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Studies on the seed biology of 100 native species of trees in a seasonal moist tropical forest, Panama, Central America

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Abstract

This study quantified various aspects of the seed biology of 100 tree species native to the seasonal moist tropical forest in the Panama Canal Watershed. Species were selected for study based on their potential for use in reforestation projects in Panama. Seeds of 32, 29, and 33 species were dispersed during the dry (DS, January–March), early rainy (ERS, April–July), and late rainy (LRS, August–December) seasons, respectively. Seed mass was correlated with moisture content (MC) but not with dispersal time, and MC was lowest for seeds dispersed in the DS. Germination of nontreated seeds ranged from 0% (6 species) to 99% and was $\geq$50% for 46 species. Seeds of *Beilschmiedia pendula*, *Castilla elastica*, *Diphysa robinioides*, *Genipa americana*, *Hura crepitans*, *Inga spectabilis*, *Jacaranda copaia*, *Protium tenuifolium*, *Pseudobambox septenatum*, and *Trattinnickia aspera* germinated $\geq$85%. Fresh seeds of 49 (52.1%) of the 94 species that germinated were nondormant and 45 (47.9%) were dormant. Only 12 species had a median length of germination time (MLG) $>$ 120 days. MLG for seeds of species dispersed in the LRS was higher than that of those dispersed in the ERS or DS. Forty-eight species had uniform germination (standard deviation of germination time $\leq$ 14 days). Seed longevity ranged from 0.5 to 36 months, and long-lived (L-L) seeds tended to be larger than short-lived (S-L) or very short-lived (very S-L) ones, but not significantly so. MC increased significantly from L-L to very S-L seeds. The highest proportion of L-L seeds was dispersed in the DS and the lowest in the LRS. Results of this study are used to make recommendations for nursery production of tree seedlings to use in forest restoration projects.

Keywords: Panama; Seasonal moist tropical forest; Seed dispersal; Seed dormancy; Seed germination; Seed longevity; Seed mass; Seed moisture content

1. Introduction

In 1998, 54% of the Panama Canal Watershed (PCW) was forested, and 43% was pasture or shrubland (Ibáñez et al., 1999). Since the watershed supplies water for the functioning of the Canal, as well for human use in the city of Panama, in the past 25 years national and international agencies have invested millions of dollars in reforestation, restoration, and sustainable development projects that involved the use of trees (Condit et al., 2001). Interest in use of native species for these reforestation projects has been increasing in the past decade. Blakesley et al. (2002) addressed the special importance of seed information for nursery planning in restoration projects that involve the use of a large number of local species. Time of collection, seed-handling procedures, germination pretreatments, and storage techniques are lacking for many tropical species (Francis, 2003). Storage also is a common problem for many tropical forest trees, since their seeds are recalcitrant or intermediate, meaning that they are sensitive to desiccation and often to low temperatures, conditions traditionally considered necessary for long-term seed storage (Vázquez-Yañes and Orozco-Segovia, 1990). There is an association between late-successional moist tropical forest trees with large, moist, nondormant seeds and desiccation sensitivity (Vázquez-Yañes et al., 2000; Dickie and Pritchard, 2002).

Few studies have been done on processing, handling, or storage of seeds of the PCW's native species. Foster (1982) found one peak of germination and two peaks of seed dispersal in phenology studies in a natural forest on Barro Colorado Island (BCI), in the center of the PCW. In a community level

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study of seed dormancy and germination on BCI, Garwood (1983) reported that mean length of time between sowing and germination for >50% of the fresh seeds of 157 woody dicot species was >4 weeks, and she recognized three germination syndromes: (1) a rapid-rainy syndrome, for seeds dispersed during the early rainy season, with a majority of the species being nondormant; (2) an intermediate-dry syndrome, for seeds dispersed during the dry season, with half of the species having an intermediate dormancy period (2–16 weeks); and (3) a delayed-rainy syndrome, for seeds dispersed during the late rainy season, with half of the species having a delayed dormancy period (≥16 weeks). Recently, Daws et al. (2005) studied traits of 225 BCI tree, shrub, and liana species related to desiccation sensitivity (recalcitrant versus orthodox). They found that even after correcting for phylogenetic dependence between taxa, desiccation-sensitive seeds were significantly larger, germinated faster, and allocated fewer resources (dry mass) to seed coat and/or endocarp than desiccation tolerant seeds.

In addition to the comprehensive studies of BCI species by Garwood (1983) and by Daws et al. (2005), which included seed mass and nursery tests, there have been a number of reports on germination patterns in natural conditions for species native to the PCW (Acuña and Garwood, 1987; Dalling et al., 1997; Garwood, 1986a; Garwood and Lighton, 1990; Kitajima and Augspurger, 1989; Silvera et al., 2003; Sork, 1985). A considerable amount of information for species that occur in the PCW comes from studies done in Costa Rica, Mexico, or Brazil (Lorenzi, 1998; Ramalho Carvalho, 1994; Salazar, 2000; Salazar and Soihet, 2001; Vázquez-Yanes and Orozco-Segovia, 1993). However, populations of widely distributed species may show significant geographical variability in germination responses among seed provenances (Vázquez-Yanes and Orozco-Segovia, 1993). Since local populations are the usual source for seeds in restoration projects, there is a clear need for information on germination responses from populations of the PCW. Information about seed ecology and management is needed to meet the objectives of conservation and sustainable projects in the PCW.

This study, at a regional scale, presents information about various aspects of the whole-seed biology of 100 tree species native to the PCW. For each species, it includes fruit collection/seed cleaning system, time of fruiting, seed mass, seed moisture content, dormancy/germination characteristics, and/or longevity in storage. This information is used to make management recommendations for nurseries that supply tree seedlings to use in restoration projects.

2. Site description

The PCW is defined as the geographic area, the surface and underground waters of which flow toward the Canal and/or are spilled into it or into its tributary lakes. The PCW encompasses 2892 km^2 of land that lie at 9°N latitude in the seasonal tropics. Most of the watershed is less than 300 m above sea level, but elevation rises to 1000 m on three peaks to the southwest and east (Condit et al., 2001). Both temperature and humidity are relatively high throughout the year. Mean annual temperature is 27 °C and varies relatively little throughout the year. Mean annual precipitation is high enough to sustain tall forest throughout the region, but there is a marked dry season from December through April (Ibáñez et al., 1999). Rainfall is higher, and the dry season shorter, on the Caribbean than on the Pacific side of the Isthmus (Condit et al., 2000). Annual rainfall varies from ca. 1600 mm/year on the Pacific coast, with a 4-month dry season from December to March, to >3000 mm/year on the Caribbean coast, with a 2–3-month dry season from January to March (Condit, 1998).

The fact that the rainy season to dry season in the seasonal tropics is a continuum calls for subjective judgment regarding division of the year into wet/dry seasons. On BCI, in the center of the isthmus, where total annual precipitation is ca. 2700 mm, rainfall is lowest in January, February, and March, begins to increase in April, plateaus in May–October, reaches the maximum in November, decreases from November to December (to about the level of the May–October plateau), declines sharply from December to January, and finally reaches the minimum in March (Croat, 1978). Based on these data, we recognized three seasons in this study: dry season, January–March; early rainy season, April–July; and late rainy season, August–December.

Most of the cities and agriculture land, mostly grassland for cattle, are located at lower elevations and on the drier Pacific side. These grasslands frequently burn during the dry season, but natural forests do not. The largest blocks of forest remain on the wetter Caribbean side of the isthmus. Most, or all, of the PCW forest is second growth and not more than 80–100 years old. Further, the forest has been subjected to major human disturbances over about the past 7000 years associated with indigenous American agricultural systems, colonization and settlement by Spaniards, and construction of the Canal (Condit et al., 2001).

The general structure of forests of the canal area is quite similar, except for small areas of mangrove, freshwater swamps, and mountain peaks. Large disturbances such as hurricanes and fires are absent; thus, individual treefalls and small windstorms are the sole natural source of canopy turnover. A closed canopy 20–40 m tall with emergent trees reaching 50 m in height and a dense understory of saplings, treelets, palms, and lianas can be found in well-drained sites (Condit et al., 2001). The majority of the watershed (90%) is classified as tropical moist forest in the Holdridge (1967) system. Small areas of wet ridges near the Atlantic are classified as wet and submontane forest, but these are not much different structurally from the moist forest (Condit, 1998).

The Missouri Botanical Garden produced a Flora of Panama that contained an estimated 2870 species of trees and shrubs, 855 of which occurred in the Panama Canal Zone, a strip 5 km wide along both sides of the canal (Condit et al., 2001). Pyke et al. (2001) reported 824 species of trees with a diameter at breast height ≥10 cm in 54 (1-ha) plots. Except for sites within 1–3 km of each other, no two forests are the same in terms of their dominant tree species, thus representing a regional flora with an exceptional β-diversity (Condit et al., 2001; Pyke et al., 2001). The abrupt change in species composition is why Panama is so rich in species. Many species are extremely rare, appearing in only one of 54 (1-ha) plots. However, only four species are endemic to Panama, and only one is restricted to the PCW (Condit et al., 2001). Seventy of our 100 study species occur in the 50-ha permanent plot on Barro Colorado Island (Condit et al., 1996).

3. Materials and methods

3.1. Species selection

We established a preliminary list of 130 species of trees native to the PCW with reforestation/restoration value and/or usefulness to rural people (Aguilar and Condit, 2001). Since number of species fruiting may vary tremendously from year to year, depending on amount of seasonal rainfall and on some other factors such as insect damage (Francis, 2003), the final set of species (Table 1) was dictated by nature. Frequent field checks indicated the occurrence of a good fruiting season for species on the list. For each of the 100 species, author, common name (in Spanish), family, reported fruiting period, month of collection, and number of trees from which fruits/seeds were collected are presented in Appendix A.

Pseudosamanea guachapele, *Dialium guianense*, *Guetarda foliacea*, *Lafoensia punicifolia*, *Beilschmiedia pendula*, and *Sapindus saponaria* were collected and germination assays run in 1993–1994. Methodology used for germination assays of these species was the same as that used for the other species reported in this paper except that studies on longevity, moisture content, and number of seeds per kg were not carried out in all cases.

3.2. Seed collection

Seeds were collected within the PCW and adjacent areas near the Pacific Ocean and Caribbean Sea, on both coastal sides of the canal corridor (block of forest east and west of the Canal). Seed collection was carried out from 1996 to 1999. Weekly fieldtrips were made to select seed trees and to monitor fruit set and degree of ripening. Most fruits were collected directly from the tree using a climbing system or a telescopic pole. Other fruits were collected from the ground if they were not decayed (Appendix B). Phenological data for individual tree species on nearby Barro Colorado Island (Croat, 1978; Foster, 1982) were used in organizing the collection effort. Collection and processing problems are species-driven, and many poorly known species in the tropics represent a challenge to handle (Francis, 2003). Thus, in each case trees were identified by number, their location recorded, and fruit/seed collecting and cleaning methods used. Seeds/diaspores were separated from the fruits and mixed.

The best method for collecting seeds was to use a telescopic pole, which allowed access to the crown of 88 (of 100) species of trees less than 20 m tall. Enough seeds of only 8 species were collected from the ground, and for 23 species both methods were needed. For 18 species, the trees had to be climbed to complete seed collection, 6 of which were only accessible by climbing (Appendix B). Unfortunately, seeds of *Platymiscium pinnatum* and *Couratari guianensis*, two species that required climbing to collect, did not germinate at all, probably due to inviability caused by insect attack.

