Interciencia
ISSN: 0378-1844
interciencia@ivic.ve
Asociación Interciencia
Venezuela

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Plant reproductive phenology in a temperate forest of the monarch butterfly biosphere reserve, México
Interciencia, vol. 32, núm. 7, julio, 2007, pp. 445-452
Asociación Interciencia
Caracas, Venezuela

PLANT REPRODUCTIVE PHENOLOGY IN A TEMPERATE FOREST OF THE MONARCH BUTTERFLY BIOSPHERE RESERVE, MEXICO

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SUMMARY

Monthly flowering and fruiting observations were recorded for the most dominant species (11 annual herbs, 72 perennial herbs, 21 shrubs, and 8 trees) in a temperate forest, during 2004, in the Cerro Altamirano Core Zone of the Monarch Butterfly Biosphere Reserve in central Mexico. Intraspecific synchrony in flowering and fruiting of eight woody species was estimated by monitoring 20 individuals of each. Flowering and fruiting occurred mainly during the rainy season and at the beginning of the dry season (Jul-Dec) and showed a low degree of seasonality. Reproductive activity within growth forms occurred in different periods: 1) annual and perennial herbs flowered principally during the rainy season and at the beginning of the dry season, while their fruiting peaked during the dry season; 2) shrubs produced flowers and fruits throughout the year without peaks in any season; and 3) nearly all trees had flowers and fruits during the dry season. Correlations of the number of flowering species at community level and perennial herbs against rainfall showed a significant positive relationship. However, a negative relationship was found between rainfall and number of fruiting species in shrubs and trees. High reproductive synchrony (>60% of individuals in the same phenological phase) was detected in five tree species. Phenological reproductive patterns in the study area, essentially a temperate high altitude forest in the tropics, were similar to those documented for the seasonal lowland tropical forests, mainly explained by annual rainfall and growth form.

One of the most important aspects of phenology studies is the search of factors that explain the phenological behavior of species. Rainfall, temperature, soil water availability and photoperiod appear to be the main abiotic factors that trigger flowering and fruiting events (van Schaik *et al*., 1993; Newstrom *et al*., 1994; Morellato *et al*., 2000; Borchert *et al*., 2004). On the other hand, biotic factors such as fruit type, pollination and seed dispersal syndromes are also very important for understanding the flowering and fruiting patterns of plant species (Bawa *et al*., 1985; Ibarra-Manríquez *et al*., 1991; Ibarra-Manríquez and Oyama, 1992; van Schaik *et al*., 1993; Newstrom *et al*., 1994; Wright and Calderón, 1995; Poulin *et al*., 1999; Spina *et al*., 2001; Bolmgren *et al*., 2003).

An additional recurring focus in plant phenology studies is the comparison of phenological patterns among different growth forms. Several studies have found that herbaceous species produce flowers and fruits during the rainy season, whereas woody species tend to have flowers during the dry season and fruits during the dry or rainy seasons (Frankie *et al*., 1974; Croat, 1975; Opler *et al*., 1980; Sarmiento and Monasterio, 1983; Ibarra-Manríquez *et al*., 1991; Ibarra-Manríquez and Oyama, 1992; Chapman *et al*., 1999; Batalha and Mantovani, 2000; Ramírez, 2002; Joshi and Janarthanam, 2004). Another important aspect is the intraspecific synchrony in reproductive events. A high degree of synchrony in flowering and fruiting could be advantageous for the plants by increasing the attraction of pollinators and seed dispersers, or the satiation of seed predators (Rathcke and Lacey, 1985; Smith and Bronstein, 1996; Olvera *et al*., 1997; Kelly and Sork, 2002). In contrast, asynchrony could minimize competition for dispersal agents, propagule predation and pathogen incidence (Rathcke and Lacey, 1985; van Schaik *et al*., 1993; Poulin *et al*., 1999).

This work describes for the first time the reproductive plant phenology in one of the core zones of the Monarch Butterfly Biosphere Reserve in

KEYWORDS / Ecosystem Conservation / Flowering Phenology / Fruiting Phenology / Growth Forms / Intraspecific Synchrony /

Received: 04/03/2007. Modified: 05/30/2007. Accepted: 06/06/2007.

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central Mexico. This reserve is the winter refuge of the monarch butterfly (*Danaus plexippus* L.) and is one of the most important protected areas of temperate forest in Mexico, in terms of diversity of vascular plants, area, and its biogeography, which includes a unique combination of northern and southern elements at high elevation within the tropics. To date, phenological studies in Mexico have been conducted mainly on woody species of tropical dry forests and tropical rain-forests (Carabias-Lillo and Guevara, 1985; Bullock and Solís-Magallanes, 1990; Ibarra-Manríquez *et al*., 1991; Ibarra-Manríquez, 1992; Ochoa-Gaona and Domínguez-Vázquez, 2000; Lobo *et al*., 2003), with few studies in the temperate forests (Ramírez and Nepamuceno, 1986; Bello, 1994; Olvera *et al*., 1997). Thus, phenological information for Mexican temperate species is scarce and only partial data can be found in some regional flora or taxonomic monographs where the phenological information comes from records in herbaria specimens rather than periodical field observations.

Understanding phenological patterns and the underlying factors is important in the Monarch Butterfly Biosphere Reserve (MBBR) to help analyze the wide array of biological processes governing forest functions and structure, and also to reflect positive or negative interactions among species (e.g., dispersal of diaspores, population biology of herbivores). Phenological data will also provide valuable information to design sustainable plans for the management and conservation of biodiversity. Specifically, such data will allow to recognize keystone fruit resources in the plant community and will also be useful in planning restoration actions in areas affected by human activities (Chapman *et al*., 1999; Wallace and Painter, 2002). Unfortunately, deforestation in the MBBR is a major problem that includes a diminished natural resource base for the local people, as well as ecosystem degradation associated with the broad changes in forest cover (Brower *et al*., 2002; Ramírez *et al*., 2003).

