



## Consequences of dry-season seed dispersal on seedling establishment of dry forest trees: Should we store seeds until the rains?

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### ARTICLE INFO

#### Article history:

Received 20 December 2007

Received in revised form 9 April 2008

Accepted 29 April 2008

#### Keywords:

*Amburana cearensis*

*Anadenanthera colubrina*

*Aspidosperma pyrifolium*

*Cavanillesia arborea*

*Cedrela fissilis*

Drought

Germination

*Myracrodruon urundeuva*

Recruitment

Seed dormancy

Shading

*Sterculia striata*

*Tabebuia impetiginosa*

### ABSTRACT

We examined the following hypotheses: (i) seeds of dry forest trees have high pre- and post-germination mortality by desiccation due to the time between seed dispersal and germination and to irregular rains at the onset of the rainy season; (ii) seedlings from seeds dispersed in the dry season which survive the dry spells are larger at the end of the first rainy season than those dispersed in the rainy season because the former have more time to grow. We evaluated the possible trade-off between few large seedlings (resulting from natural dispersal)  $\times$  many small seedlings (resulting from delayed dispersal) on seedling survival during the dry season. We sowed eight tree species in a greenhouse in September, simulating the natural dispersal timing (before the rains), and in November, when rains are more constant. Because shading can counteract the effects of desiccation, we applied three levels of shade (10%, 40% and 72% PPF). From September 2005 to December 2006, we provided the daily precipitation of a median year from a major patch of dry forest in Central Brazil. At the end of the rainy season, a subset of seedlings was collected for growth measurements (dry mass) and the remainder was left to follow the dry season survivorship. The lower germination expected for seeds dispersed in the dry season and in full sun was not confirmed for species that had some dormancy. The delayed dispersal was advantageous for the initial establishment of fast germinating species, but it was irrelevant or even disadvantageous for others. Also, the greenhouse weather was certainly milder than the natural environment, reducing the potential for mortality by desiccation. The growth of the four species of higher dormancy were not affected by timing of seed dispersal, while three out of four fast germinating species had higher root biomass when dispersed in the dry season. The growth during the rainy season did not affect seedling survival during the dry season. Keeping seeds to sow when rain is constant might be a good strategy to increase the establishment of fast-germinating tree species.

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### 1. Introduction

In tropical dry forests the timing of tree seed dispersal is highly predictable. Maturation of fleshy fruits is concentrated in the rainy season, while maturation of dry fruits occurs in the dry season (Janzen, 1967; Singh and Singh, 1992; Bullock, 1995; Justiniano and Fredericksen, 2000; Griz and Machado, 2001). Regardless of the timing of seed dispersal, most seeds of seasonal tropical forests remain dormant until the beginning of the rainy season, when they suddenly germinate (Frankie et al., 1974; Garwood, 1983). Thus,

germination at the onset of the rainy season seems to be an evolutionarily selected trait in seasonal forests (Garwood, 1983; Marod et al., 2002), which maximizes the use of the first rainy season for seedling establishment, potentially increasing the probability of surviving the next dry season (see Garwood, 1983 for a full discussion).

However, highly variable precipitation among years and frequent dry spells during the rainy season are characteristic of tropical dry forest regions (Blain and Kellman, 1991; Murphy and Lugo, 1995; Sampaio, 1995). Dry spells of up to 2 weeks occur at the beginning of the rainy season, and the exact beginning of the rainy season is unpredictable (Garwood, 1985; Blain and Kellman, 1991). The inconsistency of the first rains and the occurrence of dry spells are important sources of mortality by desiccation for seeds and recently germinated seedlings in dry forests (Ray and Brown,

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1995; McLaren and McDonald, 2003; Vieira and Scariot, 2006a), and even in low- or non-seasonal forests (Augspurger, 1980; Burslem et al., 1996; Engelbrecht et al., 2006).

Therefore, collecting seeds during the dry season and planting them when constant rains are more likely to occur, would reduce the effect of dry spells and could increase seedling establishment. On the other hand, resultant seedlings will have less time to develop before the beginning of the dry season. Some studies have simulated the absence of dry spells in dry forests by watering seeds and seedlings (Blain and Kellman, 1991; Gerhardt, 1996a; McLaren and McDonald, 2003). These studies were carried out with three, one and four species, respectively. One study (McLaren and McDonald, 2003) found a positive relationship between water supplementation and both germination and seedling survival. Here, we propose an experiment that investigates a basic ecological question and also might provide an important management practice to restore tropical dry forests.

Planting seeds after the dry season has passed would be particularly important to the restoration of open areas, where seed and seedling desiccation is more severe (Ray and Brown, 1995; McLaren and McDonald, 2003; Vieira and Scariot, 2006b). Another advantage of the delayed seeding is that it reduces the time during which seeds are exposed to predators. Seed predation is a significant barrier to seed germination and consequently to forest regeneration (Nepstad et al., 1996; Holl and Lulow, 1997). Because most dry forest tree species have high seed longevity (Baskin and Baskin, 1998; Khurana and Singh, 2001), their seeds could be stored successfully at natural temperatures (Lima et al., 2007).

Here, we tested the hypothesis that seeds from tropical dry forests trees have high mortality by desiccation (i) before germinating, due to the time between seed dispersal and germination; (ii) after germinating, due to dry spells common at the beginning of the rainy season. To test this hypothesis, we sowed seeds in September, simulating the natural dispersal timing (before the rains), and in November, simulating delayed dispersal when rains are more constant. We expected that the delayed seeding (November) would increase seed germination and seedling survival relative to natural seeding (September). We also expected variation in species responses: fast-germinating seed species would have higher mortality when dispersed in September than in November; seed species with some dormancy would have similar mortality between September and November (Blain and Kellman, 1991).

