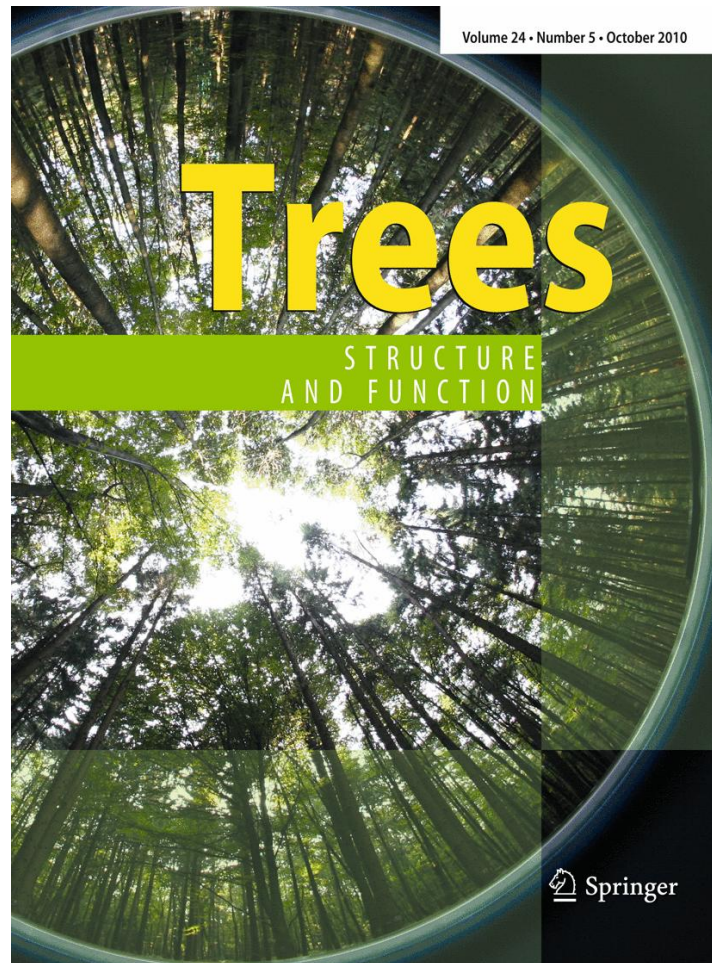


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## Seasonal variation in daily insolation induces synchronous bud break and flowering in the tropics

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**Abstract** In many temperate plants seasonal variation in day length induces flowering at species-specific times each year. Here we report synchronous bud break and flowering of tropical perennials that cannot be explained by seasonal changes in day length. We recorded flushing and flowering of more than 100 tropical trees, succulents and understory

herbs over several years. We observed the following phenological patterns throughout the northern Neotropics: wide-ranging trees flush or flower twice a year at the Equator, but annually further north; many trees leaf out in February; in autumn, wide-ranging perennials flower 4 months earlier in Mexico than at the Equator. This latitudinal variation of phenology parallels that of the annual cycle of daily insolation, a function of day length and solar irradiation. Insolation has two annual maxima at the Equator, it rapidly increases in February at all latitudes, and between Mexico and the Equator its maximum shifts from the summer solstice to the autumn equinox. These unique, manifold correlations suggest that throughout the tropics insolation, rather than day length, may control the phenology of many perennials. Our observations significantly extend current knowledge of environmental signals involved in photoperiodic control of plant development.

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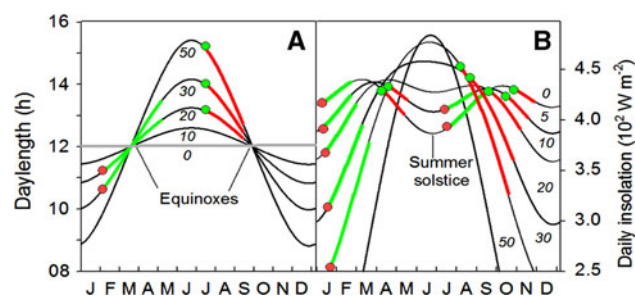
### Introduction

From the Equator to temperate latitudes, tree development is characterized by distinct periods of rest (dormancy), bud break, rapid shoot growth (flushing), and synchronous flowering, a prerequisite for efficient cross-pollination. The timing of development is well adapted to the seasonality of the environment where trees live. For example, with decreasing latitude, bud break and flowering of temperate trees induced by rising spring temperatures start progressively earlier. Between 43 and 46°N, near their northern limits of distribution, most North American broadleaved trees leaf out in May. At subtropical latitudes, wide-ranging

species, such as red maple (*Acer rubrum*), hackberry (*Celtis* sp.), beech (*Fagus grandifolia*), black cherry (*Prunus serotina*), oak (*Quercus* sp.) and others, do so in February, concurrent with sympatric evergreen tropical tree species, which replace leaves annually. In a cool mountain forest near Xalapa, Mexico (20°N), deciduous and evergreen trees of 20 species flushed in February during five consecutive years (Williams-Linera 1997; Borchert et al. 2005b). In a common garden in Gainesville, Florida (30°N), red maple seedlings grown from seed collected in southern Florida (26°N) leafed out in February, but seedlings of northern provenances did so 3 months later (Perry and Wang 1960). These examples illustrate that the time of bud break is determined genetically, varies between conspecific ecotypes adapted to different latitudes and must be controlled by different environmental signals.

The timing of synchronous bud break or flowering is highly correlated with its species-specific environmental trigger. This correlation constitutes a diagnostic tool that permits the reliable, indirect identification of the cue that induces bud break. In temperate climates, rising spring temperatures cause synchronous bud break of conspecific trees at times that vary from year to year at the same location. In many tropical trees seasonal variation in day length induces synchronous bud break or flowering at the same time each year throughout an entire region (photoperiodism; Rivera and Borchert 2001; Rivera et al. 2002). In most temperate trees, global warming has advanced the time of bud break induced by rising spring temperatures by several days (Menzel and Fabian 1999; Cleland et al. 2007), but in tropical lowlands, where mean temperatures are  $>25 \pm 3^\circ\text{C}$ , global warming is unlikely to affect the phenology of the thousands of tree species, regardless of whether it is under photoperiodic control or not (Rivera et al. 2002; Hubbell et al. 2008; Körner and Basler 2010). In tropical monsoon climates, trees at dry upland sites may stand leafless during most of the 4–6 months long dry season, and the first heavy rainfall triggers rehydration and synchronous flushing or flowering at times, that vary by several weeks from year to year and, because of the patchiness of rainfall, between nearby sites (Opler et al. 1976; Reich and Borchert 1982; Borchert 1994a, b; Eamus 1999). Studies establishing simple correlations between increasing irradiance and community-wide flowering lack the resolution necessary to identify the species-specific environmental cues inducing flowering or fruiting of tropical trees (van Schaik et al. 1993; Wright 1996; Zimmerman et al. 2007). In contrast to the synchronous phenological patterns analyzed here, many trees of tropical rain forests flush or flower at irregular intervals not correlated with any known environmental cue (Windsor 1982; Newstrom et al. 1994; S. J. Wright, personal communication).