For 75 species, fruits were collected from five or more healthy individuals that had fruits ripening at the same time, and for eight, six, three, and eight species fruits(s) were(was) collected from four, three, two, and one tree(s), respectively. Seeds of *Luehea speciosa* were collected from 30 individuals due to scarce fruit production (Appendix A).

For many species, exact timing of fruit maturation was unknown, and approximately 20% of those with fruiting phenology records were collected in a season different from that in which the fruits were reported to ripen. In agreement with data for canopy and understory trees from BCI (Foster, 1982), there were two peaks of fruiting: January–June and August–October. Only four species were collected in July, five in December, and one in November.

Seeds were collected from a total of 100 species, and for 94 of these results were obtained that allow discussion of length of germination time and dormancy. The species from which seeds were collected belong to 34 families (Appendix A). Families represented by the most species are Fabaceae (21, including all three subfamilies), Rubiaceae (8), Meliaceae (7), Tiliaceae *s. str.* (5), Bombacaceae *s. str.* (5), and Anacardiaceae (4).

3.3. Number of seeds per kg/seed mass

Following the recommended protocols of the International Seed Testing Association rules (ISTA, 1993), 8 groups of 100 seeds of 95 species were weighed and averaged to calculate the number of seeds per kilogram, after mixing seeds from parent trees. The number was also expressed as individual seed mass for comparison. We delimited six categories for seed size based on seed mass following Foster (1982) for all these species. In addition, we included four other species within these categories. Salazar (2000) reported seed mass for *Dipteryx panamensis*, and Pearson et al. (2002) reported it for *Alseis blackiana*. The seed mass category (1–10 g) for *Beilschmiedia pendula* and *Guettarda foliacea* was inferred from seed size and fruit type (drupes), respectively.

3.4. Moisture content

Moisture content for freshly collected diaspores of 94 species was calculated immediately after cleaning, following recommended protocols of the International Seed Testing Association rules (ISTA, 1993). Two replicates of 4–5 g were weighed, dried for 17 h at 103 °C, and then reweighed. Seeds larger than 1 cm were cut into smaller pieces for drying. Both diaspores (samaras) and seeds were evaluated for *Platymiscium pinnatum*. Moisture content of *Trattinnickia aspera* corresponds to seeds collected for the first time, which did not germinate at all, and germination data are for seeds from a second collection whose moisture content was not evaluated. *Tachigalia versicolor* moisture content is for the samaras

Table 1
Results of germination and other studies of seeds of 100 species native to the Panama Canal watershed

Species	Seeds/kg	Seed MC (%)	Mean LG (days)	SDT MLG (days)	MLG (days)	Total Germ (%)	SDT Germ (%)	Germ. C.V. (%)	First day	Last day	Longevity (months)
Adelia triloba	38873	6.43	11.2	13.7	11	72	9.7	13.5	8	49	+3
Albizia adinocephala	20555	8.9	10.5	6.9	7	77	4.2	5.5	4	45	+7
Alseis blackiana	5347593		36	23.9	24	50	10	20.0	24	108	+30
Amaioua corymbosa	105263	59.11	58.9	30.1	52	25	5	20.0	38	100	<1
Anacardium excelsum	300	34.76	11.6	4.8	14	51	6.6	12.9	10	17	4
Andira inermis	1616	57.2	60.3	33.6	42	55	27	49.1	31	164	<1
Annona spraguei	25363	20	117.6	94.5	73	14.8	1.3	8.8	24	283	5
Antirhea trichantha	59880	17.8	123.9	84.2	89	29	5.5	19.0	24	311	26
Apeiba aspera	62097	8.79	127.4	65.8	136	9	5.5	61.1	17	213	+6
Apeiba tibourbou	1545202	6.93	31	16.5	21	47	14	29.8	17	80	+15
Aspidosperma cruenta	551	79	30.5	18.3	25	20	2.4	12.0	13	90	<1
Beilschmiedia pendula						90			10	17	
Brosimun utile	182	67	32.9	11.6	29	77.5	7.5	9.7	17	101	2
Bursera simaruba	11376	11.41	3.8	3.8	3	38	3.7	9.7	6	27	+5
Byrsonima crassifolia			167.4	8.4	164	7[a]	2.7	38.6	161	184	
Calophyllum longifolium	73	41	17.1	8.3	15	42	11.2	26.7	5	40	<1
Calycophyllum candidissimum	1149590	10.27	11.4	1.5	7	76	5.3	7.0	10	45	+15
Carapa guianensis	20	79.7	32.7	31.7	21	38	9.6	25.3	12	159	
Cassia grandis	2830	18.8	8.5	8.9	9	43	13	30.2	8	43	+18
Castilla elastica	2035	45	12	5.3	12	86	3	3.5	3	38	<1
Cedrela odorata	36101	38.58	9.4	2.9	7	58	3.9	6.7	4	46	12–15
Ceiba pentandra	14971	7.46	4.5	0	4.5	71	4.2	5.9	8	8	+2
Chrysophyllum cainito	2902	41.5	22.9	7.4	20	76	5.5	7.2	14	76	8
Colubrina glandulosa	52459	12.06	67.7	44	61	65	7.9	12.2	12	166	+15
Copaifera aromatica	843	13.12	21	3.9	23	73	7.4	10.1	12	33	+7
Cordia alliodora	215227	9.7	17.5	0	17.5	3.5	1.3	37.1	21	21	<1
Couratari guianensis						0					
Cupania latifolia	13877	50.85	94.5	61.5	73	58	12	20.7	27	300	1
Dalbergia retusa	12315	24.3	17	8.7	16	77	11	14.3	11	60	12
Dendropanax arboreus	62485	50	23.8	5.5	21	44	5.5	12.5	10	66	<1
Dialium guianense	2919	6.06	32.5	16.9	30	2.8	1	35.7	12	57	+2
Diphysa robinioides	59075	11.81	11	4.7	9	99	0.8	0.8	5	33	+9
Dipteryx oleifera		16.42	33.3	12.8	38	27	13	48.1	14	60	<1
Enterolobium cyclocarpum	1238	12.03	131.2	113.4	75.5	36	13	36.1	4	339	+15
Enterolobium schomburgkii	14183	8.28	209.5	127.8	197	38	10	26.3	4	397	+18
Erythrina fusca	2514	14.08	25.8	21.6	16	65	6	9.2	5	89	+18
Faramea occidentalis	2593	46.73	167.1	53.7	141	66	3.4	5.2	89	298	<1
Ficus insipida	825593	12.2	34.7	29.1	22	18.5	4	21.6	19	109	7
Genipa americana	7289	36.5	28.7	12.9	24	85	5.3	6.2	27	99	3
Guarea grandifolia	2034	26.7				0					<1
Guarea guidonia	4176	30.4	71.2	39.19	56	49	13	26.5	31	241	<1
Guazuma ulmifolia	224090	11.6	52.5	40.5	35	20	6.1	30.5	10	143	+18
Guettarda foliaceae			253	134	134	22.5	5.3	23.6	60	180	
Gustavia superba	80	53.5	30.6	6.7	31	76	13	17.1	24	45	2
Hampea appendiculata	4860	44.9	12.5	5	10	50	7.9	15.8	12	39	2
Hasseltia floribunda	43589	63.3	12.8	7.5	15	40	12	30.0	11	67	<–1
Heisteria concinna	3378	30	37.9	14.8	34	40	5.9	14.8	24	115	4
Hura crepitans	829	8.7	10.8	5.8	7	87	4.3	4.9	10	31	+15
Hyeronima alcheorneoides	123762	28.5	61.1	35.5	52	61	4.6	7.5	20	223	3
Hymenaea courbaril	191	15.3	21.1	8.97	17	52	1.9	3.7	13	62	4
Inga punctata	2425	51.65	11.5	3.4	10	83	13	15.7	13	27	<1
Inga spectabilis	317	46	11.2	12.7	8	91	2.1	2.3	5	46	<1
Jacaranda copaia	116805	33.3	20.7	5	22	89	4.1	4.6	18	39	+24
Lacmellea panamensis	1616	62.56	35.5	9.1	29	75	12	16.0	18	109	1
Lafoensia punicifolia	18867	12.11	3.7	1.3	4	79	22.9	29.0	4	14	+7
Lindackeria laurina	11312	30	44.3	19.9	39	39	3.9	10.0	27	154	<–1
Lonchocarpus latifolius	13757	9.63	24.4	11.1	21	54	11	20.4	17	74	+10
Luehea seemannii	445186	11	122.3	99.7	76.5	38	12	31.6	10	311	+15
Luehea speciosa	216217	18.9	31.3	26.3	14.5	22	9.7	44.1	10	94	+18
Margaritaria nobilis	17884	22	172.9	32.2	176	5.8	3.2	55.2	117	208	<1
Miconia argentea	11682243	13.12	31.5	22.7	24	57	13	22.8	13	105	+15
Miconia minutiflora	4545454		62.4	45.4	51	45	18	40.0	27	187	+5

Table 1 (*Continued*)

Species	Seeds/kg	Seed MC (%)	Mean LG (days)	SDT MLG (days)	MLG (days)	Total Germ (%)	SDT Germ (%)	Germ. C.V. (%)	First day	Last day	Longevity (months)
Ochroma pyramidale	145985	8.8	132.7	73.7	118	21	4.6	21.9	19	284	+14
Ormosia macrocalyx	2096	13.5	62.5	36.7	59	49	3	6.1	10	136	+36
Pachira quinata	37464	12.8	7.9	4.5	10	44	5.2	11.8	15	44	5
Phoebe cinnamomifolia	4612	39.65	23.4	9.8	18	47	1.7	3.6	14	63	<1
Platymiscium pinnatum	3351 (Samara) 5365 (seeds)	30.9				0					
Posoqueria latifolia	2534	59.8	98.9	62.9	86	68	3.3	4.9	26	285	2
Prioria copaifera	17	48.6	32.9	12.6	32	50	7.1	14.2	21	70	<1
Protium panamense	1636	24.5	28.8	8.1	30	7	5.7	81.4	25	46	<1
Protium tenuifolium	4719	30.25	9.1	5.71	8	85	7.6	8.9	4	46	4
Pseudobombax septenatum	7831	41	9.1	3.1	9	86	10.8	12.6	5	33	+6
Pseudosamanea guachapele	32362	10	84.3	72	81	13	3.9	30.0	14	154	+11
Pterocarpus rohrii	3408	25.6	23.9	5.9	21	77	5.9	7.7	24	52	+8
Quararibea asterolepis	1418	47.01	31.5	11.1	26	38	2.8	7.4	15	71	1
Sapindus saponaria	1664	7.75	77.6	61.5	74	5.25	3.5	66.7	10	189	+9
Sapium glandulosum	23095	25.1	77.1	77.4	31	70	2.4	3.4	20	272	15
Schefflera morototoni	58565	14.2	39.8	11.1	35	65	2.9	4.5	38	94	3
Spondias mombin	458	60.95	79.1	110	148	9[a]	5.5	61.1	10	234	+30
Spondias radlkoferi	240	58.5	119.7	84.9	83	5	4.1	82.0	38	261	+12
Sterculia apetala	780	20.64	13.1	4.99	9	37	3.6	9.7	12	27	15
Swietenia macrophylla	1351	42.2	20.9	6.36	21	58	3.4	5.9	17	52	6
Tabebuia guayacan	51743	14.8	24	8.41	21	61	5.8	9.5	24	84	13
Tabebuia rosea	30303	21.42	7.8	3.1	11	83	4.8	5.8	7	21	11
Tachigalia versicolor	1140 (Samara with wing cut)	13.2	34.9	10.97	35	50 (seeds)	9.8	19.6	24	66	3
Tapirira guianensis	2598	23.6	12.7	7.6	14	52.5	4.3	8.2	10	82	<1
Terminalia amazonia	381862	12.9	26	42.5	21	3	3.3	110.0	24	60	
Trattinnickia aspera	5248[b]	35.1	63.6	17.8	58	87	14	16.1	42	145	
Trema micrantha	356697	9.5	76.6	37.1	68	38	2.2	5.8	36	247	26
Trichilia hirta	17391	9.2	14	2.8	14	83	3.5	4.2	17	38	12
Trichilia tuberculata	4606	40	34.4	21.9	30	11	2.6	23.6	12	89	<1
Trichospermum galeottii	454545	15.64	52.6	42.6	31	15	4.9	32.7	20	222	12
Triplaris cumingiana	33318 (Capsule with wings cut)	12				0					
Vantanea depleta	259	18.1	202.8	51.9	203	31	12	38.7	103	304	+5
Virola sebifera	1933	40	88	18.2	84	12	3	25.0	55	132	−1
Virola surinamensis	346	38.8	26.4	7.9	24	45	9.3	20.7	20	55	10
Vochysia ferruginea	65805	21.2	21.8	14.3	18	35	4.6	13.1	11	74	+2
Xylopia aromatica	43103	14.4	83.9	25	83	9	5.5	61.1			+3
Xylopia frutescens	2088	16.65	147	176	100	1.25	1	80.0	52	282	−1
Zanthoxylum panamense	28985	21.2				0					