We also tested the hypothesis that seedlings from seeds dispersed in the dry season that survive desiccation would be larger at the end of the rainy season, because they would have more time to grow. If this is the case, the larger seedlings from September would have a higher probability of surviving the dry season than seedlings from November. We also investigated the interaction between dispersal timing and shade (three levels of shade), which can diminish the desiccation effects on seeds and seedlings (Ray and Brown, 1995; McLaren and McDonald, 2003; Vieira and Scariot, 2006b), but can decrease seedling survival by reducing light levels (Balderrama and Chazdon, 2005; Baraloto et al., 2005a,b). Although the response to light levels is highly variable among species, the species studied are classified as heliophytes (for *Cedrela fissilis* Vell., *Myrcodruon urundeuva* Allemão and *Tabebuia impetiginosa* (Mart. ex DC.) Standl. see Guzmán-Gutiérrez, 2001; for *Amburana cearensis* (Allemão) A.C. Sm see Ramos et al., 2004) or lack published information about their light requirements. All studied species occupy forest canopy when mature, and seedlings are found in the understory (Vieira and Scariot, 2008).

## 2. Materials and methods

### 2.1. Seed collection

We collected seeds of all species in August and September of 2005, except *Cavanillesia*, which was in October, from tropical dry forests (seasonally deciduous forests) of São Domingos county, northeast of Goiás state, in the Paranã river basin (13°39'S, 46°45'W). Major patches of tropical dry forests occur in this region of Central Brazil (Ratter, 1992; Scariot et al., 2008; see Scariot et al., 2008; Vieira and Scariot, 2006b for a detailed description of the study area). Seeds were collected from 3 to 10 trees per species, depending on their availability, to guarantee minimum genetic variability. Thirty healthy seeds were weighed and measured to characterize species.

### 2.2. Study species

We selected five species because of their high importance value index (IVI) in tropical deciduous forests. Together they represent 10–35% of total IVI of this vegetation in the Paranã river basin (Silva and Scariot, 2003, 2004a,b; Nascimento et al., 2004; Sevilha and Scariot, unpublished data): *Anadenanthera colubrina* (Vell.) Brenan (Mimosaceae), *Aspidosperma pyrifolium* Mart. (Apocynaceae), *Cavanillesia arborea* (Willdenow) K. Schum. (Bombacaceae), *Myrcodruon urundeuva* (Anacardiaceae), *Tabebuia impetiginosa* (Bignoniaceae). Although *A. cearensis* (Fabaceae) and *C. fissilis* (Meliaceae) have low IVI in these forests, they were included in the study because they are endangered species (IUCN, 2006), and such studies are needed for their conservation demanding studies to support their conservation. *Sterculia striata* A. St.-Hil. and Naudin (Sterculiaceae), was selected because it has large seeds dispersed by vertebrates, a rare trait in this vegetation (Vieira and Scariot, 2006a). Selection criteria aimed to include high community tree representativeness by IVI and by a range of seed types (Table 1).

### 2.3. Seed storage

A portion of the collected seeds were sowed on 21 September 2005 (natural dispersal). The remaining seeds were stored in natural conditions – seeds were stored in paper bags (brown bags) at ambient room temperature and humidity – for sowing on 15 November 2005 (delayed dispersal). A sample of the seeds prepared for sowing in September and November were germinated in the laboratory simultaneously on the sowing dates (25 °C, constant moisture and 12 h photoperiod), to verify the possible viability loss during storage (Table 1; Lima et al., 2007).

### 2.4. Greenhouse experiments

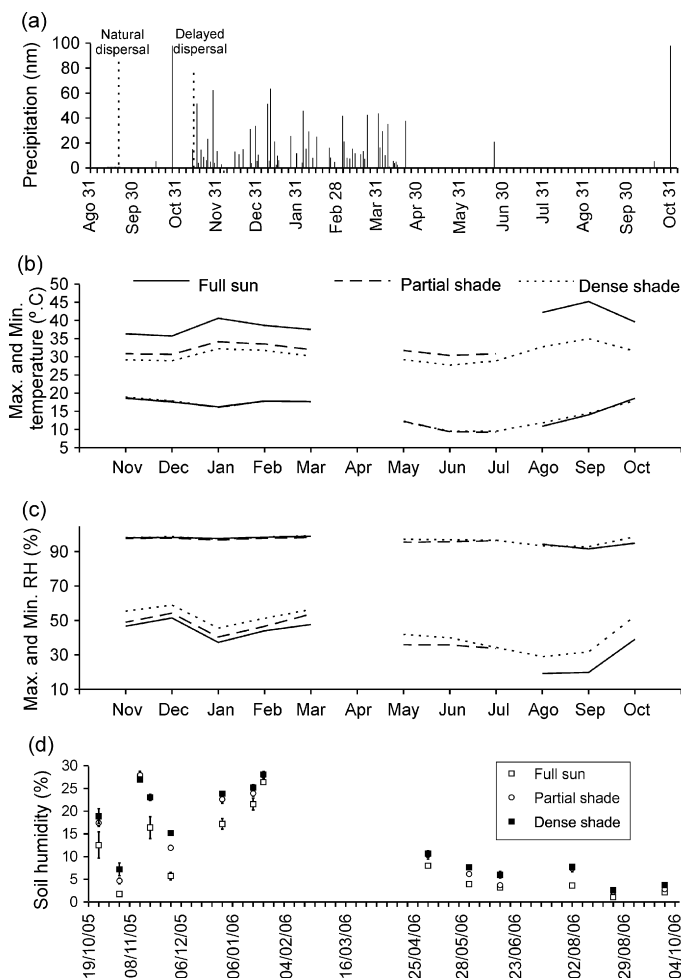
We tested the effect of dispersal timing – natural (September) and delayed (November) – in a greenhouse at Embrapa in Brasília, Federal District (15°44'S, 47°53'W). Seeds were lightly pressed against the soil, remaining partially buried, in raised beds (25 cm deep) filled with soil from the same seed collection region. Superficial soil was collected from a recently deforested and ploughed area. The precipitation in the greenhouse simulated a median year in São Domingos county (1.188 m in 1994, data from 1969 to 2001; <http://hidroweb.ana.gov.br/>; Fig. 1a). We calibrated the functioning time of the irrigation system with a pluviometer installed in the greenhouse (2 mm of precipitation in 10 min). Two dispersal timings were used: natural dispersal, 21 September (7 October for *Cavanillesia*); (ii) delayed dispersal, 15 November, when rains were regular (Fig. 1a). Three light levels were used (i) full sun (72 ± 4% SE of Photon Flux Density; measured with a

