

Guillermo Rivera · Stephen Elliott · Linda S. Caldas
Guillermo Nicolossi · Vera T. R. Coradin
Rolf Borchert

Increasing day-length induces spring flushing of tropical dry forest trees in the absence of rain

Received: 10 September 2001 / Accepted: 26 March 2002 / Published online: 20 July 2002
© Springer-Verlag 2002

Abstract In many conspecific trees of >50 species highly synchronous bud break with low inter-annual variation was observed during the late dry season, around the spring equinox, in semideciduous tropical forests of Argentina, Costa Rica, Java and Thailand and in tropical savannas of Central Brazil. Bud break was 6 months out of phase between the northern and southern hemispheres and started about 1 month earlier in the subtropics than at lower latitudes. These observations indicate that “spring flushing”, i.e., synchronous bud break around the spring equinox and weeks before the first rains of the wet season, is induced by an increase in photoperiod of 30 min or less. Spring flushing is common in semideciduous forests characterized by a 4–6 month dry season and annual rainfall of 800–1,500 mm, but rare in neotropical forests with a shorter dry season or lower annual precipitation. Establishment of new foliage shortly before the wet growing season is likely to optimize photo-

synthetic gain in tropical forests with a relatively short growing season.

Keywords Bud break · Phenology · Photoperiodic control · Tropical semideciduous forests

Introduction

In cold-temperate forests, vegetative phenology of all broad-leaved trees is strongly synchronized by winter cold. In contrast, severe seasonal drought does not synchronize vegetative phenology in tropical semideciduous forests with a dry season of 4–6 months and annual rainfall between 800 and 1,500 mm. Such forests generally constitute mosaics of trees of different functional types, in which bud break and flushing occur at different times during and after the dry season (Fig. 1; Borchert 1994a, b; Borchert et al. 2002). In early April, 3–4 months after the last rainfall and 6–8 weeks before the first major rains of the wet season (Fig. 1A), herbs and pastures remain brown and desiccated and deciduous trees on rocky hillsides are leafless in the tropical semideciduous forests of Guanacaste, Costa Rica (Fig. 1B). At the same time, the crowns of leaf-exchanging trees are covered with young, fully expanded leaves (Fig. 1C) and many other trees are just leafing out (Fig. 1D–F). Similarly, the majority of tree species in Asian monsoon forests flush during March/April, the hottest and driest months of the year (Troup 1921; Fig. 1D in Borchert 1998). In the Southern hemisphere, bud break in many species of the dry monsoon forests of Eastern Java (Coster 1923) and the tropical savannas of Northern Australia (Williams et al. 1997) occurs in September/October. “Spring flushing”, i.e., bud break during the late dry season around the spring equinox thus appears to be common in tropical dry forests around the globe.

Bud break and leaf expansion during the dry season can occur only in fully hydrated, usually leafless trees with a stem water potential (Ψ_{stem}) above -0.5 MPa (Borchert 1994a, b; Borchert et al. 2002). Thus, spring

G. Rivera
Instituto Multidisciplinario de Biología Vegetal,
Universidad de Córdoba, Casilla de Correo 495,
5000 Cordoba, Argentina

S. Elliott
Department of Biology, Faculty of Science,
Chiang Mai University, Chiang Mai, Thailand 50002

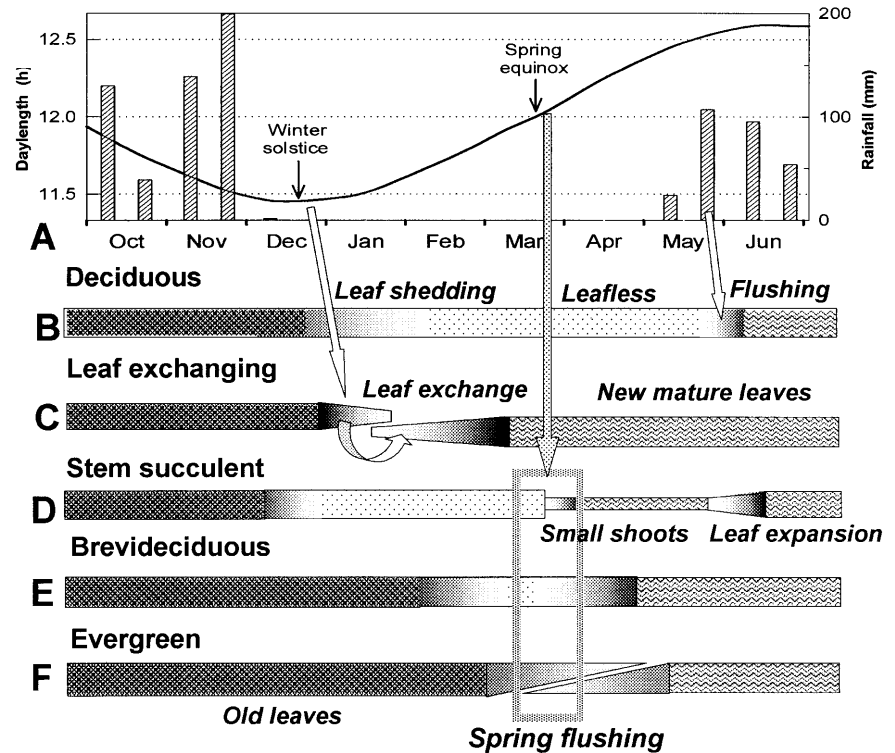
L.S. Caldas
Departamento de Botânica, C.P. 04457,
Universidade de Brasília, CEP 70919-970,
Brasília, DF, Brazil

G. Nicolossi
Intendencia Parque Nacional Calilegua, San Lorenzo s/n,
4514 Calilegua, Jujuy, Argentina

V.T.R. Coradin
Departamento de Ecologia, C.P. 04457,
Universidade de Brasília, CEP 70919-970,
Brasília, DF, Brazil

R. Borchert (✉)
Division of Biological Sciences, 1200 Haworth Hall,
Sunnyside Ave., University of Kansas, Lawrence,
KS 66045-7534, USA
e-mail: borchert@ku.edu
Tel.: +1-785-8644409, Fax: +1-785-8645321

Fig. 1 Seasonal variation in environmental factors (A rainfall, day-length) and vegetative phenology in tropical dry forest trees of various functional types (B–F) in tropical semideciduous forests. Arrows indicate causes of bud break during the dry season: B the first heavy rains of the rainy season; C drought-induced leaf shedding; D–F increasing day-length around the spring equinox. Day-length, calculated with the day-length calculator of Lammi (2001), and rainfall (1997/1998) are for Guanacaste, Costa Rica (10°30' N)



flushing raises several questions. How can leafless trees rehydrate and leaf out during the dry season without rehydration of the topsoil by rain? What causes bud break around the spring equinox, when there is no notable change in climatic conditions (Fig. 1A)? The hypothesis that spring flushing is caused by isolated rain showers during the late dry season (Frankie et al. 1974) has never been tested by phenological observations accompanied by regular monitoring of rainfall. At Hacienda La Pacifica in Guanacaste, Costa Rica, the site of phenological observations to be described below, total precipitation from February to April was below 15 mm in 15 years between 1960 and 1999 (W. Hagnauer, personal observation). Induction of spring flushing by rain is, therefore, as unlikely as the suggested induction of flushing by increasing temperature in a tropical climate, where variation in monthly mean temperatures of 27°C rarely exceeds 1°C (Walter 1971, p 207).

To identify the environmental trigger of bud break during spring flushing, we monitored rainfall, bud break and shoot expansion in >50 brevideciduous and evergreen spring-flushing species in Costa Rica, Northern Argentina and Brazil during three consecutive dry seasons. In most species, bud break of all conspecific trees in a landscape occurred each year during the same 10-day period around the spring equinox, generally after >2–3 months without rain (Fig. 1E, F).