Photoperiodic control of plant development has been studied mainly in experiments exposing herbaceous and a few woody plants to different photoperiods (Kramer 1936; Wareing 1956; Downs and Borthwick 1956; Thomas and Vince-Prue 1997). The ecological significance of photoperiodism received little attention (Thomas and Vince-Prue 1997; Jackson 2008), even though Garner and Allard (1920) recognized that flowering periods must be well adapted to the seasonal variation of day length at the latitudes where a species lives. The important role of photoperiod in inducing bud break and flowering of many tropical trees was unknown prior to our first field studies (Borchert and Rivera 2001; Rivera and Borchert 2001), because all earlier investigations focused on temperate tree species, in which bud break is induced by rising spring temperatures and only the formation of resting buds and winter dormancy is under photoperiodic control (Wareing 1956; Thomas and Vince-Prue 1997). The methods employed in our field studies differ substantially from experimental studies of flower induction, in which herbaceous plants are exposed to photoperiods of different duration and the critical day length inducing flowering is deduced from the time required for the first flower buds to appear (Thomas and Vince-Prue 1997). Under natural conditions day length increases and decreases gradually. Bud break or flowering of trees are induced when day length reaches an unknown critical value (Fig. 1, red and green circles), which can be deduced from biweekly field observations (see “Methods”). In earlier experiments conducted in a heated greenhouse at 40°N, transfer of dormant tree seedlings (*Fagus*, *Liriodendron*, *Quercus*) from the natural day length in January ( $<9$  h) to an experimental 16 h photoperiod caused rapid bud break within 3 weeks (Kramer 1936). In Brazil, the first lateral inflorescence meristems of the rubber tree (*Hevea brasiliensis*) were detected 5–6 weeks after the winter solstice on



**Fig. 1** Annual variation in day length (a) and daily insolation (b) between the Equator and 50°N. Green curves periods of bud break or flowering induced by increasing day length or daily insolation; red curves flowering periods induced by declining day length or insolation. Circles earliest times of bud break or flowering induced by increasing (red circles) or decreasing (green circles) day length or insolation. With declining latitude, autumn flowering induced by declining insolation (red circles) starts progressively later (b)

rapidly elongating new shoots (Dornelas and Rodriguez 2005). In general, photoperiodic induction of phenological phase change in tropical trees apparently takes place 2–3 weeks before the first signs of bud break or flower development become visible.

The synchronous flushing of temperate trees in February, as observed at 20°N in Mexico (Williams-Linera 1997), also indicates photoperiodic control of bud break, which is masked by low winter temperatures at higher latitudes. In most temperate tree species, rising spring temperatures cause the emergence of flowers from resting buds formed during the previous growing season, but in a few temperate outliers of tropical plant families terminal or lateral inflorescences appear on new shoots at the same time each year, in May/June (Borchert, unpublished observation). In species such as tree of heaven (*Ailanthus altissima*, Simaroubaceae), silk tree (*Albizia julibrissin*, Mimosaceae), catalpa (*Catalpa bignonioides*, Bignoniaceae), goldenrain tree (*Koelreutia paniculata*, Sapindaceae) and black locust (*Robinia pseudoacacia*, Papilionaceae) flower differentiation is therefore likely to be induced by increasing day length. In the semi-deciduous tropical forests of Costa Rica and Thailand, increasing day length causes synchronous bud break of many deciduous tree species during the late dry season, in March (Borchert and Rivera 2001; Rivera et al. 2002; Elliott et al. 2006). Similarly, bud dormancy of many spring-flushing tropical trees is likely to be induced by declining day length in autumn (Borchert and Rivera 2001).

Latitudinal variation of photoperiodic control has been studied mainly in temperate plants. For example, cocklebur (*Xanthium strumarium*, Asteraceae) plants grown in a common garden from seed collected at 47°N flowered almost 2 months earlier than those originating at 30°N (Ray and Alexander 1966). The critical day length inducing growth cessation in Norway spruce (*Picea abies*) and aspen (*Populus tremula*) in autumn ranges from 21 h at 63°N (Northern Sweden) to 15 h or less between 48 and 50°N in Germany (Heide 1974; Böhlenius et al. 2006). In Mexico (20°N), the woody short-day species *Montanoa tomentosa* (Asteraceae) flowers in July, but in Costa Rica (10°N) it does so 4 months later (Calle et al. 2009). The latitudinal variation of phenology within wide-ranging species constitutes a large-scale natural experiment revealing the role of photoperiod in the adaptation of plants to different latitudes.

In equatorial rainforests day length is constant and climate often does not vary in predictable annual patterns. Nevertheless, many tree species flush or flower at the same time each year, i.e., their phenology appears to be under photoperiodic control (Holttum 1940; Borchert et al. 2005a; Yeang 2007a). Near the Equator, more than half of >100 woody species flowered in the same month during five consecutive years (S. J. Wright, personal

communication). This raises the question: which environmental signal synchronizes the annual development of these evergreen tropical trees? Here we describe and analyze observations of synchronous flushing or flowering, made throughout the tropics and not explained by current concepts of developmental control by day length. First, several wide-ranging tree species flush or flower twice a year near the Equator, but only once a year north of 8°N. Second, from the Equator to the northern subtropics many evergreen trees leaf out in February. Third, in other wide-ranging tree species the onset of flowering shifts by 4 months with declining latitude, from July, in Mexico, to October, near the Equator. Fourth, many subtropical desert succulents flower synchronously in February (von Willert et al. 1992; Smith et al. 1998). The unknown environmental signal inducing succulent flower development in mid-winter is likely to be identical with the trigger of synchronous bud break of tropical trees at that time. In many other succulent species declining day length is known to induce flowering in autumn (e.g., *Kalanchoë*; *Sedum*, *Schlumbergera* (Christmas cactus); Thomas and Vince-Prue 1997). In arid climates with irregular rainfall seasonal variation in photoperiod appears to be the principal environmental trigger of synchronous flowering.

Daily insolation (henceforth “insolation”) is a function of day length and the intensity of irradiation, as determined by the angle at which the sun’s rays strike the earth (see “Materials and methods”; Strahler and Strahler 2005; Yeang 2007a). Between the Tropic of Cancer (23°N) and the Equator, the maximum of insolation shifts from the summer solstice to the autumn equinox (Fig. 1b). In parallel, within the wide-ranging genus *Montanoa* (Asteraceae), flowering time changes with latitude, from July, in Mexico, to November, in Colombia. The distinct latitudinal co-variation of these two variables suggests that declining insolation induces synchronous flowering in *Montanoa* (Calle et al. 2009). Here we examine the hypothesis that the above, unexplained phenological patterns might be also determined by seasonal and latitudinal variation in daily insolation (Fig. 1b), i.e., they are under photoperiodic control.

