Emerging paradigms of tree phenology in dry tropics

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The tropical dry forests constitute a mosaic composed of several phenological functional types adapted to seasonal drought in different ways. Various functional types differ with respect to phenological timing and triggering factors, water relations, extent of deciduousness (~ leaflessness), etc. Duration of deciduousness in tropical trees (reflecting integrated effect of seasonal drought, tree characteristics and soil moisture conditions) is related to leafing patterns and resource use rates. Vegetative and flowering phenology of trees in dry tropics is primarily affected by the periodicity of rainfall and soil water availability. Occurrence of leaf-flushing as well as flowering during summer in majority of Indian tropical trees, when drought is severe, seems to be a unique adaptation to survive under strongly seasonal climate having a short growth promoting wet period and a long growth constraining dry period. The key phenological themes that need research focus in the dry tropics are: duration of deciduousness, timing of vegetative bud break, leaf strategy, water relations, seasonal flowering types and asynchrony. Analysis of functional types based on the duration of deciduousness and timing of bud break may enable better assessment of future climate change impact. There is a need for long-term quantitative documentation of tree phenological patterns in India through a phenological station network in diverse climatic/vegetational zones.

Keywords: Climate change, deciduousness, flowering types, functional types, quantitative phenology.

PHENOLOGICAL analysis of trees provides a potential tool to address critical questions related to modelling and monitoring of climate change[1]. Climate change will affect many aspects of the biology of tropical trees, and its effect on plant phenology would be of immense significance[2]. In recent years, therefore, the focus of phenological studies has shifted to questions of how phenology will be affected by global climate change and what consequences any climatic change may have for species distribution and ecosystem function. The control of phenology in tropical trees is not well understood[3]. Much of the available phenological information on tropical trees is inadequate, partly because of lack of standardized terminology, and also because most studies have been for a short term and have focused on community level patterns only[4]. Expressions like per cent species showing phenological events at given times have been used frequently to describe community level phenological patterns, but such patterns eclipse a great deal of vegetative and reproductive diversity in different species. Quantitative phenology (e.g. Borchert *et al.*[3], Kushwaha and Singh[5]) involves precise documentation of timing and duration of different phenological events at species (or functional type) level, their interrelations and possible causal links between environmental variables and phenology. The patterns of phenological events may be quantitatively expressed through the time of occurrence (onset, mean, and mode), duration (range), synchrony (variance), skewness, etc.[6]. Quantitative knowledge of phenological events and levels of asynchrony amongst individuals of the same species as well as amongst different species can be useful to assess the impact of environmental perturbations on tropical trees in different geographical regions.

Here we review emerging trends in quantitative documentation of phenological patterns in tree species in tropical dry forests with emphasis on: (a) seasonality and phenological functional types and (b) current vegetative and reproductive phenological themes. We also discuss the possible causal links between climate change and phenology in the tropical dry region, and the need for further research.

Seasonally dry tropical forests

While 52% of the forests in the world are tropical, in India about 86% forests are located in the tropics, among which as much as 90% is in the dry tropics[7]. Tropical dry forests may be broadly defined as tree-dominated communities growing in climates with a pronounced seasonality in rainfall, and a drought period lasting 4–8 months during each annual cycle, when the ratio of potential evaporation to rainfall is greater than one[8]. The extent and intensity of seasonal drought may differ with the geographical location of the dry tropics; for instance, Costa Rican dry tropics (low latitude, ~ 10°N; low annual temperature variability, < 2°C; 5 dry months) sharply contrasts with Indian Vindhyan dry tropics (higher latitude, ~ 24°N; higher annual temperature variation, > 20°C; 8 dry months). Structure and ecophysiological properties of dry tropical forests are closely determined by the duration and seasonality of the dry period, which selects adaptations associated with avoidance, resistance or tolerance to water stress. Water stress is most fre-

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quently cited as a primary factor responsible for the timing of phenological events in tropical dry forests[9]. These forests show great diversity of phenological patterns and large inter-annual variation, particularly at the level of individuals.

In view of the prolonged drought in the dry tropics, the predominant tree species should be deciduous, showing early dry season leaf-fall and growth resumption after the first rains. The tropical dry forests, however, constitute a mosaic composed of several phenological functional types adapted to seasonal drought in different ways[3]. As a result, weak synchronization is often noticed between periodic growth of trees and the dry season, but a high leaf cover is maintained well beyond the rainy season. Considerable diversity in water relations may occur in different phenological functional types, possibly because drought-induced water stress is a major cause of leaf-fall[10] and stem rehydration is a prerequisite for bud break of vegetative bud[11]. The links between climate and phenology in Indian tropical forests are poorly understood to enable accurate predictions, and even the qualitative assessment is highly speculative.

Seasonality and phenology of tropical trees

Periodic shoot growth arrest as well as resumption in tropical trees is mainly caused by endogenous inherent developmental constraints, which are the consequence of size- and time-dependent changes in the functional interactions among tree organs, often referred as correlative control[12]. The largest fraction of tree water is stored in the wood, especially in the sapwood, and changes in stem water status (SWS) play a central role in correlative control of tropical trees during the dry season, when water is the principal factor limiting tree growth (Figure 1). The seasonal variation in SWS of trees forms a causal link between seasonality and phenology. SWS depends on the balance between water absorption by roots and transpiration water loss from leaves, both depending on tree characteristics and environmental factors. Such tree characteristics primarily pertain to leaf (area, age and structure), root (size and distribution) and stem wood density. Precipitation and temperature are important environmental variables that determine tree SWS in the dry tropics. Complex interactions between organ functions (e.g. transpiration, water absorption, SWS) and environmental factors (e.g. seasonal variations in rainfall, day length, temperature and soil water storage) are mainly responsible for a variety of species-specific phenological patterns in dry tropical trees. Wood density, in interaction with soil water availability and SWS, strongly affect phenology and species distribution. Water content and saturation water content increase with the amount of living parenchyma cells in the wood and are negatively correlated with wood density. The negative correlation between stem wood density and leafless period across tree species in the Vindhyan forests indicates the ecological significance of SWS[5]. The importance of studying functional wood anatomy of tropical trees has been emphasized[13]; such studies may help understand the rehydration processes in species showing variable durations of deciduousness.

