

Flooding and profuse flowering result in high litterfall in novel *Spathodea campanulata* forests in northern Puerto Rico

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Abstract. The African tulip tree, *Spathodea campanulata*, dominates many post-agricultural secondary forests in the moist tropics. Some consider these novel forests have no ecological value, yet they appear to restore ecosystem processes on degraded sites. This study describes the litterfall mass and seasonality, canopy phenology, and microclimate of *S. campanulata* forests on alluvial and karst substrates in northern Puerto Rico. These substrates have different water drainage properties and I hypothesized that (1) annual leaf fall mass and seasonality would differ between substrate types; because (2) leaf fall would be related to water availability and seasonality. I used analysis of variance to compare annual and biweekly litterfall mass across three sites on each substrate type, and multiple linear regression analysis to relate biweekly litterfall to environmental variables. Litterfall mass was high ($13.8 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, $n = 6$, $\text{SE} = 0.60$) yet its components did not differ by substrate type except for reproductive part mass which was higher on karst due to more *S. campanulata* flowers. Leaf fall had a bimodal seasonality and was negatively related to the number of dry days indicating it occurs when water is readily available or in excess as during floods. Observations show systematic leaf senescence in this deciduous species can be caused by water and nutrient demand from flowering. Litterfall mass and seasonality of novel *S. campanulata* forests is similar to that of native forests in Puerto Rico, yet flower fall appears to be higher than that of tropical forests worldwide. The environmental variables that affect litterfall seasonality and canopy phenology are similar to those in tropical forests in Puerto Rico and elsewhere. Litterfall seasonality and canopy phenology regulate understory microclimate, and influence the establishment and growth of juvenile trees and other organisms within *S. campanulata* forests. This study illustrates how forest ecosystem processes and properties restored by novel *S. campanulata* forests facilitate tree species establishment, growth, and turnover in deforested, abandoned, and degraded agricultural lands in Puerto Rico.

Key words: African tulip tree; canopy phenology; ecosystem processes; forest microclimate; introduced invasive species; land cover change; plant-animal interactions.

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INTRODUCTION

Most ecosystems on Earth have been altered by humans and terms such as “homogeocene” have been used to describe the times we live in

(Vitousek et al. 1997, Lugo 2009). In the Caribbean island of Puerto Rico, the development of a fossil fuel-based economy in the mid-20th century caused the abandonment of agricultural lands and this was followed by the

spontaneous growth of secondary forests (Rudel et al. 2000). Many of these secondary forests are dominated by introduced species and are considered to be novel ecosystems that have originated from deforestation, land use, and abandonment (Hobbs et al. 2006). The processes taking place in novel tropical forests have not been adequately studied and there is a need to understand these ecosystems, which are becoming more common as a natural response to anthropogenic change.

The African tulip tree, *Spathodea campanulata* Beauv. (Bignoniaceae), has been widely introduced outside its natural range and invades disturbed to deforested moist tropical lands worldwide, especially in islands (Francis 2000, Haysom and Murphy 2003). In Puerto Rico, it is the most abundant tree species and dominates secondary forests in the moist regions (Lugo and Helmer 2004, Brandeis et al. 2007). Novel *S. campanulata* forests have been studied in Hawaii (Mascaro et al. 2008) and Papua, New Guinea (Novotny et al. 2004). Although they accumulate biomass, novel *S. campanulata* forests in the Hawaiian lowlands lack regeneration of native trees due to the extirpation of remnant native forest and native avian seed dispersers (Foster and Robinson 2007, Mascaro et al. 2008). In Papua, various species of Lepidoptera larvae profit as herbivores on *S. campanulata* and other introduced tree species in novel forests, where these trophic webs have been described in detail (Novotny et al. 2004).

Other examples of novel forests come from the invasion of *Ligustrum* spp. on abandoned farmlands in Argentina (Lichstein et al. 2004) and on human-disturbed native forests in La Réunion island (Lavergne et al. 1999). In Argentina, native birds disperse introduced *Ligustrum lucidum* to abandoned farmlands where its dominance limits recruitment of other trees, although it allows the establishment of native trees in degraded lands (Lichstein et al. 2004, Ferreras et al. 2008). In La Réunion, introduced *Ligustrum robustum* invades heavily human-disturbed native forest where it dominates the canopy and acts as source of invasion to native undisturbed forest remnants through introduced avian seed dispersers (Lavergne et al. 1999, Mandon-Dalger et al. 2004). Perhaps the most striking example of a novel forest ecosystem is that described by

Wilkinson (2004) on Ascensión island. This island was barren of trees in the early 19th century, yet management practices introduced a myriad of tree species that resulted in lush cloud forests in current times. Most plant species endemic to Ascensión are missing from these novel forests yet observations suggest they provide ecosystem services by increasing soil depth, and capturing water from clouds and atmospheric carbon (Wilkinson 2004). The common denominator of these studies is the focus on the description of species assemblages and plant-animal interactions in novel forests, with no detailed focus on the ecosystem processes that inhibit or facilitate the establishment or interactions of species within novel forests.

In Puerto Rico, many native tree species are becoming established in novel *S. campanulata* forests and some suggest that this tree's deciduousness results in sunlight and litterfall pulses that enhance the photosynthetic capacity and nutrient status of juvenile trees in the understory (Aide et al. 2000, Lugo 2004, Abelleira Martínez 2010, Abelleira Martínez et al. 2010). Besides pulses of increased sunlight, the understory microclimate of these forests could facilitate the establishment and growth of native trees by regulating temperature and relative humidity extremes, and increasing soil nutrient, organic matter, and water content. On the other hand, compositional changes due to introduced invasive tree species can alter ecosystem processes and this can affect native biota (Vitousek 1990, Crowl et al. 2008). The dominance and deciduousness of novel *S. campanulata* forests could result in litterfall mass and seasonality different from native evergreen and species-rich old-growth forests of the moist regions of Puerto Rico. In consequence, ecosystem processes that depend on litterfall fluxes, such as development of forest floor litter, soil organic matter, and nutrient cycling from the canopy to the forest floor, could differ from native forests (Prescott 2002, Lugo 2004). This can have consequences for biota that depend on litterfall such as invertebrates and soil microorganisms.

Lowland tropical forest phenology and litterfall is closely related to water seasonality, particularly due to leaf senescence and fall pulses that coincide with droughts or floods (Reich and Borchert 1982, Medina 1983, Kinnaird 1992,

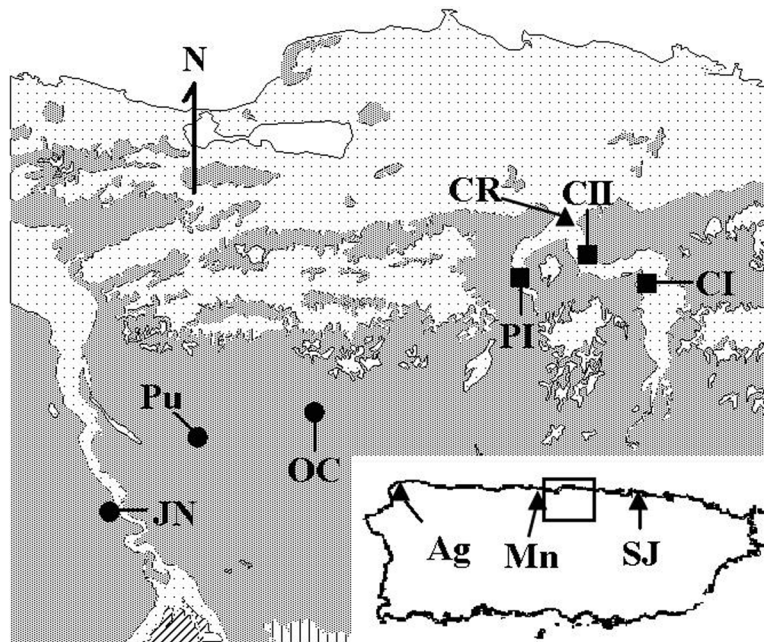


Fig. 1. Map of Puerto Rico and location of Aguadilla (Ag), San Juan (SJ), and Manatí (Mn) climate stations with respect to the enlarged section of the island, which shows the location of the study sites and the Cibuco river (CR) monitoring station. Squares denote alluvial sites, circles denote karst sites, and triangles denote stations. Site codes are as follows; CI: Cibuco I, CII: Cibuco II, JN: Juan Nieves, OC: Ollas y Calderas, PI: Paso del Indio, and Pu: Pugnado.

Kozlowski 1997, Haase 1999, Parolin et al. 2004, Haugaasen and Peres 2005, Kozlowsky 1997). In moist northern Puerto Rico, *S. campanulata* forests located on deep alluvial soil in flat riparian zones have a constant water table supply from river inputs and suffer periodic floods due to high and long rainfall events in the watershed (Abelleira and Lugo 2008). In contrast, *S. campanulata* forests on karst depressions have shallower alluvial soils underlain by porous and well-drained calcareous bedrock on sloping to nearly flat topography, similar to a soup bowl in shape, and receive most water inputs during local rain events (Monroe 1976). Thus, better drainage and inconsistent water inputs in *S. campanulata* forests on karst depressions can result in litterfall mass and seasonality different from those on alluvial valleys. In particular, I hypothesized that (1) the leaf fall of *S. campanulata* forests would differ between alluvial and karst substrates; because (2) leaf fall would be linked to water availability and seasonality.

METHODS

Study sites

I sampled six lowland *S. campanulata* forests (Fig. 1; Table 1) located on abandoned agriculture and grazing lands on alluvial and karst geological substrates in the subtropical moist life zone of northern Puerto Rico (18° N, 65° W; Holdridge 1967, Ewell and Whitmore 1973, Bawiec et al. 2001). Between 1971–2000, mean annual temperature and precipitation were 25°C and 1443 mm, respectively, and precipitation in 2006 was 1612 mm at Manatí, which is within 20 km from all sites (NOAA 2002, USGS 2007). In the Cibuco river, which is adjacent to alluvial sites, high rainfall events result in floods (USGS 2007). Climate diagrams for Aguadilla and San Juan, which lie 75 km west and 50 km east of the sites, respectively, show climate in the northern coast is moist through the year with a drier period from February to March (Rivas Martínez 2009; Lugo et al. in press).

