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The role of tree size in the leafing phenology of a seasonally dry tropical forest in Belize, Central America

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Abstract. Leafing phenology of two dry-forest sites on soils of different depth (S = shallow, D = deep) at Shipstern Reserve, Belize, were compared at the start of the rainy season (April–June 2000). Trees ≥ 2.5 cm dbh were recorded weekly for 8 wk in three 0.04-ha plots per site. Ten species were analysed individually for their phenological patterns, of which the three most common were *Bursera simaruba*, *Metopium brownei* and *Jatropha gaudieri*. Trees were divided into those in the canopy (> 10 cm dbh) and the subcanopy (≤ 10 cm dbh). Site S had larger trees on average than site D. The proportion of trees flushing leaves at any one time was generally higher in site S than in site D, for both canopy and subcanopy trees. Leaf flush started 2 wk earlier in site S than site D for subcanopy trees, but only 0.5 wk earlier for the canopy trees. Leaf flush duration was 1.5 wk longer in site S than site D. Large trees in the subcanopy flushed leaves earlier than small ones at both sites but in the canopy just at site D. Large trees flushed leaves earlier than small ones in three species and small trees flushed leaves more rapidly in two species. *Bursera* and *Jatropha* followed the general trends but *Metopium*, with larger trees in site D than site S, showed the converse with onset of flushing 1 wk earlier in site D than site S. Differences in response of the canopy and subcanopy trees on each site can be accounted for by the predominance of spring-flushing or stem-succulent species in site S and a tendency for evergreen species to occur in site D. Early flushing of relatively larger trees in site D most likely requires access to deeper soil water reserves but small and large trees utilize stored tree water in site S.

Key Words: hardwood trees, leaf flush, onset, sampling interval, soil depth, spring-flushing trees, tree size

INTRODUCTION

Although water is the limiting factor for part of the year in seasonally dry tropical forests, many tree species flush their leaves during the dry season, before the onset of the rains (Bullock & Solis-Magallanes 1990, Mooney *et al.* 1995). Two principal reasons for this have been suggested: (1) new leaves may be able to make maximum use of the higher radiation during the dry season (Wright & van Schaik 1994); and (2) new leaves avoid predation when herbivores are at their least abundant in the dry season (Murali & Sukumar 1993). Selection would be expected to operate in favour of early leaf flushing, i.e. before the start of the rainy season.

Climatic factors alone are often not sufficient to explain phenological variation in tropical dry forests (Borchert 1994a). Water stored in the tree stem, or remaining in the subsoil, buffers the impact of low water availability and allows the production of new leaves during the dry season (Borchert 1980, 1983, 1994a, b; Reich & Borchert 1984).

This indicates that tree water status, rather than climatic factors directly, is probably the principal determinant of tree phenology in the seasonally dry tropics.

Borchert & Rivera (2001) have shown that leaf buds remain dormant during the dry season in many tree species of semi-deciduous tropical forests, and bud-break is induced by an increasing photoperiod after the spring equinox. Bud-break is highly synchronous in conspecifics of these 'spring-flushing' trees, although some within-species differences occurred. One likely explanation for the latter is the amount of stem-, soil- or rain-water available to the tree. Whether leaf flush is triggered by photoperiod or other factors, sufficient water supply is a prerequisite. Bud-break and leaf expansion during the dry season occur only when the trees are fully rehydrated (Borchert 1994a, b; Borchert *et al.* 2002). The rate of shoot development and the duration of leaf expansion varies strongly with water availability (Borchert 1994b, Borchert & Rivera 2001).

One further possible explanation for variation in the timing of leaf flush is tree size, an aspect that has been observed in savannas (Shackleton 1999) but largely neglected in the study of phenology in seasonally dry tropical forests. Trees of different sizes are likely to access

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different sources of water; and soil water partitioning can strongly influence the course of leafing phenology (Meinzer *et al.* 1999). The sizes of trees of some species (or functional groups) may affect the pattern of leafing phenology through differing water use and rooting depths, and in this way explain both within-species and between-species differences in the timing of leaf flush.

The aims of this study were (1) to investigate the influence of tree size on the timing of leaf flush in two sites with contrasting soil depths and (2) to show that differences in the timing of leafing flush, previously considered as synchronous, are detectable when the sampling interval is shorter than the conventional fortnightly or monthly intervals.

STUDY SITE AND SPECIES

The study was conducted at the Shipstern Nature Reserve on the northern coast of Belize (18°18'N, 88°11'W), Central America. Rainfall is strongly seasonal with a long dry season from January to April or May, the driest months being February and March. The highest rainfall occurs during September and October. Rainfall measurements taken over a period of 4 y (from October 1989 to October 1993) (Meerman & Boomsma 1993) showed that the area around Shipstern Nature Reserve receives only *c.* 1260 mm y⁻¹ and is thus one of the driest sites in Belize. Unfortunately, no local long-term meteorological data are available. The dry season in the year of study was exceptionally dry for the area, with no rain in February (J. Aldana, *pers. comm.*) and less than 10 mm in March, whereas the data from Meerman & Boomsma (1993) show *c.* 29 mm of rain on average for February and for March. Mean monthly minimum temperatures range from 16–17 °C in winter to 24–25 °C in summer. Mean monthly maxima are around 28 °C in winter and range from 32–33 °C in summer. Extreme temperatures may exceed 40 °C (Walker 1973).

Shipstern Nature Reserve covers an area of *c.* 9000 ha. The northern part of the reserve is mainly forest. The forest vegetation is diverse, ranging from seasonally dry semi-deciduous forest to semi-evergreen forest (Bijleveld 1998), with both forest types occurring in small patches within short distances. The northern part of Belize was hit by Hurricane Janet in 1955 and the forests were almost entirely destroyed in the hurricane itself and in the fires that followed. The forest of Shipstern Reserve is therefore only 47 y old and in a stage of regeneration. The forest is a mosaic of different-sized patches that display varying degrees of deciduousness during the dry season.