Seeds/kg: number of seeds (or diaspores)/kg; Seed MC: fresh seed moisture content; Mean LG: mean length of germination time; SDT MLG: standard deviation of the mean length of germination time; MLG: median length of germination time; Total Germ: total germination percentage; SDT Germ: standard deviation of the total germination percentage; Germ. C.V.: coefficient variation of the total germination; first day: first day of germination; last day: last day of germination; longevity: number of months that seeds remained viable (total germination >5%) stored at 20 °C and 60% RH in paper bags. "+" is used in cases where longevity assays were ended due to lack of seeds and germination in final test was >5%. ISTA (1993) rules were followed.

[a] Germination values from assays in 50% of direct sun.

[b] Data from seeds of a prior collection, which did not germinate at all.

(diaspores) of the five trees from which they were collected, and germination data are for seeds from only two trees, since those from the other three trees appeared not to be viable. Thus, moisture content does not correspond to the unit evaluated in germination.

3.5. Germination tests

Seeds of 100 species were evaluated in germination tests done in Panama. Fruits collected from all trees were cleaned, and dispersal units (diaspores) were mixed and sown within the 1–7 days after cleaning. Throughout this paper, "seed" means a true seed or a diaspore. Species whose diaspores included endocarps of drupes were *Anacardium excelsum*, *Andira inermis*, *Beilschmiedia pendula*, *Dipteryx oleifera*, *Guettarda foliacea*, *Spondias mombin*, and *S. radlkoferi*. Only diaspores of *Spondias* spp. were multiseeded. Although multiple germination occurred in the two *Spondias* spp., it was very infrequent; thus, the count was done only once per diaspore (i.e. counted as one).

Four replicates of 100 seeds were sown on oven-sterilized sand in plastic trays. Large seeds were pushed into the sand for one-half of their thickness. Small seeds were covered by 3–5 mm of sand, but after watering most of them became partially uncovered. Thus, they were exposed to light. However, due to shortage of seeds for *Calophyllum longifolium*, *Lonchocarpus latrifolius*, *Luehea speciosa*, *Dipteryx oleifera*, and *Gustavia superba*, we sowed 5 replicates of 25 seeds, and for *Hymenaea courbaril* we sowed 4 replicates of 50 seeds. Two species, *Carapa guianense* and *Prioria copaifera*, had large seeds that did not fit into the trays; thus, we sowed 4 replicates of 50 seeds directly into pots. Conditions in the nursery were similar to those in commercial production nurseries in Panama, i.e. ambient temperature (25–31 °C), 30% full sunlight, and watering twice daily with an automated sprinkler system. The studies were done without any seed pretreatment to learn about natural dormancy. Exceptions were removal of the aril from seeds of *Sapium glandulosum*, *Virola surinamensis*, *V. sebifera*, and *Lindackeria laurina* and of the wing (by cutting) from those of *Swietenia macrophylla*, *Pterocarpus rorhii*, and *Aspidosperma cruenta*, to avoid fungal growth and to economize space.

Germination, defined as radicle emergence, was monitored weekly until 4 weeks without germination (after a clear peak occurred) to a maximum of 10 months, except for *Enterolobium cyclocarpum*, *E. schomburgkii*, and *Faramea occidentalis*, which were monitored for 11 months. Total germination, standard deviation of total germination, and coefficient of variation of total germination between replicates were calculated. Median (MLG) and mean (Mean LG) lengths of germination period for all seeds that germinated were calculated as measures of dormancy. Standard deviation of mean germination time (STD MLG) and total germination time (STD Germ) (time until the last seed that did so germinated) were calculated. Seeds with a fully-developed embryo and a median length of germination time (MLG) $\leq$30 days were considered to be nondormant, and those with an underdeveloped or a fully-developed embryo and an MLG $>$ 30 days or an underdeveloped embryo and a MLG $\leq$ 30 days were considered to be dormant (Baskin and Baskin, 2004).

In some cases where germination percentages were low and number of seeds collected sufficient, we tested pretreatments to break dormancy, using mechanical scarification for *Colubrina glandulosa* (Ramalho Carvalho, 1994), *Pseudosamanea guachapele*, *Enterolobium cyclocarpum*, *E. schkomburgkii* (Salazar, 2000), *Cassia grandis*, and *Sapindus saponaria*; submergence for 2 min in warm water (80 °C) for *Apeiba aspera*, *A. tibourbou*, and *Luehea seemannii* (Acuña and Garwood, 1987), then allowing them to cool to room temperature before sowing; and the latter treatment followed by 24 h in running tap water for *Guazuma ulmifolia* (Salazar, 2000).

3.6. Longevity studies

Ninety species were evaluated for seed longevity. Seeds were stored in paper bags at 20 °C and 60% relative humidity. Storage conditions were chosen considering the best conditions in many local field projects, where cold rooms are not available. Since many seeds had high moisture content, paper bags were preferred to plastic ones to avoid fungal growth. Fungicide (Vitavax) was applied to *Copaifera aromatica*, *Trema micrantha*, and *Virola surinamensis*. For each species with enough seeds collected, 5 replicates of 20 seeds were sown each month in the same nursery conditions described above for a maximum of 36 months. Viability, based on germinability, of stored seeds was monitored until germination for a species had decreased to $<$5% or until seeds in the lot were used up.

We considered seeds with a viability period of 1 month or less to be very short-lived, those with a viability period between 1 and 4 months short-lived, and those with a viability period more than 4 months long-lived. Species whose final germination percentage was $>$5% after 4 months of storage, but for which longevity studies were not continued due to lack of seeds, were considered to be long-lived. Species with initial total germination $<$10% were not considered for longevity categories. *Carapa guianensis* and *Cordia alliodora* were assigned to very short-lived and long-lived categories, respectively, based on reports by Salazar (2000) and Tweddle et al. (2003).

3.7. Month of peak germination and relevance to nursery management

Following Blakesley et al. (2002), we calculated the month of peak germination for each species, taking into consideration month of collection and median length of germination period. For example, seeds collected in November with a MLG of 62 days will have a peak of germination in January. Then, we graphed the number of species that had their peak of germination for each month. Both field work needed for collection and nursery work have been analyzed to predict nursery management constraints.

3.8. Statistical analyses

Comparisons between sowing pretreatments were done using one-way analysis of variance (ANOVA) of final germination percentages in each treatment. Linear model regressions were conducted for *Spondias mombin* to establish the relationship, if any, between total germination and length of storage period. Box plots showing median, quartiles, outliers, and extremes were generated to explore relationships between month of collection, MLG, seed size, dispersal time, longevity, and MC, after establishing categories of the latter four variables. Differences between these categories were tested using the Tukey HSD test. A scatter plot was generated to explore the relationship between MC and seed mass. Pearson correlation coefficients were calculated between all variables for germination studies. All statistical tests were carried on with Statistical software SPSS® Base 12 (2003).

4. Results

4.1. Number of seed per kg/seed mass

Number of seeds per kilogram was obtained for 95 of the 100 study species (Table 1), and it ranged from 17 to 11,682,243. Expressed as seed mass, the frequency distribution is remarkably right skewed (skewness 6.21) and peaked (kurtosis 39.69), with a mean of 1.96 g and a median of 0.13 g (Table 2).

Table 2
Descriptive statistics for variables measured in germination studies for 100 species native to the Panama Canal Watershed

	Seed weight (g)	MC (%)	Total germination percentage (days)	DST GER (%)	Mean LG (days)	DST MLG (days)	MLG (days)	Total length of germination (days)
N	95	94	100	94	94	94	94	94
Mean	1.96	27.73	45.37	6.80	51.92	29.10	41.97	119.14
S.E. of mean	.828	1.91	2.81	.49	5.35	3.55	4.51	9.73
Median	.128	21.31	46.00	5.40	31.50	13.30	24.00	83.00
S.D.	8.07	18.48	28.13	4.71	51.86	34.41	43.73	94.33
Variance	65.20	341.43	791.29	22.22	2689.55	1183.99	1912.78	8898.77
Skewness	6.21	.87	−.06	1.55	1.73	1.96	1.99	1.02
S.E. of Skewness	.247	.25	.24	.249	.25	.249	.25	.25
Kurtosis	39.69	−.13	−1.13	3.47	2.81	4.01	3.77	−.05
S.E. of Kurtosis	.490	.49	.48	.49	.49	.49	.49	.49
Range	58.82	73.64	99.0	26.2	249.30	176.00	200.00	389
Minimum	.0001	6.06	.0	.8	3.70	.00	3.00	8
Maximum	58.82	79.70	99.0	27.0	253.00	176.00	203.00	397
Percentiles								
25	.019	12.10	20.25	3.47	16.25	6.61	14.37	45.75
50	.128	21.31	46.00	5.40	31.50	13.30	24.00	83.00
75	.60	41.00	70.75	9.85	72.55	39.52	56.50	181.00

MC: seed (or diaspore) moisture content; DST GER: standard deviation of total germination; Mean LG: mean length of germination period; MLG: median length of germination period; DST MLG: standard deviation of germination period.

We grouped 99 (95 + 4, see Section 3) of the species into seed mass categories: 5 species (5.1%) had seeds that weighed less than 0.001 g (>1,000,000 seeds/kg); 12 (12.1%) 0.001–0.01 g (1,000,000–100,000 seed/kg); 30 (30.3%) 0.01–0.1 g (100,000–10,000 seeds/kg); 32 (32.3%) 0.1–1 g (10,000–1000 seeds/kg); 16 (16.2%) 1–10 g (1000–100 seeds/kg); and 4 (4%) >10 g (<100 seeds/kg) (Fig. 1). There is a slight trend for seeds dispersed in the early and late rainy season to be larger than those dispersed in the dry season, although the differences were not significant (Tukey HSD test, $p > 0.05$) (Fig. 2). All species with seeds >0.85 g are outliers or extremes.

4.2. Moisture content

Moisture content of freshly-collected diaspores ranged from 6.06 to 79.7% (Table 1). Frequency distribution of moisture content was right skewed (skewness 0.87), with a mean of 27.7% and a median of 21.3% (Table 2). Seed moisture content was correlated with seed mass (Pearson correlation coefficient 0.349, $p < 0.01$) (Table 3), and the majority of seeds <0.1 g was drier than the larger ones (Fig. 3). Species dispersed in the dry season had lower moisture content than those dispersed in the late rainy season (Tukey HSD, $p < 0.05$) (Fig. 4).