The valleys where alluvial sites are located

Table 1. Study site characteristics by geological substrate type.

Site characteristic	Alluvial				Karst			
	Cibuco I	Cibuco II	Paso del Indio	Mean	Juan Nieves	Ollas y Calderas	Pugnado	Mean
Elevation (m)	18	7	16	13	30	140	170	113
Slope (%)	0	0	0		7–15	25–50	7–15	
Land use history	SC	SC	SC, P		SA, P	SA, P	SA, P	
Age (yrs.)	24	38	24	29	38	31	24	31
Soil								
Taxon	VE	FH	FH		TU	CA	CA	
Texture	SC	SCL	SCL		GCL	GC	GC	
Bulk density (g/cm ³)								
0–15 cm depth	0.57	0.44	0.52	0.51	0.39	0.52	0.42	0.44
15–30 cm depth	0.57	0.63	0.53	0.58	0.29	0.54	0.51	0.45
Density (trees/ha)	983	994	1670	1215	579	736	804	706
Basal area (m ² /ha)	70.6	95.2	75	80.3	31.2	51	66.2	49.5
Tree species	4	3	3	3 ^A	8	9	6	8 ^B
Canopy dominance (%)	90	91.4	91.8	91.1 ^A	82.1	73.8	77.6	77.8 ^B
Canopy height (m)	22.3	25.3	24.6	24.1	24.4	24.1	29.7	26.1

Notes: Elevation of alluvial sites is from Abelleira and Lugo (2008) and of karst sites was derived from topographic maps. Slope, history, age, and forest structure data are from Abelleira Martínez et al. (2010). Soil taxon and texture are from Acevedo (1982) and Beinroth et al. (2003). Letters for land use history correspond to sugar cane (SC), pasture (P), and subsistence agriculture (SA). Letters for soil taxon correspond to vertic endoaquepts (VE), fluvaquentic hapludolls (FH), typic ustorthents (TU), and calcic arguidolls (CA). Letters for soil texture consist of combinations of the following: clay (C), loam (L), silt (S), and gravel (G). Soil bulk density is the mean of 3 to 5 soil cores per site for each depth (Abelleira and Lugo 2008). Forest structure data are for trees >10 cm diameter at breast height (DBH). Canopy dominance is the importance value of *Spathodea campanulata* amongst trees >10 cm DBH based on density, frequency, and basal area of the species (Abelleira Martínez et al. 2010). Canopy height is the mean of three upper canopy trees at each site. Means are reported per geological substrate type and letters denote significant differences between substrate types by ANOVA (df = 1, 4; $P < 0.05$).

were used for sugar cane plantations from the 17th to mid-20th century (Table 1; Picó 1937, Wadsworth 1950, Picó 1988). A crop annual cycle consisted of cane growth, harvesting, burning, and re-growth, sometimes interspersed with fallow years. Cattle plow lines are still evident on the forest floor of these sites. The depressions where karst sites are located might have been used for sugar cane as well, but if so, it was abandoned much earlier than on the alluvial sites (Picó 1988). Crops planted before abandonment at karst sites were small scale commercial to subsistence agriculture consisting of citrus, avocado, plantains, cassava, and yams. Grazing occurred in fallow years or after abandonment at most sites (Table 1).

The soil atop karst bedrock is a mixture of bedrock material with sedimentary alluvial deposits that originated in higher elevations, which are akin to soils at alluvial sites (Bawiec et al. 2001). Two sites on each substrate type were located on mollisols (calcic arguidolls and fluvaquentic hapludolls) and the others were on entisols (typic ustorthents) and inceptisols (vertic endoaquepts; Table 1). Mollisols are well-developed and amongst the most fertile soils in the tropics compared to inceptisols and entisols,

which are relatively younger and less fertile (Beinroth et al. 2003). However, I assumed no differences in soil fertility between sites because of similar sedimentary origin and disturbance by previous land use. In addition, soil bulk density at 0–15 and 15–30 cm depth is very similar across sites on both substrate types (Table 1). Tree structure is similar across sites, but alluvial sites have lower species richness and higher dominance by *S. campanulata* compared to karst sites (Table 1).

Data collection

Six 0.25 m² baskets were placed randomly along line transects set haphazardly on each site for a total of 36 baskets. The baskets were lined with 1 mm screen mesh, placed 1 to 2 m off the ground, and at least 15 m from the forest edge. I collected biweekly litterfall from each basket starting in 10 January 2006, and ending in 7 May 2007, for a total of 30 sampling dates. Litterfall samples from each basket were oven dried to constant weight at 65°C, separated into *S. campanulata* senesced and green leaves, other leaves, wood, reproductive parts, and miscellaneous components, and each component was weighed separately. The compound leaf rachis

was included with wood. Thus, leaves actually represent leaflets, but are referred to as leaves throughout this paper. The number of *S. campanulata* open flower calyxes per basket was recorded as a proxy of the number of flowers found in reproductive parts because the rest of the corolla broke apart easily during sampling and processing. I summed the litterfall mass and number of flowers per basket for the 26 sampling dates starting in 10 January 2006, and ending in 11 January 2007, to estimate annual rates per component ($\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ and $\text{flowers}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$). Litterfall mass and number of flowers per basket were divided by the number of days that integrated each sampling date to report biweekly rates ($\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ and $\text{flowers}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$).

Canopy phenology was determined from observations on seven upper canopy trees selected randomly at each site for each sampling date starting in 26 July 2006. The percentage of leaf canopy closure and the presence of flowers for each tree were determined visually from the ground. Canopy closure was estimated on a scale of 0 to 100% that corresponded to leafless to fully flushed trees, respectively. The percentage of canopy closure and of trees in flower reported is the mean value of observations on the seven trees per site for each sampling date.

Weather stations (OCC 2010) were placed at four sites in 17 May 2006 to monitor in-situ microclimate. The stations were placed on the two sites of each substrate type that were on mollisols (Table 1). Each station had sensors for temperature, relative humidity (RH), soil water content (SWC), and photosynthetic active radiation (PAR). The sensors were installed on or near large diameter *S. campanulata* trees and therefore all microclimatic data is spatially biased to the environment near trees. Temperature and RH sensors were placed at ~ 3 cm from tree trunks and ~ 2 m from the ground. The SWC sensor reached into 20 cm of soil depth, the PAR sensor was placed at 1 m above ground, and both were located between 1 to 2 m from the tree. The reason for this setup was to provide discretion because all sites had public access, suffered occasional vandalism, and preliminary conspicuous sensors were stolen or displaced. Thus, care should be taken when comparing this to other datasets. Reported values for in-situ temperature, RH, SWC, and PAR are the means of readings

that integrated each sampling date.

Data analysis

I used ANOVA to compare annual and biweekly litterfall and flower fall using the mean of six baskets per site ($n = 3$ sites per substrate type), and biweekly in-situ microclimatic means per station per site ($n = 2$ sites per substrate type) using substrate type as single factor. ANOVA was also used to compare annual and biweekly litterfall within substrate type ($n = 6$ baskets per site) using site as single factor. I used the Shapiro-Wilks test to assess data normality, the *F*-max test to assess variance homogeneity, and the Kruskal-Wallis test to compare non-normal data.

I used stepwise multiple linear regression analysis (SMLRA) to determine which variables related to biweekly litterfall rates at the substrate type ($n = 3$ sites per substrate type) and site ($n = 6$ baskets per site) levels. I used $P < 0.05$ as minimum for the inclusion of each variable in the SMLRA model. I tested the number of dry days (DD), daytime temperature (DT), daytime relative humidity (DRH), wind speed (WS), and day length (DL) as independent variables. Data for DD, DT, DRH, and WS were daily averages for 1961–1990 at San Juan (Fig. 1; USEPA 2002). The DD were the sum of days where pan evaporation exceeded rainfall in 1961–1990 daily averages for days that integrated each sampling date. Biweekly means for DT, DRH, and WS were the mean of daily values that integrated each sampling date. Data for DL were from San Juan for 2006–2007 (USNO 2008). Mean biweekly maximum and minimum values for DT, DRH, and WS (USEPA 2002) were each interchanged with corresponding variable means, and daily rainfall at Manatí (mm) and Cibuco river discharge (m^3/s) for 2006–2007 (Fig. 1; USGS 2007) were each interchanged with DD, on separate analyses and reported if the significance of the model improved. Modes of litterfall components with bimodal seasonality were analyzed separately. I used Infostat for all analyses (Di Rienzo et al. 2003).

RESULTS

Litterfall

The mean total annual litterfall of *S. campanulata* forests was $13.8 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ ($n = 6$, $\text{SE} = 0.60$) and did not differ between substrates type

Table 2. Annual litterfall mass of *Spathodea campanulata* forests on alluvial and karst geological substrates in 2006.

Litterfall component	Annual litterfall mass (Mg·ha ⁻¹ ·yr ⁻¹)	
	Alluvial	Karst
<i>Spathodea campanulata</i> senesced leaves	6.41	5.19
<i>S. campanulata</i> green leaves	0.68	0.46
All <i>S. campanulata</i> leaves	7.09	5.66
Other leaves	0.92	1.15
All leaves	8.01	6.80
Reproductive parts	1.82 ^A	2.52 ^B
Wood	3.58	3.22
Miscellaneous	0.79	0.79
All components	14.18	13.33

Notes: Each value is the average of the mean annual litterfall mass in six baskets for each of three sites per substrate type ($n = 3$). Letters denote significant differences according to ANOVA ($F [1, 4] = 18.64$, $P = 0.01$).

in 2006 (Table 2). About half the total annual litterfall mass was from *S. campanulata* leaves which constituted 85 and 75% of all leaf mass on alluvial and karst sites, respectively. Senesced leaves constituted most *S. campanulata* leaf mass and green leaves amounted to ~10%. Annual litterfall of karst sites had higher reproductive part mass than alluvial sites ($F [1, 4] = 18.64$, $P = 0.01$) but there were no differences in other components between substrate types. The difference in annual reproductive part mass was due to higher *S. campanulata* flower production at karst sites (2.17×10^6 [SE = 0.29] vs. 2.91×10^6 [SE = 0.05] flowers·ha⁻¹·yr⁻¹ at alluvial and karst sites, respectively; $F [1, 4] = 6.28$, $P = 0.07$). Annual litterfall mass did not differ between sites on the same substrate type except for *S. campanulata* senesced leaf mass which was lower on the alluvial site Cibuco II (CII; $F [2, 15] = 8.34$, $P = 0.004$) and the karst site Ollas y Calderas (OC; $F [2, 15] = 8.60$, $P = 0.003$) compared to the other sites (Table 3).

