The Impact of Annual and Seasonal Rainfall Patterns on Growth and Phenology of Emergent Tree Species in Southeastern Amazonia, Brazil

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ABSTRACT

Understanding tree growth in response to rainfall distribution is critical to predicting forest and species population responses to climate change. We investigated inter-annual and seasonal variation in stem diameter by three emergent tree species in a seasonally dry tropical forest in southeast Pará, Brazil. Annual diameter growth rates by *Swietenia macrophylla* demonstrated strong positive correlation with annual rainfall totals during 1997–2009; *Hymenaea courbaril* growth rates demonstrated weak positive correlation, whereas *Parkia pendula* exhibited weak negative correlation. For both *Swietenia* and *Hymenaea*, annual diameter growth rates correlated positively and significantly with rainfall totals during the first 6 mo of the growing year (July to December). Vernier dendrometer bands monitored at 4-wk intervals during 3–5 yr confirmed strong seasonal effects on stem diameter expansion. Individuals of all three species expanded in unison during wet season months and were static or even contracted during dry season months. Stems of the deciduous *Swietenia* contracted as crowns were shed during the early dry season, expanded slightly as new crowns were flushed, and then contracted further during 3–5 wk flowering periods in the late dry season by newly mature crowns. The three species' physiographic distribution patterns at the study site may partially underlie observed differences in annual and seasonal growth. With most global circulation models predicting conditions becoming gradually drier in southeast Amazonia over the coming decades, species such as *Swietenia* that perform best on the 'wet end' of current conditions may experience reduced growth rates. However, population viability will not necessarily be threatened if life history and ecophysiological responses to changing conditions are compensatory.

Abstract in Portuguese is available in the online version of this article.

Key words: big-leaf mahogany; climate change; dendrometer bands; diameter growth; fava bolota; jatobá; reproductive phenology; seasonal tropical forest; tropical timber species.

TREES WITHIN LOCAL SPECIES POPULATIONS GROW AT DIFFERENT RATES relative to each other and from year to year, for reasons ranging from genetic fitness to the climatic impacts of distant sea surface temperature anomalies such as the El Niño-Southern Oscillation (ENSO; Brienen *et al.* 2010). Individual tree-level factors such as stem size (diam), crown vine coverage, crown exposure to overhead sunlight, and growth history account for most observed within-population differences in growth rates (Clark & Clark 1996, Finegan *et al.* 1999, King *et al.* 2006, Grogan & Landis 2009). Climatic factors such as variation in annual and seasonal rainfall influence growth at the level of populations, affecting all individuals in roughly equivalent fashion even though individual- and species-level responses may vary widely (Clark & Clark 1994). While dendrochronological studies reconstructing growth histories from annual tree rings are increasingly being used to investigate the influence of climate on growth by tropical trees (Brienen & Zuidema 2005, Therrell *et al.* 2007), long-term studies featuring annual measurements of live trees remain rare in the literature (Clark *et al.* 2010).

Understanding growth in response to rainfall distribution is critical to predicting forest and species population responses to climate change. Global circulation models predict more than a 20 percent decline in rainfall in the eastern Amazon by the end of this century, with the biggest decline occurring during the dry season (IPCC [Intergovernmental Panel on Climate Change] 2007, Da Silva *et al.* 2008, Malhi *et al.* 2008, Nepstad *et al.* 2008). Increased intensity of ENSO events or a shift in the mean ENSO state toward more El Niño-like conditions could exacerbate an overall drying trend (Kriegler *et al.* 2009, Latif & Keenlyside 2009). Regional-scale deforestation, particularly beyond a threshold in the range of 30–40 percent of the Amazon basin, may also result in reduced rainfall (Sampaio *et al.* 2007, Nepstad *et al.* 2008). Increasing temperatures, already observed in the tropics, could intensify moisture stress experienced by trees, whereas CO_2 fertilization could lead to reduced transpiration (Wright 2010). Although uncertainty remains about the magnitude of these changes, trees will experience increased drought severity in the Amazon of the future and associated increased risk of dry season fires, especially in seasonally dry forests (Holdsworth & Uhl 1997, Nepstad *et al.* 1999, 2004, 2008). Inter-annual variability in observed growth relative to the amount and temporal distribution

of rainfall can provide insight into the sensitivity of trees to climate change.

Inter-annual and seasonal variations in stem diameter increment are well-known phenomena of seasonally dry tropical forests (Daubenmire 1972). Years during which trees grow faster than average have been shown to correspond with higher than average annual rainfall totals (Worbes 1999, Enquist & Leffler 2001, Brienen & Zuidema 2005, Shono & Snook 2006) or wetter than average dry seasons (Clark et al. 2010), although the opposite has been observed in less seasonal forests (Schuur 2003, Laurance et al. 2009). Diameter increment may be sensitive to rainfall totals – and corresponding soil water availability – during different periods of the year. For example, Dünisch et al. (2003) demonstrated significant positive correlation between annual increment and precipitation totals during the early and late months of the wet season for big-leaf mahogany (Swietenia macrophylla, Meliaceae) in southwest Brazilian Amazonia based on annual ring counts from radial disks cut from forest trees. Brienen and Zuidema (2005), using similar methods in the Bolivian Amazon, found that annual increment rates by Spanish cedar (Cedrela odorata, Meliaceae) correlated most significantly with rainfall totals during the wet to dry season transition period, whereas two other species (Cedrelinga catenaeformis, Mimosoideae and Tachigali vasquezii, Caesalpinioideae) showed strong positive increment correlation with rainfall totals at the beginning of the wet season. How widespread these patterns are, among species and geographic populations within species, and their ecophysiological bases, remain poorly understood.

