Phenology of tree species of the Osa Peninsula and Golfo Dulce region, Costa Rica

Fenologìa de especies de árboles de la Península de Osa y la región de Golfo Dulce, Costa Rica

Jorge Lobo, Reinaldo Aguilar, Eduardo Chacón & Eric Fuchs

Abstract: Data on leafing, flowering and fruiting phenology are presented for 74 tree species from the Osa Peninsula and Golfo Dulce, SE Costa Rica. Data was gathered from direct observations of phenological events from 1989 to 2007 from marked and unmarked trees in different sites in the Osa Peninsula. Flowering and fruiting peaks were observed during the dry season (December to March), with a second fruiting peak observed in the middle of the rainy season. We observed a large diversity in phenological patterns, but similar numbers of species flowered and produced fruit in the dry and rainy season. A reduction in the number of species in reproduction occurs in the months with the highest precipitation (August to October). Comparison of Osa phenological data with the phenology of wet and dry forests from Costa Rica and Panamá showed some similarities in the timing of phenological events. However, Osa species display a shift in phenological events with an earlier onset of flower and fruit production in comparison with other sites.

Key words: phenology, tropical forests, rainfall, plant reproduction, Osa Peninsula.

Resumen: Se presentan datos sobre fenología de hojas, flores y frutos de 74 especies de árboles de la Península de Osa y Golfo Dulce, al Sureste de Costa Rica. Los datos fueron obtenidos de observaciones directas de árboles no marcados y marcados en diferentes puntos de la Península de Osa durante 1989-2007. El pico de floración y fructificación se presenta durante los meses más secos (Diciembre-Marzo), con un segundo pico de fructificación en la mitad de la estación lluviosa. Se presentan una gran diversidad de patrones fenológicos, con números similares de especies floreando y fructificando tatno en la época seca y lluviosa. Durante los meses más lluviosos del año (Agosto-Octubre) se presenta una reducción en el número de especies en época reproductiva. La comparación de los datos fenológicos de Osa con los de otros sitios de Costa Rica y Panamá muestra algunas similaridades en la cronología de los eventos fenológicos, especialmente con el bosque seco del Noroeste de Costa Rica. Sin embargo, en Osa se observa un adelanto de eventos fenológicos reproductivos hacia al inicio de la época seca, en comparación con la fenología de los bosques de los otros sitios estudiados.

Palabras clave: fenología, bosque tropical, precipitación, reproducción de plantas, Peninsula de Osa.

Introduction

Phenology is the study of the chronology and periodicity of recurrent biological events. In plants, phenological events include flowering, fruiting, leaf flushing and leaf fall (Sakai 2001). A description of phenological patterns in plants allows researchers to understand how biotic and abiotic factors contribute to the onset of different events or phenophases. Additionally, phenological patterns are often related to specific reproductive strategies which maximise a species' reproductive success. A plant's phenology may influence interspecific interactions such as herbivory, pollination rate, and fruit and seed dispersal (van Schaik et al. 1993). Variations in the availability of resources associated with the duration and frequency of different phenophases may influence the population dynamics of animal species which depend on these resources, such as pollinators, frugivores and herbivores.

Tropical forest species have been shown to vary greatly in their phenological patterns. This variation may be attributed to high levels of biological diversity, a large number of ecological guilds and the great diversity of climatic conditions associated with tropical habitats (Sakai 2001). In contrast to temperate regions, a lack of winter in tropical ecosystems increases the time span of plant growth and reproduction, directly affecting the duration of phenophases. However, seasonality in tropical forests may occur due to changes in water availability (especially in tropical dry forests), variations in photoperiod (subtropical forests), strong

Stapfia **88**, zugleich Kataloge der oberösterreichischen Landesmuseen Neue Serie **80** (2008): 547-555

