

## Letters

# Insolation and photoperiodic control of tree development near the equator

## Introduction

Tree development alternates between periods of rest (dormancy), shoot growth, and flowering. At temperate latitudes, the seasonality of tree development (= phenology) is determined mainly by the annual course of temperature. However, 100 yr ago Klebs (1914) observed that in a glasshouse saplings of European beech (*Fagus sylvatica*) were dormant during the short December days, but when exposed to continuous illumination in a 'light chamber' their resting buds opened within 4 wk and 15 leaves expanded during the subsequent 4-month-long period of continuous shoot growth (Supporting Information Notes S1). In the glasshouse the increase in day length in January induced bud break of dormant saplings in February. Klebs concluded from his many experiments that the autumnal decline in 'light quantity' (duration  $\times$  intensity) induces bud dormancy, and in January the increase in light quantity, sensed by dormant buds, breaks dormancy and triggers bud break of leafless saplings in a glasshouse. He recognized that for any given latitude day length and light intensity are coupled, because solar intensity varies significantly through the year as the sun's path in the sky changes with the season. Implicitly, 'light quantity' is synonymous with 'daily insolation', the measure of integrated solar intensity and day length to be used in this paper (Calle *et al.*, 2010). Subsequent studies, in which seedlings of many temperate tree species were exposed to experimental variation in day length, confirmed Klebs' observations, but largely ignored his conclusions (Notes S1; Garner & Allard, 1923; Wareing, 1956; Romberger, 1963). We will use the term 'photoperiodic control' when referring to the control of tree development by the seasonality of daily insolation.

While knowledge of photoperiodic control of dormancy in small experimental trees expanded, photoperiodic responses of mature trees received little attention (Romberger, 1963). Many years later, we observed in tropical forests at low latitudes that the phenology of many trees is highly correlated with seasonal variation in insolation (Rivera & Borchert, 2001; Rivera *et al.*, 2002). The large size of trees precludes experimental confirmation of such field observations, but the strong correlations between seasonal variation in insolation and synchronous development of many tree species are, in fact, the results of the large-scale, long-term natural experiment conducted during the evolution of tropical trees (Calle *et al.*, 2010). These

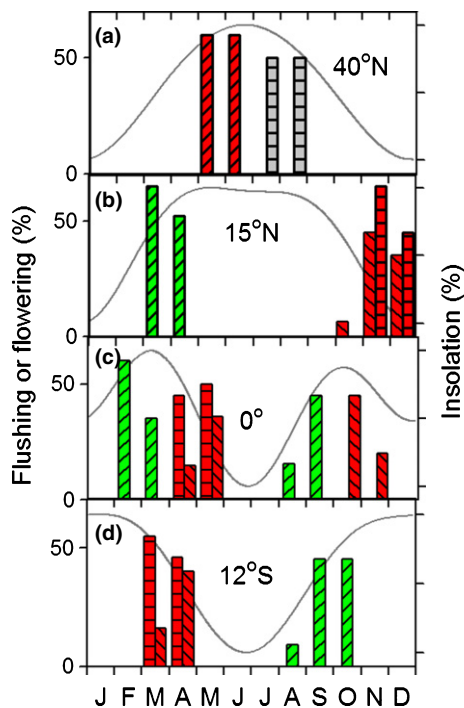
correlations were not recognized in the past (Van Schaik *et al.*, 1993; Thomas & Vince-Prue, 1997; Jackson, 2008).

In Central American semi-deciduous forests, a dry-season lasting from December to May alternates with a 6-month-long rainy season. Tree phenology is determined mainly by photoperiod or rainfall seasonality. Photoperiodic control is indicated by synchronous bud break or flowering of conspecific trees at the same time each year. The increase in insolation around the spring equinox induces flushing or flowering of leafless trees during the dry season (Rivera *et al.*, 2002; Elliott *et al.*, 2006) and its autumnal decline causes flowering of trees with mature foliage during the late rainy season (Rivera & Borchert, 2001). In other deciduous species, the timing of synchronous bud break of leafless trees varies from year to year with the first rains of the wet season, and during the dry season irrigation causes bud break within a few days (Borchert, 1984; Williams *et al.*, 1997).

