5. PHENOLOGICAL OBSERVATIONS AND TREE SEED CHARACTERISTICS IN AN EQUATORIAL MOIST FOREST AT TROMBETAS, PARA STATE, BRAZIL

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Abstract

Seasonal patterns of flowering and fruiting were studied over an 18-year period in an upland (*terra firme*) primary forest area near Trombetas, Pará in central Amazonia. The study included 160 common tree taxa. While a significant number of species produced flowers and fruits during all months, distinct seasonal patterns were observed. Flowering peaks usually occurred during the early months of the dry season (July-October). Fluctuations in the proportion of fruiting species closely followed seasonal rainfall trends for zoochoric taxa, while fruiting in the less abundant (50 of 160 species) anemochoric taxa generally peaked during the dry season (August-December). Significant year-to-year variations in phenological behavior were observed for many species. Phenomena such as synchronized (mass) flowering, relay flowering and monocarpic behavior, as well as observations on leaf phenology, are discussed. A calendar of flowering and fruiting periods, and data on seed morphology and dispersal vectors are presented for 230 taxa of primary and secondary forest trees and shrubs of the region.

Introduction

The seasonal patterns of flowering and fruiting in tropical moist forests have attracted the attention of botanists, ecologists and foresters for more than a century (Richards 1966, Longman & Jeník 1974). In an apparently aseasonal environment, what accounts for the striking variation among forest tree species in seasonal, annual, and supra-annual patterns (and irregularities) of leaf flushing, flowering and fruiting? How are these patterns related to the ecological dynamics of herbivores, pollinators, and seed dispersing agents? During the past 30 years there has been a steady increase in the number of studies conducted throughout the tropics aimed at answering these basic ecological questions and

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understanding their profound implications for tropical forest conservation and management (Bawa & Hadley 1990). These studies have elucidated species differences in the timing, duration, and frequency of flowering and fruiting as well as patterns of spatial and temporal variation in flowering and fruiting phenology (Bawa *et al.* 1990, Frankie *et al.* 1990, Wright & Cornejo 1990, Yap & Chan 1990).

As the importance of tropical forest rehabilitation and restoration becomes more widely appreciated by society, the accumulation of knowledge and experience in this field will be crucial for the development of cost-effective and ecologically viable management strategies for deforested tropical landscapes. In this context, continued research on questions related to the spatial and temporal variability in forest structure (including floristics) and ecological dynamics (including reproductive biology) is needed in most tropical forest regions to design and manage effective restoration projects. Basic phenological data from forests in the vicinity of rehabilitation or restoration project areas is critical for screening of candidate reforestation species based on their predictability of seed production and for scheduling of seed collection and nursery activities from local forests.

In the central Brazilian Amazon region, several studies of forest phenology have been conducted at upland (*terra firme*) sites in the vicinity of Manaus (Amazonas State) and western Pará State. These include studies of specific taxa such as *Bertholletia excelsa* Humb. & Bonpl. (Brazil nut) and other Lecythidaceae (Mori *et al.* 1990, Mori & Lepsch-Cunha 1995), Sapotaceae (Alencar, 1994), *Copaifera multijuga* Hayne (Alencar 1988), *Cordia alliodora* (R.&P.) Oken (Carpanezzi *et al.* 1982), and *Aniba duckei* Kostermans (Magalhaes & Alencar 1979), studies of groups of economically important timber species (Araujo 1970, Alencar *et al.* 1979, Rankin de Merona & Ackerly 1987, Botosso & Vetter 1991) and studies in western Pará State of the major primary forest tree species in the Curua-Una Forest Research Station (Pereira & Pedrosa 1973) and the Tapajós National Forest (Carvalho 1980).

The present study examines flowering and fruiting patterns over an 18-year study period for 160 tree species found in the upland (*terra* firme) forests in northwestern Pará State, Brazil. Additional data on tree seed morphology and dispersal ecology are presented for 230 primary forest tree species. This research was carried out in support of a major reforestation program conducted by a Brazilian mining company to restore native forests on bauxite-mined lands in the vicinity of Porto Trombetas (Knowles 1982, Gaunt & Bliss 1993, Knowles & Parrotta 1995)

Methods

Site Description

The study area is located near the town of Trombetas approximately 65 km north-west of Oriximiná on the peninsular formed by the Trombetas and Nhamundá rivers in western Pará State, Brazil (1°40' S., 56° 24' W.). The local

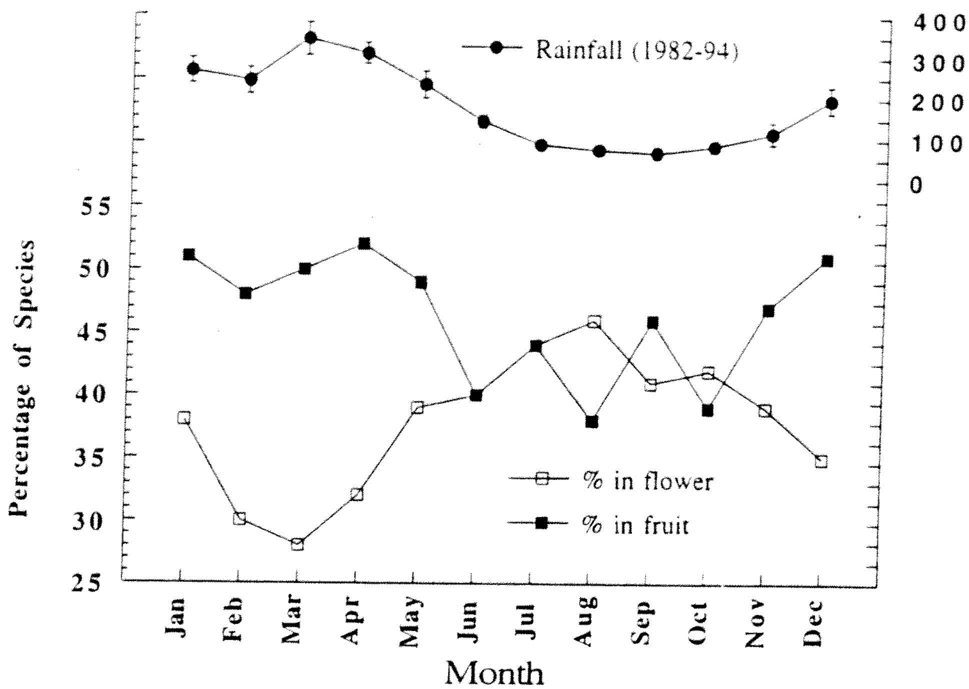

Fig. 1. Mean monthly rainfall (±S.E.) and percentage of flowering and fruiting tree taxa in terra firme forests near Porto Trombetas, Pará, Brazil.

climate is classified as Am (tropical monsoonal) in the Köppen system and corresponds to the tropical moist forest life zone in the Holdridge system (Tosi and Velez-Rodríguez 1983). Mean annual rainfall at Porto Trombetas (1970-1993) is 2185±64 (S.E.; n=24) mm, with distinctly dry (August-November) and wet (January-May) seasons, separated by short periods of showers (June-July, December). The mean monthly rainfall exceeds 100 mm in all months except July-October (see Figure 1). The mean maximum and minimum temperatures are respectively 34.6°C and 19.9°C.

The regional vegetation is climax evergreen equatorial moist forest with three basic environments: limited seasonal floodplains (*varzea*), very extensive undulating sandy uplands (*flanco*), and occasional plateaus capped by bauxite and clay (*planalto*) (Projeto RADAMBRASIL 1976). The tree floras of the upland flanco and planalto forests are rather similar, comprised principally of Leguminosae (56 spp.), Lauraceae (14 spp.), Sapotaceae (13 spp.), Annonaceae (11 spp.), Moraceae (10 spp.), Chrysobalanaceae (9 spp.), Lecythidaceae (9 spp.), and Burseraceae (7 spp.) (FCAP 1991).

The mid-story and upper-story of the flanco forests are 18 to 25 m and 25 to 35 m high, respectively, with occasional emergents reaching 45 m. The understory is comprised of stemless palms, seedlings, and occasional herbaceous plants. Lianas are common but do not form thickets. The planalto forests contain a much higher proportion of large trees, many of which are emergents reaching 45 m, and the mid-story and upper-story are clearly more heterogeneous with canopies from 5 to 18 m and 20 to 35 m high. Lianas are common but rarely form thickets. Other significant differences are associated with edaphic conditions; the sandy soils of the flanco are covered by an 8 cm thick layer of accumulated humus and loose peat interwoven with tree roots, whereas the planalto clay soils exhibit only a thin humus layer with an uneven surface created by abundant very large worm casts.

Phenology and Seed Dispersal

During an 18-year period between 1978-95, the flowering and fruiting phenologies were evaluated for 160 common tree species (or taxa) used for reforestation of bauxite-mined areas on the Saracá plateau near Porto Trombetas (Knowles & Parrotta 1995). This represents approximately 76% of the tree taxa attaining stem diameters greater than 10 cm (FCAP 1991). Field observations were made within 50 m on either side of 113 km of roads through primary and secondary forests in the vicinity of the Saracá plateau. For the vast majority of taxa, at least 10 individual mature trees were included in these observations.

