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Tree specific traits affect flowering time in Indian dry tropical forest

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Abstract Dry tropical forest tree species show variations in leafless duration (i.e. deciduousness), stem wood density (SWD), leaf mass area (LMA) and leaf strategy index (LSI, reflecting resource use rate) to overcome water limitations. We investigated the role of these tree traits in the seasonal timing of flowering and subsequent fruiting. Flowering and fruiting time of 24 tree species was recorded over two consecutive annual cycles and their relationships with the above-mentioned tree specific traits were examined across the species. In leaf-exchanging species having higher SWD and LMA, low LSI and short deciduousness, flowering coincides with leaf transitional state when vegetative growth is at its minimum, and fruit formation and leaf flushing are both supported at the same time. However, >4-months-deciduous species with lowest SWD and LMA, higher LSI and longer deciduousness showed predominantly dry season flowering, subsequent fruiting on leafless shoots and distinct separation of vegetative and flowering phenophases. In contrast, intermediate species (<2 months-deciduous, 2–4-months-deciduous) showed wider flowering range through summer, rainy, autumn or winter seasons. Fruiting duration varies considerably with variation in the flowering time; ca. 5–14 months in summer flowering species; 7–12 months in rainy flowering species; 6–10 months in autumn flowering species, 4–9 months in dry season flowering and 3–7 months in winter flowering species. In most species, fruit maturation occurred just prior to the onset of rains, ensuring seedling survival. The ability of tree species to withstand (leaf-exchange) or avoid (deciduousness) drought stress and varying seasonal flowering timings appear to be the principal mechanisms for successful survival and reproduction under extremely dry and seasonal climate. Since environmental characteristics affect flowering and fruiting either directly (e.g. through conditions in the habitat) or indirectly (e.g. through deciduousness, LMA, SWD and LSI), the impact of probable global climatic change will have long implications on reproduction of dry tropical trees.

Keywords Flowering types · Tropical deciduous forest · Wood density · Leaf mass per area · Deciduousness · Time lag

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Introduction

An understanding of the dynamics of tropical dry forest trees with special emphasis on reproductive phenology would be of great significance for proper biodiversity conservation efforts in tropics (McLaren and McDonald 2005). Flowering initiation, a precursor for the reproductive events in tree species, indicates the switch between vegetative and reproductive phases that is essential for optimal seed set and sustainable tree production systems (Bernier 1988). Reproductive events in dry tropical forest trees are not self-regulating and thus the flowering may be partly or wholly dependent on with leaf or deciduous states (van Schaik et al. 1993; Singh and Kushwaha 2006). It has been reported that the timing of tree vegetative phenology strongly determines the flowering periods, and thus flowering at least depends indirectly on environmental periodicity (Rivera et al. 2002). However, information on reproductive (flowering and fruiting) events and their functional interrelationship with vegetative (with leaf and deciduous state) phenophases in dry tropical trees is highly limited (Singh and Kushwaha 2005).

Leaf traits and stem wood density (SWD), in combination with variations in soil water availability, and stem water status have been reported to strongly affect the pattern of leaf phenology and species distribution in seasonally dry tropical forests (Borchert et al. 2002). A number of flowering patterns occur in tropical trees due to variations in flowering periods induced by a variety of factors like significant rain in winter/summer, decreasing or increasing photoperiod or drought-induced leaf fall (Borchert et al. 2004). Rainfall seasonality has been found as a major governing factor for differences in patterns of leafing, flowering and fruiting in different ecosystems (Borchert et al. 2004; Singh and Kushwaha 2006; Boulter et al. 2006). Since water availability is a prerequisite to expand growing cells during leaf flush, flower formation and fruit development (Borchert 1994), the occurrence of long and/or severe drought in seasonally dry tropical forests acts as a major factor in determining the timing of flowering and subsequent fruiting in tree species (Singh and Kushwaha 2005; Zimmerman et al. 2007). Many tropical tree species require a signal of drought or shortage of moisture to switch from vegetative growth to flower production (Borchert et al. 2004; Singh and Kushwaha 2006). However, the degree of drought adaptations in dry tropical trees varies widely as a result of temperature, soil water availability and tree characteristics like rooting depth (van Schaik et al. 1993), resulting in a variety of species-specific phenological patterns (Borchert 2000; Singh and Kushwaha 2005).

Developmental linkages between vegetative and reproductive phenology suggest that traits which affect the vegetative phenology will also have influence on reproductive phenology (Diggle 1999; Sola and Ehrlen 2007). In Indian dry tropical forests, variation in tree functional traits (e.g. leaf mass per area, LMA; stem wood density, SWD; leaf strategy index, LSI; and annual deciduousness) significantly affect the leaf (vegetative) phenological patterns (Kushwaha et al. 2010). LMA plays a significant role in inter-specific variation in relative growth rate (Garnier 1992) and has been found to be positively related to leaf life span (which is reciprocal to deciduousness) and negatively to photosynthetic rate per mass (Wright et al. 2004). SWD, apparently determined by water uptake and the ability to access soil water during dry season, affects the physiological performance of leaf and the whole plant (Bucci et al. 2004). LSI denotes the adaptations in leaf dynamics controlling the ability of a tree species to exploit/utilize resources (e.g. water, nutrients and CO_2) in relation to its ability to conserve the same (Singh and Kushwaha 2005). Deciduousness in trees, generally occurring in response to water stress, reflects the time period during the annual cycle when resources are not being exploited or are being used at a low intensity (Kushwaha and Singh 2005). LMA along with SWD and LSI (resource use or photosynthesis rate) may significantly relate to deciduousness in tropical trees because all these characteristics are closely related to leaf longevity (Reich et al. 1997). These traits have a significant role in accumulation of photosynthate during the leafing phenology. Flower initiation and subsequent fruiting mark the initiation of resource allocation from their own growth to reproduction (Roff 2002) because both these events require considerable expenditure of photosynthate accumulated during the leafing phenophase (Ashman and Schoen 1997). Considering the close link between reproductive and vegetative phenology in tropical tree species (van Schaik et al. 1993; Singh and Kushwaha 2006), it is expected that constraints imposed on vegetative growth (leafing phenophase) by LMA, SWD, LSI and deciduousness may also be reflected during flowering and fruiting phenologies.

