PHENOLOGY OF TIMBER TREE SPECIES IN A BOLIVIAN DRY FOREST: IMPLICATIONS FOR FOREST MANAGEMENT

Marcos Joaquín Justiniano & Todd S. Fredericksen*

Proyecto BOLFOR, Casilla 6204, Santa Cruz, Bolivia

Received July 1998

JUSTINIANO, M. J. & FREDERICKSEN, T. S. 2000. Phenology of timber tree species in a Bolivian dry forest: implications for forest management. The phenology of 17 timber tree species was observed in a semi-deciduous dry forest in the Lomerío region of Santa Cruz, Bolivia, during two years to obtain biological information useful for forest management. Flowering, fruiting, and leaf fall of 162 individual mature timber trees of the 17 species were observed monthly. Although phenological patterns differed between years, most trees were leafless from June through September coinciding with the middle to late dry season. The majority of species also flowered during the dry season. Peak fruiting occurred just before the beginning of the rainy season and the greatest percentage of species fruited in August and September during both years. This is also the period when most forest harvesting is conducted. Better coordination of harvest timing with seedfall will increase seed rain onto areas with increased light and scarified soils and may help maximise regeneration success. All but two species studied had wind-dispersed seeds indicating the importance of leaving productive seed trees dispersed throughout this forest. The periodicity of seed production varied widely among species. However, averaged over all species, only approximately one-third of mature trees produced seeds in either year of this study. Therefore, for most species, many more seed trees need to be retained than would normally be required if all trees produced an annual crop of seeds.

Key words: Bolivia - flowering - fruiting - leaf fall - phenology - dry forest - regeneration

JUSTINIANO, M. J. & FREDERICKSEN, T. S. 2000. Fenologi spesies pokok balak di hutan kering di Bolivia: implikasi kepada pengurusan hutan. Fenologi 17 spesies pokok balak dicerap di sebuah hutan kering separa-luruh di kawasan Lomerío di Santa Cruz, Bolivia, dalam masa dua tahun untuk mendapatkan maklumat biologi yang berguna untuk pengurusan hutan. Pembungaan, pembuahan dan jatuhan daun bagi 162 pokok balak matang secara individu bagi 17 spesies dicerap setiap bulan. Walaupun pola fenologi berbeza antara tahun-tahun, kebanyakan pokok tidak berdaun dari Jun hingga September serentak dengan pertengahan hingga akhir musim kering. Majoriti spesies juga berbunga pada musim kering. Kemuncak pembuahan terjadi sebelum permulaan musim hujan dan peratus tertinggi daripada spesies berbuah pada bulan Ogos dan September pada kedua-dua tahun. Pada masa ini jugalah kebanyakan tebangan hutan dijalankan. Penyelarasan yang lebih baik bagi masa untuk penebangan dengan penuaian biji benih akan meningkatkan hujan biji benih ke kawasan yang ditambah cahaya dan tanah gembur dan dapat membantu memaksimumkan kejayaan pemulihan. Kesemua spesies, kecuali dua

**Author for correspondence. E-mail: bolfor@bibosi.scz.entelnet.bo*

spesies yang dikaji mempunyai biji benih yang disebarkan oleh angin, menunjukkan pentingnya untuk membiarkan anak benih pokok yang produktif disebarkan ke seluruh hutan ini. Keberkalaan pengeluaran biji benih berbeza dengan meluas di kalangan spesies. Bagaimanapun, purata keseluruhan spesies hanya hampir satu pertiga daripada pokok matang mengeluarkan biji benih pada mana-mana tahun dalam kajian ini. Oleh itu, bagi kebanyakan spesies, pokok biji benih perlu dikekalkan lebih banyak daripada yang biasa diperlukan sekiranya semua pokok menghasilkan biji benih untuk tanaman tahunan.

Introduction

Knowledge of phenological patterns is basic for understanding the biology of tropical trees and organisms related to them. Understanding the phenological dynamics of trees is also essential for understanding natural forest regeneration potential (Fox 1976). For example, timing of harvests may need to coincide with seed dispersal to maximise forest regeneration. Knowledge of seed production patterns may also be important for determining the number of seed trees to be left after harvest.