## Materials and methods

### Species studied

All species analyzed in this study are angiosperms that flush or flower in synchrony at species-specific times each year. For species observed in this study, full species names are given in Tables 1 and 2 or in the text. Author names for other tree species may be found in the cited references. Tree species mentioned repeatedly will be referred to by genus name.



**Table 1** Location of phenological field observations and collection of herbarium specimens

Lat. N	Location	Species	Years	Figure	Observer or source
Field observations					
0	Galapagos Islands	<i>Cedrela odorata</i> L. <i>Cordia alliodora</i> (Ruiz & Pav.) Cham.	1	3a	Tye
0	Singapore	<i>Cedrela glaziovii</i> , <i>Couropita guianensis</i> , <i>Ficus variegata</i> , <i>Kigelia pinnata</i> , <i>Lecythis</i> sp., <i>Parkia javanica</i> , <i>Peltophorum</i> <i>Pterocarpum</i> , <i>Terminalia catappa</i>	10	3a	Holtum (1940), Borchert et al. (2005a)
4	Cali, Colombia	<i>Guazuma ulmifolia</i> Lam. <i>Montanoa quadrangularis</i> K. Koch	1.5 3	2a 3a	Calle, Piedrahita
7	Ibadan, Nigeria,	6 Species	5		Njoku (1963)
7 S	E. Java, Indonesia	<i>Pithecelobium saman</i> , <i>P. umbellatum</i>	1		Rivera et al. (2002)
10	Costa Rica	<i>Cordia alliodora</i> , <i>Delonix regia</i> (Bojer) Raf. <i>Guazuma ulmifolia</i> <i>Jacquinia pungens</i>	3 3 1	3a, b 2 3c	Borchert Rivera et al. (2002) Janzen (1970)
12 S	Northern Australia	<i>Buchania</i> , <i>Erythrophleum</i> <i>Eucalyptus porrecta</i> , <i>E. clavigera</i>	3		Williams et al. (1997)
16 S	Brasilia, Brazil	<i>Rourea induta</i> , <i>Ouratea hexasperma</i>	2		Rivera et al. (2002)
19	Chiang Mai, Thailand	<i>Anneslea fragrans</i> , <i>Dipterocarpus</i> <i>tuberculatus</i> , <i>Eugenia albiflora</i> , <i>Shorea</i> <i>siamensis</i> , <i>Tristanopsis burmanica</i> <i>Balakata baccata</i> (Roxb.) Esser, <i>Betula</i> <i>alnoides</i> Buch.-Ham., <i>Gluta usitata</i> (Wall.) Ding Hon., <i>Engelhardtia spicata</i> Blume, <i>Nyssa javanica</i> (Blume) Wang, <i>Quercus</i> <i>brandisia</i> Kz., <i>Syzygium cunii</i> Blume.	3	3c	Elliott et al. (2006)  Borchert
20	Xalapa, Mexico	13 Tropical tree species 11 Temperate tree species	5 3		Williams-Linera (1997) Borchert et al. (2005b)
20	Chamela, Mexico	<i>Forchhammeria pallida</i>	3	3c	Bullock (2002)
20	Oaxaca, Mexico	40 Cactaceae species	1	5a	Valiente-Banuet et al. (1995)
23 S	Jujuy, Argentina	<i>Cascaronia estragalina</i> , <i>Sapium saltense</i> , <i>Gleditsia amorphoides</i>	3		Rivera et al. (2002)
30	Tucson, Arizona	13 Cactaceae species	3 mo	5a	Leftin
30	San Diego, California	20 Species of <i>Conophytum</i> , <i>Lithops</i>	3 mo	5a	Hammer
48	Munich, Germany	20 Species of Cactaceae >150 Species of South African succulents (see Table 2) <i>Quercus robur</i> L.	2 2 6 mo	5b–d 5b, d 3c	Schlumpberger Schlumpberger Schlumpberger
Flowering herbarium species					
3–10	Colombia	<i>Gliricidia sepium</i> (Jacq.) Kunth	H1	3a	Piedrahita
3–25	Colombia to Mexico	<i>Guazuma ulmifolia</i>	H2	2a	Borchert
3–25	Colombia to Mexico	20 Species of <i>Montanoa</i>	H4	4	Funk (1982)
10–15	Central America	6 Species of <i>Begonia</i>	H2	6a	Borchert
25–30	Sonora, Mexico	62 Species of Cactaceae	H3	5a	Paredes-Aguilar et al. (2000)

Herbaria: H1 Herbario Nacional de Colombia, Bogotá, H2 Herbarium of the Missouri Botanical Garden, St. Louis, H3 University of Arizona Herbarium, H4 other herbaria

### Field sites and monitoring of phenology

Phenological observations were carried out at 16 field sites between the Equator and 48°N (Table 1). We combined our own observations made in the course of this (7 sites)

and earlier field studies (5 sites) with similar observations reported by others (7 sites) to increase the number of observations made at various latitudes (Table 1).

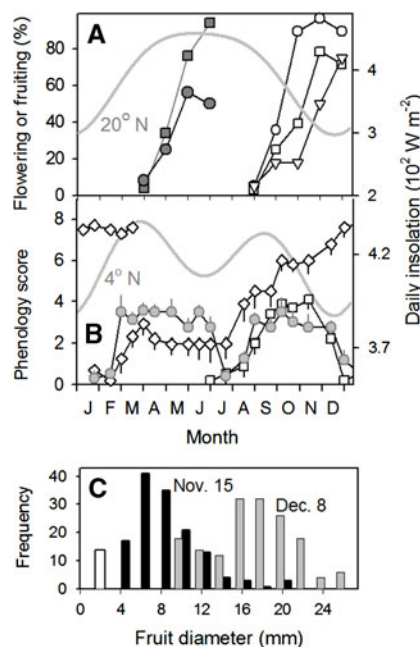
With few exceptions, bud break or expansion of flower buds started synchronously in all observed plants during the interval

**Table 2** Species of Cactaceae (1–10) and South African succulents (12–23), whose flowering periods are shown in Fig. 5d