METHODS

Two study sites with distinctly different soil types were chosen within an area of *c.* 500 m × 500 m (Sayer 2000).

Soil profiles were dug and compared with those previously described by Bijleveld (1998). The first site (henceforth 'site S'; S = shallow) was situated in low 'bajo' forest on very shallow stagno gleysol (FAO Classification) overlying limestone bedrock (Bijleveld 1998). The soil was only 20 cm deep, with the bedrock reaching the surface in several places. The area becomes temporarily inundated after heavy rains, indicating that the bedrock impedes the vertical flow of rainwater into the ground. Canopy height was 8–10 m; full canopy closure did not occur in this site. The second site (henceforth 'site D'; D = deep) was located in semi-deciduous to semi-evergreen forest above deep chromic cambisol on iron-rich chalk (Bijleveld 1998). The area was not subject to flooding. Canopy height was 10–15 m with several trees exceeding 15 m. Canopy closure occurred at the beginning of the rainy season.

Three 20-m × 20-m plots were placed randomly within both of the sites in March 2000. All trees with dbh ≥ 2.5 cm were tagged, mapped and identified as far as was possible (Sayer 2000). (Of all individuals, 88% were identified to species, 7% to generic and 1% to family levels; with 4% unidentified.) Identification was carried out using Gentry (1993), Keller (1996) and Standley & Record (1936). Samples collected were cross-checked with photographs and descriptions of specimens taken and identified during a previous floristic study of the reserve (Bijleveld 1998). Voucher specimens from this earlier study, and of unidentified species from this present one, were deposited in the herbaria of University of Neuchâtel (Switzerland), ECOSUR at Chetumal (Mexico) and the Forestry Commission in Belmopan (Belize).

The most common species in each site were chosen for phenological monitoring, six in site S and seven in site D. The criterion for the choice of species was the occurrence of ≥ 10 individuals in each of at least two plots per site. Where this was not possible, species with the most individuals in all three plots were accepted. The selection resulted in 10 species in total. Three species, *Bursera simaruba*, *Jatropha gaumeri* and *Metopium brownei*, occurred abundantly in both sites (Table 1); they were common throughout the entire forest. The other tree species recorded were *Brosimum alicastrum*, *Dalbergia glabra*, *Esenbeckia pentaphylla*, *Gliricidia sepium*, *Gynopodium floribundum*, *Hampea trilobata* and *Lysiloma latisiliquum* (Table 1). As only one species per genus was investigated in this study, all species shall henceforth be referred to by their generic names.

Data collection

Diameters at breast height were calculated from girth measurements taken with a tape. Callipers were applied to find dbh directly for trees with dbh < 10 cm. If trees had coppiced or were branching below 1.3 m, all stems

Table 1. Numbers of trees per plot of each of the species recorded for phenology in two sites (S = shallow, D = deep) at Shipstern Nature Reserve, Belize, together with the percentage of trees in the canopy (≥ 10 dbh) and species' general characteristics.

Species ¹	Site: Plot:	Number of trees							% canopy trees		Characteristics ³	
		S			D			S	D			
		1	2	3	sum	1	2	3	sum			
<i>Bursera simaruba</i> * (L.) Sarg. (Burs) ²		10	9	34	53	22	12	5	39	32	56	d,ss
<i>Metopium brownei</i> * (Jacq.) Urb. (Anac)		4	7	9	20	10	9	1	20	10	55	d,hw
<i>Jatropha gaueri</i> * Greenm. (Euph)		27	13	23	63	3	4	6	13	6	8	d,ss
<i>Lysiloma latisiliquum</i> (L.) Benth. (Mimo)		5	23	12	40	–	3	–	3	68	67	d,?
<i>Dalbergia glabra</i> (Mill.) Standl. (Faba)		15	13	18	46	–	–	–	–	9	–	d,sf
<i>Gliricidia sepium</i> (Jacq.) Kunth. ex Walp. (Faba)		10	13	4	27	–	–	–	–	56	–	d,sf
<i>Gymnopodium floribundum</i> Rolfe (Poly)		8	7	16	31	–	–	–	–	7	–	d,hw
<i>Hampea trilobata</i> Standl. (Malv)		–	–	–	–	12	5	7	24	–	8	d,sw
<i>Esenbeckia pentaphylla</i> (MacFad.) Griseb. (Ruta)		–	–	–	–	9	20	1	30	–	0	se,hw
<i>Brosimum alicastrum</i> Sw. (Mora)		–	–	–	–	21	1	28	50	–	10	e,hw
Canopy trees		16	27	29	72	25	10	8	43			
Subcanopy trees		63	57	88	208	52	44	40	136			
All trees		79	84	117	280	77	54	48	179	26	24	

¹ Species marked * were common to both sites and subject to detailed comparisons.

² Family abbreviations: Anac, Anacardiaceae; Burs, Burseraceae; Euph, Euphorbiaceae; Faba, Fabaceae; Malv, Malvaceae; Mimo, Mimosaceae; Mora, Moraceae; Poly, Polygonaceae; Ruta, Rutaceae.

³ d, deciduous; e, evergreen; hw, hardwood; se, semi-evergreen; sf, spring-flushing; ss, stem-succulent; sw, softwood; ?, status unknown.

were measured and an equivalent dbh value found from the sum of the individual stems' basal areas.