In this article, we examine relationships between tree diameter expansion (or contraction) by three emergent tree species and rainfall patterns in southeastern Amazonia at three temporal scales: (1) annual, comparing 'growing season' rainfall totals from mid dry season during one year to mid dry season during the next year (July to June) with diameter measurements repeated each dry season from 1997 to 2009; (2) seasonal, comparing rainfall totals during 4-wk intervals with stem diameter data from vernier dendrometer bands censused at the same intervals during 1997–2001; and (3) within-dry season, reporting stem diameter behavior during crown leaf loss, reflush, and flowering from dendrometer band measurements for one species at 3-d intervals in 1997. The study species are high-, medium-, and low-value timber trees with wide Neotropical distributions: big-leaf mahogany, jatobá (Hymenaea courbaril, Caesalpinioideae), and fava bolota (Parkia pendula, Mimosoideae), respectively.

STUDY SPECIES.—Big-leaf mahogany (henceforth 'Swietenia') is a canopy-emergent species associated with seasonally dry tropical forests from Mexico to Bolivia. Its local distribution in the Brazilian Amazon commonly traces seasonal streams or rivers. Population densities are typically < 1 adult tree/ha, but may be locally higher (Baima 2001, Grogan et al. 2008). Swietenia is a fast-growing, light-demanding late successional species that is deciduous during part of the dry season in southeastern Amazonia (Lamb 1966, Grogan 2001). Trees in the present study survived selective logging in the early 1990s that reduced landscape-scale densities from 0.65 to 0.19 trees > 20 cm diam/ha (Grogan et al. 2008).

Hymenaea courbaril and Parkia pendula (henceforth 'Hymenaea' and 'Parkia') are also canopy-emergent species with generally low population densities. Although now commonly harvested for timber throughout the Amazon, neither species was logged at the study site. Hymenaea has dense wood and displays slower diameter growth than Swietenia, whereas Parkia presents relatively low wood density and high growth rates relative to Swietenia (Schulze et al. 2008). Hymenaea is evergreen, with fruits ripening during July to September at the study site. Hymenaea trees have been shown to produce annual growth rings, reflecting a strong growth response to seasonal drought (Tomazello 1995, Westbrook et al. 2006, Lisi et al. 2008). Parkia is dry season deciduous within the study region, and produces mature fruits over an extended period of the dry and early wet seasons.

METHODS

STUDY SITE.—The study site is a 4100-ha forest industry-owned management area called Marajoara, located at 7°50′ S, 50°16′ W, 34 km northwest of Redenção in the southeast corner of the state of Pará. Climate is tropical dry. Annual precipitation during 1995–2001 at Marajoara averaged 1859 mm (range 1636–2170 mm), with more than 90 percent falling between November and May; in some years, no rain fell for 3–4 mo during the dry season (Grogan & Galvão 2006). All streams within the principal research area are seasonal. Swietenia is restricted to low ground adjacent to streams at Marajoara, whereas Hymenaea and Parkia are distributed evenly across slopes on the landscape (Fig. 1). The forest is dominated by evergreen trees intermixed with deciduous species. The site is surrounded by heavily logged and burned forest and pasture.

FIELD METHODS.—Daily rainfall at Marajoara was measured from October 1996–October 2001 as described by Grogan and Galvão (2006). Monthly rainfall totals from January 1998–December 2009 were extracted from Tropical Rainfall Measuring Mission (TRMM) data combining satellite and ground-based rainfall measurements in 0.25 × 0.25 degree grid boxes on a monthly basis (NASA 2010). Mean annual TRMM rainfall totals were 1892 ± 72 (SE) mm during 1998–2009 for the Marajoara site, compared with observed totals of 1859 ± 82 mm during 1996–2001 (Grogan & Galvão 2006). Observed vs. TRMM monthly rainfall totals during 46 mo of overlap (January 1998–October 2001) demonstrated strong positive correlation (Pearson $r = 0.867$). Annual rainfall totals are reported here for July to June, beginning and ending in the middle of the dry season.

The Swietenia population at Marajoara was composed of 358 trees > 10 cm diam within a core research area of 2050 ha. These trees survived logging either by being designated as seed trees in fulfillment of industry regulations or by escaping notice of logging company mateiros (woodsmen responsible for locating merchantable trees in primary forests). The largest tree included in the sample was 146 cm diam. The Hymenaea and Parkia populations were composed of 195 and 123 trees > 10 cm diam, respectively, within a smaller area of 1035 ha. The largest trees included were 124 and 90 cm diam, respectively.
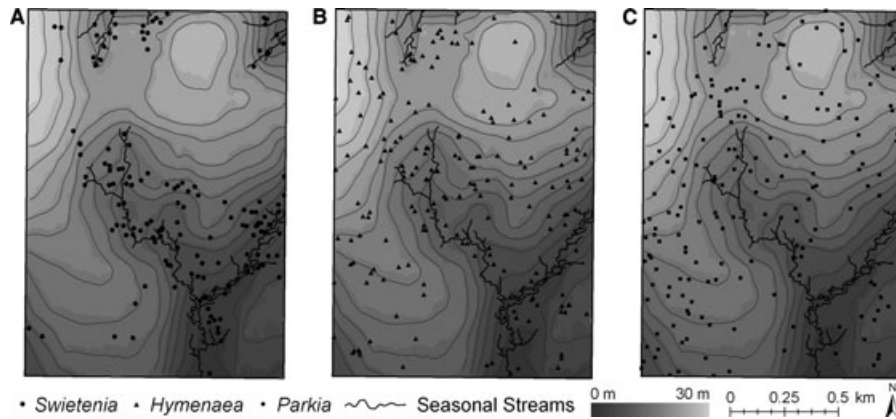
FIGURE 1. Spatial distribution patterns of three emergent timber species in southeast Pará, Brazil relative to topography and seasonal streams, for trees ≥ 20 cm diameter mapped in a 204-ha permanent plot (1200 × 1700 m) (Grogan *et al.* 2008, Schulze *et al.* 2008). (A) *Swietenia*, (B) *Hymenaea*, (C) *Parkia*.