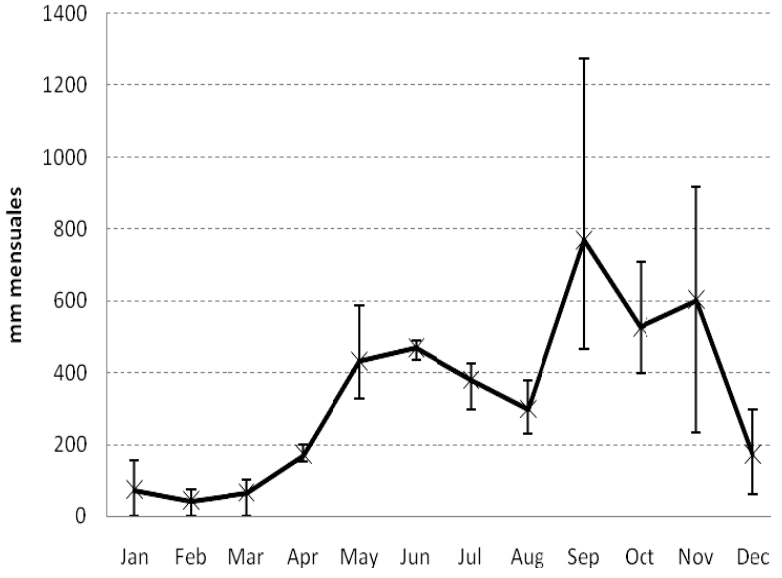

Fig. 1: Precipitation monthly averages, minima and maxima for the Golfo Dulce region. Data from Rincon meteorological station, 1999-2003.

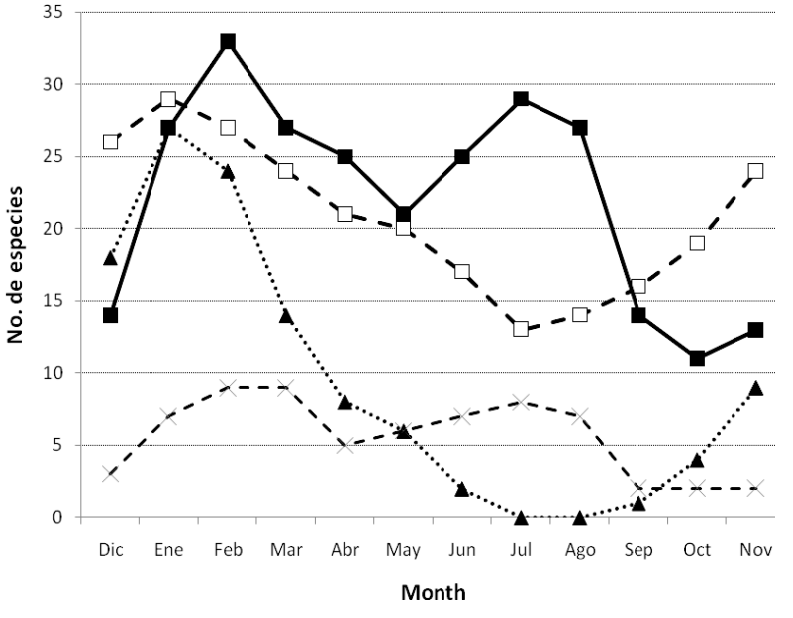

Fig. 2: Number of tree species recorded each month as flowering, fruiting or changing leaves; for a sample of 74 species from the Osa Peninsula and Golfo Dulce regions in Costa Rica. —□— species flowering, —■— fruiting, •••▲••• changing leaves, —×— fruiting in wind dispersed species.

temperature oscillations (tropical cloud forest and paramo), or changes in solar irradiance during the year (ZIMMERMAN et al. 2007).

The forests of the Osa Peninsula and coastal regions of Golfo Dulce in south-eastern Costa Rica are highly diverse habitats with high levels of endemism and a mixture of plants from different phytogeographic regions (ZAMORA et al. 2004). Climatic conditions in this area are characterised by high levels of annual precipitation (3500-5000 mm) with a short dry season between January and March (monthly precipitation <100 mm, Fig. 1). Temperatures are moderately high all year round, with a minimum of 21°C and a maximum of 33.5°C. Highest rainfall levels are observed between August and October (monthly precipitation 500-700 mm). Although the flora of the Osa Peninsula and Golfo Dulce have previously been described in detail (ALLEN 1956, WEBER 2001), to our knowledge, none of these descriptions have included detailed information on phenology of the plant community of this region.

This paper presents information on flower and fruit phenology for 73 tropical tree species from the Osa Peninsula and Golfo Dulce regions. The studied species are canopy and sub-canopy trees, many of which are endemic to the area. We also analysed trees species with restricted distributions, for which very little information on reproductive biology and leaf phenology has been produced.