At the equator, where day length is constant, many trees leaf out at irregular intervals, but others do so at the same time each year (Borchert *et al.*, 2005a). There is no consensus regarding the environmental signal that causes synchronous greening. Seasonal variation in irradiance (Van Schaik *et al.*, 1993), sunrise or sunset time (Borchert *et al.*, 2005a), sunlight (Huete *et al.*, 2006), solar radiation (Myneni *et al.*, 2007; Morton *et al.*, 2014) and high solar intensity (Renner, 2007; Yeang, 2007) have been considered. Most studies ignore that bud break preceding synchronous greening of tropical forests must be caused by an environmental signal perceived some weeks before leaf emergence (Klebs, 1914). The only environmental variable known to induce synchronous tree development near the equator is daily insolation, in short 'insolation' (Calle *et al.*, 2009, 2010; Lüttge, 2009; Guan *et al.*, 2013).

## Daily insolation

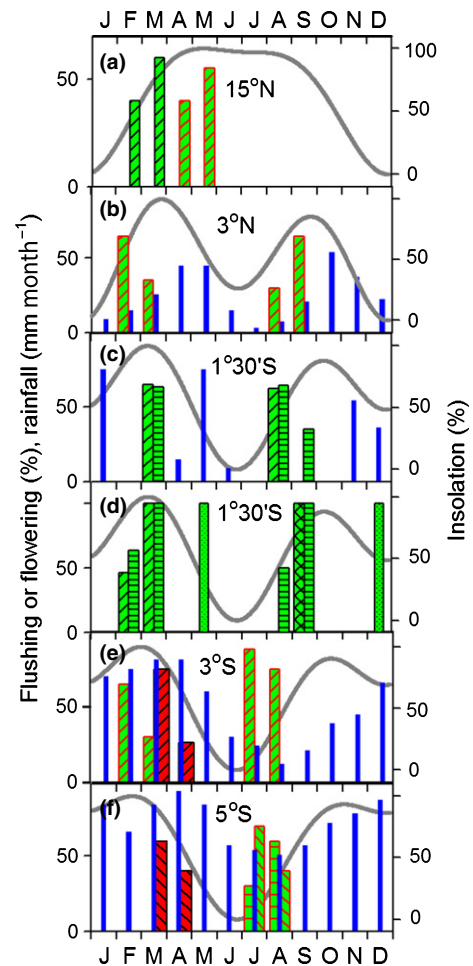
Daily insolation is a measure of solar intensity, integrated over the day, as observed without atmospheric effects at a particular latitude and day of the year (Strahler & Strahler, 2005; Yeang, 2007; Calle *et al.*, 2010; <http://en.wikipedia.org/wiki/Insolation>). Solar intensity is determined by sun angle, which varies through the day and with the seasons at each latitude. For example, at the equator, the noon sun is overhead (elevation = 90°) on the equinox, while at the solstice the sun's noon elevation is 66.5°, reducing noon solar intensity by 8.3%. Day length, defined as the time during which the sun is above the horizon, thus depends on latitude and the day of the year. The annual course of insolation varies widely with latitude (Figs 1, 2, curves; Calle *et al.*, 2010; <http://aom.giss.nasa.gov/srlocat.html>). At temperate latitudes, insolation and day length are lowest at the winter solstice and peak at the summer solstice (Fig. 1a).



**Fig. 1** Periodic flowering and flushing of trees between 40°N and 12°S. Right: annual course of daily insolation (curves). Left: seasonality of phenology (bars). (a) Flower initiation (red) and autumnal growth cessation of *Populus tremula* (gray; Böhlenius *et al.*, 2006). (b–d) Latitudinal variation in flowering periods deduced from collection dates of herbarium specimens (Missouri Botanical Garden Herbarium, St Louis, MO, USA). Green, flushing on expanding shoots: *Spondias mombin* (45). Red, flowering on mature shoots: *Cordia alliodora* (horizontal stripes; 122); *Heliocarpus americanus* (diagonal stripes; 170). Numbers, number of herbarium specimens. Bars give the first 2 months with a distinct increase in the number of flowering specimens.