Bolivia has a wealth of forest resources that are now beginning to be placed under management. It is important that this management be based upon a sound biological knowledge of the species to be managed. However, phenological patterns in dry forests have not been studied in Bolivia. The objectives of this study were 1) to describe the timing and duration of flowering, fruiting, and leaf fall for 17 timber tree species in a dry forest in eastern Bolivia, and 2) to make recommendations based on these data regarding regeneration, timing of harvests, and the quantity of seed trees to be left after harvests.

Methods

Study site

The study was carried out in the Lomerío region, in the Ñuflo de Chávez province, Department of Santa Cruz, Bolivia. The site is located near the Chiquitano indigenous community of Las Trancas (16°13'S, 61°50'W) which owns and manages the forest. The area is covered by semi-deciduous dry forest, known locally as "Bosque Chiquitano" (Navarro 1995). Mean annual precipitation taken near Concepción, Bolivia (90 km from the study site) is 1100 mm and annual mean temperature is 24 °C. Physiography is characterised by rolling hills dissected by small narrow valleys and interspersed with occasional granitic rock outcrops (Navarro 1995). Altitude ranges from 300 to 400 m. The canopy is low, with heights ranging from 12 to 18 m. Representative families are Leguminosae, Anacardiaceae, Apocynaceae and Bombacaceae. The most abundant species are *Acosmium cardenassii, Anadenanthera colubrina, Centrolobium microchaete* and *Aspidosperma* spp. Killeen *et al.* (1990) have described the plant ecological and landscape patterns in the region.

Observations

A total of 162 individuals of 17 timber species were selected (Table 1) on a 400-ha area. Species were selected because they were currently being harvested or were likely to be useful as timber species in the near future within the region. At least 5 individuals per species were included in the sample (Fournier & Charpantier 1975), with the exception of *Cordia alliodora* and *Platymiscium ulei*, for which only 3 individuals were located. Trees were selected randomly, but also met the following requirements: adult (sexually mature), diameter-at-breast-height > 15 cm, separated from other sampled trees of the same species by at least 100 m, and without any significant damage to the trunk or crown.

Table 1. Summary of the ecological traits and phenology of 17 timber species in a Bolivian dry forest

Family-Species	Leaffall	Flowers	Fruit	Seed dispersal
Anacardiaceae				
Astronium urundeuva (14)*	July–Sept.	July–Aug.	Sept.–Oct.	W**
Schinopsis brasiliensis (13)	Sept.	June–July	Sept.–Oct.	W
Apocynaceae				
Aspidosperma rigidum (9)	July–Aug.	Oct.–Nov.	July–Aug.	W
Bignoniaceae				
Tabebuia impetiginosa (9)	June–Aug.	May–June	July–Sept.	W
Boraginaceae				
Cordia alliodora (3)	July–Aug.	Aug.–Sept.	Aug.–Oct.	W
Caesalpinioideae				
Hymenaea courbaril (5)	Aug.	Nov.–Dec.	Aug.–Sept.	G
Copaifera chodatiana (13)	Aug.	Dec.–Jan.	July–Aug.	G
Pterogyne nitens (6)	Apr.	Aug.–Sept.	Aug.–Sept.	W
Lecythidaceae				
Cariniana ianeirensis (6)	July.–Sept.	Oct.	***	W
Meliaceae				
Cedrela fissilis (12)	June–Sept.	Nov.–Dec.	July–Aug.	W
Papilionoideae				
Amburana cearensis (13)	May–Aug.	Apr.	June–Aug.	W
Centrolobium microchaete (12)	Aug.	Mar.–Apr.	July–Aug.	W
Machaerium scleroxylon (12)	Aug.	Dec.–Jan.	***	W
Platymiscium ulei (3)	Aug.	Sept.	***	W
Platypodium elegans (10)	June–July	***	Oct.	W
Rubiaceae				
Calycophyllum multiflorum (12)	Aug.	Mar.–Apr.	June–Aug.	W
Ulmaceae				
Phyllostylon rhamnoides (10)	Aug.	Sept.	Oct.	W

* Figures within parentheses denote number of individuals;
** W = wind dispersed; G= animal dispersed; *** = not observed during study period.