The purpose of the present study of the reproductive phenology of 112 plant species in the Cerro Altamirano mountain massif in the core zone of the MBBR was threefold: 1) to describe phenological patterns at the community level and within growth forms (annual herbs, perennial herbs, shrubs, and trees); 2) to examine whether or not seasonal variation in rainfall and temperature was correlated with phenophase peaks; and 3) to estimate the degree of individual reproductive synchrony for important woody species. Based on preliminary findings, it was predicted that 1) flowering and fruiting would be triggered by rainfall, 2) growth forms would show different phenological patterns, and 3) woody species would display a pattern of intraspecific synchrony in flowering and fruiting.

Materials and Methods

The study was carried out in one of the three major core zones of the MBBR, the Cerro Altamirano, in the states of Michoacan and Mexico, central Mexico (19°59'42''-19°57'07''N and 100°09'54''-100°06'39''W), with a surface of 588ha and altitudes of 2500-3320masl (Cornejo *et al*., 2003). Geologically, this reserve is within the Transmexican Volcanic Belt (Ferrusquía-Villafranca, 1993). The regional climate is temperate-subhumid, with wet summers $C(w_1)$, an average annual rainfall of 830mm and a mean annual temperature of 15.7ºC (García, 1981). Rainfall is strongly seasonal, with most precipitation occurring from June to September (Figure 1). Vegetation is classified as temperate forest, with two main subtypes: *Quercus* forest at lower altitudes and *Abies* forest at higher altitudes (Rzedowski, 1978). The *Quercus* forest is a floristically rich formation found at 2500-2900masl. In this forest type the most important tree species are *Q. castanea* Née and *Q. obtusata* Humb. & Bonpl. (Fagaceae), and *Arbutus xalapensis* Kunth (Ericaceae), while the understory contains a great diversity of shrubs and herbs, predominantly Asteraceae, Lamiaceae and Scrophulariaceae. The *Abies* forest is mostly found above 3000masl, has a canopy dominated by *A. religiosa* (Kunth) Schltdl. & Cham. (Pinaceae), *Q. laurina* Humb. & Bonpl. (Fagaceae) and *Clethra mexicana* DC. (Clethraceae), and an understory of several shrub and herb species (Asteraceae and Lamiaceae; Cornejo-Tenorio *et al*., 2003).

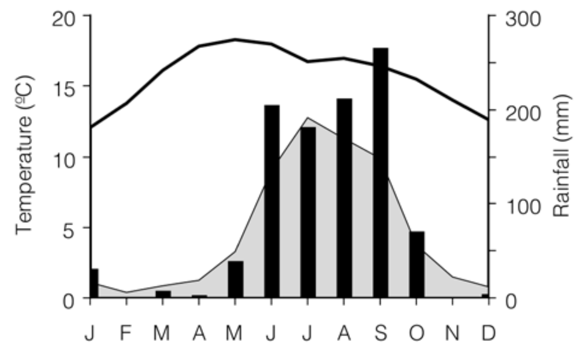

Figure 1. Climatic diagram with data from the Tepuxtepec Meteorological Station, located at Contepec, Michoacan, Mexico (19º59'S, 100º13'W, 2330masl). The values for mean monthly rainfall (curve in gray, 1970-2000), mean monthly temperature (line, 1970-2000) and monthly rainfall registered in 2004 (black bars) were obtained from the Comisión Nacional del Agua.

Phenological data and analysis

The flowering and fruiting of 112 species were observed in Cerro Altamirano during one year (Jan-Dec 2004), along a transect of approximately 3km that encompassed a 500m elevational gradient, from the lower area at 2500masl to the hill summit at 3000masl. Throughout this path observation sites were established every 100m, for a total of 35 sites. All observations were made during the first week of each month. Each observation site consisted of a 25×4m transect. Based on knowledge of the area (Cornejo *et al*., 2003), counts were limited to include only the most abundant plant species in the community (Table I): 11 annual herbs, 72 perennial herbs, 21 shrubs, and 8 trees. The presence of open flowers and ripe fruits was recorded only in those species with $\geq$10 adult individuals in at least one of the 35 observation sites. In the case of herbs, it was sometimes not possible to define individuals, in which case we recorded flowers or fruits at the level of ramets in no less than 10 sites.

To investigate phenological synchrony of the dominant woody species, 160 mature individuals were marked and observed monthly, belonging to seven tree species (*A. religiosa*; *Arbutus tesellata*, *A. xalapensis*, Ericaceae; *Clethra mexicana*, Clethraceae; *Q. castanea, Q. laurina*, and *Q. obtusata*) and to one shrub species (*Arctostaphylos pungens*, Ericaceae). Hereafter, this species group was named as tree species. Based in field experience, dominant species were recognized mainly by their numerical abundance. Observations had to be limited to this number of species and individuals for each species due to logistical reasons. However, the distance between individuals of particular species varied from 20 to 50m, depending on their relative abundance and local distribution. The presence of flowers and fruits was observed directly or with the aid of binoculars. Voucher materials of all studied species were deposited in the herbaria of Universidad Nacional Autónoma de México (MEXU) and Instituto de Ecología (IEB), Mexico.