In the tropics the winter insolation minimum is preserved, but with declining latitude the summer maximum gradually becomes a 6-months-long plateau, and the periods of increasing and declining insolation are reduced from 5 to 2.5 months (Fig. 1a,b). As the equator is approached, the plateau becomes a second minimum (Fig. 1c). Thus, near the equator there are two periods of increasing insolation; they start at the same time as those at higher latitudes, in January (northern hemisphere) and July (southern hemisphere), but last for 2 months only. At the insolation ‘equator,’ located at 3°N rather than at the true equator, the insolation curves are asymmetric, because solar intensity is strongest when the earth is closest to the sun (January 5) and weakest when it is farthest away (July 5; Fig. 2b). The decline in insolation begins progressively later with declining latitude: in July at 40°N, in September at 15°N, and in March and October at 3°N (Fig. 1a–c, July–November). South of the equator it starts 6 months later (Fig. 1d). At the earth’s surface, the intensity of insolation perceived by trees varies with cloud cover, but the duration of daily photoperiods is unaffected by the weather.

Earlier, we identified more than 50 tree species and 200 succulent species that flush or flower in synchrony during increasing or declining insolation at higher tropical latitudes (>10°N or S; Calle *et al.*, 2010). Here we analyze phenological



**Fig. 2** Seasonality of daily insolation and tree phenology near the equator. Curves, right y-axis: annual course of daily insolation between 15°N and 5°S. Bars, left y-axis: seasonality of rainfall (blue bars) and phenology as percent of observed trees or species; green, flushing; red, flowering; green/red, flowering on new shoots; yr, duration of observations; numbers, number of observed trees or species. (a) Flushing and flowering of *Spondias mombin* (green) and *Guazuma ulmifolia* (green/red) in Costa Rica (10°N, 2 yr, 10). (b) Flushing of *Guazuma* in Cali, Colombia (5°N, 2 yr, 10). (c) Flushing of *Melia volkensis* (diagonal stripes) and *Senna spectabilis* (horizontal stripes) near Nairobi, Kenya (1°30'S; 1.5 yr, 16). (d) Flushing of single trees of 76 species in the Nairobi Arboretum during increasing insolation (hatched) or after rain (stippled; Supporting Information Table S1). (e) Flushing and flowering of 42 tree species in Manaus, Brazil (3°S, 10 yr, 3 trees/species; Table S2). (f) Phenology in Loreto, Peru (horizontal; 5°S, 10 yr, 17 species, > three trees/species) and Ecuador (diagonal; 4°S, 3 yr, five species, five trees/species): *Heliocarpus americanus* (red) and *Alnus acuminata*, *Cedrela montana*, *Juglans neotropica*, *Prumnopitys montana* (green).

observations made in > 100 tropical tree species for evidence in support of two specific hypotheses. (1) If the phenology of a tree species is under photoperiodic control near the equator, then synchronous bud break or flowering should begin during the four short periods of increasing or declining insolation (Fig. 1c). (2) At higher tropical latitudes, *c.* 15°N and 12°S, new leaves or flowers should appear during the two 2.5 months-long periods of rapidly changing insolation and trees should be dormant during the 6-month-long insolation plateau (Fig. 1b,d).

## Materials and Methods

In our earlier studies of tree phenology in Central American semi-deciduous forests, we observed trees biweekly for at least 2 yr. Such studies do not exist for equatorial forests, and in this paper we analyze records of tree phenology near the equator obtained from various sources identified in the figure captions and Notes S2. Many species develop flowers during shoot growth. The time of bud break in such species can be deduced from the collection dates of flowering herbarium specimens or from field records of flowering phenology. In contrast to deciduous species, most rainforest species do not flower every year, and flowering periods can be obtained only from long-term field observations (Notes S2). The number of herbarium collections, field observations, trees, and species for which flushing and flowering times were recorded varies widely and is generally too small for statistical analysis. We therefore report the annual course of phenology as a percentage of observations (Figs 1, 2). Apparently, relative, not absolute, seasonal changes in insolation determine the periodicity of tree development in the tropics.