Tropical forests, comprising ca. 86% of forested land in India, are being rapidly transformed to various land uses due to anthropogenic activities and are facing high degree of stress due to the changing patterns of temperature, precipitation and nutrient loading (Tripathi et al. 2008; Allan et al. 2010; Kanniah et al. 2010). Alterations in temperature and precipitation patterns, often called proximate cues of vegetative phenology, are reported as strong determinants of flowering time in seasonally dry forests (Borchert et al. 2004; Singh and Kushwaha 2006). However, information on seasonal pattern of reproductive phenology and the impacting factors (abiotic and tree traits) responsible for these patterns is highly limited in tropical deciduous forests in India. Tree traits like SWD, LMA, deciduousness and resource use rate reflect environmental adaptations and eco-physiological properties of species, but their role in determining flowering timing and subsequent fruiting has not been evaluated so far. The present study tested the hypothesis that variation in the seasonal timings of flowering and fruiting across tree species is a reflection of the differences in tree specific traits like annual deciduousness, SWD, LSI and LMA. Focused on key Indian tropical deciduous forest tree species, this study addresses the following questions: (1) What is the diversity of reproductive pheno-phases of tree species in terms of seasonal timings of flowering and fruiting? (2) How do the leaf pheno-phases (especially deciduousness) and selected tree specific characteristics (LMA, LSI and SWD) affect the pattern of reproductive pheno-phases (flowering and fruiting patterns)? Outcome of the present work will be useful in biodiversity conservation through better understanding of basic factors regulating tree reproductive pheno-phases.

Materials and methods

Study site

The present study was carried out in the Hathinala Forest (24° 18′ N, 83° 6′ E; elevation, 315–485 m a.s.l., ca. 150 km away from Varanasi), which is spread over the Vindhyan plateau, in the Sonbhadra district of Uttar Pradesh, India. The Vindhyan plateau, which was originally covered with dense dry deciduous forests, has lost substantial stretches of natural forest cover, especially in the last six decades, due to sporadic illegal tree felling, extraction of non-timber resources and massive developmental activities such as mining, thermal power generation and cement industry. The forested area is continuously decreasing and the remnant forest cover exists in the form of non-contiguous patches of varying sizes. The study site was selected on the basis of field observations to represent the least-disturbed forest stand in the region. At Hathinala, several low hills rising 20 to 40 m above the general terrain, undulating ridge top and plateau are widespread resulting in highly heterogeneous landscape marked by mosaic of differing microsites, ranging from nutrient and water rich depressions to exposed dry shallow soil ridges/hills.

The vegetation of Hathinala forest belongs to Northern Tropical Dry Deciduous Forest type (subgroup 5-B of Champion and Seth 1968). The top-storey trees form a nearly continuous 15–20 m high canopy, underlain by discontinuous lower storey of trees, thin shrub layer and seasonal herb layer which includes several grasses. While leaf-exchanging species (e.g. *Albizia odoratissima* and *Shorea robusta*) are mostly distributed in relatively moist sites at hill bases, species remaining deciduous for long intervals (e.g. *Boswellia serrata* and *Sterculia urens*) are generally restricted to ridges/hill tops. Majority of other deciduous species are distributed widely from moist to dry microsites (Kushwaha et al. 2010). The forest becomes lush green during rainy season due to the presence of fully expanded leaves of trees and shrubs and a dense herbaceous layer. The summer aspect is pale and parched because of many leafless trees and shrubs and a dried-up herb layer.

Temperature and rainfall data were obtained from the weather station of the State Irrigation Department at Renukoot, located about 10 km from the study site. The climate is characterized by three seasons: warm-wet rainy (mid June–September); cool-dry winter (November–February); and hot-dry summer (April–June). October and March represent the transition months between seasons, the major part of both being closer to the season following them. The mean monthly maximum (day) temperature varies from 20 °C in January to 42 °C in May, and the mean minimum (night) temperature from 10°C in January to 24°C in May. Long-term annual rainfall varies between 850 and 1,300 mm. About 85% of the annual rainfall occurs during the rainy season from the south-west monsoon, and 7–8 dry months occur during the annual cycle (Fig. 1).

The Hathinala series of rock is composed of haematitic slates or schists together with banded jaspers and quartzites, hornblende and limestones. This rock system belongs to the transition system of Bijawar group of rock formations. According to VII approximation of the USDA soil nomenclature the soils are part of the hyperthermic formation of typical plinthustults with ustorthents.

Experimental design

To document the patterns of leaf phenological diversity, five adult individuals (>30 cm girth at 130 cm height) of the 24 species listed in Table 1 were randomly marked at Hathinala site. On each marked individual, four twigs (currently growing shoots of last-order branches) on each of four major branches (one in each direction) were marked with metal tags. Thus, for each species 80 twigs were selected to represent the whole plant canopy. On these twigs monthly observation of phenological events was made from April 2006 to May 2008. Based on previous experience (Kushwaha and Singh