The flowering and fruiting periods of every species were characterized according to rainfall seasonality

(Figure 1) as occurring in the wet (Jun-Sep) or in the dry season (Oct-May). The Pearson's correlation coefficient (Zar, 1999) was used to correlate the number of flowering and fruiting species observed each month against the monthly rainfall data registered during the study period and mean monthly temperatures (Figure 1). The Rayleigh test (Zar, 1999) was used to assess whether species had flowers or fruits uniformly throughout the year. To calculate the circular statistic parameters, months were converted to angles (0º for Jan, 30º for Feb, etc.). The Rayleigh test (z) determines the significance of the mean angle (a), which represents the period of the year throughout which flowering and fruiting is recorded for most species. If z is significant for each reproductive event, then these are concentrated in a specific period of the year, but if z is not significant, it is concluded that the phenophases were distributed uniformly throughout the year. The degree of seasonality for the reproductive activity may be indicated by a vector (R), which is a measure of concentration around the mean angle. The value of the R may vary between 0 and 1, and a high value indicates seasonal phenological behavior; R >0.75 was considered as a high value for this variable.

The activity index (Morellato *et al*., 1990; Bencke and Morellato, 2002) was used to estimate the synchrony between individuals of each woody species. This index indicates the percentage of individuals during the flowering or fruiting peak of each species. It has three categories: 1) asynchrony, when >20% of the individuals have reproductive structures; 2) low synchrony, when 20-60% when >20% of the individuals have them; and 3) high synchrony, when >60% do so.

Results

Community phenology

All the species monitored flowered and 82% fruited. About 70% of the species flowered during the rainy season and into the beginning of the dry season (Jul-Dec). The mean angle for flowering corresponds to the beginning of September (Figure 2a, Table II). A high proportion of species (73%) produced fruits during the dry season (Oct-May), with a maximum activity at the beginning of November (Figure 2b, Table II). Most species produced flowers and fruits in a specific period of the year. Nevertheless, the low values of R revealed a low degree of reproductive seasonality (Table II). A positive correlation was found among the

TABLE I
FLOWERING AND FRUITING PHENOLOGIES OF 112 SPECIES FROM CERRO ALTAMIRANO, ONE OF THE CORE ZONES OF THE MONARCH BUTTERFLY BIOSPHERE RESERVE IN CENTRAL MEXICO

Taxa	Growth form	Flowering	Fruiting
Apiaceae			
Donnellsmithia juncea (Humb. & Bonpl.) Math. & Constance	Perennial herb	9-10	11
Tauschia alpina (Coult. & Rose) Math.	Perennial herb	5-8, 10	8-9
Asteraceae			
Acourtia turbinata (Lex.) Reveal & King	Perennial herb	1-3	3
Ageratina areolaris (DC.) Gage	Shrub	1, 10-12	1, 11-12
A. glabrata (Kunth) RM King & H Rob.	Shrub	2-4	4-5
A. mairetiana (DC.) RM King & H Rob. var. *mairetiana*	Shrub	1-5, 12	2-6
A. pazcuarensis (Kunth) R.M. King. & H. Rob.	Perennial herb	10-12	—
A. petiolaris (Moc. ex DC.) R.M. King & H. Rob.	Shrub	2-4	3-6
Archibaccharis hirtella (DC.) Heering	Shrub	1-3, 11-12	3-5
A. serratifolia (Kunth) S.F. Blake	Perennial herb	1-4, 11-12	3-5, 12
Artemisia ludoviciana Nutt.	Perennial herb	10-12	12
Baccharis conferta Kunth	Shrub	3-6	4-7
B. pteronioides DC.	Perennial herb	5-6	7
Bidens odorata Cav.	Annual herb	10-12	10-12
Cosmos parviflorus (Jacq.) Kunth	Annual herb	9	10-11
C. scabiosoides Kunth	Perennial herb	8-10	—
Dahlia coccinea Cav.	Perennial herb	8-9	10-11
D. scapigera (A. Dietr.) Knowles & Westc.	Perennial herb	8-9	10-11
Dyssodia papposa (Vent.) Hitchc.	Annual herb	9-10	12
D. pinnata (Cav.) B.L. Rob. var. *pinnata*	Annual herb	10	10-12
Galinsoga quadriradiata Ruiz & Pav.	Annual herb	10	10-12
Hieracium dysonymum Blake	Perennial herb	3-5	5-6
Jaegeria hirta (Lag.) Less.	Perennial herb	10-11	10-12
Laennecia schiedeana (Less.) G.L. Nesom	Annual herb	10-11	12
Montanoa grandiflora DC.	Shrub	9-10	1, 12
Packera sanguisorbae (DC.) C. Jeffrey	Perennial herb	2-6	5-7
Piqueria trinervia Cav.	Perennial herb	8-12	10-12
Roldana barba-johannis (DC.) H. Rob. & Brettell	Shrub	1-2, 12	3-4
Stevia elatior Kunth	Perennial herb	8-9	9-12
S. monardifolia Kunth	Perennial herb	1, 8-12	10-12
S. salicifolia Cav. var. *salicifolia*	Shrub	1, 10-12	1-4, 12
S. serrata Cav. var. *serrata*	Perennial herb	8-12	10-12
Tagetes lucida Cav.	Perennial herb	8-12	12
T. lunulata Ortega	Annual herb	9-12	10-12
T. micrantha Cav.	Annual herb	8-9	10-12
Verbesina oncophora B.L. Rob. & Greenm.	Shrub	1, 12	—
Viguiera hemsleyana S.F. Blake	Perennial herb	9-10	10-11
Viguiera sessilifolia DC.	Perennial herb	9-10	11-12
Boraginaceae			
Lithospermum distichum Ortega	Perennial herb	6-8	8-9
Bromeliaceae			
Tillandsia andrieuxii (Mez) L.B. Sm.	Perennial herb	5-7	5, 8-12
Campanulaceae			
Diastatea micrantha (Kunth) McVaugh	Annual herb	10-12	—
Lobelia gruina Cav.	Perennial herb	1, 9-12	—
Caprifoliaceae			
Symphoricarpos microphyllus Kunth	Shrub	7-9	10-12
Caryophyllaceae			
Arenaria bourgaei Hemsl.	Perennial herb	5-10	5-12
Cistaceae			
Helianthemum glomeratum Lag. ex DC.	Perennial herb	1-4,8-12	2-5,8-12
Clethraceae			
Clethra mexicana DC.	Tree	1-2	3-4
Clusiaceae			
Hypericum silenoides Juss. var. *silenoides*	Perennial herb	8-12	9-12
Commelinaceae			
Commelina coelestis Willd.	Perennial herb	8-9	10
Gibasis pulchella (Kunth) Raf.	Perennial herb	7-10	—
Ericaceae			
Arbutus tessellata P.D. Sorensen	Tree	1-9, 11-12	5-6
A. xalapensis Kunth	Tree	3-6	7-12
Arctostaphylos pungens Kunth	Shrub	1-12	4-10
Comarostaphylis discolor (Hook.) Diggs subsp. *rupestris*	Shrub	2, 4-9	1-2, 5-6, 11-12
Fabaceae			
Cologania biloba (Lindl.) G. Nicholson	Perennial herb	8-10	—
Desmodium neo-mexicanum A. Gray	Perennial herb	9-10	—
Lathyrus parviflorus S. Watson	Perennial herb	7-9	—
Lupinus montanus Kunth	Perennial herb	1-3,10-12	1-5
Phaseolus pluriflorus Maréchal, Mascherpa & Stainier	Perennial herb	8-9	—
Fagaceae			
Quercus castanea Née	Tree	3-5	1-4, 12
Q. laurina Humb. & Bonpl.	Tree	4-5	12

