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ORIGINAL PAPER

Declining insolation induces synchronous flowering of *Montanoa* and *Simsia* (Asteraceae) between Mexico and the Equator

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Abstract We analyze the latitudinal shift in the onset of synchronous flowering in the woody genera *Montanoa* and *Simsia* (Asteraceae) between Mexico (28° N) and the Equator, where it cannot be caused by declining day length. Synchronous flowering of >100 *Montanoa quadrangularis* trees was observed during two consecutive years near Cali, Colombia (4° N). Analysis of herbarium specimens yielded flowering periods for 21 *Montanoa* species and 18 *Simsia* species between 4 and 28° N. Daily insolation is a function of day length and the angle at which the sun's rays strike the earth. Between Mexico and Colombia (4° N), the maximum of insolation gradually shifts from the summer solstice to the autumn equinox. In parallel, flowering of *Montanoa* and *Simsia* starts progressively later between July and November, during the period of declining insolation. Near the Equator, there are two periods of declining insolation, and correspondingly, two flowering periods. Thus, at all tropical latitudes, flowering time of *Montanoa* and *Simsia* is highly correlated with declining insolation. The seasonal decline in daily insolation, rather than in photoperiod, apparently induces synchronous flowering of *Montanoa* and *Simsia* at the same time each year.

Keywords Day length · Phenology · Photoperiod · Tropical trees

Introduction

Most plants flower synchronously at the same time each year, thus assuring cross-pollination. In many species, flowering time is determined by seasonal changes in day length (photoperiodism). Since the discovery of photoperiodism almost 100 years ago by Garner and Allen (1920), the role of photoperiod in flower induction has been studied mainly in experiments conducted under controlled environmental conditions (Thomas and Vince-Prue 1997). The ecological significance of photoperiodism has received only little attention, even though Garner and Allen recognized that flowering periods must be well adapted to the seasonal variation of day length at the latitudes where a species lives, or it could not exist there. We will show here that between the Tropic of Cancer (23.5° N) and the Equator, the latitudinal variation in flowering time within two tropical, autumn-flowering genera of the Asteraceae does not correlate with the latitudinal variation of day length. Synchronous flowering in autumn should be therefore induced by another environmental signal.

In North American cold temperate climates, *Ambrosia* (ragweed), *Helianthus* (sunflower), *Verbesina* (wingstem), *Xanthium* (cocklebur), and other autumn-flowering Asteraceae grow rapidly throughout the summer and often become the largest annuals in disturbed habitats (2–3 m tall). Declining day length induces the transformation of the shoot apex into a terminal inflorescence in late summer

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(Ray and Alexander 1966; McMillan 1970). In these Asteraceae, photoperiodic control of flowering time optimizes seasonal development and fitness in several ways: (1) synchronous flowering enhances cross-pollination; (2) delaying the onset of reproductive development to the late growing season maximizes vegetative growth and hence the capacity to produce large numbers of flowers and seeds; and (3) timing of flowering that anticipates the approaching winter assures that seed development is completed during the growing season.

Among wide-ranging temperate Asteraceae, flowering time varies with the average time of the first killing frost. In two classical studies, *Xanthium* was grown in common gardens in Michigan and Texas (Ray and Alexander 1966; McMillan 1970). In Michigan (42.3° N), flowering times of plants grown from seed collected between 30 and 47° N were highly correlated with the latitude of origin and varied little among plants from the same latitude. In ecological races from 47° N, flower buds appeared in early August, when day length was 14.3 h. Plants from the southern US around 30° N formed flower buds almost 2 months later, in late September, when day length was 12 h. In contrast, among ecological races of *Xanthium* originating from the same latitude in subtropical Mexico (20–30° N), flowering times varied widely, between late August and early November (McMillan 1970). In general, the critical day length inducing flowering in autumn is longer for ecotypes from the northern range of a species, which therefore flower first, than for southern ecotypes, which flower later. Similarly, soybean varieties with a critical day length of 14 h will flower earlier in autumn at lower than at higher latitudes (Fig. 1, 14 h day length; Cregan and Hartwig 1984).