The annual mean area averaged surface warming in India is projected to range between 3.5 and 5.5°C by 2080; around this time the country may experience between 5 and 25% decline in winter rainfall, 10 to 15% increase in summer rainfall and deviations in the monsoon onset date[14]. The projected climatic change related to precipitation and temperature in India has generated the need for mechanistic understanding of interactions between environment and tree phenology. Even a moderate deviation in annual rainfall in combination with increasing evapotranspiration, resulting from predicted increase in temperature, may affect tree phenology (Figure 1). It may be argued that in the tropics having large seasonal variation in rainfall, the tree phenology cannot always be successfully predicted from climate data because leaf-flushing and flowering are also determined by non-climatic variables, such as seasonal variation in SWS, day length and fall of old leaves[15]. The climate change impact can be better assessed through correlations amongst seasonal changes in environmental conditions, SWS and phenology at the level of functional types.

Phenological functional types

Plant functional types are defined as species groups with similar traits and functions in relation to multiple environmental factors[16], and functional diversity refers to the

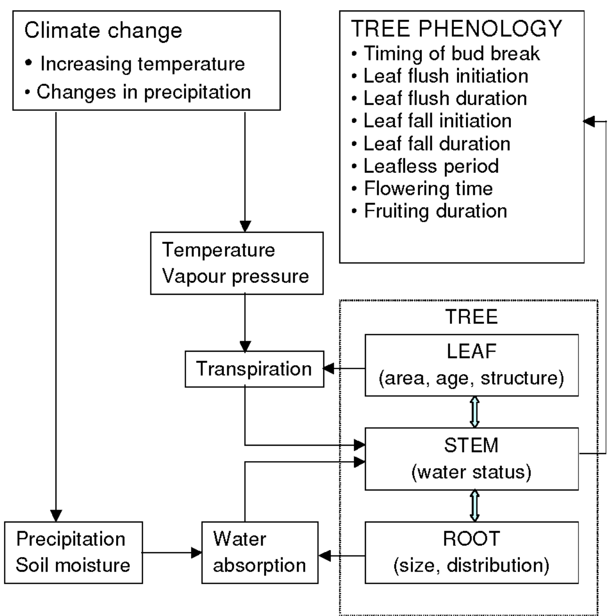

Figure 1. Climate change in relation to interactions amongst environmental inputs, stem water status of trees and its determinants, and phenological characteristics in dry tropics (adapted from Borchert[76]). Direction of arrow is from the affecting to the affected factor.

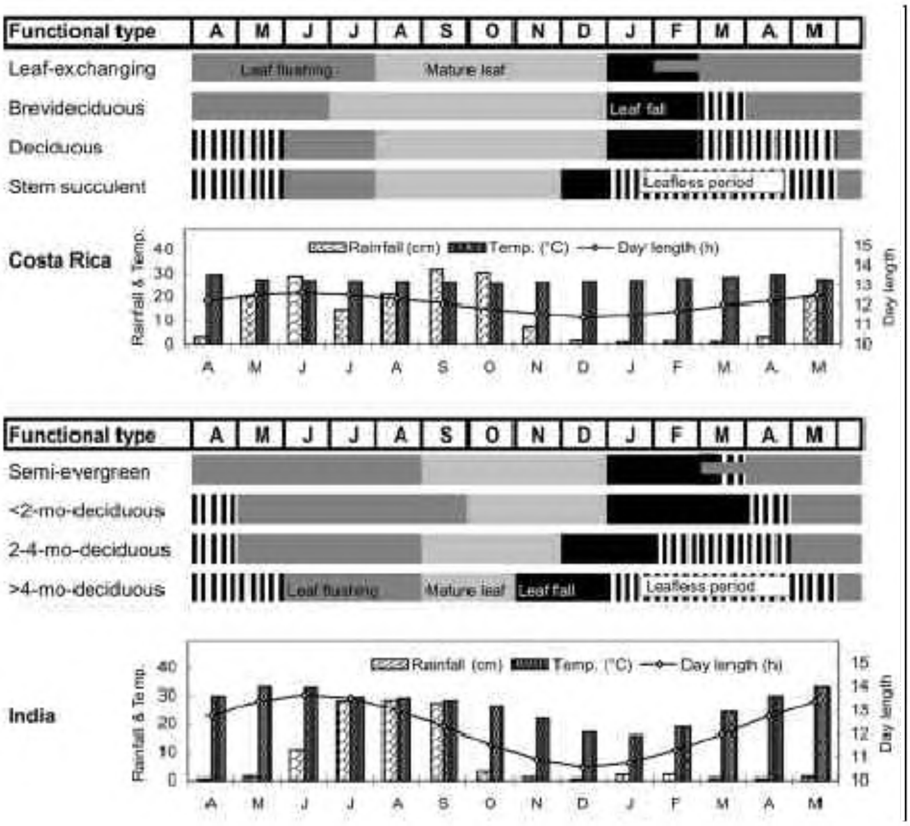

Figure 2. Leaf phenological events and duration of deciduousness in four major phenological functional types recognized in tropical dry forests of Costa Rica and India. Data source: Costa Rica, Rivera *et al.*[11]; Climate, Enquist and Leffler[74]; India, Kushwaha and Singh[5].

number of different plant functional types present in a community[17]. Identification of plant functional types and estimation of their abundance are useful in the evaluation of ecosystem functions[18]. Need for datasets of plant functional types has been emphasized by the International Geosphere Biosphere Programme, to evaluate and predict the nature of vegetation responses to future global change[19,20]. Leaf phenological variation has been considered as an important variable in distinguishing plant functional types[21,22].