Phenological observations were made with binoculars, once per month during a 2-year period (January 1995 to February 1997), except that observations were missed due to poor road conditions in January and February 1996. Notes were taken on the stage of flowering, fruiting, or leaf fall (e.g. pre-mature, mature, or senescent fruits). However, in compiling the data, a tree was noted as fruiting or flowering during a month if mature fruits or flowers were present during that month. A species was noted as fruiting or flowering if any of the sampled trees had mature fruits or flowers.

Table 2. Percentage of trees for 17 species that exhibited leaflessness, flowering or fruiting during 1995 and 1996 in a Bolivian dry forest

Family-Species	1995			1996		
	Leafless	Flower	Fruit	Leafless	Flower	Fruit
Anacardiaceae						
Astronium urundeuva	100	64	50	100	64	28
Schinopsis brasiliensis	100	69	30	92	92	23
Apocynaceae						
Aspidosperma rigidum	100	0	77	100	100	0
Bignoniaceae						
Tabebuia impetiginosa	100	0	0	100	91	75
Boraginaceae						
Cordia alliodora	100	100	100	100	100	100
Caesalpinioideae						
Hymenaea courbaril	100	20	20	60	60	0
Copaifera chodatiana	100	100	53	0	69	85
Pterogyne nitens	100	100	0	0	66	17
Lecythidaceae						
Cariniana ianeirensis	100	0	0	100	0	8
Meliaceae						
Cedrela fissilis	100	100	0	100	0	0
Papilionoideae						
Amburana cearensis	100	0	0	100	25	8
Centrolobium microchaete	100	100	58	91	92	67
Machaerium scleroxylon	100	8	0	100	42	0
Platymiscium ulei	100	0	0	0	0	0
Platypodium elegans	100	10	10	80	10	0
Rubiaceae						
Calycophyllum multiflorum	100	92	92	83	100	100
Ulmaceae						
Phyllostylon rhamnoides	100	0	0	20	80	60

Results

Phenological patterns varied by year, especially for leaf fall. In 1995, all species had some individuals that were deciduous for at least one month and several species were leafless from June to September (Table 2). In 1996, leaf fall was not as extensive nor long in duration for many species. For example, *Copaifera chodatiana, Pterogyne nitens, Aspidosperma rigidum, Platymiscium ulei* and a considerable percentage of *Hymenaea courbaril* and *Phyllostylon rhamnoides* trees did not lose their leaves in 1996 despite having been totally leafless for at least one month during 1995. Species that lost their leaves during 1996 remained leafless for a shorter period of time (July–August) than in 1995.

Flowering among species was dispersed throughout the year. However, two small peaks were evident: one during the rainy season and another at the end of the rainy season. Fruiting phenology in both years displayed a pattern of maximum production at the end of the dry season (Figure 1). However, some species produced fruit during only one year (*Amburana cearensis, Aspidosperma rigidum, Phyllostylon rhamnoides, Tabebuia impetiginosa, Cedrela fissilis, Platypodium elegans* and *Hymenaea courbaril*); and some species did not fruit in either year (*Cariniana ianeirensis, Platymiscium ulei* and *Machaerium scleroxylon*). The remaining species produced fruit during both years, but with different intensities (Table 2). Averaged over all trees in the study, only 29.1% and 36.4% of trees were observed with fruit in 1995 and 1996 respectively.