## Results

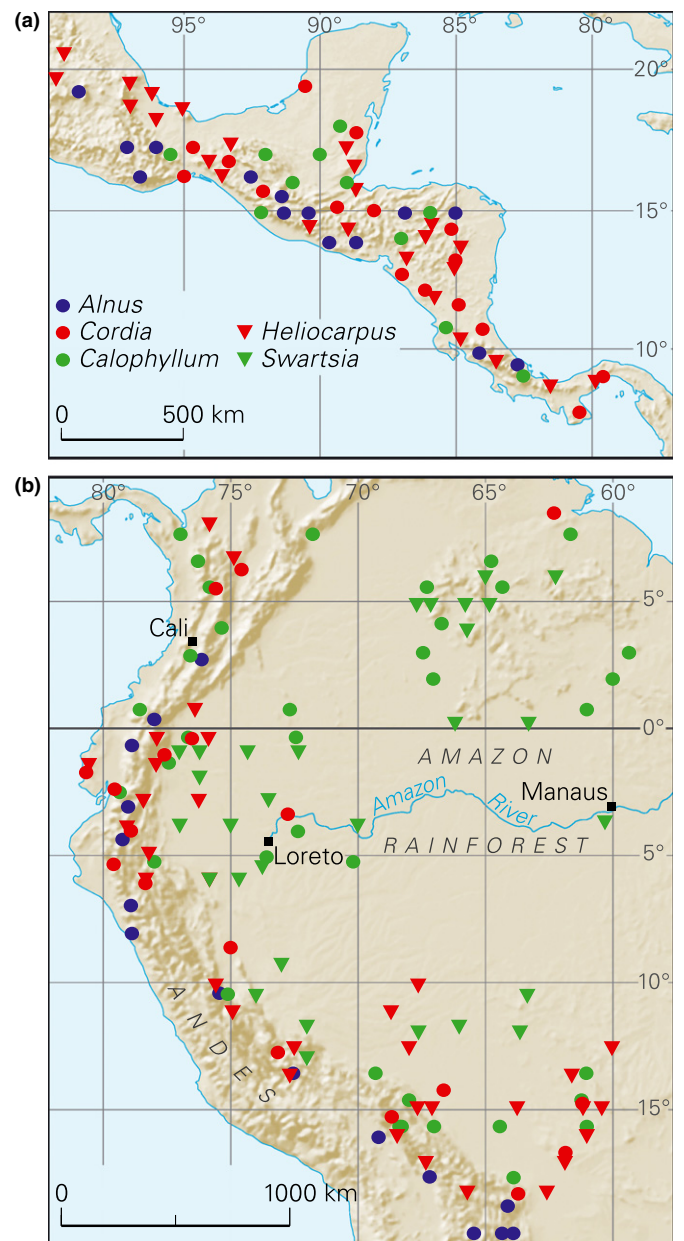
### Latitudinal range of tropical tree species

Many Neotropical tree species range over > 6000 km, from Mexico (25°N) to Argentina (25°S). Within their range, they occupy characteristic ecological niches that vary with latitude and physical geography (Fig. 3). Most high-altitude and rainforest species are evergreen throughout their range (Fig. 3, green, blue). They live in Neotropical high mountains and dominate the Amazon rainforest as well as the rainforests along the Caribbean coast of Central America. Semi-deciduous species prevail in the dry forests along the Pacific coast of Central America, where increasing insolation triggers leaf shedding, flushing, or flowering of many species during the dry season (Fig. 1b; Rivera & Borchert, 2001; Rivera *et al.*, 2002). In South America these species are confined to the eastern slopes of the Andes (Fig. 3, red), where they are evergreen near the equator and retain photoperiodic control of phenology (Fig. 1c).