Four major leaf phenological functional types, characterized by specific combinations of phenological features, seasonal variation in SWS, and structural properties affecting tree water relations have been recognized in dry tropical forests[3,11,12] (Figure 2, see Costa Rica). Ecological characteristics of these phenological functional types along with representative tree species are briefly enumerated below:

Leaf exchanging

Having long-lived coriaceous leaves and deep root systems, these tree species maintain relatively high water potentials (ψ-stem > –1 MPa) during the dry season, being confined to microsites with sub-soil water reserves[12]. These trees 'exchange leaves' because leaf-flushing usually occurs shortly before or immediately after the completion of leaf shedding during the early or mid dry season. In leaf-exchanging species, the time course of phenology is highly opportunistic and determined mainly by seasonal variation in the SWS at a given site[3]. In the seasonally dry rainforests of eastern Amazonia, maintenance of an evergreen canopy depends on the extensive utilization of sub-soil water reserves[23]. Examples are[3]: *Albizia guachapele* (Caesalpinaceae), *Hymenaea courbaril* (Caesalpinaceae), *Sideroxylon tempisque* (Sapotaceae), *Swietenia macrophylla* (Meliaceae) and *Thouinidium pentandrum* (Sapindaceae).

Brevideciduous

These species are similar in physiognomy, distribution and phenology to leaf-exchanging species; however, after a short period of deciduousness (a few days to several weeks) synchronous leaf-flushing occurs after mid-March[3]. During drought-induced leaf abscission, ψ-stem increases to high levels, indicating water absorption from sub-soil reserves by deep root systems[24]. Examples are[3]: *Cassia emarginata* (Caesalpinaceae), *Dalbergia retusa* (Fabaceae), *Diospy-*

ros nicaraguensis (Ebenaceae), *Guazuma ulmifolia* (Sterculiaceae) and *Chlorophora tinctoria* (Moraceae).

Deciduous

These trees have mesic leaves with low specific weight and water content, and often a shallow root system in association with generally high wood density[3]. They show high desiccation tolerance and during seasonal drought, leaf and stem water potentials decline to values far lower than those observed in other functional types. With increasing dryness of top soil and resultant sharp drop in stem and leaf water potentials during early dry season, strong desiccation causes the onset of leaf-fall. Deciduous species generally show large seasonal variations in trunk diameter[25] and formation of distinct annual rings[26]. Examples are[3]: *Chomelia spinosa* (Rubiaceae), *Cordia alliodora* (Boraginaceae), *Luehea candida* (Tiliaceae), *Randia* sp. (Rubiaceae) and *Tabebuia ochracea* (Bignoniaceae).

Deciduous stem succulent

Having shallow root systems and mesic leaves, these trees grow in very dry sites. Relatively short leaf lifespan assures rapid leaf-fall just following the cessation of rains (i.e. during early dry season) without being water-stressed (i.e. having high ψ-leaf). Stem succulents store large amounts of water (> 120% dry weight[27]) in the extensive parenchyma tissues of their trunks, resulting in relatively low density wood (< 0.5 g cm^{-3}). These trees maintain a high ψ-stem (>– 0.5 MPa) throughout the year, but remain leafless for several months[3]. In contrast to other deciduous and leaf-exchanging species, there is no evidence for the control of vegetative phenology by seasonal variation in SWS; rather their vegetative phenology seems to be adapted to maintain high SWS. In stem succulents, fine root proliferation into dry soil has been observed before the rainy season begins[10]. Examples are[3,28]: *Bombax malabaricum* (Bombacaceae), *Bursera simaruba* (Burseraceae), *Spondias purpurea* (Anacardiaceae), *Hildegardia barteri* (Sterculiaceae) and *Plumeria rubra* (Apocynaceae).

Several other leaf phenological functional types have been recognized, mostly by regrouping species from the four basic functional types. For example, the 'spring flushing type' (synchronous vegetative bud break induced by increasing photoperiod during spring[11]), which includes species earlier classified as brevideciduous (e.g. *D. retusa*, *C. emarginata*) and stem succulents (e.g. *B. malabaricum*, *B. simaruba*). 'Leaf exchanging evergreen' (showing emergence of young leaves during or immediately after leaf shedding in the early dry season, January–March) and 'brevideciduous spring flushing' (showing gradual leaf shedding in mid dry season and a short leafless period followed by synchronous vegetative bud break in March–April by increasing photoperiod) species have also been segregated[3].