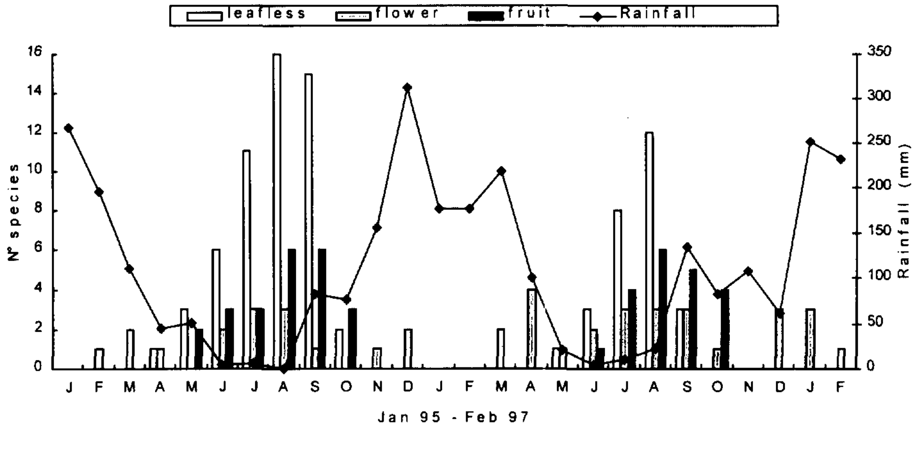

Figure 1. Monthly percentage of species with flowers, fruit, and leaves presented with monthly precipitation in Las Trancas, a dry forest in Bolivia

Discussion

Peaks in flowering and fruiting were similar to those observed in other dry forests (Bullock & Solís-Magallanes 1990, Borchert 1994, Foster 1996). While phenological changes are often caused by a variety of environmental signals such as photoperiod or temperature (Frankie *et al.* 1974, Reich & Borchert 1984, van Schaik *et al.* 1993), the phenology of this forest appears to be markedly controlled by rainfall. Although conditions are generally dry, there can be significant precipitation events during the months from May to November in this region of Bolivia coinciding with the passage of strong Antarctic cold fronts. Short drought periods are also common during the rainy season. These events often cause irregularities in the phenology of species in these forests, such as the contracted period of deciduousness observed during 1996 (Figure 1). Abnormal rainfall patterns also appeared to affect flowering phenology for some species such as *Copaifera chodatiana* and *Machaerium scleroxylon*. These species typically flower in November and December, the beginning of the rainy season. However, a 33-day drought during this period in 1996 appeared to have negatively affected flowering, and subsequent fruit production.

Bazzaz (1990) noted that in places where the dry season is not pronounced, fruiting typically starts at the end of the rainy season. Where the dry season is severe, fruiting is more concentrated at the start of the rainy season. Most of the 17 species in this study are dispersed by wind. Apparently this strategy has evolved for seed dissemination to begin when the canopy is leafless and strong north winds precede the first rains. Seed dispersal is enhanced by reducing interference from foliage, and seed germination and early seedling growth benefit from favourable soil moisture conditions (Janzen 1967, Frankie *et al.* 1974, Primack 1987, Ibarra-Manriquez *et al.* 1991, Foster 1996). Time to maturation of fruit also varied among the different species, from weeks (e.g. *Cordia alliodora*), to almost nine or more months (e.g. *Aspidos perma rigidum, Cedrela fissilis* and *Cariniana ianeirensis*) (Table 1). Time to maturation may be important in determining the seed production of a species, since retention of fruits over long periods of time increases exposure to seed predators.

Implications for management

The variability in seed production from year to year varied among species. Therefore, it will be important to plan seed tree retention on a species-specific basis. On average, however, one-third of the trees in this forest produced seeds. Based on this result, it is important not to base seed tree retention requirements for a species on the density of trees, but rather on the density and periodicity of trees producing seeds. For example, for species such as *Hymenaea courbaril, Pterogyne nitens, Cedrela fissilis, Amburana cearensis, Platypodium elegans, Cariniana ianeirensis* and *Machaerium scleroxylon*, it appears that ten times the desired number of productive seed trees should be retained to insure the desired level of seed set in most years.