Synchronous flowering at the same time each year, as observed in Asteraceae native to temperate climates, is also common in tropical trees (Borchert et al. 2005; Yeang 2007a, b). For example, in Singapore, located right at the Equator, trees of several species flushed or flowered during the same month in each of 10 consecutive years (Holttum 1940). The amplitude of the seasonal variation in day length declines with latitude and becomes zero at the Equator (Fig. 1a); therefore, day length cannot be the environmental signal controlling synchronous tree development near the Equator. Earlier, we suggested the bimodal variation in sunrise and sunset times as the potential environmental signal inducing the observed biannual flowering at the Equator (Borchert et al. 2005). Recently, high solar radiation energy has been proposed to cause synchronous flowering of *Hevea* and other tropical trees between January and the Spring equinox (Fig. 1b, *green curves*; Van Schaik et al. 1993; Yeang 2007a, b). However, none of these hypotheses can explain synchronous "autumn flowering" between September and December, as observed in many tropical tree species ranging from Panama to Mexico (Rivera and Borchert 2001). In these species, flowering time varies widely with latitude, as it does in *Xanthium*; for example, in Mexico (20° N), *Cordia alliodora* flowers in August, but in Panama (8° N) it does so 4 months later (Rivera and Borchert 2001). If induced by the decline in day length soon after the summer solstice, *Cordia* flowers should appear in July/August at all latitudes (Fig. 1a, *red curves*). Here, we propose the autumnal decline in daily insolation as the most likely signal inducing synchronous autumn flowering at times that vary widely with latitude (Fig. 1b, *red curves*; c, *circles*).

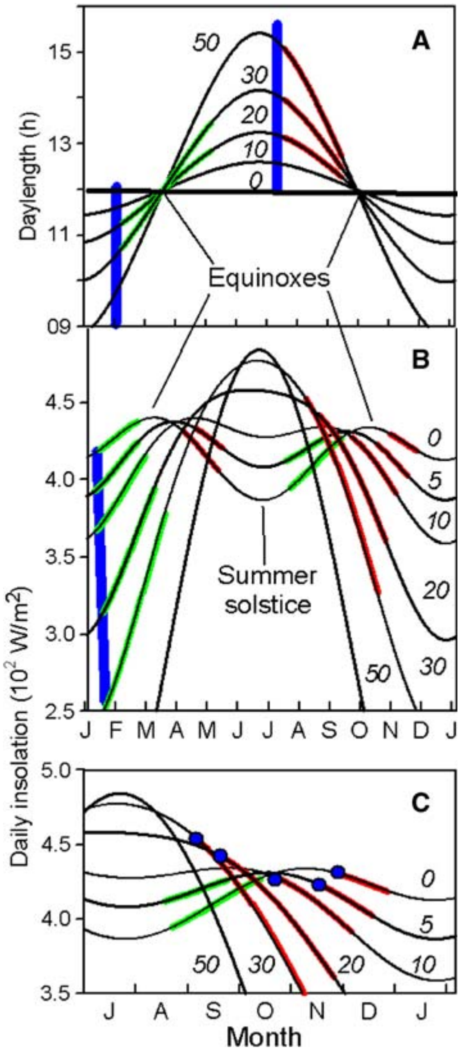

Fig. 1 Annual variation in day length (**a**) and daily insolation (**b**, **c**) between the Equator and 50° N. **a**, **b** *Red lines* periods of declining day length or insolation potentially inducing flowering *Montanoa*, *Simsia*, and other species; *green lines* periods of increasing day length or insolation potentially inducing bud break in other tree species. *Blue bars* earliest time of bud break or flowering. **c** *Blue circles* Latitudinal variation in the observed onset of *Montanoa* and *Simsia* flowering

Daily insolation (henceforth "insolation") is a measure of the solar energy flow (W m^{-2}) received at a particular location above the earth atmosphere on any day of the year (Strahler and Strahler 2003; Yeang 2007a, b). Until recently, it was not among the environmental variables known to affect plant phenology (Yeang 2007a, b). Daily insolation is a function of two variables, namely, day length and the intensity of irradiation as determined by the angle at which the sun's rays strike the earth. Whereas the annual maximum of day length occurs at the summer solstice at all latitudes, the timing of the maximum of daily insolation varies widely with latitude (Fig. 1a, b). North of 23.5° N (Tropic of Cancer) insolation—like day length—peaks at the summer solstice, but between 23.5° N and the Equator, insolation has two annual maxima, which become more distinct as they gradually shift from the summer solstice to the equinoxes (Fig. 1b, c).