**Table 1**  
Traits of studied species

Species	Position in IV ranking (mean of two intact forests) <sup>a</sup>	Fresh seed mass (g)	Seed size (cm) width/length	Dispersal timing	Germination percentage in laboratory <sup>b</sup> September/November	Main dispersal agent
<i>Amburana cearensis</i>	– <sup>c</sup>	0.53	1.1/1.6	August–September	100/98	Wind
<i>Anadenanthera colubrina</i>	29.0	0.25	1.5/1.8	August–September	93/99	Wind
<i>Aspidosperma pyrifolium</i>	12.3	0.28	2.3/2.4	August–September	85/77	Wind
<i>Cavanillesia arborea</i>	4.7	1.55	1.2/4.9	September–October	–/75	Wind
<i>Cedrela fissilis</i>	14.0	0.03	0.5/1.0	August–September	58/65	Wind
<i>Myracrodruon urundeuva</i>	1.7	0.02	0.4/0.3	August–September	83/78	Wind
<i>Sterculia striata</i>	28.0	1.37	1.1/1.7	August–September	100/100	Vertebrates
<i>Tabebuia impetiginosa</i>	3.0	0.11	1.0/1.1	August–September	88/87	Wind

<sup>a</sup> Scariot and Sevilha (2005).<sup>b</sup> Lima et al. (2007).<sup>c</sup> Not found.

quantum sensor connected to a data logger LI 2000 in open sky periods; mean  $\pm$  S.E. based on eight measures during 1 daylight period); (ii) partial shade ( $40 \pm 3\%$ ); (iii) dense shade ( $10 \pm 1\%$ ). Shade was made with 90% and 30% shade nets for partial shade and for dense shade, respectively, attached under the roof and at the four sides of



**Fig. 1.** Environmental factors in the greenhouse during the experiment. (a) Daily precipitation simulating the median year of total precipitation (1994, data from 1969–2001) in a dry forest region in northeast Goiás ( $13^{\circ}35'S$  e  $46^{\circ}46'W$ ). Sowing dates are shown. (b) Mean daily maximum and minimum temperatures for each month. (c) Mean daily maximum and minimum relative humidity for each month. The device in full sun did not work from March to July, the device in partial shade did not work in March, April, July, August or September and the device in dense shade did not work in March or April. (d) Soil moisture estimated by gravimetry on selected days during the experiment.

the greenhouse. Light treatments are those commonly found in mature forest, gaps and open areas during the wet season in dry forests of Central Brazil (Vieira and Scariot, 2008). Hence, the experiment had the factors dispersal timing (two levels), shade (three levels) and species (eight levels) ( $2 \times 3 \times 8 = 48$  experiment levels). For each experiment level, 84 seeds were sowed in a 6-cm distance between each other (Fig. 2).

## 2.5. Census and measurements

Seeds were verified every 3–5 days from the first applied rain (18 October 2005) up to 2 months, then monthly until November 2006. Survivorship was identified by the presence of green leaves

**Table 2**

Log-linear analysis testing the main effects and interactions of dispersal timing and shade on the seed germination of eight tree species

	d.f.	Partial association $\chi^2$	<i>P</i>
<i>Amburana</i>			
Dispersal timing	1	0.00	1.000
Shade	2	5.83	0.054
Interaction	2	7.87	0.020
<i>Anadenanthera</i>			
Dispersal timing	1	3.03	0.082
Shade	2	35.07	<0.001
Interaction	2	2.88	0.237
<i>Aspidosperma</i>			
Dispersal timing	1	0.15	0.700
Shade	2	9.47	0.009
Interaction	2	1.43	0.490
<i>Cavanillesia</i>			
Dispersal timing	1	13.55	<0.001
Shade	2	0.42	0.809
Interaction	2	6.52	0.038
<i>Cedrela</i>			
Dispersal timing	1	10.24	0.001
Shade	2	18.02	<0.001
Interaction	2	36.17	<0.001
<i>Myracrodruon</i>			
Dispersal timing	1	3.36	0.067
Shade	2	0.65	0.723
Interaction	2	3.33	0.189
<i>Sterculia</i>			
Dispersal timing	1	3.55	0.060
Shade	2	7.70	0.021
Interaction	2	2.63	0.268
<i>Tabebuia</i>			
Dispersal timing	1	88.12	<0.001
Shade	2	24.86	<0.001
Interaction	2	6.55	0.038

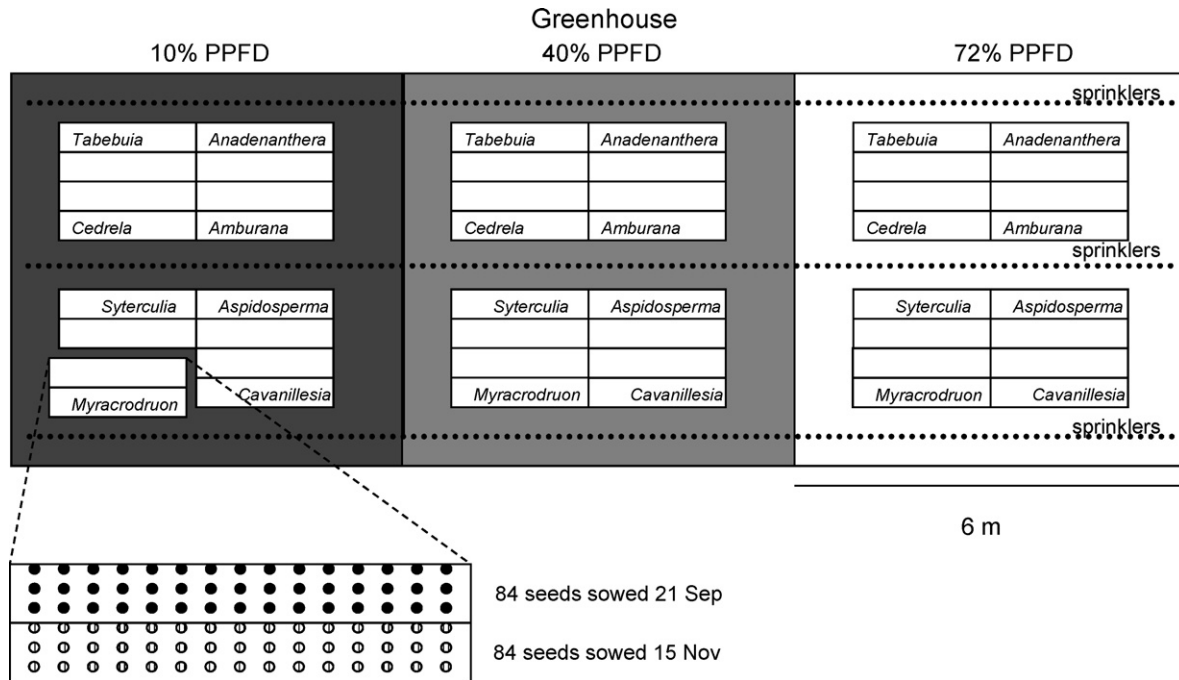


Fig. 2. Experimental design carried out in the greenhouse.