Tree stem diameters were measured annually during the dry season (July to August) from 1997 to 2009; *Parkia* trees were included in the study beginning in 1999. Population-level diameter growth rates are reported for a subset of trees (N = 252, 96, and 89 for *Swietenia, Hymenaea*, and *Parkia*, respectively) based on two criteria: they should have a minimum stem diameter of 20 cm, and a measured diameter growth rate for each full year of the study period. This eliminated trees that died during the observation period, and those that were included in the sample after the 1997 dry season (or after 1999 in the case of *Parkia*). Tree diameters were measured at 1.3 m above the ground or at least 60 cm above the reach of the highest buttress, and again 30 cm above this height; trees with tall buttresses were measured as high as 3.4 m above the ground. Aluminum nails were affixed 10 cm above the second (highest) measurement plane on opposite sides of each tree to afford precise re-location of measurement heights each year. Annual diameter increment was calculated as the difference between current and previous year's measurements at a given height on the stem, averaged between the two measurements per tree. Diameter measurements were made by a single four-person field crew throughout the study period to reduce measurement error associated with unfamiliar field and tree conditions.

Spring-loaded vernier dendrometer bands (Cattelino *et al.* 1986, Keeland & Sharitz 1993) were placed on 40 *Swietenia* trees > 10 cm diam in November 1996, divided three per 10-cm size class as far as possible given the available sample of live trees. The principal criteria for choosing trees for inclusion in the dendrometer study were that they be apparently healthy (no obvious injury, especially broken crown or stem wound) and within 1 hr walking distance of camp. Bands were placed at least 50 cm above buttresses. Trees were censused at 4-wk intervals from December 1996 to January 2001, with measurements read as mm of stem girth expansion or contraction. Twenty-one *Hymenaea* trees > 10 cm diam were banded in August 1998, and six *Parkia* trees > 20 cm diam were banded in January 1999. *Hymenaea* and *Parkia* trees were recensused at 4-wk intervals along with the original sample of *Swietenia* until January 2001.

To determine whether stem girth changes relate to *Swietenia* crown phenology during the dry season period of leaf replacement and flowering, crown phenology was observed on 23 of 40 mahogany trees with dendrometer bands at 2-wk intervals during five consecutive dry seasons from 1997 to 2001, every other observation coinciding with dendrometer band measurements. At each observation, we visually assessed crown leaf exchange by dividing crown leaf loss into four stages representing progressively thinner crowns until complete deciduousness, and by dividing crown leaf replacement into four stages representing progressively more mature crowns until leaves achieved full size and dark green (mature) color (Grogan *et al.* 2010). Flowering, which follows shortly after new leaves are mature, was confirmed either by observing receptive flowers on the crown through binoculars or fallen to the ground below. A subset of five trees was observed in this way at 3-d intervals for 42 d in the late dry season of 1997 during crown flushing and flowering, with dendrometer band measurements taken at each observation.

DATA ANALYSIS

We used the Pearson product-moment correlation coefficient (r) to test the association between observed and TRMM rainfall data, and between rainfall totals and diameter (or girth) increment. Pearson r values approaching 1.0 and −1.0 indicate perfect positive or negative correlation, respectively. Pearson r values and attendant statistical significance were computed using the R statistical software package (version 2.9.2; R Foundation for Statistical Computing, http://www.r-project.org). We investigated multiple regression models for diameter growth using best subsets of annual rainfall, total rainfall in the preceding year, dry season rainfall, early wet season rainfall, and year (Minitab v.11; Minitab Inc., State College, Pennsylvania, U.S.A.).

RESULTS

EFFECT OF VARIATION IN ANNUAL PRECIPITATION ON POPULATION-LEVEL DIAMETER GROWTH.—Annual rainfall totals from daily

observed plus TRMM-extracted monthly data over the 12-yr study period ranged from 1561 to 2232 mm/yr at Marajoara. Mean annual diameter growth rates ranged by almost a factor of two for the two fastest growing species, *Parkia* and *Swietenia* (Table 1). Growth rates by *Swietenia* demonstrated strong positive correlation with annual precipitation totals (Pearson $r = 0.8682$, $P = 0.0003$; Table 2; Fig. 2A). Mean annual diameter growth rates by *Hymenaea* demonstrated weak positive correlation with annual precipitation totals (Table 2; Fig. 2B). *Parkia* exhibited weak negative correlation between diameter growth rates and annual precipitation, growing faster, on average, during years with relatively low precipitation totals (Table 2; Fig. 2C).