Methods

The phenological data presented in this study were collected from different locations throughout the Osa Peninsula between 1989 and 2001. Phenological observations were conducted on unmarked individuals of different species; leaf, flower and fruit production were recorded on a monthly basis for all trees where the canopy was in clear view of the observer. From 2004 onwards, 1000 trees belonging to 303 species located in Piro and Banegas were permanently marked and phenology was recorded every month. Flower and fruit production was characterised using an ordinal scale from 0 to 4 depending on the percentage of the canopy covered (0 = 0%, 1 = 0-25%, 2 = 25-50%, 3 = 50-75% and 4 = 75-100%) by flowers, leaves or fruits. In this study phenological data is presented only of species with at least 5 individuals observed during 2 years (74 tree species).

Given the height of the majority of inflorescences and the monthly nature of our observations, we were not able to quantify the precise onset of flowering, nor flower longevity. Therefore we report those months when a species was found producing flowers or fruit, but we were unable to determine the exact duration of these events. In some cases we could clearly determine two or more flowering or fruiting events within a year (sub-annual phenology, sensu NEWSTROM et al. 1994). For these species, reproductive events had to be separated by at least a month so we could classify them as separate reproductive events.

Table 1: Flower, fruit and leaf production phenology for 74 tropical tree species from the Osa Península and Golfo Dulce regions, Costa Rica. Diagonal lines in leaf phenology indicate months where new leaves were produced; vertical lines indicate those months when the canopy was deciduous.

Species	Phenological phase	Dry Season				Rainy Season							
		Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
1. Anacardium excelsum	Flowers												
	Fruits												
	Leaves												
2. Apeiba membranaceae	Flowers												
	Fruits												
3. Apeiba tiborborou	Flowers												
	Fruits												
	Leaves												
4. Aspidosperma myristifolium	Flowers												
	Fruits												
	Leaves												
5. Aspidosperma spruceanum	Flowers												
	Fruits												
6. Balizia elegans	Flowers												
	Fruits												
	Leaves												
7. Bernoullia flammea	Flowers												
	Fruits												
8. Bombacopsis sessilis	Flowers												
	Fruits												
	Leaves												
9. Brosimum alicastrum	Flowers												
	Fruits												
	Leaves												
10. Brosimum costaricanum	Flowers												
	Fruits												
11. Brosimum lactecens	Flowers												
	Fruits												
	Leaves												
12. Brosimum utile	Flowers												
	Fruits												
	Leaves												
13. Bursera simarouba	Flowers												
	Fruits												
	Leaves												
14. Calophyllum longifolium	Flowers												
	Fruits												
15. Calophyllum brasiliense	Flowers												
	Fruits												

Table 1: continued

Species	Phenological phase	Dry Season				Rainy Season							
		Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
16. Carapa guianensis	Flowers												
	Fruits												
17. Caryocar costaricense	Flowers												
	Fruits												
	Leaves												
18. Caryodaphnopsis burgeri	Flowers												
	Fruits												
	Leaves												
19. Castilla tunu	Flowers												
	Fruits												
20. Cecropia insignis	Flowers												
	Fruits												
21. Ceiba pentandra	Flowers												
	Fruits												
	Leaves												
22. Chaunochiton kappleri	Flowers												
	Fruits												
	Leaves												
23. Chimarrhis latifolia	Flowers												
	Fruits												
24. Clarisia biflora	Flowers												
	Fruits												
	Leaves												
25. Compsoneura sprucei	Flowers												
	Fruits												
26. Copaifera camibar	Flowers												
	Fruits												
27. Couratari guianensis	Flowers												
	Fruits												
	Leaves												
28. Couratari scottmori	Flowers												
	Fruits												
	Leaves												
29. Cryosophila guagara	Flowers												
	Fruits												
30. Dialium guianensis	Flowers												
	Fruits												
	Leaves												
31. Dussia macroprophyllata	Flowers												
	Fruits												
	Leaves												
32. Ficus insipida	Flowers												
	Fruits												