in the rainy season and by stem turgidity during the dry season because all species were deciduous. We also visually verified the causes of mortality when possible. Half of the individuals were harvested (intercalated) on 7 January 2006 to avoid or reduce competition between seedlings. Seedling density in the experiment was 36% of that found for tree species (<100 cm in height) in dry forests where seeds were collected (Sampaio, 2001). After the rainy season (25 April 2006), half of the remaining seedlings were harvested to obtain dry mass. The other half was left to follow survivorship during the dry season. For the remaining seedlings, stem height and diameter were measured on 25 May 2006 to test the relationship between size and survival after the dry season (data not shown). Harvested seedlings were dried (70 °C) to constant weight, then weighed by parts on a precision balance 0.01 g: primary and secondary roots, stems, leaves, cotyledons and petioles, as well as the primary and secondary rachis, when applicable. We present only total mass, primary root mass and stem mass. Because the mass of roots and stems are organs of potential reserve, they are related to survivorship after the dry season.

#### 2.6. Environmental data

Air temperature, humidity and soil moisture were measured at the three light levels in the greenhouse. Air temperature and humidity were measured every 10 min with HOBO<sup>®</sup> Pro RH/Temp (one device for each light level). Daily means by month of maximum and minimum temperatures and humidity are shown (Fig. 1b and c). Soil moisture was determined by gravimetry several times after rain, totaling 14 measurements (Fig. 1d). We collected four soil samples for each light level, randomly selecting four raised beds for every soil collection.

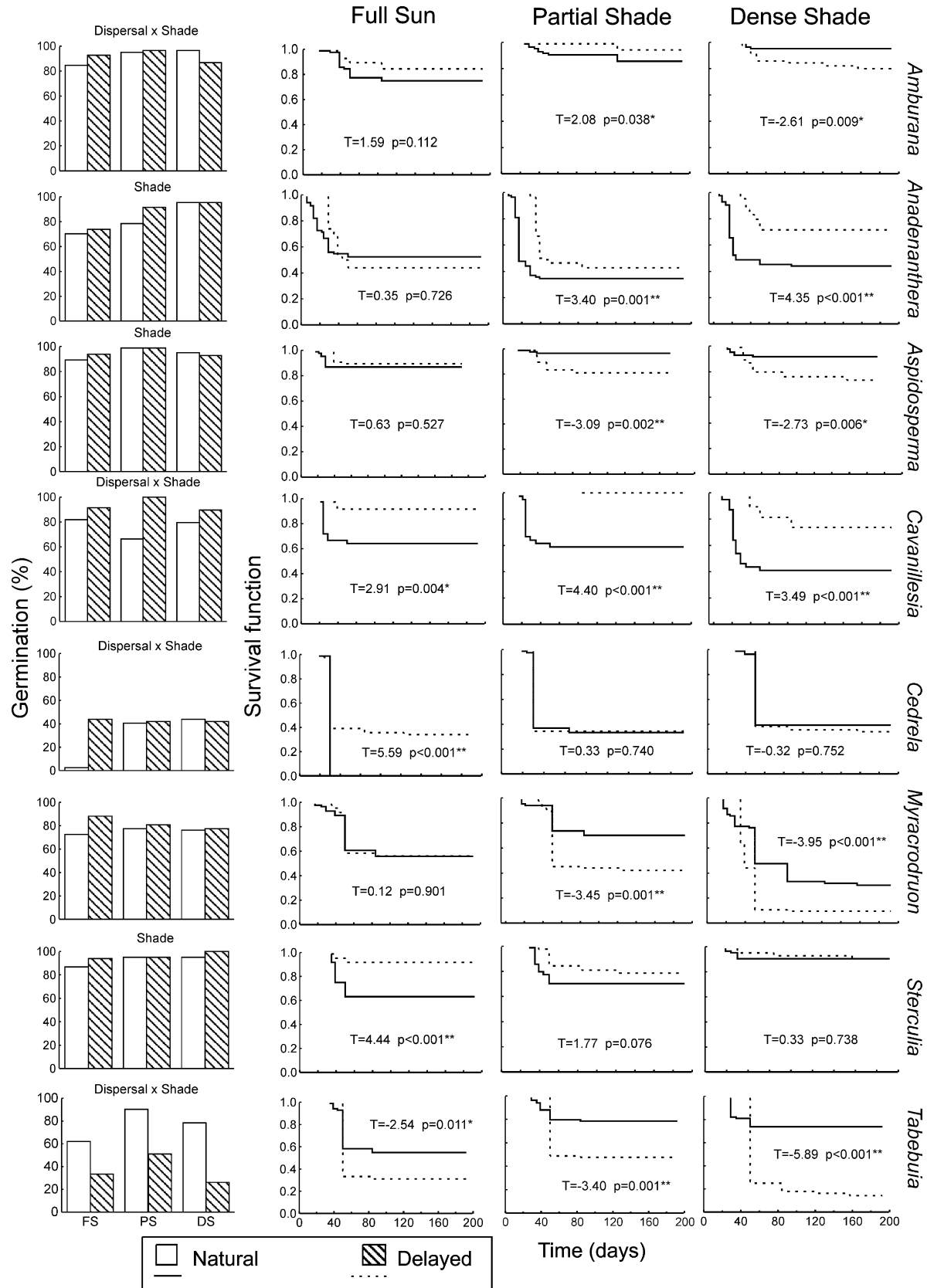
#### 2.7. Statistical analyses

Each individual seedling was considered an independent sample. There was no replication of greenhouse, light levels or

