



Research article

Leaf life-span dynamics of woody species in tropical dry forests of India

R. K. Chaturvedi^{1*} and A. S. Raghubanshi²

¹Centre for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan 666303, China

²Institute of Environment and Sustainable Development, Banaras Hindu University, Varanasi 221005, India

*Corresponding Author: ravikantchaturvedi10@gmail.com

[Accepted: 16 April 2016]

Abstract: We analysed the diversity of leaf life-span in the woody species of Vindhyan highlands and grouped the plant species according to their leaf flushing period, leaf life span and leaf fall period. We also studied the factors influencing the foliar phenology of the woody species. The study was conducted on five sites (Hathinala, Gaihat, Harnakachar and Ranitali) within the tropical dry deciduous forest in northern India. Leaf life-spans of the woody species were highly variable. About 67% species had peak of their leaf flush initiation during summer period (pre-rain leaf flushing) and rest species had their peak leaf initiation during rainy season (post-rain leaf flushing). The peak period of leaf flushing initiation at all the sites was May when 52% of the species initiated their leaf formation and the peak period of leaf flushing completion was August when 38% of the plant species completed their leaf formation. The peak period of leaf fall initiation in maximum species (54%) at all sites was November and the peak period of leaf fall completion at all the sites was February when 63% of the species shed their leaves. The peak period of leaf flush initiation as well as leaf fall initiation in most of the species at dry sites was one month before as compared to that of moist sites.

Keywords: Leaf phenology - Tropical dry forest - Soil moisture content - Deciduousness - Woody species.

[Cite as: Chaturvedi RK & Raghubanshi AS (2016) Leaf life-span dynamics of woody species in tropical dry forests of India. *Tropical Plant Research* 3(1): 199–212]

INTRODUCTION

The three most important factors influencing the phenological changes in the tropical dry forests (TDFs) are: (i) rainfall (Daubenmire 1972, Bullock & Solis-Magallanes 1990, Borchert 1994a, Eamus & Prior 2001, Bajpai *et al.* 2016); (ii) photoperiod (Bullock & Solis Magallanes 1990, Rivera *et al.* 2002, Borchert *et al.* 2004, Elliot *et al.* 2006, Bajpai *et al.* 2012, 2016); and (iii) stem water status (Borchert 1994a, b, 1998). Growth and reproduction of plant species in the TDFs are significantly influenced by the spatial and temporal variations in the foliar phenology (Suresh & Sukumar 2011, Nanda *et al.* 2014, Borah & Devi 2014). Many tree species in these forests flush their leaves during the dry season, before the onset of the rains (Bullock & Solis-Magallanes 1990, Mooney *et al.* 1995). For this mechanism, two principal reasons 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). The variations in foliar phenology in the TDFs, could be an adaptation to the pressures exerted by animals, plants and may rely on the changes in environmental conditions to trigger the event (van Schaik *et al.* 1993). Phenology is sometimes concurrently or at different times of the year, controlled by multiple factors (Nilsen & Muller 1981, White *et al.* 1997, Jolly *et al.* 2005). Therefore, it is important to understand the factors influencing the foliar phenology in the woody species of TDFs.

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, 1994b, c, Reich & Borchert 1984). This indicates that tree water status, rather than a climatic factor directly, is probably the principal determinant of tree phenology in the TDFs. 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 1994b, c, Borchert *et al.* 2002), and the rate of shoot development and the duration of leaf expansion varies strongly with water availability (Borchert 1994c, Borchert & Rivera 2001).

Intraspecific variations in leaf lifespan are reported in plant species growing in the tropics (Ackerly & Bazzaz 1995, Reich *et al.* 2004, Vincent 2006) and in temperate zones (Jurik & Chabot 1986, Oikawa *et al.* 2004). It is a general belief that plants adjust leaf life-span so as to maximize whole-plant photosynthesis (Franklin & Agren 2002, Hikosaka 2003, 2005, Kikuzawa & Lechowicz 2006, Oikawa *et al.* 2006, 2008). Models predict that when whole-plant photosynthesis is high, leaves are more frequently shed as the plant prioritizes investment in new leaves (Kikuzawa 1991, Hikosaka 2003), and this pattern is consistently observed across different biomes and taxa (Reich *et al.* 1999, Wright *et al.* 2004, Karst & Lechowicz 2007). Hence, intraspecific variation in leaf life-span should be considered as an adaptation for carbon gain (Oikawa *et al.* 2004).

In general, deciduous species have a higher photosynthetic rate and shorter leaf life span than evergreens, while evergreens are more shade-tolerant (Chabot & Hicks 1982). Similarly, within a single species, an individual in a well-lit place has a higher photosynthetic rate (Noda *et al.* 2004) than a shaded individual. Therefore, cost-benefit analysis also shows that having a higher photosynthetic rate leads to a high leaf-turnover rate, which in turn leads to a shorter leaf life span. Accordingly, a shorter mean leaf life span has been reported for individuals in well-lit environments relative to shaded conspecifics (Seiwa & Kikuzawa 1991, Ackerly & Bazzaz 1995, Hikosaka 2005, Vincent 2006). Apart from high rates of photosynthesis, species with short leaf life span also have high respiration rate, leaf nutrient concentrations and SLA (Wright *et al.* 2004).

In the present study, we analyse the diversity of leaf life-span in the woody species of Vindhyan highlands and group the plant species according to their leaf flushing period, leaf life span and leaf fall period. We also study the factor influencing the foliar phenology of the woody species.

MATERIALS AND METHODS

Study area

We selected five study sites in the forests of Vindhyan highlands (24°18'07"–25°00'17" N, 82°37'38"–83°23'05" E). Among the five sites, Hathinala, Gaighat, Harnakachar and Ranitali sites are situated in Sonebhadra district and Kotwa in Mirzapur district of Uttar Pradesh (Fig. 1). They occupy land area of 2555, 394, 1507, 2118 and 199 hectares, respectively. The selected sites represented a range in soil water availability. The area experiences tropical monsoon climate with three seasons in a year, *viz.*, summer (April–mid June), rainy (mid June–September) and winter (November–February). The months of March and October constitute transition periods, respectively between winter and summer, and between rainy and winter seasons. The mean maximum monthly temperature varies from 20°C in January to 46°C in June, and the mean minimum monthly temperature reaches 12°C in January and 31°C in May. According to the data collected from the meteorological stations of the state forest department for 1980–2010, the mean annual rainfall ranges from 865 to 1196 mm (Chaturvedi *et al.* 2011a). About 85 % of the annual rainfall occurs during the monsoon (rainy) season from the south-west monsoon, and the remaining from the few showers in December and in May–June. There is an extended dry period of about 9 months (October–mid June) in the annual cycle (Jha & Singh 1990). The monthly rainfall varies from 6 mm in April to 334 mm in August (Chaturvedi *et al.* 2012). Soils of the study area are residual, ultisols, sandy-loam in texture, reddish to dark gray in colour and extremely poor in nutrients (Chaturvedi & Raghubanshi 2011). Recently estimated physico-chemical properties of soils of the study region have been described in Chaturvedi & Raghubanshi (2015). The forest region exhibit patchiness in the species composition due to small variations in the environmental variables (Chaturvedi *et al.* 2011b). Species composition, distribution and diversity (Chaturvedi & Raghubanshi 2014), seasonal growth (Chaturvedi *et al.* 2011c, 2013, 2014), and functional traits (Chaturvedi & Raghubanshi 2013) of woody species are highly influenced by soil moisture content. The density-DBH distributions in the forest region exhibited low DBH-

biased structure, where the average density of seedlings, saplings and adults were $9,261 \pm 1,511$, 799 ± 154 and 297 ± 62 , respectively (Chaturvedi & Raghubanshi 2014).