Lack of uniform terminology

Currently, the terminology used to describe phenological functional types lacks uniformity. In most phenological studies, terminology varies with the investigator and the climatic conditions of the habitat studied. Table 1 lists, as examples, varying definitions/explanations of common leaf phenology-based functional types. It is apparent that:

1. The same phenomenon has been described by different terms, e.g. species with short leafless stage during the annual cycle has been variously termed as semi-evergreen[29], brevideciduous[12,30] or fully deciduous[31].
2. Same terms have been used to describe different phenological categories, e.g. brevideciduous for species maintaining > 50% canopy throughout the year[31] or for species having short leafless period[30].
3. Phenologically different species have been equated with each other, e.g. brevideciduous species equated with leaf-exchanging species[30,75].
4. Several contrasting criteria have been used to assign functional types, e.g. duration of deciduousness (brevideciduous[30]), triggering factor for vegetative bud break (spring flushing[11]), or SWS (stem succulents[3]).
5. The term deciduous (entire population becomes leafless, at least for a short period) has been unconsciously used, e.g. brevideciduous and semi-deciduous for species maintaining > 50 and 15–50% canopy respectively, throughout the year[31].
6. Quantitative connotation is lacking in the usage of the term 'deciduous', which has been commonly used to denote species in which leaves abscise in early dry season and bud break occurs after the first rains[12], or species remaining leafless for at least one month[32].

Deciduousness-based functional types

The use of deciduousness to classify functional types has become increasingly unsatisfactory, because every author uses deciduousness as it fits his particular forest. There is a need to standardize the terminology and incorporate, as far as possible, a quantitative perspective. A new way of expressing deciduousness, which has the advantage of being quantitative and applicable to all tropical deciduous forests, can be evolved using 'deciduous' in combination with the 'duration of leaflessness in months'. In seasonally dry tropics, where trees are characterized by functional traits like deciduousness (~ leaflessness) and drought tolerance, vegetative (leaf) phenology may be viewed from the broader perspective of a gradient of duration of deciduousness across tree species. Based on the precise extent of leafless period, leaf-flush duration, and leaf strategy index (leaf-flush rate/leaf-fall rate, reflecting rate of resource use and resource conservation), the co-existence of four tree functional types, including one semi-evergreen and three decidu-

Table 1. Various criteria used for definition of functional types based on leaf habits

Functional type	Definition(s)/description(s)
Evergreen	Species which maintain high level of canopy (> 75%) throughout the year[31]. Species which maintain at least 60% canopy throughout the year[32]. Species which flush new leaves constantly or on shoots while senescent leaves are shed. They never appear leafless during the entire year[11,30,75]. Species in which bud break of vegetative buds normally occurs during early or mid dry season, shortly before or immediately after completion of leaf shedding, i.e. trees exchange leaves[12].
Semi-evergreen	Species with a short deciduous stage[29]. Species which are hardly ever without green leaves, and if so only for a relatively short period[58,60]. Species in which individuals respond variously from leaf exchange or evergreenness to leaflessness or deciduousness, but show ≤ 1 year leaf lifespan[5,36].
Leaf-exchanging	New leaves emerge immediately after leaf abscission[11]. Young leaves emerge immediately after leaf shedding during the dry season[3].
Brevideciduous	Species showing seasonal decline in canopy, but canopy fullness remains >50% throughout the year[31]. Brevideciduous (leaf-exchanging) species shed their leaves synchronously and after remaining bare for a short period, leaf-flush follows immediately[30,75]. Species in which synchronous bud break of vegetative buds generally occurs after mid-March and is preceded by a period of deciduousness which varies from several weeks to a few days[12]. In brevideciduous species, after a brief leafless period, bud break is induced by increasing photoperiod[3].
Deciduous	Species in which leaves are shed early in the dry season followed by a strong dehydration of stems[30,75]. In these species, severely water-stressed leaves abscise during the early dry season. Rainfall exceeding 20–30 mm causes rapid rehydration and highly synchronous bud break in all leafless trees[11]. Leaves expand during early rainy season and are shed during the early dry season[3]. Leaf and stem water potentials decline to very low values during early dry season and leaves abscise. Bud break occur after the first rains[12]. Species in which every individual loses its leaves for a period of at least one month during dry season[32].
Fully deciduous	Species in which each individual loses its leaves for a period of at least one month during dry season[31].
Semideciduous	Species maintain relatively low canopy (15–50%) throughout the year[31].
Stem succulents	Leaves are shed at the end of the rainy season or early dry season and trunk rehydrates. Stem water allows flowering/fruiting during dry period[30,75]. After rapid leaf abscission during the early dry season, trees remain leafless for several months. During winter solstice and spring equinox, rain or irrigation does not induce bud break[11]. Leaves abscise soon after the end of the wet season, and trunk maintains high stem water potentials throughout the dry season. Bud break of vegetative bud is induced by increasing photoperiod[3,12].
Spring flushing	Species showing synchronous bud break induced by increasing photoperiod[11].

ous ones showing progressive increase in deciduousness has been demonstrated in the Vindhyan dry tropical forests[5]; out of eight deciduous species investigated, three were < 2-mo-deciduous, three 2–4-months-deciduous, and two > 4-mo-deciduous (~stem succulents) (Figure 2, see India). In these species, the leaf-flush duration decreases with increasing leaflessness. Significant positive relationship between the leaf strategy index and the leafless period of different species shows the adaptation of tree species to prolonged period of inactivity or low activity (when leafless) and variable resource use during the period of activity. It can be argued that in > 4-mo-deciduous trees, both resource exploitation and conservation are rapid as an adaptation to a short growing season (rainy season). However, semi-evergreen *Shorea robusta* (spring flushing), having deep roots, exploits resources at a slower rate, but conserves them at the end of the winter season for immediate leaf-flushing. In the Vindhyan region, the resource use rate decreases with decrease in deciduousness, in spite of the fact that all functional groups conserve resources at a rapid rate.