blocks due to the unavailability of other greenhouses. We opted to divide the greenhouse into three compartments (light levels) instead of applying light treatments in small blocks. Hence, each compartment had a relatively large area, permitting less influence of other compartments and higher microclimatic homogeneity inside it. The proportions of germinated seeds were compared for each species to the factors for dispersal timing, shading and interaction with Log-linear analyses (Tabachnick and Fidell, 2001). Survival curves of seeds or seedlings from the first census (3 days after the first rain, 18 October 2005) through the end of the rainy season (25 April 2006; 192 days) were compared between dispersal timings for each species in each shade level. Survival curves are the proportion of sowed seeds that survived through time (survival function), and were compared by Log-Rank test (StatSoft, 2000). For this analysis, seeds and seedlings were considered alive individuals in a continuum without distinction between them. This approach permitted the survival curve to follow the complete seed trajectory. Hence, the proportion of final survivorship was related to the total number of sowed seeds. Seedlings harvested in January were part of the analyses until the harvesting date and then were censored. Seedling survival after the dry season (November 2006) was not compared statistically because virtually no seedlings died and sprouting in December 2006 generated obvious results (see Section 3). Growth (total, root and stem dry mass) at the end of the dry season was compared by two-way ANOVAs for each species. Again, each plant was considered an independent sample.

### 3. Results

Greenhouse compartments (shade levels) were different for light, maximum air temperature, air humidity and soil moisture. Soil moisture was similar among compartments only when measured up to 2 days after a precipitation event. There was a gradient of maximum temperature, minimum air humidity and soil moisture from full sun to dense shade (Fig. 1).



**Fig. 3.** Germination percentage and survival function of seeds/seedlings of eight tree species sown on 15 September (natural-timing dispersal) and on 15 November (delayed dispersal), in three shading levels (full sun = FS, partial shade = PS and dense shade = DS). Significant effects (log-linear analyses) of dispersal timing and shade are shown. For the survival function analyses, the comparisons between dispersal timings were run independently for each shade level (Log-Rank test; shown on the graphs).

3.1. Hypothesis 1: natural-dispersal seeds have lower germination and initial seedling survival than delayed-dispersal seeds due to desiccation

3.1.1. Germination

Species were affected differently by dispersal timing, shade and interaction (Table 2; Fig. 3). There was an effect of dispersal timing on the germination in three (*Cavanillesia*, *Cedrela* and *Tabebuia*) out of eight studied species. For these species and *Amburana* there was interaction between dispersal timing and shade. *Cavanillesia* had lower germination percentage when dispersed in September, and the difference was greater with

partial shade. *Cedrela* had a strong decrease in germination percentage when dispersed in September in full sun. *Amburana* had a lower germination percentage when dispersed in September only in full sun; the inverse occurred in dense shade. For *Myracrodruon*, the effect of dispersal timing was marginal, influenced by the lower germination percentage with natural dispersal in full sun. *Tabebuia*, contrary to the expected, had a higher germination percentage when dispersed in September, mostly in dense shade. *Anadenanthera* and *Sterculia* experienced a positive effect of shade on germination because of the lessened desiccation. *Aspidosperma* had a higher germination percentage in partial shade.