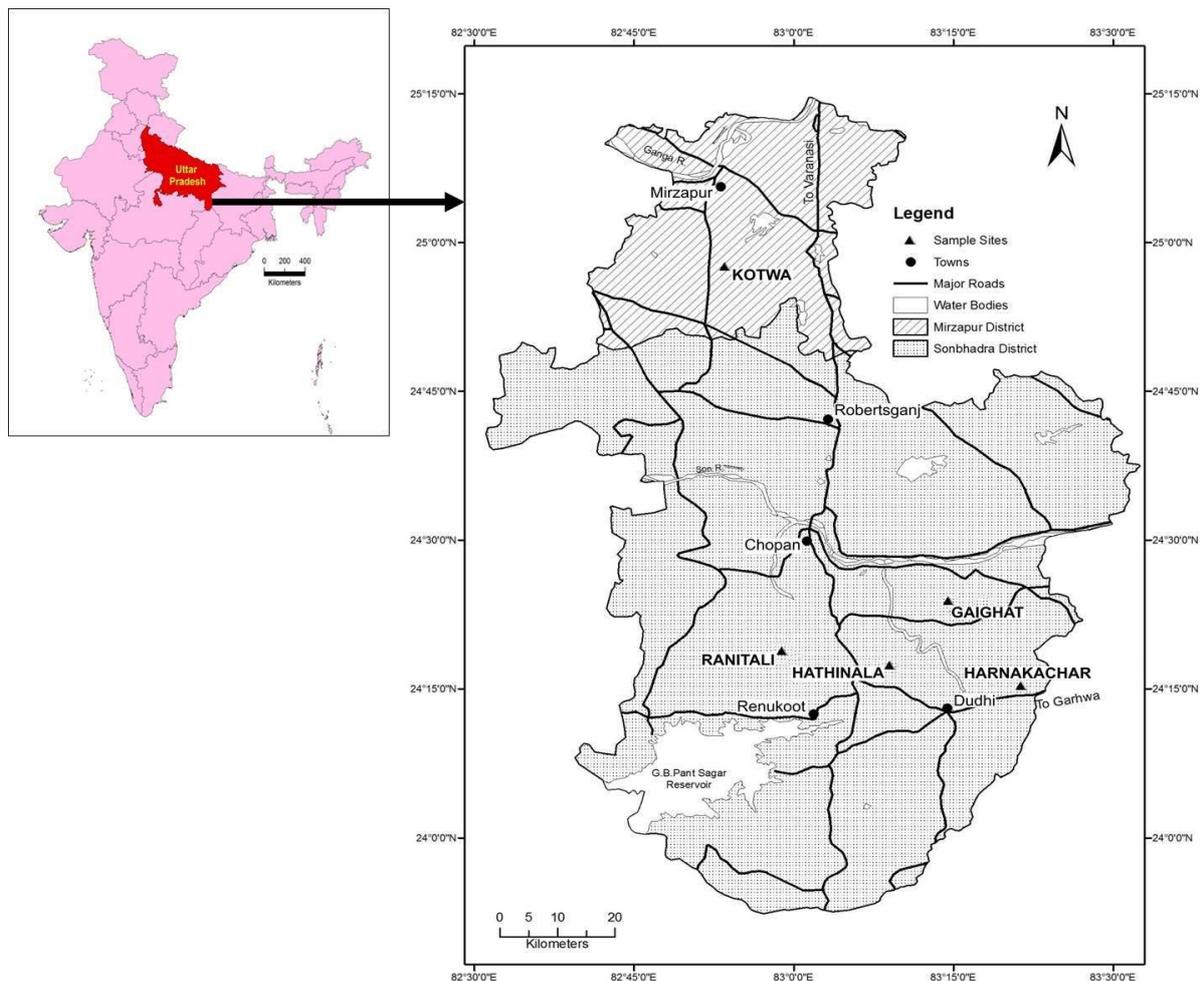


Figure 1. Map showing the location of study areas.

Study Design

For the purpose of this study, three plots, each of 4 ha (200 m × 200 m), were established randomly at each site. Fifteen individuals each, of the species were randomly selected from the three 4 ha plots at each site and were marked. Plant species which were not present at all the five sites were selected from only those sites where they were present. On each marked individual, one twig (currently growing shoots of last-order branches) on each of four major branches (one in each direction was marked with metal tags). On these twigs monthly count of leaf number was made from January 2005 to December 2006.

Soil moisture content was measured at 10 locations, randomly in each plot, at each site, as percentage by volume every month, at a depth of 10 cm at 1-month intervals for 2 years (*i.e.* January 2005 to December 2006) using a theta probe instrument (type ML 1, Delta-T Devices, Cambridge, UK). The following phenological events were derived from the monthly leaf counts: initiation of leaf flush, completion of leaf flush, leaf-fall initiation, and completion of leaf fall. Leaf-flush period of a species is the duration (days) from the first leaf flush to the last flush amongst its individuals. Leaf fall period of a species represents the time duration from the estimated first leaf fall to the last amongst individuals. The leaf life-span period for each species was calculated as the mean leaf life-span of all individuals of the species. Species were classified as Group I and Group II on the basis of pre- and post-rainfall leaf flushing, respectively. Also, on the basis of leaf life-span, species were categorized into four groups as (i) 10–12 mo life-span, (ii) 8–10 mo life-span, (iii) 6–8 mo life-span and (iv) 4–6 mo life-span, excluding the extreme values in each case. Species with 8–12 mo leaf life-span belong to Group I and with 4–8 mo leaf life-span to Group II. Site wise variations in the leaf flush and leaf fall was analysed for these two groups.

Data analysis

Soil moisture content measured at 10 locations in each plot was averaged to get three values for each site, for each month. Site wise variations of soil moisture content in each month was analysed by multivariate ANOVA using the SPSS (v. 16) package.

RESULTS

Soil moisture content

Across the five study sites, monthly measured soil moisture content was generally maximum at Hathinala and minimum at Kotwa (Fig. 2). Across the 12 months in a year, July and August showed higher soil moisture content. Lower soil moisture content was observed in November and December. Across the 12 months, site wise variations in soil moisture content were not significant only in July, August and September (Table 1).

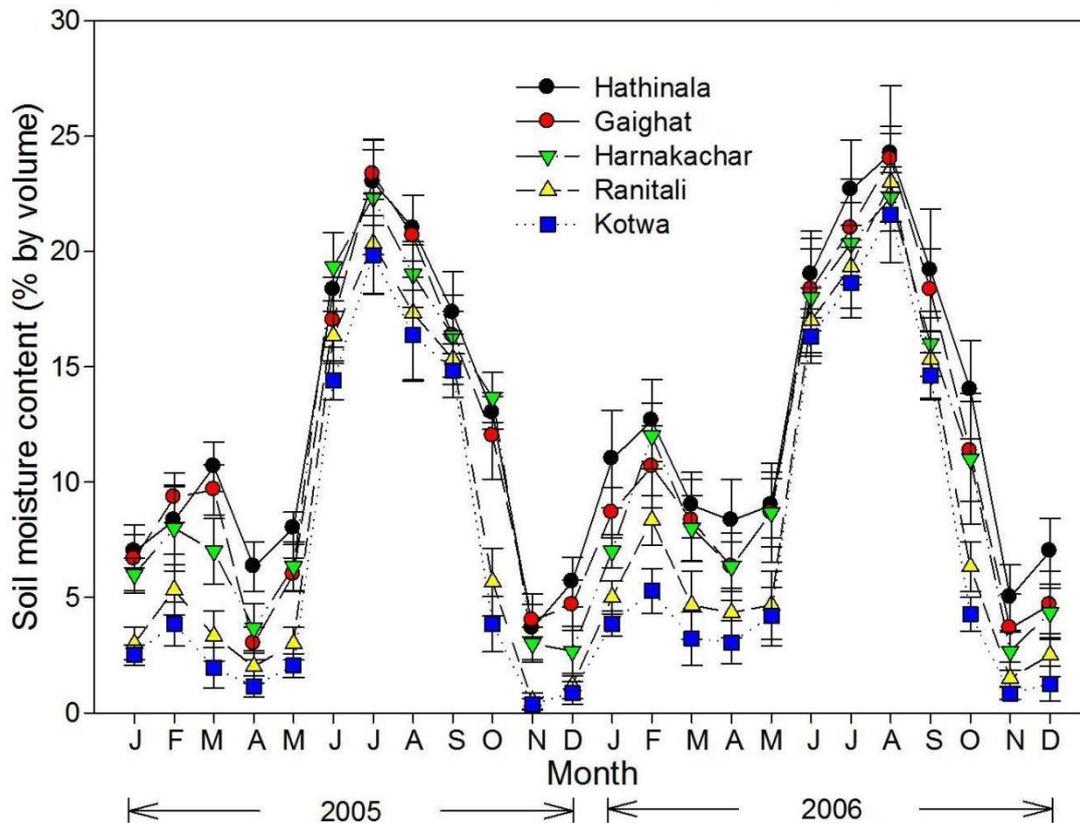


Figure 2. Monthly soil moisture content at the five study sites from January 2005 to December 2006.

