



Leaf flushing during the dry season: the paradox of Asian monsoon forests

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ABSTRACT

Aim Most deciduous species of dry monsoon forests in Thailand and India form new leaves 1–2 months before the first monsoon rains, during the hottest and driest part of the year around the spring equinox. Here we identify the proximate causes of this characteristic and counterintuitive ‘spring-flushing’ of monsoon forest trees.

Location Trees of 20 species were observed in semi-deciduous dry monsoon forests of northern Thailand with a 5–6-month-long severe dry season and annual rainfall of 800–1500 mm. They were growing on dry ridges (dipterocarp–oak forest) or in moist gullies (mixed deciduous–evergreen forest) at 680–750 m altitude near Chiang Mai and in a dry lowland stand of *Shorea siamensis* in Uthai Thani province.

Methods Two novel methods were developed to analyse temporal and spatial variation in vegetative dry-season phenology indicative of differences in root access to subsoil water reserves.

Results Evergreen and leaf exchanging species at cool, moist sites leafed soon after partial leaf shedding in January–February. Drought-resistant dipterocarp species were evergreen at moist sites, deciduous at dry sites, and trees leafed soon after leaf shedding whenever subsoil water was available. Synchronous spring flushing of deciduous species around the spring equinox, as induced by increasing daylength, was common in Thailand’s dipterocarp–oak forest and appears to be prevalent in Indian dry monsoon forests of the Deccan peninsula with its deep, water-storing soils.

Main conclusions In all observed species leafing during the dry season relied on subsoil water reserves, which buffer trees against prolonged climatic drought. Implicitly, rainfall periodicity, i.e. climate, is not the principal determinant of vegetative tree phenology. The establishment of new foliage before the summer rains is likely to optimize photosynthetic gain in dry monsoon forests with a relatively short, wet growing season.

Keywords

Deciduousness, dipterocarp–oak forest, photoperiodic control, spring-flushing, tropical dry forests, tropical tree phenology.

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INTRODUCTION

Climate exerts a dominant control over the distribution of major vegetation types (Woodward, 1987). It should also determine the characteristic vegetative phenology of major forest types often used as indicators of climate (e.g. Koeppen’s classification of climate). Deciduous, semi-deciduous and evergreen tropical forests are considered to be indicators of the amount and annual distribution of rainfall (Walter, 1971) because seasonal variation in

tree water status constitutes a major determinant of tropical tree phenology (Borchert, 1994a; Borchert *et al.*, 2002). Severe water stress enhances the abscission of old leaves and prevents the expansion of new shoots and leaves. Increasing duration and severity of the dry season should therefore result in trees being leafless for progressively longer periods and, inversely, the duration of deciduousness among trees in a landscape should be an indicator of the duration of severe drought. In common usage, the term ‘deciduous’ is applied indiscriminately to tropical tree

species being leafless for just a few weeks or as long as 4–6 months. To enhance the value of deciduousness as a quantitative indicator of seasonal tree water stress, the normal duration of deciduousness in a species will be given here (e.g. 1–2-month deciduous or 3–5-month deciduous).

The dry monsoon forests of Thailand (deciduous dipterocarp forest, mixed deciduous-evergreen forests; Rundel & Boonpragob, 1995; Maxwell & Elliott, 2001) and the Indian semi-deciduous forests of the Deccan peninsula (Troup, 1921; Puri, 1969) compared here differ widely in species composition, but share two characteristic features. First, both receive > 90% of annual rainfall of 800–1500 mm during the 5-month-long monsoon season between June and October (Fig. 1). The following 6–7-month-long dry season is subdivided into a cool ‘winter’ season with relatively low temperatures and a hot ‘spring’ season with rapidly rising temperatures (Puri, 1969; Walter, 1971; Rundel & Boonpragob, 1995). Secondly, many deciduous species shed their leaves as late as February or March and, counter-intuitively, most leaf between March and May, during the hottest and driest period of the year, 1–2 months before the first monsoon rains (Fig. 1; Troup, 1921; Walter, 1971; Sukwong *et al.*, 1975; Prasad & Hegde, 1986; Bhat, 1992; Rundel & Boonpragob, 1995; Kushwaha & Singh, 2005). Other species, including the common, wide-ranging *Shorea robusta* (sal), exchange old for new leaves between January and March (Troup, 1921; Rundel & Boonpragob, 1995; Kushwaha & Singh, 2005). Consequently, leaf cover in Asian monsoon forests is maintained well beyond the duration of the rainy season.

If amount and seasonal distribution of rainfall were the major determinants of vegetative phenology, then most trees of Asian monsoon forests should shed their leaves during the early dry season, stand leafless for several months and leaf after the first monsoon rains, i.e. they should be 3–5-month deciduous, as observed in many species of Neotropical forests with a similar climate (Frankie *et al.*, 1974; Bullock & Solis-Magallanes, 1990; Borchert, 1994a). The paradox leaf flushing of monsoon forest trees during the late dry season raises several questions. (1) How can leafless, presumably water-stressed trees rehydrate and leaf during the dry season without rehydration of the topsoil by rain? (2) Which environmental trigger causes bud break between March and May, well before the arrival of the monsoon rains? (3) Is the phenology of monsoon forest trees indeed determined mainly by rainfall periodicity and hence predictable from climatic data — as suggested by Walter (1971) and others?