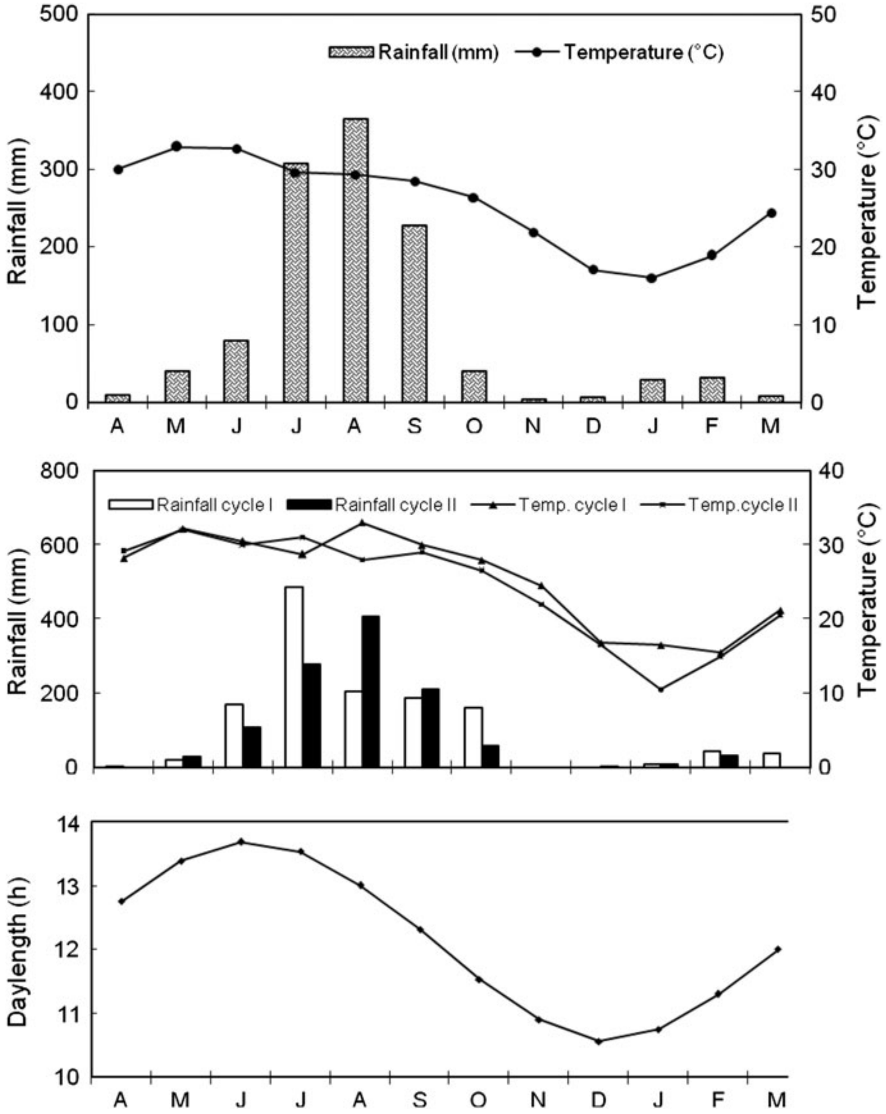


Fig. 1 Mean temperature and rainfall for 25 years (*top*), during study period (*middle*) and day length (*bottom*) in the Vindhyan tropical deciduous forest in India

Table 1 Variation in wood density, leaf mass per area (LMA), leaf strategy index (ratio of leaf fall duration to leaf flush duration) and deciduousness in tree species in Vindhyan dry forest in India

Species name	Wood density (g cm^{-3})	LMA (g cm^{-2})	Leaf strategy index	Deciduousness (days)
Leaf-exchanging				
Albizia odoratissima (L. f.) Benth.	0.625 ± 0.015	108.7 ± 1.0	0.46 ± 0.015	7 ± 3
Bauhinia racemosa Lamk.	0.667 ± 0.013	119.0 ± 1.1	0.44 ± 0.013	3 ± 1
Shorea robusta C.F. Gaertn.	0.718 ± 0.011	112.7 ± 1.2	0.44 ± 0.015	9 ± 3
Soymida febrifuga (Roxb.) A. Juss.	0.859 ± 0.021	140.2 ± 0.2	0.46 ± 0.004	6 ± 3
<2-month-deciduous				
Anogeissus latifolia (Roxb. Ex DC) Wall. ex Bedd.	0.801 ± 0.008	136.0 ± 0.9	0.61 ± 0.005	52 ± 5
Buchanania lanzan Spreng.	0.458 ± 0.006	97.6 ± 0.8	0.64 ± 0.011	47 ± 6
Cassia fistula L.	0.735 ± 0.018	92.7 ± 0.5	0.60 ± 0.005	46 ± 4
Diospyros melanoxylon Roxb.	0.685 ± 0.013	124.0 ± 0.9	0.68 ± 0.018	46 ± 3
Elaeodendron glaucum Pers.	0.666 ± 0.018	109.8 ± 0.6	0.64 ± 0.004	56 ± 4
Hardwickia binata Roxb.	0.727 ± 0.015	109.9 ± 0.7	0.68 ± 0.021	30 ± 4
Ougeinia oogeinsis (Roxb.) Hochr.	0.705 ± 0.005	116.5 ± 0.7	0.61 ± 0.012	42 ± 2
Terminalia chebula Retz.	0.642 ± 0.009	102.2 ± 0.6	0.60 ± 0.006	53 ± 5
2–4-month-deciduous				
Acacia catechu (L. f.) Willd.	0.889 ± 0.008	120.4 ± 0.7	0.89 ± 0.020	93 ± 2
Flacourtia indica (Burm. f.) Merr.	0.616 ± 0.009	101.4 ± 1.1	0.88 ± 0.028	116 ± 5
Gardenia turgida Roxb.	0.645 ± 0.027	99.4 ± 0.7	0.86 ± 0.006	75 ± 3
Lagerstroemia parviflora Roxb.	0.617 ± 0.010	112.3 ± 0.8	0.81 ± 0.007	83 ± 8
Miliusa tomentosa (Roxb.) Sinclair	0.626 ± 0.009	97.7 ± 0.8	0.84 ± 0.014	102 ± 3
Terminalia tomentosa Wt. & Arn.	0.653 ± 0.025	102.0 ± 1.2	0.80 ± 0.003	86 ± 5
>4-month-deciduous				
Adina cordifolia (Roxb.) Hook. f. ex Brandis	0.575 ± 0.005	90.8 ± 0.7	1.00 ± 0.005	129 ± 3
Bombax ceiba L.	0.335 ± 0.007	81.0 ± 0.9	1.00 ± 0.006	152 ± 3
Boswellia serrata Roxb. cx Colebr.	0.505 ± 0.008	85.4 ± 0.6	0.98 ± 0.003	144 ± 4
Chloroxylon swietenia DC	0.773 ± 0.018	99.7 ± 0.9	0.98 ± 0.003	136 ± 2
Lannea coromandelica (Houtt.) Merrill	0.509 ± 0.016	86.0 ± 0.7	0.98 ± 0.003	231 ± 8
Sterculia urens Roxb.	0.411 ± 0.007	74.9 ± 1.2	0.96 ± 0.010	224 ± 4

Values are mean ± SE

2005; Singh and Kushwaha 2006), during the intense phenological periods observations were made at 15-day interval. In addition, several other adult individuals of each species were visually observed for phenological events.

