

LEAF TRAITS OF CANOPY TREES ON A PRECIPITATION GRADIENT IN
PANAMA: INTEGRATING PLANT PHYSIOLOGICAL ECOLOGY AND
ECOSYSTEM SCIENCE

By

LOUIS STEPHEN SANTIAGO

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LEAF TRAITS OF CANOPY TREES ON A PRECIPITATION
GRADIENT IN PANAMA: INTEGRATING PLANT PHYSIOLOGICAL
ECOLOGY AND ECOSYSTEM SCIENCE

By

Louis Stephen Santiago

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Chair: Stephen S. Mulkey
Major Department: Botany

There is increasing awareness in ecology of the importance of species effects on processes at the ecosystem scale. This dissertation uses a comparative approach involving many species along a precipitation gradient (1800-3500 mm/yr) in lowland Panama to understand how species traits vary among different plant communities, and how these traits feed back into ecosystem processes such as decomposition and soil nutrient availability. As precipitation increases from South to North across the Isthmus of Panama, there is a gradual change in canopy leaf traits from short-lived leaves with high photosynthetic rates in seasonally dry forest, to relatively long-lived leaves with lower photosynthetic rates and increased allocation to structural defense in wet forest. Increases in leaf litter lignin:N also accompany increases in precipitation, indicating a decrease in potential decomposability of leaf litter in wetter sites. Leaf litter lignin:N was negatively correlated with soil N mineralization rates, and positively correlated with total soil N pools indicating that slowly decomposing litter reduces mineralization, but conserves N

in the soil organic matter matrix. Leaf litter lignin:N was the strongest litter quality predictor of decomposition at the one site where decomposition was studied.

Decomposition was positively related to specific leaf area, leaf N concentration and photosynthetic rate per unit mass suggesting that these traits may be useful predictors of the effects of species on ecosystem processes. Photosynthetic rate per unit area and stomatal conductance were positively related to leaf specific hydraulic conductivity and negatively related to branch wood density indicating that leaf traits controlling gas exchange correlate with processes at the branch and whole plant levels of organization. Overall this dissertation provides evidence that many plant traits are correlated along a minimal number of axes, and that these traits can be used to predict the movement of matter and energy between plants and their environments.

CHAPTER 1 INTRODUCTION

This dissertation is an attempt to understand how changes in plant community composition along a precipitation gradient feed back into nutrient cycling and ecosystem processes. This research area integrates plant physiology, community ecology, and ecosystem science. The ideas in this dissertation are also based on studies of how species respond to environmental factors, and the effects that species have on those factors (Cornelissen 1996; Hobbie 1992; Wardle et al. 1998). Several studies have demonstrated that many plant species traits are correlated, and that suites of traits appear to have evolved in response to specific environmental regimes vary along a minimal number of axes (Chapin 1980; Grime 1977; Tilman 1988). More recently, it has been shown that leaf physiological traits governing the carbon economy of the leaf are interrelated and reflect fundamental evolutionary tradeoffs and biochemical constraints (Reich et al. 1992). Together, these studies suggest that if we can link the effects of plant species on ecosystem processes with ecophysiological or life history characteristics, then we may augment our understanding of ecosystem functioning, by drawing upon evolutionary and ecological principles.

In this dissertation, I take two main approaches to understanding how species traits feed back into ecosystem processes. The first is along a precipitation gradient in lowland Panama. As precipitation increases in the lowland tropics, there is a gradual change in canopy species from deciduous species in seasonally dry forest, to evergreen species in wet, aseasonal forest. Leaf turnover represents a major pathway of energy and

matter between the plant and soil components of the ecosystem. Therefore, along this precipitation gradient, I present data on how patterns of canopy phenology are related to photosynthesis, and leaf life span. In turn, I relate leaf traits to indices of litter quality and discuss ways in which variation in species composition along this precipitation gradient can influence the cycling of nutrients and the size of soil nutrient pools.

The second approach I take to understanding how species traits feed back into ecosystem processes is at one wet forest site along the precipitation gradient. At this site I present data on how leaf physiological traits that control carbon assimilation and water loss are related to hydraulic and biophysical characteristics at the branch and whole plant scale, and discuss how relationships between leaf and branch physiology reflect evolutionary tradeoffs. I also compare how plant growth forms vary in the litter quality and decomposition rates of their leaves, and whether leaf litter decomposition can be predicted from leaf physiological characteristics. Together, this collection of studies provides evidence that changes in plant community composition with precipitation in lowland Panama can influence nutrient cycling, and that leaf physiological characteristics provide information about the potential effects of species on ecosystem processes.

CHAPTER 2
LEAF PHOTOSYNTHETIC TRAITS OF CANOPY TREES ALONG A
PRECIPITATION GRADIENT IN LOWLAND TROPICAL FOREST

Introduction

Tropical forests often exhibit gradients of vegetation structure and species composition in relation to precipitation (Gentry 1988; Schimper 1898; Wright 1992). Forests on the dry side of this gradient commonly have a higher proportion of deciduous canopy species that lose their leaves during seasonal dry periods when low soil water availability may limit physiological activity. Deciduous leaves of tropical forest reduce whole-plant transpiration and respiration during drought; and often have higher rates of photosynthesis per unit leaf mass (P_{mass}) than evergreen species (Chabot and Hicks 1982; Eamus and Prior 2001; Prado and DeMoraes 1997; Reich et al. 1992). 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; Cunningham et al. 1999; Vázquez and Givnish 1998). These respective costs and benefits partially explain why deciduous trees dominate seasonally dry tropical forest; why evergreen species dominate wet, aseasonal forest; and suggest that P_{mass} of canopy species should decrease with increasing precipitation in the tropics. There are few data available for photosynthetic traits on broad precipitation gradients in lowland tropical forest. On a global scale, however, P_{mass} and specific leaf area are reported to increase with increasing moisture availability (Niinemets 2001; Reich et al. 1999). The purpose of our study is to determine how patterns of canopy phenology are related to

photosynthesis and leaf life span along a regional precipitation gradient in lowland Panama.

Interest in leaf trait variation along climate gradients dates back to the time of Theophrastus and formed some of the earliest ecological works. Recent studies have focused on precipitation as a driver of resource availability with direct and indirect effects on plant processes. For example, plants of relatively dry environments in Australia exhibited more sclerified vasculature than did species in high rainfall sites, possibly reflecting adaptation to resist wilting and minimize cell damage when water availability is low (Cunningham et al. 1999). Relatively high leaf N per unit area in dry habitats in Australia may represent a mechanism by which plants capitalize on higher light availability in dry habitats (Cunningham et al. 1999; Mooney et al. 1978). Leaf N of montane forest species in Hawaii was also reported to decrease with increasing precipitation and was related to decreasing soil N availability with increasing precipitation (Schuur and Matson 2001), suggesting that evergreenness in wet tropical forest may be a response to relatively low nutrient availability (Monk 1966). Precipitation may therefore directly affect vegetation structure and community composition through constraints imposed by water deficit, or indirectly through effects on availability of light and/or nutrients (Schuur and Matson 2001).

Most studies of leaf trait variation with climate have been conducted along gradients with a maximum precipitation below 2500 mm yr⁻¹ (Cunningham et al. 1999; Mooney et al. 1978; Werger and Morris 1991). Other studies on precipitation gradients with maximum precipitation above 5000 mm yr⁻¹ have focused on phenotypic changes within individual plant species (Austin and Vitousek 1998; Schuur and Matson 2001). In

contrast, our study addresses variation in leaf traits caused by large changes in species community composition over short (10 km) distances (Condit et al. 2002). I 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 (1800 to 3500 mm yr⁻¹). Specifically I wanted to link the 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 1800 mm yr⁻¹ on the Pacific Coast to 4000 mm yr⁻¹ on the Caribbean Coast (Condit 1998). I 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 therefore temperature (Table 2-1). All sites have a mean monthly precipitation of >100 mm during the wet season (between May and December) but dry season length (mean number of 30-day periods with <100 mm precipitation) varies between 129 days at the 1800 mm site and 67 days near the 3500 mm site (ACP 2002). Between December and May, the probability of a site receiving <100 mm of monthly precipitation varies from 80% at the 1800 mm site to 22% at the 3500 mm site (Paton and Wright 2003). Variation in rainfall during the study period (2000-2002) was within 15% of MAP at all sites. Variation in the amount and distribution of annual precipitation has the potential to influence light availability and relative humidity. Average daily photosynthetically active radiation (PAR) decreases

with increasing precipitation from 32.3 mol m⁻² at the 1800 mm site (Juan Posada, unpublished data); 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 3100 mm site (Paton and Wright 2003). Mean relative humidity appears to be highest on the wet Caribbean coast (94.6% at the 3100 mm site); the 1800 mm site and Barro Colorado Island maintain values of 87.9 and 84.0%, respectively (Paton and Wright 2003).

The soils in 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; Kursar et al. 1995; Yavitt et al. 1993). All of the study sites are on volcanic substrate (except Ft. Sherman, which 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) at six randomly selected locations in each 1-ha study plot, nine times over a 14-month period (February 2001 to March 2002). One 42.5 mm diameter filter paper (Whatman no. 42, batch #711492, Whatman, Kent, UK) was equilibrated for 6 days with a fresh soil sample taken from 15 to 20 cm depth. Then the gravimetric moisture content of the filter paper was used to predict water potential using the regression equation of Deka et al. (1995). Assuming that gravitational and solute potential are negligible, the resulting values represent soil matric potential. I also determined the gravimetric soil water content on a 5 g subsample by drying at 105°C for 24 h.

At each site, I measured the eight canopy tree species with the largest relative proportion of basal area. Species composition and phenological habit of the most common canopy trees change rapidly across this gradient, as species richness increases steeply with mean annual precipitation (Table 2-2) (Pyke et al. 2001). One recent study comparing beta-diversity (how species composition changes with distance) of tree communities between lowland forests in Ecuador and Peru found that distant forests (>1000 km) with similar climate shared a much larger proportion of the most common species than would be expected by chance (Pitman et al. 2001). In contrast, tree community composition varies substantially even over 10 to 20 km distances in Panama; and such variation appears to be regulated largely by climate variation (Condit et al. 2002). All study plots are located in mature forest (>500 yr), except the 1800 mm site, which is a forest of mixed age (70-100 yr). Measurements on the largest canopy trees at the 1800 mm site are comparable to other sites even though this forest is younger, because canopy composition was representative of mature moist and dry forest (Croat 1978).

Photosynthesis

At the 1800 and 3100 mm sites, canopy 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 2300 and 3500 mm sites, leaves were collected from the upper canopy using a shotgun and then treated the same. Canopy trees were defined as individuals with approximately 80% of the crown exposed to full sun. All leaves were collected before 1030 h the day after rainfall and were transported to the laboratory within 2.5 h where photosynthesis was measured immediately.

Photosynthetic capacity was measured as the maximum rate of O₂ evolution with a Clark electrode (Model LD2, Hansatech, Norfolk, UK) (Delieu and Walker 1981) on 3 to 8 leaves of each of 2 to 4 individuals for a total of 15 leaves per species from a site. A 10-cm² leaf disk was placed in a sealed chamber containing 10% CO₂ and maintained at 29°C. Leaves were first induced with 250 and 560 μmol photosynthetic photon flux density (PPFD) before the maximum rate of O₂ evolution at 2000 μmol 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 (Model LI 190SB, Li-Cor Inc., Lincoln, NE). At each light level, a stable signal was usually obtained in 5 to 7 min. The chamber was flushed with 10% CO₂ for 2 min between changes in light intensity. The high concentration of CO₂ in the O₂ electrode chamber bypasses all stomatal and cuticular resistance, so that the measured maximum rate reflects the Rubisco-limited rate of photosynthesis; and thus is a good index of enzyme allocation to photosynthetic capacity. Maximum rates of photosynthetic O₂ evolution were correlated with measurements of CO₂ assimilation conducted with an infrared gas analyzer (Model 6400, Li-Cor, Inc.) on a subset of study species ($r^2=0.82$; $P<0.0001$; $n=12$).

Leaf Structure and Chemistry

After photosynthetic measurements, I measured lamina thickness between primary and secondary veins with a digital caliper (Mitutoyo Inc., Japan). Leaf discs were dried overnight at 65°C; weighed for determination of specific leaf area (SLA); and ball milled. All leaf discs from the same tree were pooled for chemical analysis. One composite sample from each tree was analyzed for N using an elemental analyzer (Model NCS

2500, Carlo Erba, Milano, Italy). A separate subsample was analyzed for $\delta^{15}\text{N}$ at the University of Georgia Institute of Ecology. Leaf carbon fraction analyses were performed on a single composite sample per species at a site using forest-product techniques (Ryan et al. 1989). Dried leaf samples were digested in a detergent solution by which soluble and nutritionally available cell contents were separated from neutral detergent fiber (NDF), which includes all cell wall constituents and is not immediately nutritionally available. A dilute acid detergent solution was then used to determine acid detergent fiber (ADF, lignocellulose) before lignin was separated from cellulose in 72% H_2SO_4 . Leaf toughness was measured in the field on freshly collected leaves with a penetrometer (Pesola, Switzerland), which measured the maximum force during punching through the lamina between primary and secondary veins at a steady, slow rate with a 1 mm diameter plunger. Such measurements are not equivalent to the material property of fracture toughness, which is a more theoretically relevant measure of toughness against herbivore action. However, leaf toughness was correlated with fracture toughness for species at the 1800 mm site (Kaoru Kitajima, unpublished data).

Two-Site Comparisons

Canopy access at the two crane sites allowed for ease in data collection of leaf water potential and leaf life span of study species. Leaf water potentials (Ψ_{leaf}) were measured at predawn (0600 h) and midday (1200 h) for the study species at the 1800 and 3100 mm sites using a pressure chamber (PMS Instruments, Corvallis, Oregon, USA). At both sites, canopy cranes were used to collect three terminal shoots from two individuals per species from the upper canopy in July 2001, October 2001, and February 2002 representing the early and late wet season and dry season, respectively. Leaf life span was

measured on marked sun leaves that were censused every 6 weeks for 5 years as part of a larger study on canopy leaf dynamics (S. Joseph Wright, unpublished data).

Data Analysis

Analyses of the statistical effect of climate on leaf traits were conducted with one-way general linear models, to test whether leaf traits varied significantly with precipitation. Analyses of the relationships between leaf traits were performed with one-way analyses of covariance to test for heterogeneity of means around regression slopes. Each analysis of covariance was conducted independently with P_{mass} as the dependent variable; MAP as the grouping factor; and leaf N, SLA or leaf life span as the covariate. Mean Ψ_{leaf} between sites was compared by repeated measure analysis of variance and profile analysis with site as a between-subject factor; and measurement date and time of day as multiple within-subject factors (von Ende 1993). All analyses were conducted using SAS version 6.12 (SAS 1985).

Results

Soil Water Potential

Soil water potential reinforced precipitation data, demonstrating that the main difference between sites is the length and intensity of the dry season and not differences during the wet season (Figure 2-1). Furthermore, maximum gravimetric soil moisture, an index of soil water-holding capacity, increased with precipitation from a maximum of 49.4 to 89.1% of dry soil mass from the driest to wettest site.

Photosynthesis

Mean annual precipitation (MAP) explained 13% of the variation in area-based maximum photosynthetic rates (P_{area}) of the eight most abundant canopy tree species at each of the sites (Figure 2-2A). The P_{area} showed a marginally significant decrease with

increasing MAP. When photosynthesis was expressed on a mass basis (P_{mass}), MAP explained 42% of the variation and P_{mass} decreased significantly with increasing precipitation (Figure 2-2B). There was no clear relationship between leaf N per unit area and 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 $\delta^{15}\text{N}$, both of which decreased significantly with increasing precipitation (Figure 2-3A,B). Both photosynthesis and leaf N showed stronger correlations with precipitation when expressed on a mass basis than on an area basis because there was an increase in leaf thickness with increasing MAP (Figure 2-4A). In a related index of leaf structure, SLA decreased with increasing MAP (Figure 2-4B).

Analysis of covariance revealed no heterogeneity of means around regression slopes caused by MAP in the relationship between P_{mass} and leaf life span ($F=0.23$; $P=0.58$) or leaf N ($F=0.51$; $P=0.68$), and only a marginally significant heterogeneity of slope caused by MAP in the relationship between P_{mass} and SLA ($F=2.95$; $P=0.05$). Therefore, species from all sites were regressed together in the same predictive relationships, regardless of site, although species from different sites tended to occupy different ranges of the relationship (Figure 2-5). The P_{mass} was positively correlated with leaf N across all species and sites; and this predictive relationship improved from an r^2 of 0.56 to 0.78 by removing the statistical outlier (Figure 2-5A). The P_{mass} and SLA were positively correlated across all species and sites; and were expressed as a log-linear function (Figure 2-5B).

Leaf Structure and Chemistry

Toughness of canopy leaves significantly increased with MAP and lamina thickness (Table 2-3). Fiber (NDF) and cellulose concentration were positively related to

lamina thickness; thus the proportion of leaf cell-wall material increases as leaves increase in thickness. With increasing precipitation, I also noted trends toward reduced nutritional content and increased antiherbivore defense (fiber and lignin per unit leaf N) (Table 2-3) (Cunningham et al. 1999).

Two-Site Comparisons

Median leaf life spans were longer at the 3100 mm site than they were at the 1800 mm site ($t=-6.25$; $P=0.003$; $df=4$); and were negatively correlated with P_{mass} (Figure 2-5C). Midday leaf water potential (Ψ_{leaf}) was lower at the 1800 mm site than at the 3100 mm site during the early ($F_{1,14}=6.11$; $P<0.05$) and late wet season ($F_{1,14}=3.17$; $P<0.1$; Figure 2-6); but not during the dry season. There were no significant differences in predawn Ψ_{leaf} among sites during any measurement period.

Discussion

As precipitation increases from South to North across the Isthmus of Panama, there is a gradual change in canopy leaf traits from short-lived leaves with high P_{mass} in seasonally dry forest, to relatively long-lived leaves with lower P_{mass} and increased allocation to structural defense in wet forest. Relatively high P_{mass} and short leaf life spans of canopy leaves in seasonally dry forest may allow canopy species to take advantage of high light availability when water is available; and to minimize water loss and respiration costs during rainless periods. Longer leaf life spans exhibited by canopy trees in wetter forest appear to place constraints on P_{mass} by necessitating increased allocation to structural defenses. Although substantial variation in leaf traits exist along this precipitation gradient, it is important to note that precipitation drives the expression of leaf traits through soil moisture and tree water status (Reich 1995; Reich and Borchert

1984); and potentially by influencing light and nutrient availability, although these indirect effects are less documented (Schuur and Matson 2001).

Our data show coupling between Ψ_{soil} and seasonality in precipitation and show how variation in dry season intensity among study sites appears to be the greatest source of variation in soil water availability among sites (Figure 2-1). The range of Ψ_{soil} values observed are consistent with other studies of lowland Neotropical and West African forest reporting upper soil values near 0 MPa during the wet season to -3.5 MPa or lower during dry periods (Goldstein et al. 1986; Holbrook et al. 1995; Veenendaal et al. 1996). Our values of predawn and midday Ψ_{leaf} are also comparable to studies conducted in seasonally dry tropical forest in Venezuela, Australia, and Costa Rica (Borchert 1994; Eamus and Prior 2001; Goldstein et al. 1986; Medina and Francisco 1994; Sobrado 1986). Differences in midday Ψ_{leaf} between the 1800 and 3100 mm sites during the wet season but not during the dry season (despite strong differences in Ψ_{soil} in the dry season) indicate that differences in atmospheric water content and stomatal function can affect Ψ_{leaf} independently of Ψ_{soil} . Additionally, two of the deciduous species at the 1800 mm site had no leaves during February 2002 and were therefore not measured; whereas the remaining species maintained Ψ_{leaf} values between -1.0 and -1.5 MPa and thus minimized variation between the 1800 and 3100 mm sites, resulting in no statistical difference among the measured species. Sobrado (1986) and Medina and Francisco (1994) also found a stronger decrease in Ψ_{leaf} in deciduous than in evergreen species during the dry season, suggesting that maintaining functional leaves during the dry season requires greater resistance to desiccation, possibly through allocation to deeper roots.

Several studies have addressed the effects of precipitation on nutrient availability as a factor governing the expression of leaf traits at the community scale (Austin and Vitousek 1998; Givnish 2002; Schuur and Matson 2001). Evergreen vegetation tends to dominate nutrient-poor habitats (Monk 1966). Dominance of evergreen species in wet forest is consistent with the notion of reduced nutrient availability as precipitation increases. Both Schuur and Matson (2001) and Austin and Vitousek (1998) found the lowest foliar N concentrations at highest precipitation sites along precipitation gradients in Hawaiian montane forest. Decreasing leaf N per unit mass in lowland Panamanian forest is consistent with this line of reasoning. Decreasing foliar $\delta^{15}\text{N}$ with increasing precipitation has been interpreted as signifying increasing N-limited conditions (Austin and Vitousek 1998; Schuur and Matson 2001; Shearer and Kohl 1986). However, our bulk soil $\delta^{15}\text{N}$ did not match this pattern (Chapter 3). Thus decreasing foliar $\delta^{15}\text{N}$ with increasing precipitation in lowland Panamanian canopy trees may reflect the fact that species with shorter leaf life spans retranslocate leaf N more frequently than evergreen species and that $\delta^{15}\text{N}$ becomes enriched during re-assimilation of nitrate and leaf N re-metabolism (Evans 2001).

Decreasing 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. A difference of 0.9 mol m^{-2} for average daily PAR exists across this precipitation gradient. It is unknown whether this amount could contribute to patterns of N allocation to canopy leaves. Reduced N allocation to leaves with lower light availability is consistent with the functional convergence hypothesis (which predicts that plants should only allocate

resources to photosynthetic capacity that can be used despite constraints imposed by limiting resources such as light and water) (Field 1991). One species at the 1800 mm site, *Luehea seemannii*, increased rates of CO₂ assimilation, branch growth, and fruit production in response to experimental light enrichment; supporting the notion that canopy trees of lowland forest have the potential to acclimate to higher light availability (Graham et al. 2003). Therefore, decreasing light availability with increasing precipitation may contribute to relatively low photosynthetic rates in wet tropical forest.

Our pattern of decreasing P_{mass} and SLA with increasing moisture availability on a regional precipitation gradient is consistent with the notion of a bimodal distribution of leaf longevity (Chabot and Hicks 1982; Kikuzawa 1991). On a global scale, deciduousness is highest in mid-precipitation and mid-latitude ecosystems. Our relationships between P_{mass} and leaf life span and between leaf N and SLA show slopes similar to those of global comparisons (Reich et al. 1992). This suggests that fundamental tradeoffs between leaf traits are constant; but at the high end of global precipitation range, where water availability may exceed biological demand for much of the annual cycle, P_{mass} and SLA decrease with increasing precipitation, in contrast to the pattern of increasing P_{mass} and SLA with increasing precipitation common in other biomes (Reich et al. 1999).