→

TABLE I (*cont.*)

Q. obtusata Humb. & Bonpl.	Tree	3-5	11-12
Gentianaceae			
Gentiana spathacea Kunth	Perennial herb	1-2, 12	2-3
Halenia brevicornis (Kunth) G. Don	Perennial herb	11	—
H. plantaginea (Kunth) Griseb.	Perennial herb	11	—
Geraniaceae			
Geranium potentillaefolium DC.	Perennial herb	6-8	9
G. seemanni Peyr.	Perennial herb	7-8	9
Hypoxidaceae			
Hypoxis mexicana Schult. & Schult. f.	Perennial herb	8-9	9
Iridaceae			
Sisyrinchium convolutum Nocca	Perennial herb	7-9	10
Lamiaceae			
Lepechinia caulescens (Ortega) Epling	Perennial herb	8-9	10
Salvia amarissima Ort.	Perennial herb	8-12	—
S. elegans Vahl	Perennial herb	1-5,10-12	3-5
S. fulgens Cav.	Perennial herb	7-12	10-12
S. laevis Benth.	Perennial herb	9-12	12
S. lavanduloides Benth.	Perennial herb	1, 7-12	2-4, 10-12
S. mexicana L. var. *mexicana*	Perennial herb	8-12	1-4, 10-12
S. patens Cav.	Perennial herb	8-11	—
Scutellaria caerulea Sessé & Moc.	Perennial herb	7-10	10-11
Stachys parvifolia M. Martens & Galeotti	Perennial herb	7-9	8-9
Lentiburaliaceae			
Pinguicula moranensis Kunth	Perennial herb	5-9	10
Lythraceae			
Cuphea aequipetala Cav.	Perennial herb	7-10	8-11
Onagraceae			
Fuchsia thymifolia Kunth	Shrub	5-9	10-12
Lopezia racemosa Cav.	Annual herb	1, 9-12	2
Orchidaceae			
Corallorrhiza odontorhiza (Willd.) Nutt.	Perennial herb	7-8	—
Govenia capitata Lindl.	Perennial herb	6-9	11-12
Orobanchaceae			
Conopholis alpina Liebm.	Perennial herb	4-5	5-7
Pinaceae			
Abies religiosa (Kunth) Schltdl. & Cham.	Tree	3-5	1-4
Polemoniaceae			
Loeselia mexicana (Lam.) Brand	Perennial herb	1-2, 10-12	—
Polygalaceae			
Monnina ciliolata DC.	Shrub	1, 8-9	11-12
Ranunculaceae			
Clematis dioica L.	Shrub	5-10	1
Ranunculus petiolaris Kunth ex DC. var. *arsenei* (Benson) T Duncan	Perennial herb	6-10	9-11
Rhamnaceae			
Ceanothus coeruleus Lag.	Shrub	1, 4-8, 10-12	1
Rosaceae			
Alchemilla procumbens Rose	Perennial herb	7-12	—
Rubiaceae			
Bouvardia longiflora (Cav.) Kunth	Shrub	4-10	12
B. ternifolia (Cav.) Schltdl.	Perennial herb	4-10	1, 10-12
Crusea longiflora (Willd. ex Roem. & Schult.) WR Anderson	Annual herb	8-10	—
Galium aschenbornii Nees & S. Schauer	Perennial herb	7-9	1-2, 10-12
Salicaceae			
Salix paradoxa Kunth	Tree	3	5
Scrophulariaceae			
Castilleja tenuiflora Benth.	Perennial herb	1-12	2-3, 10
Lamourouxia dasyantha (Cham. & Schltdl.) Ernst	Perennial herb	11-12	12
L. multifida Kunth	Perennial herb	9-12	10-12
Mecardonia procumbens (Mill.) Small	Perennial herb	8-10	10-12
Penstemon roseus (Cerv. ex Sweet) G Don	Perennial herb	7-12	1-2, 10-12
Solanaceae			
Cestrum thyrsoideum Kunth	Shrub	1-2, 9-11	—
Physalis orizabae Don	Perennial herb	7-9	9
Solanum demissum Lindl.	Perennial herb	7-8	—
Valerianaceae			
Valeriana barbareifolia M. Martens & Galeotti	Perennial herb	7-10	10-12
Verbenaceae			
Glandularia teucriifolia (M. Martens & Galeotti) Umber	Perennial herb	6-9	8-9
V. recta Kunth	Perennial herb	8-10	10
Violaceae			
Viola humilis Kunth	Perennial herb	6-9	10
V. painteri Rouse & House	Perennial herb	5-9	9
Viscaceae			
Cladocolea diversifolia (Benth.) Kuijt	Shrub	4-5	3-4
Phoradendron schumanni Trel.	Shrub	5	5-10