All individuals of the chosen species were recorded (using binoculars) for leafing phenology (leaf flush and leaf expansion) during the transition from the dry to the rainy season. Observations for the main data set started on 6 April 2000 (week 14 of the Julian calendar) and continued as long as half of the crown was visible from the ground. Leaf flush was regarded as any stage of leaf development from bud-break until the leaves had reached their full size. All plots were visited once a week until 2 June 2000 (week 22), except 15–21 May (week 20) which was unrecorded. One plot in each site was visited per day. The plots were visited in a randomized order, with observations (following a Latin-square arrangement) taking place on three consecutive days to ensure the smallest possible temporal differences between plots within a site and an unbiased comparison between sites.

Additional observations were also made during the period of setting up of the plots, tree tagging and identification, in weeks 10–12. These observations in the 'weeks before recording' included all plots and trees but were not made in a random order and they were spread over several days. Together they are given the nominal date of 'week 12' because 51 of the 55 trees first flushing in this period did so in that week. No individuals with flushing leaves were seen prior to 17 March 2000.

The date of onset of leaf flush was determined for each individual. Trees which flushed their leaves before recording started on 6 April 2000 were assigned a '12'; all others were assigned the number of the week in which bud-break was first observed.

Rainfall measurements were taken daily at dawn from 13 March (3 wk preceding observations) to 23 June 2000. The rainfall gauge (8 cm in diameter) was set up in a

c. 30-m \times 30-m clearing at the reserve's headquarters, less than 2 km away from the sites. As rainfall in the area could be patchy, its occurrence in the forest was checked with every rainfall event recorded at the headquarters.

Data analysis

For the following analyses, canopy trees were defined as individuals with dbh > 10 cm and subcanopy trees as individuals with dbh \leq 10 cm. This classification was supported by observations in the field which suggested two strata. Trees with dbh > 10 cm mostly reached the canopy, while those with dbh \leq 10 cm were found mostly in the understorey or subcanopy. Differences in mean dbh per plot between sites, for all trees pooled, canopy and subcanopy trees, and for each of the three common species, were tested by analysis of variance (ANOVA; F_{site} with $df = 1,4$). As the sample size (three plots/site) was small, significance was accepted at $P \leq 0.1$.

Differences between the sites with regard to frequencies of species that were flushing leaves were analysed in a similar manner but for each recorded week separately. Generalized linear modelling (GLM), with the binomial distribution and logit-link function (Payne *et al.* 1997), was employed. The response variable was the number of trees flushing leaves per plot per week and the binomial totals were the corresponding total numbers of individuals. No analyses could be carried out where multiple zeros occurred, i.e. when no leaf flush was observed in either of the sites. In this case, it was assumed that the sites did not differ from each other. Onset and duration data were analysed by ANOVA using the mean week number or mean number of weeks per plot. These variables were approximately normally distributed. Mean

onset and duration times per site were rounded to the nearest 0.5 wk.

Spearman's rank correlations of the onset and the duration of leaf flush with dbh of individual trees were found for each species and each site separately (i.e. by pooling trees across plots within a site). The correlation between dbh and leafing phenology was also analysed for all trees, and canopy and subcanopy trees within each site.

Analyses were performed using the programs GENSTAT 5.3 and 6.1 (Payne *et al.* 1997) and MINITAB versions 9 and 13 (Minitab Inc. 1993). Degrees of freedom common to several tests of the same design are given once at the start of each set of following results.

RESULTS

Rainfall

The weekly sums of rainfall correspond closely to individual events on a daily basis. The peaks in weeks 15, 22 and 24 were due to 1-d events but those in weeks 19 and 20 were an overlapping wet period of 3 d. A dry fortnight followed the first rain in week 11 (Figure 1). After the rain in week 15 there was an almost completely dry period of 3 wk before the much stronger rains in weeks 19–20. Rainfall patterns at the headquarters matched those experienced in the sites.

Tree sizes

Trees of the 10 species recorded, taken together, were slightly larger on average in site S than in site D (all trees: 8.27 vs. 7.07 cm dbh respectively, $F = 4.15$, $df = 1,4$; $P = 0.111$; canopy trees: 15.62 vs. 13.87 cm, $F = 5.07$, $P = 0.088$; and subcanopy trees: 5.76 vs. 5.10 cm, $F = 30.6$, $P = 0.005$). Individuals of *Bursera* and *Metopium* were smaller, however, in site S than in site D (8.55 vs. 9.77

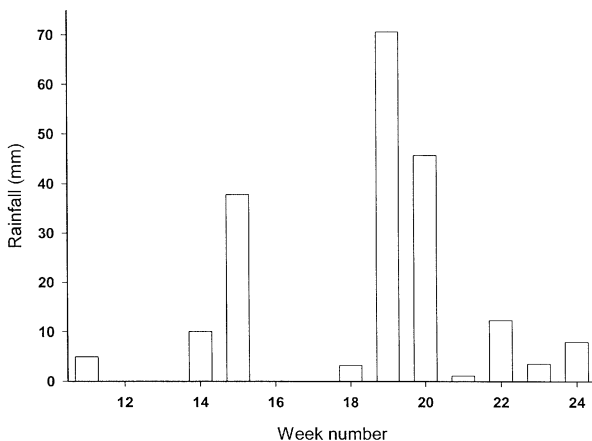


Figure 1. The pattern of rainfall at the start of the rainy season at Shipstern Nature Reserve, Belize. Julian week 10 was 6–10 March 2000. There were 5 wk (14, 15, 19, 20 and 22) with ≥ 10 mm rain.

cm, and 7.12 and 10.46 cm respectively), but similar for *Jatropha* (5.47 and 5.21 cm). Differences between sites were not significant ($P > 0.25$) for any other species.