The timing of bud break and its degree of synchrony vary widely among trees of different functional groups and are important indicators of the internal and environmental controls of phenology (Fig. 1). In shallow-rooted, deciduous hardwood species severely water-stressed

leaves abscise during the early dry season (Fig. 1A, B, December–January; Borchert 1994a; Borchert et al. 2002). Rainfall exceeding 20–30 mm causes rapid rehydration and highly synchronous bud break in all leafless trees at a micro-site. Thus, the time of bud break varies widely from year to year and from site to site with the time and local distribution of the first heavy rains (Fig. 1A, B, May–June; Bullock and Solis-Magallanes 1990; Borchert et al. 2002). Leaf-exchanging species are confined to sites with deep soils, where extraction of water from sub-soil reserves enables the maintenance of relatively high Ψ_{stem} (>–1 MPa) during the dry season (Borchert 1994a; Jackson et al. 1995; Borchert et al. 2002). New leaves emerge immediately after leaf abscission, i.e., bud break is inhibited by old leaves (Fig. 1C, January–February; Borchert 1991, 2000). The time of bud break will, therefore, vary among conspecific trees with drought-induced leaf abscission and, indirectly, with soil water reserves and the beginning of seasonal drought (Fig. 1A, C). For example, in June–August 1997, the El-Niño Southern Oscillation caused a severe, abnormal drought period in Costa Rica. This drought resulted in abnormal leaf abscission and subsequent flushing of most deciduous and leaf-exchanging trees in September/October 1997, 4–5 months earlier than normal (Borchert et al. 2002). The timing of leaf shedding and subsequent flushing may also vary by several weeks between exposed and shaded branches within the same large tree crown (Borchert 2000). In deciduous and leaf-exchanging species, bud break will thus occur whenever trees or branches have become leafless and fully hydrated, i.e., the time course of phenology is highly opportu-

nistic and determined mainly by seasonal variation in tree water status at a given site (Borchert 1994a; Borchert et al. 2002).

Deciduous stem-succulent species maintain a high Ψ_{stem} (>-0.5 MPa) throughout the year (Borchert 1994b; Borchert et al. 2002). After rapid leaf abscission during the early dry season, trees remain leafless for several months. Between the winter solstice and the spring equinox, rain or irrigation do not induce bud break of leafless trees, i.e., during this period vegetative buds are in a state of endo-dormancy similar to that of cold-temperate perennial plants during early winter (Fig. 1A, D; Bullock and Solis-Magallanes 1990; Borchert 1991; Lang 1996). Bud break of all conspecific trees occurs each year during the same species-specific 10 to 15-day period, within 2–6 weeks after the spring equinox and several weeks before the first heavy rains (Fig. 1D; Borchert and Rivera 2001; Borchert et al. 2002). The control of seasonal development in stem succulent species thus differs basically from that observed in deciduous and leaf-exchanging species, in that bud break is highly synchronous in all conspecific trees in a landscape and its timing varies minimally from year to year.

Seasonal variation in tree water status (see above) and other abiotic and biotic factors have been suggested as cues for synchronous flushing in tropical trees (Wright 1996). Among these, seasonal changes in day-length constitute the only known and conceivable environmental signal which is constant from year to year, independent of inter-annual variation in climate and capable of inducing highly synchronous developmental change in all conspecific trees throughout a landscape (Fig. 1A, D–F; Thomas and Vince-Prue 1997). In earlier experiments, shoot growth of seedlings and saplings of many cold-temperate and a few tropical woody species was found to be arrested by photoperiods shorter than 12 h and induced or enhanced by photoperiods longer than 13 h (Nitsch 1957; Njoku 1963; Romberger 1963; Longman 1978; Thomas and Vince-Prue 1997). The relevance of such experiments for photoperiodic control of seasonal development in large field-grown trees has been questioned, because periodic shoot growth patterns of vigorous, juvenile trees often differ substantially from those observed in mature trees (Romberger 1963; Borchert 1978, 1991).

Experimental variation of the photoperiod is impractical in large trees. However, as we show in this paper, photoperiodic control of bud break can be verified in carefully executed, at least 3-year-long phenological field studies with high observation frequency. Such studies constitute natural experiments testing the null hypothesis that bud break is induced by seasonal variation in climatic factors. Accordingly, in deciduous and leaf-exchanging species, the time of bud break should vary from year to year with the date of the first and last heavy rainfall of the wet season, respectively (Fig. 1A–C, empty arrows). If bud break of all trees of a species is observed each year during the same 10- to 15-day period (Fig. 1D–F, dotted arrow), this disproves the null hypothesis and, at the same time, constitutes direct proof for photoperiodic control. At a low latitude of $\sim 10^\circ$, synchronous bud break around the spring equinox must be induced by an increase in photoperiod of 30 min or less (Fig. 1A) and bud break may be induced before the spring equinox at higher latitudes.

In view of the above considerations, the observed synchronous bud break in stem succulent species must be induced by increasing day-length around the spring equinox (Fig. 1D). In keeping with this conclusion, bud break of dormant *Plumeria rubra* saplings exposed to a 13-h-photoperiod in January occurred 3 months earlier than in controls under natural day-length (Borchert and Rivera 2001). Similarly, declining photoperiod induced synchronous flowering in >25 tropical tree species of various functional types after the autumn equinox (Rivera and Borchert 2001) and the resumption of reproductive activity of Spotted Antbirds in Panama is likely to be induced by increasing day-length (Wikelski et al. 2000). Bud break in stem succulents and short-day-induced flowering vary with latitude as predicted for photoperiodic control (Table 1; Thomas and Vince-Prue 1997).

Spring-flushing brevideciduous species are similar in physiognomy, distribution and phenology to leaf-exchanging species (Borchert et al. 2002). During drought-induced leaf abscission, Ψ_{stem} increases to high levels, indicating water absorption from sub-soil reserves by deep root systems (Borchert 1994a; Jackson et al. 1995; Borchert et al. 2002). Bud break occurs in the absence of rain after trees have been leafless for several

Table 1 Effect of decreasing latitude and annual variation in day-length (Δmin) on photoperiodic induction of synchronous bud break by increasing day-length and of synchronous flowering by

declining day-length. Annual variation in day-length was calculated from latitude using the “day-length calculator” of Lammi (2001)

	Place	Latitude	Δmin	Time of bud break or flowering	Reference
Long-day induced bud break: <i>Bombax malabaricum</i>	Java	6° 10' S	43	September	Coster (1923)
	Singapore	1° 16' N	9	All year	Borchert and Rivera (2001)
Short-day induced flowering: <i>Cordia alliodora</i>	Mexico	21° N	153	September	Rivera and Borchert (2001)
	Panama	9° N	63	December	Rivera and Borchert (2001)
	Ecuador	2° N-S	14	All year	Borchert (1996)

weeks or a few days (Fig. 1E). In evergreen spring-flushing species, bud break starts weeks before all old leaves have abscised (Fig. 1F). In most of the >50 spring-flushing species described in this paper, highly synchronous bud break around the spring equinox occurred each year in all conspecific trees during the same 10- to 15-day period before the first rains of the rainy season. In these species, spring flushing is, therefore, induced by increasing photoperiod, as it is in stem succulent species, and the term “spring flushing” will be used as shorthand for “synchronous bud break induced by increasing photoperiod”.

Materials and methods

Use of scientific names of tree species

Full names of species analyzed for spring flushing are given in Table 2. Unless several species of a genus were observed, only genus names will be used in the text after the first mentioning of a species.

