Leaf flushing phenology and herbivory in a tropical dry deciduous forest, southern India

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Abstract. Patterns of leaf-flushing phenology of trees in relation to insect herbivore damage were studied at two sites in a seasonal tropical dry forest in Mudumalai, southern India, from April 1988 to August 1990. At both sites the trees began to flush leaves during the dry season, reaching a peak leaf-flushing phase before the onset of rains. Herbivorous insects emerged with the rains and attained a peak biomass during the wet months. Trees that flushed leaves later in the season suffered significantly higher damage by insects compared to those that flushed early or in synchrony during the peak flushing phase. Species whose leaves were endowed with physical defenses such as waxes suffered less damage than those not possessing such defenses. There was a positive association between the abundance of a species and leaf damage levels. These observations indicate that herbivory may have played a major role in moulding leaf flushing phenology in trees of the seasonal tropics.

Key words: Phenology – Leaf flushing – Insect herbivory – Tropical deciduous forests – Southern India

In the seasonal tropics, leaf production has been considered to be a response to the onset of rainfall. It could be disadvantageous to flush when there is moisture stress and trees may thus flush synchronously with the onset of rains (Daubenmire 1972; Frankie et al. 1974; Reich and Borchert 1984; Lieberman and Lieberman 1984; Prasad and Hegde 1986; Bullock and Solis-Magallenus 1990). Further, it has been argued that the timing of leaf flushing is influenced by the need of an individual to harvest more light and to reduce competition among physiologically active sites for vegetative and reproductive functions (Alvim 1964; Wareing and Patrick 1975). For instance, it may not be possible for a plant to allocate energy for both leaf flushing and flowering at the same time when resources such as moisture are scarce (Janzen 1967).

Leaf flush has thus been treated as a physiological response of plants to seasonal rhythms in abiotic factors. The role of biotic pressures in moulding the evolution of leaf flushing time has been less well investigated. However, some have suggested that synchronous leaf flushing serves to satiate predators and to reduce herbivore damage (Rockwood 1974; Lieberman and Lieberman 1984; Aide 1988). Young leaves are succulent, rich in nutrients and contain lower quantities of phenolic compounds and other such chemical deterrents (Feeny 1976; Rhoades and Cates 1976); hence, they are more susceptible to herbivore damage than are mature leaves which contain more waxes, lignins and other secondary compounds, making them less palatable for herbivores (Coley 1980, 1983).

This study examines the phenology of leafing in trees of a tropical dry deciduous forest and attempts to identify the selective forces that might have influenced it. Specifically, we attempt to test the hypothesis that, among other factors, risk of herbivore damage by insects during the wet season may have constituted an important selective force in shaping the timing of leaf production.

Material and methods

Study area

The study was conducted in Mudumalai Sanctuary, (11° 30' – 11° 39' N, 77° 27' – 77° 43' E) at an altitude of about 1000 m above MSL in Tamilnadu, southern India. The floristics are described in more detail elsewhere (Sharma et al. 1978; Sukumar et al. 1992). We selected two sites differing with respect to rainfall and floristic composition in the sanctuary.

Site 1. The vegetation at this site, located in the heart of the sanctuary, can be classified as tropical dry deciduous forest (Puri et al. 1983). The most common trees are *Lagerstroemia microcarpa* (Lythraceae), *Terminalia crenulata, Anogeissus latifolia* (Combretaceae), *Tectona grandis* (Verbenaceae) and *Kydia calycina* (Malvaceae), constituting about 60% of all trees greater than 10 cm DBH. This site receives about 1100 mm rainfall annually, spread from April through October. Rainfall is highest during June and July. From November onwards there is a dry spell of about 5 months during which the area receives little or no rain (rainfall distribution during

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the study period is given in Fig. 1a). At this site there are on average 308 trees above 10 cm DBH per hectare (Sukumar et al. 1992)

Site II. The second site, about 10 km east of the first site along the fringe of the sanctuary, is drier. It receives about 600 mm rainfall annually, spread from May through November with a peak in the month of September or October. The vegetation here can be classified as tropical dry thorn forest (Puri et al. 1983), the major species being *Anogeissus latifolia* (Combretaceae), *Acacia chundra* (Fabaceae), *Premna tomentosa* (Verbenaceae) and *Erythroxylon monogynum* (Erythroxylaceae) which constitute over 60% of the total number of trees in the area. The density is about 240 trees above 10 cm DBH per hectare.