Cactaceae	
1	<i>Mammillaria gracilis</i> Pfeiff.
2	<i>Eriosyce villosa</i> (Monv.) Katt.
3	<i>Stenocactus crispatus</i> (DC.) A. Berger
4	<i>Rebutia fiebrigii</i> (Gürke) Britton and Rose
5	... Under 10.5 h photoperiod
6	<i>Matucana aureiflora</i> F. Ritter
7	<i>Gymnocalycium bruchii</i> (Speg.) Hosseus
8	<i>Ariocarpus agavoides</i> (Castan.) E.F. Anderson
9	<i>Ariocarpus kotschoubeyanus</i> (Lem.) K. Schum.
10	<i>Eriosyce subgibbosa</i> (Haw.) Katt.
South African succulents	Family
12	<i>Faucaria tigrina</i> Schwantes Aizoaceae
13	<i>Lithops karasmontana</i> N.E. Br. Aizoaceae
14	<i>Conophytum bilobum</i> (Marloth) N.E. Br. Aizoaceae
15	<i>Aloe forbesii</i> Balf.f. Aspodelaceae
16	<i>Kleinia stapeliiformis</i> Stapf Asteraceae
17	<i>Euphorbia horrida</i> Boiss. Euphorbiaceae
18	<i>Monadenium guentheri</i> Pax Euphorbiaceae
19	<i>Haworthia retusa</i> Duval Aspodelaceae
20	<i>Kalanchoe sp. (var. quitense)</i> Crassulaceae
21	<i>Crassula montana</i> L.f. Crassulaceae
22	<i>Pelargonium ochroleucum</i> Harv. Geraniaceae
23	<i>Tylecodon paniculatus</i> (L.f.) Toelken Crassulaceae

between two biweekly field observations (see slopes of curves in Figs. 2a, 3). Statistical analysis of the observed phenological patterns was therefore neither necessary nor possible.

**Fig. 2** Latitudinal variation of phenology in *Guazuma ulmifolia*. **a** Flowering on elongating shoots (filled symbols) and fruit maturation (empty symbols) in Mexico (20°N; circles), Nicaragua (12°N; squares) and Panama (8°N; triangles). **b** Flowering on elongating shoots (circles) and fruit development beginning in February (diamonds) and August (squares) at 4°N in Cali, Colombia. **c** Growth of *Guazuma* fruits in Costa Rica (10°N). Fruits collected from 5 trees on Nov. 15 (black), Dec. 8 (gray), and from a branch illuminated by a floodlight (white). **d** Flowering twig with new foliage. **e** Growing fruits on leafless, lignified twig

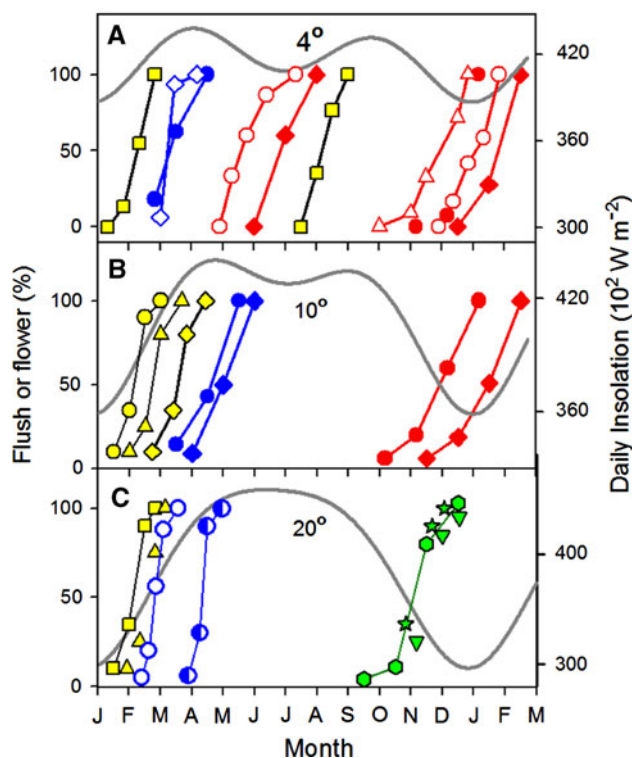


Tree phenology was monitored in 5–10 conspecific trees observed in the field and either recorded as species-specific phenology scores (Fig. 2b) or as the percentage of observed conspecific trees flushing or flowering at a given date (Figs. 2a, 3). In Munich (48°N), bud break of *Quercus robur* was monitored in two groups of 15 seedlings growing under the natural light cycle, one in a cool greenhouse, the other outdoors.

Flowering of succulents was recorded weekly by counting species with expanding flowers or as the date when flower buds or expanded flowers became visible among conspecifics. Flowering times of Cactaceae native to Mexico and Arizona were recorded in Tucson, Arizona (30°N) and obtained from the literature (Table 2). Autumn flowering of 12 species of Aizoaceae was observed in southern California (30°N; Table 2). The flowering times of 24 species of Cactaceae and >150 species of South African succulents (Table 2) were recorded over 2 years in the Munich Botanical Garden (Munich, Germany, 48°N), where the succulents were grown under the natural light cycle in a moderately heated greenhouse. In late December 2004, 10 *Rebutia fiebrigii* (Cactaceae) plants were transferred from the natural 8.3-h photoperiod then prevailing in the greenhouse to a 10.5-h photoperiod in a growth chamber to study the effects of photoperiod on the induction of flower buds.

#### Flowering times of herbarium specimens

Flowering times of a few species ranging from the Equator to Mexico (Table 1) were deduced from the collection dates of flowering herbarium specimens in the Missouri Botanical Garden's TROPICOS database at <http://www.tropicos.org>. This method has been tested repeatedly (Croat 1969;



**Fig. 3** Induction of flushing and flowering of tropical trees by seasonal variation in daily insolation (gray, right Y-axis). **a, b** Phenology of wide-ranging tree species near the Equator ( $0^{\circ}$ – $4^{\circ}$ ) and at  $10^{\circ}$ N. Flushing induced by increasing insolation (yellow): eight tree species in Singapore ( $0^{\circ}$ ; squares; Holttum 1940); *Thouinidium decandrum* (circles), *Byrsonima crassifolia* (triangles), *Delonix regia* (diamonds). Flowering on new shoots (blue): *Cedrela odorata* (diamonds), *Spondias mombin* (circles). Flowering induced by declining insolation (red): *Cordia alliodora* (circles), *Gliricida sepium* (diamonds), *Montanoa quadrangularis* (triangles). Empty symbols: field observations; filled symbols: data from herbarium collections. **c** Phenology at  $20^{\circ}$ N. Flushing of evergreen species (yellow): *Eugenia albiflora*, Chiang-Mai, Thailand (squares); *Liquidambar styracifolia*, Xalapa, Mexico (triangles). Flushing induced by decreasing insolation in Central America (green): *Andira inermis* (triangles), *Forchhammeria pallida* (hexagons), *Jacquinia pungens* (stars). Bud break of *Quercus robur* seedlings grown in Munich, Germany (blue) in a greenhouse (circles) or outdoors (half-circles)

Borchert 1996; Rivera and Borchert 2001; Primack et al. 2004) and was validated here by checking the coincidence of the flowering periods of *Cordia alliodora* and *Guazuma ulmifolia*, species monitored at several field sites, with those from herbarium observations (“Results”).

#### Daily insolation and day length

Annual variation in day length and daily insolation at different latitudes was obtained from the internet (day length: <http://www.geocities.com/jjlammi/>; daily insolation: <http://aom.giss.nasa.gov/srlocat.html>). These data were used to calculate seasonal changes in day length and daily insolation.