Table 2-1. 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 yr ⁻¹)	Elevation (m)	Basal area (m ² ha ⁻¹)	Species richness (no. ha ⁻¹)	Tree density (no. ha ⁻¹)
Parque Metropolitano	1800	60	25.39	36	318
Pipeline Road	2300	210	26.59	95	560
Fort Sherman	3100	140	32.50	87	569
Santa Rita	3500	282	25.74	162	497

Table 2-2. 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
1800 mm		
<i>Anacardium excelsum</i>	Anacardiaceae	Brevi-deciduous
<i>Astronium graveolens</i>	Anacardiaceae	Deciduous
<i>Calycophyllum candidissimum</i>	Rubiaceae	Evergreen
<i>Chrysophyllum cainito</i>	Sapotaceae	Evergreen
<i>Enterolobium cyclocarpum</i>	Fabaceae	Deciduous
<i>Luehea seemannii</i>	Tiliaceae	Brevi-deciduous
<i>Pseudobombax septenatum</i>	Bombacaceae	Deciduous
<i>Spondias mombin</i>	Anacardiaceae	Deciduous
2300 mm		
<i>Poulsenia armata</i>	Moraceae	Brevi-deciduous
<i>Pourouma bicolor</i>	Moraceae	Evergreen
<i>Sterculia apetala</i>	Sterculiaceae	Deciduous
<i>Tabebuia guayacan</i>	Bignoniaceae	Deciduous
<i>Tapirira guianensis</i>	Anacardiaceae	Evergreen
<i>Terminalia amazonica</i>	Combretaceae	Brevi-deciduous
<i>Trattinickia aspera</i>	Burseraceae	Deciduous
<i>Virola sebifera</i>	Myristicaceae	Evergreen
3100 mm		
<i>Aspidosperma cruenta</i>	Apocynaceae	Evergreen
<i>Brosimum utile</i>	Moraceae	Evergreen
<i>Calophyllum longifolium</i>	Clusiaceae	Evergreen
<i>Dussia mundia</i>	Fabaceae	Evergreen
<i>Manilkara bidentata</i>	Sapotaceae	Evergreen
<i>Marila laxiflora</i>	Clusiaceae	Evergreen
<i>Poulsenia armata</i>	Moraceae	Brevi-deciduous
<i>Tapirira guianensis</i>	Anacardiaceae	Evergreen
3500 mm		
<i>Aspidosperma cruenta</i>	Apocynaceae	Evergreen
<i>Carapa guianensis</i>	Meliaceae	Evergreen
<i>Cassipourea eliptica</i>	Rhizophoraceae	Evergreen
<i>Erisma blancoa</i>	Vochysiaceae	Evergreen
<i>Sacaglottis trygynum</i>	Hernandiaceae	Evergreen
<i>Sterculia costaricana</i>	Sterculiaceae	Brevi-deciduous
<i>Virola koschnyi</i>	Myristicaceae	Evergreen
<i>Zygia ramiflora</i>	Fabaceae	Evergreen

Table 2-3. 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 yr ⁻¹)		Lamina thickness (mm)	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Toughness (kg)	0.535	0.0016	0.843	<0.0001
Fiber—NDF (% dry mass)	0.127	0.490	0.356	0.0454
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	0.0130
NDF:N	0.470	0.0067	0.674	<0.0001
ADF:N	0.438	0.0121	0.600	0.0003
Lignin:N	0.376	0.0339	0.442	0.0113

Note: Bold type indicates significant correlation.

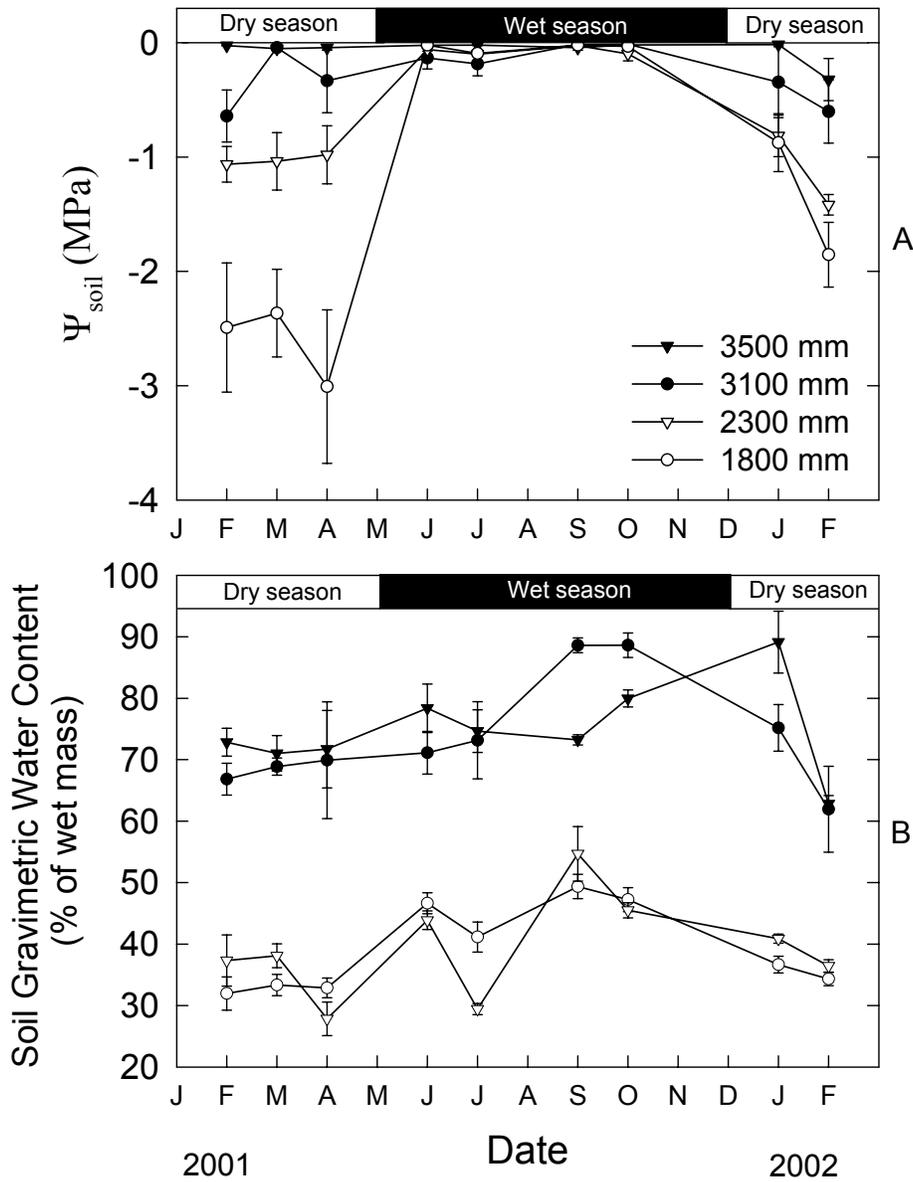


Figure 2-1. Seasonal variation in (A) soil water potential (Ψ_{soil}) and (B) gravimetric water content determined between 15-20 cm depth in four 1-ha lowland tropical forest study plots in Panama. Points represent mean ($\pm 1\text{SE}$) ($n=6$).

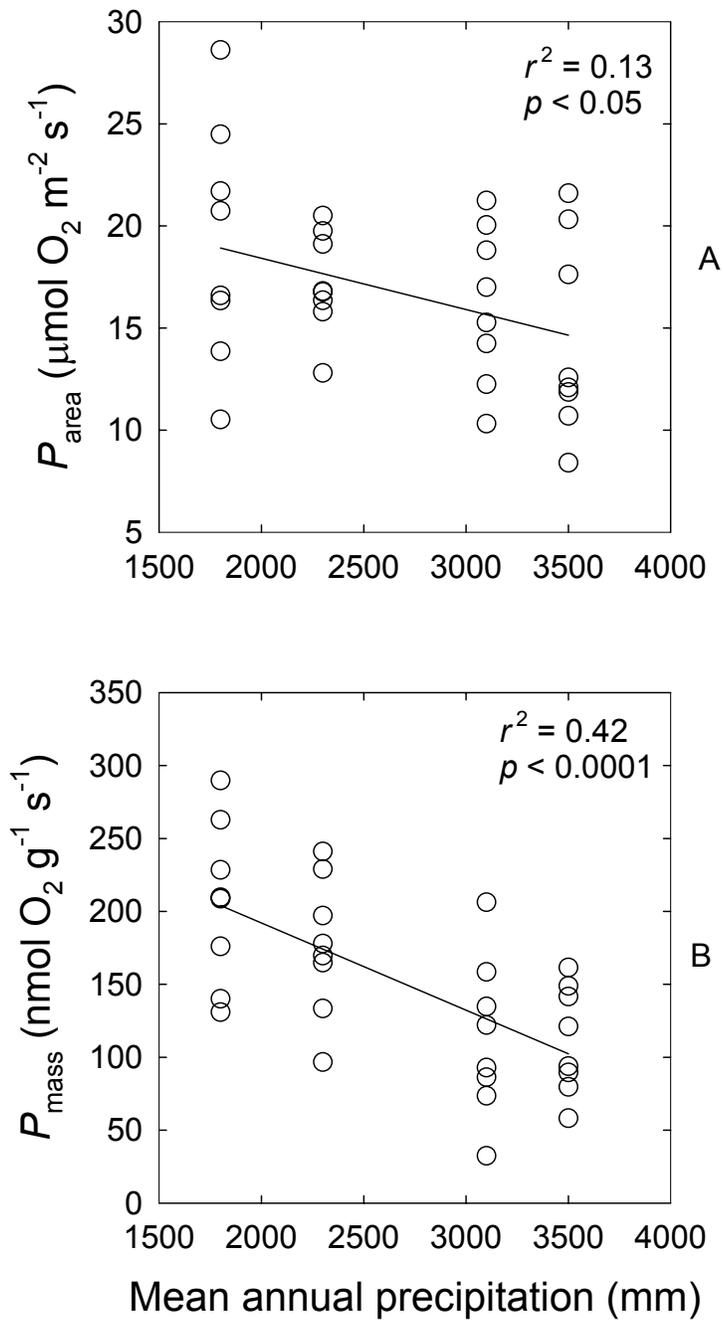


Figure 2-2. Relationship between mean annual precipitation and maximum photosynthetic oxygen evolution rate (A) per unit area (P_{area}) and (B) per unit mass (P_{mass}) for the eight most common canopy species at four sites along a precipitation gradient in lowland Panamanian forest.

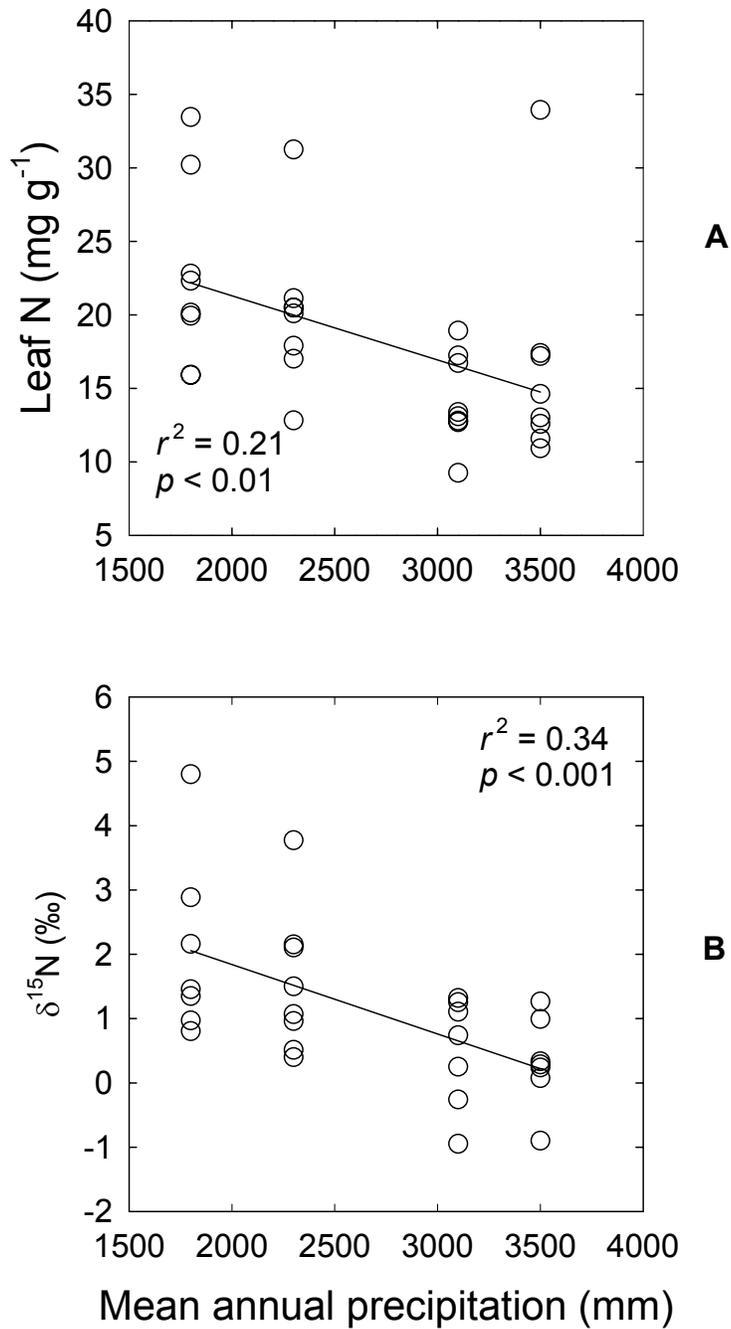


Figure 2-3. Relationship between mean annual precipitation and (A) leaf N concentration per unit mass and (B) N isotopic composition ($\delta^{15}\text{N}$) for the most common canopy species (excluding legumes) at four sites along a precipitation gradient in Panama.

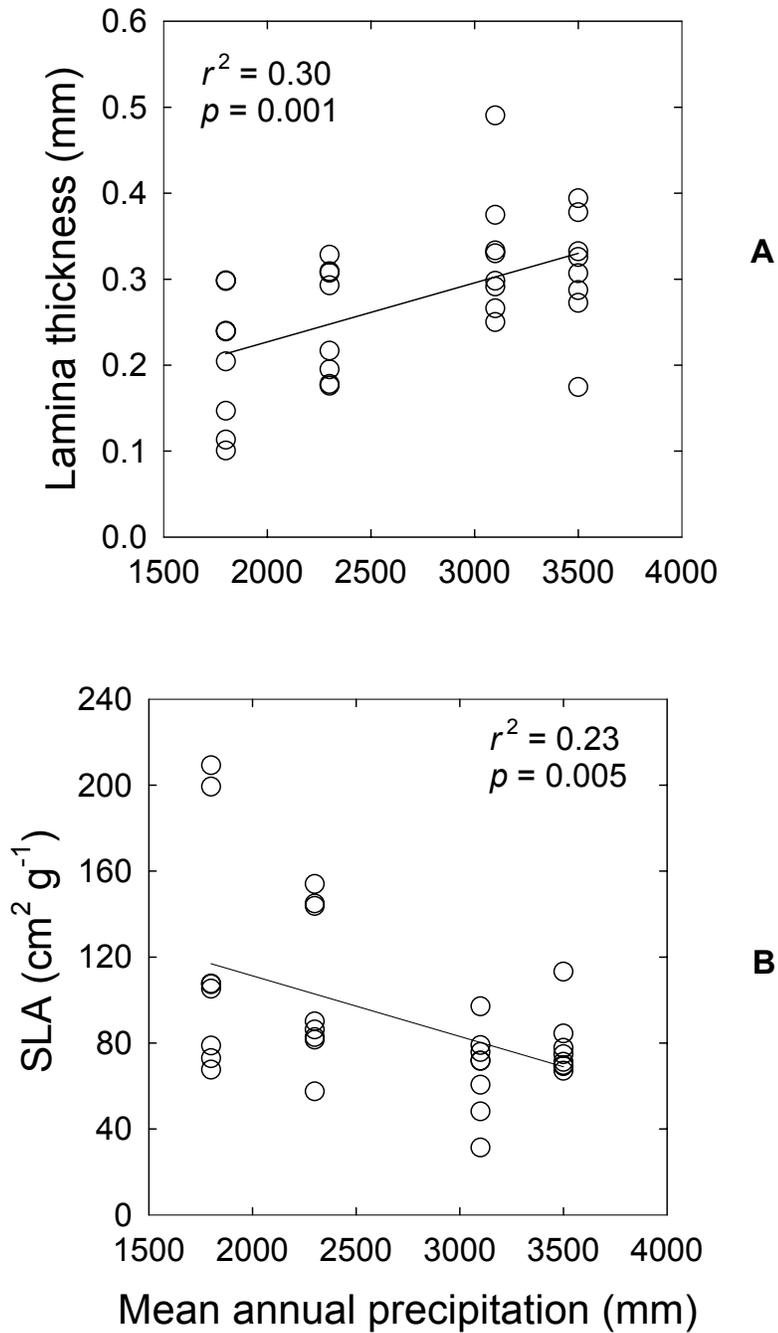


Figure 2-4. Relationship between mean annual precipitation and (A) lamina thickness and (B) specific leaf area (SLA) for the eight most common canopy species at four sites along a precipitation gradient in Panama.

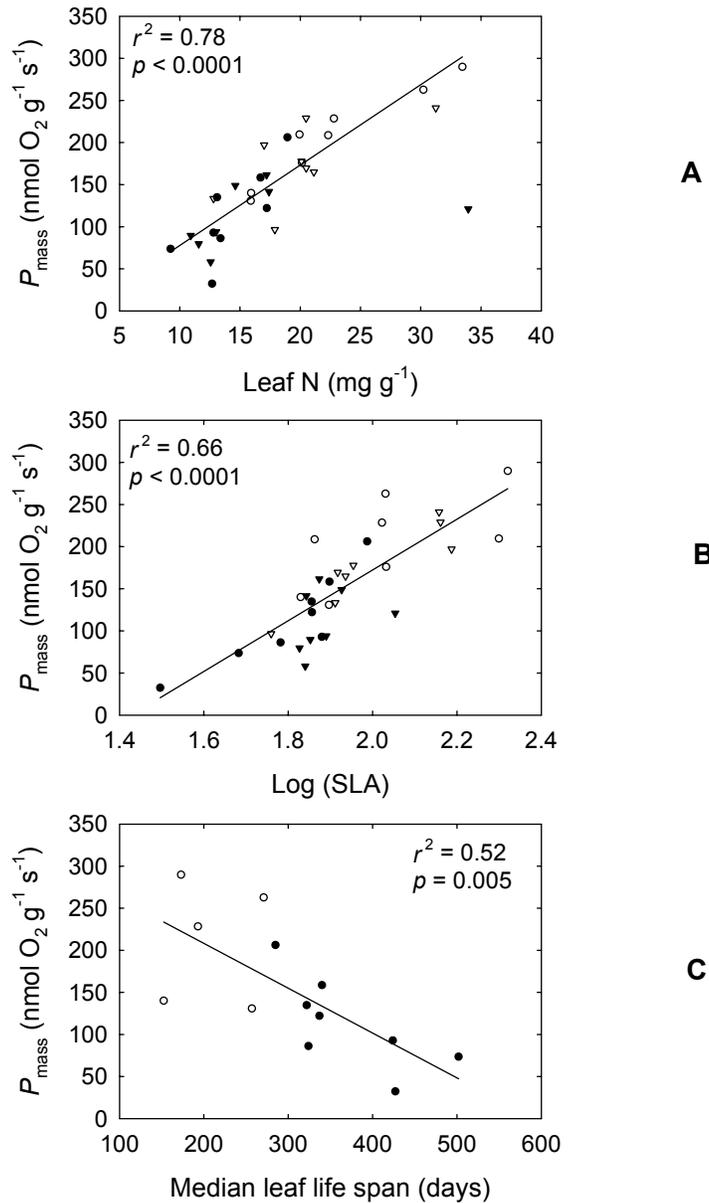


Figure 2-5. Maximum photosynthetic O_2 evolution rate (P_{mass}) as a function of (A) leaf N from study species at the 1800 mm (open circles), 2300 mm (open triangles), 3100 mm (closed circles), and 3500 mm (closed triangles) sites. The outlier from the 3500 mm site (*Zygia ramiflora*) was not included in the regression due to large studentized residuals; $P_{\text{mass}} = 95.56 \cdot (\text{leaf N}) - 17.81$. (B) P_{mass} as a function of log-transformed specific leaf area (SLA); $P_{\text{mass}} = 301 \cdot \log(\text{SLA}) - 429.7$. (C) P_{mass} as a function of median leaf life span for study species at the 1800 mm (open circles) and 3100 mm (closed circles) canopy crane sites $P_{\text{mass}} = 0.53 \cdot (\text{leaf life span}) - 314.93$.

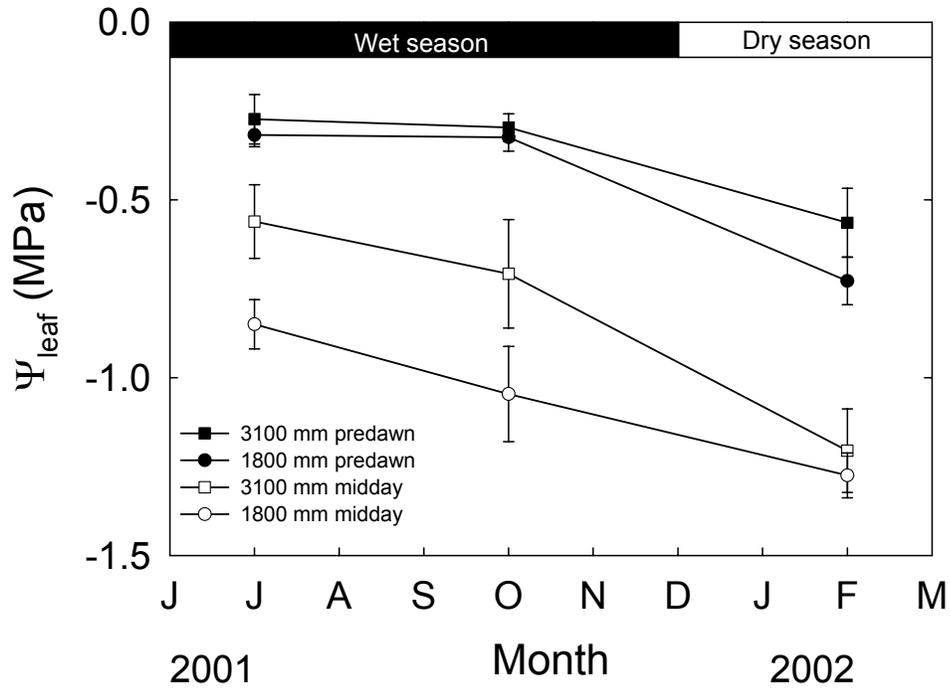


Figure 2-6. Seasonal variation in leaf water potential (Ψ_{leaf}) for canopy trees at two sites with contrasting precipitation in lowland Panama. Each point represents the mean (± 1 SE) of two individuals from 6-8 species at each site.