Sampling methods

Observations of leaf phenology. A total of 286 trees from 38 species at Site I and 167 trees from 27 species at Site II was tagged and observed for leaf flushing and extent of insect herbivore damage at 15-day intervals between April 1988 and August 1990. A total of 100 leaves in the crown of the trees was counted randomly either by eye or with the help of binoculars depending on the height of the tree. Leaves which had more than 50% of the leaf area removed by herbivores were considered damaged and expressed as a percentage. For each tree the presence or absence of each of the following leaf stages was noted: flushing leaf, expanding leaf, mature leaf (fully expanded) and old leaf (leaves which are yellow or turning yellow).

Rainfall data at fortnightly intervals were collected from the rain guages maintained by Tamilnadu Electricity Board near the study sites.

Insect collections. Modified Rothamsted light traps were placed inside the forest from 6 p.m. to 6 a.m. at 15-day intervals from January 1989 to March 1990 to collect insect samples, which were dried and weighed.

Statistical analyses. We have generally used non-parametric statistical tests, which do not assume any particular distribution of the variables, because we have treated herbivore damage to leaves as a class-variable, the levels of damage to young leaves are very low, and sample sizes are low for certain comparisons.

Differences in the patterns of frequency of leaf flushing in a month, rainfall and insect emergence were analysed using the Kolmogorov-Smirnov test (herein after called KS test). The frequency of leaf-flushing species, rainfall and insect biomass in each month were tested for differences in distribution patterns of these three variables (Zar 1984).

Spearman's rank correlation coefficients (r_s) were computed using procedures given by Zar (1984) to establish the relationship between frequency of leaf flushing in a month and amount of rainfall received in that month, between insect abundance (biomass) and amount of rainfall, and between leaf flushing frequency and insect abundance in each month. In order to know the effect of rainfall on leaf flushing frequency in subsequent months, time-lag correlations with 1–3 months lag were computed between these two variables. Similar time-lag correlations (r_s) were computed for leaf flushing frequencies and insect abundance in subsequent months. To know the effect of rainfall and insect abundance on herbivore damage, correlation coefficients (r_s) were computed between rainfall and herbivore damage and between insect abundance and herbivore damage.

Correlation coefficients (r_s) were also computed to investigate the influence of time of leaf initiation on mean herbivore damage to young leaves and mature leaves. Mean herbivore damage to young leaves for a species was correlated with the density of the species to know whether there was any difference in damage between commoner and rarer species.

Comparisons of mean levels of herbivore damage to leaves between species with and without physical defences, and to species between sites were made by Mann-Whitney *U*-test.

Results

During 1989 the earliest species to initiate leaves were *Bombax ceiba*, *Dalbergia latifolia*, *Elaeodendron glaucum*, *Garuga pinnata* and *Radermachera xylocarpa*, which began flushing in January at the beginning of the dry season. The majority of species began flushing by February and continued to flush until June or later. Two species, *Hymenodactyon orixense* and *Lagerstroemia microcarpa*, began flushing only in May and completed flushing within 1–2 months. In 1990 most species (with the exception of *Bombax ceiba* which flushed in January) began flushing relatively later, about by the month of March. Duration of flushing was also on average lower than in the previous year.

The orders of insects collected in the light traps included Lepidoptera, Coleoptera, Homoptera, Isoptera and Hymenoptera. Of these the biomass of the two major herbivorous orders, Lepidoptera and Coleoptera, was highly correlated with the total insect biomass (Lepidoptera, Site I, $r_s = 0.84$, $n = 14$, $P < 0.05$; Site II, $r_s = 0.82$, $n = 14$, $P < 0.05$. Coleoptera, Site I, $r_s = 0.81$, $n = 14$, $P < 0.05$; Site II, $r_s = 0.70$, $n = 14$, $P < 0.05$). Therefore we have used the figures of total insect biomass as representative of herbivorous insect abundance in the correlations reported subsequently.