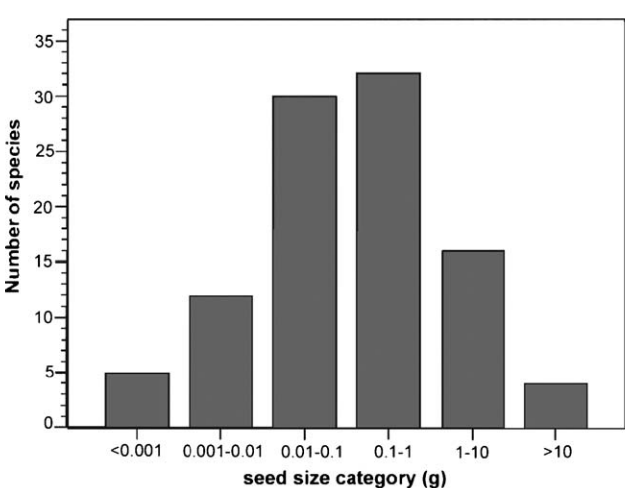

Fig. 1. Seed size distribution for 99 species native to the Panama Canal watershed.

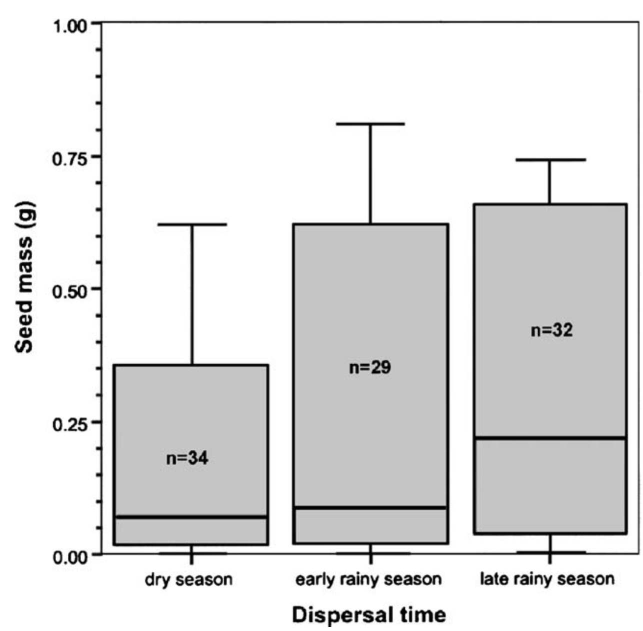

Fig. 2. Box plots showing median and quartiles of seed mass of species grouped by season of dispersal/collection. Dry season, January–March; early rainy season, April–July; late rainy season, August–December (Tukey HSD test, $p > 0.05$). All species with seeds >0.85 g were outliers or extremes.

Table 3
Pearson correlation coefficients between variables measured in germination studies of 100 species native to the Panama Canal Watershed

	MC (%)	Mean LG	SDT MLG	Total germination percentage	Coefficient variation of total germination	MLG	Total length of germination
Seed weight							
Pearson correlation	**.349****	−.060	−.051	.008	.004	−.042	−.041
Significance (1-tailed)	**.000**	.286	.316	.468	.969	.346	.351
N		91	91	95	91	91	90
MC (%)							
Pearson correlation		−.075	−.090	.128	.073	.001	−.009
Significance (1-tailed)		.241	.198	.109	.495	.497	.467
N		90	90	94	90	90	89
MLG							
Pearson correlation			**.793****	**−.454****	**.349****	**.909****	**.843****
Significance (1-tailed)			**.000**	**.000**	**.001**	**.000**	**.000**
N			**94**	**94**	**94**	**94**	**93**
DST MLG							
Pearson correlation				**−.452****	**.438****	**.674****	**.838****
Significance (1-tailed)				**.000**	**.000**	**.000**	**.000**
N				**94**	**94**	**94**	**93**
Total germination percentage							
Pearson correlation					**−.669****	**−.412****	**−.388****
Significance (1-tailed)					**.000**	**.000**	**.000**
N					**94**	**94**	**94**
Coefficient variation of total germination							
Pearson correlation						**.0309****	**.291****
Significance (1-tailed)						**.002**	**.005**
N						**94**	**93**
Median length of germination							
Pearson correlation							**.782****
Significance (1-tailed)							**.000**
N							**93**

Significant correlations are highlighted in bold. MC: seed (or diaspore) moisture content; Mean LG: mean length of germination period; MLG: median length of germination period; DST MLG: standard deviation of length of germination period; *N*: sample size. Bold numbers indicate significant correlations. **Correlation is significant at the 0.01 level (1-tailed).

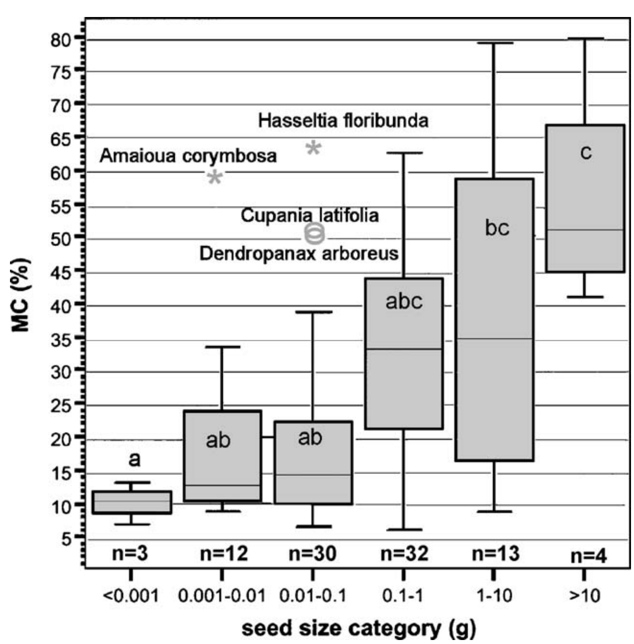

Fig. 3. Box plots showing median, quartiles, outliers (○), and extremes (*) of seed moisture content (MC) of 94 species grouped by seed size. Letters indicate subsets with significant difference (Tukey HSD test, $p < 0.05$).

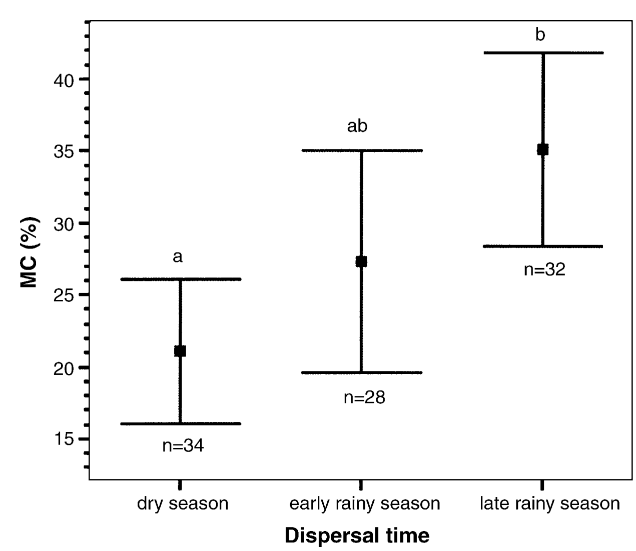

Fig. 4. Seed (or diaspore) moisture content of species grouped by dispersal season. Error bars show 95% CI of the mean. Letters indicate subsets with significant difference (Tukey HSD test, $p < 0.05$).

Table 4
Germination of species for which pretreatments to break dormancy were applied and of those whose germination increased after dry storage

Species	Pretreatment to break dormancy	With pretreatment		Control	
		Germination (%)	MLG (days)	Germination (%)	MLG (days)
Colubrina glandulosa	Mechanical scarification. Sandpaper seeds gently until the brightness is gone. Germination in shade (3% of direct sun)	76 ± 10 (NS)	15.2 ± 4.3	65 ± 7.9	67.7 ± 44
Enterolobium cyclocarpum	Mechanical scarification. Filed seed on lateral side	$94 \pm 3^{***}$	4 ± 0	36 ± 13	131.2 ± 113.4
E. schomburgkii	Mechanical scarification. Filed seed on lateral side	$79 \pm 6.9^{***}$	6.8 ± 5.8	38 ± 10	209.5 ± 127.8
Apeiba aspera	Submergence in water at 70 °C for 10 min	$74 \pm 12^{***}$	49 ± 48	9 ± 5.5	127.4 ± 65.8.
A. tibourbou	Submergence in water at 70 °C for 10 min	28 ± 9.7 (NS)	24.5 ± 7.3	47 ± 14	31 ± 16.5
Luehea seemannii	Submergence in water at 70 °C for 10 min	62^{**}		38 ± 12	122.3 ± 99.7
Guazuma ulmifolia	Submergence in water at 70 °C for 2 min, followed by washing in running water	$43 \pm 12.5^{**}$	14 ± 15	20 ± 6.1	52.2 ± 40.5
Sapindus saponaria	Mechanical scarification. Filed testa	63	14.7 ± 24.9	5.25 ± 3.5	77.6 ± 61.5
Pseudosamanea guachapele	Mechanical scarification. Cut testa opposite to micropyle	84	5.4 ± 9.5	13 ± 3.9	84.3 ± 72
Cassia grandis	Mechanical scarification. Filed testa	44 ± 5.3 (NS)	7.4 ± 7.4	43 ± 13	8.5 ± 8.9
Spondias radlkoferi	One month of dry storage	$41 \pm 13^{***}$	45.3 ± 21.9	5 ± 4.1	119.7 ± 84.9
Spondias mombin	30 months of dry storage	$43 \pm 12^{**}$	17.5 ± 7.4	9 ± 5.5	79.1 ± 110

Differences in germination tested using one-way ANOVA; NS: non significant; $^{**}0.01 \geq p > 0.001$; $^{***}0.0001 \geq p$.

4.3. Germination tests

Germination ranged from 0 to 99%, with 46 species (46%) having a germination percentage $\geq$50 (Table 1). Standard deviation of total germination ranged from 0 to 27%. Coefficient of variation calculated for species that germinated ranged from 0.8 to 100%; 47 species (50%) had a coefficient of variation <15% (Table 3).

Mechanical scarification increased germination percentages of seeds of *Colubrina glandulosa*, *Sapindus saponaria*, *Pseudosamanea guachapele*, *Enterolobium cyclocarpum*, and *E. schomburgkii*. Submergence in warm water (70 °C) increased germination percentages of *Apeiba aspera*, *Luehea seemannii*, and *Guazuma ulmifolia*. However, this same treatment did not improve germination of seeds of *A. tibourbou* (Table 4).

Table 2 summarizes statistics and Table 3 correlations for seed characteristics and germination variables. With the exception of total germination percentage, all variables have a right-skewed distribution. Although correlated between themselves, seed mass and seed moisture content are not correlated with any of the germination variables. Mean, median, and standard deviation of length of germination period and coefficient of variation of total germination percentage are positively correlated, and they are negatively correlated with total percent germination.