CHAPTER 3
NUTRIENT CYCLING ON A PRECIPITATION GRADIENT IN LOWLAND
TROPICAL FOREST

Introduction

Water availability has the potential to control components of nutrient cycles, such as nutrient pool sizes and fluxes between pools in terrestrial ecosystems. Water may affect nutrient cycling directly through soil processes such as leaching, weathering and decomposition of organic matter. Water may also influence nutrient cycling indirectly, through effects on plant community composition, since many of the plant characteristics that influence nutrient cycles, such as litter quality and productivity, vary with precipitation. Lowland tropical forest is important in global nutrient cycles and therefore, understanding how nutrient pool sizes and cycling respond to water availability is crucial. Studies of nutrient cycling in humid montane tropical forest (>2000 mm precipitation yr⁻¹) suggest that C pool sizes increase whereas N availability decreases with increasing precipitation (Austin and Vitousek 1998; Schuur et al. 2001; Schuur and Matson 2001). These montane forest studies were conducted in Hawaii, where precipitation may vary while other state factors such as parent material, species composition and temperature remain constant (Vitousek 1995). The purpose of this study is to use a precipitation gradient to sample patterns of nutrient cycling in lowland tropical forests that vary in soil parent material and plant community composition.

As precipitation inputs exceed biological demand, such as in the wet tropics, several key soil processes that influence soil nutrient cycling and storage are likely to

occur. Removal of highly mobile nutrients in the soil solution may occur via leaching, a process that may contribute to reduced nutrient availability under conditions of high water inputs (Radulovich and Sollins 1991; Schuur and Matson 2001). Where poorly drained soils are prevalent, oxygen availability may limit microbial activity that mineralizes N. Several lines of evidence also suggest that water availability may affect soil nutrient pools by weathering soil to produce secondary minerals with a higher surface area and thus higher capacity to adsorb organic matter (Torn et al. 1997). Therefore, water availability has the potential to shape ecosystem nutrient dynamics through effects on the size of soil nutrient pools and the rate at which nutrients become available for plant uptake.

Differences in water availability also result in distinct species assemblages that have the potential to influence nutrient cycling through effects on litter productivity and quality. Species in low resource environments tend to minimize tissue turnover and produce long-lived leaves with high concentrations of carbon-based defenses and slow rates of decomposition (Chapin 1980). In contrast, species from high resource habitats produce relatively short-lived leaves with higher photosynthetic rates and higher N concentrations, resulting in faster decomposition rates (Chapin 1980). The influence of litter quality in determining nutrient availability is thought to increase with actual evapotranspiration (AET) (Meentemeyer 1978). Tropical forest has high AET, so litter quality is expected to have a strong effect on nutrient availability. I present data on nutrient cycling from a precipitation gradient in lowland tropical forest in Panama. Substantial changes in species composition of canopy trees exist along this precipitation gradient (Chapter 2). The objective was to use the precipitation gradient to sample

diversity of leaf phenological patterns across plant communities, which are also affected by soil properties.

Materials and Methods

Study Site

This study was conducted in lowland tropical forest along a rainfall gradient in Central Panama (Chapter 2). Mean annual precipitation (MAP) across these sites varied from 1800 mm yr⁻¹ at the driest site to approximately 3500 mm yr⁻¹ at the wettest site (ACP 2002). 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 were used as study sites (Table 3-1). All sites have a mean monthly precipitation >100 mm during the wet season between May and December, but dry season length (mean number of 30-day periods with <100 mm precipitation) varies between 129 days at the 1800 mm site and 67 days near the 3500 mm site (Condit 1998). Variation in rainfall during the study period (2000-2002) was within 15% of MAP at all sites.

The soils in the Panama Canal forests are generally well-drained and rich in clay, Ca, Mg and N, but poor in K and P relative to other tropical soils (Dietrich et al. 1982; Kursar et al. 1995; Yavitt et al. 1993). All of the study sites lie on volcanic substrate except the 3100 mm site, which lies on sedimentary substrate (Table 3-1). The 1800 mm site is derived from the early to late Oligocene, principally agglomerate, generally andesitic in fine-grained tuff and includes stream-deposited conglomerate (Woodring et al. 1980). Soils of the 2300 and 3500 mm sites are described as derived from altered basaltic and andesitic lavas and tuff, including dioritic and dacitic intrusive rocks. The

3100 mm site is derived from the late Miocene or early Pliocene with massive, generally fine-grained sandstone (Woodring et al. 1980).

Species composition and phenological habit of the most common canopy trees change rapidly across this gradient as species richness increases steeply with mean annual precipitation (Pyke et al. 2001). The dominant canopy tree species in drier forest tend to exhibit shorter leaf life spans and a dry season deciduous leaf phenology (S.J. Wright, unpublished data).

Foliar Chemistry

As part of a larger study on photosynthetic leaf traits of canopy tree species along this precipitation gradient (Chapter 2), the eight canopy tree species at each site with the largest relative proportion of basal area were studied. Young, fully-expanded mature sun leaves were collected from 2-4 individuals for a total of 15 leaves per species from a site. Leaves were collected using canopy cranes maintained by the Smithsonian Tropical Research Institute at the 1800 and 3100 mm sites. At the 2300 and 3500 mm sites, leaves were collected from the upper canopy using a shotgun. Leaf material was dried for 48 h. at 65°C. Leaf samples from the same tree were pooled for chemical analysis. One composite sample from each tree was analyzed for C and N using an elemental analyzer (Model NCS 2500, Carlo Erba, Milano, Italy).

Litterfall Collection and Processing

Litter was collected in 0.25 m² traps randomly located at 20X20-m grid points in each 1 ha plot. Large items, such as palm fronds often fell across traps and only material that fell in the area above the trap was collected. Litter was collected 11 times at intervals ranging from 1 to 12 weeks for the period between February 2001 and February 2002. Litter used in chemical analyses was collected at intervals of 7-10 days in February-June

2001, October 2001, and February 2002. Litter collected at intervals >2 weeks were adjusted for mass loss within traps using decomposition data from the 3100 mm site (Chapter 5), and were not used in chemical analyses. Litter was sorted into four classes: (1) fine woody debris ≤ 1 cm in diameter; (2) leaves; (3) reproductive structures including fruits, flowers and seeds; and (4) other components of litterfall including insects, frass, canopy soil, and items too decomposed to identify. Litter was dried for 48 hours at 65°C and the separate classes were weighed. Entire samples from each site and pickup date were ground in a Wiley mill (mesh size 40) and homogenized. A 120-ml subsample was then retained for further chemical analyses.

Leaf Litter Chemistry

Leaf carbon fraction analyses were performed using a series of increasingly aggressive extractants (Ryan et al. 1989). Dried, ground litter samples were digested in a detergent solution to separate labile cell contents from neutral detergent fiber (NDF), which includes all cell wall components. A dilute acid detergent solution was then used to determine acid detergent fiber (ADF, lignocellulose) before cellulose was separated from lignin and insoluble ash in 72% H₂SO₄. Litter C and N concentrations were determined with an elemental analyzer (Model ECS 4010, Costech, Valencia, CA). Isotopic ratios of C ($\delta^{13}\text{C}$) and N ($\delta^{15}\text{N}$) were determined with a continuous flow isotope ratio mass spectrometer (Model Delta plus XL, Thermo Finnigan, Germany).

Nutrient Availability

Extractable nitrogen and phosphorus

Soil cores were taken at each of the four sites in July 2002, approximately 2 months after the beginning of the 8-month wet season when nutrient availability is expected to be

highest. Six 10 cm deep soil samples were taken with a slide hammer corer at random locations in each 1 ha plot. Samples were returned to the lab and hand sorted to remove roots and rocks, and three subsamples were taken. Weakly sorbed P from the first 10 g subsample was extracted in 50 ml 0.5 M NaHCO₃ (Crews et al. 1995; Miller et al. 2001). Extracts were shaken for one minute and after 24 h a 10-ml sample of the supernatant was removed and frozen until transported to the University of Florida for analysis. I extracted NH₄ and NO₃ from the second 10-g subsample for 24 h in 50 ml 2 M KCl.

Nitrogen mineralization and nitrification

The third 10-g subsample of each core was weighed into a 100-ml sample cup, covered, and allowed to incubate aerobically for 10 days in a dark cabinet at 24°C. After 10 days, incubated samples were extracted in 2M KCl as described above and the difference in NO₃ and NH₄ was recorded as net mineralization (Riley and Vitousek 1995).

Ion exchange resins

Soil nutrient availability was determined with ion exchange resins (Binkley and Matson 1983). Three grams of anion exchange resin (Biorad, AG 1-X8, 20-50 mesh, Cl⁻ form) and the same amount of cation exchange resin (Biorad, AG 50W-X8 20-50 mesh, H⁺ form) were weighed into separate 5X6 cm undyed monopolyester bags (approx. 190 µm mesh size). At each of the four sites, resin bags were placed vertically 4 to 7 cm deep. One anion and one cation resin bag were secured to a plastic stake with monofilament line at 6 random locations in each 1 ha plot. Resin bags were collected from the field after 21 days and rinsed with DI water to remove soil particles. Ions were extracted with 20 ml of 0.5 M HCl and then neutralized with 20 ml of 0.5 M NaOH. PO₄ and NO₃ from anion

extracts and NH_4 , K, Ca and Mg from cation extracts were measured colorimetrically using an autoanalyzer at the University of Florida, Food and Agricultural Sciences Soils Testing Lab to determine nutrient content per bag.

Soil nutrient pools

The remaining sample of each soil core was dried at 50°C for 48 h, and sifted to pass through a 2-mm sieve. Total soil C and N as well as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were analyzed on an elemental analyzer (Model ECS 4010, Costech) connected to a continuous flow isotope ratio mass spectrometer (Model Delta plus XL, Thermo Finnigan, Germany). Bulk density of surface 10 cm was estimated using 5 cm diameter volumetric cores dried at 105°C. Soil moisture was determined gravimetrically on bulk density samples and expressed as grams of water per unit mass of dry soil.

Results

Foliar Chemistry

Foliar N of the eight most common canopy tree species was highest at the 1800 mm site and lowest at the 3100 mm site, showing a general decrease in foliar N as precipitation increases (Table 3-2). In contrast, foliar C values were similar at all sites. Foliar C:N of the eight most common canopy tree species decreased significantly with increasing precipitation ($r^2=0.32$; $P<0.001$), and was largely driven by changes in N.

Litter Production and Chemistry

Total litter production varied from 12.47 $\text{Mg ha}^{-1} \text{ yr}^{-1}$ at the 1800 mm site to 9.80 $\text{Mg ha}^{-1} \text{ yr}^{-1}$ at the 3500 mm site. Fine woody litterfall represented 11-17% of total litter and was about 20% higher at the two wetter sites (Table 3-3). Leaf litter represented 60-75% of total litter and was 45% higher at the 1800 mm site than the other three sites (Table 3-3). Reproductive structures comprised 7-15% of total litter fall and showed no

clear pattern with precipitation (Table 3-3). Other litter components were 5-9% of total litter production (Table 3-3). Litterfall rates were seasonal with more litter falling during the dry season, and seasonal differences between maximum and minimum litterfall rates decreased with increasing precipitation (Figure 3-1).

There was significant variation in mean litter N concentration of leaf litter with precipitation ($F=5.07$; $P<0.05$) and values tended to increase with increasing precipitation (Table 3-3). There was also significant variation in litter $\delta^{15}\text{N}$ among sites with different soil parent material (Table 3-3; $F=28.05$; $P<0.0001$), but values did not vary in any predictable manner with precipitation. Litter $\delta^{13}\text{C}$ decreased linearly with increasing precipitation indicating greater integrated water use efficiency of leaves in drier forest (Figure 3-2). Litter C increased ($F=33.01$; $P<0.0001$) with increasing precipitation and may be related to variation in litter lignin concentration among sites (Table 3-3; $F=11.76$; $P<0.001$). Litter lignin:N significantly increased with increasing precipitation ($F=3.74$; $P<0.05$) whereas cellulose concentration showed no significant variation with precipitation (Table 3-3).

Nutrient Availability

Extractable nitrogen and phosphorus

Extractable P was significantly higher at the driest site than at the three wetter sites (Table 3-4; $F=3.50$; $P<0.05$). Extractable NO_3 was significantly higher at the wettest site than at the three drier sites (Table 3-4; $F=4.80$; $P<0.05$). Extractable NH_4 , net N mineralization and nitrification showed no clear pattern with precipitation (Table 3-4), but N mineralization decreased linearly with increasing litter lignin:N (Figure 3-3) indicating an effect of litter quality on N availability.

Ion exchange resins

Resin exchangeable NO_3 was about 420% higher at the two sites on pre-tertiary basalt (2300 and 3500 mm sites) compared to the other two sites (Table 3-4; $F=5.81$, $P<0.01$). There were no clear patterns in exchangeable NH_4 or K, but exchangeable Ca decreased 76% from the driest to wettest sites (Table 3-4; $F=11.75$; $P<0.0005$) and measurable quantities of exchangeable Mg were only detected at the driest site (Table 3-4).

Soil nutrient pools

Total soil N and C pools of the top 10 cm were higher at the two wetter sites than at the two drier sites (Table 3-5). Soil N showed an exponential increase in relation to litter lignin concentration (Figure 3-4A) and a strong linear increase in relation to litter lignin:N (Figure 3-4B) suggesting that lignin-bound proteins in the soil organic matter matrix comprise a large part of the total soil N pool. Soil $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were more enriched than litter inputs, possibly due to faster turnover of lighter isotopes (Figure 3-2; Table 3-5) (Nadelhoffer and Fry 1988). Soil bulk density decreased with increasing precipitation (Table 3-6).

Discussion

Foliar Chemistry

Our results suggest that patterns of foliar C per unit N reflect changes in species composition across this precipitation gradient. Decreasing foliar N of canopy species may reflect increased allocation of carbon-based leaf defenses to canopy leaves in association with longer leaf life spans in wetter forest. Decreasing foliar N with increasing precipitation does not appear to be caused by reduced N availability with increasing precipitation as has been observed on rainfall gradients in Hawaii given that soil N

availability did not decrease with increasing precipitation. This pattern, whether driven by photosynthetic or anti-herbivore allocation patterns, may provide an important feedback to nutrient availability by affecting litter quality since litter C:N is negatively correlated with decomposition rate (Chapter 5).

Litter Production and Chemistry

Patterns of litterfall suggest that the driest site may be slightly more productive than wetter forests. The primary differences are greater leaf litter production and stronger seasonality from the 1800 mm site, which has the highest proportion of dry season deciduous tree species. Therefore increased leaf litter production at the driest site may be the result of increased leaf turnover. However, in order to understand the extent to which productivity is regulated by water availability, other components of productivity such as root growth, trunk growth and respiration need to be incorporated. Nonetheless, litterfall is often the greatest fraction of productivity (Clark et al. 2001a). Several recent studies have also revealed that productivity in humid tropical forest may actually decline at high annual precipitation (>2500 mm) (Clark et al. 2001b; Schuur and Matson 2001). Therefore, assuming that all sites are at steady state, the result reported here is consistent with reduced ecosystem productivity at extremely high precipitation in the tropics due to light or nutrient limitation (Schuur and Matson 2001).

The reduction in leaf litter quality with increasing precipitation suggests that nutrient mineralization slows with increasing precipitation. Because fine root litter quality may respond similarly to leaves (Ostertag 2001), belowground litter may contribute to reduced nutrient mineralization in sites with lower litter quality (Figure 3-3). Decomposition rates at the 3100 mm site decrease substantially with increases in litter lignin:N ($r^2=0.38$; $P<0.05$; Chapter 5). Changes in litter lignin and lignin:N suggest that

compound specific changes in litter quality may be important across this gradient. The increase in lignin suggests that a higher proportion of litter will enter directly into the slow decomposing pool or organic matter (Vitousek et al. 1994). This is a potential explanation for the increase in soil C and N storage with increasing precipitation and decreasing litter quality.

Nutrient Availability

The availability of P, Ca and Mg varied in relation to precipitation, whereas N appeared more responsive to parent material. Decreasing available P, Ca and Mg with increasing precipitation is consistent with the observation that weathering can leach these elements from the soil profile and reduce availability to plants. Relatively high P availability at the 1800 mm site may contribute to higher litterfall productivity, since P is often considered to be the most limiting nutrient in lowland tropical forest, and both P availability and litterfall productivity are highest at the 1800 mm site and relatively low at all other sites. However, litterfall is extremely variable and measurements over several years are needed to determine if this trend is robust.

In contrast to P, N appeared to be under stronger regulation of parent material with both sites on tertiary basalt exhibiting high exchangeable NO_3^- . Both Austin and Vitousek (1998) and Schuur and Matson (2001) found decreasing N availability with increasing precipitation in Hawaiian montane forests in sites with consistent parent material. Our results suggest that parent material may alter the relationship between precipitation and N availability in tropical forest.

The results of increasing total soil N and C with increasing precipitation support the notion that soil organic matter increases with increasing precipitation in humid forest (Schuur et al. 2001). Soil N pools in this part of Panama are high relative to both

temperate and montane tropical forest (Austin and Vitousek 1998; Schuur and Matson 2001; Vitousek and Sanford 1986). The increases in soil N and C pools with increasing litter lignin and litter lignin:N suggest that lower quality litter may function to increase soil organic matter accumulation. Since soil waterlogging appears to be of minimal importance in these study sites, the observed increase in soil organic matter with increased precipitation may reflect an indirect effect of precipitation on species composition with more evergreen species producing lower quality litter as precipitation increases.

Total soil N increases as a function of litter lignin:N, whereas soil N mineralization rates decrease with increasing litter lignin:N (Figure 3-3) (Scott and Binkley 1997). Therefore, as lignin:N increases, it appears that a higher proportion of soil N is tightly held in the organic matter matrix and the mineralization rate of that N is slower. Lower litter quality may function as an N conservation mechanism to prevent N losses through leaching by decreasing the rate of organic N reactivity.

Conclusions

Overall, the results suggest that variation in plant community composition along this precipitation gradient can have substantial effects on soil nutrient pools and on how nutrients are cycled by vegetation. Several general patterns, such as decreasing litter quality and decreasing soil availability of PO_4 , Ca and Mg with increasing precipitation appear to corroborate patterns described for island ecosystems. Despite the diversity of soil substrates and plant community compositional changes across even short distances in Panama, there appear to be some patterns of C and N cycling and accumulation that are consistent with previous findings in Hawaiian ecosystems, where greater control over soil and species has generated theoretical predictions. Clearly, reduced litter quality and

increased soil nutrient pools with increasing precipitation, which I have shown to be related, are two components of nutrient cycling that vary similarly in Panamanian lowland forest and Hawaiian montane forest. However, other patterns of N cycling are more strongly related to soil parent material than precipitation, making some predictions developed in relatively homogeneous island systems more difficult to apply in more heterogeneous landscapes. Further studies in lowland continental tropical forest are likely to contribute to our understanding of nutrient cycling in humid ecosystems and dispel myths or corroborate patterns observed in model island systems.

Table 3-1. Characteristics of sites along precipitation gradient across the Isthmus of Panama.

Site	CTFS plot code ^a	Mean annual precipitation (mm)	Parent material ^b	Order	Suborder
Parque Metropolitano	PM	1800	<i>Panama formation</i>	<i>Ultisol</i>	<i>Ustult</i>
Pipeline Road	8	2300	<i>Pre-Tertiary basalt</i>	<i>Ultisol</i>	<i>Humult</i>
Fort Sherman	S3	3100	<i>Chagres Sandstone</i>	<i>Histosol</i>	<i>Saprist</i>
Santa Rita	31	3500	<i>Pre-Tertiary basalt</i>	<i>Ultisol</i>	<i>Humult</i>

^aPike et al. (2001)

^bWoodring et al. (1980)

Table 3-2. Percentage of N and C in canopy sun leaves from the eight most common canopy tree species across a precipitation gradient in lowland forest in Panama (Chapter 2). Values are means \pm 1 SE. ($n=8$)

Site	Foliar N (%)	Foliar C (%)
1800 mm	2.26 ^a \pm 0.24	49.02 ^a \pm 0.83
2300 mm	2.01 ^{ab} \pm 0.20	47.72 ^a \pm 1.57
3100 mm	1.43 ^b \pm 0.12	49.24 ^a \pm 1.10
3500 mm	1.64 ^{ab} \pm 0.28	49.42 ^a \pm 1.08

Table 3-3. Litterfall rates separated by component for the year between February 2001-February 2002 and litter quality of leaf litterfall from 4 sites along a precipitation gradient in lowland Panamanian forest. Values for leaf litter quality are means \pm 1 SE ($n=4$).

	Site			
	1800 mm	2300 mm	3100 mm	3500 mm
Litterfall (Mg ha⁻¹ yr⁻¹)				
Fine woody debris	1.37	1.37	1.65	1.58
Leaf	9.47	6.33	6.45	6.74
Reproductive structures	0.94	1.40	1.79	0.64
Other	0.69	0.93	0.62	0.83
Total	12.47	10.03	10.51	9.79
Litter chemistry				
N (%)	0.96 ^a \pm 0.04	1.34 ^b \pm 0.06	1.13 ^{ab} \pm 0.06	1.28 ^b \pm 0.09
$\delta^{15}\text{N}$ (‰)	-0.46 ^a \pm 0.24	1.24 ^b \pm 0.09	0.25 ^c \pm 0.10	1.23 ^b \pm 0.06
C (%)	39.7 ^a \pm 0.6	44.3 ^b \pm 0.5	47.1 ^c \pm 0.3	45.5 ^{bc} \pm 0.5
Lignin (%)	15.4 ^a \pm 1.9	20.9 ^b \pm 1.6	23.8 ^b \pm 1.6	23.7 ^b \pm 1.2
Lignin:N	16.0 ^a \pm 1.5	16.0 ^a \pm 0.9	21.1 ^b \pm 2.0	18.5 ^{ab} \pm 1.7
Cellulose (%)	20.0 ^a \pm 0.7	18.4 ^a \pm 2.5	22.6 ^a \pm 1.8	21.6 ^a \pm 1.2

Table 3-4. Soil chemistry to a depth of 10 cm. Values with different letters are significantly different at a *P*-value of 0.1.

	Site			
	1800 mm	2300 mm	3100 mm	3500 mm
Extractable nutrients (mg kg ⁻¹)				
P	5.26 ^a ± 0.78	3.21 ^b ± 0.53	2.85 ^b ± 0.77	3.33 ^b ± 0.36
NO ₃	0.07 ^a ± 0.08	0.73 ^a ± 0.61	0.23 ^a ± 0.25	3.73 ^b ± 1.59
NH ₄	2.73 ^a ± 1.19	2.95 ^a ± 0.28	3.91 ^a ± 0.40	4.73 ^a ± 0.85
Net N nitrification (mg kg ⁻¹ d ⁻¹)	0.71 ^a ± 0.20	1.13 ^a ± 0.21	0.57 ^a ± 0.20	0.94 ^a ± 0.43
Net N mineralization (mg kg ⁻¹ d ⁻¹)	0.74 ^a ± 0.18	1.17 ^a ± 0.17	0.35 ^b ± 0.15	0.74 ^a ± 0.38
Exchangeable nutrients (mg kg resin ⁻¹ 21 d ⁻¹)				
NO ₃	2.34 ^a ± 1.46	14.75 ^b ± 1.80	3.82 ^a ± 2.10	17.4 ^b ± 5.20
NH ₄	0.47 ^a ± 0.08	0.55 ^a ± 0.10	0.50 ^a ± 0.02	0.54 ^a ± 0.01
PO ₄	8.01 ^a ± 2.01	0.30 ^b ± 0.10	0.33 ^b ± 0.04	0.10 ^b ± 0.03
K	671 ^a ± 67	491 ^b ± 13	470 ^b ± 14	570 ^{ab} ± 33
Ca	41.11 ^a ± 8.45	21.96 ^b ± 5.57	3.38 ^c ± 0.93	9.93 ^{bc} ± 0.41
Mg	3.56 ^a ± 1.74	< 0.01 ^b	< 0.01 ^b	< 0.01 ^b

Table 3-5. Bulk soil chemistry from the surface 10 cm of soil. Values with a different letters are significantly different ($P < 0.05$; $n=6$)

Site	Total C (g/kg)	Total N (g/kg)	Bulk $\delta^{15}\text{N}$ (‰)
	$\bar{X} \pm 1 \text{ SE}$	$\bar{X} \pm 1 \text{ SE}$	$\bar{X} \pm 1 \text{ SE}$
1800 mm	25.21 ^a \pm 2.79	2.86 ^a \pm 0.81	2.99 ^a \pm 0.61
2300 mm	28.60 ^{ab} \pm 3.12	2.73 ^a \pm 0.17	6.57 ^b \pm 0.58
3100 mm	70.66 ^c \pm 5.40	5.25 ^b \pm 0.45	4.06 ^c \pm 0.64
3500 mm	39.57 ^b \pm 4.76	3.90 ^{ab} \pm 0.36	5.67 ^d \pm 0.72

Table 3-6. Soil bulk density and water content in the surface 10 cm of soil. Values are means ($\pm 1 \text{ SE}$) of averages measured using 6 samples per site during the early wet season of 2002.