Months are indicated by numbers. Hyphens or commas between months means continual or intermittent phenological activity, respectively.

number of flowering species and rainfall (r= 0.59, P<0.05), whereas for fruiting species the correlation was not significant (r= -0.44, P>0.05). However, for all comparisons performed at the community level and within growth forms against mean monthly temperature, there were no significant differences in flowering or fruiting periods.

Phenology and growth forms

Flowering and fruiting activity in annual and perennial herbs occurred mainly during the rainy season and the beginning of the dry season (Jul-Dec). The number of flowering and fruiting annual herbs was not uniformly distributed throughout the year (Figure 2c-d, Table II). The degree of seasonality denoted by R was high (Table II). The mean

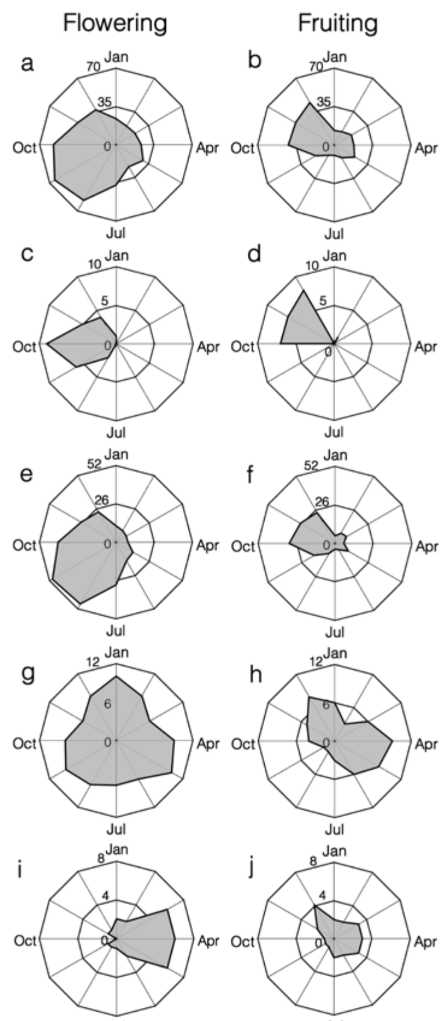

Figure 2. Flowering and fruting species throughout the year in Cerro Altamirano. a-b: community level (112 species), c-d: annual herbs (11 species), e-f: perennial herbs (72 species), g-h: shrubs (21 species), i-j: trees (8 species).

TABLE II
VALUES OF CIRCULAR STATISTIC ANALYSES FOR FLOWERING AND FRUITING SPECIES IN CERRO ALTAMIRANO CORE ZONE

	Rayleigh test (z)	Degree of seasonality (R)	Mean angle
Flowering			
Community	32.37 *	0.27	245°
Annual herbs	17.35 *	0.80	275°
Perennial herbs	50.28 *	0.42	241°
Shrubs	0.02 ns	0.01	---
Trees	8.49 *	0.54	86°
Fruiting			
Community	11.32 *	0.16	308°
Annual herbs	14.88 *	0.74	304°
Perennial herbs	12.72 *	0.21	292°
Shrubs	1.55 ns	0.13	---
Trees	0.91 ns	0.18	---

* P<0.001.

angle for flowering species corresponds to the beginning of October, whereas the mean angle for fruiting corresponds to the beginning of November. The number of flowering and fruiting annual herbs was not correlated with rainfall (r= 0.18 and r= 0.33, respectively; P>0.05). Similarly, perennial herbs also show flowering and fruiting in a specific period of the year (Figure 2e-f, Table II); although the degree of seasonality denoted by R was from medium to low (Table II). The mean angle for flowering species was at the beginning of September and the mean angle for fruiting corresponds to the end of October. The number of flowering species was positively correlated with rainfall (r= 0.67, P<0.05), while the correlation for fruiting was not significant (r= -0.23, P>0.05).

Shrubs presented flowers and fruits all year long (Figure 2g-h, Table II). Although it was observed that fruiting had two peaks (Apr and Dec, Figure 2c), the R value (0.13) indicated that this phenophase was not seasonal. Only the correlation between the number of fruiting shrubs against the rainfall was statistically significant (r= -0.62, P<0.05).

Trees did not flower uniformly throughout the year and showed a moderate degree of seasonality (Figure 2i, Table II). A large number of species produced flowers during the driest months (Mar-May) and the mean angle of 86° corresponds to the end of March. The number of fruiting species was distributed homogeneously during the annual cycle, with a low degree of seasonality (Figure 2j, Table II). The correlation between the number of flowering trees and rainfall was not statistically significant (r= -0.42, P>0.05), while for fruiting trees the correlation was negative (r= -0.64, P<0.05).