When discussing flower induction by declining insolation, we will use the conventional term "photoperiodic control," but understand it to include both, control by day length and control by seasonal variation in insolation, thereby amplifying the concept. To address common misunderstandings, we wish to stress the fundamental differences in the role of absorbed light in photosynthesis as compared to photoperiodism. The absorption of irradiation in photosynthesis results in an immediate photosynthetic energy gain, which is a function of the absorbed energy and is strongly affected by cloud cover. In contrast, the role of seasonal changes in day length or daily insolation perceived by plants is that of a signal triggering the molecular processes which result in visible flower development several days later (Engelmann 2007, Discussion). Photoperiodic control is not affected by variation in light intensity during the day (Thomas and Vince-Pruce 1997).

If induced by the decline in insolation after its maximum, the onset of autumn flowering should vary with latitude in parallel with insolation. Thus, flowering should start in July/August at subtropical latitudes (20–25° N) and 3–4 months later near the Equator, namely in October/November (Fig. 1c, *blue circles*). We sought evidence in support of this hypothesis in two ways. We analyzed the extensive herbarium records of many species in two tropical, autumn-flowering genera of the Asteracae, *Montanoa*, and *Simsia*, which range from Mexico to the Equator (see Methods), and we monitored the appearance of terminal inflorescence in 107 *Montanoa quadrangularis* trees growing near Cali, Colombia (4° N), biweekly over 2 years. With declining latitude, between Mexico and the Equator, flowering of the analyzed species started progressively later between July and October, and at 4° N, inflorescences of *M. quadrangularis* appeared in October. We conclude that between Mexico and the Equator, the synchronous onset of autumn flowering of *Montanoa*, *Simsia*, *Xanthium*, and other Asteraceae is apparently induced by declining insolation, not day length.

Materials and methods

Ranges of *Montanoa* and *Simsia*

Montanoa and *Simsia* are two genera of the Asteraceae ranging from the subtropics to the Equator. *Montanoa* species include shrubs and small trees, which range from Sonora, Mexico (28° N), to the Equator and always flower in autumn at species-specific times (Funk 1982, Figs. 2, 3). They generally grow in a variety of open, disturbed habitats, from xeric thorn forests and subtropical mountain forests in Mexico, where plants may be cold- or drought-deciduous, to tropical mountain forests, where they are evergreen. Species of *Simsia*, which include herbs and shrubs, range from the Southern US to Argentina. Most northern species start flowering between July and November (Fig. 2) and species growing near the Equator flower throughout the year (Spooner 1990).

Analyzed species

We selected 18 well-collected species of *Montanoa* with several subspecies and populations for analysis from those described by Funk (1982). For each species or subspecies, habitat, elevation, and range are listed in Table 1. Flowering times of 18 *Simsia* species were obtained from Spooner (1990) and analyzed as described below for *Montanoa*.

Latitudinal variation in flowering time

As in our earlier analysis of photoperiodic control of autumn flowering in tropical trees (Rivera and Borchert 2001), we obtained data for the analysis of latitudinal variation of flowering periodicity in *Montanoa* and *Simsia* from herbarium collections. Collection date and place of herbarium specimens provide information on flowering time and latitudinal distribution of a species (Croat 1969; Borchert 1996; Rivera and Borchert 2001; Primack et al. 2004).

Collection date and site recorded for >200 flowering collections of *Montanoa* species in the Missouri Botanical Garden Herbarium or given in Funk (1982) were entered into a spreadsheet. We used collection sites to assign the approximate latitude and considered the collection date as "flowering date." These values were used to obtain the flowering periods given in Table 1 and plot flowering time as a function of latitude for several species (Fig. 2). For the analysis of flower induction, only the earliest flowering