Table 1: continued

Species	Phenological phase	Dry Season				Rainy Season							
		Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
33. Garcinia madruno	Flowers												
	Fruits												
34. Guarea pterorachis	Flowers												
	Fruits												
35. Guarea corticosa	Flowers												
	Fruits												
36. Guatteria amplifolia	Flowers												
	Fruits												
37. Heisteria acuminata	Flowers												
	Fruits												
38. Heisteria concinna	Flowers												
	Fruits												
39. Hieronyma alchorneoides	Flowers												
	Fruits												
40. Huberodendron allenii	Flowers												
	Fruits												
	Leaves												
41. Humiriastrum diguense	Flowers												
	Fruits												
42. Inga alba	Flowers												
	Fruits												
	Leaves												
43. Lacmellea panamensis	Flowers												
	Fruits												
44. Lozania pittieri	Flowers												
	Fruits												
45. Nectandra umbrosa	Flowers												
	Fruits												
46. Newtonia suaveolens	Flowers												
	Fruits												
	Leaves												
47. Ochroma pyramidale	Flowers												
	Fruits												
48. Ocotea laetevirens	Flowers												
	Fruits												
49. Otoba novogranatensis	Flowers												
	Fruits												
50. Peltogyne purpurea	Flowers												
	Fruits												
	Leaves												
51. Pourouma bicolor	Flowers												
	Fruits												

Table 1: continued

Species	Phenological phase	Dry Season				Rainy Season							
		Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
52. Pouteria triplarifolia	Flowers												
	Fruits												
	Leaves												
53. Pseudobombax septenatum	Flowers												
	Fruits												
	Leaves												
54. Qualea paraensis	Flowers												
	Fruits												
58. Schizolobium parahyba	Flowers												
	Fruits												
	Leaves												
55. Simaba cedron	Flowers												
	Fruits												
	Leaves												
56. Simarouba amara	Flowers												
	Fruits												
	Leaves												
59. Sloanea sulcata	Flowers												
	Fruits												
	Leaves												
57. Sterculia recordiana	Flowers												
	Fruits												
	Leaves												
60. Symphonia globulifera	Flowers												
	Fruits												
	Leaves												
61. Talisia nervosa	Flowers												
	Fruits												
62. Tapirira guianensis	Flowers												
	Fruits												
	Leaves												
63. Tachigali versicolor	Flowers												
	Fruits												
	Leaves												
64. Terminalia amazonia	Flowers												
	Fruits												
	Leaves												
65. Terminalia bucidoides	Flowers												
	Fruits												
	Leaves												
66. Vantanea barbourii	Flowers												
	Fruits												

Table 1: continued

Species	Phenological phase	Dry Season				Rainy Season							
		Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
67. Virola koschnyi	Flowers												
	Fruits												
	Leaves												
68. Virola guatemalensis	Flowers												
	Fruits												
	Leaves												
69. Virola sebifera	Flowers												
	Fruits												
70. Vochysia ferruginea	Flowers												
	Fruits												
71. Welfia regia	Flowers												
	Fruits												
72. Williamodendron glaucophyllum	Flowers												
	Fruits												
	Leaves												
73. Xylopia sericophylla	Flowers												
	Fruits												

Results

Phenology data for 74 species analysed in this study are presented in Table 1. We determined that the majority of species are annual flowering species at the population level, while eleven species show a clear sub-annual flowering phenology (*Aspidosperma spruceanum*, *Carapa guianensis*, *Chimarris latifolia*, *Couratari scottmori*, *Comsponeura sprucei*, *Guarea pterorachis*, *Ficus insipida*, *Heisteria concinna*, *Hyeronima alchornoides*, *Nectandra ubmrosa* and *Welfia regia*; Table 1). This study is one of the first to report phenological data for species endemic to the Osa-Golfo Dulce region, and species with distributions limited to the southern part of Central America and Colombia (e.g. *Anthodiscus chocoensis*, *Caryodaphnopsis burgeri*, *Caryocar costaricensis*, *Copaifera camibar*, *Crysophila guagara*, *Guatteria amplifolia*, *Huberodendron allenii*, *Peltogyne purpurea*, *Sloanea sulcata* and *Tachigali versicolor*). With the exception of *Tachigali versicolor* (FOSTER 1977), very little information exists for these species concerning phenology.

Figure 2 shows the number of species flowering, fruiting or producing leaves for each month of the year. We also show fruiting periods for wind-dispersed species to determine the influence of these species, which offer no reward to animal dispersers, to our estimated fruiting peaks. Leaf flushing was only recorded for that subset (39) of species for which leaf fall and new leaf production are synchronised events which are easily recognised by an observer. A clear deciduous phase was observed only in 19 species (25%), lasting about a month (Fig. 2). A distinct flowering peak occurred during the dry season between December and February when 44 species (60%) produced flowers. Flowering intensity showed a declining trend in the following months after the dry season with a minimum of 13 species flowering in July. In contrast, two clear fruiting periods were evident from our data, the first between January and March (44 species) and the second between June and August (28 species). As shown in Figure 2, these peaks are similar for species with wind dispersed fruits and zoochorous species.