Biweekly total litterfall ranged from 1 to 6 g·m⁻²·d⁻¹ except for dates were wood increased this value up to 12 g·m⁻²·d⁻¹ (Fig. 2; Appendix A). Senesced *S. campanulata* leaves and reproductive parts had different biweekly values between substrate types for the most sampling dates, yet these only amounted to 10 to 17% of all dates. Within substrate type, differences in biweekly litterfall were found in ≤30% of sampling dates except for senesced leaf fall, which was lower in 50% of all dates on OC

compared to the other karst sites.

At most sites, *S. campanulata* senesced leaf fall had a bimodal seasonality with peaks within March to August and September to March, and a dip around March and August common to all sites (Fig. 2B). The March to August mode reached higher rates and peaked earlier at alluvial sites. The September to March mode also reached higher rates at alluvial sites, but was more irregular within sites of the same substrate type and was nonexistent at the karst site OC. The equations derived by SMLRA of *S. campanulata* senesced leaf fall to environmental variables explained between 31 to 72% of the seasonality on sites combined by substrate type (Table 4). Senesced leaf fall was negatively related to DD in equations for all sampling dates and for the March to August mode. Senesced leaf fall was also negatively related to DRH and positively to DL, but these relationships were inconsistent. No significant equations were found for the September to March senesced leaf fall mode for sites combined by substrate type.

Most *S. campanulata* green leaf fall occurred between January and July, when it reached up to half the rate of senesced leaf fall, and almost no green leaf fall occurred between September and December (Fig. 2B; Appendix A). On alluvial sites, *S. campanulata* green leaf fall was negatively related to maximum DRH but no relationship was found on karst sites (Table 4). The seasonality of other leaves, wood, and miscellaneous components resembled that of *S. campanulata* senesced leaves, but were more variable and no SMLRA equations were found for other leaves and wood.

Reproductive part fall had a bimodal season-

Table 3. *Spathodea campanulata* senesced leaf fall mass by site in 2006.

Site	Senesced leaf mass (Mg·ha ⁻¹ ·yr ⁻¹)
Alluvial	
Cibuco I	6.95 ^A
Cibuco II	5.26 ^B
Paso del Indio	7.02 ^A
Karst	
Juan Nieves	6.02 ^A
Ollas y Calderas	4.04 ^B
Pugnado	5.53 ^A

Note: Letters denote significant differences within substrate type by ANOVA-Tukey test on six baskets per site ($df = 2, 15$; $P < 0.01$).

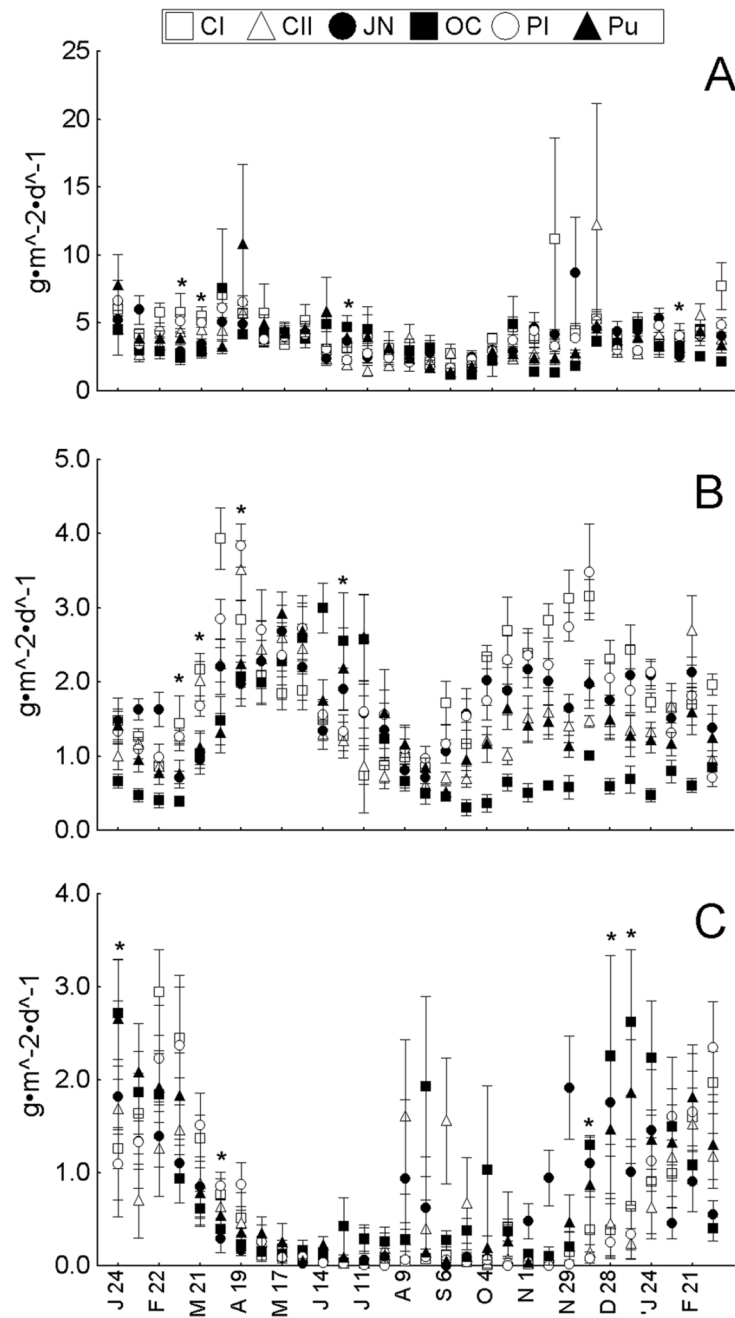


Fig. 2. Mean and standard error of biweekly (month and day) *Spathodea campanulata* litterfall for (A) all components, (B) *S. campanulata* senesced leaves, and (C) reproductive parts spanning from 24 January 2006 through 7 March 2007. Each value is the mean of six baskets per site for each sampling date. Empty symbols denote alluvial sites and dark symbols denote karst sites. Site codes follow Fig. 1. Asterisks denote significant differences between substrate type (ANOVA; $df = 1, 4$; $P < 0.05$; F [all components] = 8 March 2006: 11.86, 21 March 2006: 28.23, 27 June 2006: 11.02, and 6 February 2007: 27.90; F [senesced leaves] = 8 March 2006: 29.82, 21 March 2006: 36.87, 19 April 2006: 18.31, and 27 June 2006: 24.99; F [reproductive parts] = 24 January 2006: 9.56, 5 April 2006: 11.96, 13 December 2006: 33.26, 28 December 2006: 38.13, and 10 January 2007: 8.78).

Table 4. Statistically significant regression equations found for biweekly litterfall mass ($\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) and flower fall ($\text{flowers}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) rates in *Spathodea campanulata* forests on alluvial and karst substrates derived from stepwise multiple linear regression analysis to environmental variables.

Litterfall component	Alluvial		Karst	
	R^2	Equation	R^2	Equation
<i>Spathodea campanulata</i> senesced leaves				
All sampling dates	0.33	$y = -0.15(\text{DD}) - 0.22(\text{DRH}) + 18.57$	0.31	$y = 0.45(\text{DL}) - 0.11(\text{MinDRH}) - 0.08(\text{DD}) + 2.71$
March–August	0.72 (39)	$y = -0.46(\text{DRH}) + 1.22(\text{DL}) - 0.14(\text{DD}) + 19.44$	0.36* (39)	$y = -0.02(\text{DD}) + 3.99$
<i>S. campanulata</i> green leaves	0.33	$y = -0.07(\text{MaxDRH}) + 6.32$		
Miscellaneous	0.34	$y = 0.02(\text{RD}) - 0.06(\text{DT}) + 1.81$	0.25*	$y = -0.03(\text{MinDRH}) - 0.02(\text{DD}) + 1.86$
Reproductive parts				
All sampling dates	0.51	$y = -0.14(\text{DRH}) - 0.21(\text{DT}) + 15.82$	0.58	$y = -0.81(\text{DL}) + 0.74(\text{WS}) + 7.4$
November–May	0.62 (57)	$y = 0.09(\text{DD}) - 0.46(\text{DT}) + 12.21$	0.59 (57)	$y = -0.52(\text{DL}) - 0.47(\text{DT}) + 19.71$
<i>S. campanulata</i> flowers				
All sampling dates	0.65	$y = -0.21(\text{DRH}) - 0.32(\text{DT}) + 24.25$	0.68	$y = -1.06(\text{DT}) + 0.29(\text{DRH}) + 0.08(\text{DD}) + 9.01$
November–May	0.60 (57)	$y = 0.14(\text{DD}) - 0.51(\text{DT}) + 13.31$	0.54 (57)	$y = -1.32(\text{DT}) - 1.46(\text{WS}) + 42.8$
All components	0.22*	$y = -0.72(\text{DT}) + 23.98$	0.22*	$y = -0.28(\text{MinDRH}) - 19.06$