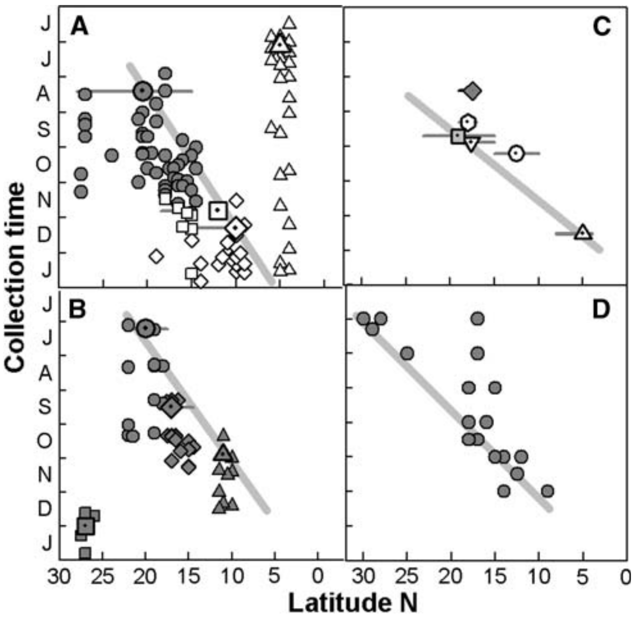

Fig. 2 Latitudinal variation in flowering time of *Montanoa* and *Simsia* (Asteraceae) in herbarium collections from the Missouri Botanical Garden herbarium and other herbaria (Funk 1982; Spooner 1990). Number of herbarium collections and species codes used in Table 1 and Fig. 3 are given in parentheses. *small*, *empty symbols* species from moist habitats; *small filled symbols* species from dry habitats; *large*, *dotted symbols* mean flowering time and latitude of the four earliest collections in a taxon; *horizontal grey line* latitudinal range of collections. **a** Month and latitude of flowering herbarium collections of four representative species. *Circles M. leucantha* (38, 8d); *squares M. hexagona* (8, 1d); *diamonds M. guatemalensis* (31, 2a); *triangles M. ovalifolia* (25, 7). **b** Variation in flowering time among subspecies and populations of *M. tomentosa* from dry habitats at different latitudes. *Squares* 26–28° N (ssp. *rosei*, 4, 2c); *circles* 18–22° N (ssp. *xanthiifolia*, 16, 8a; ssp. *tomentosa*, 8b); *diamonds* 15–17° N (ssp. *microcephala*, *17*); *triangles* 10–12° N (ssp. *xanthiifolia*, 10, 1f). **c** Means of earliest flowering times and latitudinal range of six other *Montanoa* species. *Diamond M. molissima* (10, 8c); *square M. karwinskii* (11, 9c); hexagon *M. frutescens* (17, 9d); *triangle down M. revealii* (26, 9b); *circle M. hibiscifolia* (48, 1c); *triangle up M. quadrangularis* (113, 2b; see Fig. 4). **d** Flowering times of 18 species of *Simsia*

dates are relevant. We therefore calculated, for each species, mean flowering time and latitude of the four earliest collections, rather than mean flowering time of all collections (Fig. 2, *large dotted symbols*), and excluded single, exceptionally early flowering collections. Statistical analysis of all the available herbarium collections is therefore not appropriate.

Montanoa quadrangularis

Montanoa quadrangularis is one of the few arboreal species of *Montanoa* (Funk 1982). It reaches up to 20 m in height and grows at disturbed sites throughout the Andes of Colombia and Venezuela at elevations between 1,300 and 2,500 m. We monitored the flowering phenology of 107 tagged trees biweekly from July 1998 to 2000 at 1,500 m altitude in the Colombian Cordillera Occidental near El Dovio, Valle de Cauca (4° N; Calle 2002, 2003). Flowering branches of *M. quadrangularis* develop a large, branched terminal inflorescence with as many as 1,700 composite flowers. Large trees may have up to 35,000 inflorescences on 35–40 branches. We recorded the number of branches bearing inflorescences for each tree and calculated the fraction of flowering branches in the population of 107 trees. Differences in flowering time among subsets of trees within the population were identified by sorting the phenological records for the time of maximum flowering in all branches of a tree (“peak flowering time”).

Annual variation in day length and daily insolation

Annual variation in day length and daily insolation at different latitudes was obtained from the Internet (day length: Lammi, J.J., 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.

Results

Latitudinal variation in the flowering periodicity of *Montanoa* and *Simsia* was deduced from the analysis of flowering herbarium specimens (Fig. 2; see Methods). Range and flowering period vary widely among *Montanoa* species. Some species occur within a relatively narrow latitudinal range and flower during a 1–2-month period (Fig. 2a, c; Table 1). Others extend over a latitudinal range of 13–18°, and flowering herbarium specimens were collected over 3–4 months (Fig. 2a, *circles*; b) and over 6 month for *M. ovalifolia*, between June and January (Fig. 2a, *triangles*). Within the range of *M. tomentosa*, which extends from northern Mexico (28° N) to Costa Rica (10° N), different subspecies flower between July and December (Fig. 2b, Table 1). Despite this variability, herbarium collections clearly show that in *Montanoa* and *Simsia*, the onset of flowering starts progressively later along the latitudinal gradient from Mexico to Colombia (28–4° N; Figs. 2, *gray lines*; 3; Table 1). In central Mexico, most species flower in August–September, but in Costa Rica and Colombia, they do so in November–December. In central Mexico, species native to xeric habitats flower in August, 1–2 months earlier than those in moist mountain habitats, but in the southern range of *Montanoa*, species in arid and moist habitats flower at the same time, in November/December (Figs. 2, *filled vs. empty symbols*; 3, *gray vs. black species codes*). There are a few exceptions to this trend. In northern Mexico,