Flowering data were recorded for 104 individual species and 32 groups of species; i.e., taxa that are typically grouped under a single local name during floristic inventories in the region whose botanical identifications are incomplete. Twenty-four species were excluded due mainly to the difficulty in observing inconspicuous flowers on the crowns of tall primary forest trees. Fruiting period data are complete for 128 individual species and 32 species groups.

Additional field observations on seed dispersal and measurements of seed sizes were also conducted during this period. These included 230 taxa of upland forest trees and shrubs. For each species or taxa group, the principal mode of seed dispersal was identified as either wind (anemochorous or autochorous spp.) or fauna (generally, birds, bats and terrestrial mammals in these forests). Seed sizes (length, width, and thickness) were measured by caliper, normally based on 10 fresh seeds per species.

Results and Discussion

Seasonal influences on timing and intensity of flowering and fruiting

In the upland primary forests in the vicinity of Trombetas, flowering and fruiting across all taxa are more or less continuous throughout the year, although there are distinct seasonal patterns (Figure 1). The percentages of tree species flowering show an inverse relationship with rainfall, with flowering peaks occurring during the early months of the dry season (July-October). Fruiting trends closely follow annual rainfall patterns, with a peak in the number of fruiting species occurring during the wet season (December-May). These data clearly show that phenological events in these forests reflect seasonal climatic phases.

A closer examination of fruiting seasonality among the taxa studied shows a marked difference between tree species whose seeds are dispersed by mammals

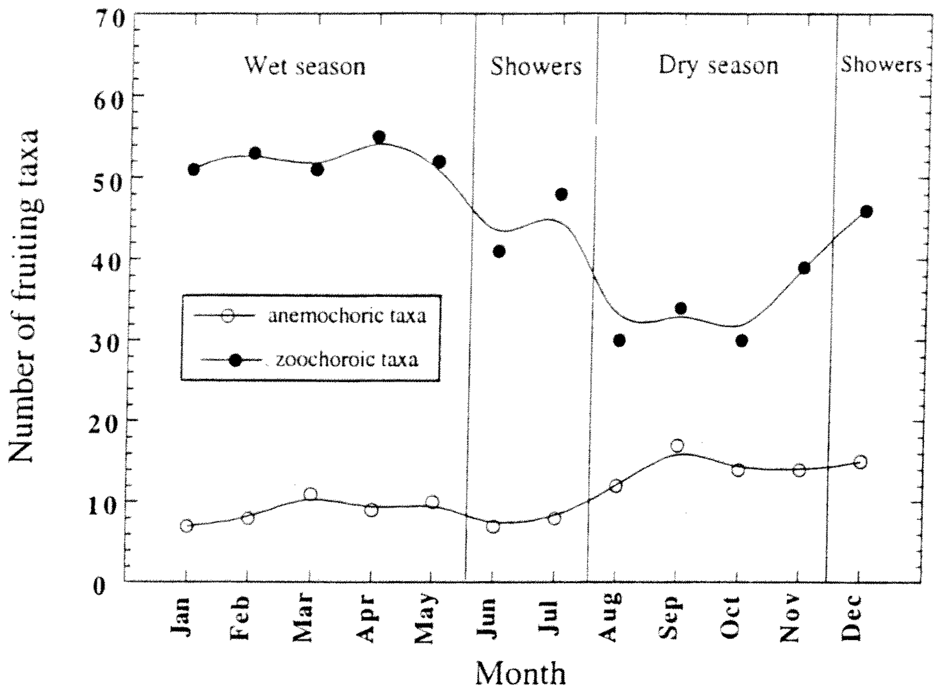

Fig. 2. Seasonal variation in fruiting among anemochoric and zoochoric primary forest tree species in terra firme forests near Porto Trombetas, Pará, Brazil.

and birds (zoochoric species) and those with wind-dispersed seeds (anemochoric species). In the case of zoochoric taxa, comprising more than two-thirds of the species studied, the numbers of fruiting species show definite seasonal patterns that closely parallel seasonal rainfall fluctuations, with a higher proportion of taxa producing fruits during the wetter months (December-May) than the drier months (Figure 2). For anemochoric taxa, this pattern is reversed, with an increase in the proportion of taxa producing fruits during the dry season (August-December).

When analyzing the individual yearly data, the taxa studied generally fall into four groups; i.e., those with (a) limited, (b) extended, (c) continuous, or (d) discontinuous flowering and fruiting periods during a given year. These divisions tends to become masked when the 18-year data is summarized as in Table 1. Three important factors contribute to the broader or discontinuous flowering and fruiting periods presented in Table 1. First, the fruiting periods for individual species can vary up to two months earlier or later than the average from one year to the next, which is likely due to yearly climatic variations. This is especially noticeable in species with flowering periods lasting no more than a few days, such as *Brosimum potabile* (Moraceae), *Caryocar villosum* (Aubl.) Pers. (Caryocaraceae), *Pterocarpus rohrii* Vahl (Leguminosae-Papilionoideae), *Tabebuia* spp. (Bignoniaceae), and *Vatairea sericea* Ducke (Leguminosae-Papilionoideae). A difference of up to 6 weeks in flowering or fruiting of individ-

Table 1. Flowering and fruiting of forest trees at Porto Trombetas, Pará, Brazil 1978-1995