Patterns of rainfall, leaf flushing and insect emergence

A plot of rainfall and leaf flushing frequencies (Fig. 1) with respect to month indicates that trees initiate leaf before the onset of rains. The distribution patterns of rainfall and leaf flushing frequency across months were significantly different for both Site I (KS test, $df = 283$, $D = 0.542$, $P < 0.01$) and Site II (KS test, $df = 166$, $D = 0.376$, $P < 0.01$). Rain usually starts during the month of April while some species are already beginning to flush leaves in December. There is no correlation between rainfall and leaf-flushing frequency during corresponding months either at Site I ($r_s = 0.09$, $n = 28$, $P > 0.05$) or Site II ($r_s = 0.23$, $n = 29$, $P > 0.05$). However, the time-lag correlations showed significant correlation between rainfall and leaf flushing frequency 2 months prior both at Site I ($r_s = 0.60$, $n = 26$, $P < 0.05$) and Site II ($r_s = 0.57$, $n = 27$, $P < 0.05$). These analyses clearly indicate that leaf flushing starts before the onset of rain and reaches a peak about two months before rainfall reaches a peak.

Abundance of insects was positively correlated with rainfall at Site I ($r_s = 0.78$, $n = 12$, $P < 0.005$) and Site II ($r_s = 0.55$, $n = 14$, $P < 0.05$). Insects emerge in response to rainfall and their abundance increases as the rainy season progresses (Fig. 1).

The distribution patterns of insect abundance and leaf flushing frequency also differ significantly at Site I (KS test, $df = 283$, $D = 0.463$, $P < 0.05$) and Site II (KS test, $df = 166$, $D = 0.415$, $P < 0.01$) (Fig. 1). The time-lag correlation between insect abundance and leaf-flushing frequency 2 months previously shows strong positive correlation at both sites (for Site I, $r_s = 0.67$, $n = 14$, $P < 0.01$ and for Site II, $r_s = 0.63$, $n = 15$, $P < 0.01$). These results suggest that leaf flushing begins before the emergence of insects and attains
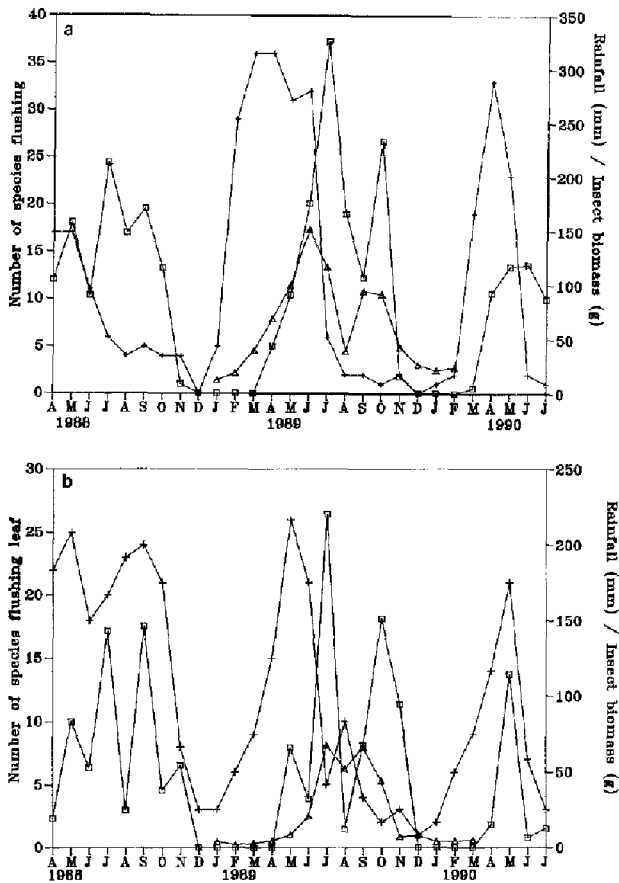
Fig. 1a, b. Patterns of leaf flushing frequency (*plus sign*), rainfall in mm (*open square*) and insect biomass in grams (*open triangle*) at monthly intervals at a Study Site I and b Study Site II
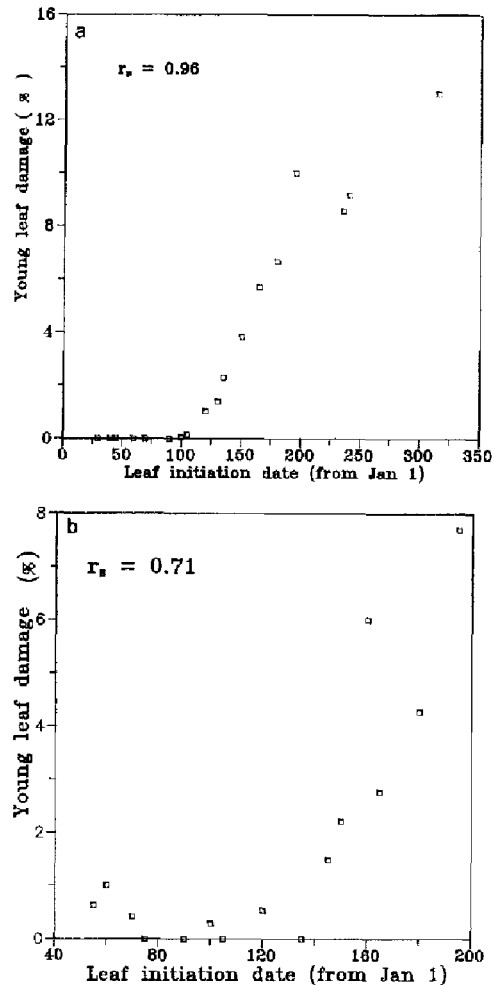