For any species, the difference between the time of highest flowering and peak fruiting time may be used as an indirect estimate of the time required for fruit maturation. For annual and sub-annual species average fruit developing time was 3.69 months (based on a 30-day month) with 1.89 months standard deviation. *Tachigali versicolor* and *Guatteria amplifolia* required the longest amount of time for fruit maturation (8 months), followed by *Virola sebifera* (7.5 months), and *Peltogyne purpurea*, *Carapa guianensis* and *Xylopia sericophylla* with 6.5 months each. Species with the shortest fruit maturation time (1 month) were *Chryosophylla guagara*, *Castilla tunu*, *Ficus insipida* and *Simarouba amara*. We did not ob-

Fig. 3: Flowers of *Peltogyne purpurea* (left) and *Copaifera camibar* (right) (Caesalpiniaceae, Fabaceae), an example of the group of species that produce flowers during the middle of the rainy season and set fruits during the dry season.

serve any species which require more than a year for fruit maturation, which is commonplace in tropical dry forest tree species (FRANKIE et al. 1974).

Discussion

Phenology data of canopy species presented in this study shows, as similarly reported for other tropical forests (NEWSTROM et al. 1994), considerable inter-specific variation in seasonality, frequency and duration of phenological events. If we limit our analysis to the seasonality of flower and fruiting periods we can create five main groups with a similar number of species in each: species that flower during the dry season and fruit in the following rainy season (e.g. *Huberodendron allenii*, *Newtonia suaveolens*, *Tapirira guianensis*), species that flower in the rainy season while fruit production occurs in the next dry season (*Peltogyne purpurea*, *Copaifera camibar*, *Dialium guianensis*, Fig. 3), species that flower and fruit in the same dry season (*Anacardium excelsum*, *Bombacopsis sessilis*, *Ceiba pentandra*, *Crysophila guagara*), species whose flowering and fruiting occur during the same rainy season (*Lacmellea panamensis*, *Lozania pittieri*, *Humiriastrum giguense*, *Williamodendron glaucophyllum*) and finally species that flower and produce fruits in both seasons (*Welfia regia*, *Compsoneura sprucei*, *Carapa guianensis*, *Hyeronima alchorneoides*).

Table 2: Comparison of phenological parameters between Osa-Golfo Dulce forests and and three tropical forests in Costa Rica and Panama.

Site	Number of studied tree species	Leaf flushing peak	% of deciduous species	Flowering peak	Fruiting peak
Osa-Golfo Dulce (Costa Rica)	74	Dec.-Feb.	25%	Dec.-Mar.	Jan.-Mar. Jun.-Aug.
La Selva (Costa Rica)	93	Feb.-Apr.	17%	May-Aug.	Aug.-Sep.
Guanacaste (Costa Rica)	113	Apr.-Jun.	60%	Jan.-Apr.	Mar.-May
Barro Colorado (Panamá)	112	-	-	Mar.-May	Mar.-May

We compared phenological patterns between Osa and other lowland tropical habitats of Southern Central America such as La Selva in the Caribbean slope of Costa Rica (FRANKIE et al. 1974, BAWA et al. 2003), Guanacaste in the dry Pacific region of NW Costa Rica (FRANKIE et al. 1974) and Barro Colorado Island (BCI) in central Panama (ZIMMERMAN et al. 2007; Table 2). From the 74 species in our study, 12 were also analysed by FRANKIE et al. (1974) in La Selva, 7 species were studied by FRANKIE et al. (1974) in Guanacaste and 17 are shared with the ZIMMERMAN et al. (2007) study in BCI. The intensity and duration of the dry season is less marked in La Selva than in BCI or Guanacaste, and Osa is intermediate in this aspect between La Selva and other sites.