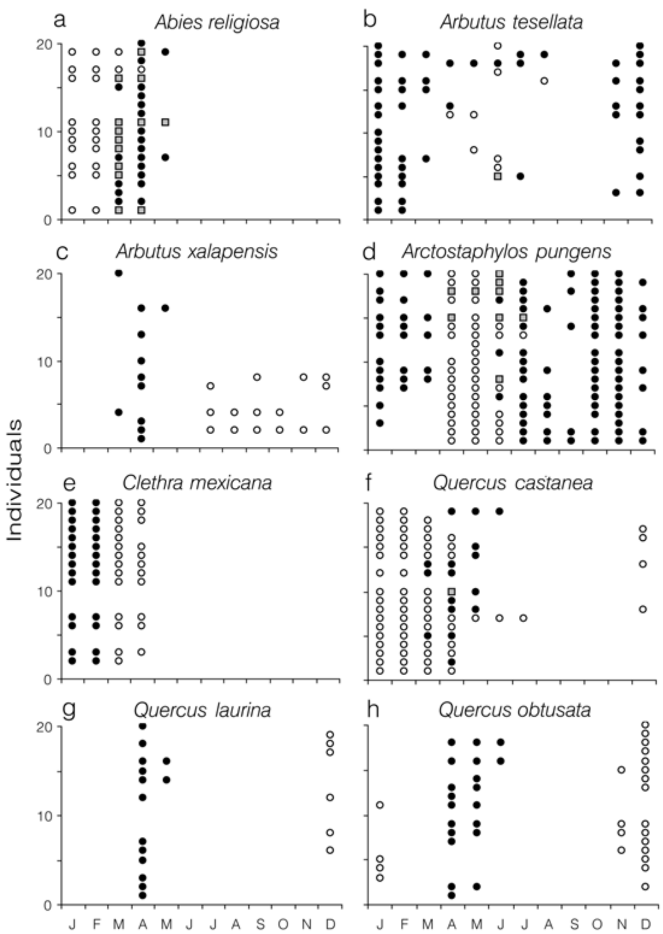

Figure 3. Reproductive phenology in marked individuals of eight woody species in Cerro Altamirano. Shaded circles: flowers, open circles: fruits, squares: both structures.

Intraspecific synchrony in tree species

Flowering of the eight tree species showed a low synchrony in half of the species and high synchrony in the other half (Table III). With regard to fruiting, only *A. xalapensis* was asynchronic, three species displayed low synchrony, and four species were highly synchronic. *Q. laurina* was the only species that exhibited a low synchrony in the production of flowers and fruits; on the contrary, *A. pungens* and *C. mexicana* were highly synchronic in both phenophases (Figure 3, Table III).

Discussion

Community phenology

The number of species flowering in Cerro Altamirano was positively correlated with rainfall. This result differs from reports for the arboreal, lianas and palms species in the tropical lowland rain forest (Carabias-Lillo and Guevara, 1985; Ibarra-Manríquez *et al*., 1991; Ibarra-Manríquez, 1992; Ibarra-Manríquez and Oyama, 1992) or tree species in the temperate forest (Ramírez and Nepamuceno, 1986; Olvera *et al*., 1997), where this

TABLE III
DEGREE OF INTRASPECIFIC SYNCHRONY* IN FLOWERING AND FRUITING AS PERCENTAGE OF INDIVIDUALS FOR EIGHT WOODY SPECIES OF CERRO ALTAMIRANO CORE ZONE

Species	Flowering %	Fruiting %
Abies religiosa	90	50
Arbutus tessellata	80	25
Arbutus xalapensis	40	15
Arctostaphylos pungens	95	95
Clethra mexicana	70	70
Quercus castanea	40	90
Quercus laurina	60	30
Quercus obtusata	50	75

* Synchrony categories: asynchrony (<20% of individuals with flowers or fruits), low synchrony (20-60%) and high synchrony (>60%). n= 20 for each species.

phenophase is associated with the season of lower precipitation. These discrepancies are understandable if it is considered that 74% of the species included in the present study are herbs. In fact, the results show that herbs, shrubs, and trees have different phenological patterns, reflecting different responses to environmental factors, particularly to rainfall seasonality, and probably also due to biotic factors such as pollination and dispersal syndromes (see below).

Phenology and growth forms

Several studies have found that flowering activity among herbaceous species is strongly associated to the rainy season (Croat, 1975; Sarmiento and Monasterio, 1983; Batalha and Mantovani, 2000; Spina *et al*., 2001; Tyler, 2001; Ramírez, 2002; Batalha and Martins, 2004), which agrees with the present findings. The strong relationship between herbs and the rainy season is due to the fact that this life form requires high water availability for their vegetative development and reproduction (Janzen, 1967; Rathcke and Lacey, 1985). Furthermore, in the study site most of the perennial herbs flower earlier than annual species. Ramírez (2002) found the same result and considered that this may be the result of the fact that perennial plants have reserve structures (rhizomes or tubers) that allow them to start their reproductive activity before annual plants. The fact that herbaceous species, the most important growth form in this plant community, produce fewer flowers during the dry season reinforces the argument of Alonso-Mejía *et al*. (1997), that the potential nectar sources for overwintering monarch butterflies become increasingly unavailable as the dry season advances. Based on their earlier blooming, it is not unexpected that fruiting herbs may also show a peak approximately two months after the maximum flowering season is reached, since this period is required for fruit formation. Fruit ripening has also been associated with the appropriate dispersal season; for instance, diaspores of wind dispersal species ripen during the dry season (Lieberman, 1982; Morellato *et al*., 1990; Ibarra-Manríquez *et al*., 1991; Batalha and Martins, 2004), a situation that also occurs in several species of Asteraceae in the study area.