FAMILY	SPECIES	COMMON NAME	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	Flowering to fruiting (months)
		Month:	FLOWERING PERIOD												FRUITING PERIOD												
		Rainfall:	Wet					Shrs		Dry				Shrs	Wet					Shrs		Dry				Shrs	
Anacardiaceae	*Anacardium giganteum* Loud. ex Steud.	Caju açu		•	•	•	•	•	•	•	•	•					□		□	□	□	□	□	□			1-2
Anacardiaceae	*Astronium lecointei* Ducke	Muiracatiara				•	•	•	•					•							□	□	□	□			3
Anacardiaceae	*Spondias mombin* L.	Taperiba										•	•	•		□	□	□	□	□	□						5
Anacardiaceae	*Tapirira guianensis* Aubl.	Tatapiririca	•	•						•	•	•	•		□	□	□	□	□	□							4
Annonaceae	*Duguetia, Guatteria, & Xylopia* spp.	Envira	•	•	•	•	•	•	•	•	•	•	•	•	□	□	□	□	□	□	□	□	□	□	□	□	2-3
Apocynaceae	*Aspidosperma exalatum* Monach	Araracanga				•				•	•	•			□	□	□	□	□	□			□	□	□	□	4-5
Apocynaceae	*Aspidosperma oblongum* A. DC.	Carapanaúba						no data								□	□	□	□	□				□	□		nd
Apocynaceae	*Aspidosperma* sp.	Marfim falso						•	•	•			•										□	□	□	□	3
Apocynaceae	*Couma guianensis* Aubl.	Sorva					•	•	•	•	•	•	•		□	□	□		□	□			□		□	□	6
Apocynaceae	*Geissospermum sericeum* (Benth.) Hook.	Quinarana	•	•	•			•									□	□	□	□							2-3
Apocynaceae	*Himatanthus sucuuba* (Spruce) Woodson	Sucuuba	•																							□	10
Apocynaceae	*Malouetia duckei* MGF	Molongó da mata				•	•	•			•	•						□		□	□	□					2-3
Apocynaceae	*Parahancornia amapa* (Hub.) Ducke	Amapá amargosa						no data								□	□										nd
Araliaceae	*Schefflera morototoni* (Aubl.) Maguire	Morototó						•	•	•										□	□	□	□	□	□	□	1-2
Bignoniaceae	*Jacaranda copaia* (Aubl.) D. Don	Parapará					•	•	•	•	•	•	•		□			□	□				□	□	□	□	4
Bignoniaceae	*Tabebuia* spp.	Pau d'arco					•	•	•	•	•	•	•	•	□	□			□				□		□	□	4
Bixaceae	*Bixa* spp.	Urucu bravo	•				•												□						□	□	4-5
Bombacaceae	*Bombax globosum* Aubl.	Mamorana da terra firme						no data																□			nd
Bombacaceae	*Ceiba pentadra* (L.) Gaertn.	Sumaúma						no data															□	□	□	□	nd
Boraginaceae	*Cordia alliodora* (R. & P.) Cham.	Uruazeiro	•	•						•	•	•	•	•	□	□	□	□							□	□	3
Boraginaceae	*Cordia goeldiana* Hub.	Freijó							•																□		4
Burseraceae	mainly *Protium* spp.	Breu	•	•	•	•	•		•	•	•	•	•		□	□	□	□	□	□	□				□	□	3
Burseraceae	*Trattinnickia rhoifolia* Willd.	Breu sucuruba	•	•	•	•	•								□			□		□	□	□	□			□	5-6
Caryocaraceae	*Caryocar glabrum* (Aubl.) Pers.	Piquiarana	•							•			•	•		□		□	□								5
Caryocaraceae	*Caryocar villosum* (Aubl.) Pers.	Piquiá							•	•	•	•			□	□	□	□	□	□	□	□					7
Celastraceae	*Goupia glabra* Aubl.	Cupiúba				•	•	•												□	□		□	□	□	□	2-3
Chysobalanaceae	*Couepia longipendula* Pilger	Castanha de galinha										•	•	•	□	□	□	□		□							3
Chysobalanaceae	*Couepia* spp.	Pajurá				•	•	•	•						□	□	□	□	□	□	□	□	□		□	□	5-6
Chysobalanaceae	*Licania* cf. *heteromorpha*	Macucu								•					□		□	□	□	□	□		□			□	5
Chysobalanaceae	*Licania* cf. *micrantha*	Caraperana	•	•	•		•			•		•	•		□	□	□	□	□	□	□	□				□	4-5
Chysobalanaceae	*Parinari montana* Aubl.	Parinari						no data							□												nd
Combretaceae	mainly *Buchenavia* spp.	Cuiarana, Tanimbouco	•	•	•					•			•			□	□	□	□	□	□	□	□		□		3-4
Connaraceae	*Connarus* sp.	Arara mirá							•	•								□	□	□							9
Ebenaceae	*Diospyros* sp.	Caqui	•																	□					□	□	5
Elaeocarpaceae	*Sloanea grandis* Ducke	Urucurana			•	•						•					□	□	□		□				□		1-2
Euphorbiaceae	*Aparisthmium & Conceveiba* spp.	Pau de índio	•		•									•	□	□	□									□	1-2
Euphorbiaceae	*Croton* sp.	Glícia						no data									□		□								nd
Euphorbiaceae	*Croton* sp.	Pau gaivota, Dima	•										•	•			□								□		4-5
Euphorbiaceae	*Hevea brasiliensis* Muell. Arg.	Seringueira								•		•			□	□	□	□	□		□						5-6
Euphorbiaceae	*Hevea guianensis* Aubl.	Seringa itaúba								•					□	□	□	□							□	□	6
Euphorbiaceae	*Hevea* spp.	Seringarana		•				•								□				□						□	6
Euphorbiaceae	*Joannesia heveoides* Ducke	Castanha arara		•					•		•												□	□		□	5-8
Euphorbiaceae	Unidentified species	Caxixá											•		□	□	□	□									2-3
Flacourtiaceae	*Laetia procera* (Poepp. & Endl.) Eichl.	Pau jacaré	•			•	•			•				•		□	□	□	□	□			□		□	□	5
Guttiferae	*Moronobea* sp.	Anani da terra firme										•	•	•			□	□									4-5
Guttiferae	*Platonia insignis* Mart.	Bacuri					•	•													□						1-
Guttiferae	*Vismia* spp.	Lacre	•	•	•	•	•	•	•	•	•	•	•	•	□	□	□	□	□	□	□	□	□	□	□	□	1-2
Humiriaceae	*Duckesia sericea* Warb.	Uchi coroa										•	•	•	□	□	□	□	□	□		□					6
Humiriaceae	*Endopleura uchi* (Huber) Cuatrec.	Uchi liso, Uchi pucú	•									•	•	•	□	□	□	□	□	□	□				□		6
Humiriaceae	*Humiria balsamifera* J. St. Hil.	Umiri					•	•			•	•	•		□	□	□	□	□		□				□		4
Humiriaceae	*Sacoglottis mattogrossensis* Malme	Achuá			•	•		•	•	•	•		•	•	□	□	□	□	□	□	□	□	□		□	□	7-8
Humiriaceae	*Vantanea parensis* L.	Uchi morcego				•	•		•	•					□	□					□				□		7
Lauraceae	*Aniba canelilla* (H.B.K.) Mez	Casca preciosa						no data											□	□		□					nd
Lauraceae	*Aniba, Nectandra & Ocotea* spp.	Louro	•	•	•	•	•	•	•	•	•	•	•	•	□	□	□	□	□	□	□	□	□	□	□	□	3-4
Lauraceae	*Mezilaurus itauba* (Meissn.) Taub. ex Mez	Itaúba				•	•	•	•									□	□	□	□	□	□				3
Lecythidaceae	*Bertholletia excelsa* Humb. & Bonpl.	Castanheira do Pará	•									•	•	•	□	□	□	□	□							□	12-14
Lecythidaceae	*Cariniana micrantha* Ducke	Tauari côco		•	•	•	•								□					□	□	□	□	□	□	□	4-5
Lecythidaceae	*Couratari oblongifolia* Ducke	Tauari branco				•	•	•	•	•	•			•	□					□	□	□	□	□	□	□	4-5
Lecythidaceae	*Eschweilera* spp.	Matamatá	•	•	•	•	•	•	•		•	•	•	•	□	□	□	□	□	□	□	□	□	□			3-4
Lecythidaceae	*Holopyxidium jarana* (Hub.) Ducke	Jarana	•	•				•	•				•			□	□	□	□			□	□				2-4
Lecythidaceae	*Lecythis usitata* Miers	Sapucaia						•	•	•	•	•	•				□	□			□	□					9-10
Legum.-Caes.	*Cassia* sp. [1]	Cassia piolho	•	•	•	•	•	•	•	•	•	•	•	•	□	□	□	□	□	□	□	□	□	□	□	□	3-4
Legum.-Caes.	*Cassia* sp. [2]	Marimari pequena da t.f.	•	•	•	•	•	•	•	•	•	•	•	•	□	□	□	□	□	□	□	□	□	□	□	□	3
Legum.-Caes.	*Cassia spruceana* Benth.	Marimari grande da t.f.				•	•				•	•	•		□					□	□	□			□		8
Legum.-Caes.	*Copaifera martii* Hayne	Copaíba				•	•												□	□	□	□	□				3-4
Legum.-Caes.	*Dialium guianensis* (Aubl.) Sandw.	Jutaí pororoca												•				□	□	□	□						4-6
Legum.-Caes.	*Dimorphandra macrostachya* Benth.	Fava pombo					•	•	•	•	•				□	□	□	□									7-8
Legum.-Caes.	*Dimorphandra* sp.	Falso angelim						no data								□									□	□	nd
Legum.-Caes.	*Hymenaea courbaril* L.	Jutaí açu, Jatobá	•			•	•	•		•	•	•			□			□	□	□	□	□	□	□	□	□	7-8
Legum.-Caes.	*Hymenaea intermedia* Ducke	Jutaí mirim	•									•										□	□	□	□	□	10
Legum.-Caes.	*Macrolobium* sp.	Fava carapalo						no data														□					nd
Legum.-Caes.	*Peltogyne lecointei*	Pau roxo							•	•	•				□								□	□	□	□	4
Legum.-Caes.	*Peltogyne paniculata* Benth.	Muirateiro				•	•	•	•	•												□	□	□	□	□	4
Legum.-Caes.	*Peltogyne paradoxa* Ducke	Coataquiçaua					•		•										□	□			□				2-3
Legum.-Caes.	*Schizolobium amazonicum* (Aubl.) Ducke	Canafístula						•															□				3
Legum.-Caes.	*Sclerolobium paniculatum* Vog.	Tachi dos campos					•	•	•					•	□						□	□	□	□	□	□	3
Legum.-Caes.	*Tachigalia paniculata* Aubl.	Tachi preto				•	•	•	•	•							□	□	□	□	□	□	□	□	□	□	3
Legum.-Caes.	*Vouacapoua americana* Aubl.	Acapú				•													□	□							2
Legum.-Mimos.	*Albizia* sp.	Fava segmentada							•			•											□				3
Legum.-Mimos.	*Cedrelinga cateniformis* Ducke	Cedrorana												•		□		□									3-4
Legum.-Mimos.	*Dinizia excelsa* Ducke	Angelim pedra				•	•			•										□	□	□	□				3-4
Legum.-Mimos.	*Enterolobium maximum* Ducke	Tamboril											•	•	□	□	□	□					□	□			10
Legum.-Mimos.	*Enterolobium schomburgkii* Benth.	Fava de rosca										•	•	•	□	□	□	□	□		□	□	□	□	□		4-5

Table 1. Cont.