Fig. 2a, b. Relationship between date of leaf initiation (number of days from January 1) and damage to young leaves at a Site I and b Site II. Data from 1989 and 1990 are combined

a peak about 2 months before insect biomass reaches its peak. By the end of March 1989 nearly 190 of the 283 trees in Site I had flushed leaves; thus 67% at Site I were in flush before onset of rains. At Site II nearly 82% (132 of 167 individuals) of trees flushed leaves before onset of rains in April 1989.

Patterns of leaf flushing, insect emergence and herbivory

A correlation of the date of leaf flushing versus percentage herbivore damage shows that trees that flush leaves later are prone to greater damage by herbivorous insects at both Site I ($r_s = 0.96$, $n = 18$, $P < 0.01$) and Site II ($r_s = 0.71$, $n = 15$, $P < 0.01$). (Fig. 2). The correlation between insect abundance and herbivore damage was also high and significant at Site I ($r_s = 0.73$, $n = 9$, $P < 0.05$) and Site II ($r_s = 0.83$, $n = 9$, $P < 0.05$). These correlations indicate that early flushers suffer less damage than do the late flushers (Fig. 3).

The pattern of young-leaf damage across species indicates that there is considerable difference in their vulnerability to herbivores. A majority of species at both sites suffered relatively little damage ($< 5\%$ of leaves showing damage as defined earlier). Trees which suffered $> 15\%$ damage usually belonged to the more abundant species

such as *Terminalia crenulata*, *Anogeissus latifolia* and *Tectona grandis* at Site I and *Anogeissus latifolia* at Site II. In addition, *Grewia tiliifolia* (at Site I) and *Ziziphus xylopyrus* (at both sites) are two species of intermediate abundance which suffered substantial damage.

Leaf morphology traits and herbivore resistance

Tree species whose leaves had a waxy coating suffered significantly lower damage to young and mature leaves than did those without such physical defenses (Table 1). The species without a waxy coating initiated leaves earlier on average than did species with a waxy coating.