Following phenological events were derived from the periodical observations on marked trees: (a) leaf flush (new leaf formation) initiation, (b) leaf flush completion, (c) leaf fall initiation, (d) leaf fall completion, (e) deciduous period, (f) initiation of flowering, (g) completion of flowering, (h) time lag between start of vegetative (first-leaf flush) and reproductive (first-visible-flower) phases, (i) initiation of fruiting, (j) completion of fruiting, (k) fruit fall initiation and (l) completion of fruit fall. Since no observations were made during the interval between two sampling dates, it was assumed that in an individual the particular phenophase began before, or continued beyond, the date of the first/last record by one-half sampling interval. Leaf flush period of a species is the duration (days) from the first-leaf flush to the last flush amongst its individuals. Similarly, leaf fall period of a species represents the time duration from the estimated first-leaf fall to the last in observed individuals. For each individual of a species, leaf flush and leaf fall periods were calculated to range 7.5 days before and after the date on which the event was recorded for the first and the last time, respectively. The deciduousness (leafless period) for each species was calculated as the mean leafless duration of individuals. Leaf strategy index for each species was calculated as the ratio of leaf fall duration to leaf flush duration (mean of 5 individuals), assuming that equal number of leaves participate in both events during the annual cycle. In this study, flowering period for each species was calculated from 7.5 days before the date on which the event was recorded for the first time to 7.5 days after the date on which the event was recorded the last time amongst individuals. Fruiting period of a species is the duration (days) from the first fruit formation to the last amongst its individuals. In the same way, fruit fall period of a species represents the time duration from the first fruit fall amongst individuals to the last.

To estimate the LMA, 125 mature leaves each from whole crown of five individuals per species were plucked during September–October. Four discs of 1 cm^2 per leaf were cut (one each from upper and lower part of mid rib and two from both side of mid rib); total 500 leaf discs per species were oven dried (80°C) and weight of leaf per unit area was reported as LMA. In the case of *Acacia catechu*, dry mass and area of leaflets were determined and converted to dry mass per unit area. Out of the five marked individuals of each species, three individuals were randomly selected for determination of sap wood density, and three stem cores per individual (total nine cores per species) were taken during March–April. Wood samples were collected with an increment borer, sealed in aluminium foils and plastic bags, and were taken to the laboratory. Bark was removed from each core and then cores were placed in water in a small graduated cylinder to determine the volume. The cores were oven dried (80°C) and weighed to obtain the dry mass. SWD was expressed as the dry mass per unit volume.

Detailed information on leaf phenology, annual deciduousness, LMA, SWD and LSI of the 24 tree species has been published elsewhere (Kushwaha et al. 2010). Briefly, the deciduousness ranged 3–9 days in leaf-exchanging species, 30–56 days in <2-month-deciduous species, 75–116 days in 2–4-month-deciduous species and 129–231 days in >4-month-deciduous species (Table 1). Across the studied species, deciduousness generally increases with decrease in SWD. Values of SWD (g cm^{-3}) varied considerably amongst tree species, being 0.625–0.859 for leaf-exchanging species, 0.458–0.801 for <2-month-deciduous species, 0.616–0.889 for 2–4-month-deciduous species and 0.335–0.773 for >4-month-deciduous species. The LMA (g m^{-2}) showed decreasing trend with increase in deciduousness; being 108.7–140.2 for leaf-exchanging species, 92.7–136.0 for <2-month-deciduous species, 97.7–120.4 for 2–4-month-deciduous species and 74.9–90.8 for >4-month-deciduous species. LSI (ratio of leaf fall duration to leaf flush duration) increased as a function of deciduousness, and ranged from 0.44 to 0.46 for leaf-exchanging species, 0.60–0.68 for <2-month-deciduous species, 0.80–0.89 for 2-4-month-deciduous species to 0.96–1.00 for >4-month-deciduous species. Species having LSI < 0.5 show semi-evergreenness (leaf-exchange), and as the duration of deciduousness increases, the LSI proportionately increases above 0.5.

In this article, the mean values of leaf phenology, annual deciduousness, LMA, SWD and LSI have been used to evaluate interactions with timings of flowering and fruiting of the species.

Statistical analysis

Relationships amongst different parameters across various species were examined with the help of SPSS package on a PC by computing correlation coefficients using species mean values.

Results

Variation in the vegetative phenology

Out of 24 species studied, four species were leaf-exchanging semi-evergreen and the rest showed variable deciduousness (Fig. 2). The leaf-exchanging species showed overlapping periods of leaf fall and leaf flush between March and May and leaf fall between December and April. In these species, leaf flush occurred between March and mid-September. Deciduous species, on other hand, showed temporally separated single leaf flush and leaf fall periods, and leaf flush always began on completely leafless twigs.

Differing dramatically with respect to the temporal patterns of leaf flush and leaf fall, deciduous species showed widely varying timings and durations of deciduousness. Although leaf flush was initiated between April and June, amongst deciduous species the timings of leaf fall varied considerably (Fig. 2): <2-month-deciduous species showed leaf fall between December and March; 2–4-month-deciduous species, between October and mid-March; and >4-month-deciduous species, between September and mid-February. With increase in deciduousness in different species their leaf flushing period decreased significantly. In contrast, leaf fall period in all species ranged closely, however, leaf fall timing amongst species varied markedly. It is evident that in the tree species studied increase in the annual duration of deciduousness is associated with earliness of leaf fall (i.e. shift towards the end of rainy season) without any marked change in the duration of leaf fall, and delayed leaf flush (i.e. closer to the onset of rainy season) with sharp decrease in flush duration.