The principal internal and environmental controls of major patterns of vegetative phenology in seasonally dry Neotropical forests have been identified in recent eco-physiological studies (Fig. 2; Borchert, 2005). In general, increasing water stress during the early dry season causes abscission of ageing leaves (Borchert *et al.*, 2002). Leaf abscission and a high water potential of twigs are prerequisites for subsequent bud break and leaf expansion (Borchert, 1994a). Leaf flushing at different times during and after the dry season is caused by three different mechanisms characteristic of different ‘functional types’ to be described below (Fig. 2b–d). In this study, environmental control of vegetative phenology in monsoon forest species will be inferred from the observed timing, synchrony and inter-annual

variation of leafing assessed by a novel method (Methods; Rivera *et al.*, 2002).

The amount and seasonality of rainfall in dry monsoon forests near Chiang Mai in northern Thailand are similar to the rainfall pattern of a semi-deciduous forest analysed in Costa Rica (Fig. 2a; Borchert, 1994a, 2002). To compare the controls of vegetative phenology in these Asian and Neotropical monsoon forests and address the questions raised above, we analysed the phenological records of 19 species observed near Chiang Mai, and the variation of phenology with tree size and subsoil water availability among 123 *Shorea siamensis* trees in another Thai forest. We found the characteristic spring flushing of many deciduous monsoon forests species to be induced by increasing daylength and dependent on root access to subsoil water reserves.

TREE SPECIES AND FIELD SITES

Doi-Suthep National Park (DSNP), Chiang Mai, Thailand

The phenology of 128 trees representing 19 species (Table 1) was monitored along a transect at 650–780 m altitude in the Doi-Suthep National Park near Chiang Mai in northern Thailand (19° N, 99° E; Elliott *et al.*, 1989; 1994). Tree species will be referred to by generic name except for the two genera with more than one species (*Dipterocarpus*, *Shorea*). The site is heavily dissected into steep gullies with mixed deciduous-evergreen forest and narrow, well-drained ridges with deciduous dipterocarp-oak forest (Rundel & Boonpragob, 1995; Maxwell & Elliott, 2001). Base rocks are mostly granitic and soils are generally deep and highly weathered. The area has a typical monsoon climate (Figs 1 and 2). Mean annual rainfall was 1120 mm during the study period. In the observed transect, temperatures are 2–3 °C lower and rainfall is probably 15–20% higher than at Chiang Mai Airport (312 m altitude, 4.5 km from the study site), where climate was recorded (Elliott, pers. obs.). For measurement of soil water content, triplicate soil samples were collected at 0–20 cm depth during each monthly phenology observation and later dried for 2 days at 120 °C.

Huai Kha Khaeng Wildlife Sanctuary (HKK), Uthai Thani Province, Thailand

The vegetative phenology of 123 *Shorea siamensis* Miqu. var. *siamensis* trees was observed in a nearly mono-specific 50 × 50-m plot in the Huai Kha Khaeng Wildlife Sanctuary, Uthai Thani Province in central Thailand (15° N, 100° E). The plot slopes slightly from 42 to 50 m elevation and an ephemeral stream bed cuts through its upper half (see Fig. 7 in Results below). Rainfall was measured at the Kapook Kapiang Ranger Station 4 km from the plot.

Functional tree types (Borchert, 2005)

The following patterns of vegetative phenology (functional types) were identified in Neotropical and Asian monsoon forests.

Table 1 Tree species of Doi Suthep National Park, Chiang Mai, Thailand, sorted by functional type (see Fig. 2; Results). Habitats: do, deciduous dipterocarp–oak forest; md, mixed deciduous–evergreen forest (Elliott *et al.*, 1994; Maxwell & Elliott, 2001). Leaf phenology at lower elevations: d, deciduous; e, evergreen

Species	Family	Number of trees	Habitat	Leaf phenology	Fig.
Deciduous, rain-induced					
<i>Antidesma acidum</i> Retz.	Euphorbiaceae	5	md	d	3, 4a, 5
Spring-flushing					
<i>Colona flagrocarpa</i> (Cl.) Craib	Tiliaceae	5	do, md	d	4b, 5
<i>Dalbergia cultrata</i> Grah. ex Bth.	Fabaceae	6	do, md	d	4d, 5
<i>Quercus kerrii</i> Craib var. <i>kerrii</i>	Fagaceae	10	do	d	4e, 5
<i>Shorea obtusa</i> Wall. ex Bl.	Dipterocarpaceae	6	do	d	4f, 5
<i>Terminalia mucronata</i> Craib & Hutch.	Combretaceae	6	md	d	4c, 5
Irregularly leaf-exchanging					
<i>Craibiodendron stellatum</i> (Pierre) W.W. Sm.	Ericaceae	5	do	d	4j, 5
<i>Dipterocarpus obtusifolius</i> Teijsm. ex Miq.	Dipterocarpaceae	12	do	d	4k, 5
<i>Dipterocarpus tuberculatus</i> Roxb.	Dipterocarpaceae	6	do	d	5
Leaf-exchanging					
<i>Anneslea fragrans</i> Wall.	Theaceae	7	do	e	4i, 5
<i>Aporusa villosa</i> (Lindl.) Baill.	Euphorbiaceae	7	do	d	5
<i>Eugenia albiflora</i> Duth. ex Kurz	Myrtaceae	5	md	e	4h, 5
<i>Metadina trichotoma</i> (Zoll. & Mor.) Bakh.f.	Rubiaceae	7	md	d	5
<i>Tristaniopsis burmanica</i> (Griff.) Wils. & Watt.	Myrtaceae	10	do	e	4g, 5
Evergreen					
<i>Castanopsis diversifolia</i> King ex. Hk.f.	Fagaceae	6	md	e	
<i>Ilex umbellulata</i> (Wall.) Loesn.	Aquifoliaceae	5	md	e	
<i>Lithocarpus sootepensis</i> (Craib) A. Camus	Fagaceae	6	md	e	
<i>Rothmannia sootepensis</i> (Craib) Brem.	Rubiaceae	5	md	e	5
<i>Wendlandia tinctoria</i> (Roxb.) D.C.	Rubiaceae	9	do, md	e	4l, 5