Table 1. ANOVA on soil moisture content measured monthly across the five study sites. The residual df is 10.

Month	d.f.	F	P
Jan	4	13.375	< 0.010
Feb	4	8.393	< 0.010
Mar	4	67.031	< 0.001
Apr	4	7.576	< 0.010
May	4	16.701	< 0.001
Jun	4	14.708	< 0.001
Jul	4	2.157	> 0.050
Aug	4	1.508	> 0.050
Sep	4	2.426	> 0.050
Oct	4	115.35	< 0.001
Nov	4	51.659	< 0.001
Dec	4	41.954	< 0.001

Diversity of Leaf Life span

Leaf life-spans of the woody species were also highly variable (Fig. 3). Leaves of *Hardwickia binata* and *Shorea robusta* had life-span of 10 to 12 months. Life-span of 8 to 10 months was observed in the leaves of seven species (*Acacia auriculiformis*, *Albizia odoratissima*, *Azadirachta indica*, *Bauhinia racemosa*, *Carissa* www.tropicalplantresearch.com

spinarum, *Diospyros melanoxylon* and *Ficus racemosa*). In 31 species (*Acacia catechu*, *Anogeissus latifolia*, *Bridelia retusa*, *Buchanania lanzan*, *Cassia fistula*, *Cassia siamea*, *Chloroxylon swietenia*, *Dendrocalamus strictus*, *Elaeodendron glaucum*, *Flacourtia indica*, *Gardenia turgida*, *Grewia hirsuta*, *Grewia serrulata*, *Hollarrhena antidysenterica*, *Holoptelia integrifolia*, *Hymenodictyon excelsum*, *Indigofera cassioides*, *Lagerstroemia parviflora*, *Madhuca longifolia*, *Miliusa tomentosa*, *Mitragyna parvifolia*, *Nyctanthes arbortristis*, *Ougeinia oogenesis*, *Pterocarpus marsupium*, *Schleichera oleosa*, *Schrebera swietenioides*, *Soymida febrifuga*, *Terminalia chebula*, *Terminalia tomentosa*, *Zizyphus nummularia* and *Zizyphus oenoplea*), life-span of 6 to 8 months was detected, whereas, in rest of the 12 species (*Abrus precatorius*, *Adina cordifolia*, *Boswellia serrata*, *Emblica officinalis*, *Eriolaena quinquelocularis*, *Gardenia latifolia*, *Lannea coromandelica*, *Lantana camara*, *Semecarpus anacardium*, *Sterculia urens*, *Woodfordia fruticosa* and *Zizyphus glaberrima*), the life-span was of 4 to 6 months (Fig. 3). In our study, about 67% species had peak of their leaf flush initiation during summer period (Group I species, pre-rain leaf flushing) and rest species had their peak leaf initiation during rainy season (Group II, post-rain leaf flushing).

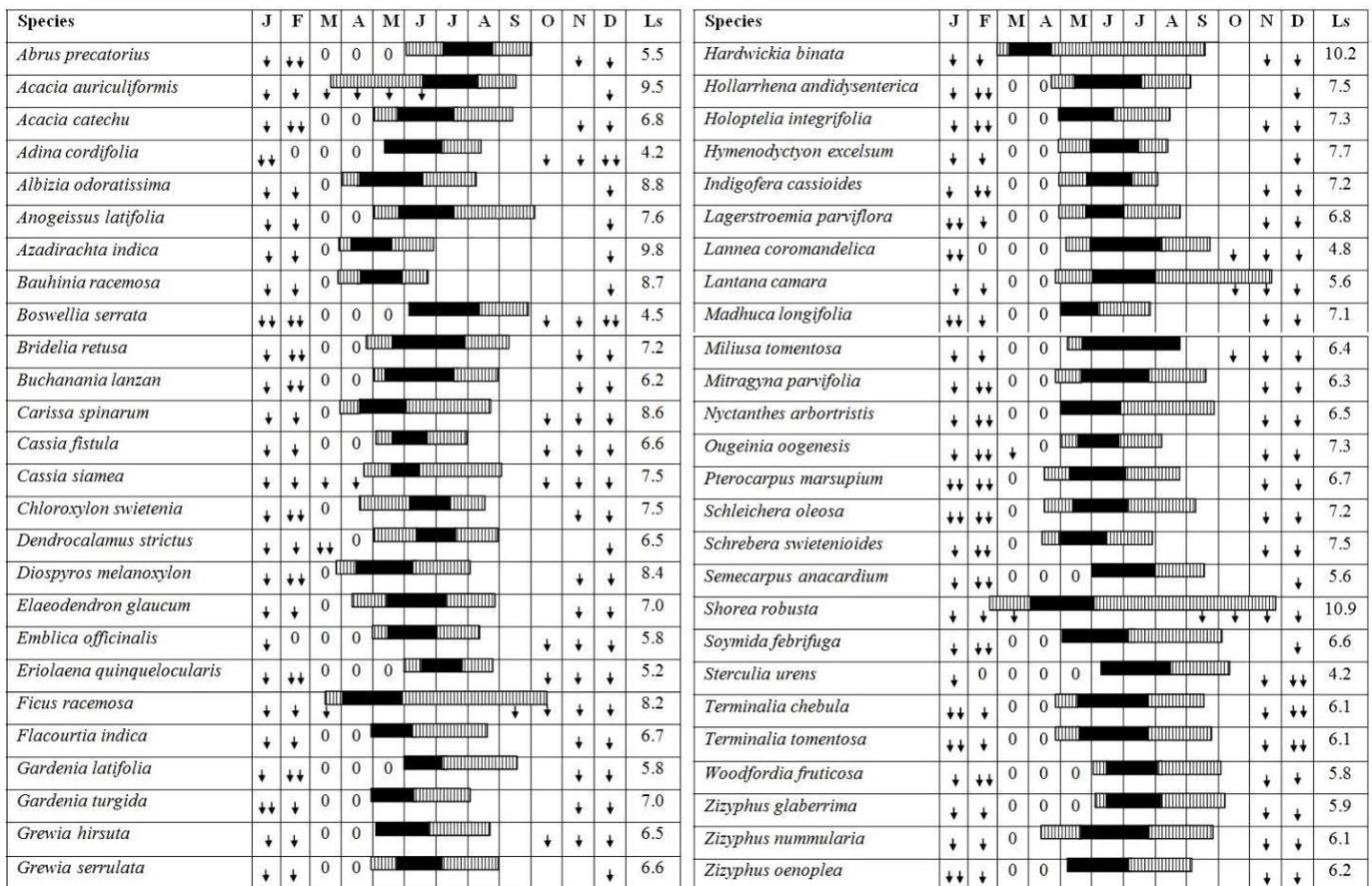


Figure 3. Periods of major (solid black horizontal bars) and minor (hatched horizontal bars) leaf flush in woody species of Vindhyan highlands. Periods of substantial leaf drop is indicated by downward arrows. ‘0’ indicates when most individuals were leafless (Ls = Life-span in months).

Diversity of Leaf Flushing

There occurred wide diversity among species in terms of duration of leaf flush (Fig. 3). *F. racemosa*, *L. camara* and *S. robusta* produced new leaves for 6-8 months. Seven species (*A. catechu*, *A. odoratissima*, *A. latifolia*, *C. spinarum*, *G. serrulata*, *H. binata* and *L. parviflora*) produced new leaves through 5-6 months, 18 species (*A. auriculiformis*, *B. retusa*, *B. lanzan*, *C. siamea*, *D. melanoxylon*, *E. glaucum*, *F. indica*, *G. latifolia*, *H. antidysenterica*, *M. tomentosa*, *M. parvifolia*, *N. arbortristis*, *S. oleosa*, *Soymida febrifuga*, *T. chebula*, *T. tomentosa*, *W. fruticosa* and *Z. nummularia*) flushed through 4-5 months and 24 species (*A. precatorius*, *A. cordifolia*, *A. indica*, *B. racemosa*, *B. serrata*, *C. fistula*, *C. swietenia*, *D. strictus*, *E. officinalis*, *E. quinquelocularis*, *G. turgida*, *G. hirsuta*, *H. integrifolia*, *H. excelsum*, *I. cassioides*, *L. coromandelica*, *M. longifolia*, *O. oogenesis*, *P. marsupium*, *S. swietenioides*, *S. anacardium*, *S. urens*, *Z. glaberrima* and *Z. oenoplea*) flushed through 3-4 months (Fig. 3).