### Latitudinal and temporal variation in tree phenology

Collection dates of herbarium specimens (Fig. 1) and field observations (Fig. 2) confirm the earlier predictions. In Central America, the expansion of flowering shoots of *Spondias mombin* starts in February (Figs 1b, 2a, green; Rivera *et al.*, 2002), in South America it begins in August (Fig. 1d), and near the equator flowering herbarium specimens were collected during both periods (Fig. 1c). At higher tropical latitudes terminal inflorescences of *Cordia alliodora* and *Heliocarpus americanus* develop either in November (Central America) or March (South America) on shoots with mature foliage (Fig. 1b,d, red; Rivera & Borchert, 2001). Herbarium specimens collected near the equator date from either period (Fig. 1c, red).

In Cali, Colombia (4°N), *Guazuma ulmifolia* trees are evergreen and flowers appear on expanding shoots in late January and July



**Fig. 3** Ranges of representative tree species from neotropical rain forests (green: *Calophyllum angulare*, *Swartzia dolichopodia*), semi-deciduous forests (red: *Cordia alliodora*, *Heliocarpus americanus*) and higher elevations (blue: *Alnus acuminata*). (a) Central America; (b) South America. Each symbol represents a herbarium specimen of the Missouri Botanical Garden Herbarium (St Louis, MO, USA). South American field collections are centered in Ecuador (0–5°S) and Bolivia (10–25°S) and the number of collections from Colombia (2–11°N) and Peru (3–17°S) is relatively small.

(Fig. 2b, green/red). In Central American semi-deciduous forests (10°N) *Guazuma* and other species shed leaves during the dry season and new shoots emerge in late March, weeks before the first rains of the wet season (Fig. 2a, green/red; Rivera *et al.*, 2002; Calle *et al.*, 2010). Photoperiodic control thus adapts the phenology of *Guazuma* to the climate of different latitudes.

Kenya is the only equatorial country with a bimodal monsoon rainfall regime (Fig. 2c, blue bars). Near Nairobi ( $1^{\circ}30'S$ ) *Melia volkensii* and *Senna spectabilis* leafed out in March and August, when soil moisture was well below field capacity (Fig. 2c; Broadhead *et al.*, 2003). In a preliminary study, we monitored flushing in single trees of 138 evergreen species in the Nairobi Arboretum. Most are native to East Africa. Half of the species did not have distinct periods of shoot growth and rest, but the others formed new leaves once a year, in February or July, or during both months (Fig. 2d, Table S1). A few species leafed out during the two rainy seasons, that is, bud break is rain-induced.

In Manaus, Brazil ( $3^{\circ}S$ ) half of the observed 54 rainforest species flush in both January and July (Fig. 2e, green; Table S2 12–28) or flower in March (Fig. 2e, red; Table S2 1–11; Alencar *et al.*, 1979; Alencar, 1990). At elevations above 2000 m in the Andes of southern Ecuador ( $4^{\circ}S$ ), *Heliocarpus* trees flower in March (Fig. 2f, red) and five other species, including *Alnus*, leaf out in August (Fig. 2f, green/red, diagonal; Fig. 3, blue; Günter *et al.*, 2008). In Loreto, Peru ( $5^{\circ}S$ ), 19 rainforest species flower on new shoots in August, at the same time as trees in Manaus and Ecuador (Fig. 2f, horizontal; Gautier & Spichiger, 1986).

Southward from the insolation equator the December insolation minimum gradually disappears (Fig. 2b–f, October–December) and the seasonality of phenology shifts correspondingly from two equivalent flushing periods in Cali ( $5^{\circ}N$ ) and Nairobi ( $1^{\circ}30'S$ ) to two unequal periods in Manaus ( $3^{\circ}S$ ) and a single period in Ecuador ( $4^{\circ}S$ ) and Loreto ( $5^{\circ}S$ ; Fig. 2b–f).