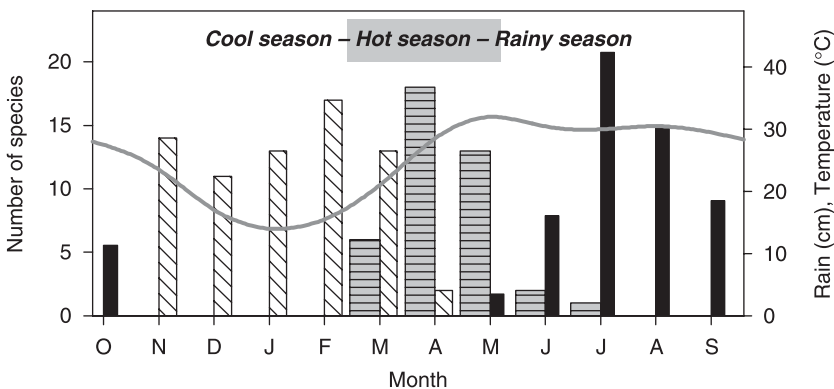


Figure 1 Rainfall periodicity and tree phenology in Indian dry monsoon forests. Information on the beginning of leaf flushing (horizontal hatching) and leaf abscission (diagonal hatching) was obtained for 81 species of the Deccan peninsula from descriptions of phenology in Troup (1921). Rainfall (black bars) and temperature (curve) are for Varanasi, India (Kushwaha & Singh, 2005).

Leaf-exchanging species are restricted to moist sites and remain well hydrated during the dry season. Shedding of old leaves during the early dry season is accompanied or immediately followed by bud break and expansion of new leaves (Fig. 2d, January/February, arrow; Williams *et al.*, 1997). As in *Shorea robusta*, leaf exchange generally occurs during the early dry season, but its timing varies widely among conspecific trees with soil water availability and between years with the time of the last major rains of the wet season (Rivera *et al.*, 2002; Borchert *et al.*, 2005; Singh & Kushwaha, 2005).

Deciduous species dehydrate strongly during the early dry season and remain leafless for 3–5 months (3–5-month deciduous).

The first wet season rainfalls of > 20–30 mm result in rapid re-hydration and synchronous bud break of all conspecific trees at a microsite (Fig. 2b, May/June, arrow; Borchert, 1994b). The variability and patchiness of the rainfall causes large variation in the timing of leafing between years and among trees at different microsites in a landscape. The opportunistic phenology of leaf-exchanging and 3–5-month deciduous species is determined mainly by seasonal variation in tree water status at a given site and trees will leaf whenever they are leafless and fully hydrated.

Leafing of *spring-flushing species* around the spring equinox, well before the first monsoon rains, is induced by increasing daylength (Fig. 2c, March/April arrow; Rivera *et al.*, 2002). It is

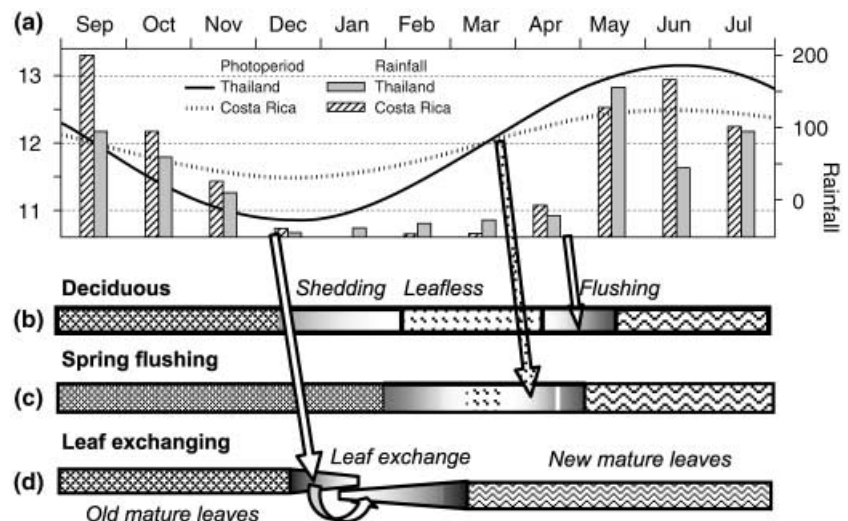


Figure 2 Seasonal variation in rainfall and daylength (a) in a Neotropical semi-deciduous forest in Guanacaste, Costa Rica (10° N) and in a dry monsoon forest near Chiang Mai, Thailand (19° N). Vegetative phenology (b–d) in Neotropical trees of three functional types. Arrows indicate the causes of vegetative bud break during the dry season: (b) the first heavy rains of the wet season; (c) increasing daylength around the spring equinox; (d) drought-induced leaf shedding.

highly synchronous among all conspecific trees in a landscape and varies minimally between years.