Mean (Mean LG) and median (MLG) lengths of germination period were 3.7–253 and 3–203 days, respectively. The Pearson correlation coefficient between mean and median length of germination period was 0.91 ($p < 0.01$). Total length of germination period ranged from 8 to 397 days, with a mean of 119 days and a median of 83 days. The standard deviation of length of germination period ranged from 0 to 176 days, with a mean of 29.10 days and a median of 13.3 days. The Pearson correlation coefficient between standard deviation of length of germination period (STD MLG) and total length of germination was 0.84 ($p < 0.01$) (Tables 2 and 3). Seeds of 45 (47.9%) of the 94 species were dormant, and 49 (52.1%) were nondormant. Species dispersed in the late rainy season had a higher MLG than those dispersed in the early rainy and dry seasons (Fig. 5). Forty-eight species (51%) had uniform germination (i.e. STD MLG $\leq$ 14 days) (Table 1).

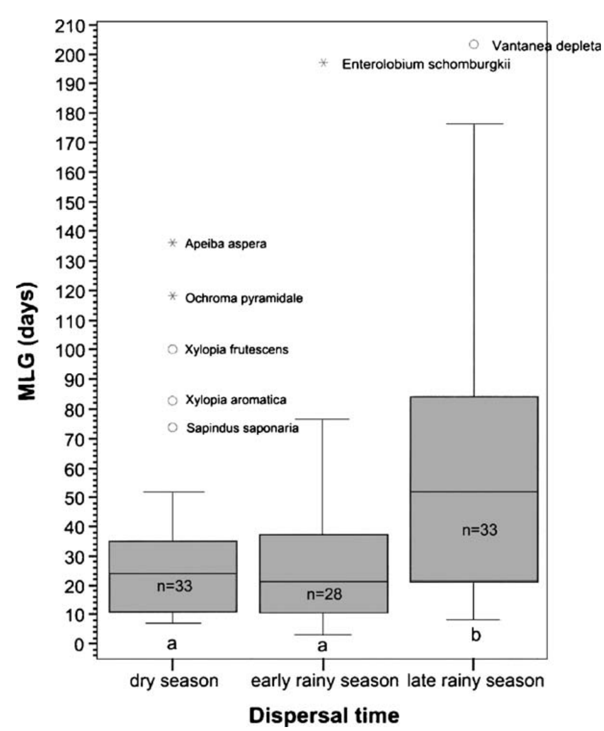

Fig. 5. Box plots showing median, quartiles, outliers (○), and extremes (*) of median length of germination period (MLG) for the species groups by dispersal season. Letters indicate subsets with significant difference (Tukey HSD test, $p < 0.05$).

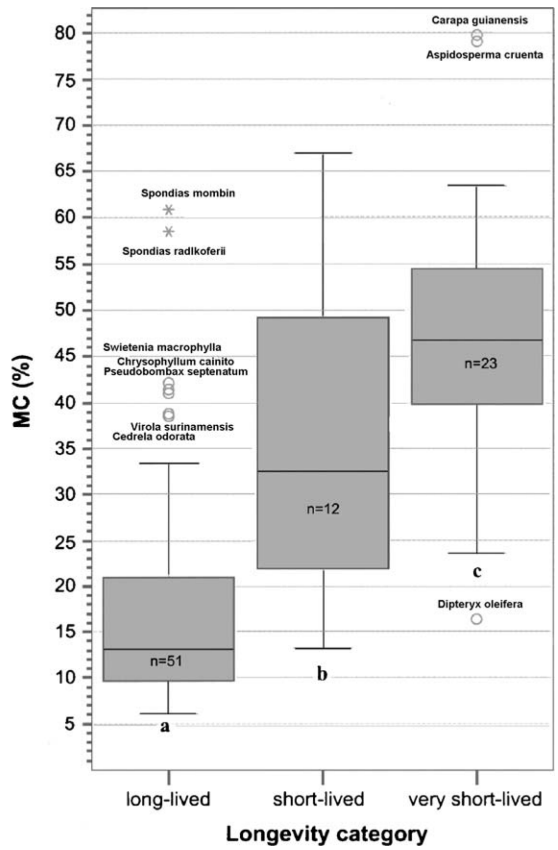

Fig. 6. Box plots showing median, quartiles, outliers (○), and extremes (*) of seed moisture content of study species grouped by longevity category. Very short, ≤1 month for germination to decrease to less than 5%; short, 1–4 months; long, >4 months. Letters indicate subsets with significant difference (Tukey HSD test, $p < 0.05$).

4.4. Longevity studies

Longevity ranged from 0.5 to 36 months (Table 1). *Byrsonima crassifolia*, *Cordia alliodora*, *Guarea grandifolia*, *Margaritaria nobilis*, *Protium panamense*, *Terminalia amazonia*, *Xylopia aromatica*, and *X. frutescens* had initial germination <10%. Based on information in the literature, *Byrsonima crassifolia*, *C. alliodora*, and *X. aromatica* were considered to be long-lived and *Carapa guianense* and *G. grandifolia* very-short lived (Geilfus, 1994; Salazar, 2000; Tweddle et al., 2003). A total of 89 species was assigned to a category: 54 (60.7%) of the species had long-lived seeds, 12 (13.5%) short-lived seeds, and 23 (25.8%) very short-lived seeds. Moisture content increased significantly from long-lived to very short-lived seeds (Fig. 6). Short and very short-lived seeds tended to be larger, but the differences were not significant (Tukey HSD test, $p > 0.05$). The proportion of very short-lived seeds dispersed in the rainy season was higher than it was in either the dry season or the early rainy season (Fig. 7).

In 88 of the 90 species, viability decreased with time of storage. However, seeds of *Spondias mombin* and *S. radlkoferi* had significantly higher germination percentages and germinated faster after dry storage at 20 °C than fresh seeds (Table 4, Fig. 8).

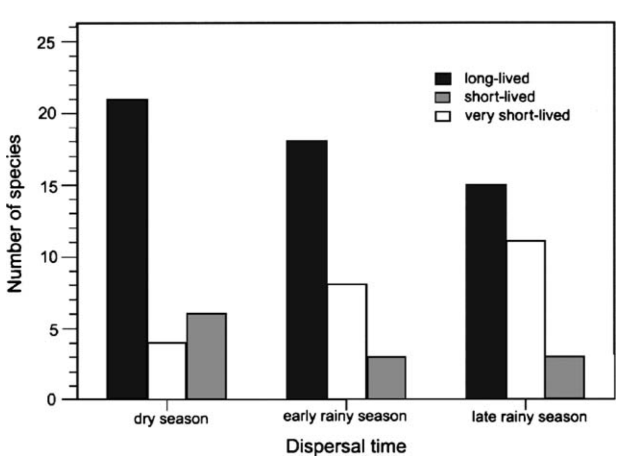

Fig. 7. Longevity of species grouped by dispersal season.

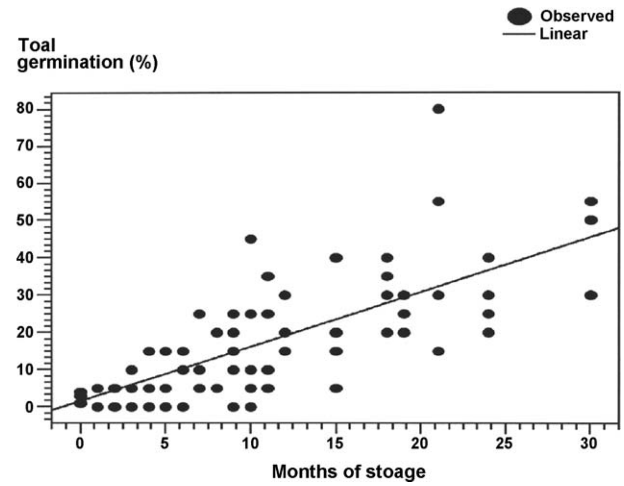

Fig. 8. Germination of seeds of *Spondias mombin* after different periods of storage in paper bags at 20 °C and 60% RH. Linear regression ($R^2 = 0.567$, $p < 0.0001$), $B = 1.463$, $\beta = 0.7528$, S.E. = 0.1334.

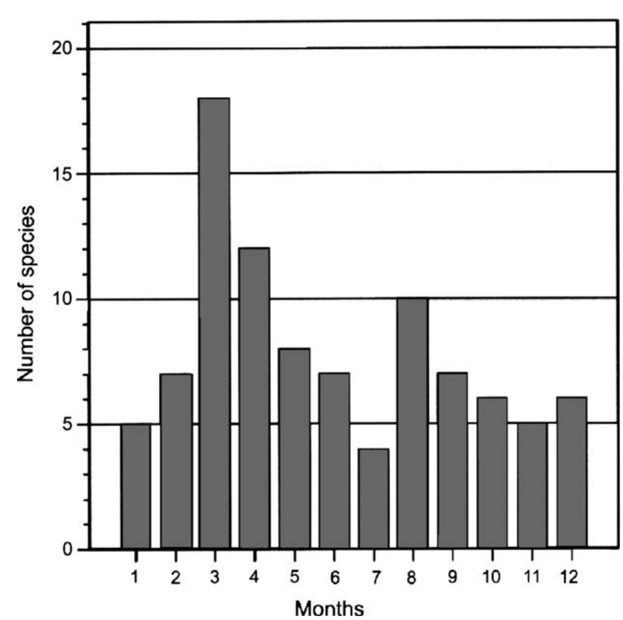

Fig. 9. Number of species whose peak of germination (calculated based on month of seed collection and median length of germination period) of non-pretreated seeds occurred in each month.

4.5. Month of peak germination and relevance to nursery management

The number of species whose peak of germination fell in each month is shown in Fig. 9. Months with the most species in their germination peak, March and August, coincided with peaks of seed collection.

5. Discussion

5.1. Germination data at the species level

There are only a few or no reports on seed germination for most of the study species, and this is particularly true for Panamanian populations of them (Acuña and Garwood, 1987; Augspurger, 1986; Daws et al., 2006; Garwood, 1986a,b; Garwood and Lighton, 1990; Ibáñez et al., 1999; Kitajima and Augspurger, 1989; Pearson et al., 2002; Sork, 1985). For 18 of the 94 species for which we present germination data, there appears to be no previous information related to seeds and germination at the species level: *Adelia triloba*, *Albizia adinocephala*, *Amaioua corymbosa*, *Antirhea trichantha*, *Aspidosperma cruenta*, *Beilschmiedia pendula*, *Brosimun utile*, *Copaifera aromatica*, *Cupania latifolia*, *Guetarda foliacea*, *Inga spectabilis*, *Lonchocarpus latifolius*, *Luehea speciosa*, *Miconia minutiflora*, *Phoebe cinnamomifolia*, *Protium panamense*, *Trattinnickia aspera*, and *Xylopia aromatica*. For another 19 species, the only information of this kind seems to be that of Garwood (1983).

Some of the germination data presented by Garwood (1983) were obtained with very few seeds, and in many cases replicates were sown in different months of the year. Mean period of time for germination between replicates varied enormously in some species. Seeds were subjected to environmental differences throughout maturation, increasing chances for different germination responses due to preconditioning in seeds (Baskin and Baskin, 1998a). Our results showing that seeds of *Calophyllum longifolium*, *Posoqueria latifolia*, and *Virola surinamensis* are dormant agree with only one of the time-replicates in Garwood's data. Seeds of *Prioria copaifera*, collected from the ground in both studies, were less dormant in our experiments for seeds sown in July (Mean LG = 32.9 days) than reported by Garwood (1983) for seeds sown in April (Mean LG = 64 days). The unknown time these seeds had been on the ground, as well as seasonal and annual climate variations, might explain some of the differences.