We have verified the ubiquitousness of deciduousness-based functional types with a large species dataset derived by us from the phenological notes included in silvicultural descriptions of over 100 Indian tropical trees by Troup[33]. Troup's notes provide approximate duration of some phenological events in these species over a wide range of habitats; hence, the duration of deciduousness has been estimated by implication (gap between reported leaf-fall and leaf-flush periods). Accordingly, we noticed that majority tree species (47%) were < 2-mo-deciduous, 18% were 2–4-mo-deciduous, 13% were > 4-mo-deciduous and 21% were leaf-exchanging. The trend of increasing deciduousness is also clearly evident in the four leaf functional types recognized in Costa Rica (Figure 2). Besides the duration of deciduousness, the linked phenotypic traits characterizing

Table 2. Proposed phenological tree functional types in tropical deciduous forests based on duration of leaflessness (deciduousness) and timing of vegetative bud break (leaf-flushing)

Functional type	Sub-type	Vegetative bud break Season[a]	Possible cue	Example
Leaf-exchanging[b]	Evergreen[c]	Early dry	Leaf fall	*Ficus bengalensis*
	Semi-evergreen[d]	Early dry	Leaf fall	*Shorea robusta*
< 2-mo-deciduous	Spring flushing	Mid dry	Increasing photoperiod	*Gmelina arborea*
	Summer flushing	Late dry	Increasing photoperiod/temperature	*Hardwickia binata*
	Rainy flushing	Early rainy	First significant rain	*Aegle marmelos*
2–4-mo-deciduous	Spring flushing	Mid dry	Increasing photoperiod	*Bombax malabaricum*
	Summer flushing	Late dry	Increasing photoperiod/temperature	*Lagerstroemia parviflora*
	Rainy flushing	Early rainy	First significant rain	*Tetrameles nudiflora*
> 4-mo-deciduous	Spring flushing	Mid dry	Increasing photoperiod	*Melia azedarach*
	Summer flushing	Late dry	Increasing photoperiod/temperature	*Lannea coromandelica*
	Rainy flushing	Early rainy	First significant rain	*Erythrina suberosa*

[a]Early dry season, cool dry; Mid dry season, warm dry; Late dry season, hot dry; Early rainy season, warm wet.
[b]Species showing leaf exchange.
[c]No leafless individual.
[d]Short leaflessness in some individuals.

the Vindhyan dry deciduous forest are leaf size, leaf texture and bark texture[34].

A phenological functional type classification for trees in the dry tropics is proposed in Table 2. This classification is based on the duration of deciduousness and timing of vegetative bud break. It is apparent that within the same range of deciduousness, bud break time and probable cue differ conspicuously.

Key phenological themes

Quantitative documentation of phenology involves periodical observations on marked trees having tagged branches/twigs. These observations include, among others, the dates of initiation and completion of phenological events (e.g. leaf-flush, flowering, fruiting). Phenological monitoring of adequate number (≥ 10) of conspecific trees in relation to seasonal variation in climate factors and daylength for 2–3 consecutive years or longer permits the determination of dates of phenological events, and more importantly the triggering factor(s) for leafing/flowering. Refinement of data quality is a prime requirement in order to evaluate the importance, benefit and limitations of phenological observations[35]. Interpretations of phenological patterns require methods that can transfer species data into useful information at the biome level, and generalize the results to broader geographic area[1]. Carefully designed experiments need to be set up on the key phenological themes discussed below.

Duration of deciduousness

The precise estimation of deciduousness (leaflessness) in tropical trees has been least attempted and no convenient categorization of deciduousness is available. As a result, self-contradictory reports have been made on leaf phenological nature of widely distributed dominant species[36]. Duration of deciduousness is the most reliable indicator of the severe drought experienced by different tree species, because it reflects an integrated effect of seasonal drought, tree characteristics and soil moisture conditions. It also denotes the time period during the annual cycle when resources (light, water, nutrients, etc.) are not being utilized or are being used at a minimum rate. Seasonally, dry forests are characterized by sudden increase (after rain onset) and by slow reduction (after rain cessation) in resource availability, but the growing period (reciprocal to leafless period) varies widely among tropical trees. Ecological differences arise among trees due to different ways of acquiring the same resource[37]. Nevertheless, phenological studies of tropical trees have largely ignored the ecological significance of the leafless period.

Wide range of leaflessness has been recorded in deciduous trees in India. In tree species of the Vindhyan dry deciduous forests, leaflessness varies widely from 3 weeks to 7 months[5]; this range may be compared with 1–3.5 mo leaflessness in Venezuela[8] and < 1–4 mo in Argentina[11]. It seems that in the tropical regions having long dry season, tree species are adapted in such a way that they can tolerate prolonged water stress, yet producing and maintaining leaves for longest duration. When water stress reaches the threshold, they shed their leaves rapidly to avoid water stress. Long leaflessness may strongly affect the water relations of trees, leading to selection of low density wood with greater water storage (as in the case of stem succulents).

Timing of vegetative bud break

Bud break of vegetative bud may be triggered by different control mechanisms, e.g. leaf-fall, first significant rainfall, or changes in photoperiod[11]. The triggering factor can be identified by careful observation of the timing, synchrony and inter-annual variation of bud break[38]. 'Spring flushing' induced by increasing photoperiod has been reported in several tree species in dry tropical forests in Argentina, Costa Rica, Java and Thailand and savanna in Brazil[11,39]. In the Vindhyan dry tropical region, deciduous tree species begin leaf-flushing during summer, the hot dry period (May–June), coinciding with maximum temperature (~ 40°C) attained about 4–8 weeks before the significant rains[5]. The tropical deciduous forests of Bandipur in South India, where the monsoon arrives about one and a half months earlier than in the Vindhyan region, also show leaf-flushing in deciduous species, including *Anogeissus latifolia* and *Lagerstroemia parviflora* common with the Vindhyan region, in the hot dry period (April–May) prior to the onset of rains[40]. In deciduous trees in the Indian dry tropics, flushing generally precedes the first significant rains by one to two months, suggesting their timing has been selected by the seasonal rainfall pattern. Houston[41] suggests that increasing day length after the spring equinox signals the approach of rainy season in the tropics. Seasonal changes in the photoperiod and thermoperiod are generally coupled, and their joint action may control growth rhythms of trees. The summer flushing enables tree species to activate canopy development before the monsoon rainfall begins, so as to make maximum use of the short rainy season for productivity. Predominant summer flushing in tropical trees in India raises the question: What is the proximal cause of vegetative bud break in dry, hot summer? In many leaf-exchanging species (e.g. *S. robusta*), flushing of new leaves during the early dry season is induced by fall of old leaves in response to the onset of drought[36]. In such species, the timing of the last significant rain, marking the beginning of the dry period, becomes indirectly important with respect to leaf-flushing.