METHODS

Analysis of phenological patterns observed at DSNP

Tree phenology in DSNP was observed monthly from December 1988 to December 1991. Each of four stages of vegetative phenology (leafless; young, light-green leaves; mature, dark-green leaves; senescent, brown leaves) was scored on a scale of 0–4 (0, phenological stage not observed; 4, phenological stage at its maximum; Elliott *et al.*, 1994) and recorded in a spreadsheet.

Species-specific timing, synchrony and inter-annual variation in leaf flushing among conspecific trees are essential for the identification of functional types (Rivera *et al.*, 2002) and for inter-specific comparisons of vegetative phenology. To identify these variables, the recorded phenological observations were analysed as follows. The sequence of phenophases during three observation years was obtained for each tree by sorting phenological records by tree number and date, subdividing them into four-column data sets and then transposing them into rows (Fig. 3a). Missing phenophases were inferred from the timing of the next phase (e.g. flushing of young leaves precedes the increase in mature leaves) and added to the record. Mean monthly phenology scores for all conspecific trees were calculated to characterize synchrony of leafing within the same year (Fig. 3b). For the evaluation of interannual variation, 3-year means of phenology scores were calculated (Fig. 3c) and graphed for each species (Fig. 4a).

Synchronous leaf exchange generally lasted less than 2–3 months and several species were leafless or had young leaves for only 2–3 weeks. At monthly observation frequency these phenophases were observed only once or not at all. Phenological patterns are therefore characterized more by the time sequence of phenophases than by changing values of phenology scores (Figs 3b,c and 4). Distinct minima of mature leaf scores

accompanied by peaks for leaflessness and young leaves indicate deciduousness and strong synchrony of leaf flushing among conspecific trees (Fig. 4a–f). Consistently low scores for young leaves and leaflessness may indicate very brief periods of partial deciduousness (Fig. 4l) or large variation in deciduousness among trees and between years (Figs 4j,k; 5, *Dipterocarpus tuberculatus*; Fig. 6). Inter-specific variation in deciduousness (Fig. 5) was quantified by counting months without leaves and with full leaf cover (mature leaf scores of < 1 and > 3, respectively) in the records of conspecific trees (Fig. 3a).

Phenology at HKK as a function of tree size and topography

Diameter at breast height (d.b.h.), location (x_i, y_i) and elevation were measured for 123 *Shorea siamensis* trees of a 50 × 50-m experimental plot in HKK. During leafing in spring 1998 and leaf shedding in early 1999, vegetative phenology was scored as percentage of crown fullness. The effects of tree size and topography on leaf flushing before the first rains in 1998 were quantified by calculating distances between each tree (x_i, y_i) and all points along the creek (x_c, y_c) as $d = [(x_i - x_c)^2 + (y_i - y_c)^2]^{-2}$ and selecting the smallest d for each tree. Trees were sorted into three size classes (6–15, 15–24, 24–56 cm d.b.h.) and classified according to their vegetative phenology as ‘flushing’ (crown cover 20–100%) or ‘dormant’ (crown cover 0%). Trees with a crown cover of 10% were ignored. For each size class, means and standard errors were calculated for the fractions of flushing vs. dormant trees, distances from the creek bed and changes in leaf cover during flushing and leaf shedding.

RESULTS

Synchronous leaf flushing of all *Antidesma* trees was triggered by the increase in soil water after the first monsoon rains, as indicated by the 1-month difference in leafing time between 1989 and 1990 (Fig. 3b, frames; high soil water in March 1990 indicates

(a) **Phenology of two individual *Antidesma* trees during 2 years**

		1989												1990																
month		J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D					
Tree #1	M	4	3			1	4	4	4	4	4	4	4	3	3			4	4	4	4	4	4	4	3					
	S	1	1			leaf senescence												1	1	1										
	B		1	4	4										1	4	4									1				
	Y					1												1	1											
Tree #2	M	mature leaves												3				4	4	3	4	4	4	4	4	4				
	S	1	1											1	1	1					1	1	1							
	B		3	4	4									1	4	4														
	Y					1												4				1								

(b) **Means for 5 trees**

M	2	3			1	3	4	4	4	4	4	4	4	3	3			4	4	4	4	4	4	3	4	
S	2	1										1	1	1	1	1	1				1	1	1	1	1	
B	1	3	4	4			2	1	1	1	1			2	2	4	4	3	1						2	2
Y					2	1												2	1		1		1			
Rainfall (cm mo ⁻¹)	3	24	12	19	24	19	16	4	0	0	4	3	2	28	5	11	18	16	13	16	0					
Soil water (10 mg g ⁻¹)	3	19	11	23	20	24	25	9	7	4	7	17	3	15	9	22	19	21	11	19	8					

(c) **3-year means for 5 trees**

M	2	2			2	4	4	4	4	4	3	4
S	1	1	1					1	1	1	1	1
B	2	3	4	4	2	3	1	1	1	1	2	2
Y					2	2	1	1		1		1

Figure 3 Identification of synchronous bud break among conspecific trees of the deciduous species *Antidesma acidum* in a mixed deciduous–evergreen forest near Chiang Mai, Thailand. (a) Seasonal development of two individual trees over 2 consecutive years. Framed scores — new leaf flush. (b) Mean phenology scores for five trees over 2 years. (c) Mean phenology scores for five trees over 3 years (December 1988–December 1991). For explanations see Methods. Phenological stages: M, mature leaves; S, senescent leaves; B, bare, leafless; Y, young light-green leaves. Grey bars indicate the time of spring-flushing induced by increasing daylength.

rainfall not recorded at the Chiang Mai airport). *Antidesma* is the only *deciduous species* with rain-induced leafing and a leafless period of 3–5 months among the 19 tree species monitored at DSNP (Figs 3–5).