More than half the trees of *Bursera* and *Metopium* were in the canopy in site D but far fewer were in the canopy in site S (Table 1). *Lysiloma* had two-thirds canopy trees in both sites; *Gliricidia* trees were mostly in the canopy in site S. All other species-site combinations showed predominance of trees in the subcanopy, the largest contrast between sites being for *Metopium* (Table 1).

Period of leaf flush

Individuals of all of the recorded species started flushing their leaves before the onset of heavier rains (defined here as ≥ 10 mm wk^{-1}), in the first week (14) of formal recording (Figure 1). Twelve canopy trees in site S and 14 in site D started flushing leaves before week 14. In site S, three trees lost all of their leaves before week 14 and five did not start fully flushing until after the more ample rainfall in week 15 (38 mm). Only individuals of *Lysiloma* were able to expand their leaves before week 15 in this site S. In site D, only three trees had finished flushing their leaves by week 14; all of the others continued to flush before the next rainfall event.

Frequency of leaf flush

Canopy/subcanopy. When all species were pooled within a site, the proportions of trees flushing leaves were higher in site S than site D in all weeks except week 21 (χ^2 -deviance change 4.9–58.8, $df = 1$; $P \leq 0.028$, six cases $P \leq 0.001$; Figure 2a). The week-by-week comparisons consisted of nine tests (for the designated 'week 12', and weeks 14–19, 21–22). The proportions of canopy trees with flushing leaves were also higher in site S than site D in only five of the recorded weeks (χ^2 -dev. 9.6–18.2, $P \leq 0.002$, four cases $P \leq 0.001$; Figure 2b); but for subcanopy trees there were significant differences for all weeks (χ^2 -dev. 4.8–74.0, $df = 1$, $P \leq 0.028$, seven at $P \leq 0.001$), frequency of flushing being higher in site S than site D in weeks 14–19 (plus the weeks before recording) yet the converse in weeks 21–22 (Figure 2c).

Species. The highest proportions of *Metopium* trees with flushing leaves occurred in site D in the first week and the weeks before recording (χ^2 -dev. 7.74–9.92, $df = 1$, $P \leq 0.005$), but this pattern reversed to being significantly higher in site S in weeks 16–18 (χ^2 -dev. 4.8–20.4, $P \leq 0.028$; Figure 2d). Re-analysis of trees with $dbh \leq 10$ cm, to remove a large part of the differences in tree size distributions between sites, still showed significant differences in leaf phenology ($P \leq 0.05$) but for only weeks 14 and 16. The proportion of individuals of *Bursera* flushing leaves was higher in site D only in weeks 14 (χ^2 -dev.