Vegetative state and flowering time

Leaf-exchanging species (*Albizia odoratissima*, *Bauhinia racemosa*, *Shorea robusta* and *Soymida febrifuga*) began flowering with or short time after leaf fall (Fig. 2). Their flowering period (January–June), coinciding with the leaf transitional state (leaf fall–leaf initiation), was associated with fruit formation and leaf flushing both at the same time. In the deciduous species, flowering initiation was seasonally separated. Out of the eight <2-months-deciduous species, three species (*Cassia fistula*, *Diospyros melanoxylon* and *Terminalia tomentosa*) initiated flowering in summer, one in rainy (*Hardwickia binata*), two (*Anogeissus latifolia*, *Elaeodendron glaucum*) in autumn and two (*Buchanania lanzan*, *Ougeinia oogeinsis*) in winter. Similarly, 2–4-month-deciduous species also showed temporal separation in their flowering timing; *Gardenia turgida* and *Miliusa tomentosa* flowered in summer, *Acacia catechu* and *Lagerstroemia parviflora* in rainy, *Terminalia tomentosa* in autumn and *Flacourtia indica* in the dry season. Except *Adina cordifolia* (which exhibited rainy flowering), all >4-months-deciduous species showed dry season flowering. Interestingly, flowering time in both <2-months-deciduous and 2–4 months-deciduous species was widely distributed in various seasons of the annual cycle. In leaf-exchanging and >4-months-deciduous species, flowering occurred predominantly in mid dry to late dry season of the annual cycle.

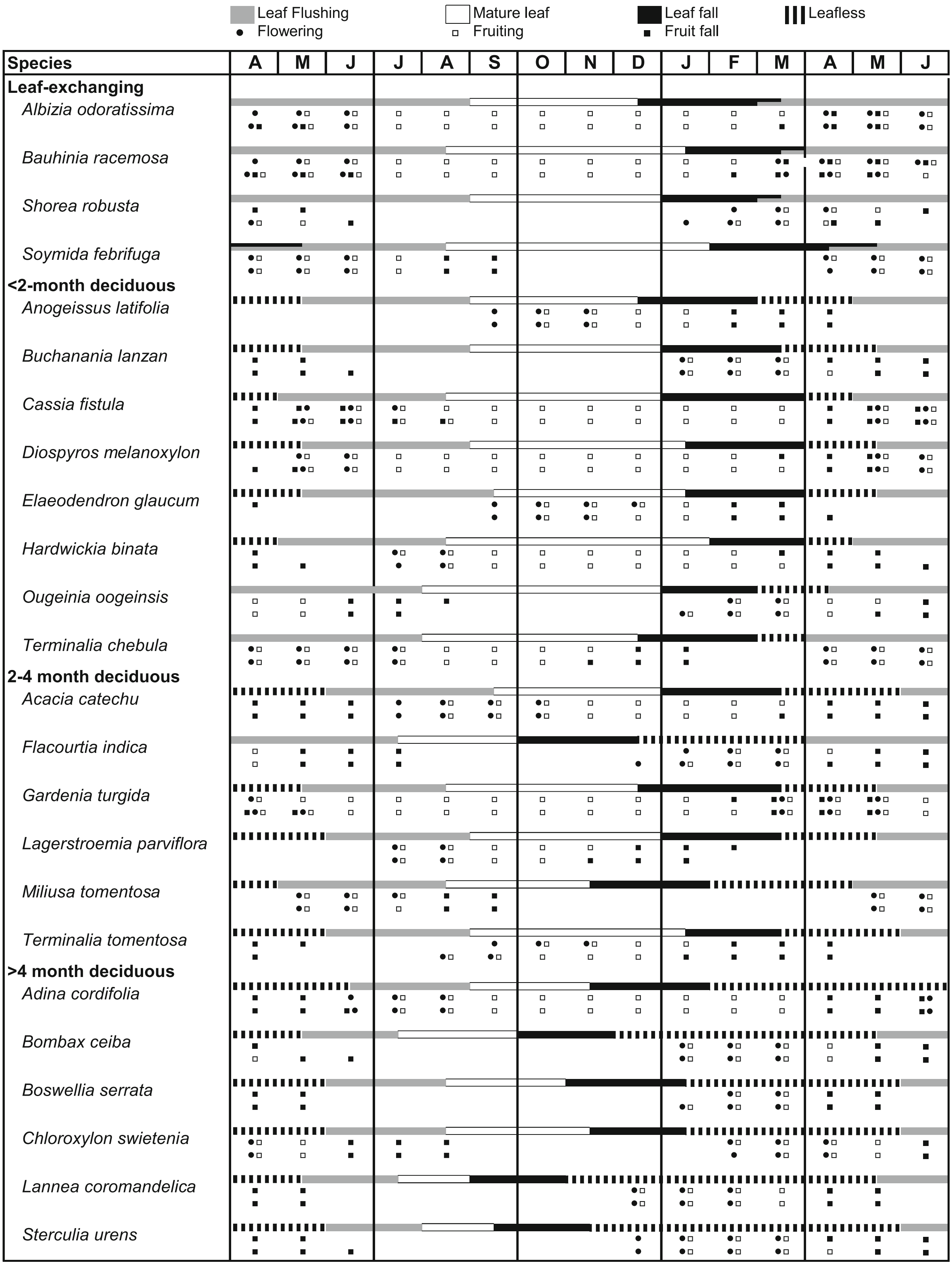
Fig. 2 Leaf phenology, flowering and fruiting of key tree ▶ species as observed during two consecutive annual cycles in Vindhyan tropical deciduous forest in India. Values of April, May and June are shown twice to clearly depict the leafless period. For each species *first row* shows the leaf phenological events (mean of two consecutive annual cycles); *second and third rows* depict the reproductive events during the two annual cycles

All deciduous tree species showed distinct time lag between the estimated dates of initiation of vegetative phase (first-leaf flush) and the succeeding reproductive phase (first-visible-flower) (Table 2). Time lag in <2-months-deciduous and 2–4-months-deciduous species ranged from 20 to 280 days. Except *Adina cordifolia*, >4-months-deciduous species showed 180–240 days time lag.