Notes: The number of data points (n) used for each regression corresponds to mean values of baskets per site ($n = 6$) for sites combined by substrate type ($N = 3$). For all sampling dates, $n = 90$ on both substrate types for all components. For separate modes, n is denoted in parenthesis next to the R^2 value. The equation for the *S. campanulata* senesced leaf fall mode of March to August includes the sampling dates of 8 March 2006 to 23 August 2006. The reproductive part and flower fall in the sampling dates of 24 January 2006 to 31 May 2006 were included with those of 15 November 2006 to 7 March 2007 and are reported as the November to May mode. The values for dependent (y) litterfall and independent (x) environmental variables used in the regressions were means for the time period that integrated each sampling date. Independent variable codes correspond to; DD: number of dry days, DRH: daytime relative humidity in percent, DL: day length in hours, DT: daytime temperature in $^{\circ}\text{C}$, RD: river discharge in m^3/day , and WS: wind speed in m^2/s . Minimum (Min) and maximum (Max) values for DRH, DT, and WS, and mean RD were included when the significance (P) of the model (R^2) was improved. The R^2 of all equations is significant to $P < 0.01$ except those marked by an asterisk which are only significant to $P < 0.05$. For empty cells, no statistically significant regression equations were found.

ality distinct from the other litterfall components with one mode in November to May of greater magnitude than a shorter mode in June to November (Fig. 2). The November to May mode coincided with *S. campanulata* flower fall (Fig. 3) and the smaller June to November mode corresponded to seedpod fall. The November to May flowering mode occurred slightly earlier and reached higher rates on karst sites (Figs. 2C and 3). The SMLRA equations explained between 51 to 68% of the variation in reproductive parts and *S. campanulata* flowers on sites combined by substrate type (Table 4). Reproductive part and *S. campanulata* flower fall were negatively related to DT in most equations, negatively related to DL and positively to DD in some equations, and related to other variables inconsistently. No significant equations were found for the June to November mode of reproductive part fall.

Canopy phenology

The canopies of *S. campanulata* forests lost their leaves by July 2006, leading to full canopy opening (Fig. 4A). Full canopy closure occurred from October to January at all sites yet lagged in time on OC. The onset of flowering coincided with full canopy closure in November on karst sites and slightly later on alluvial sites (Fig. 4B). The onset of canopy opening occurred from January to February and preceded the peak of flowering by one to two sampling dates.

Microclimate

In-situ temperature biweekly means ranged from 21 to 26 $^{\circ}\text{C}$ and were significantly higher at alluvial sites for 38% of all monitored sampling dates (Fig. 5A). In-situ temperature was highest in May to September and lowest in January to February, which matched the minimum and maximum percentage of canopy closure, respectively (Fig. 4B). In-situ RH means ranged from 85

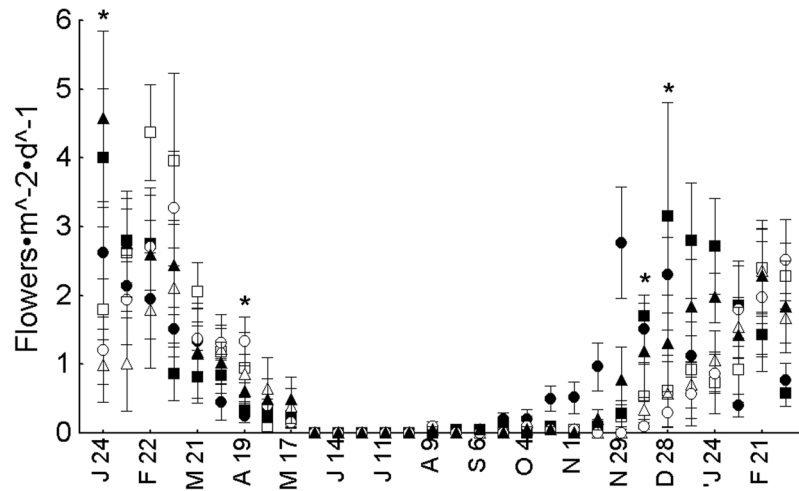


Fig. 3. Mean and standard error of biweekly (month and day) *Spathodea campanulata* flower fall spanning from 24 January 2006 through 7 March 2007. Each value is the mean of six baskets per site for each sampling date. Empty symbols denote alluvial sites and dark symbols denote karst sites. Site codes follow Fig. 1. Asterisks denote significant differences between substrate type (ANOVA; $df = 1, 4$; $P < 0.05$; F [flowers] = 24 January 2006: 14.62, 19 April 2006: 12.96, 13 December 2006: 33.99, and 28 December 2006: 10.40).

to 105% and were significantly higher at karst sites in 19% of all monitored sampling dates (Fig. 5B). After the minimum values that occurred in May, RH had a steady increase up to September when relatively constant values ranging from 93 to 95% at alluvial sites and from 97 to 100% at karst sites were maintained until January. Subsequently, there was another RH raise in February to March that coincided with peak *S. campanulata* flowering and flower fall (Figs. 2C, 3, and 4B). In-situ SWC had the greatest variability within sites of the same substrate type, and more so at karst sites (Fig. 5C). In spite of this, SWC appeared to be consistently higher at alluvial sites where means ranged from 0.21 to 0.38 m^3/m^3 compared to karst sites, which ranged from 0.15 to 0.31 m^3/m^3 . There were two drops in SWC that occurred in October and February, which coincided with high values of canopy closure and flowering, respectively (Fig. 4). In-situ PAR means ranged from 2 to 58 $\mu mol \cdot m^{-2} \cdot s^{-1}$, did not differ between substrate types, and was highest in May to June and lowest in November to January, which coincides with lowest and highest percentage of canopy closure, respectively (Figs. 4A and 5D).

DISCUSSION

The hypothesis that leaf fall mass and season-

ality would be different in *S. campanulata* forests on alluvial and karst substrates is rejected. However, *S. campanulata* senesced leaf fall was negatively related to the number of dry days, supporting the hypothesis that leaf fall relates to water seasonality (Table 4). The significant SMLRA equations found indicate leaf fall occurs when water is readily available or in excess, as during floods. Two mechanisms associated to water deficit or excess can cause leaf senescence and fall: (1) excessive water loss from high transpiration rates that cannot be compensated by xylem conductance due to low soil water potential during droughts (Medina 1983); and (2) water saturated soils that result in anoxic conditions in the roots impeding water uptake and xylem flow to leaves during floods (Kozłowski 1997). The absence of physiological drought (rainfall – evaporation < 0 , Lüttge 1997) and occurrence of leaf fall during high water availability suggests the second mechanism.

Floods were observed during February, April to May, and July to December at all sites except for OC, which does not flood because surface water runoff from higher ground is blocked by a karst wall (Monroe 1976). Based on observations, floods at alluvial sites covered more area, lasted longer for up to two weeks, and ranged in depth from 0.1 to 1.5 m, which can explain earlier and

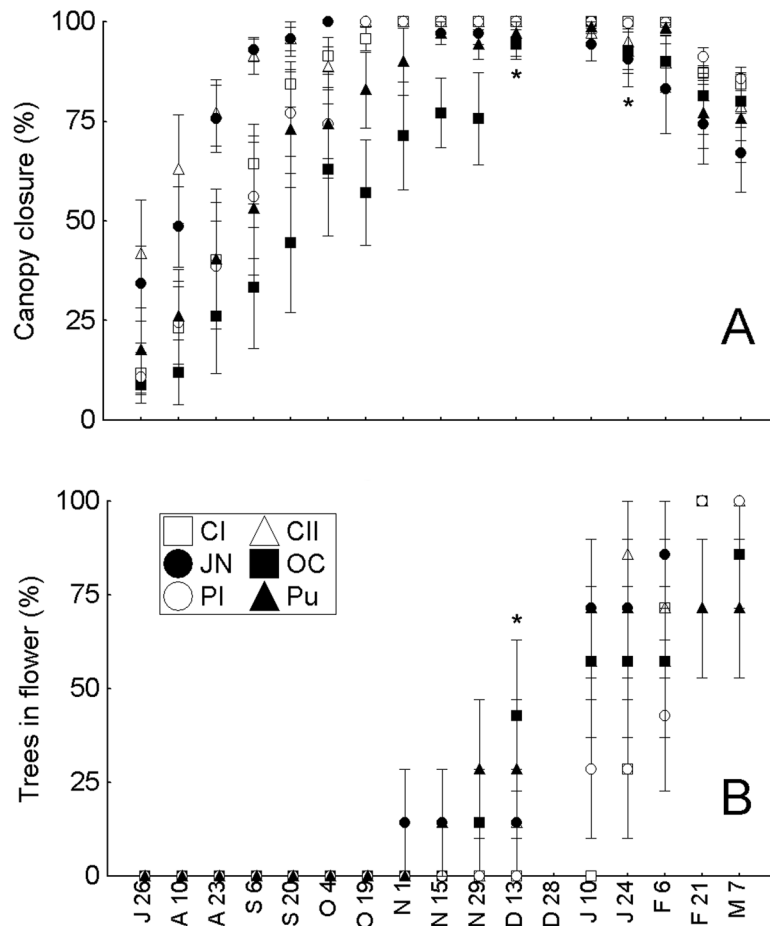


Fig. 4. Mean and standard error of (A) percentage of canopy closure and (B) percentage of trees in flower for seven *Spathodea campanulata* trees on each site spanning from 26 July 2006 through 7 May 2007. Empty symbols denote alluvial sites and dark symbols denote karst sites. Site codes follow Fig. 1. Asterisks denote significant differences between substrate type (ANOVA; $df = 1, 4$; $P < 0.05$; F [canopy closure] = 13 December 2006: 27.15, 24 January 2007: 12.03; F [trees in flower] = 29 November 2006: 16.02).

higher senesced leaf fall rates at alluvial sites in both modes. From February to June of 2010, floods were monitored with sensors on CII, Paso del Indio (PI), and Pugnado in another study (Pérez 2010), and floods were of greater magnitude and duration on the two alluvial sites (Table 1) reaching depths of 0.4 m and lasting up to a week. As the canopy is closing due to the flushing of new leaves, floods appear to cause premature leaf senescence and fall from September to March at all sites except for OC (Figs. 2B and 4A). This is further supported by SMLRA for sites individually which shows senesced leaf fall in the September to March mode was negatively related to the number of dry days on two alluvial

sites (Appendix B).