FAMILY	SPECIES	COMMON NAME	Month: 1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	
			FLOWERING PERIOD												FRUITING PERIOD												
		Rainfall:			Wet			Shrs			Dry			Shrs			Wet			Shrs			Dry			Shr	
Legum.-Mimos.	*Inga* spp.	Ingá	•		•	•	•	•	•	•	•	•	•	•	□	□	□	□	□	□	□	□	□	□		□	3-4
Legum.-Mimos.	*Parkia gigantocarpa* Ducke	Fava arara tucupi				•			•	•	•				□				□				□	□	□	□	3-4
Legum.-Mimos.	*Parkia oppositifolia* Spr. ex Benth	Fava japacamim	•	•	•													□	□	□	□	□	□	□			3-4
Legum.-Mimos.	*Parkia pendula* Benth. ex Walp.	Fava bolota								•					□								□		□		2-3
Legum.-Mimos.	*Parkia* sp.	Fava bengue				•	•	•									□				□	□	□	□	□		3
Legum.-Mimos.	*Piptadenia suaveolens* Miq.	Timborana						no data									□				□						nd
Legum.-Mimos.	*Pithecellobium racemosum* Ducke	Angelim rajado								•	•	•						□									7
Legum.-Mimos.	*Pithecellobium* sp. (1)	Fava cordão						no data							□			□	□								nd
Legum.-Mimos.	*Pithecellobium* sp. (2)	Mapuchiqui, Panca					•	•	•					•											□	□	6
Legum.-Mimos.	*Pithecellobium* sp. (3)	Fava dentinha						no data											□					□			nd
Legum.-Mimos.	*Pithecellobium* spp.	Fava olho de peixe										•							□	□	□	□					7
Legum.-Mimos.	*Stryphnodendron pulcherrimum* (Willd.) Hochr.	Barbatimão, Camuzé			•	•	•	•			•	•	•							□	□	□	□	□	□		5
Legum.-Papil.	*Andira retusa* H.B.K.	Andira uchi		•											□			□						□	□	□	8-10
Legum.-Papil.	*Bowdichia* cf. *nitida*	Sucupira amarela	•	•													□										2
Legum.-Papil.	*Bowdichia* spp.	Sucupira preta	•	•	•									•			□	□	□				□				2
Legum.-Papil.	*Dalbergia spruceana* Benth.	Jacarandá do Pará					•	•			•										□	□	□	□	□	□	2-3
Legum.-Papil.	*Diplotropis purpurea* (Rich.) Amsh.	Sucupira escamosa				•	•	•													□	□	□				3
Legum.-Papil.	*Dipteryx magnifica* Ducke	Cumaru rosa	•	•	•		•	•	•	•	•	•	•	•	□	□	□	□	□	□		□	□	□		□	6
Legum.-Papil.	*Dipteryx odorata* (Aubl.) Willd.	Cumaru			•				•	•	•	•	•	•	□	□	□	□	□	□	□	□	□	□	□		7-8
Legum.-Papil.	*Hymenolobium excelsum* (Ducke) Benth.	Angelim da mata		•	•						•	•	•		□	□		□							□	□	3-4
Legum.-Papil.	*Hymenolobium* sp. (1)	Angelim aroeira	•	•	•	•			•	•				•		□	□	□	□		□	□	□	□	□		3
Legum.-Papil.	*Hymenolobium* sp. (2)	Angelim blindado								•														□		□	3-4
Legum.-Papil.	*Ormosia* spp.	Tento	•	•	•	•	•		•				•		□	□		□	□	□	□	□	□	□	□		3-4
Legum.-Papil.	*Platymiscium duckei* Huber.	Macacauba da terra firme						•	•		•	•	•	•	□							□	□	□		□	2-3
Legum.-Papil.	*Pterocarpus rohrii* Vahl	Mututi da terra firme						•	•	•	•	•									□	□	□	□		□	2
Legum.-Papil.	*Swartzia corrugata* Benth.	Coração de negro	•	•					•	•	•	•	•		□	□	□	□	□					□	□	□	3
Legum.-Papil.	*Swartzia polyphylla* A. DC.	Pitaica							•	•	•	•	•		□			□	□						□	□	4
Legum.-Papil.	*Swartzia* spp.	Gombeira	•	•	•	•	•	•	•	•	•	•	•	•	□	□	□	□	□	□	□		□	□	□	□	2-3
Legum.-Papil.	*Vatairea sericea* Ducke	Fava amargosa							•	•					□								□	□	□		2-3
Malpighiaceae	*Byrsonima* spp.	Murici da mata	•	•	•					•	•			•		□	□	□	□	□	□	□	□		□	□	5-6
Melastomataceae	*Belucia imperialis*	Muuba, Goiaba de anta	•	•	•	•	•	•	•	•	•	•	•	•	□	□	□	□	□	□	□	□	□	□	□	□	1-2
Melastomataceae	mainly *Miconia* spp.	Maramara	•	•	•		•	•				•	•	•	□	□			□	□	□			□	□	□	1-2
Melastomataceae	*Miconia longifolia* DC.	Sapateiro						•		•	•												□		□	□	3
Melastomataceae	*Mouriri plasscharti* Lulie.	Muiraúba						•							□	□									□	□	6
Meliaceae	*Carapa guianensis* Aubl.	Andiroba	•	•	•	•					•				□	□	□	□	□	□	□						3
Meliaceae	*Cedrela odorata* L.	Cedro vermelho						•	•	•	•												□	□	□	□	3
Meliaceae	*Guarea trichilioides* L.	Jatoá												•			□	□			□						3
Meliaceae	*Swietenia macrophylla* King	Mogno						no data														□					nd
Meliaceae	*Trichilia lecointei* Ducke	Jatauba									•								□				□	□			7
Moraceae	*Bagassa guianensis* Aubl.	Tatajuba						no data																		□	nd
Moraceae	*Brosimum lactescens* (S. Moore) C.C. Berg	Janitá		•												□		□	□								2-3
Moraceae	*Brosimum rubescens* Taub.	Muirapiranga						no data							□	□	□	□							□		nd
Moraceae	*Cecropia obtusa* Trec.	Imbauba branca	•	•	•	•	•	•	•	•	•	•	•	•	□	□	□	□	□	□	□	□	□	□	□	□	1-2
Moraceae	*Clarisia racemosa* Ruiz & Pav.	Guariuba						no data							□	□	□										nd
Moraceae	*Maquira* & *Helicostylis* spp.	Muiratinga da terra firme	•	•									•	•	□		□	□	□							□	2-3
Moraceae	*Pourouma* sp.	Imbaubarana			•											□		□									2
Moracea	*Brosimum potabile*	Amapa doce						•	•	•	•											□	□	□	□	□	2
Myristicaceae	*Osteophloeum platyspermum* Warb.	Ucuubarana	•						•	•	•	•		•	□	□	□	□	□		□	□	□	□	□	□	5
Myristicaceae	*Virola* spp.	Ucuuba		•			•	•	•	•	•				□	□	□	□	□		□	□	□	□	□	□	5
Myrtaceae	*Myrcia fallax* (Rich.) DC.	Murta/Goiabinha	•	•	•							•		•	□	□	□	□		□	□			□	□	□	1-2
Myrtaceae	*Myrcia* spp.	Pixuna											•	•	□	□	□				□					□	4
Myrtaceae	*Psidium* sp.	Goiabeira						no data							□	□	□			□						□	nd
Myrtaceae	Unidentified species	Socoró da mata						no data							□		□	□								□	nd
Nyctaginaceae	*Neea* sp.	João mole						no data							□				□								nd
Olacaceae	*Minquartia guianensis* Aubl.	Acariquara							•	•							□		□		□	□	□	□	□		2-3
Olacaceae	unidentified species	Olacaceae casca grossa						no data												□	□	□					nd
Proteaceae	*Roupala montana* Aubl.	Faieira						no data							□											□	nd
Rubiaceae	*Duroia* spp.	Puruí	•										•	•		□	□	□	□	□	□	□					6
Rubiaceae	*Genipa americana* L.	Genipapo							•	•	•				□	□	□						□	□	□	□	4
Rubiaceae	*Palicourea* spp.	Erva de rato	•	•	•	•	•		•			•				□	□		□	□	□	□					3-4
Rutaceae	*Spathelia excelsa*	Pau para tudo	•															□	□								3-4
Sapindaceae	*Talisia* spp.	Pitomba					•	•													□			□		□	4
Sapotaceae	*Manilkara amazonica* (Hub.) Chev.	Maparajuba						no data							□	□	□	□	□	□						□	nd
Sapotaceae	*Manilkara huberi* (Ducke) Chev.	Maçaranduba									•	•			□	□										□	3-4
Sapotaceae	*Micropholis guianensis* (A. DC.) Pierre	Rosadinha	•	•					•	•					□	□	□	□	□							□	5-6
Sapotaceae	mainly *Pouteria* spp.	Abiurana	•		•	•	•	•	•	•	•	•	•	•	□	□	□	□	□	□	□	□	□	□	□	□	5-6
Simaroubaceae	*Simarouba amara* Aubl.	Marupá	•						•	•	•				□			□						□	□	□	3
Sterculiaceae	*Sterculia* spp.	Axixá					•	•	•	•					□	□	□	□					□	□	□	□	5-6
Sterculiaceae	*Theobroma* sp.	Cacau da mata									•	•	•		□		□	□	□							□	3-4
Tiliaceae	*Apeiba echinata* Gaertn.	Pente de macaco			•		•	•					•		□	□					□	□	□	□	□	□	4-5
Tiliaceae	*Lueheopsis divicata* Mart.	Açoita cavalo							•	•	•	•			□											□	3
Ulmaceae	*Trema micrantha* (L.) Bl.	Curumim	•	•	•	•	•	•	•	•	•	•	•		□	□	□	□	□	□	□	□	□	□	□	□	1-2
Violaceae	*Rinorea* spp.	Jacamin												•			□									□	3
Vochysiaceae	*Erisma uncinatum* Warm.	Quarubarana						no data								□	□		□								nd
Vochysiaceae	*Qualea* spp.	Mandioqueira	•	•							•	•	•	•		□	□	□									5
Vochysiaceae	*Vochysia obscura* Warm.	Quaruba rosa	•		•	•						•	•	•		□	□	□									2
	Unidentified species	Taperibarana						no data							□	□					□		□		□	□	nd
TOTAL:	TOTAL	TOTAL	51	41	38	43	53	54	60	63	56	57	53	48	81	76	80	83	78	84	70	60	73	62	75	82	