On the basis of recorded seasonal variations in flowering periods in the trees species studied, the following five flowering types can be distinguished (Table 3): (1) Summer flowering (between March and June) on young foliated shoots or old leafless shoots during the hot-dry period, (2) Rainy flowering (June–August) on young foliated shoots, following first significant rains, (3) Autumn flowering (September–December) on foliated shoots with mature leaves, (4) Winter flowering (January–March) on foliated shoots with concurrent leaf fall and (5) Cool-dry season flowering (December–March) on leafless twigs during early dry season soon after leaf shedding and/or after sporadic winter rains. Out of the 24 tree species studied, 33% showed summer flowering, 25% showed dry season flowering, 17% showed rainy flowering and remaining 25% species showed equal distribution in autumn and winter flowering. The probable flowering cues are suggested in the Table 3.

Flowering type and fruiting duration

Species flowering at different times through the year exhibited various fruiting durations (Fig. 2). Deciduous species flowering in early part of the annual cycle (summer or rainy season) showed longer fruiting duration. Whereas tree species flowering in later part of the annual cycle (autumn, winter or dry season) exhibit decreased fruiting duration. Formation of fruits occurred 2–3 months following peak


Leaf Flushing
Flowering
Mature leaf
Fruiting
Leaf fall
Fruit fall
Leafless
Species
A
M
J
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A
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O
N
D
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F
M
A
M
J
Leaf-exchanging
Albizia odoratissima
Bauhinia racemosa
Shorea robusta
Soymida febrifuga
<2-month deciduous
Anogeissus latifolia
Buchanania lanzan
Cassia fistula
Diospyros melanoxylon
Elaeodendron glaucum
Hardwickia binata
Ougeinia oogeinsis
Terminalia chebula
2-4 month deciduous
Acacia catechu
Flacourtia indica
Gardenia turgida
Lagerstroemia parviflora
Miliusa tomentosa
Terminalia tomentosa
>4 month deciduous
Adina cordifolia
Bombax ceiba
Boswellia serrata
Chloroxylon swietenia
Lannea coromandelica
Sterculia urens

Table 2 Flowering duration, fruiting duration and time lag (between first-leaf flush to first-visible flower) in tree species in Vindhyan dry forest in India

Species name	Duration (months)		Time lag (days)
	Flowering	Fruiting	
Leaf-exchanging species			
Albizia odoratissima	3.5 ± 0.10	13.0 ± 0.15	35 ± 1.6
Bauhinia racemosa	3.5 ± 0.14	14.0 ± 0.28	10 ± 1.4
Shorea robusta	3.5 ± 0.09	3.5 ± 0.13	15 ± 1.9
Soymida febrifuga	3.0 ± 0.12	6.0 ± 0.25	12 ± 1.5
<2-month-deciduous			
Anogeissus latifolia	3.0 ± 0.19	7.0 ± 0.30	105 ± 5.3
Buchanania lanzan	3.0 ± 0.12	6.0 ± 0.21	225 ± 6.1
Cassia fistula	3.0 ± 0.10	14.0 ± 0.24	30 ± 2.3
Diospyros melanoxylon	2.0 ± 0.08	11.5 ± 0.35	20 ± 1.8
Elaeodendron glaucum	3.5 ± 0.13	6.5 ± 0.22	120 ± 4.8
Hardwickia binata	2.0 ± 0.11	11.0 ± 0.28	60 ± 3.2
Ougeinia oogeinsis	2.5 ± 0.13	7.0 ± 0.20	270 ± 6.5
Terminalia chebula	4.0 ± 0.20	10.0 ± 0.32	30 ± 2.0
2–4-month-deciduous			
Acacia catechu	4.0 ± 0.19	11.0 ± 0.27	30 ± 1.4
Flacourtia indica	3.5 ± 0.13	6.5 ± 0.20	250 ± 4.8
Gardenia turgida	3.0 ± 0.21	11.5 ± 0.33	280 ± 6.0
Lagerstroemia parviflora	2.0 ± 0.11	7.5 ± 0.37	45 ± 1.2
Miliusa tomentosa	2.5 ± 0.18	5.0 ± 0.42	30 ± 2.0
Terminalia tomentosa	2.5 ± 0.14	8.0 ± 0.25	65 ± 1.8
>4-month-deciduous			
Adina cordifolia	3.0 ± 0.18	12.0 ± 0.45	20 ± 1.6
Bombax ceiba	3.0 ± 0.07	6.0 ± 0.28	195 ± 2.9
Boswellia serrata	2.5 ± 0.12	4.5 ± 0.24	210 ± 3.3
Chloroxylon swietenia	3.0 ± 0.17	4.5 ± 0.31	240 ± 2.8
Lannea coromandelica	3.0 ± 0.07	6.0 ± 0.40	195 ± 1.7
Sterculia urens	4.0 ± 0.11	8.5 ± 0.32	180 ± 2.3

Values are mean ± SE

flowering time but the time required for fruit maturation varied widely with species. Fruiting duration (interval between initiation of fruit formation to fruit fall) was conspicuously related to flowering type; fruiting duration 5–14 months long occurred in summer flowering species (March–June), 7–12 months long in rainy flowering species (June–August), 6–10 months long in autumn flowering species (September–December), 4–9 months long in dry season flowering species (December–March) and 3–7 months long in winter flowering species (January–March) (Table 2). Fruit fall was concentrated during the last 2–3 months of the fruiting phenophase in most species. In general, fruit fall was completed between April and June (i.e. less than 2 months before the rains began).