Data sets screened for photoperiodic induction of spring flushing

In autumn 1997, we observed synchronous flowering of several tree species in the semideciduous forests of Guanacaste, Costa Rica, which suggested photoperiodic control (Rivera and Borchert 2001). We, therefore, monitored synchronous bud break of two species in spring 1998 (Fig. 2) and identified all species for which flushing in March/April had been reported earlier (Frankie et al. 1974). We then planned two high-resolution (3 observations per month), multi-year observation programs, which were accompanied by daily recording of rainfall and aimed at confirming synchrony of flushing with low inter-annual variation in many species in Costa Rica and Northern Argentina. In addition, we screened weekly phenological observations from a Brazilian tropical savanna (cerrado) and monthly phenological observations from monsoon forests in Thailand and Java for spring flushing. Environmental variables and methods for phenological observations of bud break at the five observation sites are given in Table 3.

Costa Rica

In summer 1998, trees of >20 potential spring-flushing species were identified and mapped (Fig. 3). To facilitate frequent observation, most trees were located along highways and country roads in the surroundings of Hacienda La Pacifica, Cañas, the site of related field studies (Borchert 1994a, 2000; Rivera and Borchert 2001). There was no precipitation between January and May in 1998 and 2000 (Fig. 1A), but 75 mm rain fell in mid-February 1999.

Northern Argentina

The phenology of 50 species was monitored at the lower altitudes of Calilegua National Park, Province of Jujuy, Argentina. In this subtropical dry forest, less than 5% of annual precipitation occurs during the dry season. In 1999, the first heavy rains started 2 months later than in the other years.

Central Brazil

The woody vegetation on the deep, extremely nutrient-poor latosol soils of the tropical savanna (cerrado) consists mainly of shrubs and 6- to 8-m-tall, thick-leaved, brevideciduous or evergreen trees

(Eiten 1972). Phenology was monitored along transects comprising >80 trees of 22 species at the Reserva Ecológica of the Instituto Brasileiro de Geografia e Estatística located at 1,100 m elevation near Brasília, DF. The number of observed trees was sufficient to identify functional types for 9 of the observed 22 species.

Northern Thailand

Phenological observations were made in the semideciduous dip-terocarp-oak forest in Doi Suthep-Pui National Park, Chiang Mai, in a transect ranging from 650–780 m altitude (Elliott et al. 1994; Rundel and Boonpragob 1995). Monthly rainfall between January and March was less than 20 mm during the observation period.

Eastern Java

Data were obtained from the first large-scale phenological study of tropical trees, in which leaf emergence in large numbers of conspecific trees growing near highways was monitored from an automobile in the dry monsoon forests near Toeban, East Java (Coster 1923). Many of the observed trees belong to introduced neo-tropical species. Thus, this record illustrates synchronous flushing in many trees during the dry season as well as variation of leaf emergence with latitude.

Evaluation of phenological data sets

In the high-resolution data sets (3–4 observations per month; Table 3), spring flushing was quantified by phenology scores from 0 (no new leaves) to 3 (new leaves fully expanded) in Costa Rica and Argentina, but only the presence or absence of expanding buds or new leaves was recorded in Brazil. Synchrony of spring flushing is indicated by the absence of new leaves in all observed trees at one observation date and the presence of expanding buds or leaves in all trees at the next date (Fig. 2). Low inter-annual variation is indicated by synchronous bud break in consecutive years (Fig. 3) and by the rapid and synchronous increase in mean scores of leaf development in different years (Fig. 4). For species which flower during spring flushing, an abrupt increase in the number of flowering herbarium collections from one month to the next indicates low inter-annual variation in the onset of spring flushing over the >50 years during which herbarium specimens were collected (Fig. 4, right; Borchert 1996; Borchert and Rivera 2001). Collection dates of spring-flowering species were obtained from the herbarium of the Missouri Botanical Garden, St. Louis.

For several phenological stages, means and standard deviations were calculated for the dates of first observation (Figs. 5, 6). Other phenological observations were not analyzed statistically, because bud break and the emergence of new leaves, the developmental steps crucial for spring flushing, usually occur so fast (within 10–14 days) that even with sampling intervals of 7–10 days there are only 1–2 relevant observations per tree (Fig. 2). Statistical treatment of phenology scores is, therefore, irrelevant and significant variation in the timing of phenology is obtained only for non-synchronous phenological events that vary with climate, such as leaf shedding (Fig. 5, left), inter-annual variation of bud break in leaf-exchanging species (Fig. 6G–I; Table 4) and rain-induced flushing (Fig. 5A–C). In Thailand, the presence of young, light green or old, mature leaves, leaf abscission and deciduousness were scored monthly on a scale of 0–4. The low observation frequency of this data set is compensated by the observation of several consecutive stages of leaf development in 5–10 trees per species over 3 years.

Table 2 Tree species for which vegetative phenology was monitored (A Argentina, B Brazil, C Costa Rica, J Java, T Thailand)

Species	Country	Figure	Species	Country	Figure
<i>Acacia aroma</i> Gill. Ap. H. et A.	A	5	<i>Machaerium biovulatum</i> Micheli	C	3
<i>Actinophora fragrans</i> R.Br.	J	7	<i>Maclura tinctoria</i> (L.) Don ex Steudel (= <i>Chlorophora</i>)	A, C	3, 5
<i>Agonandra excelsa</i> Griseb.	A	5	<i>Myrospermum frutescens</i> Jacq.	C	3
<i>Albizia guachapele</i> (H.B.K.) Little	C	3	<i>Ouratea hexasperma</i> (St. Hil.) Baill	B	6
<i>Amburana cearensis</i> (Fr. Allem.) A.C. Smith	A	5	<i>Parkia biglobosa</i> Benth.	J	8
<i>Astronium urundeuva</i> (Fr. All.) Engl.	A	5	<i>Patagonula americana</i> L.	A	5
<i>Athyana weinmannifolia</i> (Griseb.) Radlk.	A	5	<i>Phyllostylon rhamnoides</i> (Poisson) Taubert	A	5
<i>Bombax malabaricum</i> DC	J	8	<i>Piscidia carthaginensis</i> Jacq.	C	3
<i>Bursera simarouba</i> (L.) Sarg.	C	3	<i>Pisonia ambigua</i> Heimerl.	A	5
<i>Calycophyllum multiflorum</i> Griseb.	A	5	<i>Pithecelobium saman</i> Benth.	J	8
<i>Cascaronia estragalina</i> Griseb	A	5	<i>Pithecelobium umbellatum</i> Benth.	J	8
<i>Cassia emarginata</i> L.	C	3	<i>Plumeria rubra</i> L.	C	3
<i>Cassia fistula</i> L.	C	3	<i>Pseudobombax argentinum</i> (Fries) Robyns	A	5
<i>Cassia grandis</i> L.	C	3	<i>Pseudobombax septinatum</i> (Jacq.) Dugand	C	3
<i>Cassia javanica</i> L.	J	8	<i>Pterocarpus hayesii</i> Hemsl.	C	3
<i>Cedrela angustifolia</i> Sessé et Mociño ex DC	A	5	<i>Pterodon pubescens</i> (Benth.) Benth.	B	6
<i>Chorisia insignis</i> H.B.K.	A	5	<i>Pterogyne nitens</i> Tul. ex Benth	A	5
<i>Chrysophyllum marginatum</i> (Hook. et Arn.) Radlk	A	5	<i>Qualea grandiflora</i> Mart.	B	6
<i>Coccoloba tiliaceae</i> Lindau	A	5	<i>Qualea multiflora</i> Mart.	B	6
<i>Cordia trichotoma</i> (Vell.) Arrab. Ex Steud.	A	5	<i>Qualea parviflora</i> Mart.	B	6
<i>Dalbergia fusca</i> Pierre	T	7	<i>Quercus kerrii</i> Craib var. <i>kerrii</i> .	T	7
<i>Dalbergia miscolobium</i> Benth.	B	6	<i>Rourea induta</i> Planch.	B	6
<i>Dalbergia retusa</i> Hemsl.	C	3	<i>Sapium saltense</i> Jabl.	A	5
<i>Diospyros nicaraguensis</i> Standl.	C	3	<i>Schoepfia schreberi</i> Gmel.	C	3
<i>Gleditsia amorphoides</i> (Griseb.) Taub.	A	5	<i>Shorea obtusa</i> (Wall.) ex Bl	T	7
<i>Gliricida sepium</i> (Jacq.) Steud.	C	3	<i>Solanum riparium</i> Pers.	A	5
<i>Godmania aesculifolia</i> (H.B.K.) Standl.	C	3	<i>Spondias mombin</i> L.	C	3
<i>Guapira noxia</i> (Netto) Lund	B	6	<i>Tabebuia impetiginosa</i> (Mart. Ex DC) Standl.	A, C	3, 5
<i>Guazuma ulmifolia</i> Lam.	C	3	<i>Tabebuia ochracea</i> (Cham.) Standl.	C	3
<i>Hura crepitans</i> L.	C	3	<i>Tecoma stans</i> (L.) Juss. ex H.B.K.	A	5
<i>Kielmeyera speciosa</i> St. Hil.	B	6	<i>Trema micrantha</i> (L.) Blume (3).	A	5
<i>Lonchocarpus minimiflorus</i>	C	3	<i>Trichilia hieronymi</i> Griseb.	A	5
<i>Luehea speciosa</i> Willd.	C	3			