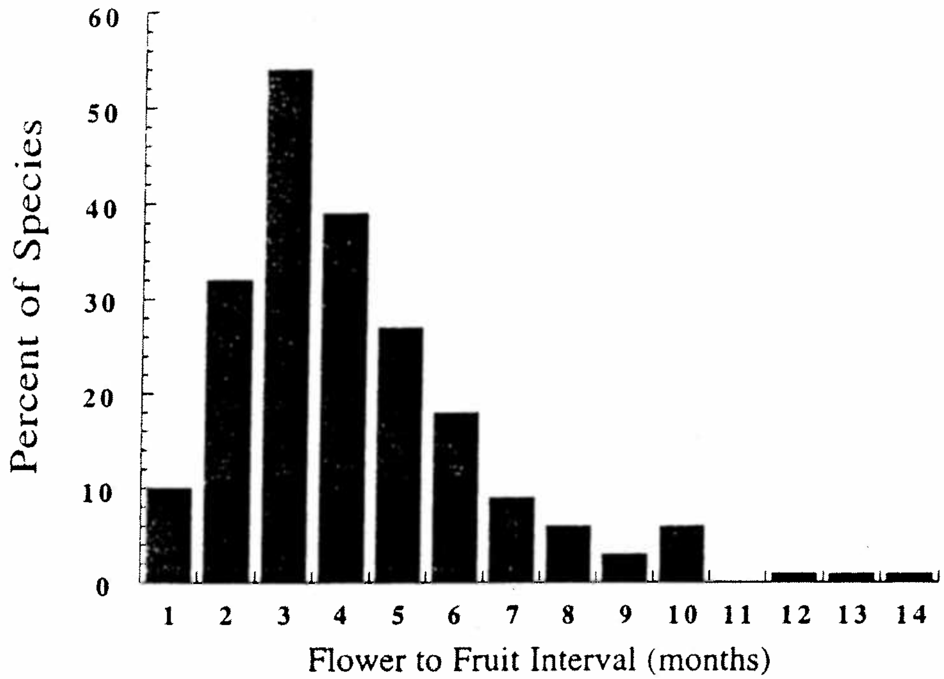

Fig. 3. Distribution of peak flowering-peak fruiting time intervals among primary forest tree taxa near Porto Trombetas, Pará, Brazil.

ual trees has been observed from one year to the next. Second, many species will flower and fruit twice in a given year and individual trees may flower "out of season" relative to others individuals of the species. Finally, some of the taxa groups included in the data embrace several individual species or even genera, each with their own specific, seasonally more restricted, flowering and fruiting periods.

In this study a few species were observed to flower and fruit continuously throughout the year. These included *Bellucia imperialis* (Melastomataceae), *Cassia* sp. [1], *Cassia* sp. [2] (Leguminosae-Caesalpinioideae), *Cecropia obtusa* Terc. (Moraceae), and *Trema micrantha* (L.) Bl. (Ulmaceae). All are medium-sized short-lived pioneer trees normally found in new clearings and forest edges. Two produce dry fruits (both *Cassia* species) while the remaining three produce fleshy fruits, all with small seeds.

The overall patterns in flowering and fruiting seasonality as well as the "irregularities" observed in the forests in the vicinity of Trombetas, are consistent with the results of earlier studies of moist forests elsewhere in the Brazilian Amazon and are in agreement with results from other moist tropical forest locations (cf. Richards 1966, Foster 1982, Terborgh 1990). In a 12-year phenological study of 27 overstory tree species in the terra firme forests of the Ducke Reserve near Manaus, Alencar *et al.* (1979) reported flowering and fruiting seasonality trends very similar to those for Trombetas. At the Ducke Reserve, peak flowering was

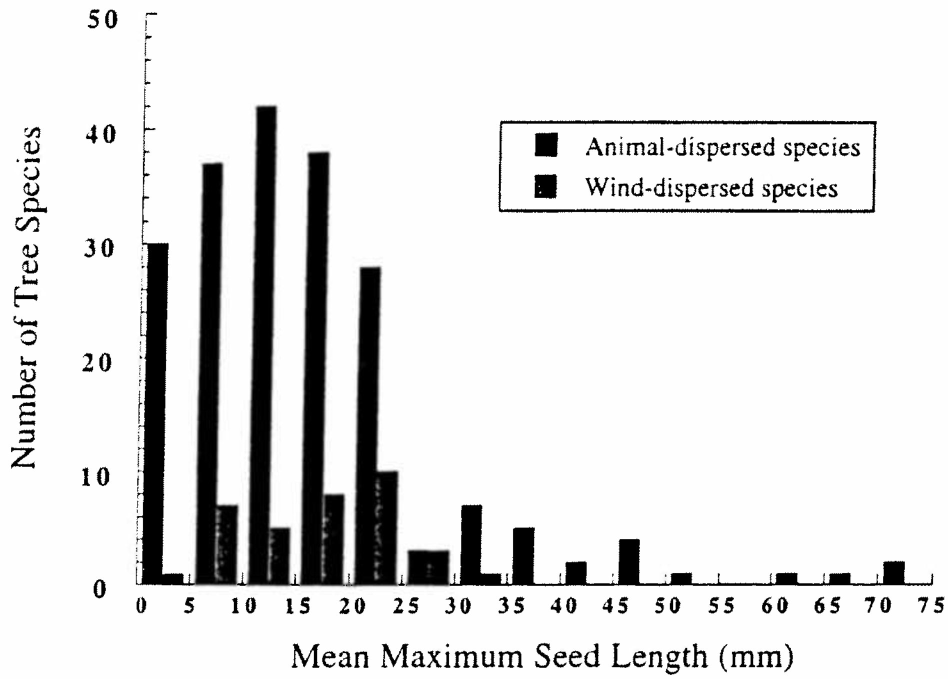

Fig. 4. Seed size distribution (mean maximum seed lengths) for animal- and wind-dispersed tree species in terra firme forests near Porto Trombetas, Pará, Brazil.

concentrated during the dry season (June-September), and peak fruit maturation during the wet season. In wet forests in Costa Rica, a marked increase in the numbers of species flowering during the dry season, and a predominance of fruit production during the wet season were reported by Frankie *et al.* (1974a, 1974b), Opler *et al.* (1976) and Newstrom *et al.* (1994).

Fruit maturation

Among the tree taxa studied, the time interval between peak flowering and peak fruiting varied widely, from less than one month up to 14 months (e.g., *Bertholletia excelsa* Humb. & Bonpl.), with a median of 3 months (Fig. 3). There were no discernible correlations between flowering-fruiting intervals and species' characteristics such as fruit or seed size or seed longevity (i.e., length of time seeds remain viable). However, there was a general tendency towards rapid fruit maturation ($\leq$2 months) among short-lived pioneer species such as *Cecropia obtusa*, *Miconia* spp., *Trema micrantha*, and *Vismia* spp., a trend that has been noted by numerous authors in studies of secondary forest ecology (cf. Budowski 1965, Gómez-Pompa & Vásquez-Yanes 1974, Opler *et al.* 1980, Brown & Lugo 1990)

Table 2. Seed sizes and dispersal mode for primary forest trees at Porto Trombetas-PA, Brazil