Our results for germination percentages and MLG are similar to those for 27 of the 75 species reported in the literature: 20 of Panamanian provenance, *Annona spraguei*, *Faramea occidentalis*, *Ficus insipida*, *Heisteria concinna*, *Lindackeria laurina*, *Margaritaria nobilis*, *Sapium glandulosum*, *Spondias mombin*, *S. radlkoferi*, *Trema micrantha*, *Vantanea depleta*, *Virola sebifera*, *Xylopia frutescens*, *Hampea appendiculata*, *Hasseltia floribunda*, *Protium tenuifolium*, *Pterocarpus rorhii*, *Quararibea asterolepis*, *Tabebuia guayacan* (Garwood, 1983), and *Miconia argentea* (Dalling and Wirth, 1998); and seven of non-Panamanian provenance, *Byrsonima crassifolia* (Geilfus, 1994; Vega et al., 1983), *Virola surinamensis* (Piña-Rodrigues and Figliolia, 2005), *Dialium guianense* (Vieira et al., 1996; Lorenzi, 1998), *Castilla elastica* (González, 1991), *Erythrina fusca* (Francis and Rodríguez, 1993; Lorenzi, 1998), *Tapirira guianense*, and *Trichilia hirta* (Lorenzi, 1998).

We suggest that differences between values reported here and those in other studies might be related to differences in initial seed MC, but MC has been reported for seeds of only a few species. Collection methods and manipulation of seeds between field and nursery or laboratory, selection of well-formed seeds, and laboratory procedures also might explain some of the differences. Seeds of *Dendropanax arboreus* from Costa Rica were reported to germinate to lower percentages (13–28%) (Salazar, 2000) and to have lower MC (26%) (González, 1991) than those in our study, which germinated to 44% and had a MC of 50%. Our results for *Virola surinamensis* (MC = 38.8%, Germ = 48%) differ from those reported by Cunha et al. (1995) for seeds of this species from Brazil (MC = 26.5%, Germ = 29%). Garwood (1983) reported yet higher germination (20–100%) for the same species from Barro Colorado Island, Panama. *Vochysia ferruginea* germinated to 35% in our study, while germination reported by González (1991), Rodríguez et al. (1997), and Salazar (2000) for selected seeds of this species from Costa Rica ranged from 80 to 90%. However, seeds in both populations were nondormant.

Most information about *Colubrina glandulosa* is for variety *reitzii*, from South America, and it is reported to have dormant (Queiroz, 1982; Ramalho Carvalho, 1994) or nondormant (Lorenzi, 1998) seeds. Our results with *C. glandulosa* var *glandulosa* indicate clearly that the seeds are dormant, due to a water-impermeable seed coat (Table 4).

At least a portion of the seeds of *Chrysophyllum cainito* from Costa Rica seems to be dormant (Salazar, 2000), while our results with Panamanian seeds clearly show that they are nondormant. *Hyeronima alcheornoides* is a colonizer species reported to have nondormant seeds (Garwood, 1983; Gonzalez, 1992) or to have "stepped" germination (Flores, 1993a). Our experiments show clearly that the seeds are dormant (MLG = 52 days). Frequently, populations of the same species with a wide geographic range show significant variability in seed viability and germination (Vázquez-Yañes and Orozco-Segovia, 1990).

Only two species, *Spondias mombin* and *S. radlkoferi*, had higher germination percentages and better synchrony after dry storage, which is described as afterripening, a progressive loss of dormancy as a function of temperature and time in dry environments (Fenner, 2000). This mechanism, perhaps best known in Poaceae (e.g. see Baskin and Baskin, 1998b), is considered to be an adaptation to survive seasonal drought. Both *Spondias* species shed their seeds in the late rainy season, and the requirement for a dry period to come out of dormancy might insure that they germinate in the next rainy season. The requirement for a dry period to overcome dormancy also is supported by the fact that fresh seeds in our study, maintained in moist conditions in trays, had a total germination of only 9 and 5% after 234 and 261 days, respectively, indicating most seeds did not afterripen. Garwood (1986b) obtained higher germination percentages in seeds of *S. mombin* sown on the surface than we did in our study, where the large seeds of *Spondias* were buried to half their size. The seeds exposed on the surface in Garwood's study could have dried to some degree between watering times, thus allowing them to afterrripen. Exposure of seeds of *S. mombin* to liquid nitrogen caused a significant increase in germination, from 11 to 53% (Salomão, 2002).

Eighteen species with mean or median length of germination around 30 days represent a challenge to decide whether or not their seeds are dormant or nondormant. Baskin and Baskin (1998a) defined dormant versus nondormant seeds based on the time needed to germinate. The rate of germination represented by mean germination time was considered a promising parameter to study germination in trees (Bonner, 1998). We used the median time of germination as the arbitrary line to define dormancy. It represents the time taken to germinate for half of the seeds that germinated and was selected based on the right skewnees that is characteristic of germination curves of most species. Nevertheless, the right tail of the germination curve could be an indication of dormancy in the remaining seeds in the lot, especially if germination percentage is low. Thus, to define dormancy in some of the species we considered supplementary information, if it was available, such as responses to pretreatments, seed characteristics, or germination percentage after storage.

One group of species common in the mature forest has large seeds with high moisture content and short longevity that are not expected to be dormant. *Carapa guianensis* was reported to take 6 weeks to germinate (Record and Hess, 1986) and to have rapid germination (15–20 days) (McHargue and Hartshorn, 1983). In our study, seeds had a MLG of 21 days, and thus they were considered to be nondormant. However, the mean length of germination (Mean LG) was 33 days, and seeds continued to germinate for 159 days after they had been sown. Thus, at least some of the seeds in the lot were dormant. *Dipteryx oleifera* seeds from Costa Rica are described as nondormant (Flores, 1992), while seeds of this species from Panama had a MLG of 38 days, longer than the mean (Mean LG = 33 days). Seeds of *Prioria copaifera* are described as nondormant by Janzen (1983) and as dormant by Garwood (1983). Our results agree with those of Garwood. Sork (1985) described the special situation of the big seeded colonizer *Gustavia superba.* This species has no preference for gaps to germinate and was dormant in the different gap situations in which it was tested. A MLG of 31 days in our study might be an underestimate, since counting was suspended once we began removing the germinated seeds, due to sprouting of small pieces of the cotyledons that remained in the trays. This cotyledonary reprouting was described by Dalling and Aizprúa (1997). These four species are dispersed in the rainy season, and their dormant period is not long enough to delay germination until the next rainy season. The ecological meaning of dormancy in these species is not clear.

A second group of species with special considerations is represented by *Apeiba tibourbou* and *Luehea speciosa*. Both species had a MLG $<$ 30 days. However, they belong to genera in the family Tiliaceae *s. str.* in which dormancy in some species is caused by a water-impermeable seed coat, and germination of both species is increased by scarification. Acuña and Garwood (1987) reported that scarification with hot water or with sulfuric acid increased germination percentage significantly in seeds of *A. tibourbou*. However, highest germination in hot-water-treated seeds was 28% and in concentrated sulfuric acid-treated seeds 52%. Salomão (2002) reported a significant increase in germination percentage of seeds exposed to liquid nitrogen (i.e. from 22 to 54%). Daws et al. (2006) obtained 80–100% germination for seeds of this species by mechanically scarifying the seed coat and by removing of the chalazal plug either mechanically or by dipping the seeds in hot water (100 °C) for 2 min. Further, about 60% of the seeds germinated after immersion in water at 70 °C for 2 min. Controls germinated $\leq$4%. In a study by Garwood (1986b), no seeds of *A. tibourbou* treated with hot water (80–85 °C) for 10 min germinated, compared to 23% for the nontreated control, suggesting that hot water killed the seeds. In our experiments, treatment with warm water (70 °C for 10 min) had no effect on germination of *A. tibourbou* seeds; germination in control seeds was prolonged until day 80, with 47% total germination. Similarly, germination of control seeds of *L. speciosa* was prolonged to day 94, with only 22% total germination. Germination of seeds of this species stored dry for 4 months increased significantly after treatment with hot water. Thus, we conclude that dormancy in these two species is caused by a water-impermeable seed coat at maturity.

In our study, seeds of *Lacmellea panamensis* sown in February germinated to 75%. At least half of the seeds were nondormant (MLG = 29 days), and they lost viability after 1 month of storage. In Garwood's (1983) study, seeds of *L. panamensis* were dormant both times she sowed them: March and April. Nevertheless, most of her seeds were collected from the ground, and additionally they were allowed to dry for 2 days before sowing them. Since Garwood's germination percentages were lower than the ones in our study, it is possible that desiccation sensitivity caused loss of viability of seeds in her study.

Discrepancies in results of germination tests for tree seeds are primarily due to the wide genetic variation present in seed lots that come from natural populations (Bonner, 1998). Time and method of collection, germination test procedures, and maternal effects also should be taken into consideration.

5.2. Dormancy, longevity, and seed characteristics

Seed size has higher variability than other traits and variables calculated for the species studied. Leishman et al. (1995) suggested that seed size is more strongly associated with other plant attributes than with environmental conditions for seedling establishment, resulting in a wide range in seed mass.

Seed mass and moisture content were weakly correlated, and neither was correlated with any of the germination variables. Mass of about 63% of the seeds was 0.01–1 g, and seeds with a mass >0.1 g tended to have higher moisture content than seeds with a mass <0.1 g. However, although the correlation is significant it does not have predictive value. Time to germination, its variation, and coefficient of variation of germination percentages are positively correlated, and all of them are negatively correlated with total germination percentage. Thus, the more dormant seeds are, the less synchronous is their germination, and they germinate to lower percentages with a high coefficient of variation.

Although longevity data from our study do not allow establishment either of the actual longevity of the seeds in the seed bank or in usual storage conditions, for 37 species it represents the first approach to their potential storage behavior, and few of the 89 species have been tested for longevity in storage. Many species have been labeled as recalcitrant just because they lost viability quickly, but this loss may be related to other causes such as poor seed-handling practices (Bonner, 1998). This is especially true for common tropical trees from natural stands, whose low density makes collection slow. Further, specific studies following international desiccation protocols are needed to determine which of the species with short longevity in laboratory storage conditions in this study can be considered to be desiccation-sensitive, especially those for which the reports are new. Of the 35 short-lived species, only *Hymenaea courbaril*, *Dipteryx oleifera*, and *Hampea appendiculata* are reported to be desiccation tolerant (probably orthodox), and 21 had no previous record. Thus, the longevity data for these 21 species reported in this paper can be considered an indication of possible desiccation-sensitivity behavior in either the intermediate or recalcitrant category.

It has been stated that a majority of dominant tree species of tropical humid moist forests have nondormant seeds that germinate rapidly and produce a carpet of very slow growing seedlings (Msanga, 1998; Ng, 1978; Vázquez-Yañes et al., 2000). Nevertheless, there are some tropical recalcitrant species reported to have an underdeveloped embryo, such as *Minquartia guianensis* (Camargo and Ferraz, 2004; Ferraz et al., 2004; Flores, 2002), *Virola kischnyi* (Flores, 1996), and *V. surinamensis* (Piña-Rodrigues et al., 2005), and thus morphological or morphophysiological dormancy (Baskin and Baskin, 2004). Seeds of *Carapa guianense* have been reported to germinate several months after dispersal (Flores, 1993b) and seeds of *Dipteryx panamensis* (*D. oleifera*) to be dormant in a reforestation project on abandoned farmland in Panama, showing dependence on shade for germination but growing better with higher light (Hooper et al., 2002). Two recalcitrant species of Lauraceae, *Beilschmiedia kweo* and *Ocotea usambarensis*, continued to germinate for 3 months and 7 weeks, respectively (Msanga, 1998), indicating that at least some seeds are dormant. Daws et al. (2005) suggest that rapid germination in desiccation-sensitive species is an adaptation for avoidance of seed predation. Nevertheless, this synchronous germination would expose an entire cohort of seedlings to predation. The association between desiccation sensitivity of large, moist seeds of shade tolerant species with dormancy might be favored by a combination of biotic evolutionary forces in the seed and seedling stages. These seeds would not dry in the shaded understory, while delay of germination would allow some seedlings to escape predation as part of the seedling bank.