Table 3 Environmental variables and phenological observation methods for five observation sites in tropical semi-deciduous forests

Parameter	Costa Rica	Northern Argentina	Central Brazil	Northern Thailand	Eastern Java
Latitude	10°N	23°S	16°S	19°N	7°S
Annual rainfall (mm)	800–2200	600–1400	1200–1600	1120	1400
Dry season (month)	5–6	4–5	4–5	4–5	4–5
Daily rainfall recorded	++	++	++	–	–
Number of species	24	25	9	3	6
Trees per species	5->50	3–12	4–10	5–10	15->100
Observations per month	3	3	4	1	1
Observation period	1998–2000	1998–2000	1997–2000	1989–1991	1922
Figure(s)	1–4	5	6	7	8

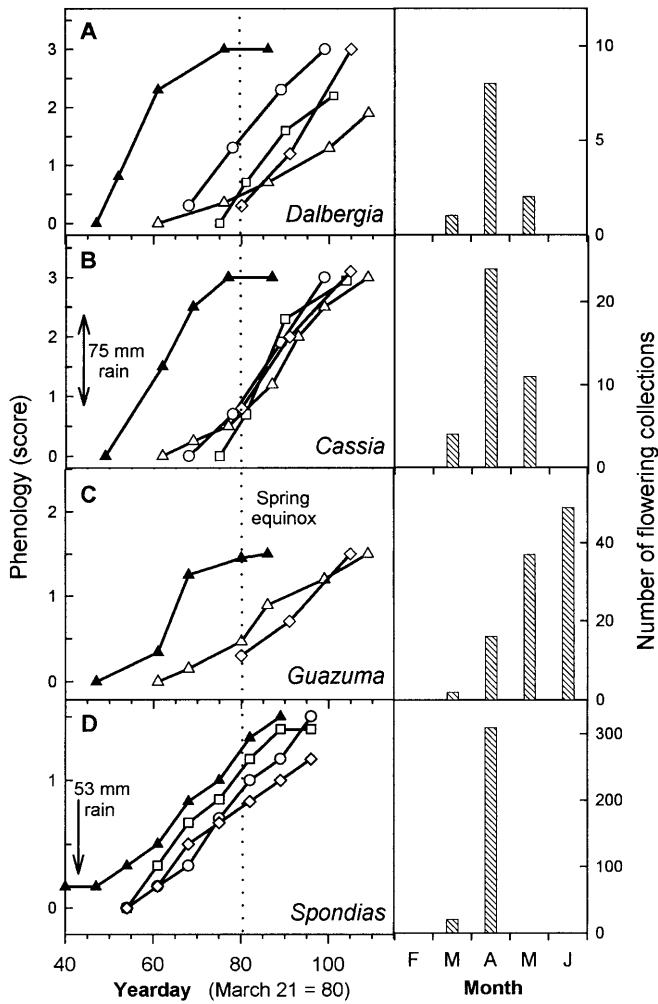
Results

Spring flushing in Costa Rica

In spring 1998, bud break in all observed *Dalbergia retusa* ($n=10$) and *Cassia grandis* trees ($n=8$) occurred within the same 10-day period, soon after leaf shedding in *Dalbergia*, but before the completion of leaf abscission in *C. grandis* (Fig. 2). It was followed by rapid leaf expansion. In 1999 and 2000, highly synchronous spring flushing was observed in many trees of 18 species between 20 March and 10 April (Fig. 3). Expansion of new shoots and inflorescences during spring flushing was fast

in trees at moist sites, but sometimes very slow in trees at dry microsites. Like the stem succulent species analyzed earlier (Fig. 3V–X; Borchert and Rivera 2001), each species flushed during the same 10-day period in consecutive years.

An exceptional 75-mm rainfall on 15 February 1999 caused flushing of many leafless trees in six spring-flushing species within 8–10 days (Figs. 3, 4, late February), but did not affect trees retaining old leaves, which flushed about 1 month later (Figs. 3, 4, late March; Borchert et al. 2002). Similarly, leafless *Godmania aesculifolia* trees receiving seepage from irrigated rice fields flushed in early February (Fig. 3H). A second set of veg-



Spring flushing versus rain-induced bud break in subtropical Northern Argentina

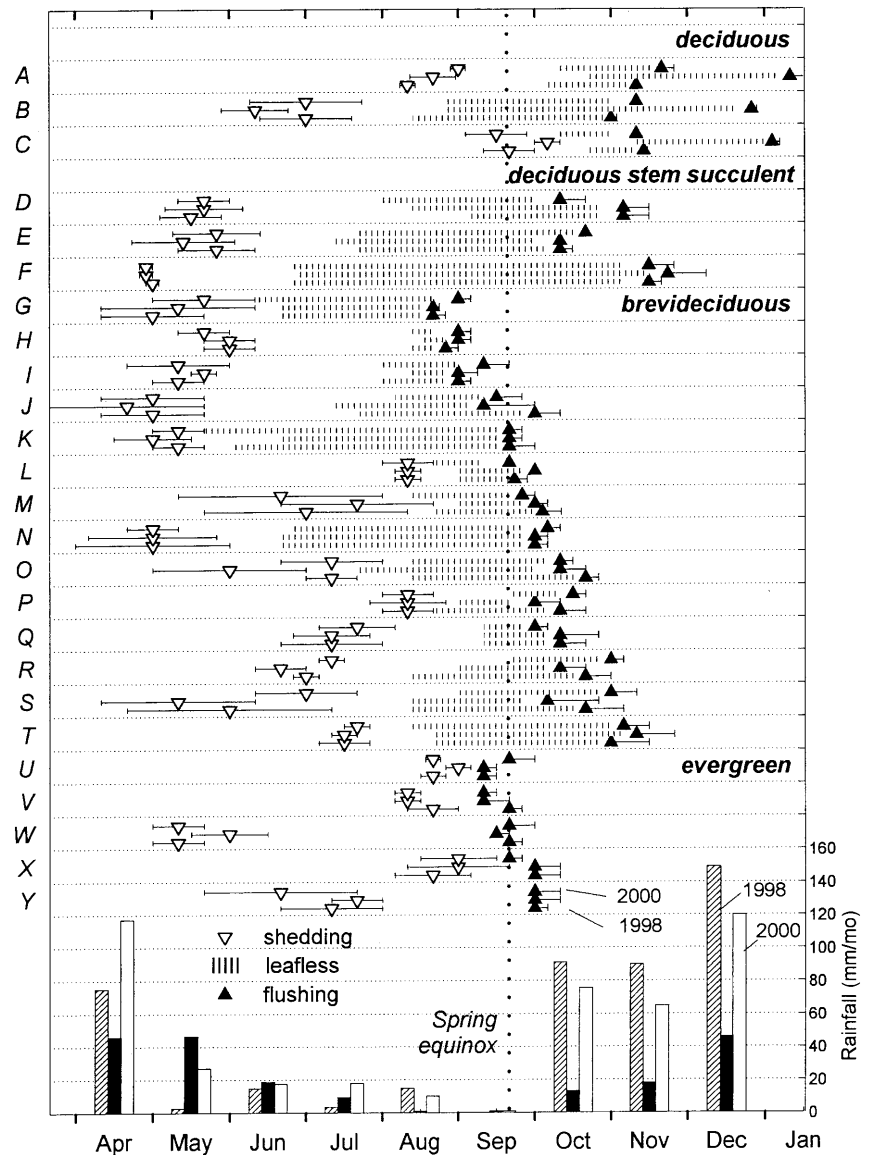
Throughout 1998 to 2000, all trees in 47 of the 50 observed species flushed during the mid- or late dry season between August and October. Highly synchronous spring flushing was observed in >25 species between 20 August and 20 October, i.e., bud break started 1 month before the spring equinox and extended over 2 months (Fig. 5D–Y). In most species, bud break occurred within the same 10-day period in 3 consecutive years, 2–6 weeks before the first major rains in 1998 and 2000 and >2 months before the rains in 1999. Leaves that expanded during spring flushing often remained wilted before the first seasonal rains, indicating that subsoil water reserves were limited. Rain-induced flushing of 3 deciduous species varied by 2 months with the timing of the first major rains (Fig. 5A–C). Ten leaf-exchanging species flushed in August/September (data not shown; compare Fig. 6G–I) and bud break was irregular in the remaining species.