Family	Species	Mean Seed Size (Length x Width x Thickness) in mm. < 8 mm	8 - 14.5 mm	15 - 24.5 mm	> 24.5 mm	Distribution method
Anacardiaceae	*Anacardium giganticum*			20 x 20 x 17		fauna
Anacardiaceae	*Astronium lecointei*			15.5 x 4.5 x 4.5		wind
Anacardiaceae	*Spondias mombim*				33 x 17 x 17	fauna
Anacardiaceae	*Tapirira guianensis*		10 x 7.5 x 5.5			fauna
Annonaceae	*Annona ambotay* Aubl.			15 x 10 x 7		fauna
Annonaceae	*Duguetia cauliflora* R.E.Fries.	6 x 4 x 3				fauna
Annonaceae	*Duguetia riparia* Huber		12 x 6 x 5			fauna
Annonaceae	*Guatteria amazonica* R.E.Fries.		10 x 8 x 7			fauna
Annonaceae	*Guatteria poeppigiana* Mart.		8 x 5 x 4			fauna
Annonaceae	*Guatteria* sp. [1]		11 x 9 x 8			fauna
Annonaceae	*Guatteria* sp. [2]		9.5 x 6 x 5			fauna
Annonaceae	*Rollinia* sp.		8 x 6.5 x 4.5			fauna
Annonaceae	*Unonopsis guatteroides* (A.DC.) R.E.Fries		12 x 9 x 7			fauna
Annonaceae	*Xylopia benthami* R.E.Fries		9.5 x 5 x 4			fauna
Annonaceae	*Xylopia* sp. [1]	5 x 3.5 x 3				fauna
Annonaceae	*Xylopia* sp. [2]	6.5 x 4 x 3.5				fauna
Anonaceae	*Xylopia* sp. [3]	7 x 4 x 3				fauna
Apocynaceae	*Aspidosperma exalatum*			24 x 22 x 2		wind
Apocynaceae	*Aspidosperma oblongum*			22 x 19 x 1		wind
Apocynaceae	*Aspidosperma* sp.				34 x 33 x 4	wind
Apocynaceae	*Couma guianensis*		12 x 7 x 2			fauna
Apocynaceae	*Geissospermum sericeum*			17 x 12.5 x 3.5		fauna
Apocynaceae	*Himatanthus articulatus*			20.5 x 9 x 1.5		wind
Apocynaceae	*Parahancornia amapa*			17 x 10.5 x 8		fauna
Araliaceae	*Schlefflera morototoni*	5 x 4 x 1				fauna
Bignoniaceae	*Jacaranda copaia*	7.5 x 6 x 1.5				wind
Bignoniaceae	*Tabebuia impetiginosa* (DC.) Standl.		8 x 6 x 1			wind
Bignoniaceae	*Tabebuia serratifolia* (Valh) Nichols		11 x 6.5 x 1			wind
Bombacaceae	*Ceiba pentandra*	6.5 x 6 x 4.5				wind
Boraginaceae	*Cordia alliodora*		12 x 8 x 6.5			fauna
Burseraceae	*Hemicrepidospermum rhiofolium* Benth.			15 x 13 x 10		fauna
Burseraceae	*Protium apiculatum* Swartz			16 x 9 x 6		fauna
Burseraceae	*Protium sagotianum* March			15 x 11 x 9		fauna
Burseraceae	*Protium* sp.			19 x 11 x 10		fauna
Burseraceae	*Tetragastris panamensis* (Engl.) O.Kuntze		13 x 9 x 6			fauna
Burseraceae	*Tetragastris trifoliata* (Engl.) Cautr.			15 x 11 x 5		fauna
Burseraceae	*Trattinnickia burserifolia* Willd.		10 x 8 x 8			fauna
Caryocaraceae	*Caryocar glabrum*				32 x 19 x 17	fauna
Caryocaraceae	*Caryocar villosum*				46 x 28 x 25	fauna
Celestraceae	*Goupia glabra*	2 x 1.5 x 1.5				fauna
Chrysobalanaceae	*Coeupia racemosa* Benth. ex Hook.				39 x 28 x 26	fauna
Chrysobalanaceae	*Couepia bracteosa*				72.5 x 52.5 x 38	fauna
Chrysobalanaceae	*Couepia longipenduncula*				52 x 26 x 26	fauna
Chrysobalanaceae	*Licania* cf. *micrantha*				37.5 x 31 x 27.5	fauna
Chrysobalanaceae	*Licania egleri* Prance				47 x 24 x 17	fauna
Chrysobalanaceae	*Licania latifolia* Benth. ex Hook.			16.5 x 8.5 x 7		fauna
Chrysobalanaceae	*Licania micrantha* Miq.			20 x 9 x 8		fauna
Chrysobalanaceae	*Licania* sp.				65 x 45.5 x 41.5	fauna
Chrysobalanaceae	*Parinari montana* Aubl.				75 x 50 x 41	fauna
Clusiaceae	*Clusia* sp. [1]	4.5 x 3 x 3				fauna
Clusiaceae	*Clusia* sp. [2]	5.5 x 2.5 x 2.5				fauna
Combretaceae	*Buchenavia* sp.			18 x 10 x 9		fauna
Ebenaceae	*Diospyros* sp.			18 x 10 x 8		fauna
Elaeocarpaceae	*Sloanea* sp.		14 x 9 x 7			fauna
Euphorbiaceae	*Conceveiba* sp.		9 x 8.5 x 7			fauna
Euphorbiaceae	*Croton* sp.	4 x 3 x 3				fauna
Euphorbiaceae	*Hevea guianensis*			16 x 13 x 10		fauna
Euphorbiaceae	*Joannesia princips*			22 x 18 x 17		fauna

Table 2.Cont.

Family	Species	Mean Seed Size (Length x Width x Thickness) in mm. < 8 mm	8 - 14.5 mm	15 - 24.5 mm	> 24.5 mm	Distribution method
Flacourtiaceae	*Laetia procera*	3 x 2 x 1.5				fauna
Guttiferae	*Calophyllum brasiliensis* Camb.		11 x 10 x 10			fauna
Guttiferae	*Tovomita macrophylla* L. O. Wms.	6 x 5 x 4.5				fauna
Guttiferae	*Vismia cayenensis* (Jacq.) Pers.	1.7 x 0.5 x 0.5				fauna
Guttiferae	*Vismia guianensis* Choisy	2 x 0.4 x 0.4				fauna
Guttiferae	*Vismia* sp.	2.7 x 0.7 x 0.7				fauna
Humiriaceae	*Duckesia sericea*				40 x 35 x 35	fauna
Humiriaceae	*Endopleura uchi*				35 x 18 x 18	fauna
Humiriaceae	*Sacoglottis mattogrossensis*			24 x 18 x 18		fauna
Humiriaceae	*Vantanea cupularis*			20 x 18 x 18		fauna
Humiriaceae	*Vantanea paraensis*			20 x 17 x 17		fauna
Lauraceae	*Aniba canellilia*			16 x 10 x 9		fauna
Lauraceae	*Aniba* cf. *permollis*			17.5 x 9 x 8.5		fauna
Lauraceae	*Aniba hostmaniana*			17 x 13 x 10		fauna
Lauraceae	*Aniba parviflora*			21 x 11 x 10		fauna
Lauraceae	*Aniba* sp. [1]			17 x 11 x 10		fauna
Lauraceae	*Aniba* sp. [2]			19 x 11 x 9		fauna
Lauraceae	*Dicypellium manauense*		14 x 7 x 6			fauna
Lauraceae	*Mezilaurus itauba*			19 x 10 x 8.5		fauna
Lauraceae	*Mezilaurus lindaviana*			21 x 10 x 9		fauna
Lauraceae	*Nectandra rubra*			17 x 12 x 11		fauna
Lauraceae	*Ocotea fragrantissima*			18 x 12 x 11		fauna
Lauraceae	*Ocotea guianensis*			16 x 9 x 8		fauna
Lauraceae	*Ocotea myriantha* Mez. ("louro abacate")		14 x 12 x 11			fauna
Lauraceae	*Ocotea sp.* . ("louro")		12.5 x 7 x 6.5			fauna
Lauraceae	*Ocotea* sp. [1]		13.5 x 9.5 x 9			fauna
Lauraceae	*Ocotea* sp. [2]			16 x 10 x 9		fauna
Lecythidaceae	*Allantoma caudata* R. Knuth			20 x 9 x 3		wind
Lecythidaceae	*Bertholletia excelsa*				48 x 21 x 20	fauna
Lecythidaceae	*Cariniana micrantha*			17 x 6.5 x 4		wind
Lecythidaceae	*Couratari* sp.				28 x 7 x 2	wind
Lecythidaceae	*Couroupita guianensis*			23 x 18 x 16		fauna
Lecythidaceae	*Eschweilera amara*			23 x 15.5 x 14		fauna
Lecythidaceae	*Eschweilera sagotiana*			23 x 22 x 15		fauna
Lecythidaceae	*Eschweilera* sp.[1]			20 x 14.5 x 11.5		fauna
Lecythidaceae	*Eschweilera* sp. [2]			17 x 11 x 8		fauna
Lecythidaceae	*Holopyxidium jarana*				40 x 35 x 25	fauna
Lecythidaceae	*Lecythis usitata*				43 x 20 x 18	fauna
Lecythidaceae	*Eschweilera odora*			22 x 17 x 13		fauna
Leg.-Caesalpinioide	*Cassia* sp. [1]		11 x 2 x 0.5			fauna
Leg.-Caesalpinioide	*Cassia* sp. [2]	7 x 2 x 1				fauna
Leg.-Caesalpinioide	*Cassia spruceana*	5.5 x 4.5 x 2.5				fauna
Leg.-Caesalpinioide	*Copaifera martii*			18 x 11.5 x 10		fauna
Leg.-Caesalpinioide	*Cynometra hostmaniana*			17 x 14 x 4		wind
Leg.-Caesalpinioide	*Dialium guianensis*		8 x 6 x 3			fauna
Leg.-Caesalpinioide	*Hymenaea courbaril*			16 x 14 x 12		fauna
Leg.-Caesalpinioide	*Hymenaea intermedia* Ducke			17 x 15 x 13		fauna
Leg.-Caesalpinioide	*Peltogyne paniculata*			24 x 12 x 3.5		wind
Leg.-Caesalpinioide	*Peltogyne paradoxa*			24 x 3.5 x 3		wind
Leg.-Caesalpinioide	*Schizolobium amazonicum*			22 x 20 x 9.5		fauna
Leg.-Caesalpinioide	*Sclerolobium paniculatum*		9 x 5 x 1.5			wind
Leg.-Caesalpinioide	*Tachigali paniculata* Aubl.				25 x 12 x 3	wind
Leg.-Mimosoideae	*Acacia auriculiformis*	5 x 3 x 2				fauna
Leg.-Mimosoideae	*Acacia mangium*	6 x 3 x 2				fauna
Leg.-Mimosoideae	*Cedrelinga catanaeformis*				30 x 19 x 4	wind
Leg.-Mimosoideae	*Dinizia excelsa*		14 x 8 x 2.5			wind
Leg.-Mimosoideae	*Enterolobium maximum*			18 x 11.5 x 6.5		fauna
Leg.-Mimosoideae	*Enterolobium schomburgkii*		8 x 4 x 2			fauna
Leg.-Mimosoideae	*Inga alba* (Sw.) Willd.			16 x 8 x 4		fauna
Leg.-Mimosoideae	*Inga cinnamomea* Spruce ex. Benth.			20 x 11 x 7		fauna

Table 2. Cont.