Site	Soil bulk density (g cm^{-3})	Water content (g g^{-1})
1800 mm	0.92 \pm 0.02	0.53 \pm 0.02
2300 mm	0.73 \pm 0.03	0.58 \pm .001
3100 mm	0.51 \pm 0.02	0.82 \pm 0.02
3500 mm	0.60 \pm 0.02	0.98 \pm .006

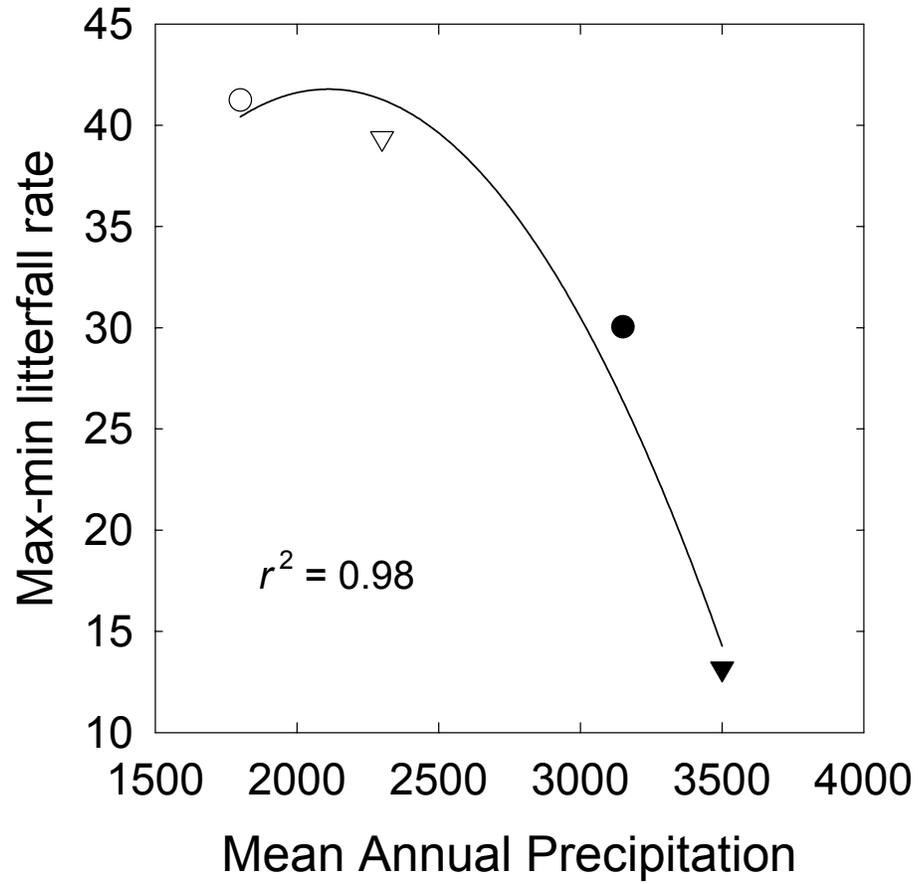


Figure 3-1. The difference between seasonal maximum and minimum litterfall rates as a function of mean annual precipitation for four forest sites along a precipitation gradient in lowland Panama. Values are means ($n=11$).

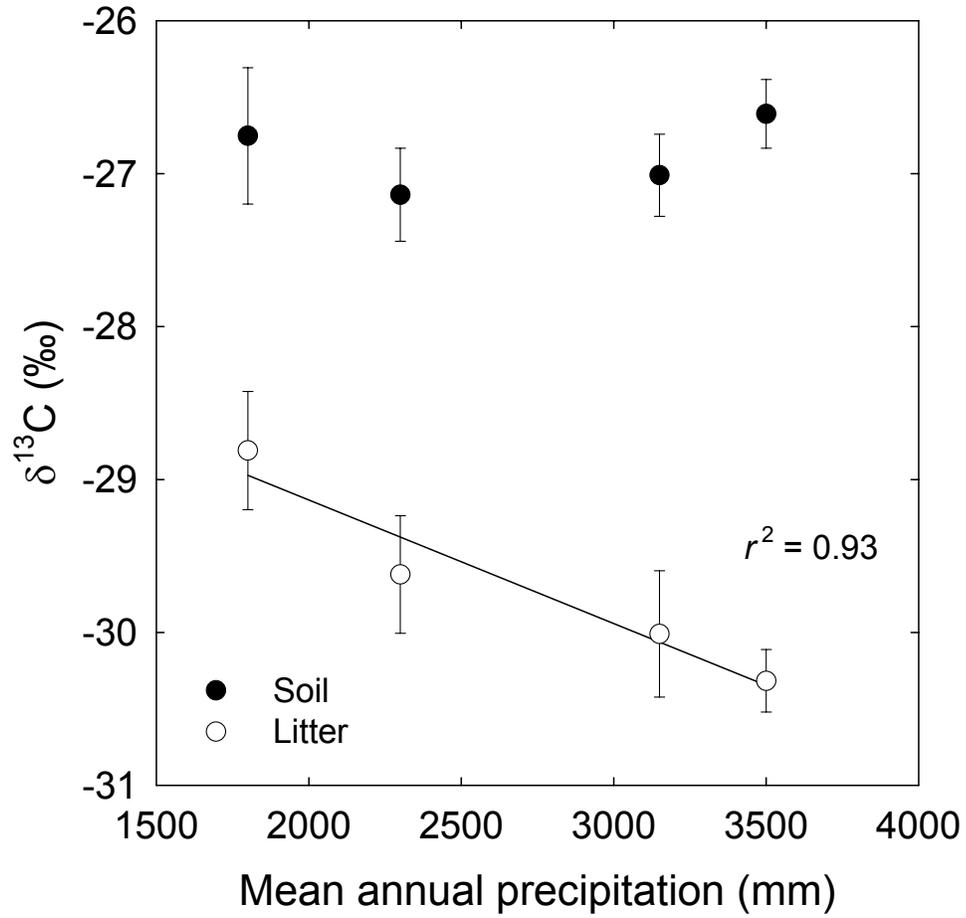


Figure 3-2. Relationship between carbon isotope composition of soil ($n=6$) and litter ($n=4$) for four 1 ha forest plots along precipitation gradient in lowland Panama. Values are means ± 1 SE.

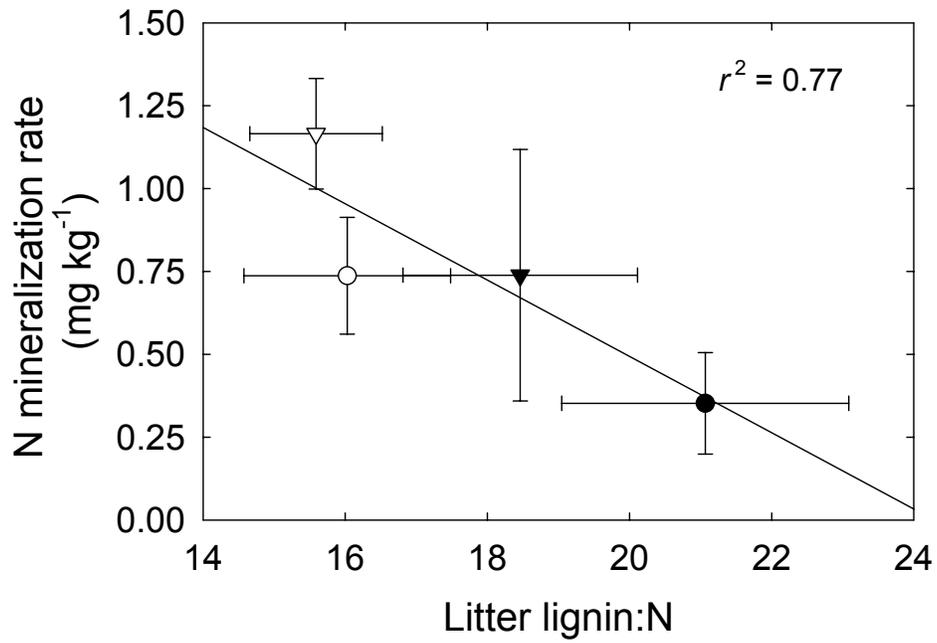


Figure 3-3. Soil N mineralization rates for the top 10 cm ($n=6$) as a function of litter lignin to N ratio ($n=4$) for four forest sites in lowland Panama that vary in mean annual precipitation: 1800 mm (open circle); 2300 mm (open triangle); 3100 mm (closed circle); 3500 mm (closed triangle). Values are means \pm 1 SE.

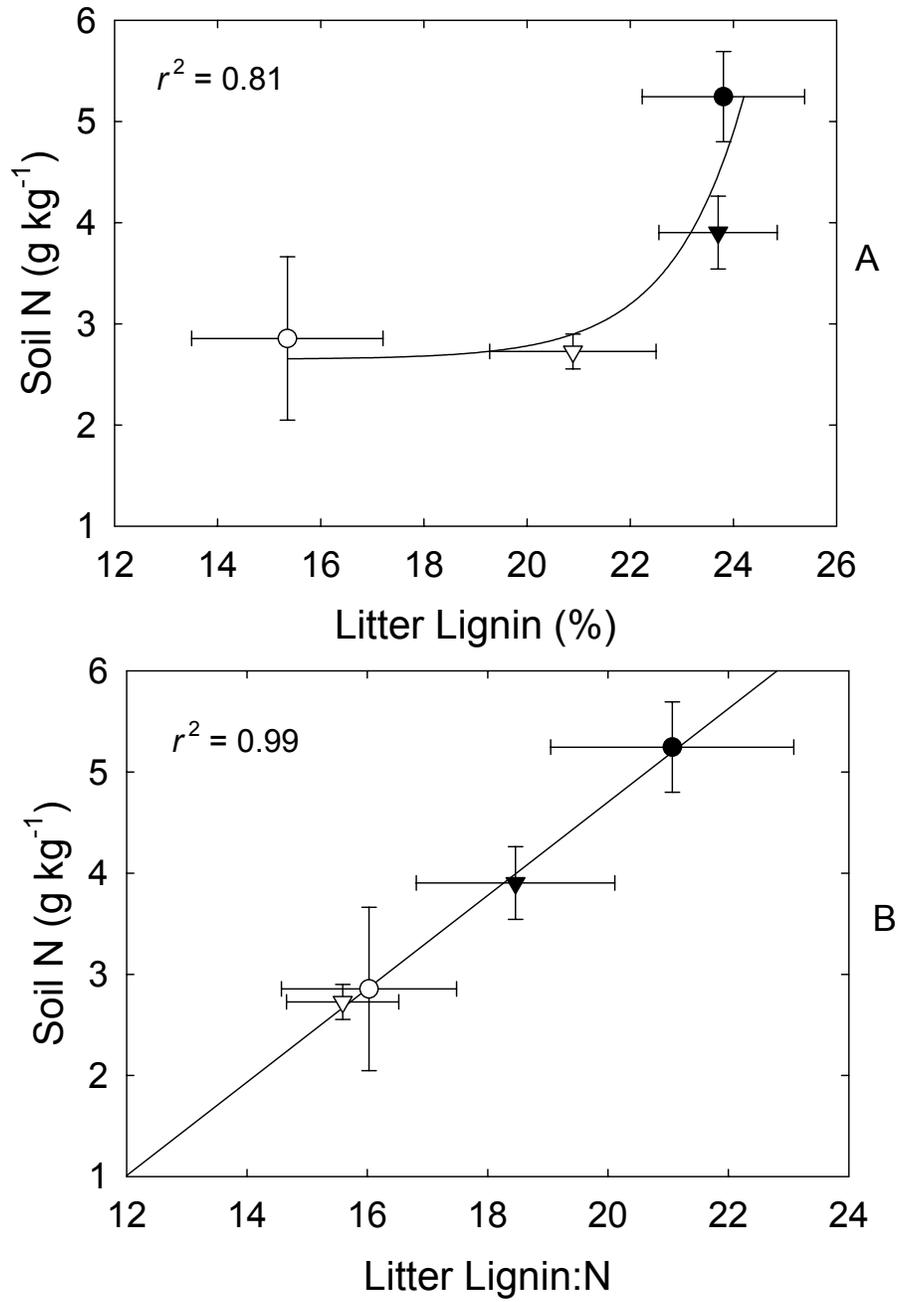


Figure 3-4. Soil N concentration as a function of (A) litter lignin and (B) litter lignin to N ratio for four forest study sites in lowland Panama. Values are means \pm 1 SE. Symbols as in Figure 3-3.

CHAPTER 4
HYDRAULIC CONDUCTIVITY AND WOOD DENSITY SCALE WITH LEAF
PHOTOSYNTHETIC TRAITS IN PANAMANIAN FOREST CANOPY TREES

Introduction

Species often exhibit substantial variation in rates of carbon gain and resource use. In species-rich tropical forests, the extent to which observed patterns of resource utilization and carbon gain are species-specific is uncertain. Results of recent studies point to substantial convergence in plant functioning among species from diverse biomes (Reich et al. 1997). For example, maximum photosynthetic rates, stomatal conductance, and leaf surface area per unit mass (specific leaf area; SLA) are positively correlated and tend to decrease with increasing leaf life span across a wide array of study sites and angiosperm taxa (Ackerly and Reich 1999; Reich et al. 1999; Reich et al. 1997). However, within sites, variation in photosynthetic rate and leaf life span is as great or greater than variation in mean differences among biomes (Reich et al. 1999). Understanding hydraulic properties of the branch or whole plant scale may explain additional within-site variation in leaf characteristics among individuals and species (Meinzer and Goldstein 1996).

Convergence in regulation of carbon economy at the leaf level may also be related to the life history features of a species. Photosynthesis, SLA, and leaf nitrogen concentration are generally related to rapid growth, high allocation to photosynthetic tissue, early attainment of reproductive age, and regeneration in high resource habitats (Cornelissen et al. 1997; Poorter and Remkes 1990; Reich et al. 1992; Wright and

Westoby 1999). In addition, leaf photosynthetic traits are correlated with many of the same whole-organism traits that can be predicted by plant hydraulic conductance. Interspecific variation in leaf physiology may be related to xylem hydraulic properties, because stomatal conductance, a leaf area-based property, is often closely coordinated with the apparent hydraulic conductance of the soil-to-leaf pathway (Andrade et al. 1998; Küppers 1984; Meinzer and Grantz 1990; Sperry and Pockman 1993). Recent studies have suggested that allometric scaling of plant vascular systems is universal and thus reflects convergence among many species to overcome similar physical limitations of long-distance water transport (Enquist et al. 1998; Meinzer 2003; West et al. 1999). Furthermore, similar relationships in the scaling of plant transpiration and animal metabolism suggest that both share common scaling laws that reflect how resource requirements of organisms affect distribution in ecological communities (Enquist et al. 1998). Since photosynthesis is the sole mechanism of carbon assimilation in most vascular plants, and water is likely to limit photosynthesis at some time scale in most terrestrial environments, I expect coordination between photosynthetic capacity and plant hydraulic properties. Therefore, measurements of plant hydraulic properties may be related to other plant processes such as nutrient use and gross photosynthesis, thus integrating leaf level processes into a more complete understanding of whole-plant function.

This study was designed to examine the allometry of branch hydraulic architecture, xylem biophysical properties and suites of leaf photosynthetic traits among 20 species of canopy trees growing in two Panamanian lowland forests. The primary objective was to determine the extent to which variation in leaf area-based hydraulic properties and xylem

biophysical properties can explain variation in leaf gas exchange characteristics. Specific questions included: 1) Does allocation to leaf photosynthetic capacity correspond to capacity for hydraulic water supply? 2) Is hydraulic conductivity correlated with physiological leaf traits such as life span, nitrogen concentration and water use efficiency? 3) Does wood density constrain hydraulic conductivity to affect leaf gas exchange? 4) Can photosynthetic traits be predicted from xylem biophysical properties?

Materials and Methods

Study Site and Species

The study was conducted from two canopy cranes operated by the Smithsonian Tropical Research Institute (STRI) in the Republic of Panama. Each crane is equipped with a gondola suspended by cables from a rotating boom that allows coverage of approximately 0.82 ha of forest. One crane is located in Parque Metropolitano, a secondary dry forest on the edge of Panama City that receives approximately 1800 mm of precipitation annually with a distinct dry season between December and April (Condit 1998). The other crane is located in an old-growth forest at Fort Sherman on the Caribbean side of the Panamanian Isthmus where mean annual precipitation is 3100 mm and the dry season is shorter and less intense than at Parque Metropolitano. During the dry season of 2002 (Feb-Mar), physiological and morphological characteristics in the upper crown of one to four individuals of 20 canopy tree species were measured. Both rare and common species were included in the study (Table 4-1). I measured at least five sun-exposed terminal branches in all species. In rare species with only one individual at the study site, sample branches were taken from different portions of the crown.

Gas Exchange Measurements

Maximum rates of net CO₂ assimilation (A) and stomatal conductance (g_s) were measured with a portable photosynthesis system (Model 6400, Li-Cor, Inc., Lincoln, NE, USA) between 0700 and 1100 h. Two to four newly formed mature leaves per branch were measured at 400 $\mu\text{mol CO}_2$, and 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD) provided by a red blue light source (model 6400-02B #SI-710, Li-Cor, Inc.). Only gas exchange values measured at a leaf to air vapor pressure deficit (VPD_l) below 1.5 kPa were used because significant stomatal closure above this value was observed.

Hydraulic Conductivity

Hydraulic conductivity (k_h) was measured on twigs excised from 1.0-1.5-m- long branches. Branches were longer than the measured maximum vessel length determined by the air pressure technique (Ewers and Fisher 1989). Upper crown branches exposed to full sun were cut directly after gas exchange measurements on days with similar environmental conditions and transported to the laboratory. In the laboratory, the first fully developed twigs supporting the leaves on which gas exchange was measured were excised from the rest of the branch under filtered water (0.2 μm) to prevent xylem embolism. After removing 3 to 4 mm of bark from each end, the cut ends were shaved with Teflon coated razor blades and connected to the hydraulic conductivity apparatus (Sperry et al. 1988). Pith areas were plugged with plasticine when necessary. The hydraulic conductivity apparatus consisted of a beaker supplying filtered (0.2 μm) water under low (1.4 kPa) gravitational pressure to the stem. A low hydraulic head insured no embolisms were removed and the apparatus was frequently flushed with 10% bleach

solution to avoid microbial growth. Flow rates were determined volumetrically 5-15 minutes after connection when they became steady. Initial k_h was estimated as the rate of water flux (J , mmol s^{-1}) in a stem when a pressure gradient (dP/dx , MPa m^{-1}) was applied across the stem

$$k_h = J / (dP/dx). \quad (4-1)$$

Maximum k_h was measured after a 20-min high-pressure flush from a captive air tank when flow rates reached steady values. After hydraulic measurements, stem length, xylem diameter and pith diameter were measured for the calculation of k_h and specific conductivity (k_s), k_h per unit xylem area. Leaf area distal to the branch segment where k_h was measured was recorded with a leaf area meter (model LI-3100, Li-Cor Inc.), and used to calculate leaf specific conductivity (LSC), k_h per unit leaf area.

Wood Density

After conductivity measurements, outer bark, phloem and pith were removed from sample stems, wet mass was determined and stems were dried for 48 h at 65°C and weighed to determine the saturated water content (SWC). Wood density was measured as the ratio of xylem dry mass to xylem volume. Percent loss of conductivity (PLC) was calculated from the ratio of initial to maximum k_h .

Foliar Analysis

After measurement of their area, gas exchange leaves were dried for 48 h at 65°C and weighed for the determination of specific leaf area (SLA; $\text{cm}^2 \text{g}^{-1}$) so that photosynthesis could be calculated both on a unit leaf area and leaf mass basis. Leaves were ground in a Wiley mill and one composite sample per branch was analyzed for total leaf nitrogen and carbon isotope discrimination ($\delta^{13}\text{C}$) on an elemental analyzer

connected to a continuous flow mass spectrometer at the University of Idaho. This allowed us to express photosynthesis per unit leaf nitrogen (A_N) and to evaluate intrinsic water use efficiency estimated by discrimination against ^{13}C (Farquhar and Richards 1984).

Results

There were significant positive relationships between mean species A_{area} and stomatal conductance (g_s) when plotted against leaf specific hydraulic conductance (LSC; Figure 4-1). A_{area} and g_s showed substantial increases with increasing initial ($\text{LSC}_{\text{initial}}$) and maximum (LSC_{max}) measurements, but LSC_{max} was a much stronger predictor (Figure 4-1) suggesting that plants allocate photosynthetic capacity proportionally to the maximum operational capacity of the xylem. There were also significant positive relationships between A_{area} and specific conductivity (k_s). When A_{area} was regressed against initial and maximum k_s , the relationships were again stronger with maximum than initial conductance ($r^2=0.22$; $P<0.05$ and $r^2=0.39$; $P<0.005$, respectively), consistent with the pattern observed in LSC.

Leaf nitrogen per unit area (N_{area}) varied independently of LSC_{max} (Figure 4-2). However, photosynthesis per unit N (A_N) increased significantly with increasing LSC_{max} suggesting that hydraulic constraints limit the instantaneous efficiency with which N appears to be used (Fig 4-2). Median leaf life span was negatively related to LSC_{max} suggesting that there is an evolutionary tradeoff between long-lived leaves and high LSC ($r^2=0.24$; $P<0.1$) similar to the functional relationship between leaf photosynthetic capacity and leaf life span (Reich et al. 1992). Leaf carbon isotope discrimination ($\delta^{13}\text{C}$), a measure of intrinsic water use efficiency was not significantly related to $\text{LSC}_{\text{initial}}$

($r^2=0.00$; $P=0.86$) or LSC_{max} ($r^2=0.00$; $P=0.78$) when measurement branches were averaged per species. However, instantaneous water use efficiency (A_{area}/g_s) declined with increasing LSC_{max} , indicating a tradeoff between hydraulic conductivity and water loss per unit carbon gain (Figure 4-2).