The dominance of *S. campanulata* at CII and OC is nearly the same as the other alluvial and karst sites, respectively, and yet these sites had significantly lower senesced leaf mass (Tables 1 and 3). The lower senesced leaf mass at OC compared to the other sites is due to lack of flooding and absence of the September to March leaf fall mode (Fig. 2B). It is possible that floods at CII are less significant or of shorter duration than at the other alluvial sites, which could account for the lower September to March leaf fall mode at this site. An alternative explanation for lower senesced leaf mass on CII than the other alluvial sites could be that CII is more

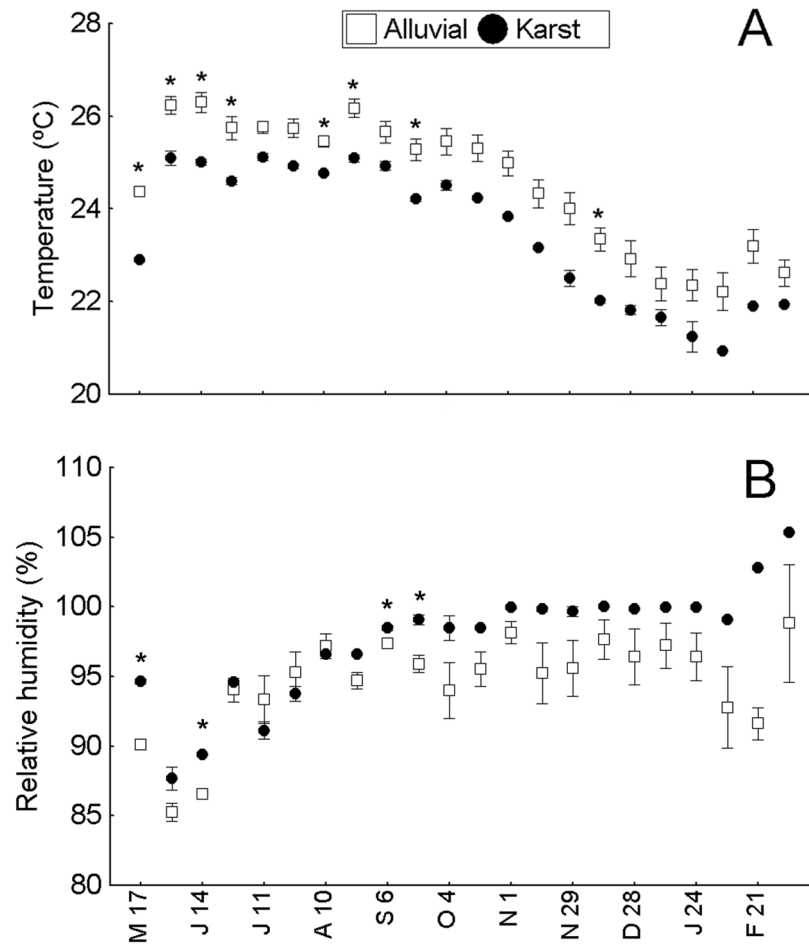


Fig. 5. Mean and standard error of in-situ (A) temperature, (B) relative humidity (RH), (C) soil water content (SWC), and (D) photosynthetic active radiation (PAR) measured inside two alluvial (Cibuco II and Paso del Indio) and two karst (Ollas y Calderas [OC] and Pugnado) *Spathodea campanulata* forest sites spanning from 17 May 2006 through 7 March 2007. For each sampling date, $n = 2$ on each substrate type except for all variables in 19 October 2006, temperature during the dates after 24 January 2007, and RH during the dates after 13 December 2006 on karst for which $n = 1$ (OC). Asterisks denote significant differences between substrate type (ANOVA; $df = 1, 2$; $P < 0.05$; F [temperature] = 17 May 2006: 166.22, 31 May 2006: 21.53, 14 June 2006: 32.99, 27 June 2006: 19.19, 9 August 2006: 31.12, 23 August 2006: 24.31, 20 September 2006: 20.65, 13 December 2006: 28.08; F [RH] = 17 May 2006: 214.06, 14 June 2006: 831.51, 6 September 2006: 28.22, 20 September 2006: 19.90; F [SWC] = 26 July 2006: 27.77; F [PAR] = 14 June 2006: 219.57).

mature (Odum 1969, Ewell 1976) yet the small difference in age makes this unlikely (Table 1).

Unexpectedly, higher reproductive part mass and *S. campanulata* flower production at karst sites were the only differences found between substrates (Table 2). The negative relation of flower fall to daytime temperature could account for higher flower production at karst sites because their in-situ temperature was consistent-

ly lower (Table 4; Fig. 5A). However, it is unclear how temperature measured in the understory relates to the canopy where these processes occur. It is more likely that daytime temperature is only correlated to changes in day length or insolation that induce flowering in plants sensitive to short days or to days with less cloud cover (Appendix C; Evans 1971, Wright and Van Schaik 1994, Calle et al. 2010). If this is the case, earlier

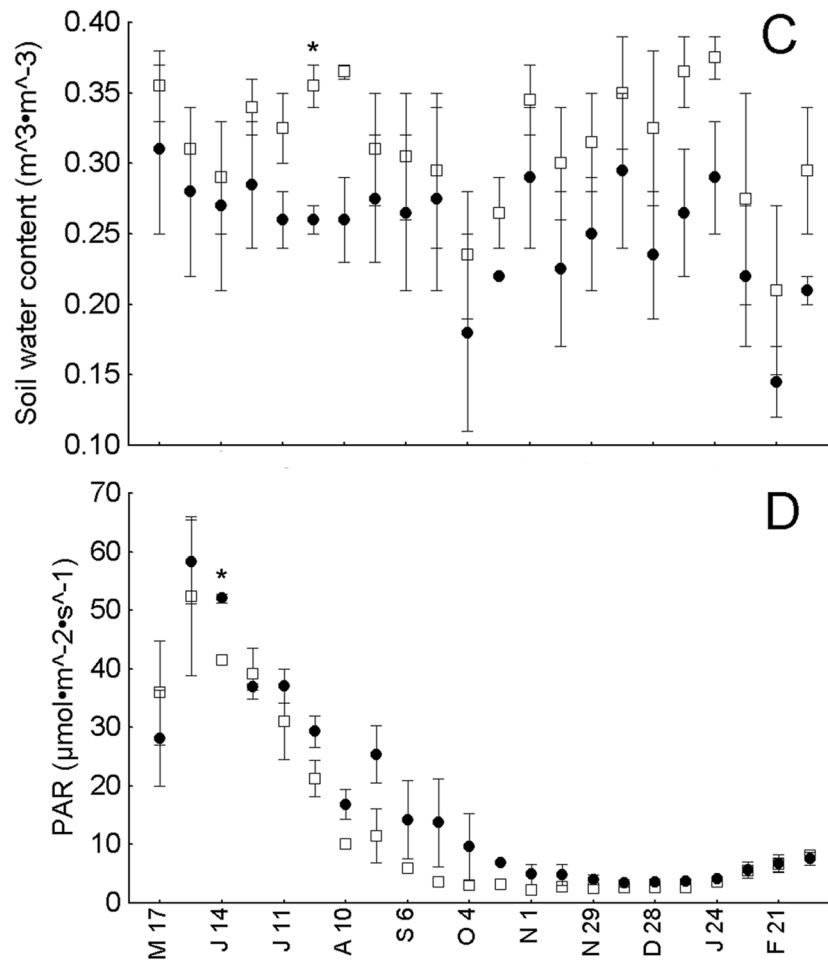


Fig. 5. Continued.

and longer flowering time on karst depressions compared to alluvial sites can be due to differences in incident solar radiation due to surrounding topography or cloud cover, but showing this is beyond the scope of this study.

In dry climate, drought causes the inhibition of vegetative growth, leaf shedding, and flower induction in *Tabebuia neochrysantha* (Bignoniaceae), but anthesis is delayed for months and occurs when the rainy season arrives (Reich and Borchert 1982, Borchert 1983). No time lag between flower induction and anthesis occurs in *S. campanulata* due to the absence of physiological drought (Lüttge 1997). Instead, it appears flowering itself inhibits vegetative growth because the onset of flowering coincided with full canopy closure and the onset of leaf shedding

preceded the peak of flowering (Figs. 2, 3, and 4). “There is no reason to presuppose that any single environmental factor controls the timing of leaf fall for large numbers of tropical plants” (Wright and Cornejo 1990:1173) and I present an alternate hypothesis for this species. Before anthesis, *S. campanulata* flower buds are filled with an aqueous solution that has a high content of enzymes related to N and P metabolism (Charyulu and Rao 1990, Charyulu and Rao 1995). Increased N, P, enzymatic, and water demand by flower buds can decrease leaf metabolic rates, turgor pressure, and growth. This resource demand from flowering can cause systematic leaf senescence in *S. campanulata* starting around February and lead to full canopy opening in July.

High peaks of wood and miscellaneous parts

during April to May and September to December seemed to match storm events (Appendix A). In contrast, *S. campanulata* green leaf fall was lowest during the rainy months of September to December when trees are flushing out new leaves, and highest during flowering from January to March (Fig. 4; Appendix A). The negative relation of green leaf fall to maximum daytime relative humidity at alluvial sites suggests it occurs when evaporation low, which can be decreasing turgor pressure (Table 4). This could be exacerbated by increased water demand from flowering and facilitate premature knocking of leaves by wind.

The dip in total litterfall common to most components occurred during the warmest months of August to September, coinciding with full canopy opening and the onset of leaf flushing (Figs. 2, 3, 4 and 5; Appendix A). This suggests *S. campanulata* forests are tuned to have lost most of their litterfall components when it is warmest and there is high evaporative demand such that the canopy is devoid of most surfaces conductive to water loss. The exception is *S. campanulata* seedpod fall, which occurred from July to August, suggesting high temperatures cause the ripening and opening of the woody seedpods. Seedpod opening and fall coincided with canopy opening and the hurricane season, which can facilitate seed dispersal by wind and water.