Table 1 Flowering periodicity and distribution of 21 species and subspecies of *Montanoa,* Asteraceae (from Funk 1982)

Code	Species/Subspecies	Flowering period								Habitat	Elevation (m)	Distribution	Latitude (°N)	Ref.
		J	A	S	O	N	D	J	F					
7	*ovalifolia*	x	x		x		x	x		Wet subparamo	1900–3000	Colombia	6–4	10a
8a	*xanthiifolia* N*		x	x	x					Xeric–semi-xeric	1000–1500	Jalisco	20	1d
8b	*tomentosa**		x	x	x					Xeric thorn forest	1900–2800	Central Mexico	19	1a
8c	*molissima*		x	x	x					Hot, dry slopes	1600–2100	Puebla, Oaxaca	17	4
8d	*leucantha***		x	x						Dry rocky sites	2000–2400	Central Mexico	17	15a
9a	*arborescens* N**			x	x	x				Cool, wet forests	1000–2300	Sonora–Oaxaca	28–20	15b
9b	*revealii [= gigas]*			x	x	x	x			Wet, mesophytic forest	2200–2700	Guerrero	18	9
9c	*karwinskii*			x	x					Semideciduous forest	500–2000	Sierra Madre del Sur	17	16
9d	*frutescens*			x	x	x				Cool, wet	2300–2800	Central Mexico	19	2
0a	*imbricata*				x	x				Oak forest	800–1450	Sierra Madre del Sur	17	24
0b	*grandiflora*				x	x				Pine–oak forest	800–2500	Sierra Madre del Sur	17	22
0c	*speciosa*				x	x				Deciduous forest	150–1400	Sierra Madre del Sur	17	23
0d	*pteropoda*				x	x	x			Wet pine–oak forest	1700–3800	Chiapas–Guatemala	15	18
1a	*bipinnatifolia*					x	x			Pine–oak forest	450–2000	Sinaloa–Oaxaca	24–16	25
1b	*atriplicifolia*					x	x	x		Roadsides in cool forests	500–2000	Chiapas–Costa Rica	15–10	17a
1c	*hibiscifolia*					x	x	x		Low to mountain forest	400–2500	Chiapas–Panama	15–9	19
1d	*hexagona*					x	x			Cloud forest	2000–3000	Chiapas–Guatemala	15	20
1e	*arborescens* S**					x	x	x		Cool, wet forests	1000–2300	Chiapas–Guatemala	15	15b
1f	*xanthiifolia* S*					x	x	x		Xeric–semi-xeric	1000–1500	Costa Rica	10	1d
1g	*fragrans*					x				Dry hillsides	300–400	Venezuela	9	11
2a	*guatemalensis*						x	x	x	Below cloud forest	1200–2000	Nicaragua–Costa Rica	15–10	3
2b	*quadrangularis*						x	x		Cool, wet forests	1900–2700	Venezuela, Colombia	8–4	13
2c	*rosei**						x	x	x	Deciduous thorn-forest	100–600	Sonora, Sinaloa	28–24	1c

Species codes as in Fig. 1. N, S—population at the N or S extremes of large species ranges. *, **—Subspecies of *M. tomentosa** or *M. leucantha***. Ref—references to species descriptions and distribution maps in Funk (1982)

M. bipinnatifolia (Table 1, *1a*) and *M. tomentosa* ssp. *rosei* flower in November/December, i.e., 3–4 months later than *Montanoa* species in central Mexico (Figs. 2b, *squares*; 3, (*2c*)). Near the Equator (2–4° N), *M. ovalifolia* starts flowering 6 months before *M. quadrangularis* (Fig. 2a, c, *triangles*). Different *Simsia* species also flower progressively later with declining latitude (Fig. 2d).