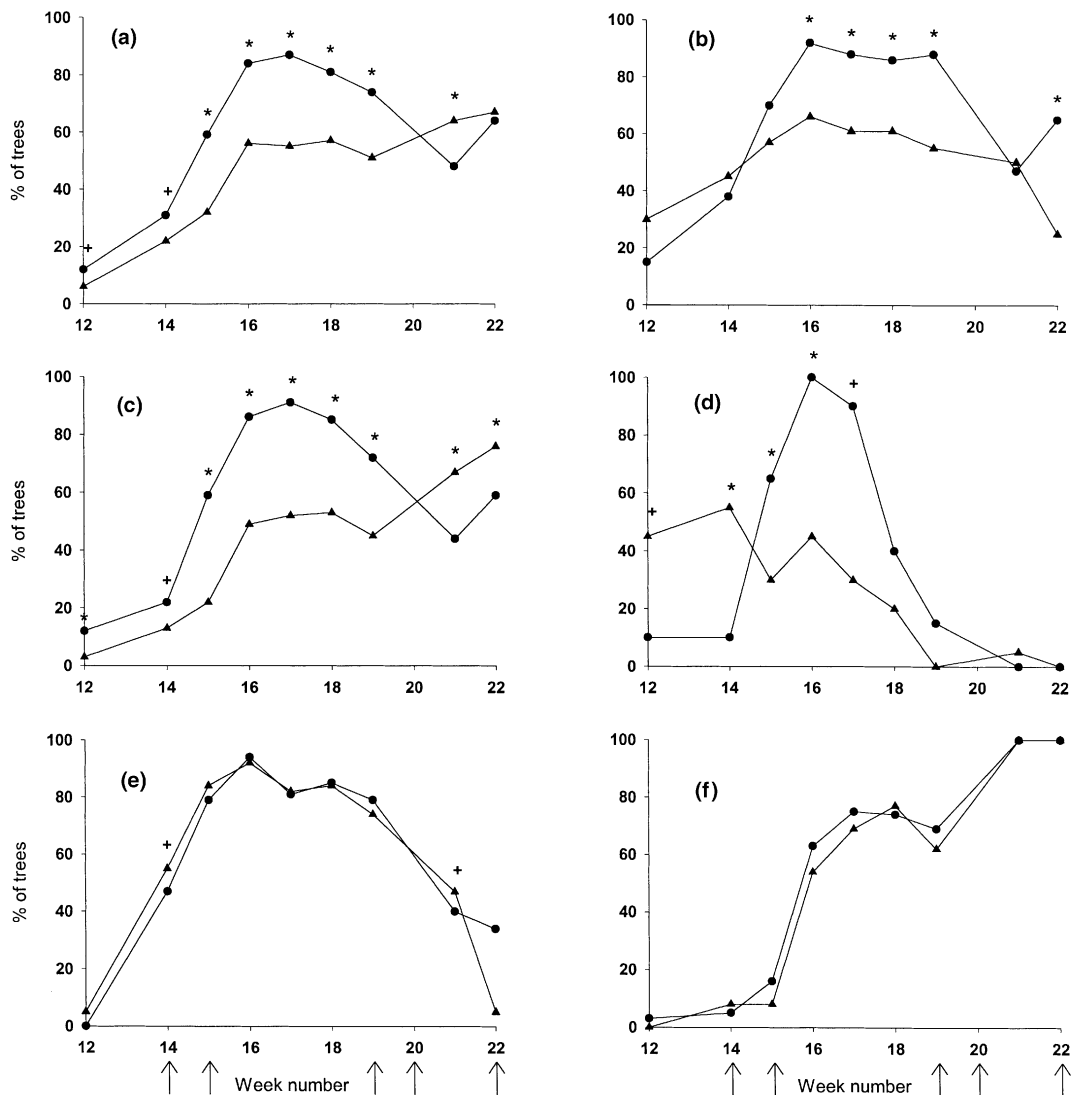


Figure 2. Relative frequencies of individuals flushing leaves per recording week at Shipstern Reserve, Belize (start 6 April 2000; Julian week 14), expressed as percentages of the total number of individuals per group or species at two sites (S, circles; D, triangles): (a) all, (b) canopy and (c) subcanopy trees; and trees of (d) *Metopium brownei*, (e) *Bursera simaruba* and (f) *Jatropha gaueri*. ‘*’ and ‘+’ denote significant differences at $P < 0.01$ and $P < 0.05$, respectively. Arrows denote weeks with > 10 mm rainfall (see Figure 1).

4.84, $P = 0.028$) and 21 (χ^2 -dev. 4.62, $P = 0.032$) (Figure 2e), while the leafing phenology of *Jatropha* showed no significant differences ($P > 0.05$) between sites in any week (Figure 2f).

Onset of leaf flush

Canopy/subcanopy. When all trees were pooled, leaf flush started 1.5 wk earlier in site S than in site D but not significantly so ($F = 3.59$, $df = 1,4$; $P = 0.135$; Figure 3a). Canopy trees were only 0.5 wk earlier in site S than site D ($F = 0.33$, $P = 0.60$; Figure 3b) whilst those in the subcanopy were significantly 2 wk earlier ($F = 5.99$, $P = 0.077$; Figure 3c).

Species. Individuals of *Metopium* started to flush leaves significantly 1 wk earlier in site D than in site S ($F = 13.77$, $df = 1,4$; $P = 0.021$; Figure 3d), non-significantly 0.5 wk earlier for *Bursera* ($F = 4.00$, $P = 0.116$; Figure 3e), with the weak converse by 1 wk for *Jatropha* ($F = 1.22$, $P = 0.33$; Figure 3f). There was, however, no significant difference between sites in the onset of leaf flush in *Metopium* when canopy trees (dbh > 10 cm) were excluded ($P = 0.282$).

Duration of leaf flush

Trees flushed their leaves longer in site S than site D ($F = 3.94$, $df = 1,4$; $P = 0.118$; 5.5 vs. 4.0 wk respectively),