It is evident that canopy phenology significantly modifies the microclimate inside *S. campanulata* forests. When the canopy was devoid of leaves in June to July, day length was at its highest values resulting in higher in-situ temperature and PAR, and lower RH (Figs. 4A and 5). I expected that higher evaporation rates associated to higher PAR and temperature during canopy opening in June to July would have lowered SWC (Fig. 5). However, the highest values of SWC happened around June to July and this could be due to a drop in transpiration from leaf surfaces in the canopy (Fig. 4A). The lowest SWC values occurred during leaf flushing to canopy closure in the months of October to January with another drop at the peak of flowering in February. Increased water demand by growing leaf surfaces and flower buds during those months can be decreasing SWC through uptake by roots. This further suggests that increased water and resource demand by flowering during

February can be a cause of leaf senescence.

Lower in-situ temperature at karst sites can be associated to their low position in depressions and enclosed topography, which minimizes the exposed forest edges that can cause higher temperatures at alluvial sites (Table 1; Fig. 5A). A parallel explanation for higher in-situ RH at karst sites is that the air inside forests in depressions does not mix as much with the atmosphere (Fig. 5B). The sudden raise in RH during February to March coincided with the peak of flowering on both substrate types (Fig. 4B). In those months, evaporation of aqueous nectar in fallen flowers on the forest floor can increase RH.

The microclimate of *S. campanulata* forests during canopy opening from May to August can enhance the growth of juvenile trees in the understory (Figs. 4A and 5). Favorable in-situ SWC and RH coupled with higher PAR and temperature during those months can be enhancing photosynthetic and enzymatic activity in understory leaves. New leaf flushing during forest canopy opening was observed in some juvenile tree species such as *Cinamomum elongata*, *Cordia laevigata*, *Ocotea coriacea*, and *Thespesia grandiflora*. Preceding and coincident pulses of flower and leaf fall, respectively, can be further enhancing the growth of juvenile trees by increasing the rate of nutrient return to the forest floor (Figs. 2 and 3). This marked seasonality in which the canopy is open for about two months of the year following a leaf and flower fall pulse has implications for juvenile tree species growth that can be the focus of other studies.

Spathodea forests vs. others

How does the litterfall of novel *S. campanulata* forests compare to those of other forests in Puerto Rico and elsewhere? The annual leaf and litterfall mass of *S. campanulata* forests is in the high range of tropical moist forests (Table 5; see Klinge 1978, Brown and Lugo 1982, Cannell 1982, Proctor 1984, Vitousek 1984, Lugo et al. 1988, and Brinson 1990 for reviews). In Puerto Rico, they are comparable to or exceeded by that of riparian and saline fringe *Rhizophora mangle* mangroves, *Prestoea montana* palm, and *Pterocarpus officinalis* forests subject to periodical flooding or saline intrusions (Table 5). In contrast, *P. officinalis* swamp forests on permanently flooded condi-

Table 5. Annual litterfall mass ($\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) of lowland (<1000 m) moist to wet tropical and subtropical forests on alluvial, karst, and volcanic substrates in Puerto Rico and elsewhere.

Forest type†	Year	Total litterfall	Leaves	Reproductive parts	Reference
Alluvial					
<i>Pterocarpus officinalis</i> coastal riverine forest‡	1981	14.1			Álvarez López 1990
<i>P. officinalis</i> coastal flooded basin forest‡	1981	11.9			Álvarez López 1990
		8.7			
<i>Rhizophora mangle</i> saline fringe forest§	1986	16.6	10.2	5.3	Lugo et al. 2007
<i>P. officinalis</i> low salinity forest	1995	12.0	4.1	0.2	Eusse and Aide 1999
<i>P. officinalis</i> mid salinity forest		9.8	1.8	0.1	
<i>P. officinalis</i> high salinity forest		13.8	4.8	0.0	
<i>Spathodea campanulata</i> novel forest	2006	14.2	8.0	1.8	This study
Native forest, Sarawak	1978	11.5	6.6	0.4	Proctor et al. 1983
Terra firme native forest, Venezuela	1981	10.3	7.6	0.4	Cuevas and Medina 1986
Caatinga native forest, Venezuela		5.6	4.0	0.2	
Bana native forest, Venezuela		2.4	2.1	0.1	
Terra firme native forest, Brasil	1987	9.3	6.3	1.2	Scott et al. 1992
Pantanal seasonally flooded native forest, Brasil	1991–1994	8.8	5.8	0.6	Haase 1999
		7.5	4.9	0.7	
		10.3	6.2	1.1	
		9.5	7.1	0.2	
Pantanal non-seasonally flooded native forest, Brasil	1991–1994	4.9	2.8	0.6	Haase 1999
		5.1	3.6	0.3	
		7.5	5.3	0.3	
		7.7	5.1	0.5	
Karst					
Hilltop native forest‡	1977–1978	5.4	4.7		Dugger et al. 1979
Hillside native forest‡	1977–1978	9.3	8.3		Dugger et al. 1979
Valley secondary forest‡	1977–1978	9.2	7.4		Dugger et al. 1979
<i>S. campanulata</i> novel forest	2006	13.3	6.8	2.5	This study
<i>Castilla elastica</i> novel forest	2008	9.6	6.7	1.3	Fonseca da Silva 2011
Native forest, Malaysia¶	1975	5.2	3.8	0.7	Crowther 1987
		5.7	4.0	1.2	
		12.1	8.9	1.3	
		6.4	4.5	0.9	
Dipterocarp native forest, Sarawak	1978	12.0	7.3	1.6	Proctor et al. 1983
<i>Dyospyros maritima</i> native forest, Taiwan	2004	9.1			Liao et al. 2006
		7.1			
		7.0			
		8.7			
Volcanic					
<i>Prestoea montana</i> forest	1980	8.7	6.2	1.4	Frangi and Lugo 1985
		17.0#			
<i>Tabebuia heterophylla</i> secondary forest	1987	8.0	6.7	0.3	Cuevas et al. 1991
	1988	8.3	6.4	0.4	
<i>P. montana</i> secondary forest	1991	5.3	4.3	0.5	Lugo et al. 1999
	1992	7.5	4.8	2.1	
	1991	5.3	4.3	0.5	
	1992	5.8	4.4	0.9	
Native secondary forest	2003	7.5	4.9	1.0	Zalamea and González 2008
<i>Syzygium jambos</i> novel forest††	1998	31.9	8.7	0.9	Lugo et al. 2011
	1999	7.2	5.5	0.8	
Native forest, Sarawak	1978	8.8	5.4	1.1	Proctor et al. 1983
Tableland native forest, Australia	1980–1985	11.0	6.1	2.5	Stocker et al. 1995
Lowland native forest, Australia	1980–1985	8.0	5.2	1.2	Stocker et al. 1995
Native forest, Hong Kong‡‡	1983	12.2	8.4	1.5	Lam and Dudgeon 1985

Table 5. Continued.

Forest type†	Year	Total litterfall	Leaves	Reproductive parts	Reference
Native forest, Cameroon§§	1983	13.6	8.7	1.7	Songwe et al. 1988
		13.9	8.6	1.4	
Lowland native forest, La Réunion	2000–2002	7.6	5.3	0.8	Kirman et al. 2007

Notes: For each substrate type, sites are ordered by year of study within studies conducted in Puerto Rico and studies conducted elsewhere. Empty cells indicate data were not specified in the study.

† The dominant species or family is stated for forest types when specified by the study. Forest types are located in Puerto Rico unless otherwise stated.

‡ Extrapolated to a year from mean daily ($\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) values. Miscellaneous and reproductive parts were included with all leaves (Dugger et al. 1979).

§ This forest is in subtropical dry life zone in the south coast (Ewell and Whitmore 1973).

¶ Reproductive parts include miscellaneous non-woody components, labeled as “thrash”.

Corrected for decomposition of senesced palm fronds while clinging to trunks.

†† Hurricane Georges struck this forest during 1998.

‡‡ A typhoon struck this forest in 1983.

§§ This forest had been selectively logged and was described as “broken forest”.

tions have lower annual litterfall mass (Table 5). Comparative studies of permanently vs. periodically flooded forests also find higher annual leaf and litterfall mass on periodically flooded conditions (Van et al. 2002, Meier et al. 2006). Periodic floods allow for higher annual productivity due to longer growing seasons as opposed to permanently flooded conditions where the soil is anaerobic (Kozłowski 1997). Studies that compare periodically flooded forests to non-flooded counterparts also find higher litterfall in periodically flooded conditions (Haase 1999; Table 5). Further delving into comparisons of permanently vs. periodically vs. non-floodable forests is complicated by the simultaneous effect that soil nutrients can have on forest productivity (Cuevas and Medina 1986, Kaspari et al. 2008). Other factors that result in high leaf and litterfall mass are stress from soil water salinity (Table 5; Lugo et al. 1988, Kozłowski 1997) and young secondary forest stand age (Ewell 1976, Barlow et al. 2007). Despite all the factors that affect litterfall mass, many undisturbed forests growing on lowland alluvial, karst, and volcanic substrates have annual leaf and litterfall mass equal or similar to *S. campanulata* forests, which suggests the relatively high values found in this study is not an anomalous feature exclusive of this novel forest type (Table 5).

Most litterfall studies on the moist forests of Puerto Rico are from higher elevations on volcanic substrate (Table 5). Except for *P. officinalis* swamp forests, studies on the litterfall of non-saline lowland alluvial forests are unavailable and data for karst forests are scant. In *P.*

officinalis swamps in the northern coast, Eusse and Aide (1999) found leaf fall peaks of similar magnitude during March to June and September to October in 1995, which coincide with the leaf fall peaks observed in *S. campanulata* forests (Fig. 2B). In the only litterfall study available on moist karst in Puerto Rico, Dugger et al. (1979) found leaf and litterfall peaks during March to April in 1977 and 1978, which coincide with the first annual senesced leaf fall peak observed in this study (Fig. 2B). Similar to our study, a second peak was observed during June to November in valley bottoms but this peak was absent on hillsides where flooding is unlikely to occur. Both of these studies were undertaken within tens of kilometers from the sites in this study and should have similar environmental seasonality.