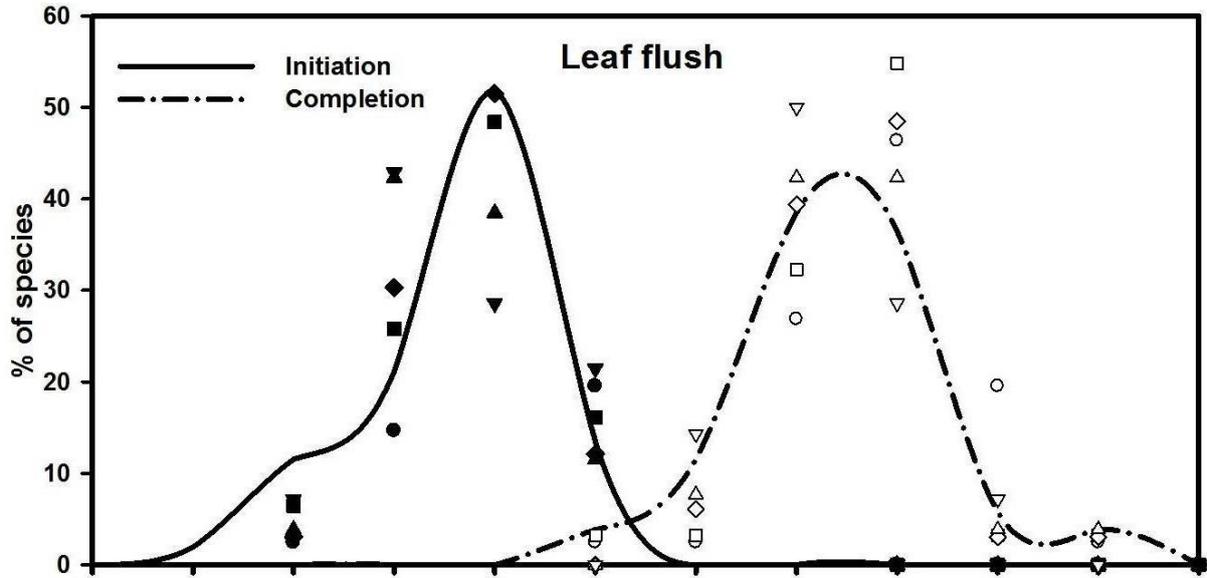


Figure 4. Initiation and completion of leaf flushing. Data for Hathinala are represented by circles, for Gaighat by squares, for Harnakachar by diamond, for Ranitali by up triangle and for Kotwa by down triangle. Solid symbols are for initiation and open symbols are for completion of phenological event. The smooth solid curves represent initiation and dash dotted curves represent completion of phenological event.

In general, the peak period of leaf flushing initiation at all the sites was May when 52% of the species initiated their leaf formation and the peak period of leaf flushing completion was August when 38% of the plant species completed their leaf formation (Fig. 4). At the community level, May constituted the peak period of leaf flushing initiation at Hathinala (63%), Gaighat (48%) and Harnakachar (51%), whereas, the peak period leaf flushing initiation at Ranitali (42%) and Kotwa (43%) was April (Fig. 5). Similar to the peak period leaf flushing initiation, the peak period of completion of leaf flushing was same for Hathinala, Gaighat and Harnakachar where 46%, 55% and 48% of the species have shown completion of their leaf formation respectively. In the drier sites, the completion of leaf flushing was August and September (both 42%) for Ranitali and August (50%) for Kotwa (Fig. 5).

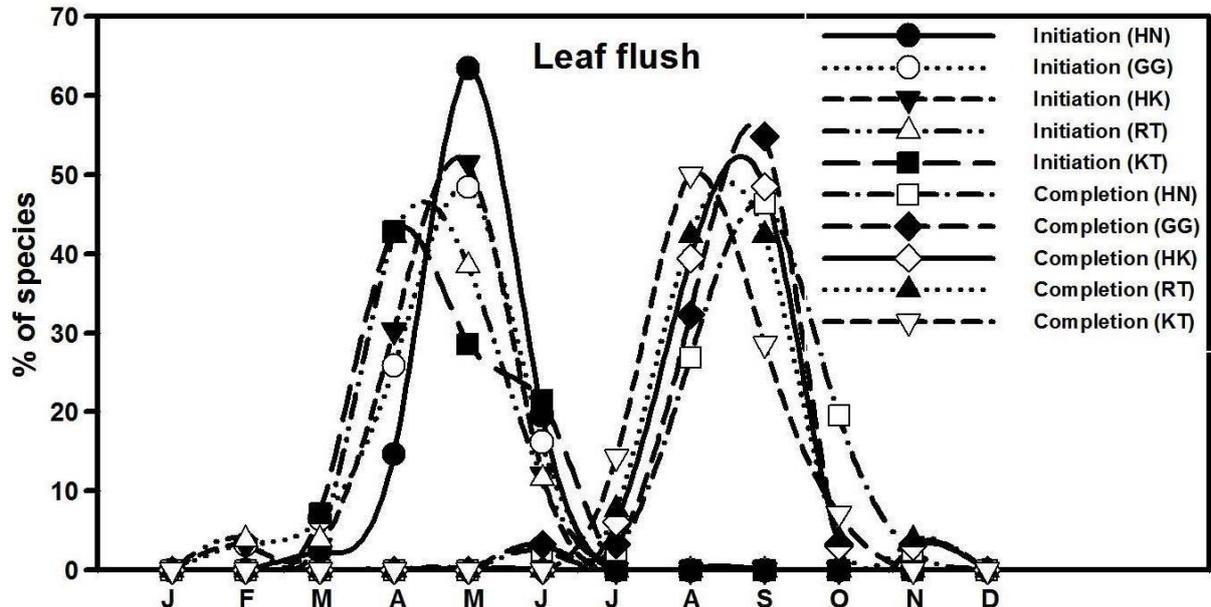


Figure 5. Initiation and completion of leaf flush of species in the study sites. HN, Hathinala; GG, Gaighat; HK, Harnakachar; RT, Ranitali; KT, Kotwa.

Leaf Flush Initiation

Peak period of leaf flush initiation in majority of species in group I (pre-rainfall group) occurred in March (67%), however, species in group II (post-rainfall group) were highly deciduous and most of them (63%) showed their peak period of leaf flush initiation in May (Fig. 6). In group I, 80% species at Hathinala, 50%

species at Gaighat and Harnakachar showed their peak period of leaf flush initiation in April (Fig. 6). At Ranitali, *S. robusta* showed peak period of leaf flush initiation in February, *H. binata* in March and *D. melanoxylon* in April. Only two species at Kotwa were in group I, in which the peak period of leaf flush initiation was in April (for *D. melanoxylon*) and March (for *F. racemosa*). Most of the species at Hathinala (72%), Gaighat (63%) and Harnakachar (59%), belonging to group II showed their peak period of leaf flush initiation in May (Fig. 6). At Ranitali, most of the species (43%) showed the peak period of leaf flush initiation equally in April and May, whereas, at Kotwa, majority of the species (42%) showed the peak period of leaf flush initiation in April (Fig. 6).