Daily insolation is a measure of the instantaneous solar energy flow ( $\text{W m}^{-2}$ ) received at a particular location above the earth atmosphere on any day of the year (Strahler and Strahler 2005; Yeang 2007a). It is a function of day length and the intensity of irradiation as determined by the angle at which the sun’s rays strike the earth. North of the Tropic of Cancer ( $23.5^{\circ}\text{N}$ ), daily insolation—like day length—is largest at the summer solstice (Fig. 1). South of the Tropic of Cancer, insolation has two annual maxima at the times when the sun passes directly overhead. Towards the Equator these maxima become more distinct as they shift from the summer solstice towards the equinoxes and become separated by a growing second minimum (Fig. 1b). At the Equator itself, seasonal change in insolation is a function of irradiation intensity alone, because day length is constant. In the southern hemisphere, latitudinal and seasonal changes in daily insolation are 6 months out of phase with those described for the northern hemisphere.

#### Terminology

We will use the conventional term “photoperiodic control” when referring to developmental responses induced by seasonal variation in either day length or daily insolation. To prevent common misunderstandings, we wish to emphasize the fundamental difference between the functions of absorbed light in photoperiodism as compared to photosynthesis. In natural settings, only the relative lengths of the daily light and dark periods are important for photoperiodic control, and variation in light intensity due to variable cloudiness is irrelevant (Thomas and Vince-Prue 1997; Renner 2007). Seasonal changes in day length or daily insolation trigger the molecular processes leading to subsequent developmental changes at the organ level (“Discussion”). In contrast, the absorption of solar irradiation in photosynthesis results in an immediate photosynthetic energy gain, which is strongly affected by cloud cover.

## Results

### Latitudinal variation in the annual course of insolation

The annual course of insolation varies widely with latitude (Fig. 1b). Under the hypothesis that seasonal changes in insolation induce synchronous plant development, the following should be true in the Northern hemisphere. (Expectation 1) Long-day (LD) plants flush or flower during periods of increasing insolation. With increasing latitude, these periods start slightly later in January–February and become longer (Fig. 1b, red circles, green curves). Near the Equator there is a second increase in

insolation in July/August, and hence LD plants should exhibit a second flowering period at that time. (Expectation 2) Short-day (SD) plants flower during periods of decreasing insolation. With decreasing latitude, these periods start progressively later between July and November and become shorter (Fig. 1b, green circles, red curves). Near the Equator there is a second decrease in insolation in April/May, and hence SD plants should exhibit a second flowering period at that time. Between the Tropic of Cancer (23.5°N) and the Equator, the time course of insolation differs strongly from that of day length (Fig. 1a, b) and the phenology of SD-plants should reflect this difference.

Earlier, we reported synchronous flowering of many tree species near the Equator, but could not identify the inducing signal with certainty, because we were unaware of the bimodal course of insolation at the Equator (Borchert et al. 2005a). Here we compare the latitudinal shift in the annual course of insolation with that recorded for the phenology of wide-ranging tropical tree species that flush or flower at the same time each year.

#### Latitudinal variation of the phenology of *Guazuma ulmifolia*

Latitudinal variation of phenology has been recorded only in a few tropical tree species. *Guazuma* is a fast growing pioneer-species ranging from Mexico to Paraguay (Borchert 1996). In the semi-deciduous forests of Mexico and Central America, the LD-species *Guazuma* is brevi-deciduous. After a short leafless period, young shoots emerge synchronously during the late dry season in early March, 1–2 months before the first summer rains (Rivera et al. 2002). Vigorous shoots may continue to grow for several months and form up to 20–30 leaves. Axillary inflorescences bearing small, inconspicuous flowers appear during shoot elongation (Fig. 2a, d). Development of the small fruits formed soon after flowering remains arrested at an early stage (3 mm diameter) until September, when fruit expansion resumes, first in Mexico (20°N), and then in Central America (10–14°N) and Panama (8°N) (Fig. 2a, right). During final expansion fruits attain a diameter of ~25 mm and increase ~250-fold in volume (Fig. 2c, e; Janzen 1982). In Costa Rica, nocturnal exposure of branches to a floodlight inhibited fruit growth and induced abnormal flushing and flowering in October (Fig. 2c, white bar).

Near the Equator (4°N, Cali, Colombia), *Guazuma* is evergreen and synchrony among the branches of individual trees and between different trees is less distinct than further North. There are two annual periods of shoot growth and flowering, one from February to June, the other from August to November (Fig. 2b, circles). As in Central

America, growth of the “Spring fruits” is arrested at an early stage, but resumes in July and continues until December/January (Fig. 2b, diamonds). Consequently, between July and November trees bear growing, flowering shoots of the second annual flush as well as expanding fruits on the older, leafless branch sections (Fig. 2d, e). Small fruits formed during the second flush abscise in November, i.e., only one set of fruits matures each year.

Several phases of the seasonal development of *Guazuma* are highly correlated with the annual course of insolation, i.e., they appear to be under photoperiodic control. Near the Equator, where day length is constant, the two periods of shoot growth coincide with the two periods of increasing insolation in February and August (Figs. 1b, 0, 5°N; 2b). At higher tropical latitudes, *Guazuma*, like many other brevi-deciduous species, leaves out synchronously during the increase in insolation in March, at the end of the dry season (Fig. 2a; Rivera et al. 2002). The synchronous onset of fruit expansion in autumn (Fig. 2a, c) and its inhibition by nocturnal illumination indicates photoperiodic induction of fruit development by declining insolation, which to our knowledge has not been observed in any other species. Between Mexico and Panama the summer maximum of insolation shifts to the autumn equinox, and fruit growth induced by declining insolation starts correspondingly later (Figs. 1b, 2a).

#### LD trees

Many evergreen tropical trees shed and replace leaves at the same time each year. During this “leaf exchange” synchronous bud break and expansion of new shoots may begin weeks before all old leaves have abscised. Leaf exchange is therefore less conspicuous than drought-induced leaf abscission, leaflessness and subsequent flushing of deciduous trees. It has been observed throughout the tropics (Table 1), but its environmental trigger has not been identified before (Borchert 1994a; Williams-Linera 1997; Elliott et al. 2006).

The time of synchronous flushing of evergreen LD species can be deduced from records of both flushing and flowering, because lateral or terminal flowers generally appear on new, rapidly expanding shoots (Figs. 2d; S1). Flushing and flowering of conspecific trees is usually completed within 2 months, and only the periods of rapid change in phenology are therefore graphed in Fig. 3 for numerous species.