Fig. 4 Spring flushing and flowering in the brevideciduous species *Dalbergia retusa* (A), *Cassia grandis* (B) and *Guazuma ulmifolia* (C) in the semideciduous forest of Guanacaste, Costa Rica. Left: Empty symbols: spring flushing after >3 rainless months in 1991 (circles), 1998 (squares), 1999 (triangles) and 2000 (diamonds). Filled triangles: flushing induced by a 75-mm rain-shower on 15 February 1999. Right: Periodicity of spring flowering obtained from herbarium collections of the Missouri Botanical Garden, St. Louis, Mo. D Spring flushing in 1975–1978 (left) and flowering in 1992–1995 (right) of *Spondias mombin* in the seasonally dry rainforest of Barro Colorado Island, Panama (Data from Rand and Rand 1982; Windsor 1982; Adler and Kielipinski 2000)

Table 4 Variation in the time of leaf exchange with time of last rains in three species of the Brazilian cerrado. Number of observed trees is given in brackets. Soil water available during the mid dry season was estimated from amount and time of last rainfall

		Time (yearday ± day) or interval (Δ±day)				Means 97–2000	
		1997		1998			2000
Rainfall	Last rain	143 (23-May)		120 (30-Apr)		118 (28-Apr)	
	mm rain last 10 days	108 mm		40 mm		170 mm	
	Estimated soil water	high		low		intermediate	
	First rain >30 mm	268 (25-Sep)		283 (10-Oct)		242 (30-Aug)	
	Δ Last-first rains	125		163		124	
<i>Guapira</i> [8, 8, 14] Brevideciduous	Leafless	242±8.1		227±11.9		228±10.3	
	Bud break	249±8.5		239±14.5		234±13.1	
	Δ leafless-bud break	6±5.5		13±8.5		6±8.5	
	Δ Last rain-leafless	99		107		110	
<i>Guapira</i> [first, last trees]	Leafless	225	245	204	240	220	250
	Bud break	240	262	220	263	221	258
	Δ Earliest-latest tree	22		43		37	
	Δ Last rain-leafless	82	102	84	120	102	132
<i>Ouatea</i> [8, 8, 7] Evergreen	Bud break	253±7.5		231±11.3		231±8.5	
	Δ Last rain-bud break	110		111		113	
<i>Rourea</i> [4, 4, 4] Evergreen	New leaves	260±11.2		244±8.7		241±10.2	
	Δ Last rain-new leaves	117		124		123	

Fig. 5 Rainfall and vegetative phenology in the semideciduous subtropical forest of Calilegua National Park, Jujuy, Argentina. Beginning of leaf shedding (*empty triangles*), deciduous period (*vertical hatching*), bud break during spring flushing (*filled triangles*) and monthly rainfall (*vertical bars*) were observed in 1998–2000. Number of observed trees in parentheses. **A–C** Deciduous species with rain-induced flushing. **A** *Athyana weinmannifolia* (4); **B** *Calycophyllum multiflorum* (5); **C** *Phyllostylon rhamnoides* (6); **D–F** Deciduous spring-flushing stem succulents. **D** *Chorisia insignis* (6); **E** *Pseudobombax argentinum* (5); **F** *Cedrela angustifolia* (8); **G–T** Brevideciduous spring-flushing species. **G** *Cascaronia estragalina* (3); **H** *Sapium saltense* (3); **I** *Gleditsia amorphoides* (3); **J** *Coccoloba tiliaceae* (8); **K** *Acacia aroma* (4); **L** *Tecoma stans* (6); **M** *Tabebuia impetiginosa* (9); **N** *Amburana cearensis* (7); **O** *Pisonia ambigua* (4); **P** *Patagonula americana* (5); **Q** *Pterogyne nitens* (3); **R** *Maclura tinctoria* (3); **S** *Cordia trichotoma* (8); **T** *Astronium urundeuva* (8); **U–Y** Evergreen spring-flushing species. **U** *Agonandra excelsa* (4); **V** *Trichilia hieronymi* (8); **W** *Chrysophyllum marginatum* (4); **X** *Solanum riparium* (5); **Y** *Trema micrantha* (3)



Among the spring-flushing species, leaf phenology varied widely from the deciduous stem succulents, which were leafless for up to 5 months, to evergreen species, which generally lost more than half their old leaves before spring flushing, but completed abscission of old leaves weeks later. Like synchronous spring flushing, leaf shedding occurred at species-specific times, but the duration of leaf abscission and deciduousness varied widely between species (Fig. 5).

Spring flushing versus drought-induced leaf exchange in the Central Brazilian savanna

Synchronous flushing with low inter-annual variation in August/September make induction of bud break by increasing photoperiod very likely for six brevideciduous species of the Central Brazilian savanna (Fig. 6A–F). In three other species, one brevideciduous and two ever-

green, leaf shedding and bud break consistently occurred 2–3 weeks later in 1997 than in the other years (Fig. 6G–I; Table 4). This phenological pattern was not correlated with the first seasonal rains (Fig. 6, bottom), but well correlated with the last precipitation before the dry season, which in 1997 occurred 3 weeks later than in the other years (Table 4). In these 3 species, the 3.5- to 4-month interval between the last significant rainfall and leaf shedding or the resumption of growth was remarkably constant from year to year (Table 4). In *Guapira noxia*, bud break always occurred a few days after leaf abscission was complete (Table 4), but the time of bud break varied by 22–43 days between the first and last-flushing trees (Table 4). This interval was shortest in 1997, when late, heavy rains provided ample soil water reserves (Table 4) and longest after the early onset and long duration of drought in 1998 (Table 4). These observations indicate that *Guapira*, *Rourea induta* and *Ouretea hexasperma* are leaf-exchanging species, in which