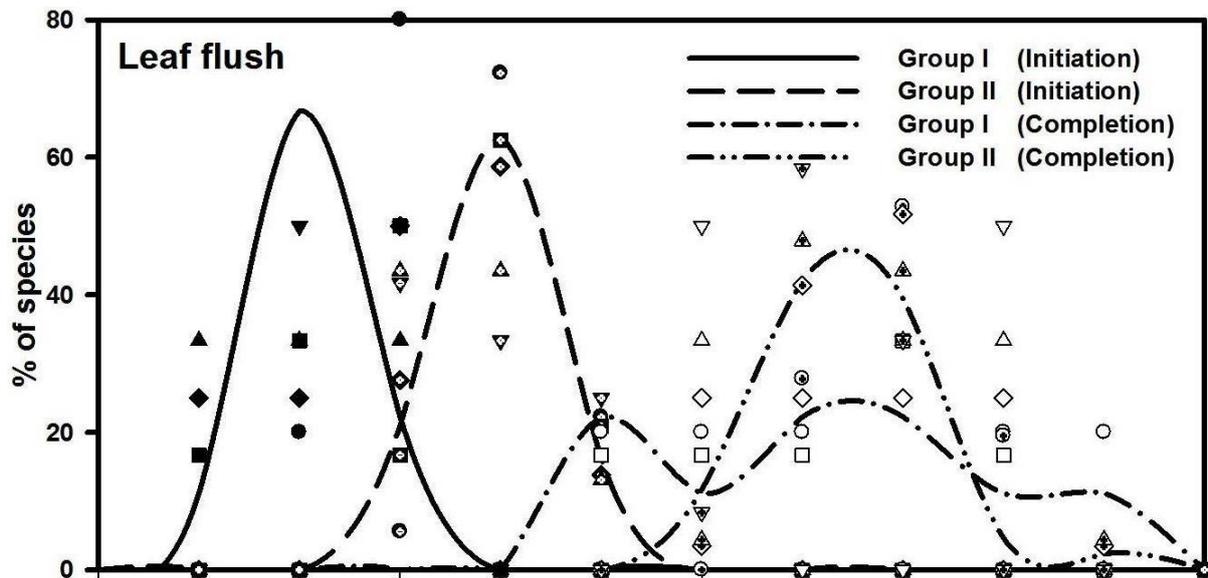


Figure 6. Initiation and completion of leaf flushing of species having 8-12 months (Group I) and 4-8 (Group II) months of leaf life span. Data for Hathinala are represented by circles; Gaighat by squares; Harnakachar by diamond; Ranitali by up triangle; Kotwa by down triangle. Solid and solid cross haired symbols are for initiation; open and open cross haired symbols are for completion of phenological event. The smooth solid curves represent initiation in Group I species; broken curves represent initiation in Group II species; dash dotted curves represent completion in Group I species; dash double dotted curves represent completion in Group II species.

Leaf Flush Completion

Phenological event of leaf flush completion was much variable among species, the peak period in group I for *A. indica* and *B. racemosa* was June, for *A. odoratissima*, it was July, for *C. spinarum* and *D. melanoxylon* it was August, for *H. binata* and *A. auriculiformis* it was September, for *F. racemosa* it was October and for *S. robusta* it was November. The peak period of leaf flush completion in species of group II was also variable but majority of species showed their peak period in August for 42% and September for 40% of the species (Fig. 6). The species of group II were highly deciduous and leaf flush completion ended in October, however, in *L. camara*, the peak period of leaf flush completion was November. The peak period of leaf flush completion at Hathinala was much variable among the species where, *B. racemosa* showed the peak in June, *A. odoratissima* in July, *D. melanoxylon* in August, *H. binata* in October and *S. robusta* in November.

At Gaighat, *A. indica* showed maximum peak in June, *D. melanoxylon* in July (similar at Harnakachar, Ranitali and Kotwa), *C. spinarum* in August (similar at Harnakachar), *H. binata* (similar at Harnakachar and Ranitali) and *A. auriculiformis* in September and *S. robusta* in October (similar at Harnakachar and Ranitali). At Kotwa, the site specific species *F. racemosa* showed the peak in October. In group II most of the species at Hathinala (53%), Gaighat (63%) and Harnakachar (52%) showed their peak of leaf flush completion in September, however, at Harnakachar and Kotwa the peak for most of the species was observed in August (48% for Ranitali and 58% for Kotwa) (Fig. 6).

Duration of Leaf Fall

Generally, the duration of leaf fall for most of the species ranged through 3–4 months (Dec–Mar), however, in *F. racemosa* and *S. robusta* minor leaf fall was also observed in September and October. Duration of leafless period ranged from one to three months, however, individuals of *A. auriculiformis*, *C. siamea*, *F. racemosa* and

S. robusta were never found completely leafless in their annual cycle. The only species leafless for 4 months was *S. urens* (Fig. 3).

Leaf Fall Initiation

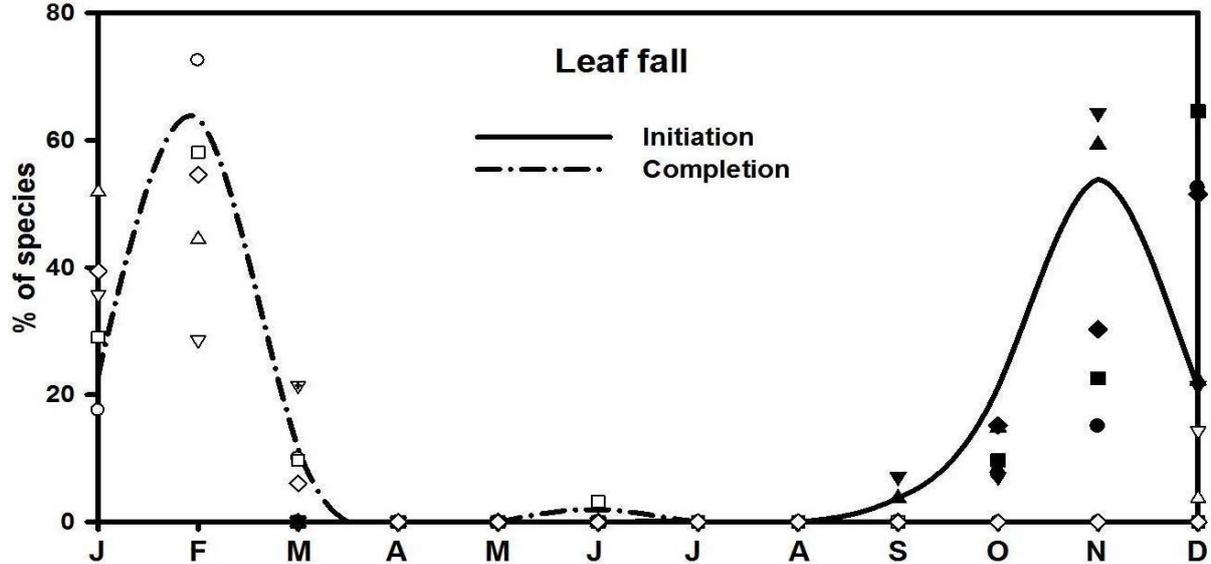


Figure 7. Initiation and completion of leaf fall. Data for Hathinala are represented by circles, for Gaighat by squares, for Harnakachar by diamond, for Ranitali by up triangle and for Kotwa by down triangle. Solid symbols are for initiation and open symbols are for completion of phenological event. The smooth solid curves represent initiation and dash dotted curves represent completion of phenological event.

The peak period of leaf fall initiation in maximum species (54%) at all sites was November and the peak period of leaf fall completion at all the sites was February when 63% of the species shed their leaves (Fig. 7). When the leaf fall in plant species was studied at different sites, it was observed that the peak period of leaf fall initiation for majority of species at Hathinala (53%), Gaighat (65%) and Harnakachar (52%) was December, whereas at drier sites, *i.e.* Ranitali and Kotwa, the peak period of leaf fall initiation for most of the species was November (59% at Ranitali and 64% at Kotwa) which is one month before than that of the moist sites (Fig. 8). The peak period of leaf fall completion at the three comparatively moist sites was February when 73% of the species at Hathinala, 58% at Gaighat and 55% at Harnakachar shed their leaves. At the drier sites, the peak period of leaf fall completion was January when 52% of species at Ranitali and 36% of species at Kotwa shed their leaves (Fig. 8).