Near the Equator, there are two periods of increasing insolation (Fig. 1b, 0, 5°N, green). Evergreen LD species such as *Guazuma ulmifolia*, *Hevea brasiliensis* and *Terminalia catappa* flush during both of these periods, others, such as *Cedrela* sp., *Ficus* sp., and *Spondias mombin* do so only in February (Figs. 2b, 3a, yellow, blue



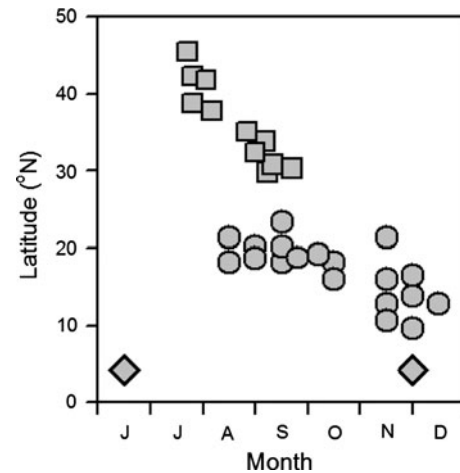
symbols; S1) (Holtum 1940; Borchert et al. 2005a). In *Hevea*, as in other LD trees, rapid shoot elongation in February is accompanied by the differentiation of lateral flower primordia (Figs. 3a; S1; Dornelas and Rodriguez 2005) and flowering of the rubber tree is therefore not induced by high solar irradiance around the spring equinox, as proposed by Yeang (2007a, b).

Further North, all evergreen LD species flush during the single period of increasing insolation in February (Fig. 3b, c, yellow symbols) (Rivera et al. 2002; Borchert et al. 2005a). Brevi-deciduous species adapted to drier sites tend to leaf out slightly later, in March (Figs. 2a, 3b, blue symbols).

In the northern hemisphere, “winter flushing”, i.e., bud break of evergreen, leaf-exchanging trees in February, has been observed from the Equator to the subtropics (Table 1), namely in Singapore, 0° (Fig. 3a, squares; Holtum 1940), Colombia, 4°N (Fig. 2b, circles), Nigeria, 7°N (Njoku 1963), Costa Rica, 10°N (Fig. 3b, yellow symbols; Rivera et al. 2002), Thailand, 19°N (Fig. 3c, squares; Elliott et al. 2006) and Mexico, 20°N (Fig. 3c, yellow triangles; Williams-Linera 1997; Borchert et al. 2005b). In the southern hemisphere leaf exchange in August has been recorded in Java, 6°S (Rivera et al. 2002), tropical Australia, 12°S (Williams et al. 1997), Brazil, 16°S (Rivera et al. 2002) and Argentina, 23°S (Rivera et al. 2002). Throughout the tropics, synchronous bud break in February or August coincides with, and is likely to be caused by, increasing insolation 4–6 weeks after the winter solstice (Figs. 1b, Jan–Feb; 3a–c, gray curves).

In mid-February 2010, 4 months after the last rainfall, most trees of a montane monsoon forest in northern Thailand (Doi-Suthep National Park near Chiang-Mai, Thailand, 19°N, 600–1,000 m) carried senescent, dark-green or brownish leaves, but in about 5% of the trees, belonging to 12 species, new shoots with light green, immature leaves were expanding, indicating that bud break had started synchronously in late January (Table 1). Both in North America and Southeast Asia the January–7°C-isotherm, which runs along the 30°N parallel, constitutes the boundary between cold-temperate and frost-free subtropical climates (Pohlmann 1976; Borchert et al. 2005b). In subtropical Mexico flushing of broadleaved evergreen trees starts in early February (“Introduction”; Fig. 3c). The forests of subtropical SE China contain >350 species of evergreen tropical and temperate trees. Many genera (e.g., *Albizia*, *Camellia*, *Cinnamomum*, *Daphne*, *Helicia*, *Machilus*, *Neolitsea* and others) flush in early February, as others do in Mexico and Thailand (Kira 1991; Jian et al. 2009; Jian, personal communication).

Near Xalapa, Mexico (20°N), wide-ranging temperate trees such as *Celtis*, *Fagus*, and *Quercus* and others flush in February, at the same time as sympatric tropical species



**Fig. 4** Latitudinal variation in flowering time induced by declining insolation. *Squares* flowering of *Xanthium* (Compositae) at temperate latitudes (Ray and Alexander 1966). *Circles* flowering start in 20 subspecies of *Montanoa* (Asteraceae) between Mexico and 4°N. *Diamonds* flowering start of *M. ovalifolia* and *M. quadrangularis* near the Equator

(Table 1). At 48°N (Munich), oak seedlings (*Quercus robur*) growing in a greenhouse under the natural light regime leafed out in February, 2 months earlier than those growing outdoors (Fig. 3c, blue circles).

#### SD trees and shrubs

At 10°N, the wide-ranging SD species *Cordia alliodora* and *Gliricidia sepium* flower once a year, in late autumn, but near the Equator, they do so twice, in May and November (Fig. 3a, b, red; Rivera and Borchert 2001). The transition from vegetative growth to the development of terminal inflorescences starts more than 3 months earlier in *Montanoa* species growing in Mexico (20°N) than in those near the Equator (Fig. 4), where *Montanoa quadrangularis* flowers in November, but prolonged flowering of *M. ovalifolia* starts in June (Fig. 4, diamonds) (Calle et al. 2009). In parallel, the autumnal decline in insolation begins progressively later moving from the Tropic of Cancer towards the Equator, where there are two periods of declining insolation (Figs. 1b red, 2b–d). In contrast to most other tree species, declining—rather than increasing—insolation induces flushing of *Andira inermis*, *Forchhammeria pallida* and *Jacquinia pungens* in November (Fig. 3c, green symbols) (Janzen 1970; Bullock 2002).

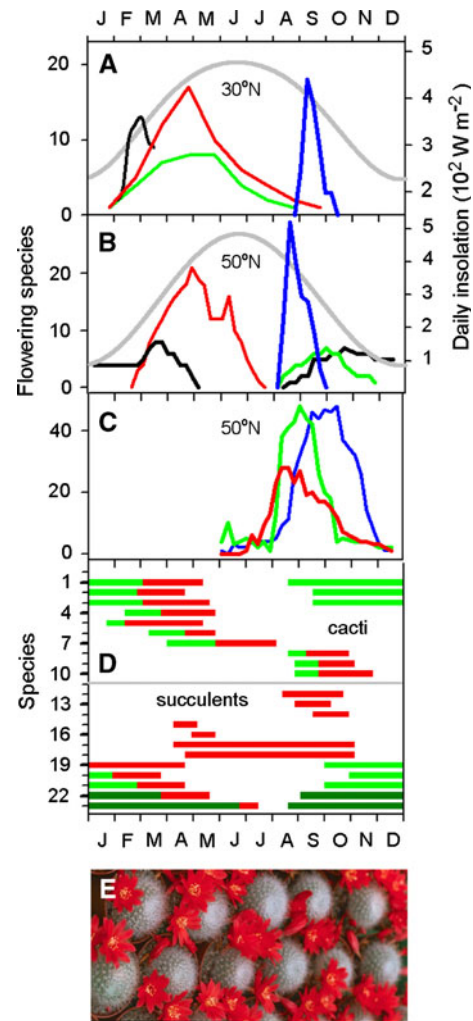
The above observations show that throughout the tropics, LD tree species flush or flower during the single period (at 10–25°N) or double periods (near the Equator) of increasing insolation. With declining latitude, SD trees flower progressively later during periods of decreasing insolation. This fits precisely with the expectations of the insolation hypothesis.