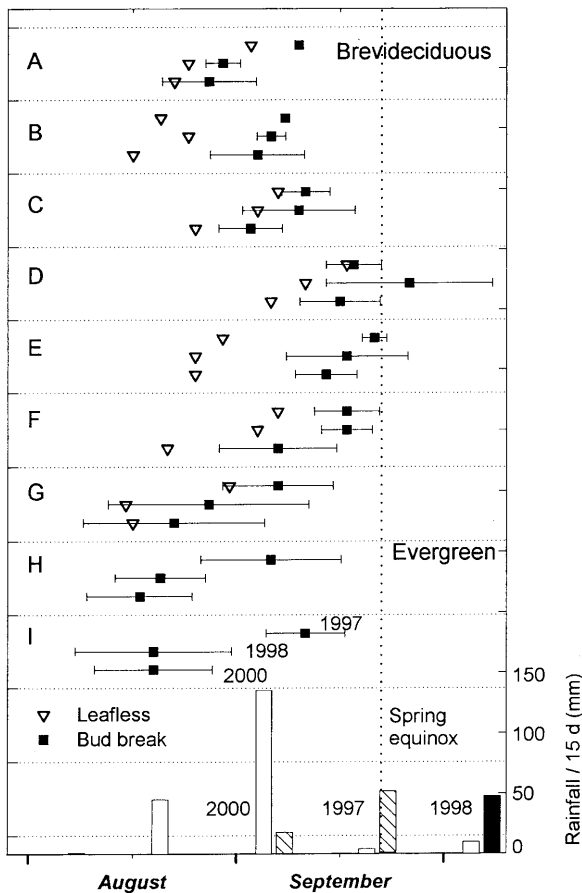


Fig. 6 Rainfall (vertical bars) and phenology (symbols) during the late dry season in spring flushing (A–F) and leaf-exchanging species (G–I) of the tropical savanna (cerrado) in Central Brazil. The number of observed trees is given in parentheses (two numbers indicate a larger number of observed trees in 2000). **A** *Dalbergia miscolobium* (4–5); **B** *Kielmeyera speciosa* (4–5); **C** *Pterodon pubescens* (4); **D** *Qualea grandiflora* (4–10); **E** *Qualea multiflora* (6); **F** *Qualea parviflora* (6); **G** *Guapira noxia* (8–14); **H** *Rourea induta* (Planch.) Baker (4); **I** *Ouratea hexasperma* (8)

bud break is caused by drought-induced leaf abscission and varies with the onset of seasonal drought and micro-site water availability (Fig. 1C).

Spring flushing in Northern Thailand

Although the low time resolution of observations in the subtropical dry dipterocarp forest of Northern Thailand precludes demonstration of synchrony and low inter-annual variation of bud break with the same precision as in the observations from Central and South America, flushing of new leaves during the hot, rainless March/April period was highly synchronous within species (Fig. 7A) and occurred each year at the same time, as indicated by the sharp rise in the 3-year means of leaf formation (Fig. 7B–D). Like *Dalbergia* in Costa Rica (Fig. 2), most spring-flushing trees are leafless for a few

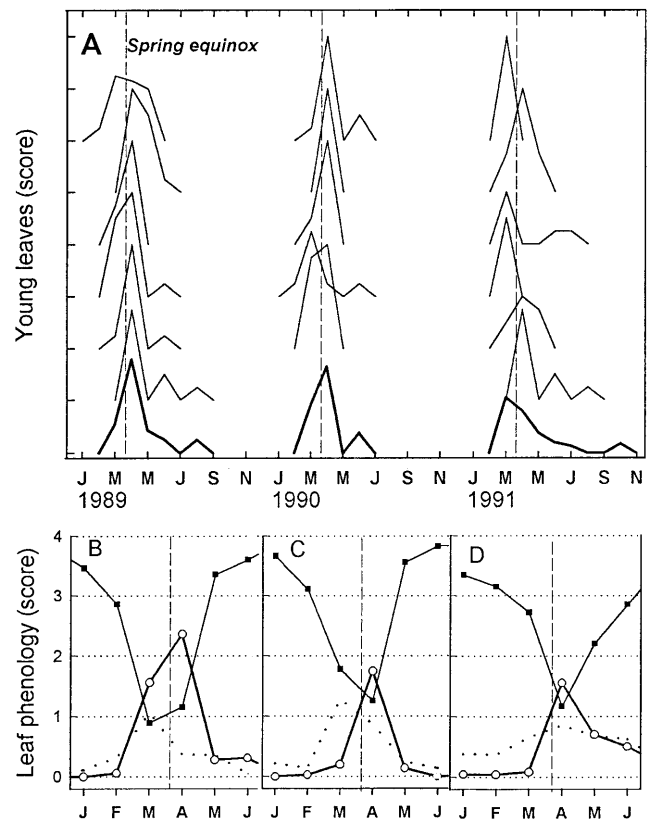


Fig. 7A–D Spring flushing in brevideciduous tree species of the dry dipterocarp-oak forest in Doi Suthep National Park, Chiang Mai, Thailand. **A** Formation of new leaves in six trees of *Shorea obtusa* during 3 consecutive years (thick lines means of 6 trees). **B–D** Three-year means of phenology scores for mature leaves (filled squares), leaf shedding (dotted line) and young leaves (empty circles) calculated from 5–10 trees in three species. **B** *Shorea obtusa*; **C** *Dalbergia fusca* Pierre; **D** *Quercus kerrii*

weeks (S. Elliott, personal observation). Minimum scores for mature leaves greater than zero result from averaging monthly scores of many trees over 3 years (Fig. 7B–D). Other brevideciduous species in the same forest flush irregularly and, because of large inter-annual variation, 3-year means of flushing show no distinct peaks (data not shown).

Spring flushing versus leaf exchange in Eastern Java

In the dry monsoon forest of Eastern Java, species of different functional types flush at different times after the winter solstice in June, as they do in Central America (Figs. 1, 8; Coster 1923). Leaf-exchanging species such as the neotropical *Pithecelobium saman* and the paleotropical *P. umbellatum* flush within 2 months after the winter solstice (Fig. 8, July/August) and spring flushing of the brevideciduous *Cassia javanica* and the stem succulent *Bombax malabaricum* takes place around the spring equinox (Fig. 8, September), as it does in their neotropical relatives *C. grandis* and *Pseudobombax* (Fig. 3D, X).

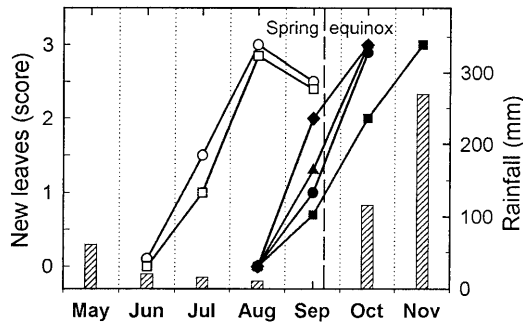


Fig. 8 Vegetative phenology (symbols) and rainfall (vertical bars) in the dry monsoon forest of East Java. Two leaf-exchanging species [*Pithecelobium saman* (30; empty circles); *Pithecelobium umbellatum* (15; empty squares)], three spring-flushing brevideciduous species [*Actinophora fragrans* (15; filled triangles); *Cassia javanica* (10; filled squares); *Parkia biglobosa* (5; filled diamonds)] and one stem succulent species [*Bombax malabaricum* (200; filled circles)] were observed during the 1922 dry season (number of observed trees in brackets; data from Coster 1923)