Relationships between wood density and photosynthetic and hydraulic characteristics generally showed negative correlations. Stem saturated water content (SWC) was negatively correlated with wood density demonstrating a possible tradeoff between sapwood water storage and mechanical strength (Figure 4-3). LSC_{max} was negatively related to wood density suggesting that high LSC can be achieved by producing larger vessels or higher vessel density at the expense of having lighter wood with potentially reduced mechanical strength (Figure 4-3). Both A_{area} (Figure 4-3) and A_{mass} ($r^2=0.50$; $P<0.001$) were negatively correlated with wood density; thus wood density appears to be negatively related to photosynthetic capacity through its effect on hydraulic conductance per unit leaf area.

Discussion

The results suggest that plant traits regulating photosynthetic and hydraulic capacity are highly interdependent. Leaf specific hydraulic conductivity (LSC) varied proportionally with photosynthetic CO_2 assimilation (A) and this relationship is consistent within a group of canopy trees in Panamanian lowland forest. Additionally, it appears that tradeoffs in relation to wood density and leaf life span allow diversity of allocation patterns among coexisting species in the plant community. For example, species with low photosynthetic and hydraulic capacity exhibited longer leaf life spans, potentially minimizing the nutrient cost of leaf replacement (Chapin 1980). Species with lower photosynthetic and hydraulic capacity also have denser wood, which may be a result of

smaller diameter vessels that constrain maximum xylem conductance but also allow increased biomechanical support and an increased xylem pressure threshold (Hacke et al. 2001). Furthermore, species with lower photosynthetic and hydraulic capacity show evidence of higher water use efficiency, thus tradeoffs result in several solutions to balancing carbon gain with water loss. These results indicate that understanding xylem hydraulic capacity adds information to leaf level measurements when comparing species and links photosynthetic allocation patterns with processes at the branch and whole organism levels of organization.

The relationship between photosynthesis and hydraulic conductance reflects a balance between carbon gain and water loss, thus the primary feature regulated by LSC is probably stomatal conductance (g_s), and therefore transpiration. Species usually have specific operating ranges or minimum values of leaf water potential governed by stomatal regulation (Meinzer and Grantz 1991). Thus, if LSC increases as a result of partial defoliation or leaf shading, g_s usually increases, but leaf water potential remains about the same because the transpiration/LSC relationship is conserved (Meinzer and Grantz 1991; Pataki et al. 1998). Therefore, the coordination of photosynthetic and hydraulic capacity may be more a consequence of the often reported coupling of A and g_s , and of g_s with LSC rather than a direct relationship between A and LSC. A appears to belong to a suite of coordinated characteristics related to plant hydraulic architecture and wood density. High rates of photosynthesis in relation to LSC will not impair plant functioning, but excessive transpiration can result in xylem cavitation and turgor loss. Therefore, the data showing proportional allocation to photosynthetic and hydraulic capacity may mean that

species only invest in transport capacity that can be supported without experiencing physiological damage.

Understanding the contributions of individual species to productivity and resource use in species-rich tropical forest is challenging. Previous attempts to understand and model inter-species physiological variation have involved dividing species into discrete functional groups. Recent studies of regulation of water use among diverse tropical forest canopy tree species have shown that contrasting patterns of regulation at the leaf level tend to converge when appropriate scaling and normalizing factors are applied (Andrade et al. 1998; Goldstein et al. 1998; Meinzer et al. 1997). The data suggest that continuous scaling relationships work to collapse inter-species variation into functional relationships that reflect plant capacity for carbon gain and tradeoffs that allow a broad spectrum of capacities. Therefore, understanding where a species falls along a functional evolutionary tradeoff continuum may be more informative than the discrete functional group approach.

Table 4-1. Area-based maximum photosynthetic rate (A_{area}), maximum leaf specific hydraulic conductivity (LSC_{max}), and wood density for study species from two lowland tropical forest sites in Panama.

Species	Family	A_{area} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	LSC_{max} ($\text{mmol m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$)	Wood density (g cm^{-3})
Fort Sherman				
<i>Aspidosperma cruenta</i>	Apocynaceae	9.7	15.81	0.70
<i>Dussia mundia</i>	Fabaceae	12.3	37.44	0.53
<i>Guateria dumentosa</i>	Annonaceae	12.2	38.42	0.42
<i>Humiriastrum diguense</i>	Hernandiaceae	11.2	34.05	0.58
<i>Manilkara bidentata</i>	Sapotaceae	10.3	42.04	0.61
<i>Marila laxifolia</i>	Clusiaceae	9.9	29.89	0.48
<i>Miconia borealis</i>	Melastomataceae	16.8	81.00	0.50
<i>Nectandra purpurescens</i>	Lauraceae	11.1	58.91	0.55
<i>Ocotea ira</i>	Lauraceae	12.6	45.78	0.58
<i>Poulsenia armata</i>	Moraceae	11.8	39.49	0.43
<i>Pourouma bicolor</i>	Moraceae	13.7	49.90	0.45
<i>Simarouba amara</i>	Simaroubaceae	17.5	102.37	0.41
<i>Tapirira guianense</i>	Anacardiaceae	12.9	61.99	0.43
<i>Trattinickia aspera</i>	Bursuraceae	12.2	43.00	0.57
<i>Virola sebifera</i>	Myristicaceae	13.5	60.78	0.50
<i>Vochysia ferruginea</i>	Vochysiaceae	18.3	120.69	0.35
Parque Metropolitano				
<i>Chrysophyllum cainito</i>	Sapotaceae	9.9	33.84	0.61
<i>Cordia alliodora</i>	Boraginaceae	15.4	61.59	0.47
<i>Ficus insipida</i>	Moraceae	19.2	123.14	0.34
<i>Luehea seemannii</i>	Tiliaceae	17.0	115.19	0.33

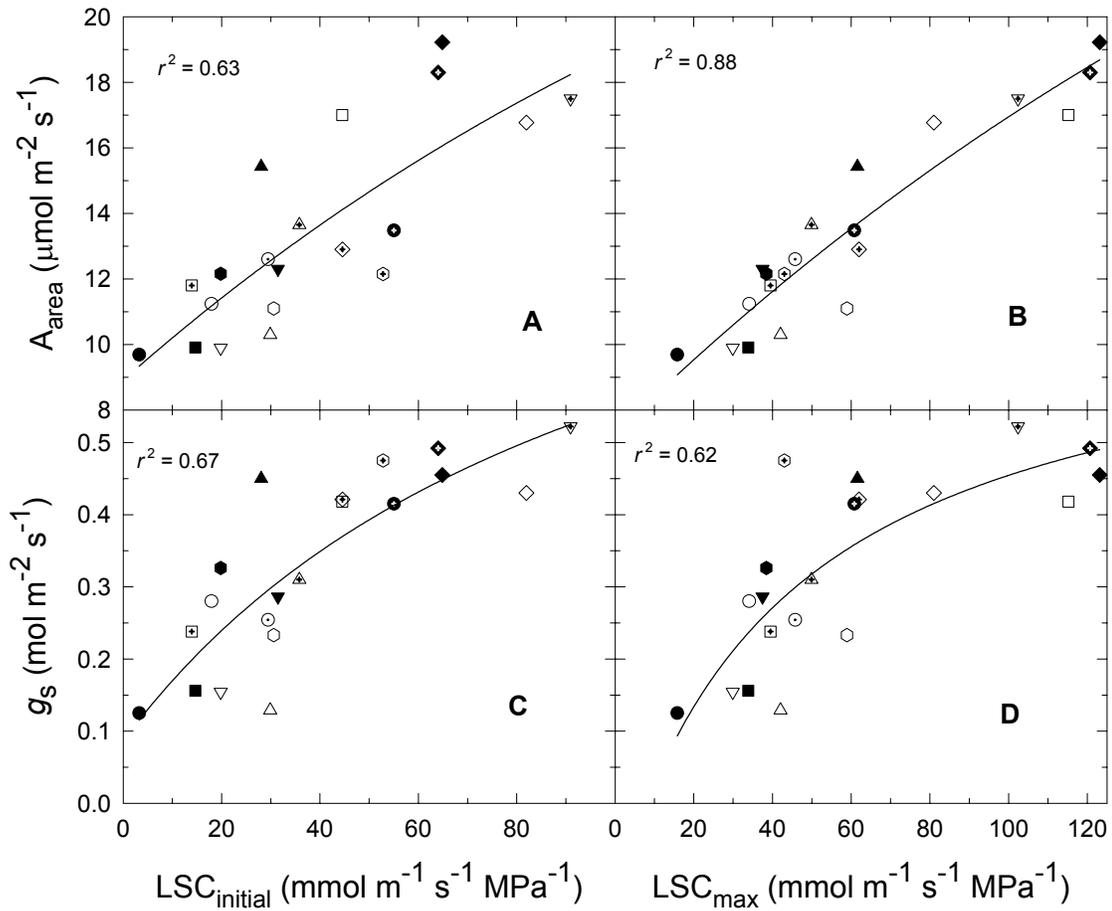


Figure 4-1. Leaf photosynthetic rate per unit area (A_{area} ; A-B) and stomatal conductance (g_s ; C-D) as a function of initial and maximum leaf specific hydraulic conductivity (LSC) for 20 canopy tree species of lowland tropical forest in Panama. Symbols: *A. cruenta* (black circle), *C. cainito* (black square), *C. alliodora* (black triangle), *D. mundia* (black upside down triangle), *F. insipida* (black diamond), *G. dumentosa* (black hexagon), *H. diguense* (white circle), *L. seemannii* (white square), *M. bidentata* (white triangle), *M. laxifolia* (white upside down triangle), *M. borealis* (white diamond), *N. purpurescens* (white hexagon), *O. ira* (white crosshair circle), *P. armata* (white crosshair square), *P. bicolor* (white crosshair triangle), *S. amara* (white crosshair upside down triangle), *T. guianense* (white crosshair diamond), *T. aspera* (white crosshair hexagon), *V. sebifera* (black crosshair circle), *V. ferruginea* (black crosshair diamond).

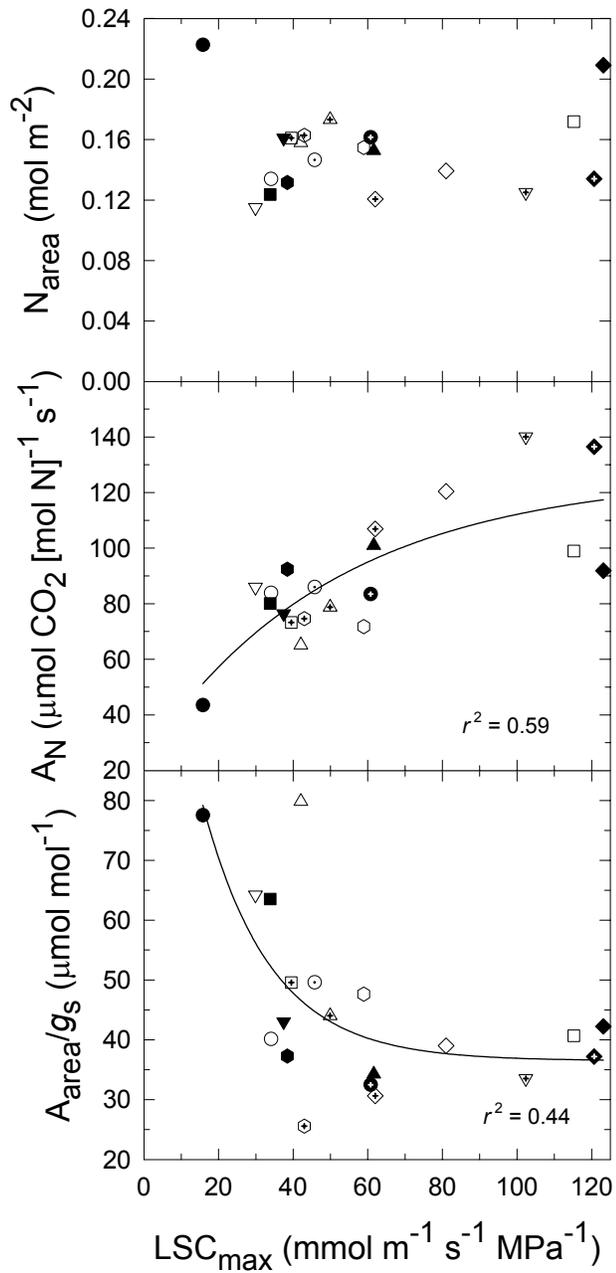


Figure 4-2. Leaf nitrogen per unit area (N_{area}), leaf photosynthetic rate per unit leaf nitrogen (A_N), and instantaneous water use efficiency (A_{area}/g_s) as a function of maximum leaf specific hydraulic conductivity (LSC_{max}) for 20 canopy tree species in lowland Panama. Symbols as in Figure 4-1.

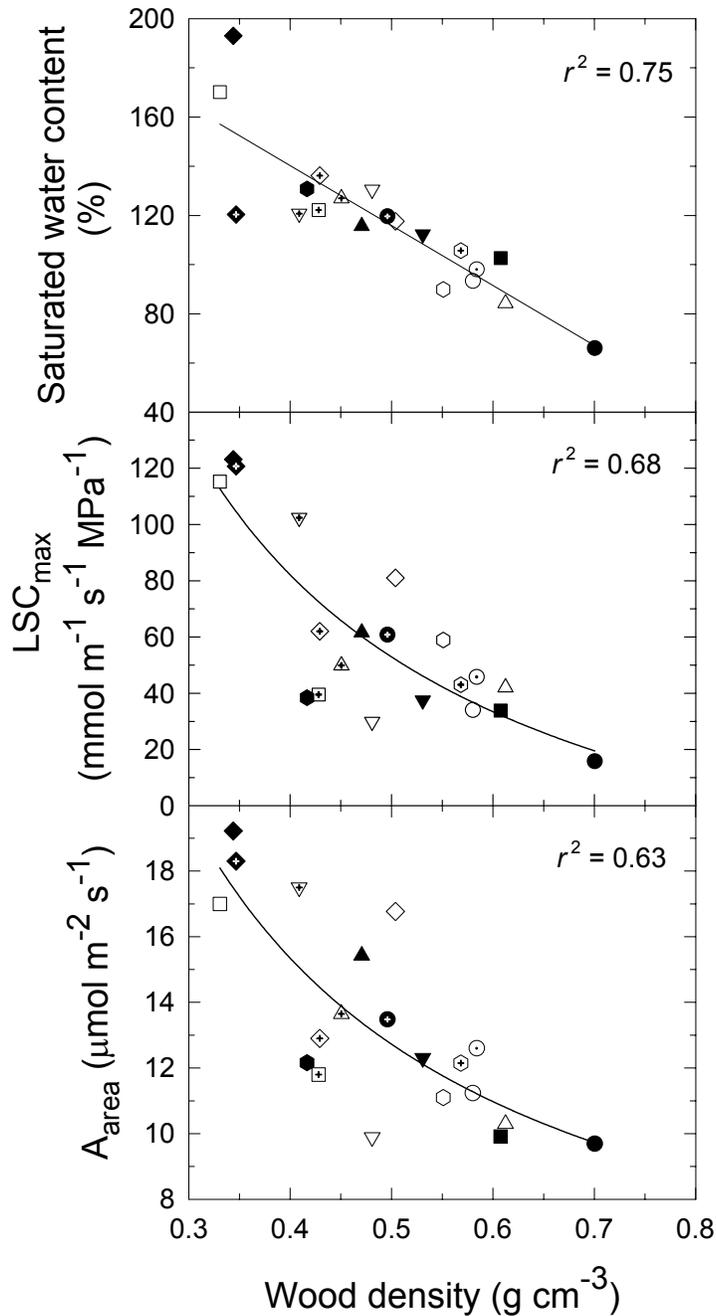


Figure 4-3. Stem saturated water content, maximum leaf specific hydraulic conductivity (LSC_{max}), and photosynthetic rate per unit leaf area (A_{area}), as a function of stem wood density for 20 species of lowland forest canopy trees in Panama. Symbols as in Figure 4-1.

CHAPTER 5
LEAF DECOMPOSITION IN A WET TROPICAL FOREST: LINKING LEAF TRAITS
WITH NUTRIENT CYCLING

Introduction

Climate, substrate, and the decomposer community are the three primary factors controlling decomposition processes. In tropical wet forest, it has been proposed that the structure and chemistry of substrate should have a relatively large effect, because tropical forest tends to have warm moist climate and high biological diversity (Meentemeyer 1978). Substrate chemistry of leaf litter is a product of the resources allocated to the living leaf, minus the nutrients retranslocated during senescence. Several general patterns relating species to litter quality have been noted. For example, species from low resource habitats often have leaves of low nutrient content that may decompose relatively slowly, whereas species in high resource habitats generally produce leaves that have higher nutrient content and decomposable readily (Chapin 1980). Furthermore, leaves share interdependent characteristics such as photosynthetic rate, N concentration, specific leaf area and leaf life span (Reich et al. 1997). The purpose of this paper is to evaluate the extent to which such functional leaf characteristics predict litter quality and decomposition rates among species in a wet lowland tropical forest.

Of the variety of leaf chemical components that are correlated with decomposition rate, it is generally accepted that litter lignin:N ratio is the strongest predictor (Cornelissen 1996; Hobbie 1996; Melillo et al. 1982). Considerably less work has gone into investigating which leaf chemical, structural, or physiological traits of functioning

leaves predict decomposition (Cornelissen 1996; Cornelissen and Thompson 1997; Grime et al. 1996; Wardle et al. 1998). This approach is of interest because it allows the potential for understanding how growth and reproduction are related to the decomposability of plant tissue. For example, Cornelissen and Thompson (1997) found that specific leaf area (SLA), leaf life span, and leaf N were significant predictors of % mass loss during decomposition among herbaceous monocots, suggesting that relationships between leaf physiological traits of living leaves may be extended into leaf litter decomposition. Furthermore, antiherbivore defenses have been found to continue to work against decomposing organisms (Grime et al. 1996; Wardle et al. 2002). Thus leaf physiology and antiherbivore defenses, two major determinants of leaf structure and function, might be related to the effects of any one species on decomposition and nutrient cycling.

It would be informative to link leaf physiology and antiherbivore defense to decomposition because of the body of ecological literature that relates suites of leaf functional traits to growth strategies in specific environmental regimes (Chapin 1993; Coley et al. 1985; Grime 1977; Westoby 1998). Leaf physiological traits, especially photosynthesis and water use efficiency, have been correlated with fitness in some studies, although mostly through correlations with other traits (Arntz and Delph 2001; Dudley 1996; Geber 1990; Lechowicz 1984). Therefore, it appears that many traits are correlated along a minimal number of functional axes. The goal of this study is to determine if it is possible to extend our understanding of correlated plant traits to include leaf decomposition rate.

Materials and Methods

Study Site and Species

The study was conducted at the Fort Sherman canopy crane site on the Caribbean coast of Central Panama. The site contains a 5-ha plot of lowland tropical forest within the 12,000 ha San Lorenzo protected area. Mean annual rainfall at the site is 3100 mm, with a mild dry season from January to March. I accessed the canopy with a 52-m-tall construction crane equipped with a gondola and operated by the Smithsonian Tropical Research Institute. Thirty six plant species that represent a broad selection of growth forms including palms, lianas, monocot herbs, canopy trees and pioneer trees were selected for study (Table 5-1).

Litter Collection and Decomposition

Leaf litter was collected during the dry season, between January and April, 2001, when many species shed or exchange leaves. Senescent leaves were collected by hand directly from at least three individuals of each study species. Entire leaves with complete discoloration were gently shaken and harvested only if they came off the plant with a light touch, indicating a well-formed abscission zone. Palm fronds and monocot herb leaves remain on the plant for several months after retranslocation, so the most recent senescing leaf or frond that had no remaining green pigmentation was selected.

Leaves were air dried in an air-conditioned laboratory (45% RH and 24°C) for >1 month. Ten grams of litter from each species was set aside for initial litter quality chemical analyses. Two to three grams of litter from each species were placed in 1X1 mm mesh nylon-covered fiberglass window screen. Leaves of several species can weigh more than 3 g and for these species one entire leaf was placed in each bag. For palms, a leaflet was separated from the rachis and treated as a leaf. Four sizes of litter bags: 10X10,

10X30, 20X20 and 30X30 cm were used to accommodate different leaf sizes and minimize folding. Litterbags were heat sealed with a dry iron and placed in the field on March 30, 2001, about one month before the beginning of the rainy season that year. Dowel rods (1/4" diameter, 15 cm long) were placed in the field with litterbags as a standard to compare with other decomposition studies (LIDET 1995).

At 1, 3, 6, 14, and 24 months, 5 bags per species were collected from the field. Bags were gently rinsed with distilled water to remove adhered soil particles and any roots that had grown into the bags were removed with tweezers. A subsample of each species was weighed fresh for moisture content, while the rest of the bags were placed in the freezer overnight. The contents of each litterbag were then dried for 48 hours at 65°C. Dried samples were weighed and ground in a Wiley mill through a 40 size mesh.

Initial Litter Quality

A subsample of litter from each species was dried for 48 hours at 65°C for the determination of initial litter quality. Carbon fraction analyses were performed using a series of increasingly aggressive extractants (Ryan et al. 1989). Dried litter samples were digested in a detergent solution which separated non-polar extractives (cell contents) from neutral detergent fiber (NDF), which includes cell wall constituents and fractions that are not immediately nutritionally available. A dilute acid detergent solution was then used to determine acid detergent fiber (ADF, lignocellulose) before lignin was separated from cellulose in 72% H₂SO₄. A separate subsample was analyzed for C and N using an elemental analyzer (Carlo Erba, Milano, Italy).

Gas Exchange and Leaf Chemistry

In the wet season of 2000 and 2001 (June-November), maximum rates of net CO₂ assimilation (*A*) and stomatal conductance (*g_s*) were measured with an infrared gas

analyzer (Model 6400, Li-Cor, Inc., Lincoln, NE, USA) between 0700 and 1100 h. Five newly formed mature leaves from three individuals of each species were measured at 370 $\mu\text{mol mol}^{-1}$, (slightly higher than ambient CO_2 concentration), and 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD) provided by a red blue light source (model 6400-02B #SI-710, Li-Cor, Inc.). Only gas exchange values measured at a leaf-to-air vapor pressure deficit (VPD_l) below 1.5 kPa were used because significant stomatal closure was observed above this value. Gas exchange was measured on leaves growing in the highest light environment in which the species tends to grow. For canopy trees, lianas, pioneer trees and some palms, terminal leaves were accessed using the canopy crane. For monocot herbs and understory palms, measurements were made from the forest floor.

Following photosynthetic measurements, lamina thickness was measured between primary and secondary veins with a digital caliper (Mitutoyo, Japan). Leaves were dried for 48 hours at 65°C, weighed for determination of specific leaf area (SLA) and ball milled to a fine powder. All leaves from the same individual were pooled for chemical analysis. One composite sample from each individual was analyzed for C and N using an elemental analyzer (Carlo Erba, Milano, Italy). Leaf toughness was measured in the field on freshly collected leaves with a penetrometer (Pesola, Switzerland), which measured the maximum force during punching through the lamina between primary and secondary veins at a steady, slow rate with a 1 mm diameter plunger. Such measurements do not replicate the action by which herbivores puncture leaves (fracture toughness) but leaf toughness was correlated with fracture toughness in a study of 42 tropical tree species (Choong et al. 1992), so I use it as an index of allocation to structure and potential

resistance to decomposition. Leaf polyphenol concentration was analyzed with the Prussian Blue Procedure in a subset of the species studied, including canopy trees, pioneer trees, lianas, and one palm (S. Joseph Wright, unpublished data).