## Subtropical succulents

Flowering of Cactaceae (24 species) and South African succulents (>150 species; Table 2) was monitored in Arizona (30°N), California (30°N) and in the greenhouses of the Munich Botanical Garden at 48°N (Fig. 5a–d; Table 1). Each year, the observed plants flowered at the same species-specific time in spring or autumn. In most Cactaceae flower buds emerged shortly before blooming in spring and autumn, but in some species they appeared in autumn, remained dormant during the winter, and opened in spring (Fig. 5a, b, d species 1–10). Species native to subtropical deserts with irregular spring or summer rainfall flowered in spring, and species from regions with late summer or winter rains did so in autumn. In Sonora and Arizona (25–30°N), the first LD cacti bloomed in early February (Fig. 5a), and those growing under the natural light cycle in a Munich greenhouse flowered 2 weeks later (Fig. 5b, d). Transfer of 10 *Rebutia fiebrigii* (Cactaceae) plants from the natural 8.3-h photoperiod in late December to a 10.5-h photoperiod in a growth chamber induced the appearance of flower buds 3 weeks later (Fig. 5e). By extrapolation, flower buds that opened in the greenhouse in late February probably were induced 3 weeks earlier by the natural 9.5-h photoperiod prevailing then (Fig. 5d, species 4 and 5).

In Southwest Africa, at 20–30°S latitude, succulent species in the Aizoaceae and other families flower in autumn or spring, remain dormant during the hot and dry summer (November–December), and grow during the relatively cool and moist winter months (May–August; Smith et al. 1998). In Munich, watering of Aizoaceae between May and July induced neither vegetative growth nor the emergence of flowers, i.e., the plants were dormant (Fig. 5d, species 12–23). The flowers of *Conophytum* and *Lithops* species opened in late August (Fig. 5b, blue; c, d, species 12–14), and the same species cultivated in California (30°N) started flowering 2 weeks later (Fig. 5a, blue). As in *Montanoa* (Fig. 4; Calle et al. 2009), autumnal flowering of SD succulents thus begins earlier at higher than at lower latitudes (Fig. 5a, b), fitting with the earlier onset of the decline in insolation at higher latitudes (Fig. 1b). As expected under the insolation hypothesis, increasing and decreasing insolation act as the signal for, respectively, summer dormancy and autumn flowering of these succulents.

The timing of flower development and anthesis varied widely among the studied succulents of other families (Fig. 5d, species 15–22; plant names see Table 2), but flowering and, in a few species, shoot growth started consistently at the same time, in spring or autumn, in each of the two study years.

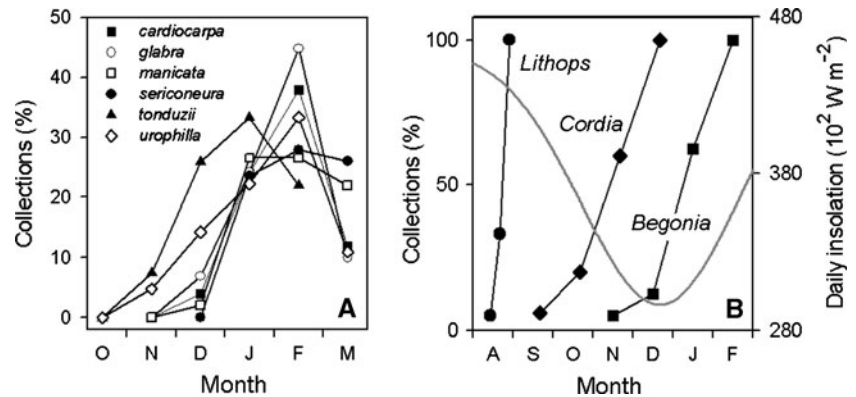


**Fig. 5** Flowering periods of succulents between 20 and 50°N. **a, b** Annual course of daily insolation at 30 and 50°N (gray, right legends). **a** Flowering periods of Cactaceae: Oaxaca, 20°N (green), Sonora, Mexico, 25–30°N (red); Tucson, Arizona, 30°N (black). Flowering starts of *Conophytum* and *Lithops* (Aizoaceae) in California, 30°N (blue). **b** Flowering of Cactaceae and South African succulents in the greenhouses of the Munich Botanical Garden (48°N). Cactaceae: spring flowering (red); autumn flowering (green); flower buds develop in autumn, remain dormant in winter, and open in spring (black). Synchronous flowering in *Conophytum* and *Lithops* (blue). **c** Flowering periods of >150 species of South African succulent in Munich. *Conophytum* (red), *Lithops* (green), and five other genera (*Argyroderma*, *Faucaria*, *Fenestraria*, *Ophthalmophyllum*, *Pleiospilos*) (blue). **d** Phenology of Cactaceae (rows 1–10) and other South African succulents (rows 12–23) grown in Munich. Flowering time of *Rebutia fiebrigii* under natural (row 4) and under an experimental 10.5 h photoperiod (row 5). Flower buds (green), flowers (red), vegetative growth (brown). Species names given in Table S2. **e** Synchronous flowering in February of *Rebutia fiebrigii* in a Munich greenhouse

## Tropical herbs

Synchronous flowering of a tropical SD herb, *Begonia urophylla*, has been documented in Costa Rica at 10°N,

**Fig. 6** Flowering periods induced by declining insolation. **a** Flowering periods of six Central American *Begonia* species as deduced from herbarium collections. **b** Comparison between the flowering periods of *Lithops* (Fig. 5a), *Cordia alliodora* (Fig. 2c), and *Begonia* (Fig. 6a)



where this species flowers in December (Rivera and Cozza 2008). Under experimental conditions, flower buds appeared 80 days after initial exposure to an experimental 11-h-light/13-h-dark regime, implying that the flowers opening naturally in December had been induced 80 days earlier, in late September, when photoperiod was declining and had reached ca. 12 h. To examine whether photoperiodic flower induction may be more widespread in *Begonia*, we compiled flowering dates for well-collected species from the herbarium of the Missouri Botanical Garden (“Materials and methods”). In Central America, very few flowering *Begonia* specimens were collected in November/December and most are from January and February. This fits with the hypothesis that synchronous onset of flowering in *Begonia* is induced by declining insolation in October or November (Fig. 6a). *Begonia* species collected between Panama and Ecuador flower throughout the year, and the wide-ranging *B. glabra* flowers synchronously in Central America, but asynchronously in Colombia (data not shown).