At the altitude of the observed transect, deciduousness varies widely among the five *spring-flushing species* (Figs 4b–f and 5), which at lower elevations are 1–3-month deciduous. These species leafed each year synchronously in March/April, well before the first monsoon rains (Fig. 4b–f). In the five *leaf-exchanging species*, moderately synchronous leaf flushing in January/February was preceded and hence probably caused by the shedding of many old leaves (Figs 4g–i and 5; Williams *et al.*, 1997; Borchert, 2000). As in many Neotropical leaf-exchanging species, early monsoon rains in May/June triggered a minor second leaf flush (Fig. 4g,i, filled circle in May/June). In the five *evergreen species* (Table 1), there was almost no discernable seasonality of vegetative development (Fig. 4l), i.e. old leaves were apparently replaced throughout the year.

In *D. obtusifolius*, *D. tuberculatus* and *Craibiodendron*, 3-year mean phenology scores show low levels of mature leaves, deciduousness and new leaves throughout the year (Figs 4j,k and 5). Phenological records of individual trees in these species indicate that throughout the year some branches were leafing while others shed old leaves or were leafless (Fig. 6). Thus, in contrast to the other deciduous species, seasonal development at higher elevations was asynchronous within the crowns of these species. Most leaf flushes were preceded by a distinct decline in the fraction of mature leaves, i.e. irregular leaf shedding caused leaf flushing unrelated to climatic seasonality (Fig. 6).

To assess the crucial role of subsoil water reserves in dry-season flushing, we monitored the vegetative phenology of 123 *Shorea siamensis* trees of different size classes growing at HKK on

a gentle slope transected by an ephemeral stream bed, the probable location of the largest subsoil water reserves (Fig. 7). In mid-March 1998, 2 weeks before the first monsoon rains, the fractions of flushing (20–100% crown cover) and dormant trees were, respectively, correlated directly and inversely with tree size (Fig. 8a, symbols). Small trees had formed new leaves only when growing within 2 m of the creek bed (Fig. 7). The mean distance of small flushing trees from the creek bed was therefore one-third that of dormant trees, but the difference between distances of large flushing and dormant trees was relatively small (Fig. 8a, bars). Two weeks before the first rains, the largest trees (> 24 cm d.b.h.) had expanded most of their new leaves, but in medium-sized trees leaf cover was only approximately 20% (Fig. 8b left, circles, squares); leaf buds had just begun to expand in about half of the many small trees with d.b.h. < 15 cm (Fig. 7), in which rapid leaf expansion started immediately after the first rains (Fig. 8b, triangles). During the following dry season, trees of all size classes shed leaves at the same rate (Fig. 8b right).

DISCUSSION

Control of vegetative phenology in Thailand and India

At the altitude of the observed transect in DSNP (650–780 m) the transition from deciduous to evergreen phenology is more gradual than at lower elevations (Fig. 5), but the environmental and endogenous controls of vegetative phenology (Fig. 2) can be deduced reliably from timing and synchrony of the phenophases established by the novel analysis of phenological records (Figs 3 and 4; Methods). Distinct minima in mature leaf scores followed by maxima for young leaves in the 3-year mean phenological scores indicate synchronous leaf shedding and flushing of