Based on data shown in Table 2 we can conclude that Guanacaste and Osa are similar in the presence of a flowering and fruiting peak during the dry season (December to March). However, Osa tree species show differences in phenological patterns with dry forests in Guanacaste. In Osa, leaf production generally occurs during the beginning of the dry season (Table 2), in contrast to Guanacaste and La Selva where new leaves are produced at the beginning of the rainy season. The percentage of deciduous species in Osa resembles those found in La Selva, and are both significantly lower than the proportion of deciduous species found in Guanacaste. In Osa, the flowering peak (i.e. maximum number of species flowering) both starts and ends one month earlier than the flowering peak in Guanacaste (Table 2). Additionally, in Osa we only observed one flowering peak at the beginning of the dry season, while in La Sel-

va a second flowering peak was recorded during the beginning of the rainy season. Fruiting phenology follows a similar pattern; the majority of species in Osa fruit during the dry season and half-way through the rainy season, but in both instances the fruiting peak occurs one month earlier than in Guanacaste and La Selva. This shift towards earlier flowering and fruiting observed in Osa, does not correspond to changes in species composition, since changes in phenological patterns were recorded within the same species. If we compare the 12 species shared between La Selva and Osa, nine exhibit precocious flowering and fruiting phenology in Osa. Six out of the seven species shared between Osa and Guanacaste also flower and fruit earlier in Osa than in Guanacaste. Phenological shifts in flower and fruit phenology experienced by Osa species are between one and two months earlier than those observed in other localities. Comparisons between Osa and Zimmerman's study at BCI are harder to conduct since the latter used seed traps to infer phenology, and only reported species in those months where seed traps recorded 75% of total seed production. Nevertheless, six out of the 17 species found in both Osa and BCI also indicate an earlier displacement of the reproductive phenology of Osa trees. A larger data set is needed to confirm phenological shift observed in this study and to formulate hypotheses to explain this observation.

Phenological comparisons between the forests of SE Costa Rica and other neotropical sites presented in this study are in need of a higher number of species in order to better support our conclusions. We also need data from different forest strata, as well as information on the relative abundance of these species, to determine if the differences in phenological patterns, specifically the reduction in fruiting intensity observed at the end of the rainy season in Osa, may impact the availability of resources for the frugivorous fauna in the Golfo Dulce and Osa regions.

References

Allen P.H. (1956): The rainforest of Golfo Dulce. — University of Florida Press.

Bawa K.S., Kang H. & M.H. Grayum (2003): Relationships among time, frequency, and duration of flowering in tropical rainforest trees. — Am. J. Bot. **90**: 877-887.

Foster R.B. (1977): *Tachigali versicolor* is a suicidal neotropical tree. — Nature **268**: 624-626.

Frankie G., Baker H.G. & P.A. Opler (1974): Comparative phenological studies of trees in Tropical wet and dry forests in the lowlands of Costa Rica. — J. Ecol. **62**: 881-899.

Newstrom L.E., Frankie G.W., Baker H.G. & R.K. Colwell (1994): Diversity of long-term flowering patterns. — In: L.W. McDade, Bawa K.S. & Hespenheide H.A. (eds), La Selva: ecology and natural history of a neotropical rainforest. Chicago University Press, Chicago, Illinois, USA: 142-160.

Sakai S. (2001): Phenological diversity in tropical forests. — Pop. Ecol. **43**: 77-86.

Van Schaik C.P., Terborgh J.W. & S.J. Wright (1993): The phenology of tropical forests: adaptive significance and consequences for primary consumers. — Ann. Rev. Ecol. Syst. **24**: 353-377.

Weber A. (2001): An introductory field guide to the flowering plants of the Golfo Dulce rainforests, Costa Rica. — Stapfia **78**: 1-462.

Zamora N., Hammel B.E. & M.H. Grayum (2004): Vegetación. — In: Hammel B.E, Grayum M.H., Herrera C. & Zamora N., Manual de Plantas de Costa Rica. Vol. 1, Missouri Botanical Garden Press. St. Louis, Missouri, USA: 91-299.

Zimmerman J.K., Wright S.J., Calderón O., Aponte Pagan M. & S. Paton (2007): Flowering and fruiting phenologies of seasonal and aseasonal neotropical forests: the role of annual changes in irradiance. — J. Trop. Ecol. **23**: 231-251.

Addresses of authors:

Jorge Lobo
Escuela de Biología
Universidad de Costa Rica
San José, Costa Rica
E-mail: jorgelobosegura@gmail.com

Reinaldo Aguilar
Eduardo Chacón
Recinto Universitario de Golfito
Universidad de Costa Rica
Costa Rica
E-mail: raguilarster@gmail.com
edchacon@gmail.com

Eric Fuchs
Escuela de Biología
Universidad de Costa Rica
San José, Costa Rica
E-mail: e.j.fuchs@gmail.com