Leaf strategy

Tree species adjusted to variable micro-habitat conditions often show differing leaf strategies. Leaf strategy primarily denotes adaptations in leaf dynamics controlling the ability of a tree species to exploit/utilize resources (e.g. water, nutrients, CO_2) in relation to its ability to conserve the same. While the magnitude of resource utilization may be related to duration and number/mass of leaves produced, the duration of leaf-fall and leaflessness has a bearing on resource conservation. Tree species showing different leafless periods (reciprocal to the growth period) exhibit substantial differences in their leafing (vegetative growth) pattern, as reflected by the leaf strategy index[5]. Species having leaf strategy index <0.5 show semi-evergreenness (leaf-exchange), and as the duration of deciduousness increases, the index proportionately increases above 0.5.

Various aspects of phenology are related to survival adaptation as well as capacity adaptation in trees. While survival adaptation refers to the ability of a tree to survive under unfavourable circumstances, capacity adaptation is related to features enabling the tree to use available resources effectively[42]. Tropical dry forest trees having varying leafless periods (survival adaptation, indicating the period of least activity) show variable leaf strategy indices (capacity adaptation, indicating rates of resource use and conservation). In tropical trees, survival adaptations are highly linked with capacity adaptation. It may be possible that changes in survival adaptation (e.g. duration of leafless period) will substantially change capacity adaptation (e.g. resource use rate). With respect to adaptations promoting nutrient conservation, dry tropical forest tree species show varying pre-litter-fall nutrient resorption abilities and efficient internal nutrient cycling[43]. The resorption ability, however, varies with leaf habit, generally being greater in deciduous species relative to evergreen ones[44].

Water relation patterns

Tropical dry region trees exhibit considerable diversity in seasonal water relations[45]. Interactions between water availability, tree structure and ecophysiological characteristics lead to varying phenological patterns[10]. Shallow-rooted species have access only to variable sub-surface soil water, but deep-rooted species have access to less variable soil water reserves and can maintain positive water balance throughout the dry season[46]. Rainfall occurring early in the season would first be experienced by species with relatively shallower roots. However, deep-rooted species would mainly benefit from rain percolating into deeper layers during the peak of the rainy season. Ultimately, initiation of growth at an early date would lead to earlier leaf expansion and a longer growing season. Trees in the dry tropics must survive 4 to 8 months long dry season by either avoiding (deciduous) or tolerating (evergreen) drought. Some deciduous tree species (e.g. fully deciduous of northern Australia[47]) show complete leaf-fall while water potentials are still high, whereas others (e.g. Venezuelan dry forest[48]) are severely dehydrated before leaf-fall.

Given the extent and diversity of dry tropical forests worldwide, there have been relatively few detailed studies of seasonal patterns of tree water status[13]. Few available tree water relation studies in the Indian subcontinent pertain to the Himalayan region[49–51] and the dry tropics is unexplored. Predominant summer flushing coupled with variable leafless periods in the Indian tropical trees raises several questions relating to water relations. For example: What is the diversity in water relations in different phenological tree functional types? What are seasonal relationships among climatic factors, tree water status and phenology in different tree functional types? How do different functional types rehydrate and leaf out during the dry season without rehydration of the top soil by rain? Long-term analysis of water relations in different tree functional types is essential for understanding relationships between tree growth and climatic variation.

Table 3. Characteristics of different flowering types in tropical dry deciduous forest at Hathinala in the Vindhyan region

Flowering type/time/species	Possible flowering cue	Vegetative phenology	Time lag[a] (mo)	Leafless period (day)	Fruiting duration (mo)
Deciduous species[b]					
Summer (March–June)	Increasing day length and temperature	Leaf-flushing	0.8	33	11
Rainy (June–August)	First significant rain	Leaf-flushing	1.3–2.7	18–78	7–9
Autumn (September–December)	Decreasing day length	End of leaf-flushing	4.2–4.5	62–69	6–7
Dry season (December–March)	Leaf-fall or winter rains	Leafless shoots	7.7–8.2	138–201	3–4
Semi-evergreen (leaf-exchanging) species[c]					
Winter (January–March)	Drought-induced leaf shedding	During and after leaf exchange	0	0	3–4

[a]Estimated time lag between first leaf flush and first visible flower.
[b]Deciduous species – Summer: *Diospyros melanoxylon*; Rainy: *Acacia catechu, Hardwickia binata, Lagerstroemia parviflora*; Autumn: *Anogeissus latifolia, Terminalia tomentosa*; Dry season: *Boswellia serrata, Lannea coromandelica.*
[c]Semi-evergreen species: *Shorea robusta*.