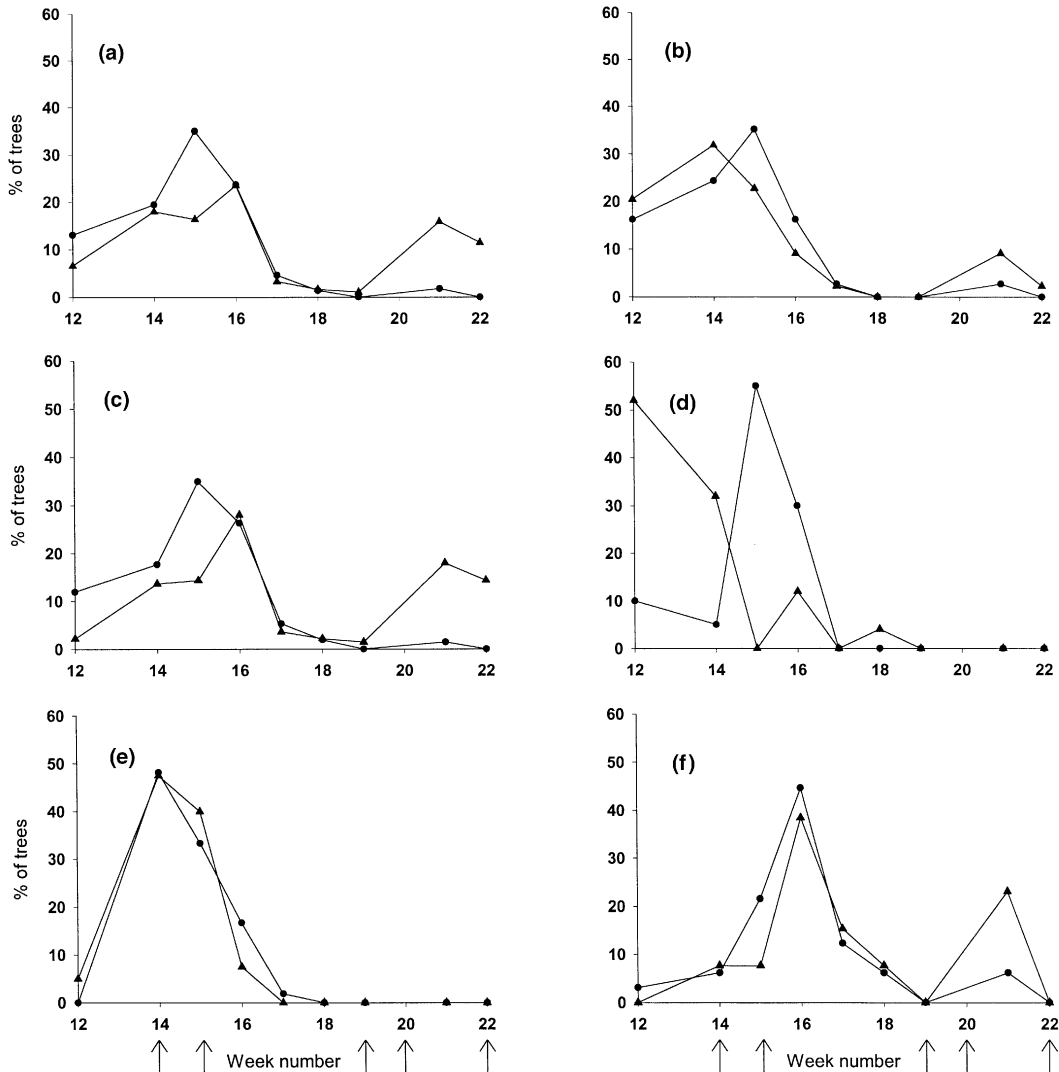


Figure 3. The timing of onset of leaf flush, expressed as the relative frequencies of trees starting to flush in each week, at Shipstern Reserve, Belize (start 6 April 2000; Julian week 14), expressed as percentages of the total number of individuals per group or species at two sites (S, circles; D, triangles): (a) all, (b) canopy and (c) subcanopy trees; and trees of (d) *Metopium brownei*, (e) *Bursera simaruba* and (f) *Jatropha gaumeri*. Arrows denote weeks with high rainfall, as in Figure 2.

significantly so in the canopy ($F = 5.53$, $P = 0.078$; 6.0 vs. 4.5 wk) but less strongly in the subcanopy trees ($F = 3.45$, $P = 0.137$; 5.5 vs. 4.0 wk). For *Bursera*, *Metopium* and *Jatropha* there were no significant differences between sites ($P = 0.14$ – 0.55).

Leaf flush and rainfall

The first main increase in leaf flushing occurred with the first rain events in weeks 14 and 15 (Figure 2). In the subcanopy of site D (Figure 2c) and for *Jatropha* in both sites S and D (Figure 2f) the frequency of leaf flushing rose again with the heavier rains in weeks 19 and 20. Trees of *Bursera* and *Metopium*, as well as the canopy

trees in site D and the canopy and subcanopy trees in site S, did not respond to these later rains.

Tree size and leaf flush

Onset. For all trees pooled, larger trees flushed their leaves earlier than small ones in both sites (site S: $r_s = -0.211$, sample sizes in Table 1, $P < 0.01$; site D: $r_s = -0.493$, $P < 0.01$), and the same was the case for subcanopy trees (site S: $r_s = -0.208$, $P < 0.01$; site D: $r_s = -0.339$, $P < 0.01$). In the canopy large trees flushed earlier only in site D ($r_s = -0.355$, $P = 0.02$; in site S there was no trend ($r_s = -0.019$, $P = 0.87$)). Among the common species, only large trees of *Metopium* in site D flushed earlier than small ones

($r_s = -0.700$, $P < 0.01$). Of the other species, large trees of *Gymnopodium* (site S) ($r_s = -0.496$, $P < 0.01$), and *Brosimum* (site D) ($r_s = -0.296$, $P = 0.04$) also flushed earlier than small trees.

Duration. Trees flushed their leaves longer with increasing dbh in site S, but not in site D, when all trees were pooled ($r_s = 0.191$, sample sizes in Table 1; $P < 0.01$). No significant relationship was found for either canopy or subcanopy trees at either site ($P > 0.10$). However, large trees of *Bursera* flushed longer than small ones at both sites (site S: $r_s = 0.275$, $P = 0.046$; site D: $r_s = 0.428$, $P < 0.01$), as did large trees of *Lysiloma* ($r_s = 0.361$, $P = 0.017$).

Integrating measures of leaf flushing

The time by which at least 50% of trees had started, and were continuing, to flush leaves (TLF₅₀) was used as a cumulative measure of the onset of leaf flush at the level of canopy/subcanopy trees or of a species. The time of peak flushing (TLF_{max}) was defined as the time when the maximum number of trees were fully flushing (75–100% of the crown). These two measures, summarized in Figure 4, integrate leaf flushing over time. This was valuable because (1) some species had small sample sizes (Table 1) and individual onset times were erratic, (2) the rate of leaf flushing could vary greatly within a species and (3) some species started to flush for a second time (e.g. after heavier rains or herbivore attack).

Peak flushing (TLF_{max}) was at week 16 for canopy and subcanopy trees in both sites S and D (Figure 4). Onset (TLF₅₀), however, was earliest for the canopy trees (week 14) and latest for subcanopy trees (week 16) in site D. In site S, TLF₅₀ was intermediate at week 15 for both canopy and subcanopy. Among the species, subcanopy trees of *Metopium* and *Bursera* had TLF_{max} at 16 weeks in both sites but canopy trees tended to peak 1–2 wk earlier. *Jatropha* and the other species all had a TLF_{max} later than week 16. For canopy trees of *Metopium* at site D, TLF₅₀ was unusually early at week 12 (Figure 4), followed by subcanopy trees of this species and site and *Bursera* (except for the subcanopy in site S) in week 14. The other species and size classes had largely reached TLF₅₀ by weeks 15–16. *Brosimum* was also exceptional in having a TLF₅₀ at week 21.

DISCUSSION

Sampling interval

Peaks in leaf flush (TLF_{max}) occurred within 3 wk of onset in all but two of the 10 tree species. When leaf flush takes place in such a short period of time, important small differences in onset and duration, both within and between species, are only detectable when a sampling interval of

1 wk is used. Most phenological studies in the tropics to date have been based on monthly observations, although Williams *et al.* (1997) did detect asynchronous phenological activity in individuals of the same species with a 2-wk sampling interval.