In the mountains of western Colombia (4° N), synchronous flowering of 107 *M. quadrangularis* trees (called “daisy trees” because of their daisy-like flowers) started in October/November of two consecutive years (Fig. 4a). Within the observed tree population, flowering time varied. In most trees, flowering peaked during three biweekly observation periods (Fig. 4b), but a few trees flowered almost 3 months before those flowerings last. In most individual trees, flowering peaked during the same 2-week period in consecutive years, indicating genetic differences in peak flowering time between the different cohorts (Fig. 4b). In 1999, the average number of inflorescences/tree was three times larger than in 2000 (Fig. 1c), when rainfall between September and November was twice that in 1999 and may have affected flower development adversely.

Discussion

Between Mexico and the Equator, the species-specific flowering periods of *Montanoa* and *Simsia,* as deduced from herbarium collections (see Methods), start progressively later with declining latitude (Figs. 2, 3; Table 1). The synchronous development of terminal inflorescences is likely to begin at the same time every year in all conspecific plants, as it is in *M. quadrangularis*, whose flowering periodicity we monitored over 2 years in the field (Fig. 4), and other tree species (Borchert and Rivera 2001; Rivera et al. 2002). This raises the question: which environmental signal induces synchronous flowering at species-specific times that vary with latitude? The latitudinal gradient in flowering time of *Montanoa* and *Simsia* is paralleled by latitudinal changes in the seasonal time course of day length, daily insolation, and rainfall (Fig. 3). Synchronous

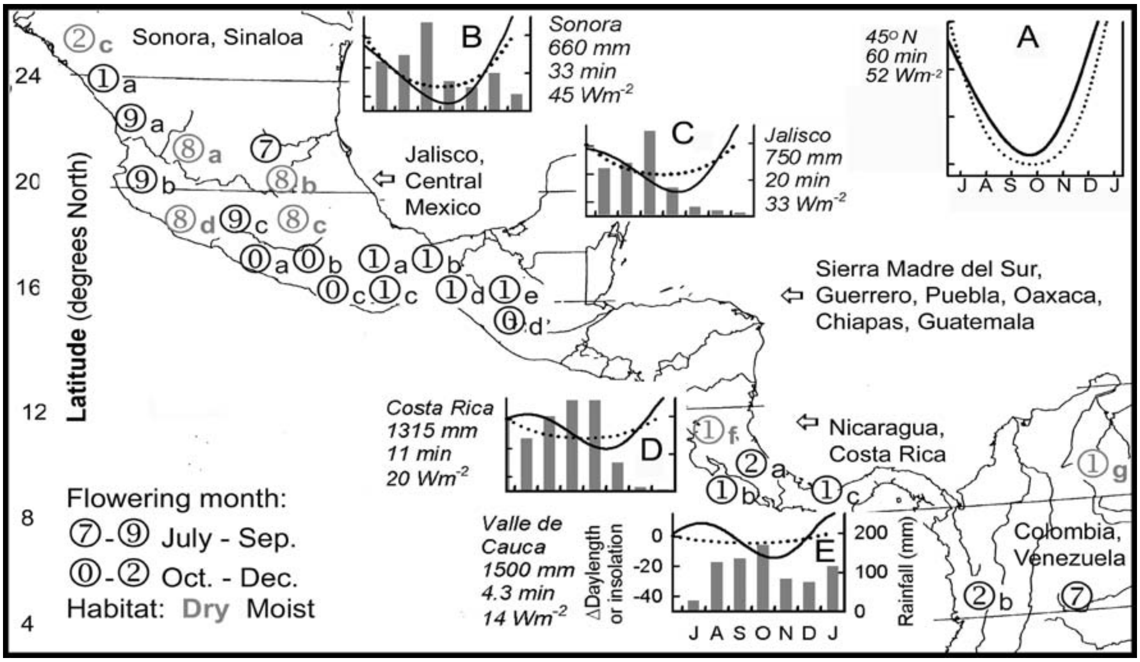

Fig. 3 Latitudinal variation in flowering times of *Montanoa* between Mexico and the Equator, rainfall seasonality, and autumnal decline in day length and daily insolation. Each *Montanoa* species listed in Table 1 is identified by a circled number (last digit of flowering month between July and December) and a lowercase letter (Table 1, *first column*; Funk 1982). *Gray numbers* dry habitat; *black numbers* mesic or moist habitat. *Graph insets* **a**–**e** Rate of autumnal decline in day length (min 20 day^{-1}, *dotted*) and daily insolation (W m^{-2} 20 day^{-1}, *solid*) and rainfall (mm/months, *bars*; legends in **e**). Annual rainfall and largest change in day length and daily insolation given below station names. Rainfall for **b**–**d** from Borchert et al. 2004, for **e** from Calle (unpublished)

flowering at the same time each year cannot be induced by rainfall, which varies widely both locally and between years (Fig. 3b–e *bars*), but is indicative of photoperiodic control.