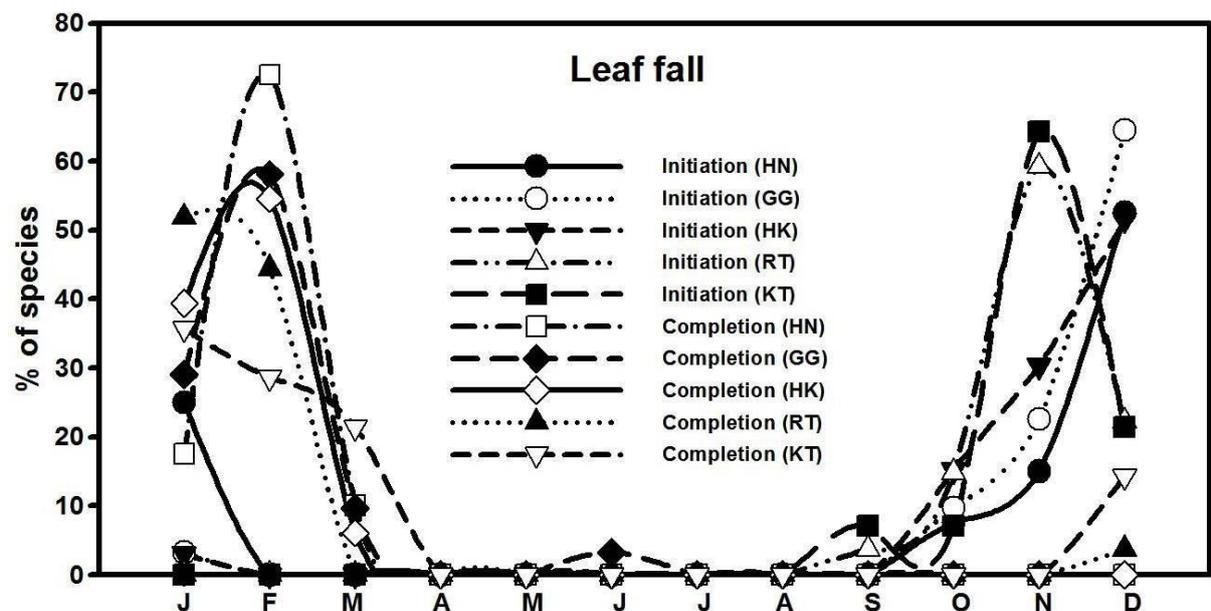


Figure 8. Initiation and completion of leaf fall of species in the study sites. HN, Hathinala; GG, Gaighat; HK, Harnakachar; RT, Ranitali; KT, Kotwa.

Similar to the peak period of leaf flush initiation, the peak period of leaf fall initiation for most of the species in group I was one month after that of group II species. In group I, the peak reached in December whereas in group II, the peak was in November (Fig. 9). At Hathinala, the peak period of *H. binata*, *A. odoratissima* and *B. racemosa* was November, whereas, for the other two species (*S. robusta* and *D. melanoxylon*), it was September.

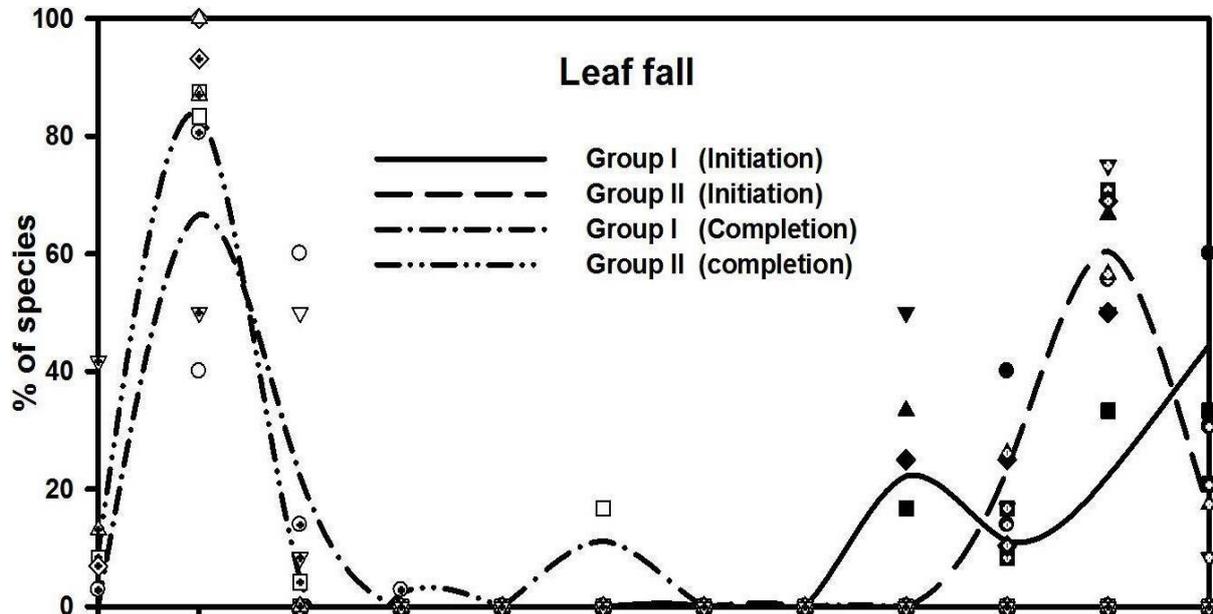


Figure 9. Initiation and completion of leaf fall of species having 8-12 mo (Group I) and 4-8 mo (Group II) of leaf life span. Data for Hathinala are represented by circles; Gaighat by squares; Harnakachar by diamond; Ranitali by up triangle; Kotwa by down triangle. Solid and solid cross haired symbols are for initiation; open and open cross haired symbols are for completion of phenological event. The smooth solid curves represent initiation in (Group II) species; broken curves represent initiation in (Group I) species; dash dotted curves represent completion in (Group II) species; dash double dotted curves represent completion in (Group I) species.

At Gaighat, the peak for *S. robusta* reached in September (similar for Harnakachar and Ranitali), for *C. spinarum* in October (similar for Harnakachar), for *H. binata* and *D. melanoxylon* in November (similar for Harnakachar, Ranitali and Kotwa) and for *A. auriculiformis* in December. *F. racemosa*, the site specific species at Kotwa showed its peak of leaf fall initiation in September. Species in group II at all the five sites had same peak period of leaf fall initiation *i.e.* November (Fig. 9), where 56% species at Hathinala, 71% at Gaighat, 69% at Harnakachar, 57% at Ranitali and 75% species at Kotwa started their leaf fall.

Leaf Fall Completion

Peak period of leaf fall completion for most of the species in group I (67%) and group II (84%) was February (Fig. 9). In the species of group I at Hathinala, *A. odoratissima* and *B. racemosa* showed the peak of leaf fall in February, whereas, *H. binata*, *S. robusta* and *D. melanoxylon* attained their peak in March. At Gaighat, *A. auriculiformis* reached the peak in June, however, the other five species showed the peak in February. All the species at Harnakachar and Ranitali reached the peak of leaf fall completion in February, whereas, at Kotwa, *D. melanoxylon* showed its peak in February and *F. racemosa* in March. Similar to the leaf fall initiation, the peak period of leaf fall completion for most of the species in group II was same at all the five sites (Fig. 9), where 81% species at Hathinala, 88% at Gaighat, 93% at Harnakachar, 87% at Ranitali and 50% at Kotwa were leafless in February.

DISCUSSION AND CONCLUSION

In deciduous woody species of TDFs, both spring flushing and summer flushing generally precede the first rains by 1–2 months, suggesting their timing has been selected for by the rainfall pattern. The rates of leaf flush and leaf fall in different plants vary with available soil moisture, leaf structure, depth of root system, and other variables and, therefore, leaf phenology is asynchronous within a population. Our study showed variations in leaf phenological events of woody species in moist and dry sites. Within site variation of leaf flushing and leaf fall events were also very prominent.

The characteristic phenology of dry period flushing species is also controlled by non-climatic environmental variables, such as water storage in deep soils and photoperiodic induction of leafing, which also determine tree phenology in TDF species around the globe (Borchert 1994d, Rivera *et al.* 2002). These variations may be due to patchy distribution of microhabitats in the TDF soils (Roy & Singh 1994). To exploit the resources present in these microhabitats, species evolve differently which causes variations in their leaf phenology.

In our study, most of the species had peak of their leaf flush initiation during dry period (Group I species, pre-rain leaf flushing) while rest species had their peak leaf initiation during rainy season (Group II, post-rain leaf flushing). Species belonging to Group I are often capable of physiological adjustment in low soil moisture condition when atmospheric humidity is also low, resulting in greater photosynthetic carbon gain and lower transpirational water loss than otherwise would be possible (Mulkey *et al.* 1992). In contrast, the species belonging to Group II are not able to adjust to dry season conditions because they are produced during period of high water availability.

Besides the adjustment of plant species to low soil water availability, early leaf flushing has been reported to protect the young leaves from the herbivore damage which occurs when a leaf is young (Coley & Aide 1991). This damage affects growth, survivorship, and reproduction of the plant species (Crawley 1985, Dirzo 1984, Krischik & Denno 1983, Louda 1984, Marquis 1984). Chemical and physical defenses, particularly leaf toughness, are effective herbivore defense of mature leaves (Coley 1983), but these defenses are not as well developed in young leaves. However, because young leaves are an ephemeral stage in the life of a leaf, characteristics of leaf phenology also may influence the degree of vulnerability of young leaves to herbivores (Aide 1988, Clark & Clark 1991). Therefore, in TDFs, some species "anticipate" the wet season and produce leaves under drought conditions during the dry season (Frankie *et al.* 1974, Rockwood 1973; Shukla & Ramakrishnan 1982). Herbivore abundances are usually low during the dry season (Wolda 1978, but see Boinski & Fowler 1989), and thus leaves produced at this time should temporally escape herbivores (Aide 1988).