Differences in leaf flushing between the sites

Canopy and subcanopy trees in site S had a more synchronous leafing phenology than those in site D (Figures 2 and 3). Of the seven species recorded in site S, only *Bursera* and *Dalbergia* started to flush before week 15 (Figure 4) and only *Jatropha* started flushing in week 16. The more uniform response to the first rain showers after the dry season in site S may have been due to the species composition, as most of the species recorded in this site were 'spring flushing' or stem-succulent trees (see below).

Subcanopy trees started flushing their leaves earlier in site S than site D (Figures 3b and 4). The analyses of the subcanopy trees are, however, biased by the presence of *Brosimum* in site D (Table 1). *Brosimum* is an evergreen leaf-exchanging species, and therefore belongs to a different phenological type than the species recorded in site S, all of which are deciduous. *Brosimum* only started flushing leaves towards the end of the recording period (week 21). Most individuals of this species were found in the subcanopy and they comprised more than a quarter of all subcanopy trees in this site (Table 1).

The difference in species composition of the canopy layer explains why large canopy trees flushed earlier than small ones in site D but not in site S. The commonest canopy trees were *Gliricidia*, *Bursera* and *Lysiloma* in site S and *Metopium*, *Bursera* and *Brosimum* in site D (Table 1), and leaf flush was only correlated with dbh in *Metopium* and *Brosimum*. However, the lack of a correlation between the onset of leaf flush and tree size among the common canopy trees in site S is striking and may have resulted from the large number of 'spring-flushing' canopy trees in that site.

The duration of leaf flush in subcanopy trees was shorter in site D than in site S. The TLF₅₀ of all trees in site D coincided with TLF_{max} since most trees had finished flushing their leaves within 3 wk (Figure 4). Smaller trees may have benefited from flushing their leaves more rapidly when radiation levels were high and finishing expansion of their leaves before the canopy closed in site D. The canopy was not fully closed in site S.

Although rainfall of > 30 mm is considered to be sufficient to induce leaf flush in non-spring-flushing trees (Borchert 1994a, Borchert & Rivera 2001), individuals of all species started flushing some leaves before the rains (Figures 1 and 2). The leaf loss and arrested expansion of leaves in canopy trees in the dry fortnight following the first rainfall was observed only in site S and may have been an indication of deep reserves of soil water in site

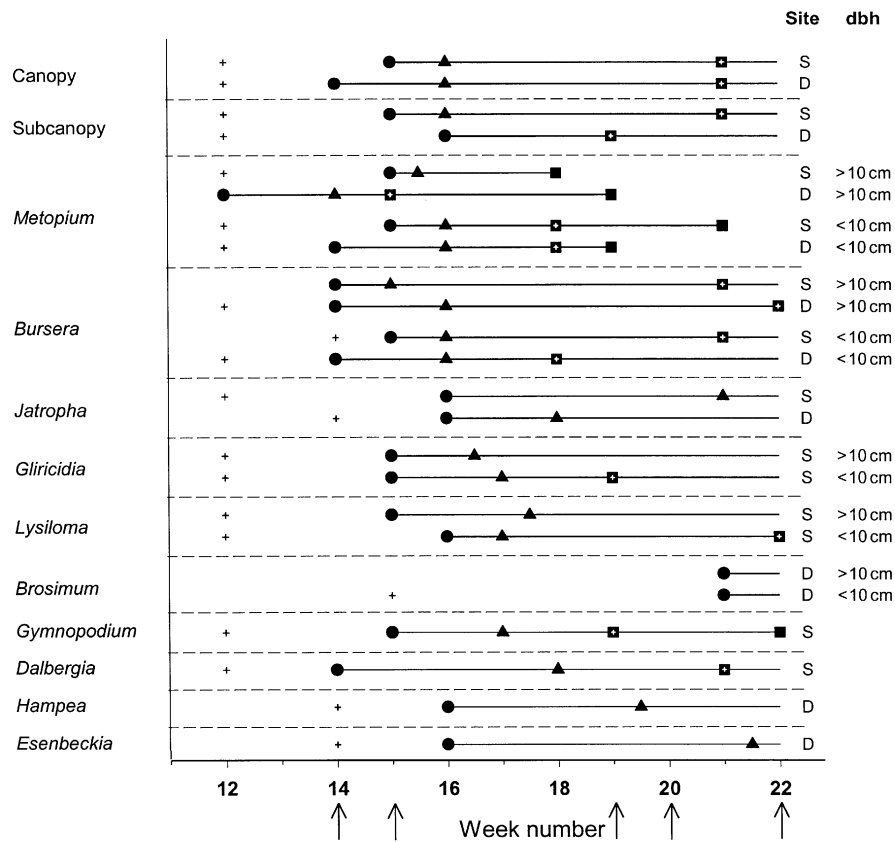


Figure 4. Integrated patterns of leaf flushing of 10 tree species at two sites (S, D) in Shipstern Reserve, Belize, recorded from 6 April–2 June 2000 (Julian weeks 14–22). Observation in the previous weeks 10–12 are shown as week 12. Crosses (+) indicate the onset of leaf flush of the first individual; circles, the first week at which there was $\geq 50\%$ trees that had flushed (TLF_{50}); triangles, the week(s) with peak leaf flush (maximum number of trees with 75–100% of canopy flushed, TLF_{max}); and squares, end of leaf flush. Where TLF_{max} coincided with TLF_{50} , and where end of leaf flush was not before the end of the recording period, no symbols are shown. Where TLF_{max} is shown at a half-week interval it was the average of 2 weeks with the same measure. A square with a cross indicates the end of leaf flush for $> 50\%$ of all individuals. Phenology of those species with many large individuals is given in two dbh classes. Arrows denote weeks with high rainfall, as in Figure 2.

D, which would make leaf flush possible despite the insufficient rainfall.

Functional groups of species

The species studied can be divided into two groups according to the structure of their stem wood (hardwood, softwood and succulent), their general leafing phenology (deciduous or evergreen) and whether they are ‘spring’ flushers.