The time courses of day length and insolation between July and November differ substantially. Daylength follows the same sinusoidal time course at all latitudes, with its maximum and minimum attained at the summer and winter solstice, respectively (Fig. 1a). The largest rate of decline occurs at the autumn equinox and varies with latitude, from 60 min 20 day^{-1} at 45° N to zero at the Equator (Fig. 3a–e, *dotted curves*). If induced by declining day length, flowering of Montanoa should start in July/August at all tropical latitudes. In contrast to day length, the annual course of insolation varies significantly with latitude (Fig. 1b; Introduction). In the tropics, the maximum of insolation gradually shifts from the summer solstice, at 23° N, to the autumn equinox, at the Equator. Near the Equator, where day length is constant, the amplitude of annual changes in insolation still amounts to ca. 25% of that at 45° N (14 vs. 52 Wm^{-2}; Fig. 3a, e, *solid curves*). Between 25 and 4° N, the beginning of the distinct autumnal decline in insolation shifts from July to October (Fig. 1c, *blue circles*), and the decline lasts for progressively shorter periods (Fig. 1b). Flowering periods induced by declining insolation should change correspondingly with declining latitude (Fig. 1b, *red curves*).

The flowering periods observed in *Montanoa* and *Simsia* confirm this prediction (Figs. 2, 3). In Mexico (20–28°), the decline in insolation lasts from July to November (Fig. 1b). Accordingly, different species flower at various times between July and December (Fig. 3, Table 1), and other environmental variables apparently co-determine species-specific flowering times. *Montanoa* species adapted to dry lowlands tend to flower during the late rainy season, in July/August (Fig. 3c), 1–2 month earlier than species of moist habitats (Fig. 3, *18–22° N, gray vs. black numbers*). Flowering depending on winter rains occurs last, in December (Fig. 3, *24–28° N*). Within the wide range of *M. tomentosa* (10–28° N), different subspecies flower at various times between July and December (Fig. 2b, Table 1), i.e., like the ecological races of *Xanthium,* they are adapted to latitudinal and seasonal variations in insolation (Introduction; Ray and Alexander 1966; McMillan 1970). Several *Montanoa* and *Simsia* species flower 2–3 months later than Asteraceae of the temperate zone, where flowering and fruit development must be completed before the first frost in autumn.

Around 10° N, in Costa Rica and Venezuela, all *Montanoa* and *Simsia* species flower during the relatively short period of declining insolation in October/November (Figs. 1, 2, 3, *10° N*), as do other woody Asteraceae (*Trixis*, *Verbesina*, *Vernonia*) and tree species (Opler et al. 1980;

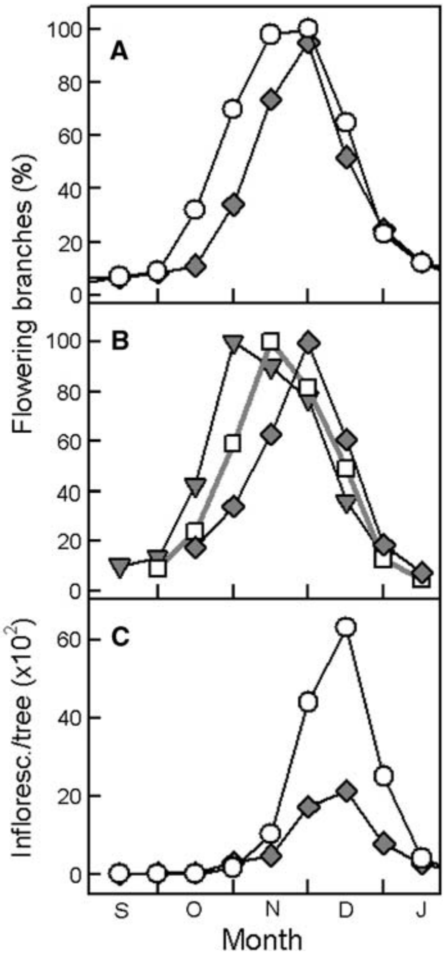

Fig. 4 Synchronous flowering of 107 *Montanoa quadrangularis* trees in El Dovio, Valle del Cauca, Colombia (4° N) between September 1998 and March 2000. **a** Fraction of flowering branches observed during the first (*circles*) and second observation year (*diamonds*). **b** First-year flowering periods of three subsets of trees representing 85% of the population. **c** Number of inflorescences formed in first (*circles*) and second observation year (*diamonds*)

Rivera and Borchert 2001). Near the equator, *M. quadrangularis* flowers during the brief decline of insolation in October/November (Fig. 4), but the prolonged flowering period of *M. ovalifolia* starts during declining insolation in May/June (Fig. 2a).