Although, there was wide variation in the leaf flush initiation and leaf fall initiation in the woody species across the study sites, the peak period of leaf flush initiation as well as leaf fall initiation in most of the species at dry sites was one month before as compared to that of moist sites. Plant species growing at the dry sites tolerate water stress to a greater extent as compared to moist site. Early leaf flushing helps them to extend the wet growing season which is shorter than the moist site due to early leaf fall in the dry season.

During rainy season, when soil moisture becomes uniform across the landscape, the period of leaf flush initiation and completion at different sites for most of the species form similar pattern. This similarity of leaf flushing event was clearly seen in Fig. 5 where similar curves having sharp boundary was observed for all the five study sites. This synchrony in leaf flushing event is due to similarity in soil moisture availability for the plant species at different sites. Therefore, site variability is not the determining factor for leaf flush initiation in the rainy season. However, during the phenological event of leaf fall, there occurs much difference in the phenological pattern which is seen in Fig. 8, where the peak period of leaf fall for most of the species at different study sites form variable curves. Here, the asynchrony is due to site-wise variation in soil moisture availability. Plants acquire water according to their rooting depth and the water holding capacity of the site.

Woody species in the Vindhyan region exhibit a broad range of deciduousness, and four classes can be recognized; semi-evergreen, <2-month deciduous, 2–4-mo-deciduous and >4-month deciduous. This study detected two species in semi-evergreen category, seven species in 2-4-months deciduous and 43 species in >4-month deciduous category. Leafless period in woody species, generally occurring in response to water stress, represents the time period during the annual cycle when resources (light, water, nutrients etc.) are not being exploited or are being used at a low intensity. The duration of the tolerance of water stress in different leaflessness categories should decrease in the order: semi-evergreen, <2-mo-deciduous, 2–4-mo-deciduous, >4-mo-deciduous. Prolonged leaflessness may strongly affect the water relations of woody species, leading to selection for low-density wood with greater water storage (*e.g.* >4-mo-deciduous *B. serrata* and *L. coromandelica* which show characteristics equivalent to stem succulents of Borchert 2000).

Semi-evergreen and short-deciduous woody species show adaptations such as deep root systems with access to subsoil water. Skarpe (1996) reported that evergreen species have deep root systems, deciduous fine leaved trees have deep to moderately shallow roots, and deciduous broad-leaved trees have moderately deep to moderately shallow roots.

Our study area experience a long dry season, the woody species are adapted in such a way that they can tolerate water stress for the maximum possible duration to maintain relative growth rate by retaining leaves for longest duration. When water stress reaches the threshold, they shed their leaves rapidly to avoid water stress. Site wise variation in the foliar phenology reveals that the soil moisture content is an important factor in TDFs, influencing foliar phenology of the woody species. However, many other factors still needs to be studied to completely understand the phenological event.

ACKNOWLEDGMENTS

We thank the Divisional Forest Officer, Renukoot, Sonbhadra, Uttar Pradesh, India, for granting permission to work in the forest. The study was financially supported by Research Associate scheme of Council of Scientific and Industrial Research (award no. 09/13(452)/2012-EMR-I; to R.K.C.).

REFERENCES

- Ackerly DD & Bazzaz FA (1995) Leaf dynamics, self-shading and carbon gain in seedlings of a tropical pioneer tree. *Oecologia* 101: 289–298.
- Aide TM (1988) Herbivory as a selective agent on the timing of leaf production in a tropical understory community. *Nature* 336: 574–575.
- Bajpai O, Kumar A, Mishra AK, Sahu N, Behera SK & Chaudhury LB (2012) Phenological study of two dominant tree species in tropical moist deciduous forest from the northern India. *International Journal of Botany* 8(2): 66–72.
- Bajpai O, Pandey J & Chaudhury LB (2016) Periodicity of different phenophases in selected trees from Himalayan Terai of India. *Agroforestry Systems* [DOI: 10.1007/s10457-016-9936-9]
- Boinski S & Fowler NL (1989) Seasonal patterns in a tropical lowland forest. *Biotropica* 21: 223–233.
- Borah M & Devi A (2014) Phenology, growth and survival of *Vatica lanceaefolia* Bl.: A critically endangered tree species in moist tropical forest of Northeast India. *Tropical Plant Research* 1(3): 1–12.
- Borchert R & Rivera G (2001) Photoperiodic control of seasonal development and dormancy in tropical stem-succulent trees. *Tree Physiology* 21: 213–221.
- Borchert R (1980) Phenology and ecophysiology of tropical trees: *Erythrina poeppigiana* O. F. Cook. *Ecology* 61: 1065–1074.
- Borchert R (1983) Phenology and control of flowering in tropical trees. *Biotropica* 15: 81–89.
- Borchert R (1994a) Induction of rehydration and budbreak by irrigation or rain in deciduous trees of a tropical dry forest in Costa Rica. *Trees* 8: 198–204.
- Borchert R (1994b) Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Biotropica* 15: 81–89.
- Borchert R (1994c) Water status and development of tropical trees during seasonal drought. *Trees-Structure and Function* 8: 115–125.
- Borchert R (1994d) Water storage in soil or tree stems determines phenology and distribution of tropical dry forest trees. *Ecology* 75: 1437–1449.
- Borchert R (1998) Response of tropical trees to rainfall seasonality and its long-term changes. *Climate Change* 39: 381–393.
- Borchert R (2000) Organismic and environmental controls of bud growth in tropical trees. In: Viemont JD & Crabbe J (eds) *Dormancy in plants: from whole plant behavior to cellular control*. Wallingford: CAB International, pp. 87–107.
- Borchert R, Meyer SA, Felger RS & Porter-Bolland L (2004) Environmental control of flowering periodicity in Costa Rican and Mexican tropical dry forests. *Global Ecology and Biogeography* 13: 409–425.
- Borchert R, Rivera G & Hagnauer W (2002) Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain. *Biotropica* 34: 27–39.
- Bullock SH & Solis-Magallanes JA (1990) Phenology of canopy trees of a tropical deciduous forest in Mexico. *Biotropica* 22: 22–35.
- Chabot BF & Hicks DJ (1982) The ecology of leaf life spans. *Annual Review of Ecology and Systematics* 13: 229–259.
- Chaturvedi RK & Raghubanshi AS (2011) *Plant Functional Traits in a Tropical Deciduous Forest: An Analysis*. Berlin, Germany: Lambert Academic Publishing GmbH and Co. KG.