Dividing annual precipitation totals into 3- and 6-mo sub-totals (Dünisch *et al.* 2003, Brienen & Zuidema 2005), both July–September (first 3 mo of the growing year) and October–December (second 3 mo) correlated strongly with mean annual diameter growth rates by *Swietenia*, and July–December (first 6 mo of the growing year) sub-totals yielded significant positive correlation (Table 2). Sub-totals for the second half of the growing year correlated weakly with annual growth rates. *Hymenaea* demonstrated significant positive correlation between annual growth and rainfall totals during the second 3-mo period (October–December) and the first 6 mo (July–December); otherwise

TABLE 1. *Range of population-level mean annual diameter growth rates (1997–2009, cm/yr), from lowest year to highest, for the three study species (except Parkia = 1999–2009). Numbers in parentheses indicate one standard error of the mean.*

	Lowest (SE)	Highest (SE)
Swietenia	0.48 (0.022)	0.84 (0.030)
Hymenaea	0.34 (0.040)	0.60 (0.043)
Parkia	0.68 (0.043)	1.21 (0.073)

TABLE 2. *Pearson product-moment correlation coefficients (r) and P-values for annual precipitation vs. mean annual diameter growth rates (1997–2009, N = 12 except for Parkia as noted). Annual totals are growing season totals, measured from the middle of the dry season (July–June). Sub-totals divide the year into 3- and 6-mo periods. Bold values indicate significant P-values at α = 0.05.*

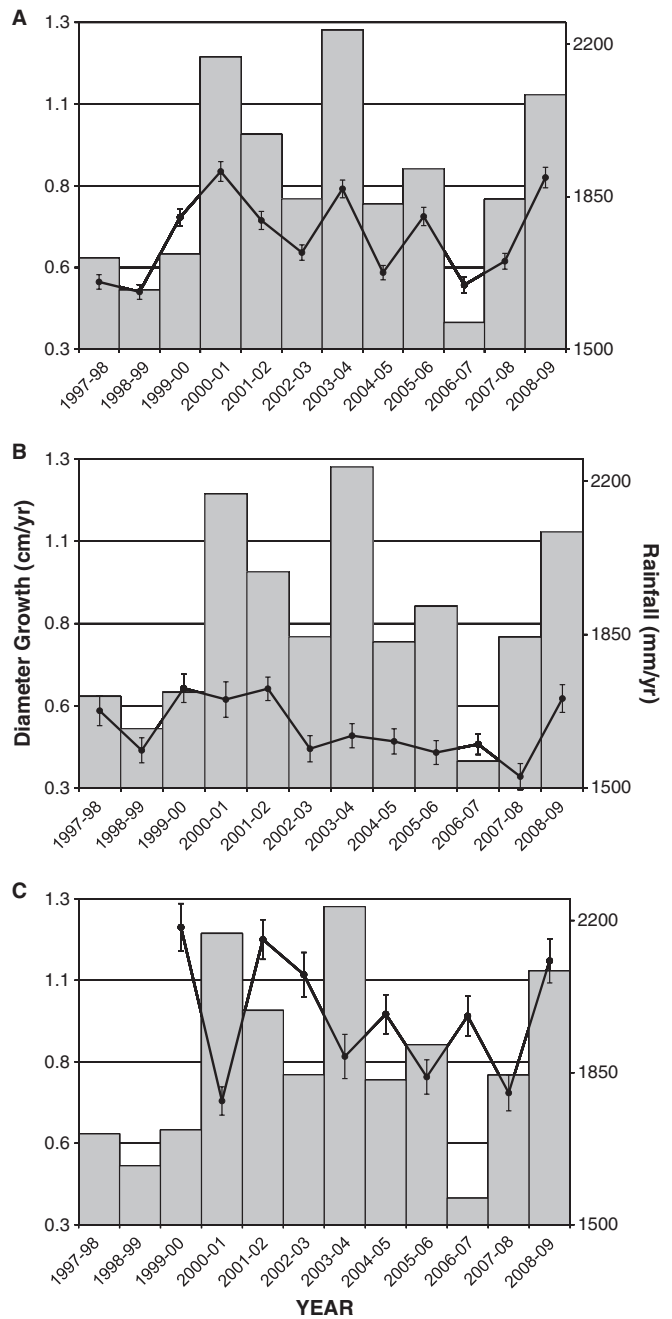|	*Swietenia*		*Hymenaea*		*Parkia*	
	r	P	r	P	r	P
July–June total	0.8682	**0.0003**	0.2875	0.3649	−0.2877	0.4203
July–Sept	0.5340	0.0737	0.3079	0.3303	−0.3246	0.3601
Oct–Dec	0.5232	0.0809	0.8024	**0.0017**	0.2251	0.5318
July–Dec	0.6506	**0.0220**	0.7469	**0.0053**	0.0187	0.9592
Jan–March	0.2775	0.3826	−0.1619	0.6151	−0.4201	0.2268
Apr–June	0.3220	0.3074	−0.2499	0.4335	−0.0119	0.9740
Jan–June	0.4695	0.1236	−0.3206	0.3096	−0.3578	0.3101

FIGURE 2. Mean annual diameter growth rates by sample populations during 1997–2009 (lines), with annual precipitation totals (July–June) in mm (bar columns). (A) *Swietenia*, N = 252; (B) *Hymenaea*, N = 96; (C) *Parkia*, N = 89. Trees are ≥ 20 cm diam. Error bars show ± SE. Increment data for *Parkia* are not available during 1997–1999.