Results

Decomposition rate (k) varied from a minimum of 0.41 in the canopy tree *Vochysia ferruginea* to a maximum of 4.58 in the pioneer tree, *Piper hispidum*. Overall, there were no significant differences in k among plant growth forms ($F=1.76$; $P=0.1617$; Table 5-2). Several indices of litter quality varied significantly between the monocots, (palms and monocot herbs), and dicots (canopy trees, pioneer trees, and lianas). For example, non-polar extractives were significantly lower in monocot herbs and palms than other growth forms ($F=7.86$; $P=0.0002$). Litter cellulose concentration was significantly higher in monocot herbs and palms ($F=7.16$; $P=0.0003$), and acid detergent fiber (ADF) was higher in palms than other growth forms ($F=6.43$; $P=0.0007$).

Litter lignin concentration was negatively related to decomposition rate (Table 5-3, Figure 5-1). Although litter N concentration was not a significant predictor of decomposition, the composite variable, litter lignin:N, was the strongest predictor of decomposition rate (Table 5-3, Figure 5-1). Litter C concentration and C:N were also negatively related to decomposition (Table 5-3, Figure 5-2). No other indices of litter quality were related to decomposition except ADF, and this relationship was weak (Table 5-3).

Several chemical and structural traits of living leaves were significantly related to decomposition. Leaf N and C:N were significantly related to decomposition (Table 5-4, Figure 5-3). SLA was positively related to decomposition (Table 5-4, Figure 5-4), and species with tougher leaves tended to decompose more slowly (Table 5-4). Leaf N and

SLA, two of the strongest leaf predictors of decomposition were also significant predictors of photosynthetic rate (Figure 5-5), indicating a relationship between leaf physiology and decomposition through these structural and chemical traits.

Although lignin and lignin:N were the strongest predictors of decomposition, there were several species with low lignin concentrations that decomposed slowly. A general linear model including the effects of lignin and polyphenol concentration explained more of the variance in decomposition than lignin alone (Table 5-5). This result suggests that although lignin is probably the best general leaf defensive characteristic for predicting decomposition, other antiherbivore defenses may play a similar role in deterring decomposers following senescence (Grime et al. 1996; Wardle et al. 2002), and when combined with lignin appear to explain a greater proportion of the variance.

Discussion

Plant Growth Forms and Ecosystem Processes

In high diversity tropical ecosystems, it has been difficult to relate resource use characteristics of individual plant species to system-wide processes such as nutrient storage and cycling. This predicament has led to the functional group approach, in which species with similar resource use characteristics are grouped into a smaller, more manageable number of functional groups. This approach greatly simplifies modeling of plant processes and has achieved success in many ecosystems (Chapin et al. 1995; Ewel and Bigelow 1996; Körner 1993; Tilman et al. 1997). However, it appears that continuous functions reflecting convergence in leaf physiology can also be used to simplify the effects of many species. Therefore, my results suggest that for predicting the effect of a species on an ecosystem process such as litter decomposition, it is more

important to know the value of a continuous variable such as litter lignin:N than any discrete classification such as growth form, canopy position, successional status, or phylogenetic association.

Litter Quality and Decomposition

The result that litter lignin:N is the strongest predictor of decomposition reported in this study is consistent with numerous other decomposition studies (Cornelissen 1996; Hobbie 1996; Melillo et al. 1982; Ostertag and Hobbie 1999). Similarly, the result that litter C concentration and C:N are significantly related to decomposition corroborates much of what exists in the ecological literature. Mechanistically, it is important to note that the ratio of lignin to N reflects a ratio between leaf defense and photosynthetic potential. High leaf lignin concentration is a characteristic of species in low resource habitats and species with long-lived leaves, and is considered a general antiherbivore defense (Chapin 1980; Coley 1983; Reich et al. 1997). To some degree, litter N is a reflection of the physiological capacity of the leaf. Therefore, litter lignin:N is a ratio of defense and structure to physiological capacity, although effects on decomposition are more strongly driven by lignin. Viewed in this respect, the strongest predictor of litter decomposition integrates plant allocation along the axes of defense and potentially carbon gain.

Photosynthesis and Decomposition

Photosynthesis is the primary function of leaves and therefore most of the features of leaves are under strong selection to maximize carbon gain over the life of the leaf (Kikuzawa 1991; Mulkey et al. 1995; Reich et al. 1997). Ecologists have identified a suite of highly interdependent leaf characteristics that occur repeatedly and appear important in the exploitation of specific habitats (Chapin 1980). Specific leaf area (SLA)

and leaf N are two of these leaf characteristics that are positively related with photosynthesis across broad groups of plant species (Reich et al. 1992). SLA and leaf N are also the strongest leaf predictors of decomposition in this study and suggest that allocation to photosynthetic capacity is related to decomposition through these correlations (Figure 5-6). Interestingly, leaf N was correlated with decomposition rate, but litter N was not. Leaf N may be related to a host of other leaf characteristics that influence decomposition. Although photosynthetic rate and decomposition rate may show a positive correlation, litter does not photosynthesize. Therefore, it is necessary to consider chemical and structural leaf components that are related to photosynthesis to understand how decomposition is a product of selection to maximize carbon gain in leaves.

Table 5-1. Summary of study species and leaf litter decomposition rate (k) organized by growth form. All leaf litter material was collected in lowland wet tropical forest at Fort Sherman, Panama.

Species	Family	Growth form	k (yr ⁻¹)
<i>Aspidosperma cruenta</i>	Apocynaceae	Canopy tree	1.27
<i>Brosimum utile</i>	Moraceae	Canopy tree	0.47
<i>Calophyllum longifolium</i>	Clusiaceae	Canopy tree	0.46
<i>Carapa guianensis</i>	Meliaceae	Canopy tree	0.45
<i>Dussia mundia</i>	Leguminosae	Canopy tree	1.11
<i>Manilkara bidentata</i>	Sapotaceae	Canopy tree	0.66
<i>Nectandra purpurascens</i>	Lauraceae	Canopy tree	0.57
<i>Pourouma bicolor</i>	Cecropiaceae	Canopy tree	0.44
<i>Simarouba amara</i>	Simaroubaceae	Canopy tree	1.01
<i>Tapirira guianensis</i>	Anacardiaceae	Canopy tree	0.96
<i>Vochysia ferruginea</i>	Vochysiaceae	Canopy tree	0.41
<i>Apeiba membranaceae</i>	Tiliaceae	Pioneer tree	1.05
<i>Cecropia insignis</i>	Cecropiaceae	Pioneer tree	1.00
<i>Jacaranda copaia</i>	Bignoniaceae	Pioneer tree	0.80
<i>Clidemia octona</i>	Melastomataceae	Pioneer tree	0.69
<i>Ochroma pyramidale</i>	Bombacaceae	Pioneer tree	0.58
<i>Piper hispidum</i>	Piperaceae	Pioneer tree	4.58
<i>Trema micrantha</i>	Ulmaceae	Pioneer tree	1.55
<i>Arrabidaea verrucosa</i>	Bignoniaceae	Liana	0.72
<i>Cayaponia granatensis</i>	Cucurbitaceae	Liana	0.72
<i>Doliocarpus dentatus</i>	Dilleniaceae	Liana	0.44
<i>Heisteria scandens</i>	Olacaceae	Liana	1.40
<i>Maripa panamensis</i>	Convolvulaceae	Liana	0.82
<i>Phryganocydia corymbosa</i>	Bignoniaceae	Liana	1.24
<i>Pleonotoma variabilis</i>	Bignoniaceae	Liana	0.48
<i>Tontelea richardii</i>	Hippocrateaceae	Liana	0.56
<i>Costus pulverulentus</i>	Zingiberaceae	Monocot herb	0.64
<i>Diffenbachia pittieri</i>	Araceae	Monocot herb	3.18
<i>Heliconia pogonantha</i>	Heliconiaceae	Monocot herb	0.81
<i>Stromanthe jacquinii</i>	Maranthaceae	Monocot herb	0.80
<i>Zingiber officinale</i>	Zingiberaceae	Monocot herb	1.76
<i>Calyptrogyne costatifrons</i>	Palmae	Palm	0.61
<i>Carloduvica palmata</i>	Cyclanthaceae	Palm	0.90
<i>Genoma cuneata</i>	Palmae	Palm	0.79
<i>Oenocarpus mapora</i>	Palmae	Palm	0.64
<i>Socratea esxorrhiza</i>	Palmae	Palm	0.46
Dowels			0.18

Table 5-2. Leaf litter decomposition rates and initial litter quality of study species from Fort Sherman, Panama, averaged by growth form. Values are mean \pm 1 SE. Values with the same letter are not significantly different ($P > 0.05$).

	Canopy trees ($n=11$)	Pioneer trees ($n=7$)	Lianas ($n=8$)	Monocot herbs ($n=5$)	Palms ($n=6$)
k (yr^{-1})	$0.71^a \pm 0.10$	$1.47^a \pm 0.58$	$0.80^a \pm 0.13$	$1.44^a \pm .054$	$0.68^a \pm 0.08$
C (%)	$47.27^a \pm 1.38$	$43.23^a \pm 2.66$	$46.45^a \pm 2.07$	$40.71^a \pm 1.40$	$41.98^a \pm 1.11$
N (%)	$0.90^a \pm 0.09$	$1.22^a \pm 0.18$	$1.10^a \pm 0.08$	$1.02^a \pm 0.06$	$1.14^a \pm 0.16$
C:N	$58.42^a \pm 6.42$	$39.23^a \pm 5.95$	$44.42^a \pm 5.57$	$40.29^a \pm 1.44$	$38.69^a \pm 3.89$
Lignin (%)	$16.03^a \pm 1.66$	$13.67^a \pm 2.71$	$16.46^a \pm 3.17$	$11.96^a \pm 1.62$	$21.48^a \pm 3.19$
Lignin:N	$19.90^a \pm 3.34$	$11.81^a \pm 2.76$	$16.80^a \pm 4.93$	$11.74^a \pm 1.37$	$19.9^a \pm 4.30$
Non-polar extractives (%)	$54.23^a \pm 3.49$	$55.48^a \pm 5.07$	$50.35^a \pm 3.01$	$35.81^b \pm 6.33$	$29.59^b \pm 1.65$
Cellulose (%)	$18.41^a \pm 1.90$	$18.01^a \pm 3.00$	$19.56^a \pm 2.72$	$27.67^b \pm 1.71$	$32.61^b \pm 1.82$
Fiber—ADF (%)	$45.77^a \pm 3.49$	$44.52^a \pm 5.07$	$49.65^a \pm 3.01$	$64.18^a \pm 6.33$	$70.39^b \pm 1.64$

Table 5-3. Regressions of litter chemical parameters and leaf litter decomposition rate (k). All plant growth forms were combined for analyses. Only statistically significant regressions ($P < 0.1$) are reported. ADF, acid detergent fiber. ($n=36$)

Parameter	Regression equation	r^2	Significance
Litter C	$\ln(k) = 6.91 - 1.89 \cdot \text{Litter C}$	0.17	0.0122
Litter C:N	$\ln(k) = 2.29 - 0.66 \cdot \text{Litter C:N}$	0.15	0.0181
Lignin	$\ln(k) = 1.66 - 0.70 \cdot \text{Lignin}$	0.30	0.0005
Lignin:N	$\ln(k) = 1.53 - 0.65 \cdot \text{Lignin:N}$	0.38	<0.0001
ADF	$\ln(k) = 1.78 - 0.55 \cdot \text{ADF}$	0.09	0.0772

Table 5-4. Regressions of leaf chemical and structural parameters and leaf litter decomposition rate (k). All plant growth forms were combined for analyses. Only statistically significant regressions ($P < 0.1$) are reported. SLA, specific leaf area. ($n=36$)

Parameter	Regression equation	r^2	Significance
Leaf N	$\ln(k) = -0.97 + 1.15 \cdot \text{Leaf N}$	0.20	0.0059
Leaf C:N	$\ln(k) = 2.48 - 0.85 \cdot \text{Leaf C:N}$	0.19	0.0077
Lamina toughness	$\ln(k) = 0.66 - 0.18 \cdot \text{lamina toughness}$	0.10	0.0575
SLA	$\ln(k) = -2.43 + 0.48 \cdot \text{SLA}$	0.21	0.0050

Table 5-5. Results of general linear model for combined effects of leaf phenol (measured with the Prussian Blue Procedure) and litter lignin on litter decomposition rate. This analysis was conducted on a subset of the study species for which phenol data was available. The analysis included canopy trees, pioneer trees, lianas and one palm.

Parameter	k	
	Estimate	P
Intercept	2.005	0.0052
Phenols	-1.243	0.0589
Lignin	-0.839	0.0026
Phenols*Lignin	0.439	0.1146
Overall model p -value		0.0044
Model R^2		0.49
n		23

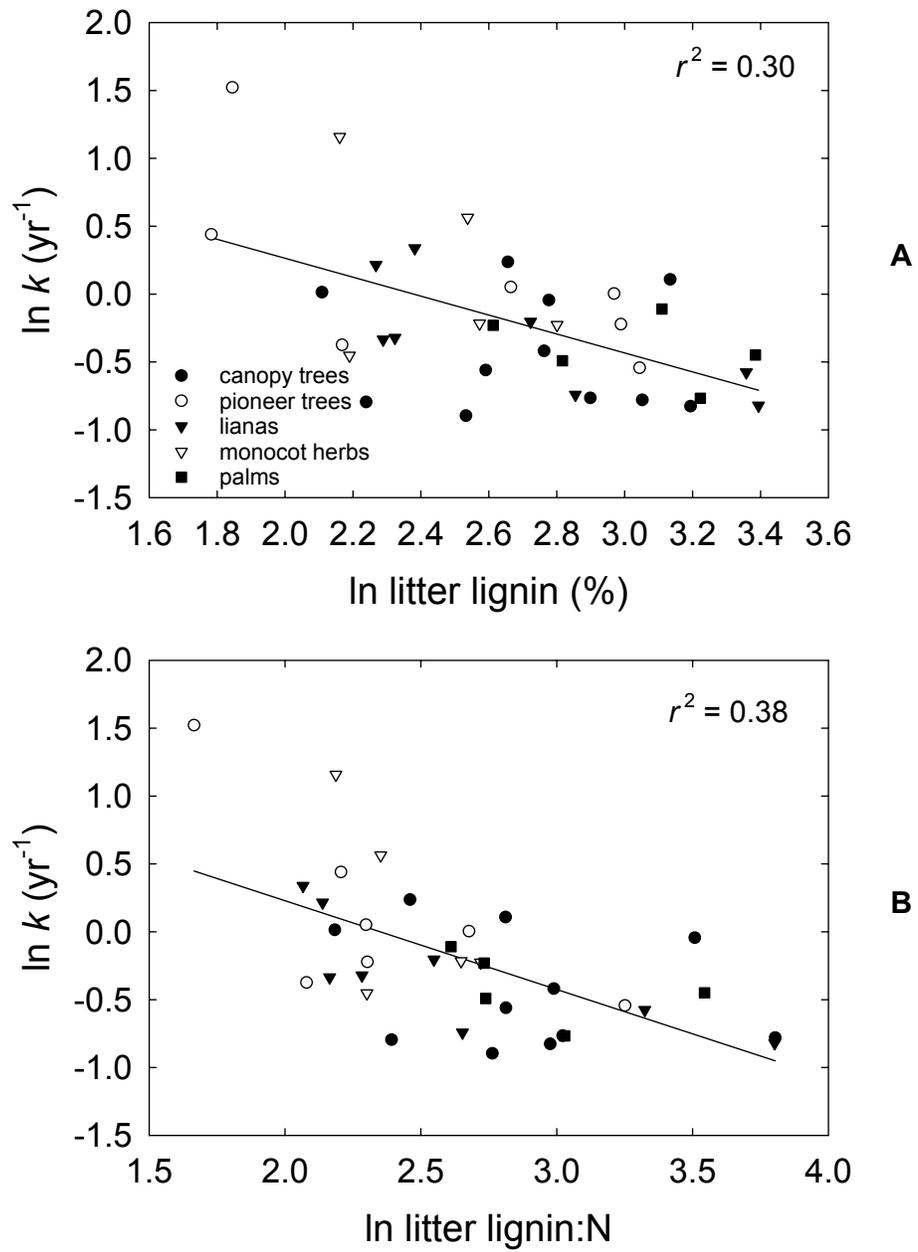


Figure 5-1. Relationship between leaf litter decomposition rate (k) and (A) initial litter lignin concentration and (B) initial litter lignin to nitrogen ratio for 36 lowland tropical wet forest plant species from Fort Sherman, Panama.

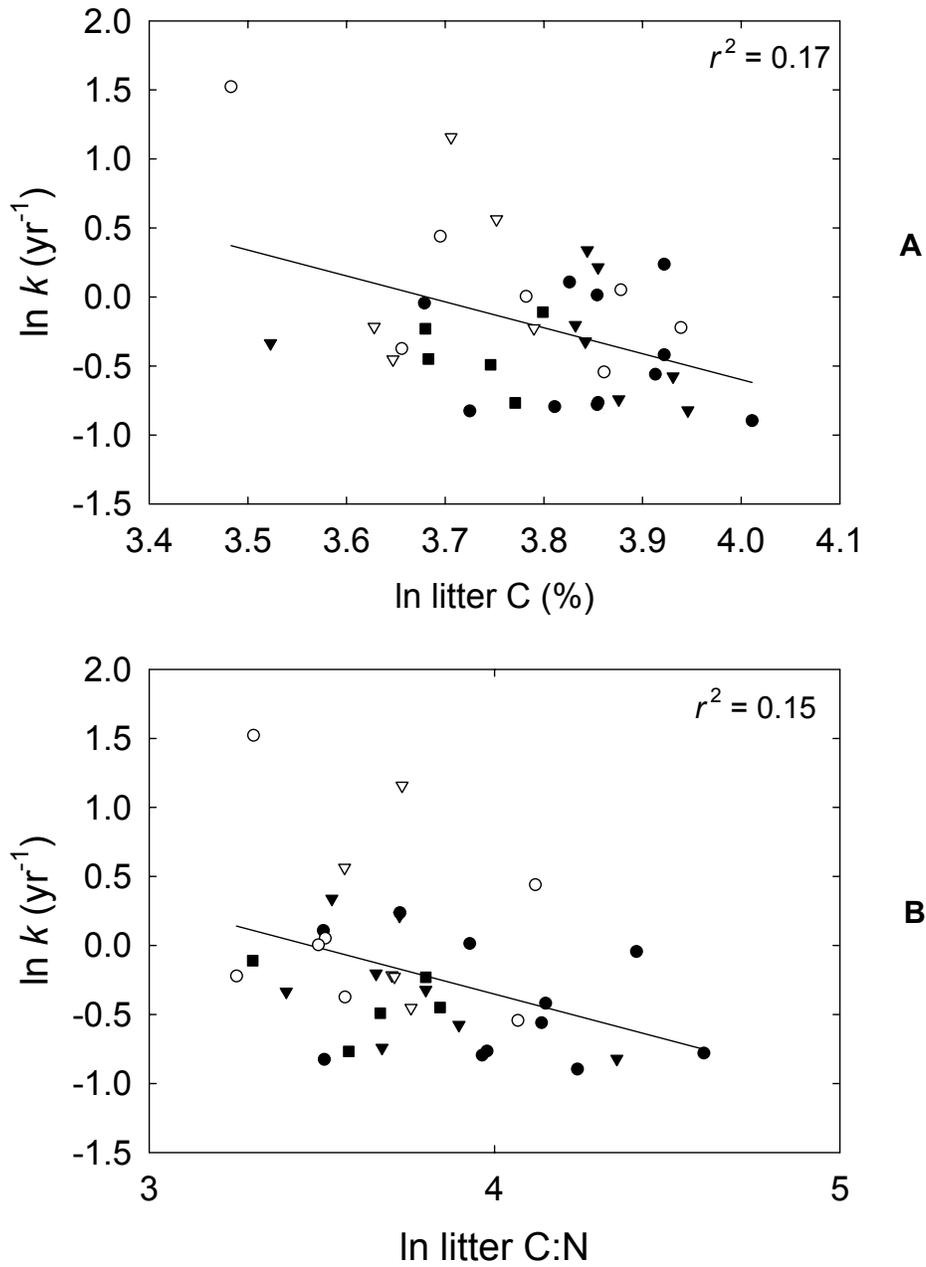


Figure 5-2. Relationship between leaf litter decomposition rate (k) and (A) initial litter carbon concentration and (B) initial litter carbon to nitrogen ratio for 36 wet forest species. Symbols as in figure 5-1.

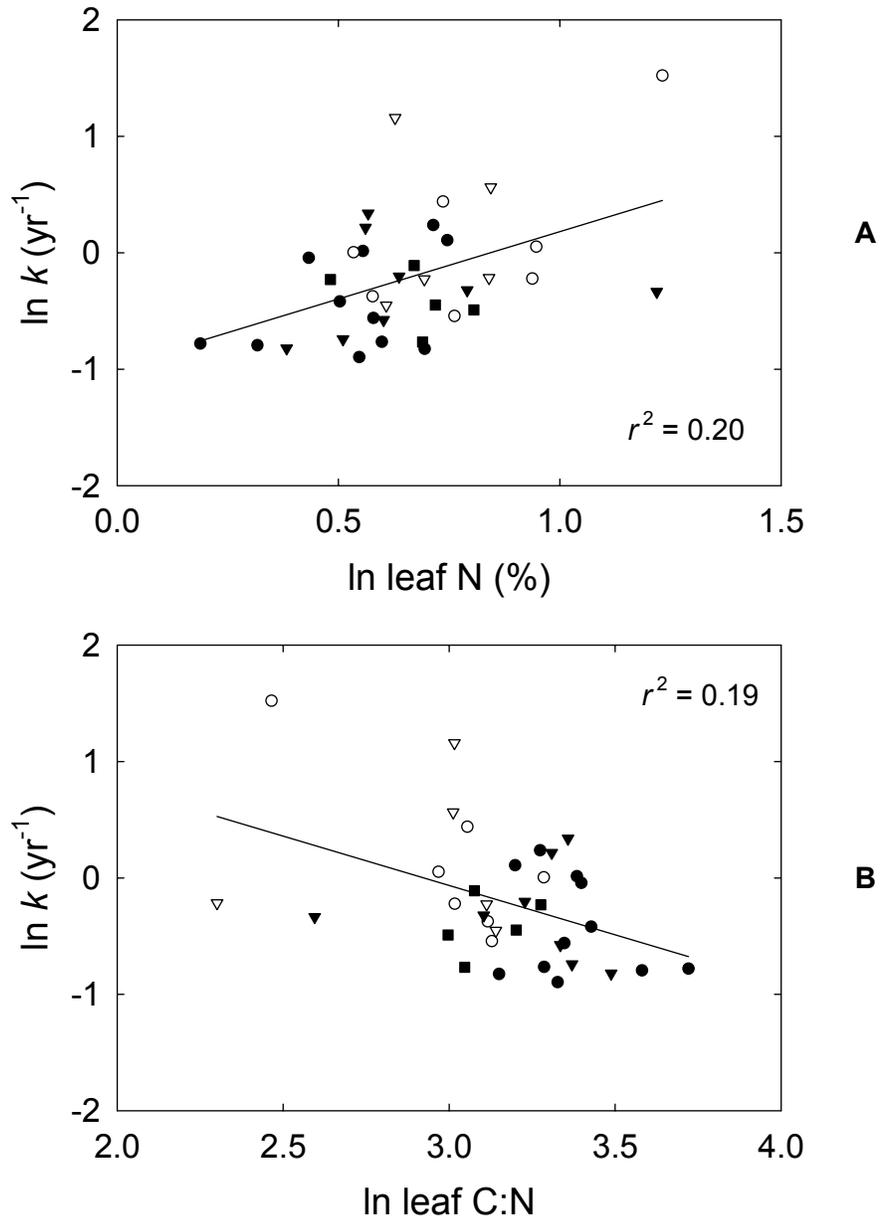


Figure 5-3. Relationship between leaf litter decomposition rate (k) and (A) nitrogen concentration of living leaf and (B) carbon to nitrogen ratio of living leaf for 36 wet forest species. Symbols as in figure 5-1.