The annual reproductive part mass of *S. campanulata* forests is more than twice that of most other moist tropical forests (Table 5). Exceptions are *R. mangle* saline fringe forest, *P. montana* forests, and *Castilla elastica* novel forests in Puerto Rico, and Dipterocarp forests in Malaysia and Sarawak, tableland forests in Australia, and native forests in Hong Kong and Cameroon (Table 5). In tableland forests, these high values were attributed to weekly sampling, which limited decomposition of flowers in litter traps compared to biweekly sampling used in most studies. Native forests in Hong Kong and Cameroon were affected by disturbances, which could have increased flower productivity and fall (Table 5). It is possible that dominance by a species or family results in high reproductive mass by synchronicity of flowering (Figs. 2C, 3,

and 4B; Sakai et al. 2006). Since most reproductive part mass consists of flowers, high annual litterfall mass in *S. campanulata* forests is largely due to flower production (Tables 2 and 5).

Conclusion

This study illustrates how novel forests dominated by the African tree *S. campanulata* in northern Puerto Rico restore forest ecosystem processes between the canopy and forest floor in deforested post-agricultural sites. Dominance by one species and a pulsating environment driven by periodical flooding result in high leaf and flower litterfall mass in *S. campanulata* forests. In other tropical regions or islands where *S. campanulata* is found, local climate and substrate properties are likely to affect its litterfall and phenology. Thus, the results from this study can only be extrapolated to areas experiencing similar environmental conditions such as rainfall seasonality, floods, temperature, and insolation. However, it is likely that the effects of environmental variables on the ecophysiology of *S. campanulata* forests in this study will be the same in areas subject to equivalent environmental variations.

The high leaf and litterfall of *S. campanulata* forests can facilitate the establishment of litter and soil invertebrates and microorganisms by increasing soil standing litter and nutrients (Lugo et al. 2006, McGlynn et al. 2007, Rivera et al. 2008, Templer et al. 2008). Profuse flower and seedpod production of *S. campanulata* in Puerto Rico is not common to all places where this species occurs. In La Réunion island, *S. campanulata* trees flowered but did not produce seedpods until a native bird, *Zosterops* spp., started visiting and pollinating the self-incompatible flowers (Bitten-court et al. 2003, PIER 2011). In Puerto Rico, the presence of native bats and birds that act as pollinators have aided the reproduction and spread of *S. campanulata* to abandoned farmlands (Ayensu 1982, Kress and Horvitz 2005). This can have evolutionary implications for *S. campanulata* in Puerto Rico through the selection of trees that flower profusely and are suited to available pollinators (Abelleira Martínez 2008, Pérez et al. 2008).

High rates of leaf and flower fall, marked canopy seasonality, and *S. campanulata*'s introduced origin distinguish these novel forests, yet

they are affected by environmental factors in the same way as other tropical forests. Moreover, most tree species that invade these forests, which benefit from the coupling of canopy opening with increased sunlight and litterfall nutrient pulses, are native and ecosystem process rates can change with age and species turnover (Odum 1969, Abelleira Martínez 2010, Abelleira Martínez et al. 2010, Flynn et al. 2010). If this happens, any differences in litterfall mass and seasonality between *S. campanulata* forests and old-growth forests are successional as well. In the short-term, forest ecosystem processes and properties restored by novel *S. campanulata* forests, such as litterfall, canopy phenology, and microclimate, appear to facilitate tree species establishment and turnover in deforested and abandoned agricultural lands.

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APPENDIX A

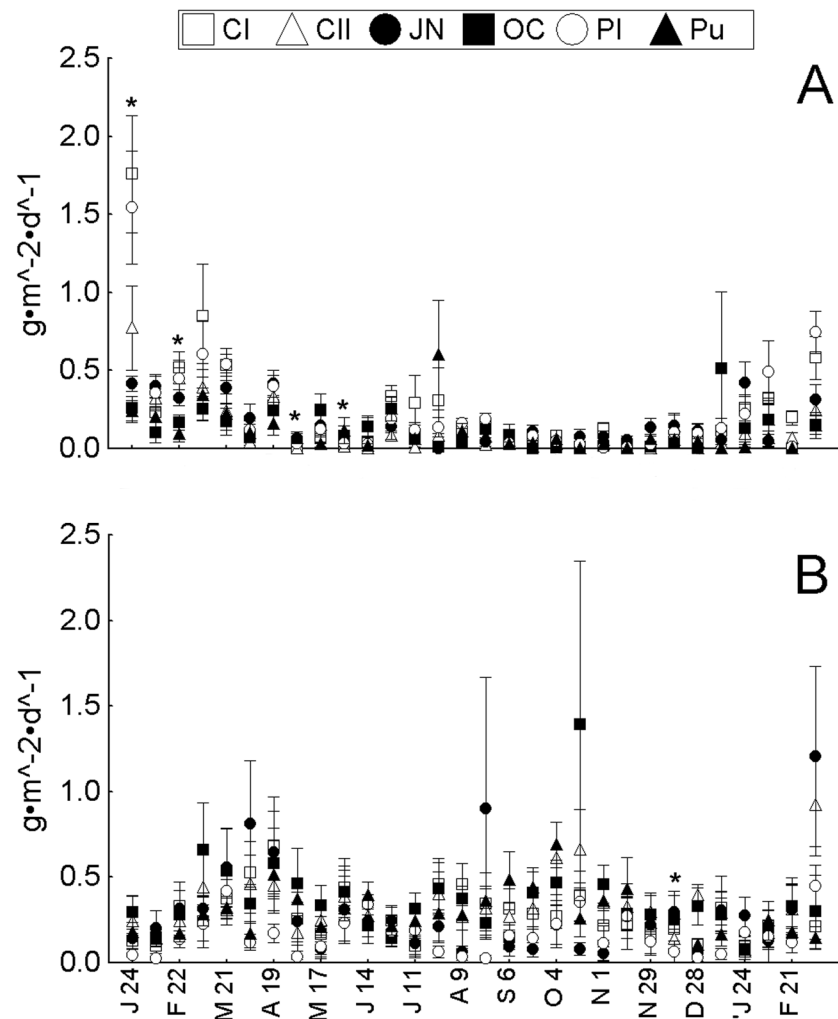


Fig. A1. Mean and standard error of biweekly *Spathodea campanulata* litterfall components of (A) *S. campanulata* green leaves, (B) other (non-*S. campanulata*) leaves, (C) wood, and (D) miscellaneous parts spanning from 24 January 2006 through 7 March 2007. Each value is the mean of six baskets per site for each sampling date. Empty symbols denote alluvial sites and dark symbols denote karst sites. Site codes follow Fig. 1. Asterisks denote significant differences between substrate type (ANOVA; $df = 1, 4$; $P < 0.05$; F [green leaves] = 24 January 2006: 11.93, 22 February 2006: 13.86, 3 May 2006: 19.69, and 31 May 2006: 14.70; F [other leaves] = 13 December 2006: 11.46; F [miscellaneous] = 8 March 2006: 17.65, and 21 March 2006: 25.71).

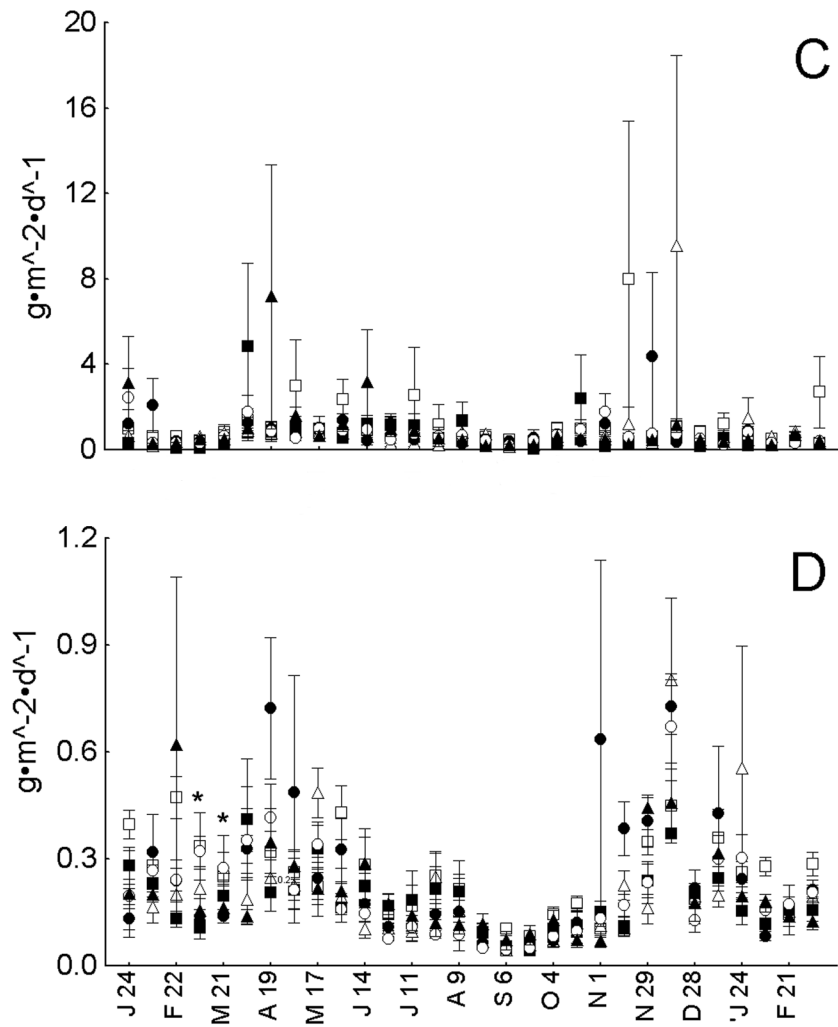


Fig. A1. Continued.

APPENDIX B

Table B1. Statistically significant regression equations found for biweekly litterfall mass ($\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) and flower fall ($\text{flowers}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) rates in *Spathodea campanulata* forest sites on alluvial substrate obtained from stepwise multiple linear regression analysis to environmental variables.