Like other Neotropical localities (Opler *et al*., 1980; Smith-Ramírez and Armesto, 1994; Batalha and Mantovani, 2000; Spina *et al*., 2001; Ramírez, 2002; Batalha and Martins, 2004), flowering and fruiting of shrubs was observed during the whole year, even though the greatest number of species presented fruits during the dry season. This pattern could be explained considering that woody species have a deep root system that allows them to reach available water, or they have water storage structures that buffer the negative impact of seasonal drought (Sarmiento and Monasterio, 1983).

On the other hand, one of the factors proposed to explain flowering activity of trees in the dry season is that wind pollinated species need specific environmental conditions (dry and windy weather) for optimum pollen dispersion (Frankie *et al*., 1974; Bawa *et al*., 1985; Ramírez and Nepamuceno, 1986; Bello, 1994; Olvera *et al*., 1997; Barnes *et al*., 1998). This argument is useful to explain the present findings, since the wind pollinated trees in the study area (*A. religiosa*, *Q. castanea*, *Q. laurina*, *Q. obtusata* and *S. paradoxa*) flower during the driest months of the year (Mar-May; Figures 1 and 3). Fruiting periodicity depends principally on flowering, but it is also influenced by environmental conditions appropriate for fruit development, diaspore dispersal, and seedling establishment (Rathcke and Lacey, 1985; Ibarra-Manríquez *et al*., 1991; van Schaik *et al*., 1993). Available information from several Neotropical regions indicate that during the dry season the number of species with anemochorous or autochorous diaspores is higher, while species with zoochorous diaspores seem to produce them most often in the rainy season (Morellato *et al*., 1990; Ibarra-Manríquez *et al*., 1991, 2001; Batalha and Mantovani, 2000; Batalha and Martins, 2004). These reproductive patterns were observed in tree species of Cerro Altamirano, where anemochorous and autochorous trees have fruits in the dry season (*A. religiosa*, *C. mexicana*, *Q. castanea*, *Q. laurina*, Q. *obtusata*, and *S. paradoxa*), and zoochorous species fruit mainly in the wet season (*A. tessellata* and *A. xalapensis*).

Intraspecific synchrony in tree species

Considering the results of both reproductive cycles, 50% of the woody species showed high synchrony and the other 50% showed low synchrony or asynchrony (Table III). Rabinowitz *et al*., (1981) found that in comparison with insect-pollinated species, flowering phenology in wind-pollinated plants showed greater intrapopulation synchronization or individuals with shorter flowering times. In Cerro Altamirano, wind-pollinated species (*A. religiosa* and three species of *Quercus*) had short periods of flowering, but only *A. religiosa* was highly synchronic (Figure 3; Table I). Also, *A. tesellata*, *A. pungens*, and *C. mexicana*, which are probably pollinated by diurnal insects (e.g., bees), presented high synchrony during their flowering period, which would allow for the attraction of a higher number of generalist pollinators (Rathcke and Lacey, 1985; Ims, 1990).

From the eight tree species studied, four showed a high fruiting synchrony (Table III). It has been widely proposed in the literature that the mast fruiting effect leads to satiation of specialist and generalist predators, which allows for a part of the fruit crop to escape predation (Rathcke and Lacey, 1985; Crawley, 2000 and references therein). This event probably occurred in *Q. castanea* and *Q. laurina*. Both oak species had a high fruit production during 2004 but also showed many damaged nuts, probably by squirrels or mice. Mast fruiting in oak species is a widely documented phenological behavior in other localities of temperate forest and has been considered as an evolved reproductive strategy, because it is not simply a response to weather conditions (Sork *et al*., 1993; Kelly and Sork, 2002).

Conclusions

The results obtained indicate that the reproductive phenology patterns of the temperate flora of Cerro Altamirano are similar to those documented for seasonal tropical communities. Nevertheless, it is necessary to perform phenological studies in the other core zones of the reserve, with the purpose of contrasting the findings and to obtain long-term data. This last issue has special significance as temporal changes in plant resources profoundly affect animals, and also because cycles of plant reproduction are crucial for an understanding of ecosystem functioning (Rathcke and Lacey, 1985; van Schaik *et al*., 1993; Barnes *et al*., 1998; Chapman *et al*., 1999; Poulin *et al*., 1999; Wallace and Painter, 2002). Furthermore, it has been detected that the reproductive season of particular species may change through the years and also that many species have multiyear reproductive cycles (Frankie *et al*., 1974; Bawa *et al*., 1985; Ibarra-Manríquez *et al*., 1991; Newstrom *et al*., 1994; Chapman *et al*., 1999). In fact, recently (Oct-Dec 2006) a high number of reproductive *A. religiosa* trees were detected in each one of the three core zones of the MBBR, a condition never observed along the previous six years of floristic inventory. This situation suggests that *A. religiosa* could be considered as a supra-annual flowering species, (*sensu* Newstrom *et al*., 1994), but in order to confirm this hypothesis long-term phenological observations (at least 12 years; Newstrom *et al*., 1994) are needed.