Rainfall periodicity does not cause synchronous bud break at the equator

Synchronous flushing of rainforest trees observed near the equator was ascribed earlier to the seasonality of rainfall or water availability (Alencar *et al.*, 1979; Gautier & Spichiger, 1986; Alencar, 1990; Van Schaik *et al.*, 1993). However, equatorial rainforests are evergreen because trees are rarely exposed to water deficits sufficient to cause leaf shedding (Nepstad *et al.*, 1994). The seasonality of rainfall ranges from 12 rainy months in western Amazonia (Figs 2f, blue; 3; Loreto, 2900 mm rain  $yr^{-1}$ ) to Manaus with four moderately dry months (Figs 2e, 3; 1840 mm  $yr^{-1}$ ), Cali with two rainfall minima (Figs 2b, 3; 1200 mm  $yr^{-1}$ ) and Nairobi with two distinct dry seasons (Fig. 2c; 900 mm  $yr^{-1}$ ). As shown in Fig. 2, none of these rainfall patterns matches the observed patterns of flushing and flowering.

Observations from spacecraft and aircraft

In the Amazon rainforest, monitoring the phenology of tall evergreen canopy trees from the forest floor is difficult, because light-green flushes appear on branches with older, dark-green foliage and bud break is not as well synchronized as in deciduous forests at higher tropical latitudes (Fig. 4a; see the Introduction section). However, satellite-based monitoring of canopy reflectance in Amazon rainforests reveals a distinct increase in canopy greenness in July, which coincides with the seasonal rise in



**Fig. 4** South American forests photographed from low-flying aircraft. (a) Light-green flushing trees, trees with dark green old leaves and leafless trees (but no flowering trees) in the Amazon rainforest (Yasuni National Park, Ecuador,  $1^{\circ}S$ ;  $> 3000$  mm rain  $yr^{-1}$ ; August 2012). Photograph by I. Kashinsky, Quito, Ecuador. (b) Trees with new light-green or old dark-green foliage and leafless flowering trees in a semi-deciduous forest (Madidi National Park, Bolivia,  $14^{\circ}S$ ; c. 1600 mm rain  $yr^{-1}$ ; mid-May 2007). Photograph by A. Baertschi (wildtropix.com).

insolation and flushing in Manaus (Fig. 2e; Huete *et al.*, 2006; Myneni *et al.*, 2007; Morton *et al.*, 2014). In African equatorial rainforests remote sensing shows two greening periods starting in February and August. They coincide with the two periods of increasing insolation and synchronous flushing in Nairobi (Fig. 2c,d; Table S1; Guan *et al.*, 2013).

In a photograph taken from a low-flying airplane in early August many tree crowns in Ecuador's Yasuni National Park (1°S) are covered with light-green foliage (Fig. 4a; 1°S; Wallace, 2013). Whereas trees observed in Manaus and Loreto (Fig. 2e,f) represent only a tiny fraction of the > 3200 Amazonian tree species (Hubell *et al.*, 2008), satellite images and photographs confirm that synchronous flushing during increasing insolation is common in equatorial rainforests.

In the semi-deciduous Peruvian forests at the foot of the Andes (10°S), increasing insolation probably triggers leaf shedding and expansion of the red flowers of *Erythrina* and yellow flowers of *Tabebuia* in August (Fig. S1; Borchert, 1985a,b). In Bolivia (14°S) declining insolation apparently induces both flowering of leafless trees and unfolding of young, light-green foliage in mid-May (Fig. 4b).

#### Earlier studies of photoperiodic control of phenology

In Central American semi-deciduous forests most evergreen trees growing near rivers exchange old for new leaves during increasing insolation in February. Many semi-deciduous tree species occupy dry sites where deep roots reach the water table. They shed leaves gradually during the early dry season and leaf out synchronously in late March, at the end of the short period of rising insolation, > 3 months after the last rainfall, and weeks before the first heavy rains of the wet season (Borchert & Rivera, 2001; Rivera *et al.*, 2002). Bud break during seasonal drought is counter-intuitive and appears to be suboptimal, but constitutes strong evidence for induction by the rapid increase in insolation between February and March, rather than by slowly rising day length, the only photoperiodic signal known when these field studies were conducted.