Litterfall component	Cibuco I (175)		Cibuco II (180)		Paso del Indio (179)	
	Equation	R^2	Equation	R^2	Equation	R^2
<i>Spathodea campanulata</i>						
senesced leaves						
All sampling dates	$y = -0.19(\text{DD}) - 0.24(\text{DRH}) + 20.59$	0.27	$y = -0.34(\text{DRH}) - 0.16(\text{DD}) + 0.44(\text{DL}) + 21.12$	0.34	$y = -0.21(\text{DD}) - 0.23(\text{DRH}) + 0.27(\text{DL}) + 16.86$	0.25
March–August	$y = -0.43(\text{DRH}) + 0.97(\text{DL}) + 18.84$	0.48 (75)	$y = -0.46(\text{DRH}) - 0.21(\text{DD}) + 1.1(\text{DL}) + 21.68$	0.57 (78)	$y = -0.48(\text{DRH}) + 1.6(\text{DL}) - 0.16(\text{DD}) + 16.63$	0.49 (78)
September–March	$y = -0.13(\text{DD}) + 3.22$	0.27 (100)			$y = -0.13(\text{DD}) - 0.63(\text{DL}) + 10.3$	0.36 (101)
<i>S. campanulata</i> green leaves	$y = -0.09(\text{MaxDRH}) + 7.72$	0.23*			$y = -0.12(\text{DT}) + 0.03(\text{DD}) + 3.15$	0.21
Miscellaneous	$y = -0.09(\text{DT}) + 0.06(\text{DL}) + 1.91$	0.22			$y = -0.12(\text{DT}) - 0.02(\text{DD}) + 0.07(\text{DL}) + 2.64$	0.29
Reproductive parts						
All sampling dates	$y = -0.43(\text{DT}) + 0.08(\text{DD}) + 11.69$	0.42			$y = -0.19(\text{DRH}) - 0.24(\text{DT}) + 20.49$	0.42
November–May	$y = -0.57(\text{DT}) + 0.09(\text{DD}) + 15.29$	0.35 (111)			$y = 0.18(\text{DD}) - 0.92$	0.31 (113)
<i>S. campanulata</i> flowers						
All sampling dates	$y = -0.65(\text{DT}) + 0.12(\text{DD}) + 17.69$	0.41	$y = -0.27(\text{DRH}) + 19.45$	0.28	$y = -0.36(\text{DRH}) + 25.77$	0.39
November–May	$y = 0.14(\text{DD}) - 0.76(\text{DT}) + 20.12$	0.31 (111)	$y = 0.16(\text{DD}) - 0.68$	0.19* (114)	$y = 0.22(\text{DD}) - 1.15$	0.30 (113)
All components					$y = -0.74(\text{DT}) + 24.3$	0.22

Notes: Sampling dates (month and day) below *S. campanulata* senesced leaves, reproductive parts, and *S. campanulata* flower fall components correspond to separate modes where significant equations were found. The number of data points (n) used for each regression corresponds to values of baskets per site ($N=6$). For all sampling dates, n is in parenthesis next to the site name. For separate modes, n is denoted in parenthesis next to the R^2 value. The values for dependent (y) litterfall and independent (x) environmental variables used in the regressions were means for the time period that integrated each sampling date included in each equation. The equation for the *S. campanulata* senesced leaf fall mode of March to August includes the sampling dates of 8 March 2006 to 23 August 2006. The senesced leaf fall in the sampling dates of 24 January 2006 to 22 February 2006 were included with those of 6 September 2006 to 7 March 2007 and are reported as the September to March mode. The reproductive part and flower fall in the sampling dates of 24 January 2006 to 31 May 2006 were included with those of 15 November 2006 to 7 March 2007 and are reported as the November to May mode. Independent variable codes correspond to: DD: number of dry days, DRH: daytime relative humidity in percent, DL: day length in hours, DT: daytime temperature in $^{\circ}\text{C}$, RD: river discharge in m^3/day , and WS: wind speed in m^2/s . Minimum (Min) and maximum (Max) values for some variables, and RD were included when the significance (P) of the model (R^2) was improved by their incorporation. The R^2 of all equations is significant to $P < 0.01$ except those marked by an asterisk which are only significant to $P < 0.05$. For empty cells, no statistically significant regression equations were found.

Table B2. Statistically significant regression equations found for biweekly litterfall mass ($\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) and flower fall ($\text{flowers}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) rates in *Spathodea campanulata* forest sites on karst substrate obtained from stepwise multiple linear regression analysis to environmental variables.

Litterfall component	Juan Nieves (178)		Ollas y Calderas (175)		Pugnado (180)	
	Equation	R^2	Equation	R^2	Equation	R^2
<i>Spathodea campanulata</i>						
senesced leaves						
All sampling dates			$y = 1.49(\text{DL}) - 0.59(\text{DT}) - 0.1(\text{DD}) + 0.53$	0.48	$y = 0.93(\text{DL}) - 0.12(\text{DD}) - 0.43(\text{DT}) + 3.56$	0.23
March–August	$y = 0.22(\text{RD}) + 0.71$	0.28* (76)	$y = 3.53(\text{DL}) - 1.28(\text{DT}) - 7.22$	0.45 (78)	$y = -0.23(\text{DD}) + 4.5$	0.24* (78)
September–March						
<i>S. campanulata</i> green leaves	$y = -0.04(\text{DRH}) + 2.72$	0.17*				
Reproductive parts						
All sampling dates	$y = -0.61(\text{DL}) + 7.97$	0.25	$y = -0.91(\text{DL}) + 0.17(\text{DD}) + 0.15(\text{DRH}) - 0.55$	0.25	$y = -0.56(\text{DT}) + 16.3$	0.37
November–May	$y = -0.74(\text{DL}) + 9.64$	0.27 (112)	$y = -1.3(\text{DT}) + 0.23(\text{DRH}) + 20.08$	0.35 (109)	$y = -0.97(\text{DT}) + 27.22$	0.30 (114)
<i>S. campanulata</i> flowers						
All sampling dates	$y = -0.88(\text{DL}) + 11.37$	0.35	$y = -1.33(\text{DT}) + 0.46(\text{DRH}) + 0.14(\text{DD}) + 4.51$	0.42	$y = -0.81(\text{DT}) + 23.33$	0.39
November–May	$y = -0.9(\text{DL}) + 11.79$	0.22* (112)	$y = -1.71(\text{DT}) + 0.28(\text{DRH}) + 27.86$	0.30 (109)	$y = -1.26(\text{DT}) + 35.19$	0.25* (114)

Notes: See Appendix B: Table B1 for notes and independent variable code meanings. No significant equations were found for miscellaneous and the total of all components on karst sites.

APPENDIX C

Table C1. Correlation matrix showing Pearson correlation coefficients/probabilities of environmental variables used in stepwise multiple linear regression analysis of biweekly litterfall.

Variable	DT (°C)	Min DT (°C)	Max DT (°C)	DL (hrs)	WS (m/s)	Min WS (m/s)	Max WS (m/s)
DT (°C)	1	0	0	9.60E-06	0.23	0.7	2.00E-05
Min DT (°C)	0.96	1	8.80E-12	1.00E-06	0.79	0.73	7.30E-04
Max DT (°C)	0.94	0.9	1	2.70E-08	0.45	0.78	3.30E-05
DL (hrs)	0.71	0.76	0.82	1	0.04	0.02	0.2
WS (m/s)	-0.23	-0.05	-0.14	0.38	1	2.10E-08	2.60E-05
Min WS (m/s)	-0.07	0.07	0.05	0.41	0.82	1	0.01
Max WS (m/s)	-0.7	-0.58	-0.68	-0.24	0.69	0.46	1
DRH (%)	0.76	0.7	0.55	0.25	-0.49	-0.49	-0.66
Min DRH (%)	0.68	0.62	0.48	0.14	-0.41	-0.28	-0.6
Max DRH (%)	0.68	0.61	0.55	0.31	-0.43	-0.5	-0.55
DD	-0.26	-0.16	-0.14	0.2	0.65	0.78	0.48
DRF (mm)	0.17	0.07	0.15	0.1	-0.09	-0.04	-0.07
RD (m^3/d)	0.04	-4.70E-03	0.11	0.08	-0.19	-0.23	-0.03

Note: Abbreviations follow Appendix B: Table B1 except for daily rainfall (DRF) at Manatí (Fig. 1).

Table C2. Correlation matrix showing Pearson correlation coefficients/probabilities of environmental variables used in stepwise multiple linear regression analysis of biweekly litterfall.

Variable	DRH (%)	Min DRH (%)	Max DRH (%)	DD	DRF (mm)	RD (m ³ /d)
DT (°C)	1.10E-06	3.40E-05	3.70E-05	0.16	0.36	0.82
Min DT (°C)	1.90E-05	2.40E-04	3.50E-04	0.39	0.72	0.98
Max DT (°C)	1.50E-03	0.01	1.70E-03	0.46	0.41	0.55
DL (hrs)	0.18	0.45	0.09	0.29	0.61	0.69
WS (m/s)	0.01	0.02	0.02	8.90E-05	0.63	0.31
Min WS (m/s)	0.01	0.13	0.01	4.00E-07	0.83	0.23
Max WS (m/s)	6.50E-05	4.10E-04	1.50E-03	0.01	0.73	0.89
DRH (%)	1	4.90E-09	5.80E-08	2.10E-04	0.95	0.88
Min DRH (%)	0.84	1	1.90E-03	0.06	0.49	0.15
Max DRH (%)	0.81	0.54	1	2.30E-06	0.39	0.33
DD	-0.63	-0.35	-0.75	1	0.48	0.14
DRF (mm)	0.01	-0.13	0.16	-0.13	1	1.00E-03
RD (m ³ /d)	-0.03	-0.27	0.18	-0.28	0.57	1

Note: Abbreviations follow Appendix B: Table B1 except for daily rainfall (DRF) at Manatí (Fig. 1).