Relationship between vegetative and reproductive events

Leaf-exchanging species (having higher SWD and LMA, lowest LSI and shortest annual deciduousness) showed winter and summer flowering (Table 3). On the other hand, >4-month-deciduous species (with lowest SWD and LMA, higher LSI and longest deciduousness) mainly showed dry season flowering. Species intermediate between leaf-exchanging and >4-month-deciduous (<2-month-deciduous and 2–4-

Table 3 Characteristcs of different tree species in Vindhyan dry forest in India

Functional type	Flowering type/time	Possible flowering cue	Species
Leaf exchanging	Summer (Mar–Jun)	Increasing day length and/or temperature	*Albizia odoratissima*, *Bauhinia racemosa*, *Soymida febrifuga*
	Winter (Jan–Mar)	Drought induced leaf fall	*Shorea robusta*
<2-month-deciduous	Summer (Mar–Jun)	Increasing day length and/or temperature	*Cassia fistula*, *Diospyros melanoxylon*, *Terminalia chebula*
	Rainy (Jun–Aug)	First significant rain	*Hardwickia binata*
	Autumn (Sep–Dec)	Decreasing day length	*Anogeissus latifolia*, *Elaeodendron glaucum*
	Winter (Jan–Mar)	Drought induced leaf fall	*Buchanania lanzan*, *Ougeinia oogeinsis*
2–4-month-deciduous	Summer (Mar–Jun)	Increasing day length and/or temperature	*Gardenia turgida*, *Miliusa tomentosa*
	Rainy (Jun–Aug)	First significant rain	*Acacia catechu*, *Lagerstroemia parviflora*
	Autumn (Sep–Dec)	Decreasing day length	*Terminalia tomentosa*
	Dry season (Dec–Mar)	Leaf fall or winter rains	*Flacourtia indica*
>4-month-deciduous	Rainy (Jun–Aug)	First significant rain	*Adina cordifolia*
	Dry season (Dec–Mar)	Leaf fall or winter rains	*Bombax ceiba*, *Boswellia serrata*, *Chloroxylon swietenia*, *Lannea coromandelica*, *Sterculia urens*

month-deciduous) mostly flowered during summer, rainy and autumn seasons. Interesting is the occurrence of winter flowering in <2-month-deciduous *Buchanania lanzan* and *Ougeinia oogeinsis* and dry season flowering in 2–4-month-deciduous *Flacourtia indica*. It is apparent that in different species flowering time gradually shifted with changes in the annual deciduousness and associated traits.

Relationships amongst deciduousness, LSI, LMA and SWD, time lag between onset of vegetative and reproductive phases and fruiting duration were examined across the 24 species studied. Deciduousness was significantly positively correlated with LSI ($r = 0.89$, $P < 0.01$, $n = 24$), and significantly negatively correlated with SWD ($r = -0.58$, $P < 0.01$, $n = 24$) and with LMA ($r = -0.73$, $P < 0.01$, $n = 24$). Across species, LSI showed significant negative correlation with LMA ($r = -0.66$, $P < 0.01$, $n = 24$) and with SWD ($r = -0.46$, $P < 0.05$, $n = 24$). LMA and SWD were positively correlated with each other ($r = 0.79$, $P < 0.01$, $n = 24$). Time lag showed significant negative relationships with SWD ($r = -0.41$, $P < 0.05$, $n = 24$), LMA ($r = -0.42$, $P < 0.05$, $n = 24$) and fruiting duration ($r = -0.41$, $P < 0.05$, $n = 24$) and significant positive relationship with deciduousness ($r = 0.47$, $P < 0.05$, $n = 24$) and LSI ($r = 0.48$, $P < 0.05$, $n = 24$).

Discussion

Differences in tree leaves and SWD, arising from phylogeny and adaptations, are expected as helpful determinants for species co-existence in forests (King et al. 2006; Kitajima and Poorter 2008). Relating with a suit of other tree traits, both SWD and LMA characterize environmental adaptations and ecophysiological properties of species (Green et al. 2003; Enquist et al. 1999) and interspecific variation in relative growth rate (Lambers and Poorter 1992; Swenson and Enquist 2007). Low SWD species tend to have highly conductive sapwood (Wright et al. 2007), storing large quantities of water in the extensive parenchyma tissues in their trunks (Borchert and Rivera 2001). With increase in SWD, the sapwood water storage decreases substantially (Meinzer 2003; Bucci et al. 2004). Species with low LMA tend to have short average leaf life span and exhibit greater photosynthetic rates (Field and Mooney 1986; Niinemets 1999) as a result of increase in mass-based assimilation with decreasing leaf life span (Reich et al. 1992:

Prior et al. 2003). Deciduousness is an adaptation to avoid water stress, and water stress affects flowering time in tropical forest trees (Bullock 1995). Increased annual deciduousness of species results in reduction in the vegetative growth period, and drought stress is not only reflected in terms of deciduous period, but is also evident from the greater seasonal separation between the vegetative and reproductive phases. Significant negative relationship of LMA and SWD with LSI (reflecting the resource use rate) and the extent of deciduousness suggest that with increase in deciduousness (inverse of leaf life span, as in our study) species tend to exploit resources at rapid rate during their short vegetative growth period.