correlations were positive during the first half of the year and weakly negative during the second half. Mean annual growth rates by *Parkia* were negatively correlated with precipitation sub-totals except for the second 3-mo period (October–December) and the first 6 mo (July–December); no relationships were statistically significant.
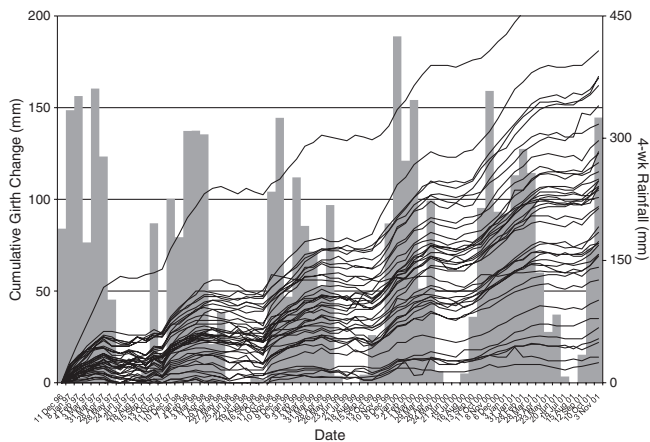
FIGURE 3. Stem girth change by 40 mahogany trees with vernier dendrometer bands from start in December 1996 at 4-wk intervals during 1997–2001. Bar columns show precipitation totals during the 4 wk prior to each measurement.

FIGURE 4. Mean stem girth change from dendrometer bands at 4-wk intervals for (A) *Swietenia* from December 1996 to November 2001, $N = 40$; (B) *Hymenaea* from August 1998, $N = 21$; and (C) *Parkia* from January 1999, $N = 6$. Error bars show ± SE. Bar columns show precipitation totals during the 4 wk prior to each measurement. Note different left y-axis for *Swietenia*.

No two- or three-factor regression model outperformed single-factor models in explaining variation in mean annual growth; no multi-factor model was found where all factors were significant. For *Swietenia*, total rainfall during the growth year explained most of the variation in annual increment ($R^2 = 72.9$, F = 30.6, $P < 0.001$). October–December rainfall sub-total was the best predictor of *Hymenaea* annual increment ($R^2 = 60.7$, F = 18.0, $P = 0.002$). No valid regression model could be constructed for *Parkia*.

EFFECT OF SEASONAL VARIATION IN PRECIPITATION ON STEM DIAMETER: DENDROMETERS.—Vernier dendrometer measurements show that stem diameters of 40 *Swietenia* trees expanded during successive wet seasons and discontinued expansion or contracted during successive dry seasons (Fig. 3). The relationship between stem expansion/contraction and precipitation during 4-wk observation periods was positive and significant (Pearson $r = 0.7427$, df = 64, $P < 0.0001$). While some trees grew much faster than others, ranging from 0.07 to 1.41 cm/yr of diameter expansion over the 5 yr of observation, periods of expansion, dormancy, and contraction were timed essentially the same for all individuals. Mean dendrometer measurements during each census period demonstrate this seasonal growth pattern more clearly (Fig. 4A). In 3 of 4 yr with complete seasonal data, a sharp spike in diameter expansion occurred near the beginning of the wet season (September–November depending on the year). Mean stem expansion then declined through the mid to late wet season (January–April) until trees contracted at the beginning of the dry period (May) as seasonal rainfall stopped. During 3 of 5 yr, tree stems then expanded during the dry season after rainfall had stopped completely before contracting again. This pattern was repeated twice during the 1997 and 1999 dry seasons when the wet season's onset was delayed.

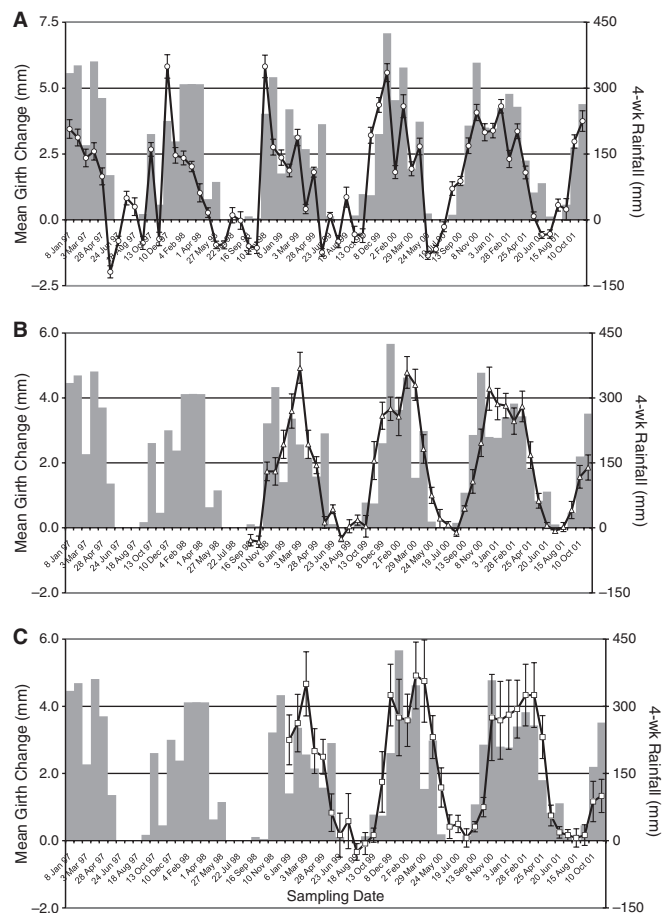Dendrometer measurements for *Hymenaea* and *Parkia* trees showed seasonal patterns similar to *Swietenia*'s, with wet season expansion and dry season dormancy or contraction (Figs. 4B and C). Dormancy and contraction were timed essentially the same for all individuals. The relationship between stem expansion/contraction and precipitation during 4-wk observation periods was positive and highly significant (Pearson $r = 0.7424$ & 0.7421, df = 41 & 37, respectively; $P < 0.0001$). Expansion rates by *Hymenaea* and *Parkia* trees during the measurement period ranged from 0.05–1.31 and 0.34–1.54 cm/yr, respectively.