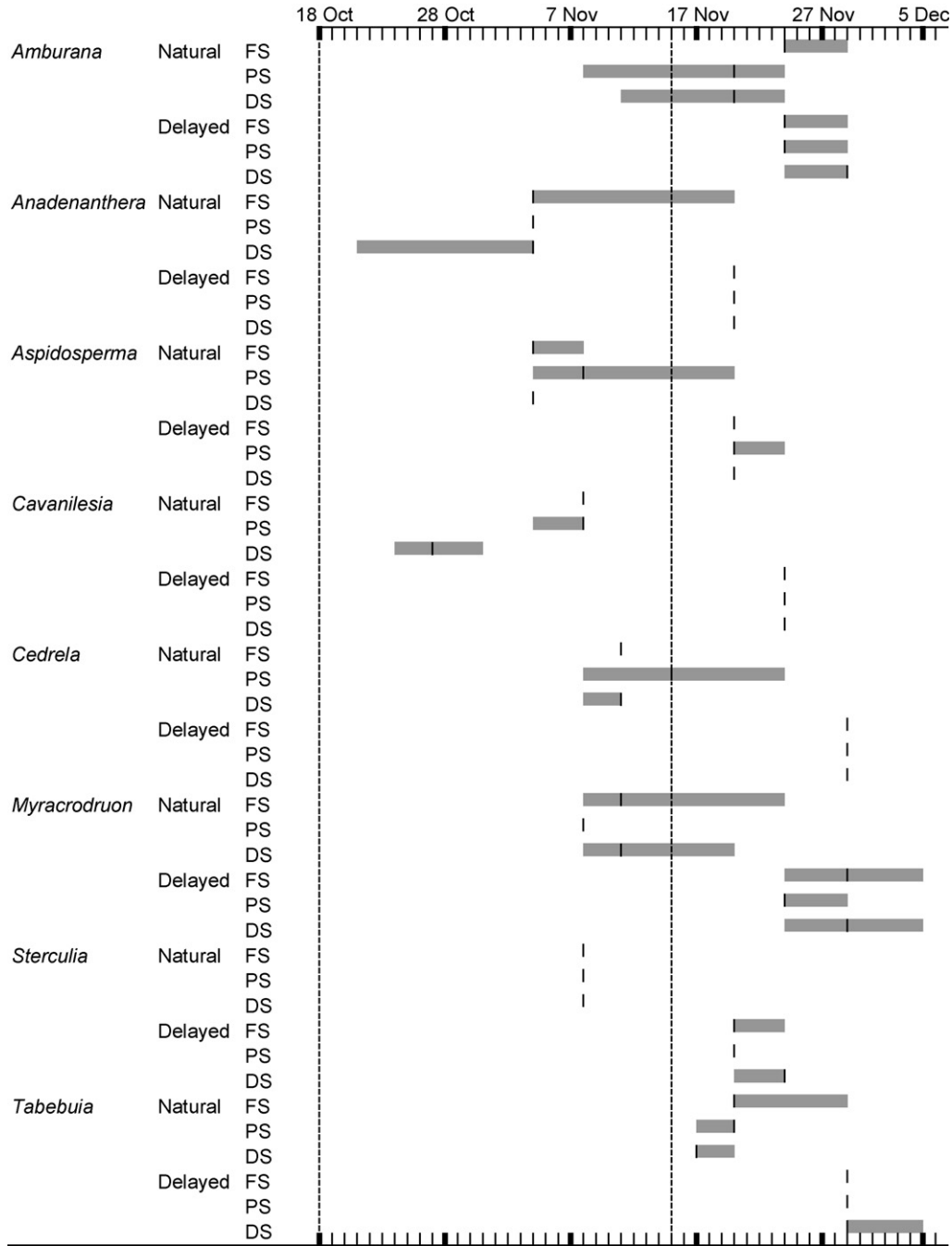
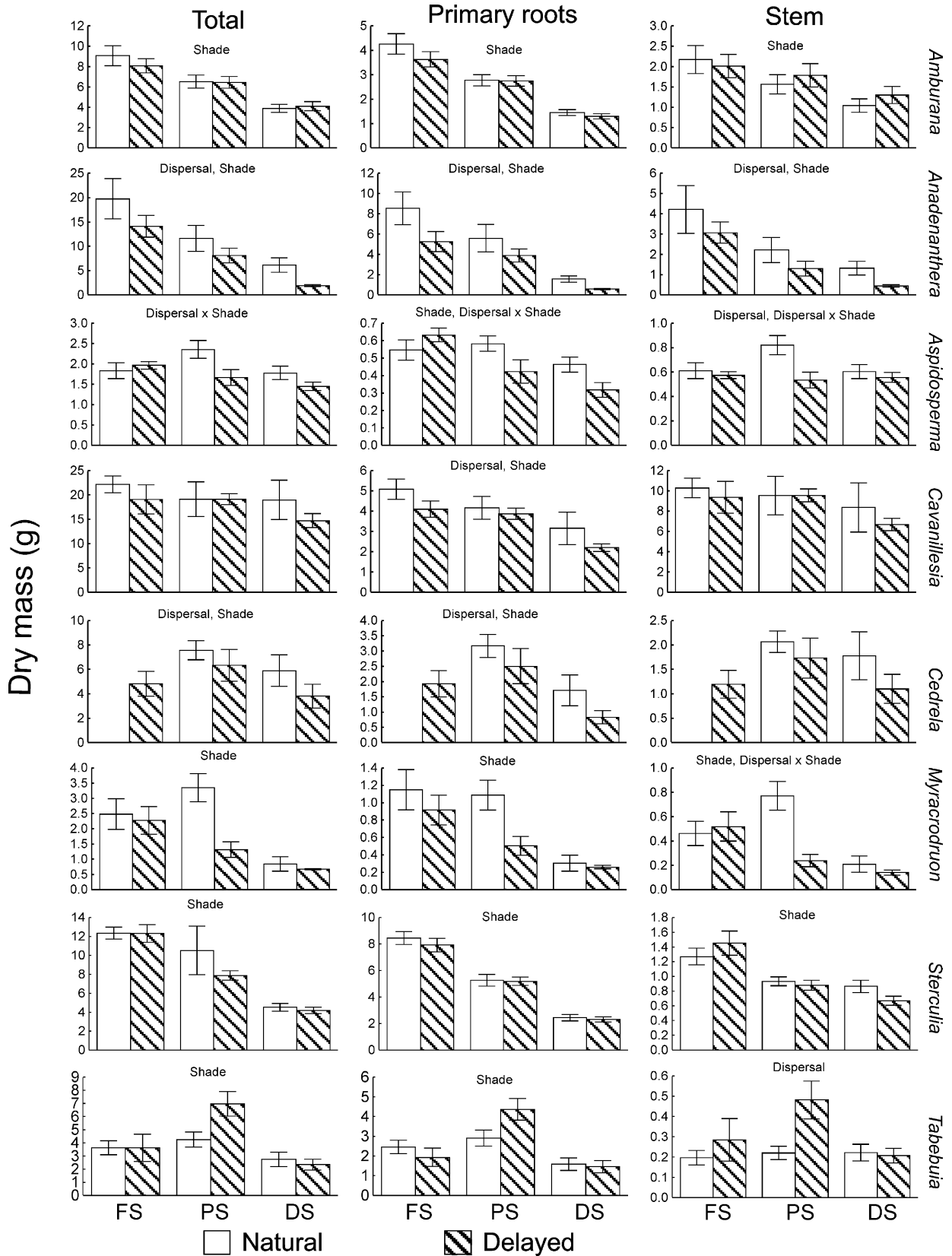


Fig. 4. Germination date of tree species dispersed on 15 September 2005 (natural dispersal) and on 15 November 2005 (delayed dispersal), in three shade levels (full sun = FS, partial shade = PS and dense shade = DS). Gray bars are 1° quartile–3° quartile and solid vertical lines are median values of germination date. Vertical dashed lines are the first rain date (18 October 2005) and the delayed-dispersal date (15 November 2005). The date of natural dispersal for *Cavanillesia* was 7 October 2005.





**Fig. 5.** Total, root and stem dry mass of seedlings of eight tree species sown on 15 September 2005 (natural dispersal) and on 15 November 2005 (delayed dispersal), in three shade levels (full sun = FS, partial shade = PS and dense shade = DS). Seedlings were collected at the end of the rainy season (25 April 2006). Significant effects (ANOVAs) of the factors dispersal timing and shade are shown.