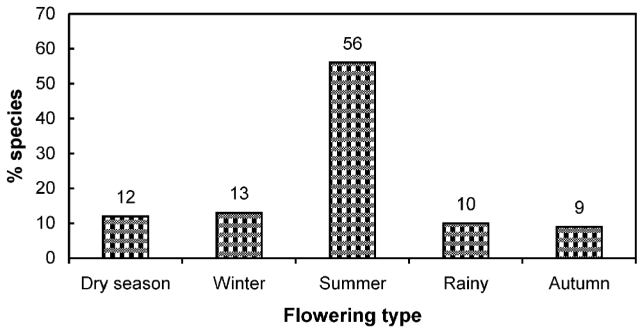

Figure 3. Proportion of five seasonal flowering types among Indian tropical trees (derived from Troup[33]).

Seasonal flowering types

Leafing and flowering phenophases are not mutually independent in woody species and flowering may be partly or wholly dependent on leafing activity[52]. Nevertheless, tree species having similar leaf phenological rhythms often differ in the timing of their flowering[53]. Like vegetative phenology, flowering phenology of trees is affected by the periodicity of rainfall and soil water availability. Variation in the timing of flower bud break relative to vegetative phenology in dry tropical trees results in several flowering types[38]. After seasonal growth has ended, flowering may be triggered by various environmental cues. In some species declining day length in autumn induces the highly synchronous development of lateral or terminal flowers during the late rainy season or early dry season[54]. In many deciduous species, flower buds formed during the growing season remain dormant until bud expansion and anthesis are triggered during the following dry season by rehydration of leafless twigs caused by leaf shedding, or exceptional dry season rain showers[12,55], or the first rain of the wet season[56]. In other species, increasing day length induces synchronous flowering during the late dry season between March and May, weeks/months before the first rains of the wet season[28].

In the Vindhyan tropical forests, the following five flowering types have been recorded (our unpublished work): summer flowering (probably induced by increasing day length and/or higher temperature), rainy flowering (induced by first significant rain), autumn flowering (induced by declining day length), winter and dry season flowering (induced by leaf-fall; Table 3). Interestingly, in deciduous trees, longer the leafless period, more delayed is the appearance of flowers (greater time lag between first-leaf-flush and first-visible-flower). Drought stress is not only reflected in terms of leafless period, but is also evident from the seasonal separation between the two phases. Various physiologically active sites or sinks (e.g. leaves and leaf buds, flowers and flower buds) usually compete for water, nutrients and metabolites within a tree, resulting in partitioning in time of plant functions like leafing and flowering. The temporal separation of leafing and flowering in deciduous species serves as an important adaptation to a strongly seasonal dry climate, where optimization of vegetative growth during the short growing season may be crucial for tree reproduction and survival.

Our synthesis of Troup's[33] notes on flowering period for 119 Indian tropical trees showed that summer flowering species were dominant (56% of total species), followed by winter flowering (13%), dry season flowering (12%), rainy flowering (10%) and autumn flowering species (9%) (Figure 3). Amongst Indian tropical trees, 81% species (winter, dry season and summer flowering species) flower during the dry period, when vegetative growth is at its minimum. In tropical deciduous forests in other parts of the world, the proportion of species flowering during the dry period (December–May) varies widely; e.g. Guanacaste (Costa Rica) 53%, Yucatan (Mexico) 54%, Jalisco (Mexico) 19% and Sonora (Mexico) 73% of total species[38]. In Sonora, having long dry season and short wet season, 45% species flower between mid March and May. Large fraction of species flowering during the dry season suggests the availability of water required for the growing organs; water availability, however, varies widely depending on rainfall patterns and soil conditions. The water requirement can be met by sporadic winter rains, water absorption from sub-soil water reserves (leaf-exchanging species) or stored stem water (stem succulents).

Different flowering types in the Vindhyan region are related to varying durations of fruiting phenophases, but all flowering types complete the fruiting phenophase during the late dry season before the onset of the succeeding rainy season, ensuring that some, if not all, seeds are available for germination when the soil is sufficiently moist (Table 3). In tropical dry forests fruit maturation and suitable conditions for dispersal are closely synchronized because of the pronounced differences of biotic and abiotic conditions between dry and rainy seasons[57]. Environmental characteristics affect flowering and fruiting either directly (e.g. through habitat conditions) or indirectly (e.g. through leafless period).

Asynchrony

Asynchrony[52], intra-species variability[58] or plasticity[53] in a species denotes the existence of individuals showing differing morphological, physiological and behavioural responses to environmental conditions. Trees display asynchrony to a wide variety of ecological conditions, including variations in the abiotic environment, disturbance, herbivory, identity of neighbours, etc. Tropical trees display varying behaviour from complete intra-specific synchrony to complete asynchrony[52]. Asynchrony helps in population maintenance and expansion[58], withstanding water stress[31], contributing to species becoming dominant[59], and promoting multi-species phenological diversity to face changing conditions[60]. It has been demonstrated that in dry forest conspecific asynchrony is guided by differences in water availability[39]. Tree size, greatly neglected in phenological studies in seasonally dry forests, may affect the pattern of leafing phenology through differing water use and rooting depths, and explain both inter- and intra-species asynchrony in the timing of leaf-flush[61]. Asynchrony in leaf phenological events in dominant tree species can have significant influence on several ecosystem functions (e.g. nutrient return from vegetation to soil, release of nutrients from decomposing litter) and adaptation of asynchronous leaf development may determine the distribution of species both within and across the forest stands[49].

Due to patchiness and inter-annual variation of rainfall at landscape level, tree species showing vegetative or flower bud break due to rain onset or leaf-fall are expected to exhibit high conspecific asynchrony. On the other hand, trees showing photoperiod-induced bud break are likely to be least asynchronous, as reported in equatorial forests[62]. As a corollary, quantification of asynchrony may help determine the bud break causal factor. Community-level studies in Indian tropical dry forests[40,63] and moist forests[64] suggest phenological asynchrony among tree species. Varying conspecific asynchrony for different phenological events has been recorded in tree species in dry tropical Vindhyan region[5,36].