Equivalent correlation values for the three species between 4-wk rainfall totals and mean dendrometer stem increments were largely a function of extreme values associated with zero or negative increment (contraction) during dry season periods of little or no rain. Stem expansion patterns during the rainy season, defined here as months with ≥ 100 mm of rainfall, tell a different story. *Swietenia* demonstrated statistically significant correlation between rainfall totals and stem increment under this condition (Pearson $r = 0.4155$, df = 37, $P = 0.0103$), whereas *Hymenaea* (Pearson $r = 0.1260$, df = 23, $P = 0.5575$) and *Parkia* (Pearson $r = 0.1690$, df = 21, $P = 0.4521$) did not.

SWIETENIA CROWN PHENOLOGY AND STEM CONTRACTION/
EXPANSION.—*Swietenia* trees at Marajoara began shedding leaves as
the wet season subsided during May. Complete leaf loss by indi-
vidual trees occurred over 1–3 mo. The leafless period was short,
lasting 5–10 d before new leaves emerged. Crown reflush to full-
sized mature leaves took approximately 1 mo. Inflorescences
emerged with new leaves, and flowering initiated 1–2 wk after
new crowns were mature.

Coupling dendrometer data with crown phenology data col-
lected at 2-wk intervals during the 1997–2001 dry seasons, a con-
sistent pattern emerged: (1) stems contracted as crowns shed
leaves until the deciduous state; (2) stems expanded slightly as
crowns flushed new leaves; (3) stems contracted again as crowns
flowered over the course of 3–5 wk. This pattern would be more
visibly pronounced at the sample level – the magnitude of nega-
tive diameter increment during each dry season would be greater
in Figure 4A – if crown and reproductive phenology were more
tightly synchronized among trees (Grogan 2001). During years
with short dry seasons and or early wet season onset, stem con-
traction during flowering did not occur, as early rains caused
stems to expand instead (*e.g.*, in 2000 and 2001, Fig. 4A).

Five trees monitored for stem girth change at 3-d intervals
during the latter part of the 1998 dry season (26 August–7 Octo-
ber during which 10 mm of rain fell) demonstrate this pattern
with variations (Table 3). Tree #40302, relatively small at
22.3 cm diameter and growing in shallow, excessively draining soil
on a boulder outcrop, remained leafless throughout the observa-
tion period and contracted slightly in stem girth at the end of this
period. The other trees contracted in girth as new crowns
approached maturity or as flowering proceeded.

DISCUSSION

Changes in stem diameter through time as measured externally by
diameter tapes and vernier dendrometer bands do not necessarily

reflect true 'growth' or wood increment. Stems may also expand
and contract as bark moisture content increases and declines
during respective wet and dry seasons (Zweifel *et al.* 2000, Stahl
et al. 2010), and as xylem tension rises and falls as a function of
soil moisture availability through the seasons (Borchert 1980,
1994, Reich & Borchert 1982, 1984). We consider results from
annual diameter measurements of the three study species
equivalent to true growth increment because the timing of each
year's census, in the middle of the dry season (July–August),
ensured that bark moisture content and xylem tension were
approximately equal from one year to the next (but see Baker
et al. 2002). The source (or sources) of seasonal changes as mea-
sured by dendrometers, however, remains ambiguous in the
absence of data on bark moisture content and stem water status.

ANNUAL DIAMETER GROWTH PATTERNS.—Mean annual *Swietenia*
diameter growth increment increased predictably with total annual
(July–June) rainfall and with rainfall totals during the first half
of the growing season at Marajoara. This finding corroborates
results from field studies in Mexico, Belize, and southwestern
Amazonia showing that diameter growth rates by *Swietenia*
increase with annual precipitation totals (Whigham *et al.* 1998,
Dünisch *et al.* 2003, Shono & Snook 2006). Our data suggest
that rainy season duration influences annual growth patterns
more than total precipitation, that is, whether wet season onset
occurs in September vs. October or even late November. As a
result of *Swietenia*'s marked response to early rains (see below),
early wet season onset may extend the growing season by
2–3 mo regardless of total rainfall.