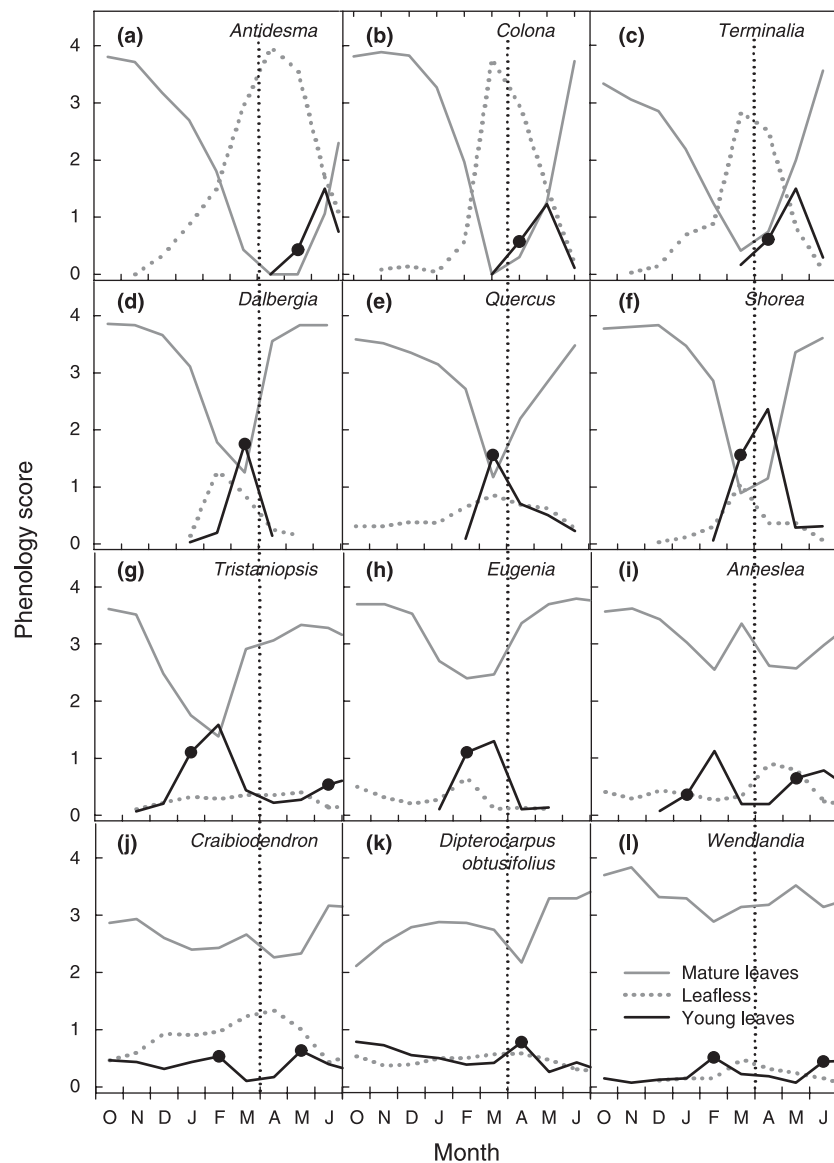


Figure 4 Three-year mean scores of vegetative phenology (see Fig. 3c) for 12 tree species of five functional types observed in Doi Suthep National Park near Chiang Mai, Thailand. Filled circles indicate the first distinct increase in the formation of young leaves, i.e. the start of leafing. (a) Deciduous species: flushing induced by the first heavy monsoon rains after the spring equinox. (b–f) Spring-flushing species: synchronous flushing induced by increasing daylength at the same time each year around the spring equinox (March/April, dotted vertical lines). (g–i) Leaf-exchanging species: flushing induced during the early dry season (January/February) by partial leaf-shedding. Early monsoon rains (May/June) may induce a second flush (filled circles in May/June). (j–k) Irregularly leaf-exchanging species: leaf-shedding and flushing vary widely among trees and between years (compare with Fig. 6). (l) Evergreen species.

conspecific trees at species-specific times with low interannual variation (Fig. 4a–h, filled circles). Such regular patterns of phenology are controlled by seasonal variation in environmental factors (Fig. 2). In contrast, the absence of distinct maxima or minima for these phenophases indicates that the replacement of old by young leaves is determined mainly by endogenous factors such as leaf ageing (Fig. 4i–l).

Antidesma is the only deciduous species with rain-induced leafing, because leafing time varied with the first monsoon rains (Fig. 3b). Highly synchronous leafing of ‘spring-flushing’ species at DSNP and in the majority of deciduous tree species in Indian monsoon forests (Fig. 1; Kushwaha & Singh, 2005) occurs every year around the spring equinox, well before the first monsoon rains (Fig. 4b–f); it is therefore induced by increasing daylength (Rivera *et al.*, 2002).

At lower elevations of DSNP, spring-flushing species of the dipterocarp–oak forest are leafless between late January

and March (2–3 months deciduous; Elliott *et al.*, 1994; Maxwell & Elliott, 2001), i.e. deciduousness is similar to that observed in Indian dry monsoon forests of the Deccan Peninsula (Fig. 1; Troup, 1921; Kushwaha & Singh, 2005). Increasing deciduousness with decreasing altitude has been also described for the Neotropical *Erythrina poeppigiana* and *Tabebuia rosea* (Borchert, 1991).

Differences in phenology between Asian and Neotropical monsoon forests

The amount and seasonal distributions of rainfall are similar in the monsoon forests of northern Thailand and Costa Rica (Fig. 2a), yet the fractions of evergreen vs. deciduous species vary widely between these forests (Table 2; Rundel & Boonpragob, 1995). The low degree of deciduousness in DSNP indicates that water stress during the dry season is distinctly lower than in

Table 2 Fraction of species of three major functional types in a Neotropical semi-deciduous forest (Costa Rica: Frankie *et al.*, 1974) and in three Asian monsoon forests (India: *Troup, 1921; †Kushwaha & Singh, 2005; Thailand: this study). At all sites > 90% of annual rainfall of 800–1600 mm is received during the wet season between May/June and October/November

Functional type	Costa Rica		India*		India†		Thailand	
	species	%	species	%	species	%	species	%
3–6 month deciduous	38	41	23	23	2	22	1	5
Spring-flushing	32	34	62	63	6	67	8	42
Leaf-exchanging: evergreen	23	25	13	13	1	11	10	53
Species total	93		98		9		19	