- Chaturvedi RK & Raghubanshi AS (2013) Phenotypic plasticity in functional traits of woody species in tropical dry forest. In: Valentino JB & Harrelson PC (eds) *Phenotypic Plasticity: Molecular Mechanisms, Evolutionary Significance and Impact on Speciation*. New York: Nova Science Publishers, Inc, pp. 35–66.
- Chaturvedi RK & Raghubanshi AS (2014) Species composition, distribution and diversity of woody species in tropical dry forest of India. *Journal of Sustainable Forestry* 33: 729–756.
- Chaturvedi RK & Raghubanshi AS (2015) Assessment of carbon density and accumulation in mono- and multi-specific stands in Teak and Sal forests of a tropical dry region in India. *Forest Ecology and Management* 339: 11–21.
- Chaturvedi RK, Raghubanshi AS & Singh JS (2011a) Carbon density and accumulation in woody species of tropical dry forest in India. *Forest Ecology and Management* 262: 1576–1588.
- Chaturvedi RK, Raghubanshi AS & Singh JS (2011b) Effect of small scale variations in environmental factors on the distribution of woody species in tropical deciduous forests of Vindhyan Highlands, India. *Journal of Botany* 2011: Article ID 297097. [doi:10.1155/2011/297097]
- Chaturvedi RK, Raghubanshi AS & Singh JS (2011c) Leaf attributes and tree growth in a tropical dry forest. *Journal of Vegetation Science* 22: 917–931.
- Chaturvedi RK, Raghubanshi AS & Singh JS (2012) Effect of grazing and harvesting on diversity, recruitment and carbon accumulation of juvenile trees in tropical dry forests. *Forest Ecology and Management* 284: 152–162.
- Chaturvedi RK, Raghubanshi AS & Singh JS (2013) Growth of tree seedlings in a dry tropical forest in relation to soil moisture and leaf traits. *Journal of Plant Ecology* 6: 158–170.
- Chaturvedi RK, Raghubanshi AS & Singh JS (2014) Relative effects of different leaf attributes on sapling growth in tropical dry forest. *Journal of Plant Ecology* 7: 544–558.
- Clark DB & Clark DA (1991) Herbivores, herbivory, and plant phenology: patterns and consequences in a tropical rain-forest cycad. In: Price PW, Lewinsohn TM, Fernandes GW & Benson W (eds) *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*. New York: John Wiley & Sons, Inc, pp. 209–225.
- Coley PD & Aide TM (1991) Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. In: Price PW, Lewinsohn TM, Fernandes GW & Benson W (eds) *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*. New York: John Wiley & Sons, Inc, pp. 25–49.
- Coley PD (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs* 53: 209–233.
- Crawley MJ (1985) Reduction of oak fecundity by low density herbivore populations. *Nature* 314: 163–164.
- Daubenmire R (1972) Phenology and other characteristics of tropical semi-deciduous forest in northeastern Costa Rica. *Journal of Ecology* 60: 147–170.
- Dirzo R (1984) Insect-plant interactions: some ecophysiological consequences of herbivory. In: Medina E, Mooney HA & Vazquez-Yanes C (eds) *Physiological ecology of plants in the wet tropics*. The Hague, Netherlands: Dr. Junk W, pp. 209–224.
- Eamus D & Prior L (2001) Ecophysiology of trees of seasonally dry tropics: Comparisons among phenologies. *Advances in Ecological Research* 32: 113–197.
- Elliot S, Baker PJ & Borchert R (2006) Leaf-flushing during the dry season: The paradox of Asian monsoon forests. *Global Ecology and Biogeography* 15: 248–257.
- Frankie GW, Baker HG & Opler PA (1974) Comparative phenological studies of trees in tropical wet and dry forest in the lowlands of Costa Rica. *Journal of Ecology* 62: 881–913.
- Franklin O & Agren GI (2002) Leaf senescence and resorption as mechanisms of maximizing photosynthetic production during canopy development at N limitation. *Functional Ecology* 16: 727–733.
- Hikosaka K (2003) A model of dynamics of leaves and nitrogen in a plant canopy: An integration of canopy photosynthesis, leaf life span, and nitrogen use efficiency. *American Naturalist* 162: 149–164.
- Hikosaka K (2005) Leaf canopy as a dynamic system: ecophysiology and optimality in leaf turnover. *Annals of Botany* 95: 521–533.
- Jha CS & Singh JS (1990) Composition and dynamics of dry tropical forest in relation to soil texture. *Journal of Vegetation Science* 1: 609–614.

- Jolly WM, Nemani R & Running SW (2005) A generalized, bioclimatic index to predict foliar phenology in response to climate. *Global Change Biology* 11: 619–632.
- Jurik TW & Chabot BF (1986) Leaf dynamics and profitability in wild strawberries. *Oecologia* 69: 296–304.
- Karst AL & Lechowicz MJ (2007) Are correlations among foliar traits in ferns consistent with those in the seed plants? *New Phytologist* 173: 306–312.
- Kikuzawa K & Lechowicz MJ (2006) Toward synthesis of relationships among leaf longevity, instantaneous photosynthetic rate, lifetime leaf carbon gain, and the gross primary production of forests. *American Naturalist* 168: 373–383.
- Kikuzawa K (1991) A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. *American Naturalist* 138: 1250–1263.
- Krischik VA & Denno RR (1983) Individual, population, and geographic patterns in plant defense. In: Denno RF & McClure MS (eds) *Variable plants and herbivores in natural and managed systems*. New York: Academic Press, pp. 463–512.
- Louda S (1984) Herbivory effects on stature, fruiting, and leaf dynamics of a native crucifer. *Ecology* 65: 1379–1386.
- Marquis RJ (1984) Leaf herbivores decrease fitness of a tropical plant. *Science* 226: 537–539.
- Mooney HA, Bullock SH & Medina E (1995) Introduction. In: Mooney HA, Bullock SH & Medina E (eds) *Seasonally dry tropical forests*. Cambridge: Cambridge University Press, pp. 1–8.
- Mulkey SS, Smith AP, Wright SJ, Machado JL & Dudley R (1992) Contrasting leaf phenotypes control seasonal variation in water loss in a tropical forest shrub. *Proceedings of the National Academy of Sciences USA* 89: 9084–9088.
- Murali KS & Sukumar R (1993) Reproductive phenology of a tropical dry forest in Mudumalai, southern India. *Journal of Ecology* 82: 759–767.
- Nanda A, Suresh HS & Krishnamurthy YL (2014) Phenology of a tropical dry deciduous forest of Bhadra wildlife sanctuary, southern India. *Ecological Processes* 3: 1–12.
- Nilsen ET & Muller WH (1981) Phenology of the drought-deciduous shrub *Lotus scoparius*: climatic controls and adaptive significance. *Ecological Monographs* 51: 323–341.
- Noda H, Muraoka H & Washitani I (2004) Morphological and physiological acclimation responses to contrasting light and water regimes in *Primula sieboldii*. *Ecological Research* 19: 331–340.
- Oikawa S, Hikosaka K & Hirose T (2006) Leaf lifespan and lifetime carbon balance of individual leaves in a stand of an annual herb, *Xanthium canadense*. *New Phytologist* 172: 104–116.
- Oikawa S, Hikosaka K & Hirose T (2008) Does leaf shedding increase the whole-plant carbon gain despite some nitrogen being lost with shedding? *New Phytologist* 178: 617–624.
- Oikawa S, Hikosaka K, Hirose T, Shiyomi M, Takahashi S & Hori Y (2004) Cost-benefit relationships in leaves emerging at different times in a deciduous fern *Pteridium aquilinum*. *Canadian Journal of Botany* 82: 521–527.
- Reich PB & Borchert R (1984) Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *Journal of Ecology* 72: 61–74.
- Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC & Bowman WD (1999) Generality of leaf trait relationships: a test across six biomes. *Ecology* 80: 1955–1969.
- Reich PB, Uhl C, Walters MB, Prugh L & Ellsworth DS (2004) Leaf demography and phenology in Amazonian rain forest: a census of 40,000 leaves of 23 tree species. *Ecological Monographs* 74: 3–23.
- Rivera G, Elliott S, Caldas LS, Nicolossi G, Coradin VTR & Borchert R (2002) Increasing day-length induces spring flushing of tropical dry forest trees in the absence of rain. *Trees* 16: 445–456.
- Rockwood LL (1973) The effect of defoliation on seed production of six Costa Rican tree species. *Ecology* 54: 1363–1369.
- Roy S & Singh JS (1994) Consequences of habitat heterogeneity for availability of nutrients in a dry tropical forest. *Journal of Ecology* 82: 503–509.
- Seiwa K & Kikuzawa K (1991) Phenology of tree seedlings in relation to seed size. *Canadian Journal of Botany* 69: 532–538.
- Shukla R & Ramakrishnan P (1982) Phenology of trees in a sub-tropical humid forest in north-eastern India. *Vegetatio* 49: 103–109.

- Skarpe C (1996) Plant functional types and climate in a southern African savanna. *Journal of Vegetation Science* 7: 397–404.
- Suresh HS & Sukumar R (2011) Vegetative phenology of tropical montane forests in the Nilgiris, South India. *Journal of the National Science Foundation of Sri Lanka* 39: 337–347.
- van Schaik CP, Terborgh JW & Wright SJ (1993) The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24: 353–377.
- Vincent G (2006) Leaf life span plasticity in tropical seedlings grown under contrasting light regimes. *Annals of Botany* 97: 245–255.
- White MA, Thornton PE & Running SW (1997) A continental phenology model for monitoring vegetation response to interannual climatic variability. *Global Biogeochemical Cycles* 11: 217–234.
- Wolda H (1978) Seasonal fluctuations in rainfall, food and abundance of tropical insects. *Journal of Animal Ecology* 47: 369–381.
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin FS, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ & Villar R (2004) The worldwide leaf economics spectrum. *Nature* 428: 821–827.
- Wright SJ & van Schaik CP (1994) Light and the phenology of tropical trees. *American Naturalist* 143: 192–199.