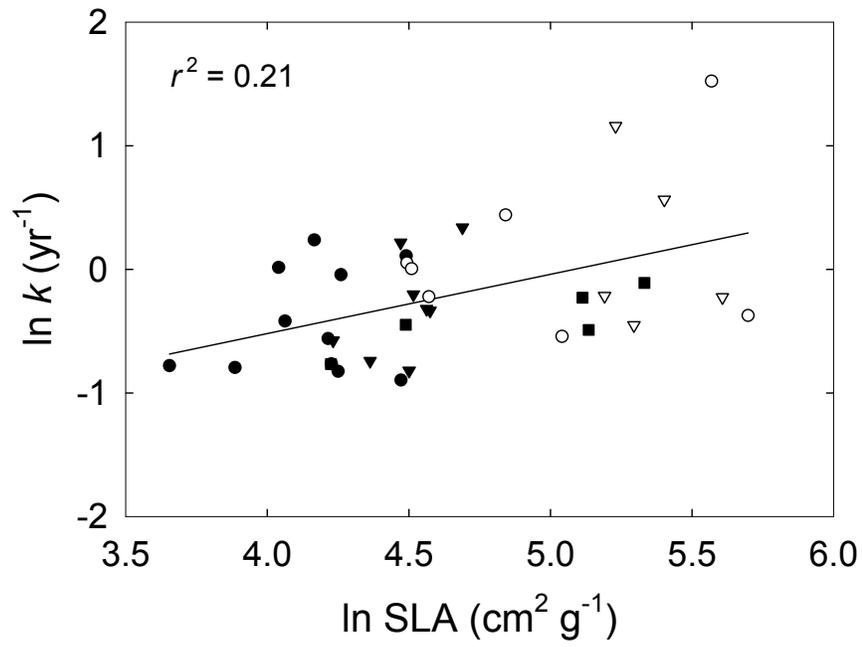


Figure 5-4. Relationship between leaf litter decomposition rate (k) and specific leaf area (SLA) for 36 wet forest species. Symbols as in figure 5-1.

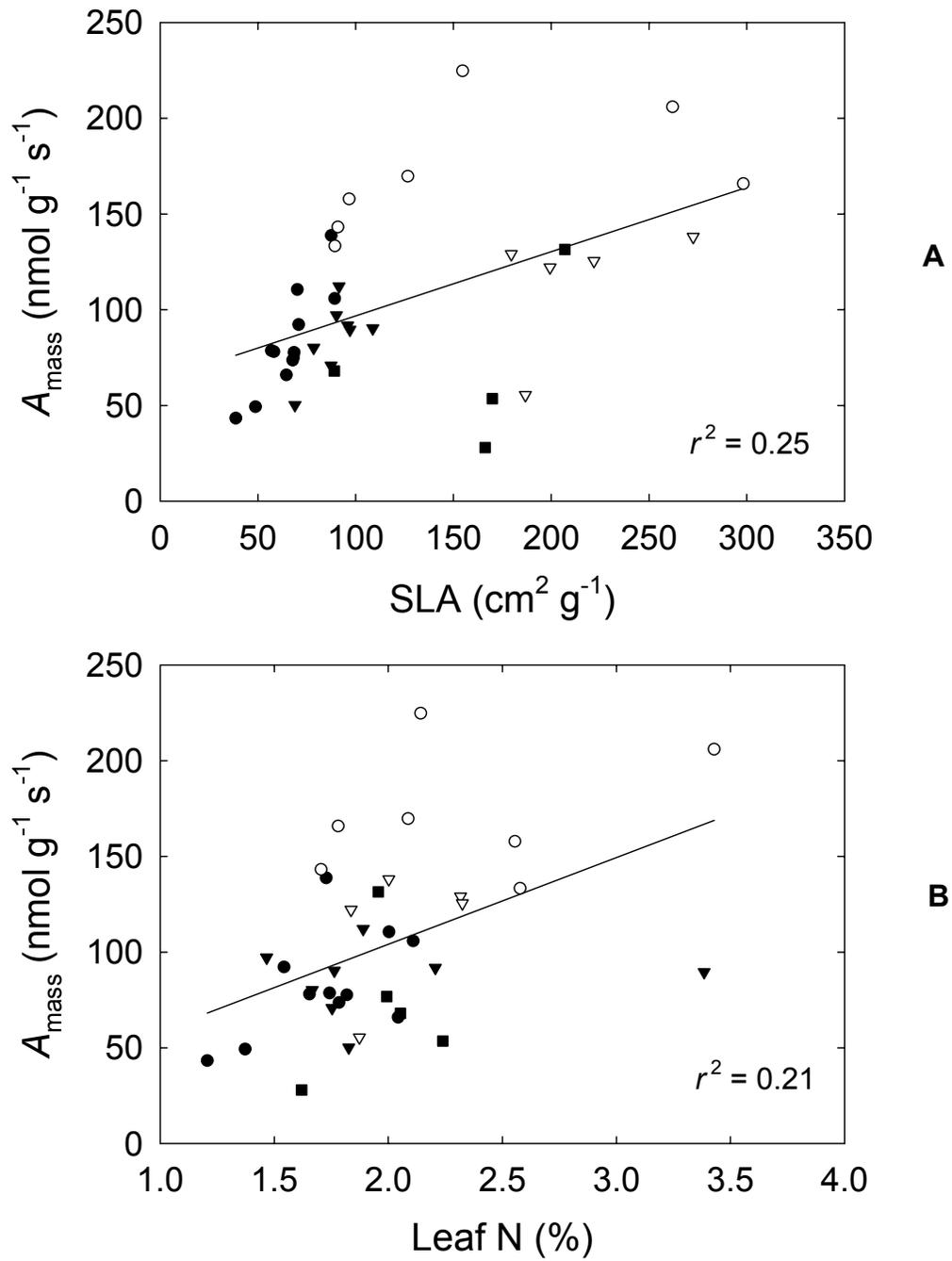


Figure 5-5. Relationship between leaf photosynthetic rate per unit mass (A_{mass}) and (A) specific leaf area (SLA) and (B) leaf nitrogen concentration for 36 wet forest species. Symbols as in figure 5-1.

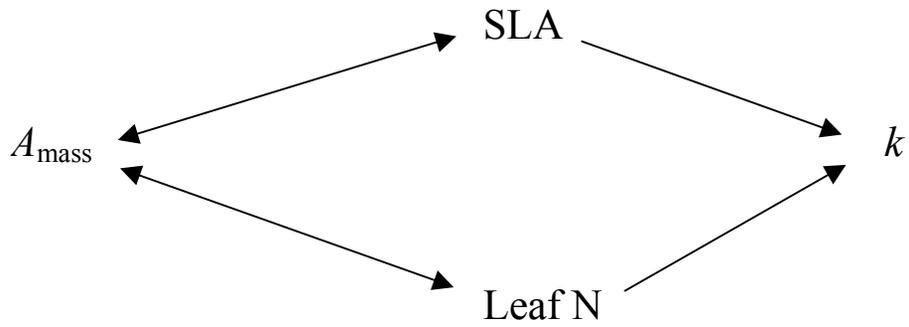


Figure 5-6. Schematic diagram depicting how photosynthesis is related to decomposition rate (k) through correlation with specific leaf area (SLA) and leaf nitrogen concentration.

CHAPTER 6
TEST OF GAS EXCHANGE MEASUREMENTS ON EXCISED BRANCHES OF TEN
TROPICAL TREE SPECIES: A TECHNICAL REPORT

Introduction

Plant physiological parameters that describe CO₂ uptake and water loss are used to model biosphere-atmosphere interactions at local and regional scales (Running and Coughlan 1988; Williams et al. 1996) and to predict the sensitivity of vegetation to climate change at regional to global scales (Neilson and Marks 1994). Measurements from the upper canopy are important for calculations of net primary productivity (NPP) and direct gas exchange measurements are needed to understand the extent to which NPP is controlled by plant community type and environmental heterogeneity (Haxeltine and Prentice 1996; Woodward et al. 1995). Towers, scaffolds, walkways and construction cranes have been employed to obtain physiological parameters from intact branches in the upper canopy of mature forest (Mulkey et al. 1996). However, these structures are not available everywhere and there is a need for reliable estimates of leaf-level processes in places where it is not practical or feasible to build such structures. Researchers have measured gas exchange of canopy leaves by cutting or shooting small branches and re-cutting stems under water to re-establish the xylem water column in the form of a potometer before measurement (Dang et al. 1997; Koyama 1981; Reich et al. 1995; Reich et al. 1998). Other researchers have measured gas exchange of montane forest trees (Gerrish 1992) or conifers (Ginn et al. 1991; Samuelson 1998) by simply detaching a group of leaves or fascicles and placing them in a cuvette for immediate measurement.

Although numerous physiological observations on excised foliage have been published, there is evidence that excision may alter gas exchange measurements in several ways. Even if a stem is double cut to re-establish the xylem water column, cavitation, changes in xylem pressure, and reductions in hydraulic conductance can result (Boari and Malone 1993; Stahlberg and Cosgrove 1995). These alterations in the xylem stream can influence stomatal responses (Sperry et al. 1993; Williamson and Milburn 1995) and inhibit the transport of hormones and nutrients, which are important for regulating shoot water potential and stomatal control (Tardieu and Davies 1993; Zhang and Davies 1990). The time scale at which these changes occur is likely to be important in determining the degree of excision-induced effects on gas exchange. However, these responses vary widely across the plant kingdom leaving us with little information regarding the reliability of gas exchange measurements on excised foliage; few studies provide verification of how leaves on excised stems perform (Dang et al. 1997; Ginn et al. 1991).

The purpose of this study is to compare gas exchange rates measured on excised and attached branches of tropical forest canopy trees. I investigated how measurements of gas exchange and biochemical parameters derived from photosynthetic light and CO₂ response curves varied between leaves on excised and attached branches. Our main objective was to determine if excision causes significant effects on measured gas exchange rates and parameters, i.e. I wanted to know if the effect of excision on gas exchange parameters is greater than the range of values observed on intact branches. Second, I hoped to evaluate whether species differ in their gas exchange responses to excision, and if there are any characteristics that might be used to predict the degree

excision-induced effects. Although measuring gas exchange on excised branches is a convenient technique for acquiring data, it seems important to address the limitations of this approach so as to prevent the collection of spurious data and to interpret the results of studies that reported gas exchange results from excised stems.

Materials and Methods

Study Sites and Species

The study was conducted from two construction cranes operated by the Smithsonian Tropical Research Institute (STRI) in the Republic of Panama. Each crane is equipped with a gondola suspended by cables from a rotating boom that allows coverage of approximately 0.82 ha of forest. The first crane is located in Parque Metropolitano, a secondary dry forest on the edge of Panama City that receives approximately 1800 mm of precipitation annually with a distinct dry season between December and April. The second crane is located at Fort Sherman, on the Caribbean side of the Panamanian Isthmus in old growth forest that receives approximately 3100 mm of precipitation annually with a shorter and less intense dry season.

Ten tree species from 9 families, representing a variety of leaf morphology and gas exchange rates were investigated. At Fort Sherman, *Apeiba membranacea* Spruce ex. Benth. (Tiliaceae), *Jacaranda copaia* (Aubl.) D. Don (Bignoniaceae) and *Vochysia ferruginea* Mart. in Mart. & Zucc. (Vochysiaceae) have relatively high rates of photosynthesis and stomatal conductance (Table 6-1). *Aspidosperma cruenta* Woods (Apocynaceae), *Brosimum utile* (Moraceae), *Manilkara bidentata* (Sapotaceae) and *Simarouba amara* Aubl. var. typica Cronq. (Simaroubaceae), in contrast, have lower rates of photosynthesis and stomatal conductance, and tend to have thicker leaves. At Parque Metropolitano, *Anacardium excelsum* (Bertero & Balb.) Skeels (Anacardiaceae) has

relatively low rates of photosynthesis and stomatal conductance, whereas *Pseudobombax septenatum* (Jacq.) Dug. (Bombacaceae) and *Luehea seemannii* Tr. & Planch. (Tiliaceae) have higher rates of photosynthesis and stomatal conductance. All nomenclature follows (Croat 1978).

Gas Exchange Measurements

Net CO₂ assimilation (A) and stomatal conductance (g_s) were measured with an infrared gas analyzer (Model 6400, Li-Cor, Inc., Lincoln, NE, USA) on leaves of branches with full sun exposure. One gas exchange measurement was taken on a newly formed mature intact and attached leaf at ambient temperature, 37.26 Pa CO₂ (equivalent to 370 $\mu\text{mol mol}^{-1}$, slightly higher than ambient), and 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD) provided by a red blue light source (model 6400-02B #SI-710, Li-Cor, Inc.). The segment of branch was then excised 100 cm from the measured leaf and immediately shortened to 50 cm by re-cutting under water to re-establish the xylem water column. Successive gas exchange measurements were taken within 3 min and then several times up to 60 min after excision.

The response of A to PPFD was measured on newly formed fully expanded mature leaves at a range of PPFD from 0 to 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, 37.26 Pa CO₂, and ambient relative humidity. Measurements were made at ambient temperature unless leaf temperature exceeded 33° C, in which case, peltier plates adjacent to the cuvette were used to maintain the block temperature at 33° C. I first measured A at 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, then light was decreased in a stepwise fashion for a total of 10 measurement points down to 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Once the light response curve was completed, the branch was immediately re-cut under water as described above and the curve was repeated in the

gondola with the stem in a potometer on a leaf of similar age adjacent to the original leaf. An attempt was made to maintain the cut stem in sunlight to prevent stomatal closure as a result of low light availability in the gondola. Trials were performed on two to four branches per species. Parameters for light response curves were fit to a nonrectangular hyperbola (Sims and Pearcy 1991), which allows calculation of apparent quantum yield on the basis of incident photons (Φ), the light-saturated rate of gross CO₂ assimilation at saturating irradiance (A_{\max}), the radius of curvature (Θ) and dark respiration (R_d).

The response of A to intercellular CO₂ partial pressure (p_i) was measured on three branches per species. I conducted measurements on intact branches by first inducing the leaf with 1700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PFD and 37.26 Pa CO₂. Measurements were then taken at 0 Pa CO₂ and the concentration was increased over a total of 14 measurement points to a final concentration of 151 Pa. The branch was then cut and re-cut as described above and a second CO₂ response curve was conducted on a leaf of similar age adjacent to the original leaf to avoid feedback inhibition.

Parameters for CO₂ response curves were modeled by two equations that describe CO₂-limited and rubisco-limited rates of photosynthesis (Lambers et al. 1998; von Caemmerer and Farquhar 1981). CO₂-limited rate of photosynthesis [$A(c)$] can be calculated as

$$A(c) = \frac{V_{c \max}(p_i - \Gamma)}{p_i + K_m} - R_{day} \quad (6-1)$$

Where $V_{c \max}$ is the rate of CO₂ assimilation at saturating p_i , Γ is the CO₂ compensation point, K_m is the Michaelis-Menten constant for the carboxylation reaction

and R_{day} is the rate of respiration during photosynthesis. The rubisco-limited rate of photosynthesis [$A(j)$] can be calculated as:

$$A(j) = \frac{J_{\text{max}}(p_i - \Gamma)}{4(p_i + 2\Gamma)} - R_{\text{day}} \quad (6-2)$$

Where J_{max} is the maximum rate of electron transport and all other parameters follow equation 1. Repeated measure analysis of variance (ANOVA) was used to assess the effect of excision on light and CO₂ response curves with branches as a random factor nested within treatments.

Results and Discussion

Time Course Measurements

After excision, all species showed a reduction in both A and g_s within 3 min (Figures 6-1 and 6-2). However, after 10 min, most species showed fewer fluctuations and appeared to stabilize for the remainder of the 60 min measurement period. This pattern indicates that hurrying to take a measurement on an excised branch may minimize, but not necessarily avoid changes in gas exchange rates caused by excision. At Ft. Sherman, the three species with the highest A for attached leaves, *A. membranacea*, *J. copaia*, and *V. ferruginea* (Table 6-1), also maintained the highest A at 60 min after excision (Figure 6-1). The other four species at Ft. Sherman, *A. cruenta*, *B. utile*, *M. bidentata*, and *S. amara*, suffered a greater reduction in A 60 min after cutting (Figure 6-1) and all produce latex or resin in the stem. *A. cruenta*, *B. utile* and *M. bidentata*, are from plant families well-known for this characteristic: the Apocynaceae, Moraceae, Sapotaceae, respectively. *Simarouba amara* has a clear yellow resin, also characteristic of its family, the Simaroubaceae (Croat 1978). Wounding stimulates latex and resin production (Kramer and Kozlowski 1979), which acts as a wound response and can

physically clog the xylem and prevent water loss and pathogen attack. However, once an excised stem is in water, if latex or resin leaks in the vicinity of the cut section of active xylem it can clog the xylem thus inhibiting water supply to the leaf and reducing A and g_s . Therefore, these data suggest that species with latex or resin do not perform well following excision.

At Parque Metropolitano, *L. seemannii* maintained a mean of 86.5% of intact photosynthetic rates 60 min after excision (Figure 6-1), whereas *P. septenatum* maintained only 13.4 and 5.5% of the average intact values for A and g_s , respectively, after excision (Figs. 6-1 and 6-2). *A. excelsum*, maintained only 26.6 and 48.6% of intact A and g_s , respectively after excision. With the exception of *P. septenatum*, species at Parque maintained higher percentages of intact g_s than A 60 min after excision (Figs. 6-1 and 6-2). In contrast, all species in the wetter forest at Ft. Sherman maintained a higher percentage of intact A , relative to g_s 60 min after excision (Figs. 6-1 and 6-2). This trend may be indicative of greater stomatal sensitivity in wet forest trees as a result of acclimation to humid conditions.

Response to Light

Photosynthetic light response curves following excision varied among species (Figure 6-3). Species such as *A. membranacea* and *L. seemannii* showed no differences between intact and excised branches, whereas *B. utile* and *S. amara* showed substantial differences in light-saturated photosynthesis (Figure 6-3). Although the curve from the excised branch was always lower, this difference was less than the variation between leaves from different branches, so excision did not significantly reduce A as a function of PFD in any of the six species investigated (Table 6-2). Therefore, the light response curve of any excised leaf is likely to reach lower values than measurements on the same leaf

when it is attached, but these lower values are also likely to fall within the range of values for attached leaves.

Excision decreased the calculated value of A_{\max} in *A. cruenta*, *B. utile*, and *S. amara* (Table 6-3) but not in the other three species investigated. Since A_{\max} is probably the most widely used parameter derived from light response curves and half of the species tested showed significant reductions upon excision, estimates of A_{\max} derived from light response curves on excised foliage must be interpreted with caution. Minor differences between Θ , Φ , and R_d from intact and excised light response curves were also observed in some cases (data not shown), but these differences were generally within the 95% confidence interval of the parameter in curve fitting.

Overall, most species appeared to perform better during light response curves than over time course measurements. Maintaining a portion of the leaf in the constant environment of the cuvette may help maintain consistency. How a leaf's ability to respond to short-term changes in light and VPD is affected following excision is unknown, but measurements suggest that constant conditions may result in more accurate measurements. (Reich et al. 1995) kept excised branches in sunlight, which is likely to have maintained the leaf in an induced state. In that study, attached foliage from pioneer species was compared with excised foliage from mature canopy species and it was found that the excised foliage of canopy species produced lower gas exchange rates. Since excision can negatively affect gas exchange rates in a systematic way, it is difficult to discern whether the lower gas exchange rates of canopy trees observed by Reich et al. (1995) are the result of excision-induced effects or represent characteristics that have evolved to specific environmental regimes. In either case, the species-specific responses

to excision presented in this paper suggest that it is important to consider the sensitivity to excision when comparing species or functional groups.

Response to CO₂

The effect of branch excision on leaf photosynthetic CO₂ responses was again species specific (Figure 6-4). Excision changed the general shape of the curve in *A. cruenta*, *B. utile*, and *S. amara*, whereas in *A. membranacea*, *L. seemanii*, and *V. ferruginea*, lower maxima were the main effect. *L. seemanii* and *V. ferruginea* were the only species exhibiting a significant effect of excision on photosynthetic responses to p_i (Table 6-2). In the other four species, A as a function of p_i was reduced following excision, but the magnitude of the effect of excision was small compared to the range of values encountered between branches and therefore, no statistical effect was detected.

The reduction in A during CO₂ response curves following excision may be indicative of non-uniform stomatal closure. Heterogeneous gas exchange over small areas of the leaf has been shown to occur in response to water stress (Downton et al. 1988). Heterogeneous stomatal closure has also been implicated in causing errors in estimating p_i and may explain observed reductions in A even when p_i does not appear to be limiting (Mansfield et al. 1990). Cheeseman (1991) demonstrated through simulation models that the effects of heterogeneous stomatal behaviour can only account for minor effects in calculating p_i , and therefore, on CO₂ response curves. Yet, the effects of patchy stomatal closure on CO₂ response curves presented by (Cheeseman 1991) are similar to the patterns of reduction following excision in this study, suggesting that stem water status is altered by excision and the reduction in g_s is heterogeneous over the leaf surface. Therefore, non-uniform stomatal behaviour may explain why for several species the main effect of excision on the CO₂ response curve was a slight reduction of the maximum. This

reduction probably reflects changes in stomatal behaviour rather than a reduction of the biochemical functioning of the photosystem.

Excision reduced the calculated values of both $V_{c_{\max}}$ and J_{\max} in *L. seemannii* and *S. amara* whereas in *A. membranacea* and *A. cruenta*, only the calculation of $V_{c_{\max}}$ was significantly affected (Table 6-3). In spite of multi-fold variation in $V_{c_{\max}}$ and J_{\max} among species, and in some cases between treatments, there was strong correlation between these two parameters ($r^2=0.89$). Excision did not produce a significantly different relationship ($t=-0.174$; $P>0.25$) between J_{\max} and $V_{c_{\max}}$, so a single linear regression was used. A slightly positive intercept of $13.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ was observed, along with a slope of 1.63. These results are consistent with those reported in a review of 109 species (Wullschleger 1993). In that study, Wullschleger (1993) also reported linear regression between J_{\max} and $V_{c_{\max}}$ with a positive intercept and a slope of 1.64. The consistency of the relationship between J_{\max} and $V_{c_{\max}}$ suggests that effects on water transport and patchy stomatal behavior are responsible for the differences in calculating biochemical parameters, rather than changes in biochemical activity.