Overall, large, moist, short-lived, dormant seeds are more frequent in the rainy season, especially in the late rainy season, with significant differences only for moisture content and kind of dormancy. A longer germination time in the late rainy season agrees with the delayed-rainy syndrome described by Garwood (1983). She considered dormancy to be the primary mechanism controlling time of germination of seeds dispersed in the rainy season.

5.3. Implications for nursery management

In seasonal tropical regions, time for planting is restricted to the beginning of the rainy season, and commercial-tree nurseries that depend on market seeds work basically from the mid-dry season until the rainy season is established. For restoration projects, nurseries should emphasize seed-collection efforts during months when the highest number of species is in fruit in order to take advantage of field workers and time. Overall, for restoration projects that involve the use of large numbers of native species about which little is known, there will be a considerable increase in nursery costs and time required for nursery production in comparison to commercial tree nurseries (Blakesley et al., 2002).

To improve nursery production, germination pretreatments should be determined for species that germinate to low percentages and/or at low rates without pretreatment, thus facilitating use of space and scheduling of seedling production. This is especially true if the species has an optimal field performance and is also a promising timber or agroforestry species. If no pretreatment is applied, and considering MLG, dormancy, and desiccation sensitivity of seeds, there will be an "overlap" of time for seed collection and seedling production during most parts of the year. At the end of the dry season and the beginning of the rainy season, there will be a peak of all activities in the nursery: collecting seeds, sowing seeds, and transplanting seedlings to containers. From the mid rainy season to the beginning of the next rainy season, space in the nursery will be used for both seeds in their germination beds and seedling in their containers, waiting for the next planting season.

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Appendix A

Scientific name (including author), common name (in Spanish), family, reported fruiting time, month of fruit collection, and number of trees from which fruits were collected, for each of the 100 study species. The acronyms CAES, FAB, and MIM attached by a dash to FABACEAE designate subfamilies Caesalpinioideae, Faboideae, and Mimosoideae, respectively. Fruiting as reported by Croat (1978), Foster (1982), and J. Wright (personal communication).

Genus	Species	Author	Common name	Family	Fruiting as reported (months)	Month of collection	No. of trees
Adelia	*triloba*	(Muell. Arg.) Hemsl.	Espino amarillo	Euphorbiaceae	1–4	5	1
Albizia	*adinocephala*	Britton & Rose ex Record	Frijolillo	Fabaceae-MIM		3	5
Alseis	*blackiana*	Hemsl.	Mameicillo	Rubiaceae	3, 5, 7–12	2	5
Amaioua	*corymbosa*	Kunth	Madroño de montaña	Rubiaceae	7–2	1	6
Anacardium	*excelsum*	(Bert. & Balb.) Skeels	Espavé	Anacardiaceae	4–5–	5	5
Andira	*inermis*	(W. Wright) Kunth	Almendro de río. Harino	Fabaceae-FAB	8–12	6	5
Annona	*spraguei*	Saff.	Chirimoya	Annonaceae	6–10	9	5
Antirhea	*trichantha*	(Griseb.) Hesml.	Candelo	Rubiaceae	6–10	8	5
Apeiba	*aspera*	Aubl.	Peine de Mico	Tiliaceae	11–5	3	5
Apeiba	*tibourbou*	Aubl.	Peine de mico	Tiliaceae	1–7	5	5
Aspidosperma	*cruenta*	Woods.	Alcarreto	Apocynaceae	2–5	10	5
Beilschmiedia	*pendula*	(Sw.) Hemsl.	Agucatillo	Lauraceae	5–6	6	3
Brosimun	*utile*	(Kunth) Pittier	Arbol vaca	Moraceae	7	6	5
Bursera	*simaruba*	(L.) Sarg.	Cholo pelao	Burseraceae	1–3, 8	5	5
Byrsonima	*crassifolia*	(L.) Kunth	Nance	Malpighiaceae	5–10	8	5[1]
Calophyllum	*longifolium*	Willd.	María	Clusiaceae	5–12	9	5
Calycophyllum	*candidissimum*	(Vahl) DC.	Madroño	Rubiaceae	2–3	5	4
Carapa	*guianensis*	Aubl.	Bateo, Tangaré	Meliaceae	5–8, 10	11	5
Cassia	*grandis*	L. f.	Caña Fístula	Fabaceae-CAES	2–3	3	5
Castilla	*elastica*	Cerv. *var. costaricanum* (Liebm.) C. Berg.	Caucho	Moraceae	5–6	6	5
Cedrela	*odorata*	L.	Cedro cebolla, Cedro amargo	Meliaceae	1–11	2	5
Ceiba	*pentandra*	(L.) Gaertn.	Ceiba	Bombacaceae	1–5	5	1
Chrysophyllum	*cainito*	L.	Caimito	Sapotaceae	1–4	2	5
Colubrina	*glandulosa* var. *glandulosa*	(Perkins) M.C. Johnst.	Carbonero	Rhamnaceae	2–4	4	5
Copaifera	*aromatica*	Dwyer	Cabimo	Fabaceae-CAES	2–4, 8–9	2	4
Cordia	*alliodora*	(R. & P.) Oken	Laurel	Boraginaceae	4–5	4	4
Couratari	*guianensis*	Aubl.	Coquito	Lecythidaceae	2–3	2	1
Cupania	*latifolia*	Kunth	Gorgojero	Sapindaceae	9–10	10	5
Dalbergia	*retusa*	Hemsl.	Cocobolo	Fabaceae-FAB	1–5, 10	2	3
Dendropanax	*arboreus*	(L.) Dec. & Planch.	Muñequito	Araliaceae	8–10	9	5
Dialium	*guianense*	(Aubl.) Sandwith	Tamarindo de montaña	Fabaceae-CAE	11–3	3	1
Diphysa	*robinioides*	Benth.	Macano	Fabaceae-FAB	2–3	1	5
Dipteryx	*oleifera*	(Pitier) Record & Mell	Almendro de montaña	Fabaceae-FAB	10–3	12	5
Enterolobium	*cyclocarpum*	(Jacq.) Griseb.	Corotú	Fabaceae-MIM	3–6	5	5
Enterolobium	*schomburgkii*	(Benth.) Benth.	Guabino	Fabaceae-MIM	4–9	4	5
Erythrina	*fusca*	Lour.	Palo bobo	Fabaceae-FAB	2–5, 10	4	5
Faramea	*occidentalis*	(L.) A. Rich.	Huesito, Jazmín	Rubiaceae	3–1	12	5
Ficus	*insipida*	Willd.	Higuerón	Moraceae	2–4, 8, 10	7	5
Genipa	*americana*	L.	Jagua	Rubiaceae	1–12	2	5
Guarea	*grandifolia*	DC.	Cedro macho	Meliaceae	2–6, 11	4	5
Guarea	*guidonia*	(L.) Sleumer	Cedro blanco. Cedro macho	Meliaceae	1–7, 12	4	4
Guazuma	*ulmifolia*	Lam.	Guácimo	Sterculiaceae	3–5, 9	3	5
Guettarda	*foliaceae*	Standl.	Guayabo de monte, espino amarillo	Rubiaceae	5–12	10	1
Gustavia	*superba*	(Kunth) Berg.	Membrillo	Lecythidaceae	4–8	7	8
Hampea	*appendiculata*	(Donn. Sm.) Standl.		Malvaceae	1–3	1	5
Hasseltia	*floribunda*	Kunth	Parimontón	Flacourtiaceae	3–6, 8	6	5
Heisteria	*concinna*	Standl.	Ajicillo Naranjillo	Olacaceae	2–4	3	5
Hura	*crepitans*	L.	Tronador, Javillo, Ceibo	Euphorbiaceae	2–4	2	5
Hyeronima	*alcheorneoides*	Allemão	Zapatero, Pilón, Piedro	Euphorbiaceae	3–8, 11	12	5
Hymenaea	*courbaril*	L.	Algarrobo	Fabaceae-CAES	11–12, 2, 8	1	5
Inga	*punctata*	Willd.	Guabita cansaboca	Fabaceae-MIM	3–5	6	2

Appendix A (*Continued*)

Genus	Species	Author	Common name	Family	Fruiting as reported (months)	Month of collection	No. of trees
Inga	*spectabilis*	(Vahl) Willd. *var. spectabilis*	Guaba machete	Fabaceae-MIM	2–5	4	4
Jacaranda	*copaia*	(Aubl.) D. Don.	Jacaranda	Bignoniaceae	7–8, 10, 1	9	5
Lacmellea	*panamensis*	(Woodson) Markgr.	Lagarto negro	Apocynaceae	1–7	3	2
Lafoensia	*punicifolia*	D.C.	Roble coral, Cascarillo	Lythraceae	1–4	4	1
Lindackeria	*laurina*	C. Presl.	Chiriquí	Flacourtiaceae	9–2	2	4
Lonchocarpus	*latifolius*	Kunth	Zorro, Gallote	Fabaceae-FAB	3–5	9	2
Luehea	*seemannii*	Planch. and Triana	Guácimo colorado	Tiliaceae	4–5, 8	6	5
Luehea	*speciosa*	Willd.	Guácimo pacheca	Tiliaceae	4–6	2	30
Margaritaria	*nobilis*	L. f.	Clavito	Euphorbiaceae	7–10	10	5
Miconia	*argentea*	(Sw.) DC.	Papelillo, Dos caras	Melastomataceae	1–6	4	5
Miconia	*minutiflora*	(Bonpl.) DC.	Dos caras	Melastomataceae	2–3	4	5
Ochroma	*pyramidale*	(Lam.) Urb.	Balso	Bombacaceae	1–3, 5–8	2	5
Ormosia	*macrocalyx*	Ducke	Conejito colorao	Fabaceae-FAB	3–11	8	5
Pachira	*quinata*	(Jacq.) W.S. Alverson	Cedro Espino	Bombacaceae	1–6	3	5
Phoebe	*cinnamomifolia*	Rich. ex Griseb.	Sigua blanco	Lauraceae	4–8	8	5
Platymiscium	*pinnatum*	(Jacq.) Dugand	Quira	Fabaceae-FAB	8–3	1	5
Posoqueria	*latifolia*	(Rudge) Roem. & Schult.	Boca de vieja	Rubiaceae	1–12	12	5
Prioria	*copaifera*	Griseb.	Cativo	Fabaceae-CAES	3–6,10	7	5
Protium	*panamense*	(Rose) I.M. Johnst.	Chutrás	Burseraceae	9–11, 2–6	12	3
Protium	*tenuifolium*	Engl.	Chutrás	Burseraceae	9–10	9	5
Pseudobombax	*septenatum*	(Jacq.) Dugand	Barrigón	Bombacaceae	2–4	4	5
Pseudosamanea	*guachapele*	(Kunth) Harms	Guachapalí	Fabaceae-MIM	10–3	11	3
Pterocarpus	*rohrii*	Vahl	Sangre de gallo	Fabaceae-FAB	8–11	8	3
Quararibea	*asterolepis*	Pittier	Guayabillo	Bombacaceae	8–11, 1, 5	9	5
Sapindus	*saponaria*	L.	Jaboncillo	Sapindaceae	11–5	3	1
Sapium	*glandulosum*	(L.) Morong	Olivo	Euphorbiaceae	5–10	9	5
Schefflera	*morototoni*	(Aubl.) Maguirre, Stey., & Frod.	Guarumo de Pava	Araliaceae	1–12	2	5
Spondias	*mombin*	L.	Jobo	Anacardiaceae	7–9	8	5
Spondias	*radlkoferi*	Donn. Sm.	Jobo	Anacardiaceae	9–12	10	5
Sterculia	*apetala*	(Jacq.) Karst.	Panamá	Sterculiaceae	1–3	2	5
Swietenia	*macrophylla*	King	Caoba	Meliaceae	1–4, 8	1	5
Tabebuia	*guayacan*	(Seem.) Hemsl.	Guayacán	Bignoniaceae	3–6	5	4
Tabebuia	*rosea*	DC.	Roble	Bignoniaceae	3–5	4	5
Tachigalia	*versicolor*	Standl. & L.O. Wms.	Arbol suicida	Fabaceae-CAES	8–3	2	5
Tapirira	*guianensis*	Aubl.	Palo de gusano	Anacardiaceae		9	7
Terminalia	*amazonia*	(J.F. Gmel.) Exell	Amarillo	Combretaceae	2–6	4	5
Trattinnickia	*aspera*	(Standl.) Swart	Caraño hediondo	Burseraceae	2–4, 10–12	10	1
Trema	*micrantha*	(L.) Blume	Jordancillo Capulín macho	Ulmaceae	6–10	8	5
Trichilia	*hirta*	L.	Matapiojo	Meliaceae		3	5
Trichilia	*tuberculata*	C. DC.	Alfajía Colorado	Meliaceae	5–8, 10–11	9	6
Trichospermum	*galeottii*	(Turcz.) Kosterm.	Burrilico	Tiliaceae	2–4	1	5
Triplaris	*cumingiana*	Fischer & Meyer	Palo Santo	Polygonaceae	3–5	4	5
Vantanea	*depleta*	McPherson	Chiricano	Humiriaceae	2	2	3
Virola	*sebifera*	Aubl.	Velario	Myristicaceae	7–2	9	4
Virola	*surinamensis*	(Rol.) Ward	Velario	Myristicaceae	2–8, 10	5	5
Vochysia	*ferruginea*	Mart.	Mayo	Vochysiaceae	6–9	10	5
Xylopia	*aromatica*	(Lam.) Mart.	Malagueto hembra	Annonaceae		12	5
Xylopia	*frutescens*	Aubl.	Malagueto macho	Annonaceae	11–2	1	5
Zanthoxylum	*panamense*	P. Wilson	Arcabú	Rutaceae	8–12	12	5