Family	Species	Mean Seed Size (Length x Width x Thickness) in mm. < 8 mm	8 - 14.5 mm	15 - 24.5 mm	> 24.5 mm	Distribution method
Leg.-Mimosoideae	*Inga falcisti*		13 x 8 x 5			fauna
Leg.-Mimosoideae	*Inga obrusata* Spruce ex. Benth.		13 x 7.5 x 6			fauna
Leg.-Mimosoideae	*Inga* sp. [1]		14 x 9 x 6			fauna
Leg.-Mimosoideae	*Inga* sp. [2]			24 x 12 x 10		fauna
Leg.-Mimosoideae	*Inga* sp. [3]		9 x 8.5 x 5			fauna
Leg.-Mimosoideae	*Inga* sp. [4]		9.5 x 7.5 x 5			fauna
Leg.-Mimosoideae	*Inga* sp. [5]			23 x 9.5 x 6		fauna
Leg.-Mimosoideae	*Inga* sp. [6]			15 x 7.5 x 6.5		fauna
Leg.-Mimosoideae	*Inga* sp. [7]			15 x 8 x 6		fauna
Leg.-Mimosoideae	*Inga velutina* Willd.			15 x 8 x 5		fauna
Leg.-Mimosoideae	*Parkia gigantocarpa*				46 x 12 x 10	fauna
Leg.-Mimosoideae	*Parkia multijuga* Benth.			18 x 12 x 6		fauna
Leg.-Mimosoideae	*Parkia oppositifolia*			22 x 8 x 6		fauna
Leg.-Mimosoideae	*Parkia pendula*	7 x 6 x 3				fauna
Leg.-Mimosoideae	*Parkia ulei*		14 x 10 x 4			fauna
Leg.-Mimosoideae	*Piptadenia suaveolens* Miq.			24 x 6 x 1		wind
Leg.-Mimosoideae	*Pithecelobium* sp.		8.5 x 5.5 x 2.5			fauna
Leg.-Mimosoideae	*Pithecolobium racemosum*	3.5 x 3.5 x 2				fauna
Leg.-Mimosoideae	*Stryphnodendron pulcherrium*	7 x 5 x 3				fauna
Leg.-Papilionoideae	*Andira retusa*				35 x 26.5 x 25	fauna
Leg.-Papilionoideae	*Bowdichia* cf. *nitida*			19.5 x 5 x 3		wind
Leg.-Papilionoideae	*Bowdichia* sp.		12 x 4 x 2			wind
Leg.-Papilionoideae	*Clitoria racemosa*			15 x 14 x 3		fauna
Leg.-Papilionoideae	*Dalbergia spruceana*			15 x 7 x 1		wind
Leg.-Papilionoideae	*Diplotropis purpurea*	6.5 x 4 x 2				wind
Leg.-Papilionoideae	*Dypteryx magnifica*				31 x 16 x 13	fauna
Leg.-Papilionoideae	*Dypteryx odorata*				32 x 17 x 14	fauna
Leg.-Papilionoideae	*Hymenolobium* sp. [1]			23 x 5 x 1.5		wind
Leg.-Papilionoideae	*Hymenolobium* sp. [2]				27 x 9 x 2	wind
Leg.-Papilionoideae	*Hymenolobium excelsum*			18 x 6 x 1.5		wind
Leg.-Papilionoideae	*Ormosia discolor*		11 x 10 x 9.5			fauna
Leg.-Papilionoideae	*Platymiscium duckei*			17 x 11 x 2		wind
Leg.-Papilionoideae	*Pterocarpus rohrii*		12 x 5 x 3			wind
Leg.-Papilionoideae	*Swartzia corrugata* Benth.			24 x 17.5 x 16		fauna
Leg.-Papilionoideae	*Swartzia platygyne* Ducke				36 x 23 x 10	fauna
Leg.-Papilionoideae	*Swartzia polyphylla*				70 x 35 x 32	fauna
Leg.-Papilionoideae	*Vatairea sericea*			24 x 13 x 4.5		wind
Malpighiaceae	*Byrsonima ciliata* Cuatr.	4 x 3 x 3				fauna
Malpighiaceae	*Byrsonima crispa*		14.5 x 11 x 10.5			fauna
Malpighiaceae	*Byrsonima* sp.	7 x 6.5 x 6.5				fauna
Melastomataceae	*Bellucia imperialis*	0.5 x 0.3 x 0.3				fauna
Melastomataceae	*Miconia longifolia*	1 x 0.5 x 0.5				fauna
Melastomataceae	*Miconia* sp. [1]	1.5 x 0.6 x 0.6				fauna
Melastomataceae	*Miconia* sp. [2]	1.8 x 1.2 x 1				fauna
Melastomataceae	*Miconia* sp. [3]	1 x 0.6 x 0.4				fauna
Melastomataceae	*Mouriri plasschaerti*		10 x 9 x 7			fauna
Meliaceae	*Carapa guianensis*				25 x 25 x 25	fauna
Meliaceae	*Cedrela odorata*		9.5 x 4 x 2			wind
Meliaceae	*Guarea trichiloides*		9 x 7 x 6			fauna
Monimiaceae	*Siparuna amazonica*	5.5 x 4 x 3				fauna
Moraceae	*Brosimum acutifolium* Hub.		12 x 11 x 10			fauna
Moraceae	*Brosimum lactescens*		8.5 x 7 x 6			fauna
Moraceae	*Brosimum potabile*		11 x 16 x 15			fauna
Moraceae	*Brosimum rubescens*		10 x 8 x 6			fauna
Moraceae	*Cecropia* sp.	1.5 x 1 x 0.8				fauna
Moraceae	*Clarisia racemosa*			19 x 13 x 12		fauna
Moraceae	*Maquira* sp.			23.5 x 21 x 19		fauna
Moraceae	*Noyera mollis* Ducke		14 x 13 x 13			fauna
Moraceae	*Pourouma* sp.		14 x 8 x 6			fauna
Myristicaceae	*Osteophloem platyspermum*				25.5 x 16 x 16	fauna
Myristicaceae	*Virola multicostata* Ducke			20.5 x 12.5 x 12		fauna
Myristicaceae	*Virola* sp.			17 x 12 x 11		fauna
Myrtaceae	*Myrcia atramentifera* Barb.		10 x 8 x 5			fauna

Table 2.Cont.

Family	Species	Mean Seed Size (Length x Width x Thickness) in mm. < 8 mm	8 - 14.5 mm	15 - 24.5 mm	> 24.5 mm	Distribution method
Myrtaceae	*Myrcia fallax*		9 x 8.5 x 6			fauna
Myrtaceae	*Psidium araca* Raddi	3 x 2 x 1.5				fauna
Myrtaceae	*Psidium guajava* L.	3 x 2.5 x 2				fauna
Olacaceae	*Minquartia guianensis*			21 x 12 x 12		fauna
Olacaceae	*Minquartia punctata* Aubl.			21 x 12 x 12		fauna
Olacaceae	*Ptychopetalum olacoides* Benth.		12 x 8 x 8			fauna
Opiliaceae	*Agonandra brasiliensis* Benth.		13 x 9 x 6			fauna
Palmae	*Astrocaryum murumuru*			22 x 13 x 12		fauna
Palmae	*Attalea* sp.				45 x 21 x 20	fauna
Palmae	*Desmoncus polyacanthos*			15 x 15 x 15		fauna
Palmae	*Euterpe oleracea*		12 x 12 x 12			fauna
Palmae	*Iriartella setigera*				25 x 15 x 15	fauna
Palmae	*Jessenia bataua*			18 x 18 x 17		fauna
Palmae	*Oenocarpus bacaba* Mart.				35 x 35 x 33	fauna
Palmae	*Oenocarpus minor*			20 x 20 x 19		fauna
Polygonaceae	*Cocoloba latifolia* Lam.		10 x 8 x 5			fauna
Rubiaceae	*Chimarrhis turbinata* DC.	2 x 1 x 0.5				fauna
Rubiaceae	*Duroia macrophylla* Huber		11 x 9 x 2			fauna
Rubiaceae	*Duroia* sp.		8 x 5 x 1.5			fauna
Rubiaceae	*Genipa americana*		9 x 8 x 1.5			fauna
Rubiaceae	*Palicourea* sp. [1]	3 x 2.5 x 2.5				fauna
Rubiaceae	*Palicourea* sp. [2]	0.8 x 0.8 x 0.8				fauna
Sapindaceae	Unidentified species		13 x 9 x 7.5			fauna
Sapindaceae	*Talisia cupularis*			18 x 11 x 10		fauna
Sapotaceae	*Chrysophyllum prieurii* A. DC			22 x 10 x 6		fauna
Sapotaceae	*Chrysophyllum* sp. [1]			22 x 10 x 6		fauna
Sapotaceae	*Chrysophyllum* sp. [2]			21 x 8 x 6		fauna
Sapotaceae	*Glycoxylon inophyllum* Ducke			22 x 10 x 6		fauna
Sapotaceae	*Lucuma dissepala* (Krause) Ducke				27.5 x 14.5 x 1	fauna
Sapotaceae	*Manilkara amazonica*		13.5 x 8 x 4.5			fauna
Sapotaceae	*Manilkara huberi*			20 x 11 x 5		fauna
Sapotaceae	*Micropholis guianensis*			15 x 15 x 8		fauna
Sapotaceae	*Micropholis venulosa* (Mart. ex Eichl.) Pierre			20 x 11 x 8		fauna
Sapotaceae	*Pouteria guianensis* Aubl.		14 x 10 x 5			fauna
Sapotaceae	*Pouteria* sp.			19 x 11 x 8		fauna
Sapotaceae	*Radlkoferella macrocarpa* Hub.			22 x 21 x 19		fauna
Simarubaceae	*Simarouba amara*		11 x 6.5 x 5.5			fauna
Solanaceae	*Brunfelsia hospeana*	4 x 3 x 2				fauna
Sterculiaceae	*Sterculia* sp.			22 x 13.5 x 10		fauna
Sterculiaceae	*Theobroma sylvestris* Aubl. ex. Mart.			22.5 x 14 x 8		fauna
Tiliaceae	*Apeiba echinata*	5.5 x 4 x 2				fauna
Tiliaceae	*Luehea divicata* Mart.	5 x 3 x 1.5				wind
Violaceae	*Rinorea* sp. [1]	4 x 4 x 4				fauna
Violaceae	*Rinorea* sp. [2]	4 x 4 x 4				fauna
Vochysiaceae	*Erisma uncinatum*			17 x 2.5 x 2.5		wind
Vochysiaceae	*Vochysia* sp.			16 x 5 x 2.5		wind