The majority of tree species in this study have small seeds that are wind-dispersed with their phenology coinciding with strong winds at the end of the dry season. Given that forest harvesting occurs during the dry season, it is possible to coordinate logging activities so that trees are not felled before they have a chance to disperse seeds. Only a few species produce fruits after harvesting is likely to occur (i.e. *Platypodium elegans* and *Phyllostylon rhamnoides*). An abundance of seeds in well-lit logging gaps with soils scarified by logging would also make it more likely to achieve an abundance of forest regeneration. A problem with regeneration of timber species has been noted in this forest (Guzmán 1997) and the most important timber species appear to be shade-intolerant (Guzmán 1997), thus any activities that increase seedfall and optimise the timing of seedfall should be encouraged. Scarification of soil near seed trees may improve seedbed conditions for many of these species with light, wind-dispersed seeds.

Acknowledgements

The authors wish to thank Daniel Nash for his translation of this document and Glenn Garson for assistance in data analysis and graphics. We also thank Rudy Gúzman, Bonifacio Mostacedo, William Cordero and John Nittler for their critical reviews.

References

BAZZAZ, F. A. 1990. Regeneration of tropical forests: physiological responses of pioneer and secondary species. Pp. 91–118 in Gómez-Pompa, A., Whitmore, T. C. & M. Hadley (Eds.) *Rain Forest Regeneration and Management.* UNESCO, Paris and Parthenon Publishing Group, UK.

BORCHERT, R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* 75:1437–1449.

BULLOCK, S.H. & SOLIS-MAGALLANES, J. A. 1990. Phenology of canopy trees of a tropical deciduous forest in Mexico. *Biotropica* 22:22–35.

FOSTER, R. B. 1996. The seasonal rhythm of fruitfall in Barro Colorado Island. Pp. 7-12 in Leigh, E. G. Jr. (Ed.) *The Ecology of a Tropical Forest.* 2nd edition. Smithsonian Inst. Press, Washington, DC.

FOURNIER, L. A. & CHARPANTIER, C. 1975. El tamaño de la muestra y la frecuencia de observaciones en el estudio de las características fenológicas de los árboles tropicales. *Turrialba* 25:45–48.

FRANKIE, G. W., BAKER, H. G. & OPLER, P. A. 1974. Comparative phenological studies of trees in tropical wet and dry forest in the lowlands of Costa Rica. *Journal of Ecology* 62:881–913.

FOX, J. E. D. 1976. Constraints on the natural regeneration of tropical moist forests. *Forest Ecology and Management* 1:37–65.

GUZMÁN, R. 1997. Caracterización de Especies Forestales en Gremios Ecológicos en el Bosque Subhúmedo Estacional de la Región de Lomerío Santa Cruz, Bolivia. M.S. thesis, CATIE, Turrialba, Costa Rica. 59 pp.

IBARRA-MANRIQUEZ, G., SANCHEZ, B. & GONZALES, L. 1991. Fenolog a de lianas y árboles anemocoros en la selva cálido-húmeda de México. *Biotropica* 23(3):242–254.

JANZEN, D. H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution* 21:620–37.

KILLEEN, T. J., LOUMAN, B. T. & GRIMWOOD, T. 1990. La ecología paisajística de la región de Concepción y Lomerío en la Provincia de Nuflo de Chavez, Santa Cruz, Bolivia. *Ecología en Bolivia* 17:53–71.

NAVARRO, G. 1995. *Clasificación de la Vegetación de Lomerío en el Departamento de Santa Cruz, Bolivia.* Doc. Tec. 10, Proyecto BOLFOR, Santa Cruz, Bolivia.

PRIMACK, R. B. 1987. Relationships among flowers, fruits, and seeds. *Annual Review of Ecology and Systematics* 18:409–430.

REICH, P. B. & BORCHERT, R. 1984. Water stress and tree phenology in a tropical dry forest in lowlands of Costa Rica. *Journal of Ecology* 72:61–74.

VAN SCHAIK, C. P., TERBORGH, J. W. & WRIGHT, S. J. 1993. The phenology of tropical forest: adaptative significance and consequences of consumers. *Annual Review of Ecology and Systematics* 24:353–377.