanian Isthmus only in early successional stands, and may be less competitive for resources than evergreen species that dominate mature wet forests. However, these dry-forest dominants can maintain their competitive advantage where evergreen species fail to persist due to seasonal drought. The common functional relationship between leaf life span, photosynthetic capacity, leaf N, SLA and structural toughness identified across the study

sites suggests that community-wide changes in leaf trait association and phenological habit should be understood from the perspective of costs and benefits associated with contrasting leaf longevity that applies to both regional and global scales.

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