In the present study, leaf-exchanging species having high SWD, high LMA and slower resource use rate through the long growing season (reflected by LSI), least deciduousness and confinement to relatively moist sites, initiate flowering and fruiting during winter or early summer, overlapping with leaf transitional stage, at a time when vegetative growth is at its minimum. Leaf-exchanging and short (<2 month) deciduous tree 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. However, >4-months-deciduous species (low SWD, low LMA and greater resource use rate during short vegetative phase with maximum deciduousness and distribution on drier sites) show distinct separation of vegetative and reproductive events to avoid intense competition for limited availability of resources like water, nutrients and plant metabolites. Various physiologically active sites or sinks (e.g. leaf buds and leaves, flower buds and flowers and fruit) may compete for water, nutrients and metabolites within a plant (Lieberman 1982). Such internal competition may lead to the partitioning of plant functions like leafing and flowering in time. Significant positive relationships of time lag (between first-leaf flush to first-visible flower) with the annual deciduousness (reciprocal to growing period) and leaf strategy, recorded in the present study, suggests that with increase in the deciduousness, or decrease in the vegetative growth period, there is an increase in resource utilization rate during the vegetative growth and thus greater separation of vegetative and reproductive events. Such temporal separation of leafing and flowering in tropical deciduous tree species serves as an important adaptation mechanism to a strongly seasonal dry climate, where optimization of vegetative growth during the short growing season may be crucial for the survival of trees. The long held contention that in dry tropics flowering on leafless trees during dry summer has evolved as a result of interactions between plant and pollinator or disperser (Janzen, 1967), has been strongly contested and climatic periodicity has been suggested as the principal cause for flowering on leafless tress during dry summer (Borchert et al. 2004).

Most of the tree species with lesser deciduousness (<2-months-deciduous and 2–4-months-deciduous), showing intermediate values of SWD, LMA, LSI, growing season duration and leaf fall occurrence in mid or late dry season, initiate flowering at different times during summer, rainy, autumn or winter seasons. In these species, both phases begin relatively close in time, possibly, due to slower resource use rate (reflected by LSI and longer leaf flush period) and greater tolerance to water stress (as suggested by shorter leafless period) than the >4-months-deciduous tree species (having short leaf flush period and longer leafless period). It may be suggested that, as observed in the present study, tree species with lesser deciduousness duration (indicating milder seasonal water stress) encompass the whole spectrum of flowering and fruiting timings through the year (cf. >4-months-deciduous, predominant dry season flowering). In contrast, species at both ends of the deciduousness gradient (leaf-exchanging to >4-months-decidous) generally have restricted flowering time.

In the present study, large fraction of species (ca. 70% species) produces flowers during the dry period (from December to June) when vegetative growth is at its minimum, reflecting the strategy to avoid intense completion for water required by growing organs. The water requirement at this time can be met by sporadic winter rains, water absorption from sub-soil water reserves (leaf-exchanging species) or stored stem water (>4-months-deciduous species having low SWD) (Singh and Kushwaha 2006). However, the water availability and intensity of drought during the dry period varies widely amongst tropical deciduous forests depending on rainfall patterns and soil conditions, resulting in differing proportion of species flowering during the dry period; e.g. 53% of total species in Guanacaste, 54% in Yucatan, 19% in Jalisco and 73% in Sonora (Borchert et al. 2004). Occurrence of flowering during dry period (December–June) of the annual cycle on foliated or leafless shoots (Dry season flowering, Winter flowering and Summer flowering; Table 3) in majority of tree species seems to be a unique adaptation to survive under strongly seasonal climate having short wet period (growth promoting) and a long dry (growth suppressive) period. Under strongly seasonal climate, tree species have evolved a variety of flowering times to maximize their reproductive efforts.

Varying durations of fruiting pheno-phase in different flowering types, recorded in the present study, may be an adaptation for fruit maturation during the late dry season or just before the onset of the succeeding rainy season. Such maturation timing of fruits ensures maximum seed germination and establishment of seedlings due to the favourable climatic condition during the rainy season. Presence of several flowering types with specific fruiting duration may be responsible for the seasonal variation in the fruit availability. Fruit bearing species vary through time resulting in seasonal variation in the fruit availability in most plant communities (Ting et al. 2008).

Drought has been reported as a critical climate change factor in regulating growth of tropical forests (Bazzaz 1998). The varying ability to withstand (as in leaf-exchanging species) or avoid (as in deciduous species) drought stress in association to different seasonal flowering timings appear to be the principal mechanism that allow these tree species to successfully survive and reproduce in extremely dry and seasonal climate. In most of the tropical regions including India, future prediction suggests a longer dry season or shorter wet season (Hulme and Viner 1998); thus, increasing drought stress as a result of climate change in this region may become a crucial determinant for changing structural and functional traits. Apart from tree traits, increased drought in this region may have profound effects on flowering and fruiting phenology of tropical plants because of their sensitivity to environmental cues such as temperature, precipitation, photoperiod and soil moisture availability (Rathcke and Lacey 1985; Borchert et al. 2004; Singh and Kushwaha 2006). Reproductive phenological events directly or indirectly triggered by several meteorological parameters indicate a species-specific interval between climate event and phenological response (Bendix et al. 2006). The changes in LMA, SWD and deciduousness in tropical tree species caused by climate change will likely exert significant selection pressure not only on flowering but also on trophic levels that depend on them.

Consistent and predictable annual cycles in the biotic and abiotic factors that affect tree growth and reproduction over evolutionary time are expected to shape tree phenology (Anderson et al. 2005). In tropical tree species, SWD, LMA, annual deciduousness and LSI may vary due to variations in their growing conditions as a result of changes in climatic variables like temperature, precipitation and soil moisture availability (Swenson and Enquist 2007; Kushwaha et al. 2010). Abiotic factors (e.g. rainfall, day length, irradiance and temperature) in association with biotic and evolutionary factors have been suggested to regulate the flowering timing in tropical trees (Boulter et al. 2006). Indian tropical dry deciduous forests, evolved as result of long evolutionary processes under monsoonic bioclimate, exhibit wide diversity of seasonal flowering and fruiting patterns with linkage to vegetative phenology, deciduousness and other tree traits. Acquiring strategies to enhance ability of tree species to store/access water during dry period helps in their survival in stressful dry tropical conditions. Since environmental characteristics affect flowering and fruiting either directly (e.g. through conditions in the habitat) or indirectly (e.g. through deciduousness, LMA, SWD and LSI), the impact of probable global climatic change will have long implications on reproductive phenology of dry tropical trees. More studies relating the variation in deciduousness and associated tree specific traits with flowering and fruiting events of tropical trees are needed in widely distributed locations, facing high degree of threats and alteration in climatic conditions.

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