based on approx. 2000 observations.

Dispersal: wind = 34; fauna = 196

'Abnormal' and noteworthy flowering and fruiting behavior

The failure to produce fruit, even after intense flowering, has been frequently observed in the primary forests around Trombetas. This has been reported in other tropical locations, although the causes remain open to discussion. Insect predation during the flowering period can cause severe or even total loss, especially with Leguminosae taxa. A typical response by a tree following severe floral predation is to flower again outside the usual period for that species. In the present study, it was observed that following a second flowering, such trees often succeed in producing a modest fruit crop, also outside of the species' normal fruiting period. An unusual drought can provoke a similar reaction, as was observed several times during this study with *Brosimum potabile*.

A few taxa were noted to flower sporadically, with several years elapsing between flowering events. These include all of the *Hymenolobium* spp. studied. In the case of *H. excelsum*, flowering intervals of up to 7 years were observed in this study.

Year-to-year variations on flowering and/or fruiting periodicity, the occurrence of two or more flowering events in a given year, and asynchrony of flowering and fruiting within populations have been reported for other neotropical moist forests in Amazônia (Alencar *et al.* 1979, Roth 1987, Figliolia & Aguiar 1993, Kageyama & Piña-Rodrigues 1993, Piña-Rodrigues & Piratelli 1993).

The spectacular, brief, synchronized display of yellow or magenta flowers in *Tabebuia* spp. is a notable event in the Trombetas upland forests. Other taxa exhibiting similar mass flowering at Trombetas include: *Cassia spruceana* Benth. (Leguminosae-Caesalpiniodeae) (yellow), *Diplotropis purpurea* (Rich.) Amsh. (Leguminosae-Papilionoideae) (blue), *Hymenolobium* spp.(Leguminosae-Papilionoideae) (magenta), *Platymiscium duckei* Huber (Leguminosae- Papilionoideae) (yellow), *Qualea* spp. (Vochysiaceae) (white or blue), *Pterocarpus rohrii* (yellow), *Vatairea sericea* (blue), and *Vochysia obscura* Warm. (Vochysiaceae) (yellow). The environmental cues which synchronizes flowering among widely scattered trees of these species remain undefined.

A 'cascade' or 'relay' strategy was observed in *Dipteryx magnifica* (Leguminosae-Papilionoidae) whose dominant crowns are totally covered by deep pink blossoms when in flower. In this species, as the flowers of one tree fade other trees will burst into flower. This results in extended flowering and subsequent fruiting periods for the species in spite of a 7- to 10-day flowering period for individual trees. A similar phenomenon was observed for *Couma guianensis* Aubl. (Apocynaceae), which has deep pink flowers, *Jacaranda copaia* (Aubl.) D.Don (Bignoniaceae) which produces large panicles of deep blue flowers, and *Sclerolobium paniculatum* Voc.(Leguminosae-Caesalpiniodeae) with large panicles of small cream-colored flowers. All of these species have flowers that are readily observable from great distances and therefore easily documented. It is probable that other taxa in the study area with less conspicuous flowers also follow this strategy.

Monocarpic behavior, where trees flower only once and die after fruiting, is a noteworthy phenomenon observed in many tropical forests, bamboo species being perhaps the best known examples of this behavior. In the Trombetas region of Amazonia the monocarpic taxa are mainly *Spathelia excelsa* (Rutaceae), a tall, slender, branchless tree with a life span of about 20 years; and several species of *Tachigalia* (Leguminosae-Caesalpinioideae), canopy trees with a life span of about 50 years. In places where *Tachigalia* spp. are especially abundant (e.g. at Portel near Belém, Pará), the exceptionally high frequency of standing dead trees had previously led to erroneous conclusions regarding sustainability of these species. In fact, the huge quantities of anemochorous fruits produced by the dying tree germinate readily under shade and assure adequate regeneration of the species.

Observations on leaf phenology

Deciduousness is not a typical feature of the tree flora in the Trombetas region, although it does occur in few taxa over very short periods early in the dry season. The majority of taxa substitute leaves on a continuous basis, but with a marked increase in leaf turnover during the first months of the dry season. Total leaflessness is limited to only a few taxa for a very short period during the early stages of the dry season.

The principal taxa remaining totally leafless for a period of 5 to 10 days per year are: *Anacardium giganteum* Loud. ex Steud. (Anacardiaceae), *Brosimum potabile, Caryocar villosum, Cassia spruceana, Cedrela odorata* L. (Meliaceae), *Ceiba pentandra* (L.) Gaertn. (Bombacaceae), *Couma guianensis, Couratari oblongifolia* Ducke (Lecythidaceae), *Enterolobium schomburgkii* Benth. (Leguminosae-Mimosoideae), *Hymenolobium* spp., *Jacaranda copaia, Tabebuia* spp., *Parkia pendula* Benth. ex Walp. (Leguminosae-Mimosoideae), *Spondias mombim* L. (Anacardiaceae), and *Trattinnickia rhoifolia* Willd. (Burseraceae). The *Cassia* and *Tabebuia* spp. flower while leafless; the remainder of the above taxa flower as new leaves are produced. During flowering years for *Hymenolobium* spp., trees typically lose their leaves immediately prior to flowering. If fertilization is successful, the green pods substitute leaves for photosynthesis and evapo-transpiration, and new leaves will only appear after fruit maturity and abscission. But if fertilization fails the tree will promptly produce new leaves and not flower again that year.

The new leaves of some taxa have brilliant colors such as: bright pastel green (*Cedrela odorata*); pink (*Inga* spp., Leguminosae-Mimosoideae); deep red (*Eschweilera* spp.); Violet (*Swartzia* spp., Leguminosae-Papilionoideae); and white (*Couratari* spp.). The deep coloring of some species' new leaves, which fades rapidly with leaf maturity, is reputed to serve a protective role against ultra-violet radiation during the tender leaf formation. Loggers commonly use the distinctive new leaf color of these species to locate mature trees in the forest.

Seed morphology and dispersal

Average seed sizes ranged greatly among the 230 tree taxa studied (Table 2). Mean maximum seed lengths of up to 75 mm were recorded for a few taxa, although the majority were ≤25 mm in length. The frequency distributions of mean maximum seed lengths were similar between wind- and animal-dispersed species. Species with the largest seeds (maximum seed lengths >50 mm) included several species of Chrysobalanaceae (*Couepia* spp., *Licania* sp., *Parinari montana* Aubl.) and *Swartzia polyphylla* A. DC. (Leguminosae-Papilionoideae). Species with minute seeds (≤2 mm long) tended to be short-lived early pioneer species. These included *Bellucia* and *Miconia* spp. (Melastomataceae), *Cecropia* spp. (Moraceae) and *Vismia* spp. (Guttiferae).

For the overstory tree species surveyed, birds, bats and terrestrial mammals are the principal seed dispersal agents. Approximately 85% of the 230 taxa included in Table 2 are zoochoric, the remaining 15% (34 taxa) being anemochoric, or wind-dispersed. Similar frequencies of zoochoric and anemochoric species in upland moist tropical forests have been reported for other sites in the Brazilian Amazon region and Central America (Foster 1982, Hartshorn 1980, Piña-Rodrigues & Aguiar 1993, van Roosmalen 1985). The importance of wildlife for seed dispersal and forest regeneration in these and moist tropical forests has been discussed by many authors (cf. Sutton 1983, Gautier-Hion 1990, Howe 1990, Terborgh 1990). In the Trombetas region of central Amazonia, this topic has yet to be explored and represents an important area for future research.

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