Hardwoods. This first group includes *Metopium*, *Gymnopodium*, *Esenbeckia* and *Brosimum* and consists of trees with high wood density, the hardwoods (Record & Hess 1947). Tree size plays an important role in the pattern of leaf flush in these species, with large trees flushing leaves earlier than small ones. In *Metopium* the differences between sites apparent from the GLMs and the timing of onset of leaf flush were largely due to the difference in size (dbh) distributions (Table 1). *Metopium* was the most common

canopy species in site D, while only two individuals in site S had dbh > 10 cm.

Individuals of *Gymnopodium* rarely grow very large, according to Record & Hess (1947), and it is possible that they can flush leaves in response to the first rains after the dry season. However, in the year of study, those individuals flushing immediately after the first rain in week 11 lost their leaves in the subsequent dry fortnight and did not produce new ones until week 15. Thus, the observed relationship between tree size and the onset of leaf flush may have been the result of a trade-off between the opportunity to produce leaves when light levels were high and the risk of losing leaves after small isolated rainfall events and subsequent dry periods (Reich & Borchert 1984).

Although *Esenbeckia* (site D) is also a hardwood tree (Record & Hess 1947), no influence of tree size on leafing phenology was found. It is possible that the lack of a significant relationship between tree size and leaf flush was due to the narrow dbh range (2.6–7.1 cm). None of the trees of this species reached the canopy.

Stem-succulents and spring-flushing species. The second group includes all stem-succulent and 'spring-flushing' species; *Bursera*, *Jatropha*, *Dalbergia* and *Gliricidia*. The sizes of these species had no inferred influence on the onset of leaf flush and had little or no influence on the pattern of their leafing phenology. Borchert & Rivera (2001) have shown that leaf flush in stem-succulent and 'spring-flushing' tree species is triggered by changes in day length. Stem-succulents can store large amounts of water and softwood trees also have high water storage capacities (Borchert 1994a, Borchert & Rivera 2001). Water stored in these species enables them to flush their leaves before the onset of the rainy season (Borchert 1994a). Although large trees can store more water than can small ones (Goldstein *et al.* 1998), they also require more water as they generally have more growing shoots and transpiring leaves (Borchert 2000). Thus, the stored water in these trees may not only buffer the impact of seasonal dryness (Borchert 1994a) but it will also lessen or eliminate the effects of tree size on leafing phenology.

Bursera is a shallow-rooted, stem-succulent tree (Borchert 1994a, Holbrook *et al.* 1995, Olivares & Medina 1992). Both *Bursera* and *Gliricidia* have recently been identified as a spring-flushing species too by Borchert & Rivera (2001), as has *Dalbergia retusa*. It is therefore likely that *Dalbergia glabra* is also a spring-flushing species. *Jatropha* is a stem-succulent species and it seems likely that *Lysiloma* is also a spring-flushing tree, as the pattern of leaf flush is similar to that of *Gliricidia*. *Hampea* (site D) is a small deciduous softwood tree (Record & Hess 1947).

The only observed influence of tree size on the leaf flush of trees in this group was that smaller individuals of *Bursera* flushed their leaves more rapidly than larger ones in both sites (Figure 4) and small individuals of *Lysiloma* flushed leaves more rapidly in site S. In *Bursera*, small trees in the subcanopy layer may have benefited from flushing their leaves rapidly in order to make full use of the high radiation before the canopy closes. This suggestion is supported by the correlation between duration and dbh which was much stronger for individuals of *Bursera* in site D, where less light reaches the subcanopy after canopy closure, than in site S.

Lysiloma has very shallow, widely spreading roots according to Stratton *et al.* (2000). Small trees of this species may have been able to obtain enough rainwater after the first light showers to expand their leaves more rapidly than large trees.

Tree size and leaf flushing

Tree size has been shown to influence either the onset or the duration of leaf flush in five of the 10 species recorded in this study and is therefore an important factor in determining patterns of leafing in the seasonally dry tropical

forest of Shipstern Reserve. Two important factors may explain how tree size affects leaf flushing:

Rooting. Large trees may be able to flush their leaves earlier if they have access to ground water or soil moisture reserves at greater depths (Meinzer *et al.* 1999), while small trees may be better able to expand their leaves more rapidly after light showers and thus benefit from higher light levels before canopy closure. Although water availability may not necessarily be the factor triggering leaf flush, a sufficient water supply is nevertheless a prerequisite for leaf expansion (Borchert 1994a, b), and the rate of shoot development varies greatly with soil water availability (Borchert & Rivera 2001). That trees most likely were rooting more deeply in site D than site S is supported by observations on fallen trees in the field. These showed that trees in site S had very shallow, widely spreading root systems, whereas broken-off tap roots were observed for fallen trees in site D. Several evergreen species were present in site D, and these are usually found in sites with deep soils where extraction of water from subsoil reserves is possible (Borchert 1999, Jackson *et al.* 1995). A substantial gap in detailed understanding of these dry forest ecosystems is the knowledge of where precisely the roots of trees are and from what depths is water taken up.

Radiation. Large trees may be better able to afford flushing leaves earlier than small ones and thereby make maximum use of the higher seasonal radiation levels (Wright & van Schaik 1994). If insufficient water is available in the subsequent weeks, the leaves will fall or remain only partially expanded (Reich & Borchert 1984). Furthermore, as leaf flush requires large amounts of non-structural carbohydrates (Tissue & Wright 1995), large trees may be more likely to afford this strategy and the associated risk than small trees, as they have the larger reserves (Rathcke & Lacey 1985). How much water, carbon and nutrients is stored within not just stems but also roots over the dry season is an important aspect for further study.

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