Likely impact of climate change

Tropical trees are expected to respond variously to changes in rainfall and temperature, because they widely differ with respect to adaptations to drought and cues for bud break of vegetative and flower buds, rendering it difficult to generalize potential climate change impact on phenology. Probably, the climate change impact can be better assessed at the level of functional types based on the duration of deciduousness and timing of bud break. Global climate change may force variation in timing, duration and synchronization of phenological events (e.g. dates of initiation and completion of leaf-flush and leaf-fall and leafless period) in the tropical forests[65]. Trends of erratic precipitation and increasing temperature are likely to reduce the length of the growing season by affecting the timing of leaf-flush and leaf-fall and increasing the leafless period, though to varying extents in different functional types. The competition among species (or functional types) is likely to get modified, if their phenological behaviour is differently sensitive to environmental conditions[66]. Due to changed competitive relationships, the species composition of forests and possibly geographic range of species will change in the long run. Climate change forced deviations in the length of growing period and competition among species may alter the resource use patterns in different species. In the < 2-mo-deciduous, summer flushing and summer flowering trees, which are most abundant in India, bud break will be independent of rainfall patterns, but survival of young leaves and flowering and fruit setting may be affected adversely if the rainfall period is shifted. Variations in fruiting responses of trees, in Kibale National Park, Uganda, both at species and community levels, over a three decade period have been attributed to climate change[67].

The timing of leaf-flushing and flowering in species showing rain-induced bud break will vary greatly according to the onset of rainy season (earlier or delayed); this will affect the length of their growing season and the reproductive success. With respect to leaf-exchanging species, deviations in summer and/or winter rains may affect the timings of leaf exchange and flowering through drought-induced leaf-fall and depletion of sub-soil water reserves. Any marked delay in the onset of rains will expose relatively young leaves to prolonged severe drought, which in turn, may strongly reduce the leaf activity period. The direct effect of climate change on phenology may be less serious than the effect of changed phenology on pollinators and seed dispersal agents[2].

Drought during rainy season or rain spell during dry season may cause a shift in flushing and/or flowering. In seasonally dry forests of Gunacaste, Costa Rica, a 10 week long severe drought (caused by El-Nino) during the mid rainy season forced phenological deviations such as replacement of deciduous species leaves by new leaves during the rainy season and shortening of leaf lifespan, abscission of flower buds in some species, precocious leaf exchange in evergreen species during drought and recurrent flushing after drought. However, no notable change occurred in the phenology of spring flushing brevideciduous and stem succulent trees[3]. Experimental irrigation studies designed to alter the timing of early season rainfall have shown that some species differentially respond in terms of growth and/or phenology to change in the timing of soil wetting[68,69]. In Costa Rican forest, biweekly irrigation during pre-monsoon season induced three-month early leaf-flushing than those formed under natural conditions, and leaves of pre-monsoon irrigated trees attained three month longer lifespan[3].

Perspectives in India

Phenological stations

Phenological changes will probably be the most obvious short-term result of rapid climate change, and indications of shift in plant phenology in the boreal and temperate zones of the northern hemisphere have already been reported[70]. Differences in phenological responses of tree species to temperature change can have long-term consequences on their geographic distribution[71]. It is predicted that 1°C increase in mean air temperature is associated with an extension of growing season by about 5 days in Europe[72]. A five-decade long first-flowering-date analysis of 385 British plants, showed significant advancement of flowering date in many species as well as significant delay in others[73]. Most of the phenological data originating from last 4 to 5 decades predominantly reveal advancing of leaf-flush and flowering in Europe and North America by 1.2 to 3.8 days/decade on average[35]. To accurately monitor such changes, a systematic development of phenological data network on regional and global scales is required. International Phenological Gardens (IPGs) are parts of the phenological network in Europe, and presently about 50 IPGs across Europe record phenological observation from 23 species[72]. The UK government has included phenology in its climatic change indicators[35]. India being endowed with great variations in climate and vegetation urgently needs a phenological station network. The existing network of Biosphere Reserves, National Parks and Sanctuaries may be utilized for establishing phenological stations; and even meteorological data stations can also be considered for the purpose.

Future research needs

In the dry tropics, high functional diversity and multiple triggering factors for bud break (vegetative and flower) are major causes for weak synchronization of community-level phenological events with the onset of growth-suppressive seasonal drought or growth-promoting rainy season. Long-term quantitative documentation of phenological patterns in a tree species is required in a standardized way in the tropical regions to assess the range of variation within and between species, and to segregate them among functional types. The following major objectives may be pursued to understand the possible impact of climate change on phenology of Indian tropical trees: (a) to screen-out tree species into functional types based on deciduousness and triggering factors; (b) to evaluate the interrelationships between vegetative and reproductive phenological events; (c) to explore the cause(s) of vegetative and flower bud break in different species; (d) to model how different functional types interact with seasonal variation in climatic factors and soil moisture storage through their water relations and phenological events; (e) to examine functional wood anatomy and root systems in different functional types; (f) to evaluate the patterns of resource use and to establish the links among water relations, phenology and primary productivity. It is important to develop capabilities to detect and predict the impact of climate change on phenology of tropical trees. Thus, tropical tree phenology has emerged as an important focus for ecological research, not only because of its relevance to forest structure and functions, but more importantly due to its potential to address critical questions in global modelling, monitoring, and climate change.

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