Swietenia is restricted to fast-draining sandy soils on low
ground adjacent to seasonal streams at the study site (Grogan
et al. 2003), whereas *Hymenaea* and *Parkia* are topographic and soil
generalists, exhibiting a faint repulsion from *Swietenia* habitat
(Fig. 1). *Swietenia* is one of many buttressing, shallow-rooted tree
species dominating low-ground areas where phreatic water

TABLE 3. *Interaction between stem girth (mm) and crown phenology of five mahogany trees at 3-d intervals over 42 d during the late dry season in 1998 when trees were leafless and or*
leafing out and flowering. Crown flushing and flowering were associated with stem girth contraction. Rainfall accumulation during this period was 8 mm on day 12 and 2 mm
on day 22 (10 mm total). Legend for crown stages: - = leafless; n1 = new leaves 0–25 percent full size; n2 = new leaves 25–50 percent full size; n3 = new leaves 50–
75 percent full size; n4 = new leaves full size; m = mature leaves; b = flower buds; f = active flowering (Grogan et al. *2010).*

		Days from 26 August 1997														
Tree ID		0	3	6	9	12	15	18	21	24	27	30	33	36	39	42
40302	Crown	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
(22.3cm)	Girth	0	0	0	0	0	0	0	0	0	0	0	−0.5	−1	−1	−1
40501	Crown	n2	n2	n2	n3	n4	n4	mb	mb	mb	f	f	f	f	f	m
(30.3cm)	Girth	0	0	0	−1	−1	−3	−3	−3	−4	−4.5	−5	−5.5	−5	−5	−5
41005	Crown	n3	n4	n4	mb	mb	f	f	f	f	f	f	f	m	m	m
(39.3cm)	Girth	0	0	0	−0.5	−1	−2	−2	−2	−2	−2	−2	−3	−2.5	−3	−3
40503	Crown	n2	n3	n3	n4	n4	mb	f	f	f	f	f	f	f	m	m
(53.0cm)	Girth	0	0	0	0	0	0	0	0	−1	−1	−1	−1	−1	−1	−1
41003	Crown	n1	n2	n4	n4	n4	mb	mb	f	f	f	f	f	f	f	f
(67.9cm)	Girth	0	0	0	0	−1	−2	−2	−2.5	−3	−4	−5	−5.5	−5	−6	−6

frequently perches at ground level during the rainy season. The low-ground community experiences higher mortality rates during years with extended dry seasons compared with largely evergreen communities on higher ground (J. Grogan & M. Schulze, unpubl. data). Successive drought years lowering phreatic water below average dry season levels can retard wet season recharge and exacerbate mortality in low-ground areas at the study site (Grogan & Galvão 2006). Studies demonstrating that shallow-rooting species are more sensitive to rainfall patterns (Noldt *et al.* 2001, Dünisch *et al.* 2003) support results reported here for *Swietenia*.

This study's second deciduous species, *Parkia*, demonstrated quite different stem behavior with respect to annual rainfall totals, tending to grow more robustly during years with lower rainfall. This pattern has been observed in other tropical regions for canopy and emergent species (Laurance *et al.* 2004, 2009) and attributed to causes such as increased solar radiation during drier years (Graham *et al.* 2003, Nemani *et al.* 2003, Wright 2005, Saleska *et al.* 2007, Laurance *et al.* 2009) and, for less seasonal sites, increased soil oxygen availability (Schuur 2003). In the absence of appropriate data, we cannot address these possible causes. However, why some light-demanding deciduous species would increase growth rates during sunnier (drier) years whereas others – see *Swietenia* – would not, remains an open question. Most *Parkia* and *Hymenaea* trees occur at mid- to upper-slope topographic positions at Marajoara, where soil moisture relations are moderated by finer texture and non-waterlogged conditions during the wet season (Grogan & Galvão 2006). We suggest that soil moisture relations tend to dominate annual growth patterns by shallow-rooting species and or species associated with poorly or excessively draining soils. The evergreen *Hymenaea*'s weak positive growth response to annual rainfall totals indicates that tree species respond to climatic variation across a broad spectrum of subtle differences (Enquist & Leffler 2001).

SEASONAL STEM EXPANSION AND CONTRACTION PATTERNS.—Dendrometer bands revealed that *Swietenia* stem expansion rates peaked during the early part of each year's rainy season, declining steadily thereafter through the wet season. *Hymenaea* and *Parkia* experienced slower onset of stem expansion and relatively consistent expansion through the rainy season irrespective of month-to-month fluctuations in precipitation, with stem expansion extending somewhat further into the wet-dry transition period. Stahl *et al.* (2010) found that seasonal variation in atmospheric relative humidity is responsible for measurable stem expansion and contraction depending on a species' bark water content and thickness. Of the three study species, *Swietenia* has the thickest, most exfoliating bark that we presume may also be most responsive to relative humidity. Thus, early rainy season stem expansion to some extent represents restoration of pre-dry season bark moisture content, whereas abrupt stem contraction at the dry season's onset may reflect bark dry-down in response to sharply reduced atmospheric relative humidity. Possible reasons for reduced mid rainy season stem expansion rates concurrent with reduced rainfall totals include: (1) photosynthetic efficiency of recently flushed leaves may decline through the rainy season (Aide 1993, Larcher

1995); and (2) soil oxygen availability facilitating nutrient uptake may decline through the rainy season as phreatic water perches near the soil surface on low ground, creating waterlogged conditions (Kozlowski 1984, Brady 1990, Grogan & Galvão 2006).

Stem contraction by *Swietenia* occurred each May during 1997–2000, as the rainy season tapered off (Fig. 4A). The data in Figure 4A are somewhat misleading: in fact, the last significant rain fell in late April or early May in these 4 yr, meaning that phreatic water and moisture content in low-ground soils where mahogany occurs had already begun to fall by the end of May when dendrometer measurements were taken (Figs. S1 and S2). In 2001, the rainy season persisted into the first week of June, and stem contraction was not recorded until the late June measurement. Stem contraction thus occurred in tandem with falling atmospheric relative humidity's effect on bark moisture content and or the onset of soil moisture stress. Reich and Borchert (1982) attributed early dry season leaf shedding by *Tabebuia neochrysantha* in Costa Rica to lowered stem xylem potential, as transpiration losses exceeded absorption from water-depleted soils.