Discussion

Photoperiodic control of spring flushing in tropical semideciduous forests

In the past, photoperiodic control of shoot growth in woody plants was analyzed by comparing growth responses in saplings exposed to different photoperiods. In this study, we established photoperiodic control of mature trees in the field by monitoring the timing of bud break at frequent intervals (7–10 days) during 3 consecutive years and by comparing the time of bud break in trees of various functional groups in semideciduous forests of Argentina, Brazil and Costa Rica. In Argentina and Brazil, the timing of the first and last heavy rainfalls of the wet season varied widely between years and caused characteristic and predictable inter-annual variation of rain-induced bud break in deciduous species (Figs. 1B, 5A–C) and of drought-induced leaf abscission in leaf-exchanging species (Figs. 1C, 6G–I; Table 4). In spite of this strong inter-annual variation in climate, synchronous bud break of spring-flushing species occurred each year during the same species-specific 10-day period and in the absence of rain (Figs. 5, 6). The time of bud break was, therefore, determined by seasonal variation in day-length and not by climatic seasonality. Synchronous bud break with minimal inter-annual variation was also observed in numerous trees of many species in Costa Rica and Thailand (Figs. 2, 3, 4, 7) and was 6 months out of phase between the northern and southern hemispheres (Figs. 3, 7 versus 5, 6, 8). Bud break around the spring equinox indicates induction by increasing photoperiod (Fig. 1A). As also observed for short-day induced flowering of dry forest species (Table 1; Rivera and Borchert 2001), spring flushing started about 1 month earlier in the subtropics (Figs. 5, 6, 7) than at lower latitudes (Figs. 3, 8). This indicates that critical day-length for the induction of bud break ranges from ~11.5 to

~12.5 h in the subtropics and is ~12 h at low latitudes. At a latitude of ~10° N, spring flushing in late March (Fig. 3) must be induced by an increase in photoperiod of 30 min (Fig. 1A, D, E). The synchronous bud break of >60 *Cedrela odorata* trees observed in early November 2001 in Manaus, Brazil (2:30° S; O. Duenisch, personal communication), where annual variation in day-length is 18 min (Lammi 2001), suggests that trees are capable of responding to changes in photoperiod of <10 min.

Patterns of leaf abscission

In contrast to the relatively narrow time frame for bud break during spring flushing, patterns of leaf abscission vary widely among spring-flushing species (Figs. 1D, E, 5). They range from deciduous species, which shed leaves during the early dry season and remain leafless for 3–5 months (Fig. 5D–G, K, N), through brevideciduous species with late leaf abscission and a leafless period of a few days or weeks (Figs. 5H–J, L–T, 6A–G), to evergreen species in which leaf fall starts before spring flushing but is completed several weeks after the emergence of new leaves (Fig. 5U–Y). In contrast to leaf-exchanging species (Fig. 1C; Table 4; Borchert et al. 2002), there is no indication of a direct causal relation between the completion of leaf abscission and subsequent bud break. Generally, the timing of leaf abscission varied widely within species and between years, but in some species leaf abscission was remarkably synchronous and started at the same time each year, indicating that it might be induced by declining (Fig. 5F) or increasing day length (Fig. 5L, P, T). In Argentina, leaf shedding of several species began during the last months of the wet season (Fig. 5D–K, N, April/May), i.e., it is probably caused by a combination of increasing leaf age and declining photoperiod rather than increasing drought (Borchert and Rivera 2001; Borchert et al 2002).

Distribution of spring-flushing species in tropical forests

Expansion of new leaves in spring-flushing and leaf-exchanging species during the dry season determines the physiognomy of semideciduous as opposed to deciduous tropical forests. Spring flushing is common in semideciduous forests, but rare in seasonally dry evergreen forests, where many species exchange leaves during or after the short dry season (e.g., Amazonia: Alencar et al. 1979; Barro Colorado Island in Panama: Windsor 1982; Atlantic forest of Brazil: Morellato et al. 2000), and in deciduous forests, where rehydration and flushing of all trees is induced by the first heavy rains of the wet season (Mexico: Bullock and Solis-Magallanes 1990). In the semideciduous forest of Costa Rica, ~25% of >100 observed species are spring flushing (Frankie et al. 1974) and the distribution of functional tree types varies strongly with topography and water availability. Leaf-exchanging and spring-flushing hardwood species are

confined to moist microsites and deciduous species are dominant at dry upland sites (Borchert 1994a; Borchert et al. 2002). In subtropical Northern Argentina, where the dry season is 1–2 months shorter and notably cooler than in Costa Rica, most trees remain leafless for <6–8 weeks and flush during the dry season. More than 50% of all species appear to be spring-flushing. (Fig. 5; Table 3). Under similar climates, most trees in the monsoon forests of Northern Thailand and the tropical savannas of Brazil are evergreen or leafless for very short periods and spring flushing is less common than in Argentina (6 of 20 observed species in Thailand; Elliott et al. 1994). Finally, a few observations with species of wide-ranging pan-tropic genera suggest that functional types are preserved within taxa. Thus, several species of *Cassia* (Figs. 3B–D), *Cedrela* (Fig. 5F; Borchert, personal observation) and *Dalbergia* (Figs. 3E, 6A, 7C) are spring flushing, whereas both observed species of *Pithecelobium* exchange leaves (Fig. 8).

Physiological control of spring flushing

Bud break during the dry season is generally prevented by dry soils causing a low Ψ_{STEM} and by the presence of old leaves with poor stomatal control and high transpiration rates, which are strong sinks for available water (Borchert 1994a, b, 2000; Borchert et al. 2002). Leaf-exchanging and spring-flushing species are, therefore, confined to moist microsites, and low subsoil water reserves may slow down spring flushing and cause wilting of new leaves. In leaf-exchanging species, bud break occurs as soon as trees have become leafless and fully hydrated (Fig. 1C), but these prerequisites are not sufficient for bud break in spring-flushing species, which require an inductive increase in day-length to break bud dormancy. Bud break before complete leaf abscission in evergreen trees indicates that emerging buds are capable of escaping correlative inhibition by old leaves (Figs. 5, 6).

During most of the dry season, vegetative buds of spring-flushing stem-succulent species are in a state of endo-dormancy induced and terminated by declining and increasing photoperiod, respectively (Borchert and Rivera 2001). In Argentina, irrigation during the dry season did not induce bud break in any spring-flushing species prior to photoperiodic induction (G. Rivera, personal observation), but in Costa Rica abnormal rain during the dry season caused bud break in vegetative or flower buds of leafless trees in several, but not all, spring-flushing species (Figs. 3, 4, February). Apparently, either rainfall or increasing photoperiod may induce bud break in these brevideciduous species. Thus, in tropical as in temperate trees, there appear to be different types of bud dormancy, the molecular controls of which are not understood (Romberger 1963; Lang 1996).

Spring flowering is the result of bud break in dormant flower buds formed during the previous growing season and does not involve photoperiodic induction of flowering meristems (Rivera and Borchert 2001). As with veg-

etative buds (see above), bud break may be induced before spring flowering by rainfall or irrigation (Reich and Borchert 1982; Borchert 1994c). In *Tabebuia*, partial flowering induced by sparse rain showers during the early dry season may be followed by expansion of the remaining flower buds during spring flowering (Fig. 3T, U).

In deciduous cold-temperate trees, rising spring temperatures induce the transformation of reserve starch into sugars, sugar secretion into the xylem, slow upward water shifting from the root system and osmotic water uptake by bark tissues (sap rise or osmotic water shifting; Braun 1984; Borchert 1994b). The resulting high water and sugar content of bark tissues is a prerequisite for bud break (Braun 1984). Similarly, during flushing of several leaf-exchanging and spring-flushing neotropical tree species, the parenchyma sheaths surrounding the vessels remain free of starch and the activity of acid phosphatases regulating sugar secretion into the xylem is high (Fink 1982; Braun 1984). If increasing photoperiod should induce osmotic adjustment in bud tissues of spring-flushing trees via starch-sugar conversion, as increasing spring temperatures do in temperate trees, this might trigger bud break via increased water absorption and availability of sugars.