Declining values of A at high p_i in CO_2 response curves on both attached and excised branches indicate an apparent limitation by triose phosphate utilization (Sharkey 1985) in *L. seemannii* and *V. ferruginea* (Figure 6-4). Limitation of A by TPU was once thought to occur rarely, but there is now increasing evidence that this limitation may be more common under conditions of high light and high p_i (Harley et al. 1992; Wullschleger 1993). Tropical forest canopies often experience high light and our data indicate that TPU limitation can be important for at least two species in these forests.

This finding has implications for modeling the responses of tropical forest to increases in atmospheric CO₂.

Conclusions

I investigated the utility of a technique for measuring gas exchange on excised foliage in tropical forest canopy trees. Responses to excision were species specific and there is some evidence that responses are related to phylogeny, potentially allowing prediction of how a species might perform. All species with latex or resin performed relatively poorly after excision and I suggest that these types of wound responses can clog cut xylem ends, thus reducing water transport. Patterns of reduction of A and g_s in time course measurements, light and CO₂ response curves appear to be mediated by stomatal closure as opposed to reductions in biochemical photosynthetic capacity. I recommend individual trials on all species to be investigated. It appears that anatomical, morphological, and possibly, phylogenetic differences can influence the response of gas exchange measurements to excision. Therefore, patterns of response to excision at taxonomic levels higher than species, and different growth forms, such as trees, vines and shrubs, should also be considered in broad species comparisons of photosynthetic measurements on excised branches.

Table 6-1. Light-saturated rate of net CO₂ assimilation per unit mass (A_{mass}) and area (A_{area}), leaf diffusive conductance (g_s), and specific leaf area (SLA) \pm 1 S.D. for 10 tropical tree species from the Republic of Panama.

Species	A_{mass} (nmol g ⁻¹ s ⁻¹)	A_{area} ($\mu\text{mol m}^{-2}$ s ⁻¹)	g_s (mmol m ⁻² s ⁻¹)	SLA (cm ² g ⁻¹)
Parque Metropolitano				
<i>Anacardium exelsum</i>	65.1 \pm 19.1	7.0 \pm 2.0	129.7 \pm 37.7	93.1 \pm 6.8
<i>Luehea seemannii</i>	114.8 \pm 12.6	14.8 \pm 1.6	592.2 \pm 140.0	79.5 \pm 11.9
<i>Pseudobombax septenatum</i>	146.8 \pm 20.3	12.4 \pm 1.7	347.0 \pm 57.1	118.6 \pm 7.7
Fort Sherman				
<i>Apeiba membranacea</i>	200.4 \pm 16.1	16.1 \pm 1.3	659.7 \pm 103.6	124.8 \pm 9.6
<i>Aspidosperma cruenta</i>	104.5 \pm 5.3	14.2 \pm 0.7	387.3 \pm 68.9	74.4 \pm 7.3
<i>Brosimum utile</i>	94.5 \pm 14.2	10.4 \pm 1.6	298.2 \pm 83.8	91.2 \pm 4.2
<i>Jacaranda copaia</i>	157.8 \pm 27.1	14.6 \pm 2.5	538.0 \pm 212.7	96.6 \pm 6.4
<i>Manilkara bidentata</i>	58.1 \pm 16.6	11.8 \pm 3.4	199.3 \pm 83.9	49.4 \pm 1.7
<i>Simarouba amara</i>	106.3 \pm 11.4	15.7 \pm 1.7	443.8 \pm 113.2	68.1 \pm 5.4
<i>Vochysia ferruginea</i>	134.5 \pm 7.5	15.2 \pm 0.8	670.2 \pm 83.9	89.5 \pm 9.7

Table 6-2. Repeated measures analysis of variance for the effects of excision on photosynthetic light and CO₂ response curves for 6 canopy tree species from the Republic of Panama.

Species	Light			CO ₂		
	SS	F	P	SS	F	P
<i>Apeiba membranacea</i>	13.20	4.38	0.171	0.22	2.98	0.227
<i>Aspidosperma cruenta</i>	9.27	12.90	0.173	50.93	40.84	0.099
<i>Brosimum utile</i>	10.36	2.46	0.361	76.13	1.35	0.452
<i>Luehea seemannii</i>	3.75	4.96	0.156	16.24	523	0.002
<i>Simarouba amara</i>	13.17	2.21	0.377	404.86	3.47	0.314
<i>Vochysia ferruginea</i>	4.58	18.30	0.146	13.82	4.97	0.038

Table 6-3. Means of model parameters from photosynthetic light and CO₂ response curves on leaves of intact (IN) and excised (EX) branches determined by least-squared estimates. Values of light-saturated rate of gross photosynthesis (A_{\max}) from light response curves, and maximum rate of carboxylation ($V_{c_{\max}}$) and electron transport (J_{\max}) from CO₂ response curves followed by the same letter are not significantly different ($P < 0.05$) based on Duncan's multiple range test. Comparisons are only valid within species.

Species	Method	A_{\max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	$V_{c_{\max}}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	J_{\max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
<i>Apeiba membranacea</i>	IN	20.0 ^a	51.9 ^a	102.9 ^a
	EX	18.9 ^a	42.5 ^b	86.3 ^a
<i>Aspidosperma cruenta</i>	IN	16.0 ^a	56.2 ^a	92.3 ^a
	EX	13.8 ^b	45.1 ^b	81.4 ^a
<i>Brosimum utile</i>	IN	12.8 ^a	35.0 ^a	64.5 ^a
	EX	9.8 ^b	29.2 ^a	54.5 ^a
<i>Luehea seemanii</i>	IN	14.9 ^a	38.3 ^a	82.7 ^a
	EX	13.3 ^a	27.5 ^b	65.2 ^b
<i>Simarouba amara</i>	IN	17.9 ^a	61.4 ^a	108.8 ^a
	EX	15.6 ^b	32.9 ^b	59.9 ^b
<i>Vochysia ferruginea</i>	IN	16.6 ^a	50.9 ^a	108.1 ^a
	EX	14.8 ^a	53.6 ^a	104.0 ^a

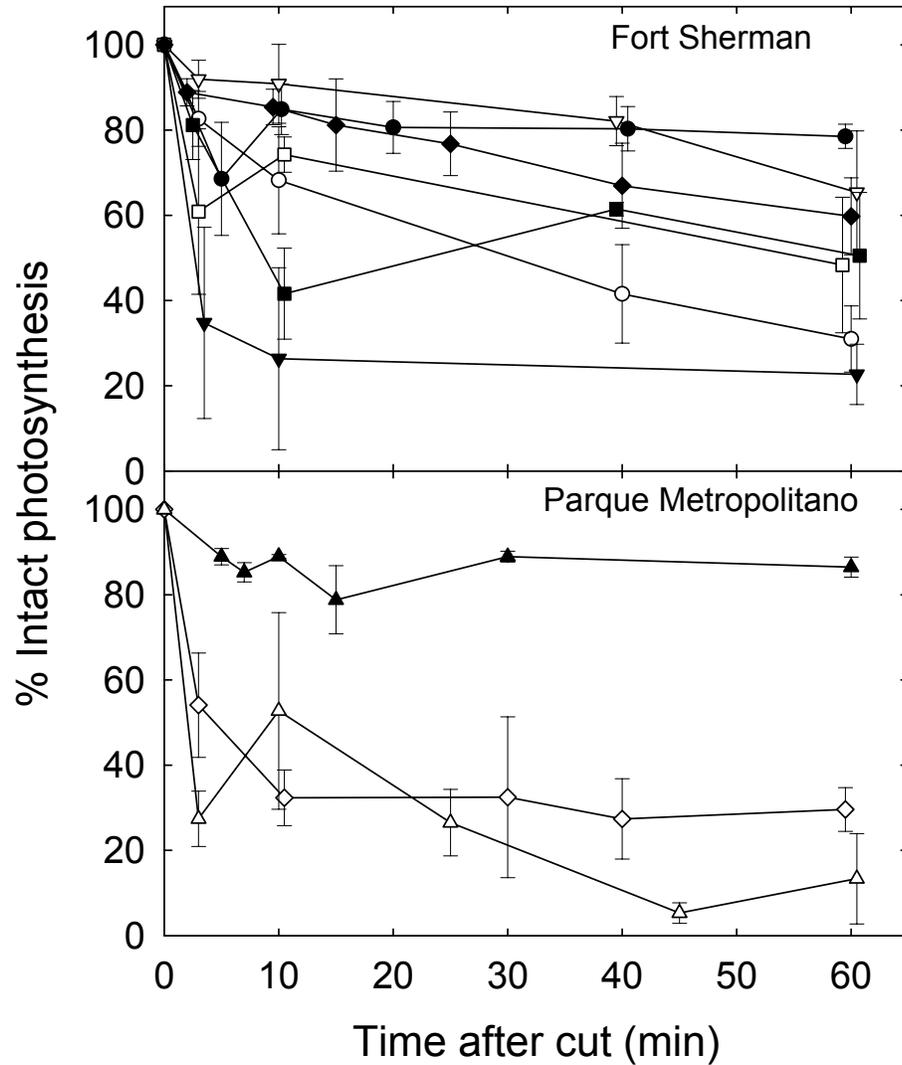


Figure 6-1. Percent of maximum photosynthesis of 3-5 leaves from excised branches at two canopy crane sites: Fort Sherman and Parque Metropolitano, Republic of Panama. Species at Fort Sherman: (filled circle) *Apeiba membranacea*, (open circle) *Aspidosperma cruenta*, (filled upside down triangle) *Brosimum utile*, (open upside down triangle) *Jacaranda copaia*, (filled square) *Manilkara bidentata*, (open square) *Simarouba amara* var. *typica* and (filled diamond) *Vochysia ferruginea*. Species at Parque Metropolitano: (open diamond) *Anacardium excelsum*, (filled triangle) *Luehea seemannii*, and (open triangle) *Pseudobombax septenatum*.

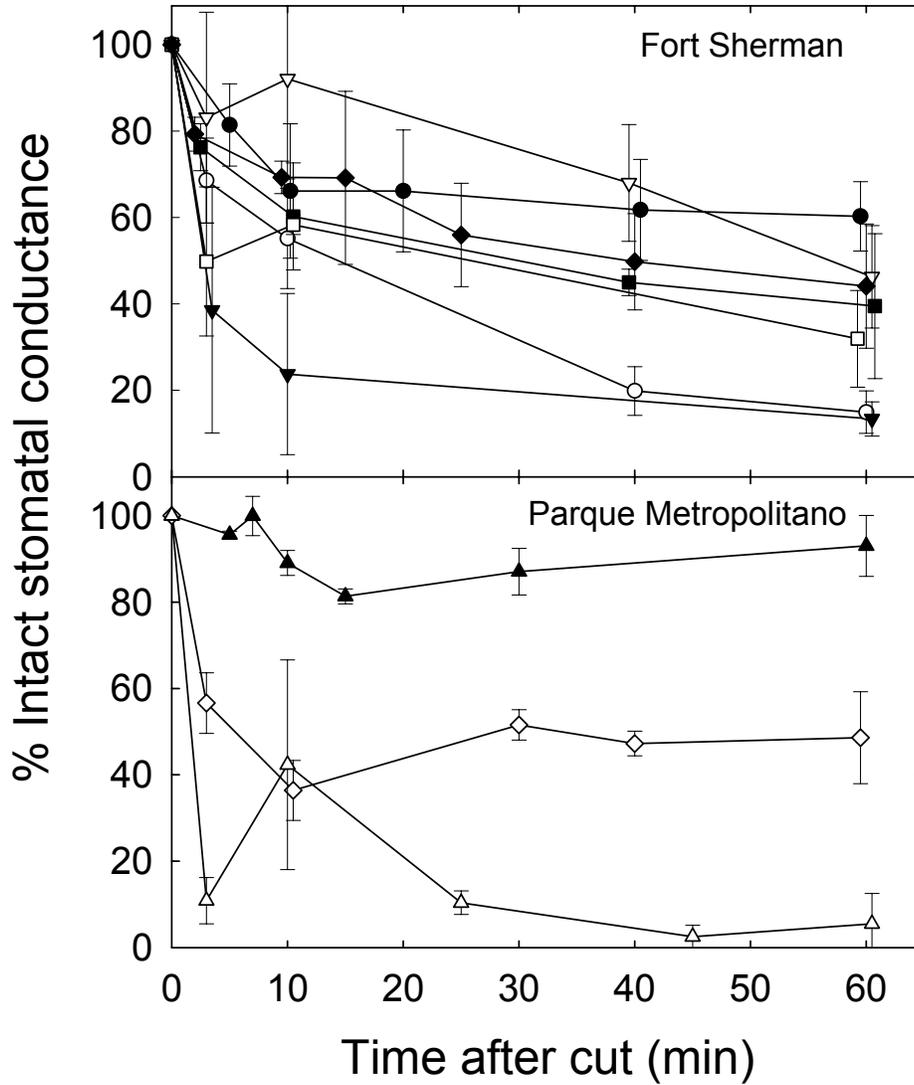


Figure 6-2. Percent of maximum stomatal conductance of 3-5 leaves from excised branches at two canopy crane sites: Fort Sherman and Parque Metropolitan, Republic of Panama. Symbols as in Figure 1.

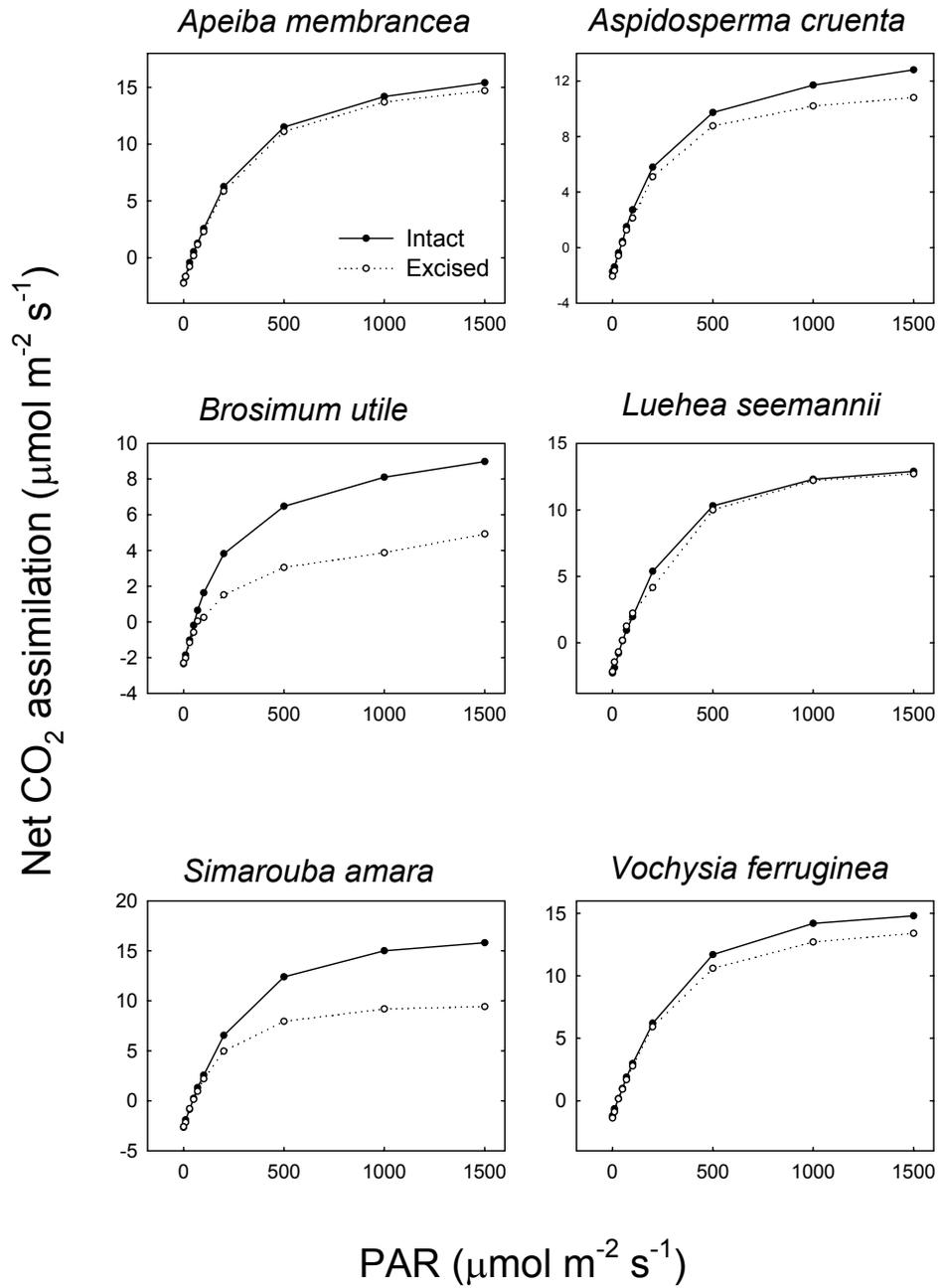


Figure 6-3. Representative curves of net CO₂ assimilation as a function of PFD, under 370 μmol mol⁻¹ CO₂, and ambient temperature (30-33 °C) and relative humidity (70-85%) for leaves of intact and excised branches.

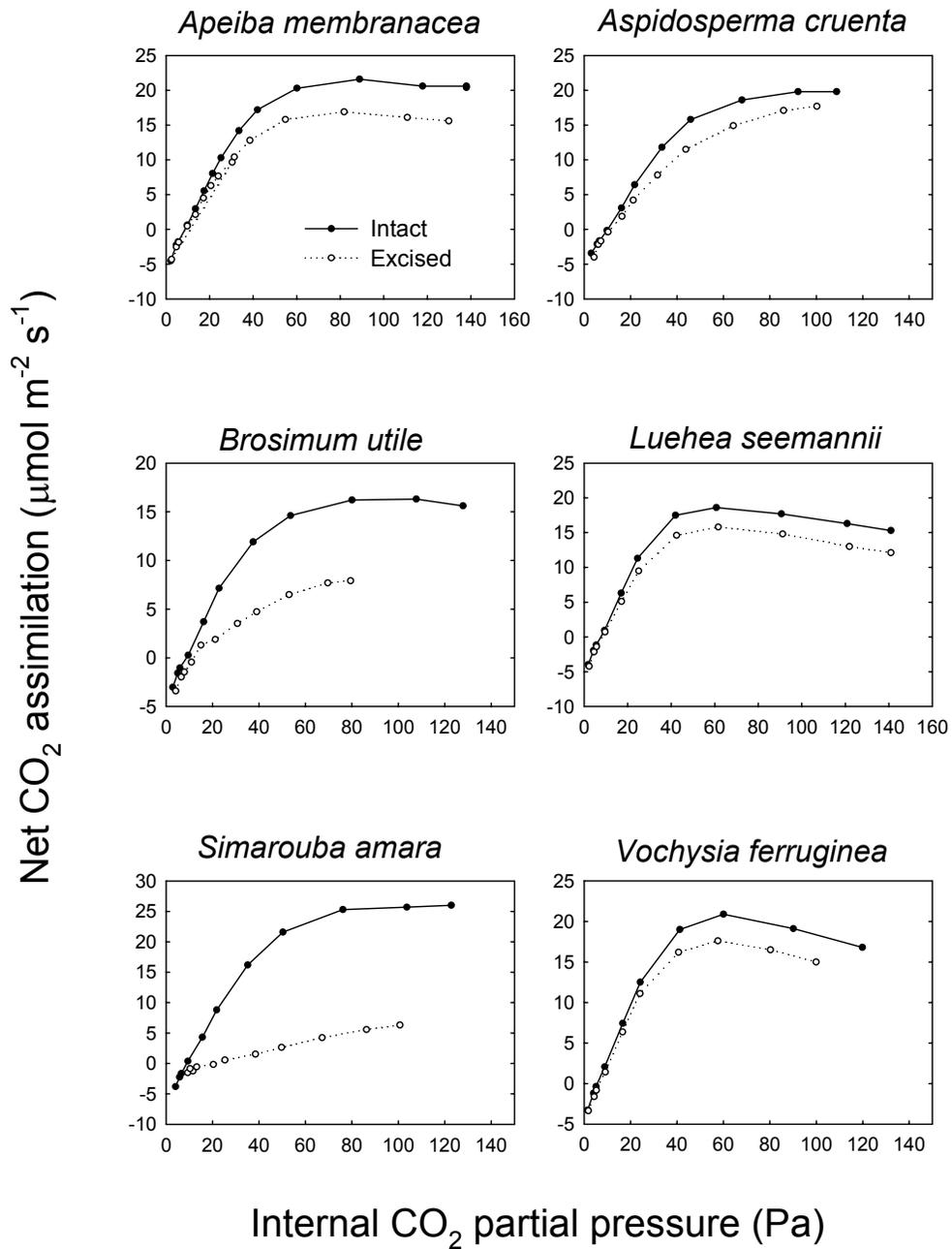


Figure 6-4. Representative curves of net CO₂ assimilation as a function of internal CO₂ partial pressure (p_i) under 1700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PFD, and ambient temperature (30-33 °C) and relative humidity (70-85%) for leaves of intact and excised branches.

CHAPTER 7 CONCLUSIONS

This dissertation emphasizes the relationship between leaf physiological traits and effects of plant species and communities on processes at the ecosystem scale. It appears that plant allocation to leaf photosynthetic capacity has the potential to reveal itself at larger spatial and temporal scales. The leaf traits evaluated in this dissertation have been shown to be interrelated and appear to have evolved in response to specific environmental regimes (Chapin 1980; Reich et al. 1992). The result that there is a relationship between leaf physiology and leaf litter decomposition suggests that the body of ecological literature on plant traits and life history characteristics may be extended to understand the effects of species on ecosystem processes.

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BIOGRAPHICAL SKETCH

Louis Stephen Santiago was born on February 13, 1970 in Aiea, Oahu, Hawaii. After several years, he moved with his family to San Francisco Bay, where he was raised. During his youth, Louis spent time playing in the dunes of Half Moon Bay, and walking in the East Bay hills and Sierra Nevada foothills with his father. These activities stimulated an interest in the natural world. For undergraduate studies, Louis attended the University of California at Berkeley. Although he began in Chemistry, he soon switched to Integrative Biology. He had the opportunity to work on several independent projects in the East Bay hills, in the Mojave Desert, and on the island of Moorea, Tahiti, in the South Pacific. These experiences inspired a strong interest in tropical biology. After graduating from the University of California in 1993, Louis began a masters program at the University of Hawaii, under the direction of Dr. Guillermo Goldstein. Louis pursued a masters project in the cloud forests of Waikamoi, Maui. Before graduating from the University of Hawaii, however, he spent five months at Dr. Goldstein's lab in Panama; and began developing the doctoral project presented in this dissertation. Louis then returned to Hawaii, graduated in 1998, and immediately began a doctoral program at the University of Florida with Dr. Stephen Mulkey. After completing his doctoral studies, Louis will return to the University of California at Berkeley for a postdoctoral position in stable isotope ecology.