Latitudinal variation of the flowering periods of *Montanoa* illustrates the ecological significance of photoperiodic control of flowering time. To assure cross-pollination, flowering should be synchronous among individuals of a population. From Equatorial forests with low climatic seasonality to strongly seasonal forests at higher tropical latitudes, seasonal variation in insolation constitutes the only reliable environmental signal for inducing synchronous flowering at the same time each year.

Daily insolation is measured above the earth atmosphere. As solar irradiation passes through the atmosphere, it is reduced by light scattering and absorption in clouds (Strahler and Strahler 2003; Yeang 2007a, b). Most *M. quadrangularis* trees flowered at the same time in consecutive years, but the number of inflorescences formed was much higher in the year with relatively low rainfall during the flowering period (Fig. 4a, c). This suggests that absorption of solar radiation by cloud cover affects the energy-dependent flower aspects of flower development, but not the timing of flower induction in a significant way (compare Introduction).

For over 80 years, seasonal variation in day length has been known to induce flowering of many plant species at temperate latitudes (Thomas and Vince-Prue 1997; Lüttge and Hertel 2009). Identification of daily insolation as the environmental variable that may determine the course of seasonal development of many perennials resolves the problem of photoperiodic control at lower latitudes, because insolation is a function of both day length and the intensity of solar irradiation. Near the Equator, day length is constant, and the seasonality of insolation is a function of irradiation alone. At temperate latitudes, the annual variation of insolation is similar to, but not identical with, that of day length (Fig. 1, *50° N*; Strahler and Strahler 2003; Yeang 2007a, b). We conclude that between Mexico and the Equator, the observed synchronous onset of autumn flowering of *Montanoa*, *Simsia,* and other perennials is likely to be induced by declining insolation, not day length.

The pathway from the perception of the inducing environmental signal to early developmental changes in the apical meristem includes the following major components: day-length (signal) > biological clock (reference) > phytochromes and cryptochromes (photoreceptors) > CONSTANS (CO-protein) > FLOWERING LOCUS (FT-protein) > meristem identity genes (Engelmann 2007). In *Arabidopsis*, the latter can direct development of the apical meristem into either a flower or a vegetative stem with secondary growth forming a wood cylinder (Melzer et al. 2008). In the aspen tree (*Populus tremula*), this pathway controls both the induction of flower buds by increasing day-length in spring and of vegetative resting buds by declining day-length in autumn (Böhlenius et al. 2006). The development of both organs remains arrested in winter and is completed when temperatures rise again in early spring. FT expression peaks during floral initiation and declines strongly before bud set. The critical day-length arresting shoot growth in autumn varies among aspen provenances from 22 h at 63° N to 17 h at 51° N (Introduction: *Xanthium*). FT expression declines earliest at 63° N, i.e., it is a critical determinant of the timing of bud set. Latitudinal variation of flowering time in *Montanoa* (Figs. 2, 3) is probably determined by variation in the time course of CO and FT expressions in autumn. The molecular composition of the biological clock and its interactions with the various photoreceptors are complex (Engelmann 2007). *Montanoa* probably perceives seasonal variation of daily insolation at lower latitudes via unidentified sensors interacting with the biological clock.

The annual cycle of insolation was suggested earlier as a potential time giver for synchronous flowering in tropical tree communities (Van Schaik et al. 1993; Wright 1996). Recently, Yeang (2007a, 2007b) suggested that high solar radiation intensity induces flowering of the rubber tree (*Hevea brasiliensis*) around the spring equinox. He overlooked that in *Hevea* and other tropical trees, lateral flower primordia differentiate during rapid shoot expansion induced by increasing insolation in January/February, i.e., weeks before the spring equinox (Fig. 1b, *February*; Borchert et al., unpublished). Nor does the solar radiation intensity hypothesis explain synchronous flowering in November/December, as described here.

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