### 3.1.2. Germination timing

There was a difference of 61 days between natural and delayed dispersal (39 days for *Cavanillesia*). However, in this simulation the first rain occurred on 18 October so germination could only happen after that, because the soil was too dry to permit any germination before this date. Thus, although the difference between sowing dates is 61 days, possible differences in germination is 28 days, which is the difference between the first rain and the delayed dispersal. Seeds dispersed in September germinated slower than those dispersed in November; few seeds germinated promptly after the first rains (Fig. 4). Seeds dispersed in November, when soil moisture was high, germinated quickly, making differences in germination time frequently less than 28 days (variation among species from 0 to 28 days). *Amburana* and *Tabebuia* dispersed in September had the slowest germination, resulting in a difference in germinating date of 0–9 and 9–13 days respectively (ranges are the variation in number of days among the shade treatments), between seeds dispersed in September and seeds dispersed in November. *Aspidosperma* and *Sterculia* differed by 12–16 days, *Cedrela* by 13–18 days, *Anadenanthera* by 16 days (all seeds dispersed in a dispersal timing germinated at the same census interval), *Myracrodruon* by 16–18 days and *Cavanillesia* by 16–28 days.

### 3.1.3. Survival to the end of the rainy season

Seedling survival did not follow the germination results for the most species (Fig. 3). Only *Cedrela* and *Sterculia* followed the expected results; seed germination and seedling survival were

higher for seeds delayed dispersed in the full sun treatment. In partial and dense shade, dispersal timing did not affect survival curves. On the other hand, survival was not greater for *Amburana*, *Aspidosperma*, *Myracrodruon* and *Tabebuia* when dispersed in November. Conversely, they had lower survival in partial shade, and especially in dense shade, when dispersed in November. *Anadenanthera* had higher survival when dispersed in November in partial shade, and especially in dense shade. *Anadenanthera* seeds dispersed in September germinated quickly, particularly in dense shade, and were killed by desiccation due to irregular rains in that period.

*Cavanillesia*, another fast germinating species, also had high mortality when dispersed in September. Similar to *Anadenanthera* seedlings, most mortality in partial and dense shade is associated with faster germination in these compartments. Hence, in full sun three species had higher survival in delayed dispersal, one had lower survival and four showed no difference. In partial shade three had higher survival with delayed dispersal, three had lower survival and two showed no difference. In dense shade two had higher survival with delayed dispersal, four had lower survival and two showed no difference.

### 3.2. Hypothesis 2: natural-dispersal seedlings are larger at the end of the rainy season than delayed-dispersal seedlings, resulting in higher survival probability at the end of the dry season

Among the eight species studied, two had higher total mass, three had higher primary root mass and two had higher stem mass

**Table 3**  
Results of two-way ANOVAs for each species testing the effects of dispersal timing, shade and interaction on the total, root and stem biomass of seedlings at the end of the rainy season

	d.f.	Total		Primary		Stem	
		F	P	F	P	F	P
<b><i>Amburana</i> (n = 99)</b>							
Dispersal timing	1	1.05	0.307	2.03	0.157	0.81	0.370
Shade	2	36.48	<0.001	56.39	<0.001	22.03	<0.001
Interaction	2	1.63	0.202	0.96	0.387	1.40	0.253
<b><i>Anadenanthera</i> (n = 62)</b>							
Dispersal timing	1	7.25	0.009	7.81	0.007	4.52	0.038
Shade	2	27.98	<0.001	40.03	<0.001	16.27	<0.001
Interaction	2	1.60	0.212	0.35	0.708	0.69	0.504
<b><i>Aspidosperma</i> (n = 97)</b>							
Dispersal timing	1	3.59	0.061	3.34	0.071	5.42	0.022
Shade	2	1.98	0.144	6.85	0.002	1.16	0.318
Interaction	2	3.94	0.023	4.37	0.015	3.23	0.044
<b><i>Cavanillesia</i> (n = 46)</b>							
Dispersal timing	1	1.47	0.233	4.46	0.042	0.64	0.430
Shade	2	0.96	0.392	10.91	<0.001	1.71	0.196
Interaction	2	0.94	0.398	0.68	0.515	0.52	0.601
<b><i>Cedrela</i> (n = 39)</b>							
Dispersal timing	1	4.33	0.045	5.25	0.028	3.19	0.083
Shade	1	5.11	0.030	17.84	<0.001	2.89	0.098
Interaction	1	0.26	0.616	0.12	0.728	0.12	0.733
<b><i>Myracrodruon</i> (n = 59)</b>							
Dispersal timing	1	2.29	0.136	1.29	0.260	2.99	0.090
Shade	2	5.10	0.009	4.76	0.013	3.78	0.029
Interaction	2	3.12	0.052	1.98	0.149	4.45	0.016
<b><i>Sterculia</i> (n = 97)</b>							
Dispersal timing	1	1.11	0.294	0.30	0.585	0.55	0.461
Shade	2	65.97	<0.001	106.89	<0.001	19.70	<0.001
Interaction	2	0.16	0.848	0.22	0.801	1.96	0.147
<b><i>Tabebuia</i> (n = 62)</b>							
Dispersal timing	1	0.86	0.359	0.26	0.612	4.07	0.049
Shade	2	7.89	0.001	11.08	<0.001	2.75	0.072
Interaction	2	1.83	0.170	2.40	0.100	2.22	0.118

Significant *P* are in bold.



with natural dispersal than with delayed dispersal (Fig. 5; Table 3). Only for *Anadenanthera* where seedlings from natural dispersal larger for both primary roots and stem, resulting in four species with higher mass in reserve organs in natural dispersal than in delayed dispersal (*Anadenanthera*, *Aspidosperma*, *Cavanillesia* and *Cedrela*). Only *Tabebuia* had significant higher stem dry mass with delayed dispersal. *Aspidosperma* and *Myracrodruon* seedlings also had interaction effects (dispersal timing  $\times$  shade) on dry mass. *Aspidosperma* seedlings in partial and dense shade had higher total, primary roots and stem dry mass with natural dispersal. *Myracrodruon* had higher stem dry mass with natural dispersal in partial shade. Shade affected at least one growth parameter for all species. Four species increased dry mass with light availability (*Amburana*, *Anadenanthera*, *Cavanillesia* and *Sterculia*). *Cedrela*, which could not be evaluated in full sun (100% mortality), *Myracrodruon* and *Tabebuia* had greater growth in partial shade.