Crown observations coupled with dendrometer readings at 3-d intervals demonstrated that *Swietenia* stems gradually contract during leaf shedding – concurrent with environmental dry-down as the dry season progresses – and then expand during crown reflush, followed by further contraction during flowering by newly mature crowns (Table 3). Daubenmire (1972) observed similar behavior by *Swietenia* in Costa Rica. Borchert (1980, 1983) hypothesized that slow re-absorption of soil water after crown loss is sufficient to increase tree water potential and allow bud break. Further stem contraction after flowering may be associated with transpirational losses by new crowns, and additional moisture losses associated with floral nectaries.

All three species demonstrate strong signals of annual dormancy of diameter growth concurrent with the strong dry season. *Swietenia* and *Hymenaea* have been shown to produce annual rings in adult wood at other locations with a similar wet-dry annual cycle (Dünisch *et al.* 2002, Westbrook *et al.* 2006, Lisi *et al.* 2008). The genus *Parkia* has been identified as a candidate for annual growth rings (Vetter & Botosso 1989, Worbes 2002). Together, these observations suggest strong potential for retrospective analysis of long-term growth-climate relationships in southeastern Amazonia, as well as lifetime trends in growth and recruitment of canopy emergent trees.

CONCLUSIONS

This study illustrates that even within what might be described as a single ecological species group – light-demanding, canopy emergent trees (*e.g.*, MacPherson *et al.* 2010) – variation in environmental responses can be pronounced. The study species differ in spatial distribution patterns within the forest, with *Swietenia* largely restricted to low-ground areas subject to extreme dry season moisture stress, alternating with inundation and reduced soil oxygen availability during the wet season. In compensation, low-ground sites where *Swietenia* occurs have richer soils, experience

more frequent canopy disturbance, and on average have higher understory light levels (Grogan *et al.* 2003). While *Parkia* and *Hymenaea* are largely spatial generalists at Marajoara, they (especially *Parkia*) exhibit faint repulsion from the sites where *Swietenia* resides. As such, it is difficult to distinguish between inherent differences in species drought resistance and topographically mediated climate response. That *Swietenia* commonly achieves relatively high abundance on microsites subject to extreme seasonal drought and or inundation throughout its range in Central and South America (Lamb 1966, Schulze & Whitacre 1999) argues for high tolerance to edaphic extremes. This tolerance, combined with other aspects of *Swietenia* life history that together constrain its local distribution may, at Marajoara, result in greater sensitivity to variability in rainfall.

Although many of the responses to climate change of interest to policymakers will occur at the scale of large forest tracts or even regions (Brando *et al.* 2008, 2010, Phillips *et al.* 2008, 2009, Costa *et al.* 2010), species-level responses to climate variability may provide useful insights into forest-level responses to a drying Amazon basin. One current strategy for reducing carbon emissions from deforestation and retaining adequate forest cover in Amazonia to avoid catastrophic feedbacks in the hydrologic system (*cf.* Nobre *et al.* 2009) is sustainable forest management (Putz & Nasi 2009). Sustainability requires, at minimum, that valuable species persist in managed forests through multiple cutting cycles to provide economic returns. Models of timber species population dynamics under logging pressure indicate that current best practices under assumptions of a stable climate will not sustain viable commercial populations of *Swietenia, Hymenaea,* and many other high-value species (Grogan *et al.* 2008, Schulze *et al.* 2008). Stand-level models predict dramatic changes in species composition in logged stands over relatively short time frames (Van Gardingen *et al.* 2006, Valle *et al.* 2007, MacPherson *et al.* 2010). A changing climate, and species-specific responses to these changes, may lead to more dramatic shifts in forest composition than current models suggest. If harvests of threatened species such as *Swietenia, Hymenaea,* and *Tabebuia* are to be maintained, current approaches to harvest regulation and silviculture must be re-examined (Schulze *et al.* 2008).

In eastern Amazonia, impacts of land use changes over the past 30 yr on forest species swamp the effects of climate variability and change at all scales greater than the local site. In the region surrounding Marajoara, extensive forest conversion means that direct anthropogenic disturbance will continue to dominate this landscape for the foreseeable future. Even so, most current models project that changes in regional climate patterns combined with continued deforestation will yield drier conditions in southeast Amazonia over the coming decades (Malhi *et al.* 2008, Brando *et al.* 2010, Wright 2010). While species such as *Swietenia* that perform best on the 'wet end' of current conditions may experience reduced growth rates under future conditions, population viability will not necessarily be threatened if other life history strategies and ecophysiological responses (*e.g.*, drought tolerance through prolonged deciduousness, or increased recruitment rates under new disturbance regimes) compensate for slower growth

rates. As Amazonia becomes dryer, community composition and forest structure may change at different rates across landscapes. We can expect transitional forests such as those at Marajoara to respond relatively rapidly to climate change compared with wetter forests to the north and west (*cf.* Nepstad *et al.* 2004). In the near future, a species' capacity to survive and capitalize on conditions created by increasingly common dry season ground fires in natural forests may be the critical aspect of life history determining winners and losers on anthropogenic seasonal landscapes (Grogan *et al.* 2010).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Depth to the water table at three topographic positions across a slope from high to low ground representing 5.8 m elevation change at Marajoara.
FIGURE S2. Seasonal changes in gravimetric soil moisture by soils at high-ground and low-ground topographic positions.

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