## Discussion

We monitored synchronous bud break and flowering that occurs every year at the same time in many arborescent, shrubby, succulent, and herbaceous tropical species. The observed phenological patterns support the hypothesis that in many tropical perennials seasonal changes in daily insolation, rather than day length, synchronize phenology.

First, in evergreen trees growing near the Equator, where day length is constant, the two annual periods of synchronous flushing (in LD species) and flowering (in SD species) coincide with the two periods of increasing or decreasing insolation, respectively (Figs. 1b, 0°, 5°N; 2b; 3a) (Borchert et al. 2005a). In equatorial rainforests the density of conspecific trees may be as low as 1 tree/ha (Black et al. 1950) and photoperiodic induction of synchronous flowering is probably the best way to achieve successful pollination

among the >11,000 Amazonian tree species (Hubbell et al. 2008).

Second, between the Equator and 10°N, both insolation and the phenology of wide-ranging tree species change from a bimodal to a unimodal annual cycle (Figs. 2a, b, 3a, b). For example, near the Equator *Guazuma* flushes in February and August, but at higher latitudes it does so only in Spring (Fig. 2a, b).

Third, throughout the tropics, many evergreen LD tree species have been observed to flush synchronously about 6 weeks after the winter solstice in response to an unknown environmental trigger (Table 1; Borchert 1994a), which we identify here as increasing insolation (Figs. 1b, 3). In the subtropics, increasing insolation causes flowering of cacti in February (Fig. 5a), spring flowering of South African succulents (Fig. 5d, 15–18) and summer dormancy of autumn-flowering Aizoaceae. In greenhouses at Northern latitudes, increasing insolation triggers bud break of oak seedlings and succulent flowering in February (Figs. 3c, circles, 5b, d). In future experiments, such observations should be confirmed and extended under controlled environmental conditions.

Fourth, if induced by declining day length, autumn flowering should start about 1 month after the summer solstice at all latitudes (Fig. 1a, green circles). De facto, flowering begins progressively later with declining latitude, as does the autumnal decline in insolation (Figs. 1b, green circles; 3c, d, August–December; 4, 5a, b). These specific correlations constitute strong evidence for the photoperiodic induction of flowering by declining insolation (Calle et al. 2009). In a few species, declining insolation induces flushing (Fig. 3c, green symbols) or fruit development, as reported here for the first time; like autumn flowering, late fruit development of *Guazuma* starts progressively later with declining latitude (Fig. 2a).

In conclusion, any one of the phases of seasonal development may be under photoperiodic control in tropical perennials, and the observed complex latitudinal changes in phenology are highly correlated with those in insolation. Unlike the seasonal variation in temperature and

day length at temperate latitudes, the seasonal variation of insolation at lower latitudes is too small to be perceived by humans, and its role in the control of tree phenology therefore has been recognized only recently (Yeang 2007a; Calle et al. 2009).

The annual cycle of daily insolation constitutes the principal signal synchronizing the seasonal development of the species analyzed here, but other environmental variables may interact with photoperiodic control of phenology. In tropical monsoon forests, leaf-exchanging LD trees growing along rivers flush synchronously during the early rise in insolation (Fig. 3b, c), but at drier sites deep-rooted brevi-deciduous species, such as *Guazuma*, and deciduous, stem-succulent LD trees do so during the late dry season, in March/April (Fig. 3c, yellow, blue) (Borchert and Rivera 2001). Synchronous spring flushing has been observed in >80 tree species in monsoon forests throughout the world. In the light of the observations described here, it is likely to be induced by increasing insolation, rather than day length, as proposed earlier (Borchert and Rivera 2001; Rivera et al. 2002; Kushwara and Singh 2005; Elliott et al. 2006).

Among SD species, the specific periods of declining insolation that induce flowering vary widely with latitude and climate. In the subtropics, succulent Aizoaceae flower during the early decline in insolation, in August, which in South Africa coincides with the end of the summer drought (Figs. 5a, blue; 6b). At lower latitudes, Costa Rican dry forest trees flower (e.g., *Calicophyllum*, *Cordia*) or flush (e.g., *Andira*) during the decline of insolation in late October, at the end of the rainy season (Figs. 3b, c, November; 6b). Understory begonias flower even later, when leaf-exchanging trees are shedding their leaves and canopy density is lowest (Fig. 6a, b). In frost-free climates (<30°N), bud break of wide-ranging temperate trees is triggered by increasing insolation in February, but at higher latitudes it is induced progressively later by rising spring temperatures (Borchert et al. 2005b).

The molecular biology of photoperiodic control of plant development deals mainly with the transition from vegetative growth to flowering in herbaceous annuals, such as *Arabidopsis* (Jackson 2008; Melzer et al. 2008). The repeated transition between relatively short periods of shoot growth and prolonged periods of dormancy, characteristic of the tropical perennials analyzed here, has been analyzed only recently, in a temperate tree species. In aspen (*Populus tremula*) the pathway from the perception of day length to the expression of meristem identity genes is similar to that in *Arabidopsis* (Jackson 2008) and controls both the differentiation of flower buds in spring (see “Introduction”) and of vegetative buds in autumn, as induced by increasing or declining day length, respectively (Böhlenius et al. 2006). The critical day length for the arrest of shoot growth varies from 22 h in aspen

provenances collected at 63°N to 17 h in those originating at 51°N. Expression of the FT-Protein, a precursor of the meristem identity genes, declines earliest at 63°N, i.e., it is a critical determinant of the timing of bud set. The same may be the case for the tropical, autumn-flowering tree species *Montanoa tomentosa*, which flowers 3 months earlier in Mexico (20°N) than in Costa Rica (10°N; Calle et al. 2009). The molecular biology of tropical tree development apparently differs threefold from that in aspen and other temperate trees. First, the pigment systems sensing the photoperiodic signal perceive seasonal variation in daily insolation, rather than day length. Second, they are quite sensitive and capable of triggering phenological change even at the Equator, where seasonal variation in insolation is small (Fig. 1b). Third, any one of the stages of seasonal development may be under photoperiodic control in tropical perennials. North of the Arctic Circle (66°N), where day length is a constant 24 h during mid-summer, the rapid decline in insolation after its maximum in June (Fig. 1b, 50°N) might be also involved in the growth cessation of *Betula*, *Picea*, *Populus* and *Salix* in July/August (Juntilla 1980; Böhlenius et al. 2006; Lüttge and Hertel 2009; R. Guy, personal communication).

In this study, we describe synchronous bud break and flowering of a large number of perennial species throughout the tropics (Table 1). Synchronous development observed at the same time each year constitutes evidence for photoperiodic control, in general, and for the role of seasonal variation in daily insolation, in particular. Our findings are likely to apply to hundreds of evergreen tree species in tropical forests around the globe.

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