Another important point to extend phenological studies to other areas of the reserve is that the floristic composition of each core zone (Cerro Altamirano, Chincua-Campanario-Chivati, and Cerro Pelón) is very particular and each should be considered as a distinct plant community. The floristic inventory carried out in these sanctuaries reached around 650 species (2000-2006), of which only ~14% (92 species) was shared in all three areas (Ibarra-Manríquez, unpublished data). In fact, Cerro Altamirano area has 213 species (33%) registered exclusively in its forests. Consequently, phenological information must be generated for other species that inhabit these temperate forests together with monarch butterflies. For implementing restoration actions to recover disturbed areas near overwintering sites, or for degraded ground recovery, the information obtained should be a guide to know the appropriate timing for collecting mature seeds of several species (e.g., *A. religiosa*, *Ceanothus coeruleus*, *Lupinus* spp., *Quercus* spp.).

Finally, it would be advisable that the reproductive phenology of plants in temperate forests of Mexico be addressed in a more comprehensive way, where phenological patterns could be related to other reproductive attributes, such as pollination syndromes and seed dispersal or sexual systems (monoecious, dioicious or hermaphroditic). A better understanding of phenological patterns at both the level of species and of ecosystems is crucial for the management and long term conservation of ecosystems (Newstrom *et al*., 1994; Joshi and Janarthanam, 2004). A better habitat management of existing overwintering sites and buffer areas in the MBBR is a critical element for the preservation of the mass of wintering aggregations of monarch butterflies in Mexico, an exceptional biological phenomenon highly threatened by human activities (Brower *et al*., 2002; Ramírez *et al*., 2003).

ACKNOWLEDGMENTS

The authors acknowledge the careful and extensive revision and edition of this paper by Lincoln B. Brower, and thank Ellen Andresen and William C. Burger for criticism of earlier version of the manuscript, Juan Martínez-Cruz, Fernando Pineda-García, Miguel Ángel Salinas-Melgoza and Roberto Sáyago-Lorenzana for their help in the field work. The first author received a scholarship from the Consejo Nacional de Ciencia y Tecnología (CONACyT; Nº 181848).

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FENOLOGÍA REPRODUCTIVA DE LAS PLANTAS DE UN BOSQUE TEMPLADO DE LA RESERVA DE LA BIOSFERA MARIPOSA MONARCA, MÉXICO

Guadalupe Cornejo-Tenorio y Guillermo Ibarra-Manríquez

RESUMEN

Para documentar la fenología reproductiva de las especies más importantes (11 hierbas anuales, 72 hierbas perennes, 21 arbustos y 8 árboles) del bosque templado en la zona núcleo Cerro Altamirano, Reserva de la Biosfera Mariposa Monarca, México, se realizaron observaciones mensuales durante 2004. La sincronía intraespecífica de floración y fructificación se estimó en ocho especies leñosas por medio de la observación de 20 individuos por especie. La floración y fructificación ocurrió principalmente durante la estación de lluvias e inicios de la estación seca (jul-dic), con baja estacionalidad. Las formas de crecimiento mostraron diferencias temporales en su actividad reproductiva: i) las hierbas anuales y perennes florecieron principalmente durante la estación de lluvias e inicios de la seca, mientras que la mayoría de especies con frutos fue observada en la estación seca; ii) los arbustos presentaron flores y frutos a lo largo del año, sin máximo en alguna época particular, y iii) la mayoría de los árboles concentraron su actividad reproductiva en la época de menor precipitación. El número de especies en floración a nivel comunitario y de hierbas perennes se correlacionó positivamente con la precipitación, y el número de especies arbustivas y arbóreas en fructificación mostró una correlación negativa con la precipitación. Se determinó una alta sincronía reproductiva (>60% de los individuos en una fase fenológica específica) en cinco de las especies arbóreas. Los patrones fenológicos reproductivos en el área, un bosque templado de elevada altitud en una zona tropical, fueron similares a los documentados para bosques tropicales estacionales de bajas altitudes, y explicados principalmente por la precipitación total anual y la forma de crecimiento de las especies.

FENOLOGIA REPRODUTIVA DAS PLANTAS DE UM BOSQUE TEMPERADO DA RESERVA DA BIOSFERA MARIPOSA MONARCA, MÉXICO

Guadalupe Cornejo-Tenorio e Guillermo Ibarra-Manríquez

RESUMO

Para documentar a fenologia reprodutiva das espécies mais importantes (11 ervas anuais, 72 ervas perenes, 21 arbustos e 8 árvores) do bosque temperado na zona núcleo Cerro Altamirano, Reserva da Biosfera Mariposa Monarca, México, se realizaram observações mensais durante 2004. Estimou-se a sincronia intra-específica na floração e frutificação em oito espécies lenhosas por meio da observação de 20 indivíduos por espécie. A floração e frutificação ocorreram principalmente durante a estação de chuvas e inícios da estação seca (jul-dez), com baixa estacionalidade. As formas de crescimento mostraram diferenças temporais na sua atividade reprodutiva: i) as ervas anuais e perenes floresceram principalmente durante a estação de chuvas e inícios da seca, enquanto que a maioria de espécies com frutos foi observada na estação seca; ii) os arbustos apresentaram flores e frutos ao longo do ano, sem máximo em alguma época em particular, e iii) a maioria das árvores concentraram sua atividade reprodutiva na época de menor precipitação. O número de espécies em floração a nível comunitário e de ervas perenes se correlacionou positivamente com a precipitação, e o número de espécies arbustivas e arbóreas em frutificação mostrou uma correlação negativa com a precipitação. Determinou-se uma alta sincronia reprodutiva (>60% dos indivíduos em uma fase fenológica específica) em cinco das espécies arbóreas. Os patrões fenológicos reprodutivos na área, um bosque temperado de elevada altitude em zona tropical, foram similares aos documentados para bosques tropicais estacionais de baixas altitudes, e explicados principalmente pela precipitação total anual e a forma de crescimento das espécies.