Appendix B

Methods of collecting and processing seeds of each of the 100 study species.

Species	Collection method	Fruit/seed cleaning method
Adelia triloba	From tree with pole	Capsules opened in paper bags. Seeds extracted manually
Albizia adinocephala	From tree with pole and from ground	Break legumes manually
Alseis blackiana	From tree with pole	Break capsules manually
Amaioua corymbosa	From tree with pole	Break capsules manually
Anacardium excelsum	From ground	Drupe; seeds + endocarp = diaspore, does not need cleaning

Appendix B (*Continued*)

Species	Collection method	Fruit/seed cleaning method
Andira inermis	From tree with pole	Drupe; extract exocarp with knife
Annona spraguei	From tree with pole	Separate seeds from fleshy fruit wall under water
Antirhea trichantha	From tree with pole	Separate seeds from fleshy fruit wall under water
Apeiba aspera	From ground	Break capsules manually
Apeiba tibourbou	From tree with pole	Break capsules manually
Aspidosperma cruenta	From tree, climbing	Break capsules manually
Beilschmiedia pendula	From tree with pole	Separate seeds from fleshy fruit wall manually
Brosimun utile	From tree, climbing	Separate seeds from fleshy fruit wall manually
Bursera simaruba	From tree with pole	Break capsules manually
Byrsonima crassifolia	From tree with pole	Separate seeds from fleshy exocarp manually
Calophyllum longifolium	From tree, climbing	Separate seeds from fleshy fruit wall manually. Seeds germinated in bag
Calycophyllum candidissimum	From tree with pole and with sheets	Winged seeds are collected in sheets and do not need cleaning
Carapa guianensis	From tree, climbing	Capsule opens on its own
Cassia grandis	From tree with pole	Break legume manually
Castilla elastica	From tree with pole and from ground	Separate seeds from fleshy fruit wall under water
Cedrela odorata	From tree with pole	Let capsules open in dry area, and extract winged seeds manually
Ceiba pentandra	From tree with pole and from ground	Let capsules open in dry area, and separate kapok (fibers around the seeds) manually
Chrysophyllum cainito	From tree, climbing	Separate seeds from fleshy fruit wall under water
Colubrina glandulosa	From tree with pole and with sheets	Let capsules open in dry area, and extract seeds manually
Copaifera aromatica	From tree with pole and from ground	Legume dehiscent. Extract aril manually
Cordia alliodora	From tree with pole	Break capsules manually, and extract seeds manually
Couratari guianensis	From tree, climbing	Let capsules (pixid) open in dry area, and extract seeds manually
Cupania latifolia	From tree with pole	Let capsules open in dry area. Extract seeds manually, and extract aril
Dalbergia retusa	From tree with pole	Break legume manually
Dendropanax arboreus	From tree with pole	Separate seeds from fleshy fruit wall manually
Diphysa robinioides	From tree with pole	Break legume manually
Dipteryx oleifera	From ground	Drupe; seed + endocarp = disapore, does not need cleaning
Enterolobium cyclocarpum	From ground	Break legume manually (easier in a bag), separate seeds, and wash them to extract sweet mesocarp
Enterolobium schomburgkii	From ground	Break legume manually (easier in a bag). Separate seeds, and wash them to extract sweet mesocarp
Erythrina fusca	From tree with pole	Break legume manually
Faramea occidentalis	From ground	Separate seeds from fleshy fruit wall under water
Ficus insipida	From tree with pole and climbing	Let the fleshy fruit dry, and extract seeds manually. Flotation method probably could be used to separate empty seeds, which float, from filled ones, which sink
Genipa americana	From tree with pole	Separate seeds from fleshy fruit wall under water
Guarea grandifolia	From tree with pole	Let capsules open in dry area
Guarea guidonia	From tree with pole	Let capsules open in dry area
Guazuma ulmifolia	From tree with pole and from ground	Break capsules, and extract seeds manually
Gustavia superba	From tree with pole and from ground	Open pixids carefully with a knife to extract seeds
Hampea appendiculata	From tree with pole	Let capsules open in dry area. Extract aril
Hasseltia floribunda	From tree with pole	Separate seeds from fleshy fruit wall manually. Select black fruits
Heisteria concinna	From tree with pole and climbing	Remove tiny fleshy exocarp. Endocarp is part of the diaspore
Hura crepitans	From tree with pole	Put capsules in a cloth bag. Then, hit them or let them fall, so they will explode, liberating the seeds
Hyeronima alcheorneoides	From tree, climbing	Drupe; seed + endocarp = disapore, does not need cleaning
Hymenaea courbaril	From tree with pole, climbing, and from ground	Break fruit and extract seeds manually. A hammer is needed to break the indehiscent fruit
Inga punctata	From tree with pole and from ground	Break legume and extract seeds manually. Extract sweet aril by hand, or better eat it
Inga spectabilis	From tree with pole	Break legume and extract seeds manually. Extract sweet aril by hand, or better eat it
Jacaranda copaia	From tree, climbing	Let capsules open in dry area
Lacmellea panamensis	From ground	Separate seeds from fleshy exocarp manually. Seeds germinated in the bag
Lindackeria laurina	From tree with pole	Let capsules open in dry area
Lonchocarpus latifolius	From tree with pole	Break indehiscent legume manually
Luehea seemannii	From tree with pole	Let capsules open in dry area
Luehea speciosa	From tree with pole	Let capsules open in dry area
Margaritaria nobilis	From tree with pole	Let capsules open in dry area
Miconia argentea	From tree with pole	Separate seeds from fleshy fruit wall under water. Collect the tiny seeds in cheesecloth
Miconia minutiflora	From tree with pole	Separate seeds from fleshy fruit wall under water. Collect the tiny seeds in cheesecloth

Appendix B (*Continued*)

Species	Collection method	Fruit/seed cleaning method
Ochroma pyramidale	From tree with pole	Break capsules manually. Separate hairs from the seed using a sieve
Ormosia macrocalyx	From tree with pole and from ground	Let legumes open in dry area
Pachira quinata	From tree with pole	Let capsules open in dry area
Phoebe cinnamomifolia	From tree with pole and from ground	Separate seeds from fleshy fruit wall under water and wash
Platymiscium pinnatum	From tree, climbing	We extracted seeds from the samaras, but are not completely confident about their maturity
Posoqueria latifolia	From tree with pole	Separate seeds from fleshy fruit wall under water
Prioria copaifera	From ground	Indehiscent pods = diaspore (with only one seed) are collected clean
Protium panamense	From tree with pole	Break capsules manually. Eliminate aril
Protium tenuifolium	From tree with pole	Break capsules manually. Eliminate aril
Pseudobombax septenatum	From tree with pole	Let capsules open in dry area. Separate hairs from seeds using a sieve
Pterocarpus rohrii	From tree, climbing	Cut wing of samara
Quararibea asterolepis	From ground	Separate seeds from fleshy fruit wall, and let seeds air-dry
Sapium glandulosum	From tree with pole and climbing	Let capsules open in dry area, and extract aril manually under water
Schefflera morototoni	From tree with pole and from ground	Separate seeds from fleshy fruit wall under water
Spondias mombin	From tree with pole and from ground	Remove fleshy exocarp under water. Endocarp is part of diaspore
Spondias radlkoferi	From tree with pole and from ground	Remove fleshy exocarp under water after making several cuts. Endocarp is part of diapore
Sterculia apetala	From tree with pole and from ground	Let capsules open in dry area. Extract seeds manually, being very careful with hairs on fruit wall
Swietenia macrophylla	From tree with pole and climbing	Let capsules open in dry area. Cut wing
Tabebuia guayacan	From tree with pole	Let capsules open in dry area. Cover them to avoid seed loss by wind
Tabebuia rosea	From tree with pole	Let capsules open in dry area. Cover them to avoid seed loss by wind
Tachigalia versicolor	From ground	Samara = diaspore, does not need cleaning. Mature fruit can be recognized by the rattle-sound dry seeds make inside when fruit is shaken. Also, seeds can be extracted from samaras and sown
Tapirira guianensis	From tree with pole	Break fruit and extract seeds manually
Terminalia amazonia	From tree with pole and from ground	Winged fruit = diaspore, does not need cleaning. However, it is very difficult to distinguish empty fruits from filled ones
Trattinnickia aspera	From tree with pole	Separate seeds from fleshy fruit wall manually
Trema micrantha	From tree with pole	Drupe; seed + endocarp = diaspore, does not need cleaning
Trichilia hirta	From tree with pole	Let capsules open in dry area
Trichilia tuberculata	From tree with pole	Let capsules open in dry area
Trichospermum galeottii	From tree with pole	Let capsules open in dry area
Triplaris cumingiana	From tree with pole	Winged fruit = diaspore, does not need cleaning. We cut wings
Vantanea depleta	From tree with pole	Separate seeds from flesh exocarp manually with a knife
Virola sebifera	From tree with pole	Let capsules open in dry area
Virola surinamensis	From tree with pole	Let capsules open in dry area
Vochysia ferruginea	From tree with pole	Let capsules open in dry area
Xylopia aromatica	From tree with pole	Let capsules open in a plastic bag
Xylopia frutescens	From tree with pole	Let capsules open in a plastic bag
Zanthoxylum panamense	From tree with pole	Let capsules open in dry area

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