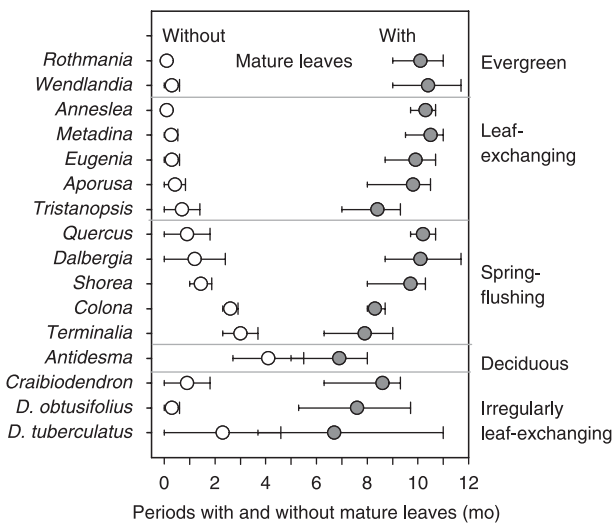


Figure 5 Variations in deciduousness (period with mature leaf score < 1) and full crown cover (period with mature leaf score > 3) among 16 species of five functional types in Doi Suthep National Park near Chiang Mai, Thailand.

Costa Rica. This probably has two main causes. First, because of higher latitude (19 vs. 10° N) and altitude (600,800 m vs. 40 m), temperatures and hence evaporative water loss are substantially lower at DSNP than in lowland Costa Rica during the early dry season (22–24 °C vs. 28 °C). Secondly, subsoil water storage is likely to be larger in the deeply weathered soils at DSNP than at the prevailing dry upland sites in Costa Rica.

Tree phenology at lower elevations of DSNP and in Indian monsoon forests is intermediate between that described here (Fig. 4) and observed in Costa Rica (Table 2; Fig. 2). The majority of Indian tree species leaf during the late dry season before the arrival of the monsoon rains (Table 2; Fig. 1), indicating that substantial subsoil water storage in old, deeply weathered soils permits spring-flushing during the late dry season.

Soil water reserves and spring flushing

The dramatic variation in the time of leafing with tree size and topography among *Shorea siamensis* trees at HKK (Figs 7 and 8)

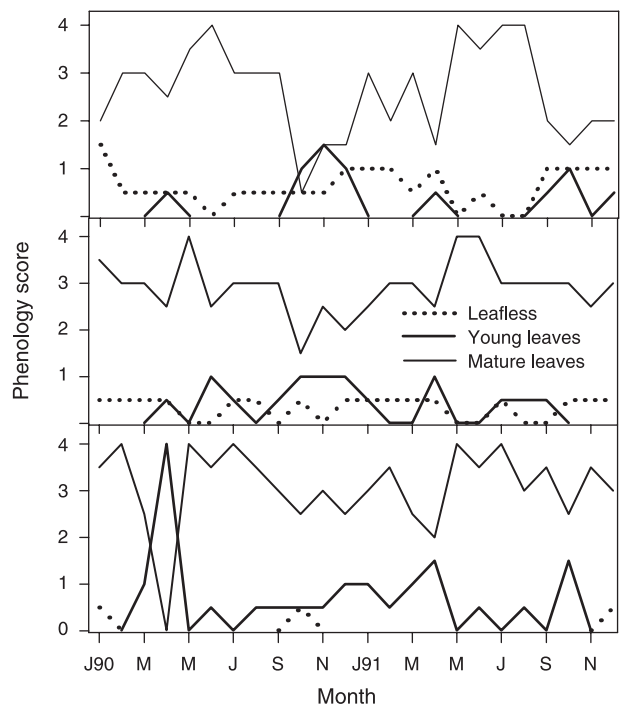


Figure 6 Seasonal variation of vegetative phenology in three *Dipterocarpus obtusifolius* trees in Doi Suthep National Park near Chiang Mai, Thailand.

constitutes the first quantitative assessment of the crucial role of subsoil water reserves for leaf expansion during the dry season. Different rates of leafing indicate that near the dry creek bed subsoil water reserves were accessible by trees of all sizes, but at uphill sites they were within the reach of large, deep-rooted trees only (Figs 7 and 8a). The rapid increase in leaf cover of small trees within a week after the first rains (Fig. 8b, week 13) indicates that growth of non-dormant buds had been inhibited by water stress and resumed immediately after rehydration. Leaf abscission was independent of subsoil water reserves (Fig. 8b, 1999) and was probably caused by increasing leaf water stress in ageing leaves (Borchert *et al.*, 2002).

The effect of tree size, topography and soil quality on dry-season phenology depending on subsoil water reserves has been