Adaptive significance of spring flushing

The evolution of the above, unique set of physiological mechanisms in spring-flushing species suggests that bud break during the late dry season is adaptive. In the tropics, increasing day-length after the spring equinox signals the approach of the rainy season (Fig. 1; Houston 1994). Induction of spring flushing by increasing photoperiod assures that a full complement of young, photosynthetically efficient leaves is in place when the rainy season begins, yet precludes prolonged exposure of young leaves to severe drought. Spring flushing may, therefore, be an adaptation for optimizing photosynthetic gain during a relatively short wet growing season, but it might also reduce damage by herbivorous insects emerging from diapause after the first rains (Wright 1996).

Acknowledgements We thank the Program of Terrestrial Ecology of the Andrew W. Mellon Foundation for financial support of field work in Costa Rica, and the managers of Hacienda La Pacifica for generous logistical support and permission to work in the ranch. Field work in Argentina was supported by Proyungas-Liey and a grant by the International Foundation of Science (D/2996–1). Observations in Central Brazil were supported by PRONEX and IBGE and species identifications were confirmed by Ana Palmira Silva, Benedito A. S. Pereira and Mardocheu Rocha. Wildlife Conservation International and the Department of Biology of Chiang-Mai University supported field work in Thailand.

References

- Adler GH, Kielpinski KA (2000) Reproductive phenology of a tropical canopy tree, *Spondias mombin*. *Biotropica* 32:686–692
- Alencar JC, Almeida RA, Fernandes NP (1979) Fenologia de espécies florestais em floresta tropical úmida de terra firme na Amazônia Central. *Acta Amazonica* 9:163–198
- Borchert R (1978) Feedback control and age-related changes of shoot growth in seasonal and non-seasonal climates. In: Tomlinson PB, Zimmermann MH (eds) *Tropical trees as living systems*. Cambridge University Press, Cambridge, pp 497–515
- Borchert R (1991) Growth periodicity and dormancy. In: Raghavendra AS (ed) *Physiology of trees*. Wiley, New York, pp 221–245
- Borchert R (1994a) Water storage in soil or tree stems determines phenology and distribution of tropical dry forest trees. *Ecology* 75:1437–1449
- Borchert R (1994b) Water status and development of tropical trees during seasonal drought. *Trees* 8:115–125
- Borchert R (1994c) Induction of rehydration and bud break by irrigation or rain in deciduous trees of a tropical dry forest in Costa Rica. *Trees* 8:198–204
- Borchert R (1996) Phenology and flowering periodicity of neotropical dry forest species: evidence from herbarium collections. *J Trop Ecol* 12:65–80
- Borchert R (1998) Responses of tropical trees to rainfall seasonality and its long-term changes. *Clim Change* 39:381–393
- Borchert R (2000) Organismic and environmental controls of bud growth in tropical trees. In: Viemont JD, Crabbè J (eds) *Dormancy in plants: from whole plant behavior to cellular control*. CAB International, Wallingford, pp 87–107
- Borchert R, Rivera G (2001) Photoperiodic control of seasonal development and dormancy in tropical stem-succulent trees. *Tree Physiol* 21:213–221
- Borchert R, Rivera G, Hagnauer W (2002) Modification of vegetative phenology in a tropical semideciduous forest by abnormal drought and rain. *Biotropica* 34:27–39
- Braun HJ (1984) The significance of the accessory tissues of the hydrosystem for osmotic water shifting. *IAWA Bull* 5:275–294
- Bullock SH, Solis-Magallanes JA (1990) Phenology of canopy trees of a tropical deciduous forest in Mexico. *Biotropica* 22:22–35
- Coster C (1923) Lauberneuerung und andere periodische Lebensprozesse in dem trockenen Monsungebiet Ost-Javas. *Ann Jard Bot Buitenzorg* 33:117–189
- Eiten G (1972) The cerrado vegetation of Central Brazil. *Bot Rev* 38:201–341
- Elliott S, Promkutkaew S, Maxwell JF (1994) Flowering and seed production phenology of dry tropical forest trees in Northern Thailand. In: Drysdale RM, John SET, Yapa AC (eds) *Proceedings of the International Symposium on Genetic Conservation and Production of Tropical Forest Tree Seed*. ASEAN – Canada Forest Tree Seed Centre, Saraburi, Thailand, pp 52–61
- Fink S (1982) Histochemische Untersuchungen über Stärkeverteilung und Phosphatase-Aktivität im Holz einiger tropischer Baumarten. *Holzforschung* 36:295–302
- Frankie GW, Baker HG, Opler PA (1974) Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J Ecol* 62:881–919
- Houston MA (1994) *Biological diversity. The coexistence of species in changing landscapes*. Cambridge University Press, Cambridge
- Jackson PC, Cavellier J, Goldstein G, Meinzer FC, Holbrook NM (1995) Partitioning of water resources among plants of a lowland tropical forest. *Oecologia* 101:197–203
- Lammi J (2001) Online photoperiod calculator. <http://www.netti.fi/~jjlammi/sun.html>
- Lang GA (ed) (1996) *Plant dormancy: physiology, biochemistry and molecular biology*. CAB International, Wallingford
- Longman KA (1978) Control of shoot extension and dormancy: external and internal factors. In: Tomlinson PB, Zimmermann MH (eds) *Tropical trees as living systems*. Cambridge University Press, Cambridge, pp 465–495
- Morellato LPC, Talora DC, Takahasi A, Bencke CC, Romera EC, Ziparro VB (2000) Phenology of Atlantic rain forest trees: a comparative study. *Biotropica* 32:811–823
- Nitsch JP (1957) Photoperiodism in woody plants. *Proc Am Soc Hortic Sci* 10:526–544
- Njoku E (1964) Seasonal periodicity in the growth and development of some forest trees in Nigeria. II. Observations on seedlings. *J Ecol* 52:19–26
- Rand AS, Rand WM (1982) Variation in rainfall on Barro Colorado. In: Leigh EG Jr, Rand AS, Windsor DM (eds) *The ecology of a tropical rainforest. Seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, D.C. pp 47–59
- Reich PB, Borchert R (1982) Phenology and ecophysiology of the tropical tree *Tabebuia neochrysantha* (Bignoniaceae). *Ecology* 63:294–299
- Rivera G, Borchert R (2001) Induction of flowering in tropical trees by a 30-min reduction in photoperiod: evidence from field observations and herbarium specimens. *Tree Physiol* 21:201–212
- Romberger JA (1963) Meristems, growth and development in woody plants. *USDA Technical Bulletin No. 1293*
- Rundel PW, Boonpragob K (1995) Dry forest ecosystems of Thailand. In: Bullock SH, Mooney HA, Medina E (eds) *Seasonally dry tropical forests*. Cambridge University Press, Cambridge, pp 93–123
- Thomas B, Vince-Prue D (1997) *Photoperiodism in plants*. Academic, San Diego
- Troup RS (1921) *The silviculture of Indian trees*. Clarendon, Oxford
- Walter H (1971) *Ecology of tropical and subtropical vegetation*. Oliver & Boyd, Edinburgh
- Wikelski M, Hau M, Wingfield JC (2000) Seasonality of reproduction in a neotropical rain forest bird. *Ecology* 81:2458–2474
- Windsor D (1982) The phenology of leaf production for selected trees on Barro Colorado Island, Republic of Panama. Preliminary data report. *Smithsonian Tropical Research Institute, Panama*
- Williams RJ, Myers BA, Muller WJ, Duff GA, Eamus D (1997) Leaf phenology of woody species in a Northern Australian tropical savanna. *Ecology* 78:2542–2558
- Wright SJ (1996) Phenological responses to seasonality in tropical forest plants. In: Mulkey SS, Chazdon RL, Smith AP (eds) *Tropical forest ecophysiology*. Chapman and Hall, New York, pp 440–460