At all northern tropical latitudes, increasing insolation causes bud break between February and March. By contrast, autumnal flowering starts progressively later as the early decline in insolation shifts from July in Mexico (20°N) to October in Costa Rica (10°N) (Fig. 1a–c, curves; Calle *et al.*, 2009, 2010). In Mexico flowers of the wide-ranging *Montanoa tomentosa* appear in July, but in Costa Rica trees flower in October, in synchrony with *Cordia*, *Heliocarpus* and > 20 other species which bloom during the 2-month-long decline in insolation after the summer plateau (Fig. 1b, red; Rivera & Borchert, 2001).

In Central America declining insolation causes rapid leaf shedding of the stem-succulent, deciduous *Plumeria rubra* in November and increasing insolation induces bud break in March (Borchert & Rivera, 2001). *Plumeria* is one of the few tropical trees in which photoperiodic responses have been manipulated experimentally. Rainfall or irrigation do not cause bud break of dormant *Plumeria* between November and March, when day length declines to 11.7 h. In leafless saplings exposed to experimental 13-h

photoperiods in December, buds begin to swell within 3 wk (compare Introduction section). Buds of plants transferred to northern Argentina (25°S) expand 6 months later than in Central America. These observations imply that in *Plumeria* insolation is perceived in leafless, green succulent stems, and dormancy can be broken by increasing insolation as well as exposure to constant inductive photoperiods.

More than 15 North American tree genera range from 45°N in Canada to 20°N in subtropical Mexico (Borchert *et al.*, 2005b). At temperate latitudes, rising spring temperatures cause bud break of these species, but in subtropical Mexico their new leaves emerge concurrently with those of cohabiting tropical trees during the increase in insolation between January and March (Williams-Linera, 1997).

At temperate latitudes, insolation, like day length, rises continuously from January to June, twice as long as in the tropics (Fig. 1a). Whereas autumnal flowering of tropical trees with mature foliage is triggered by declining insolation (Fig. 1b–d, red), in adult trees of temperate species such as *Catalpa bignonioides*, *Koelreuteria paniculata* and *Robinia pseudoacacia* increasing insolation apparently induces synchronous flowering in May/June, several weeks after rising spring temperatures cause bud break and leaf expansion (Fig. 1a, June; Romberger, 1963).

#### Molecular control of tree phenology

In many herbaceous plants flowering in response to variations in photoperiod is controlled by the CO/FT regulatory module. In *Populus tremula* (aspen) this module controls not only flower initiation caused by increasing day length in spring, but also short-day induced growth-cessation and bud set in fall (Fig. 1a; Böhlenius *et al.*, 2006; Jackson, 2008). Recent studies confirm the central role of the FT-module in the development in several trees (Hsu *et al.*, 2011; Srinivasan *et al.*, 2012). Synchronous bud break and flowering of tropical tree species are therefore likely to be manifestations of FT-control (Notes S3).

#### Concluding remarks

Synchronous flushing or flowering of tropical trees during the short periods of rising or declining insolation, respectively, has been observed at all tropical latitudes in adult trees of numerous species. In the absence of a distinct day-length signal, near the equator these correlations confirm the adaptation of tropical tree phenology to the annual course of daily insolation. They imply that at all latitudes, tropical and temperate, the environmental signal sensed by plants is likely to be seasonal change in daily insolation rather than day length, as Klebs (1914) discovered 100 yr ago.

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## Supporting Information

Additional supporting information may be found in the online version of this article.

**Fig. S1** Flowering of leafless deciduous trees observed from boats travelling rivers in South American semi-deciduous forests.

**Table S1** Flushing times in trees of 76 species at the Nairobi Arboretum

**Table S2** Flushing or flowering of rainforest species in Manaus, Brazil

**Notes S1** The discovery of photoperiodism by G. Klebs (1914).

**Notes S2** Methods.

**Notes S3** Molecular controls of tree development.

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**Key words:** African monsoon forest, daily insolation, latitudinal variation of tropical tree phenology, photoperiodic control of tree development, South American equatorial rainforest, tropical semi-deciduous forest, tropical trees.

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