Herbivory in relation to species abundance

The correlation between mean damage to young leaves in a species and the density of the species was not significant at Site I ($r_s = 0.29$, $n = 38$, $P > 0.05$) but positively significant at Site II ($r_s = 0.41$, $n = 27$, $P < 0.05$). However, when two outliers (*Ziziphus xylopyrus* and *Grewia tiliifolia*) were
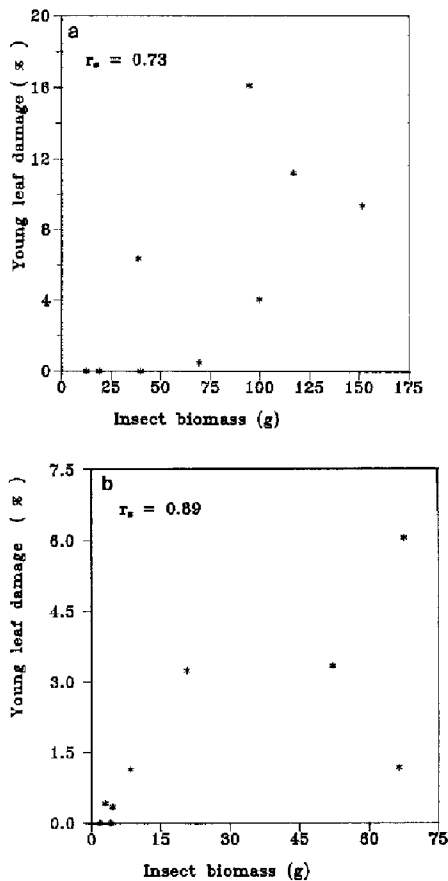
Fig. 3a, b. Relationship between percent herbivore damage to young leaves and insect biomass (g) at **a** Site I and **b** Site II

removed the correlation was significant and positive in Site I ($r_s = 0.43$, $n = 36$, $P < 0.05$). Although this pattern cannot be established with a high degree of statistical rigor, it may nevertheless be an indication of an underlying biological phenomenon.

Herbivory levels in different habitats

Rates of herbivore damage to young and mature leaves were higher at Site I than at Site II (Table 2). There were nine species common to both sites but only one of these (*Ziziphus xylopyrus*) suffered significantly higher damage at Site I (Site 1: $\bar{x} = 8.4 \pm 1.93$; Site 2: $\bar{x} = 1.5 \pm 0.60$; Mann-Whitney $U = 55$, $P < 0.05$). The proportion of species at the two sites showing characters such as waxy coating were, however, were not significantly different ($\chi^2 = 0.04$, $df = 1$, $P > 0.5$). There were nine such species at Site I and seven at Site II.

Discussion

This study shows that trees at two sites in a tropical deciduous forest in southern India reach a peak in leaf flushing during the dry season before the onset of rains. It is not clear how the flushing trees are able to overcome soil moisture stress during the dry period. They may have deep tap roots that reach ground water. Another possibility is that, in the absence of transpiration during the leafless phase, trees are able to store some water in their conductive tissues for subsequent use during the early leaf flushing phase (Bullock and Solis-Magallenus 1990). By flushing

Table 1. Differences between resistant and non-resistant species with respect to herbivory

Site I

	Leaf initiation date (from Jan 1) (Mean ± SD)	Young leaf damage (%) (Mean ± SD)	Mature leaf damage (%) (Mean ± SD)
Non-waxy coating ($n = 216$)	98.4 ± 10.72	2.1 ± 3.53	11.9 ± 13.67
Waxy coating on leaves ($n = 59$)	103.8 ± 6.22	0.8 ± 0.92	6.8 ± 4.15
Test statistic	3.19^t	2.18^z	2.43^z
Prob. limits	<0.005	<0.05	0.05