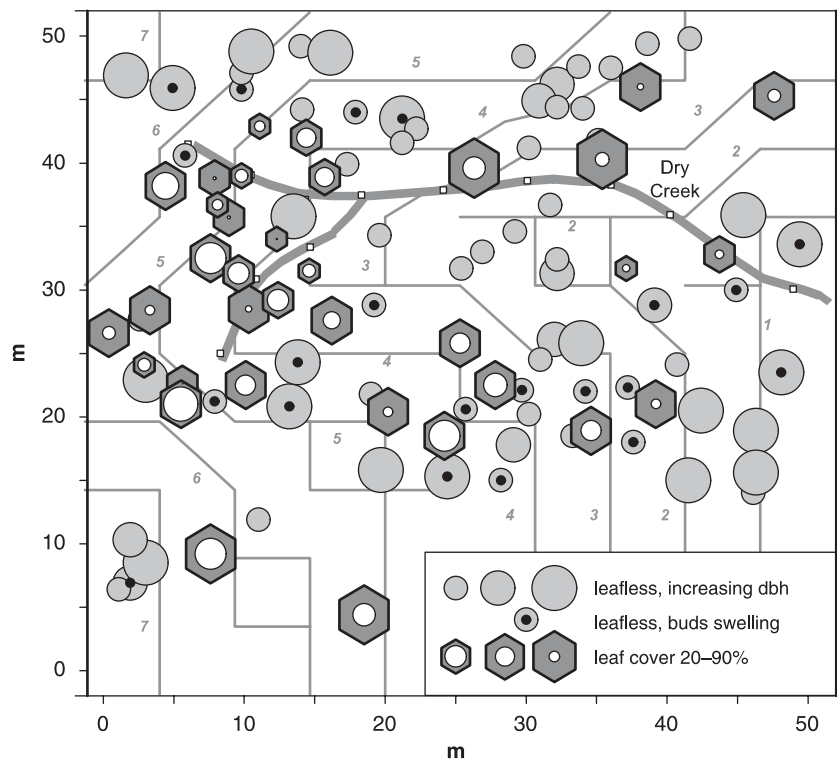


Figure 7 Distribution, size and leaf cover of 123 *Shorea siamensis* trees observed in mid-March 1998, 2 weeks before the first rainfall of the wet season. The 50 × 50-m experimental plot at the Huai Kha Khaeng Wildlife Sanctuary in central Thailand is slightly sloped and crossed by a dry creek bed (thick grey line with squares to calculate distances of trees from the creek bed). Numbers on straight grey contour lines give elevation in m above the lowest point at right. Diameters and tree numbers (in parentheses) in the four size classes shown are: 6–13 cm (32); < 17 cm (29); < 22 cm (34); 23–56 cm (28).

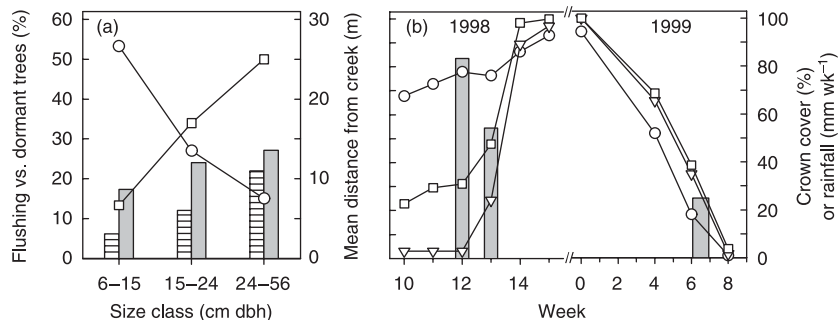


Figure 8 Variation of vegetative phenology in 123 *Shorea siamea* trees with tree size and topography at the Huai Kha Khaeng Wildlife Sanctuary in central Thailand (see Fig. 7). (a) Size-dependent fraction of flushing (squares) and dormant trees (circles) and their mean distance from the creek bed (flushing trees, hatched bars; dormant trees, grey bars). (b) Leaf flushing before (weeks 10–12) and after the first rainfall (bars) in week 12 of 1998 (left) and leaf shedding during the mid-dry season in 1999 (right). Mean d.b.h. and fraction of all trees for the three experimental groups are 25.5 cm (14%, circles), 19 cm (15%, squares) and 16.7 cm (71%, triangles). Standard errors of all means for crown cover, d.b.h. and distances from creek are < 0.1 (not shown).

observed elsewhere (Sayer & Newbery, 2003; Borchert *et al.*, 2004). It is particularly well documented for the life history of *Shorea robusta*. During the monsoon season *Shorea* seedlings grow well in a variety of soils; during the dry season those on sandy riverbanks usually die, whereas those on sandy loam survive, but die back regularly until they have developed deep roots (Troup, 1921). The vegetative phenology of mature trees varies with topography from evergreen to 1-month deciduous (Singh & Kushwaha, 2005). During consecutive years of severe drought, mortality is low at moist sites with deep sandy loams and high at

relatively dry sites (Troup, 1921; Seth *et al.*, 1960; Borchert, 1998). Deep-rooted trees of evergreen forests in eastern Amazonia maintain full leaf cover during exceptional drought by extracting > 500 mm water from a potential reservoir of > 800 mm of plant-available water (Nepstad *et al.*, 1994).

The opportunistic phenology of other drought-resistant dipterocarp species also appears to be determined by tree water balance during the dry season. Trees exchanged leaves irregularly at higher elevations with moderate water loss (Fig. 6), but were 1–3-month deciduous at lower elevations, where

they leafed whenever their water balance became positive (Fig. 8b, left).

Adaptive significance of spring flushing

In India and Thailand, increasing daylength after the spring equinox signals the approach of the monsoon season. Induction of leaf flushing by increasing daylength assures that a full complement of young, photosynthetically competent leaves is in place when the monsoon rains begin, yet precludes prolonged exposure of young leaves to severe drought. The predominance of spring-flushing species among Indian monsoon forest trees (Table 2; Fig. 1; Kushwaha & Singh, 2005) suggests that this phenological strategy is particularly advantageous, probably because it optimizes use of large subsoil water reserves for photosynthetic activity during seasonal drought and thus extends the relatively short, wet growing season. The characteristic phenology of spring-flushing species is controlled mainly by two non-climatic environmental variables, water storage in deep soils and photo-periodic induction of leafing, which also determine tree phenology in other tropical dry forest species around the globe (Borchert, 1994a; Rivera *et al.*, 2002).

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