Site II

	Leaf initiation date (from Jan 1) Mean ± SD	Young leaf damage (%) Mean ± SD	Mature leaf damage (%) Mean ± SD
Non-waxy coating ($n = 117$)	121.4 ± 4.00	1.1 ± 4.00	6.0 ± 9.08
Waxy coating on leaves ($n = 51$)	125.0 ± 13.14	0.1 ± 0.64	0.8 ± 1.14
Test statistic	2.15^t	6.49^z	6.45^z
Prob. limits	<0.005	<0.001	<0.001

Table 2. Comparison between the two study sites with respect to leaf herbivory and leaf flushing time

	Site I ($n=275$) Mean $\pm$ SD	Site II ($n=168$) Mean $\pm$ SD	Test statistic	P
Leaf flushing time (days from Jan 1)	99.6 ± 11.61	122.5 ± 16.07	16.24^1	<0.01
Young leaf damage (per cent)	1.8 ± 3.15	0.8 ± 3.37	4.35^z	<0.01
Mature leaf damage (per cent)	10.8 ± 12.77	4.4 ± 7.91	7.72^z	<0.01

leaves before the onset of rains, the plants are in a position to expand their leaves rapidly through photosynthesis once the rains arrive.

Early flushers certainly have an advantage over the late flushers with respect to damage by herbivores. Insects, including the herbivorous Lepidoptera and Coleoptera, emerge with the onset of rains and attain a peak biomass during the wet months. Lepidopteran adults emerge, mate and lay eggs within 2 days. The eggs hatch within 3–4 days and the larvae start feeding on leaves. Coleopteran adults start feeding on leaves soon after they emerge from the soil at the beginning of the rains. The peak in leaf flushing is clearly attained before the peak in insect biomass; the former preceeds the latter by about 2 months at both sites.

These results clearly show that the degree of herbivorous damage to young leaves is related to the date of leaf initiation; early flushers or those flushing synchronously during the peak period suffer significantly lower damage than those which flush late. In this case the significance of lower damage during synchronous flushing does not seem to be merely due to predator satiation as suggested by Aide (1988), but simply a consequence of low population levels of predators. Not only do late flushers suffer greater damage to young leaves, they also suffer more damage to mature leaves.

Our observations also show that mature leaves are significantly more damaged than are young leaves. This could be simply because the trees pass through the young leaf stage when insect herbivores are scarce, while the mature leaf stage is attained during the wet season when the herbivore populations are also abundant. Although we have not checked levels of chemical defenses in plants, those species which possess physical defenses such as a waxy coating on the leaves suffered lower damage to young and mature leaves than did species not having such defenses.

It has been suggested that early-successional gap-colonizing plants that are fast growing are also difficult for herbivores to find ('unapparent') owing to their patchy distribution in time. Hence, they may be less prone to herbivore damage (Feeny 1976; Coley 1980). Extending this line of argument to rare or 'unapparent' versus common or 'apparent' plants it can be seen that herbivore damage does broadly increase with increasing abundance of a species. This could also be due to commoner plants initiating leaves later on the average, when insects are more abundant.

One rather puzzling result is the higher degree of herbivore damage at Site I compared to Site II. We are unable to explain this in terms of any differences in insect abundance. It is possible that plants growing under stressed conditions, such as in a drier locality, could have evolved better defenses against herbivory (Janzen 1974; Coley et al. 1985). This could be in the form of secondary chemicals, which we have not screened for. Of the nine species common between the sites, eight did not show any difference in damage. This implies that the difference in damage levels between the two sites largely arises as a result of difference in vulnerability of species not common to the sites.

Although the precise impact of folivore damage on individual fitness is not clear, it is reasonable to assume that plants would evolve life-history traits so as to minimize the risk of herbivory. Sub-lethal bouts of herbivory may stimulate compensatory production over a short time period (Mattson and Addy 1975). On the other hand, severe defoliation may also result in inhibition of cambial growth and death of trees (Kramer and Kozlowski 1979) or reduced fruit production (Rockwood 1973). Herbivory is thus an important selective agent influencing the phenology of leaf flushing in plants of the seasonal tropics.

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