### 3.3. Does seedling size at the end of the rainy season affect survival during the dry season?

No seedlings died during the dry season (census from May to November 2006) except for one seedling of *Aspidosperma* in partial shade with delayed dispersal. Although seedlings virtually did not die during the dry season, seedlings did not sprout when the rains started for half of the species and in December we uprooted these seedlings to confirm that roots were decayed. All *Anadenanthera* seedlings died at the onset of the rainy season. All *Aspidosperma* seedlings died except in dense shade with natural dispersal (44% sprouted;  $N = 18$ ). All *Tabebuia* seedlings died except in dense shade, natural and delayed dispersal (7% sprouted;  $N = 14$  and 50% sprouted;  $N = 4$ , respectively). For *Myracrodruon*, 8% ( $N = 13$ ) sprouted in full sun, 57% ( $N = 14$ ) sprouted in partial shade and 40% ( $N = 10$ ) sprouted in dense shade with natural dispersal; 13% ( $N = 16$ ) sprouted in full sun, 8% ( $N = 12$ ) sprouted in partial shade and no seeds ( $N = 3$ ) sprouted in dense shade with delayed dispersal. *Amburana*, *Cavanillesia*, *Cedrela* and *Sterculia* had high sprouting at the onset of the rainy season. All *Cavanillesia* and *Sterculia* seedlings sprouted. All *Cedrela* seedlings sprouted, except 10% ( $N = 10$ ) in full sun with delayed dispersal. All *Amburana* seedlings sprouted, except 5% ( $N = 20$ ) in dense shade with natural dispersal.

## 4. Discussion

### 4.1. Hypothesis 1: natural-dispersal seeds have lower germination and initial seedling survival than delayed-dispersal seeds due to desiccation

The lower germination expected for seeds with natural dispersal and in full sun was not evident because most species delayed germination to a point where germination was simultaneous to that of delayed-dispersal seeds (e.g. *Amburana*). Hence, we conclude that seeds had a certain dormancy to minimize mortality after the first rains. However, seedlings of *Anadenanthera* and *Cavanillesia*, which had the fastest germination, had higher survival when their dispersal was delayed, mainly in the shaded areas where germination of both species was very fast. The longer lasting soil moisture in shaded treatments promptly started germination of these species and consequently increased seedling mortality in the following dry spells. Even for *Cavanillesia*, which has mucilaginous seeds to avoid desiccation after imbibing, dry spells decreased germination and early seedling survival. Similar results were found for seedlings of *Cavanillesia platanifolia* (Bonpl.) Kunth, which had higher survival with constant watering than in non-watering for up to 2 weeks (Garwood, 1985).

Delayed dispersal decreased by half the germination percentage of *Tabebuia*, probably because in this season the microbial activity is much higher, mainly in shaded areas (D.L.M. Vieira, pers. obs. in field and greenhouse), favoring pre-germination seed decay. Some *Aspidosperma* seeds dispersed in dense shade also decayed. At the time of delayed dispersal, rains were constant outside of the greenhouse, and the light intensity was lower than that found in September during natural dispersal. In October there were 4 rainy days in Brasília, in November there were 18 days and in December, 24 days. The low light intensity, together with the high biological activity during the season of constant rains, caused mortality of imbibed seeds and seedlings (as *Tabebuia*) by pathogens. Seedlings from seeds subjected to natural dispersal were more developed in November, which conferred higher resistance to pathogens (Gilbert et al., 2001; Baraloto et al., 2005a).

Although precipitation in the greenhouse simulated a median year in a dry forest region (1994, São Domingos county, Goiás state), climate outside the greenhouse was certainly milder than in São Domingos county in 1994. From September 2005 to April 2006, Brasília had 102 days with some precipitation while we provided seedlings with 62 days of some precipitation (there is no temperature data for São Domingos). This amelioration of extreme temperatures may have reduced mortality by desiccation. Also, in this experiment we applied the median total precipitation, but there are many possible precipitation distributions that were not evaluated. The date of the first rain, the volume and frequency of the first rains affect germination and seedling survival (Augspurger, 1980). Another consideration about this experiment is that treatments simulated light levels found in mature forest, gaps and open areas during the wet season (Vieira and Scariot, 2006b, 2008). However, in the dry season, canopy cover of Central Brazil dry forests is much lower than the applied experiments, reaching mean values of ca. 40% (Vieira and Scariot, 2006b; Nascimento et al., 2007). Again, desiccation of natural-dispersal seeds would be higher if light levels were higher from September to November, when canopy is still deciduous.

### 4.2. Hypothesis 2: natural-dispersal seedlings are larger at the end of the rainy season than delayed-dispersal seedlings, resulting in higher survival probability at the end of the dry season

Under the hypothesis that seedlings from natural-dispersal seeds are bigger than those from delayed-dispersal seeds, natural-dispersal seeds are expected to germinate before delayed-dispersal seeds. Because several species delayed germination with natural-dispersal, the hypothesis cannot be accepted for all species studied. Hence, the four species that delayed germination did not develop bigger primary roots under delayed dispersal, while three out of four fast-germinating species had higher primary root biomass with natural dispersal. *Myracrodruon* had fast germination, but did not develop bigger roots with natural dispersal than with delayed dispersal. Seeds of *Myracrodruon* natural-timing dispersed that germinated fast had high mortality, while seeds with some dormancy had high seedling survival.

### 4.3. Trade-off of survival $\times$ growth between dispersal timings

Germination and early seedling survival of dry forest trees improve with shade because soil retains moisture longer and microclimate is milder than open areas (Gerhardt, 1996b; Ray and Brown, 1995; McLaren and McDonald, 2003; Woods and Elliott, 2004; Vieira and Scariot, 2006b; Vieira et al., 2007). However, in open areas seedling growth is higher than in shaded areas (Fetene and Feleke, 2001; Marod et al., 2004). This study corroborates these statements: with natural dispersal, partial or dense shade

increased the germination percentage of four species and the survival at the end of the rainy season of six out of eight species, even though differences were small except for *Cedrela*. Seedling growth in dense shade was much lower than in partial shade and full sun, with full sun leading to more growth than partial shade for three species, in congruence with the literature.

There was not consistent higher mortality in full sun relative to other shade treatments (except for *Cedrela*), and increased growth in full sun did not increase survival during the dry season. However, because delayed dispersal increased germination and early survival of fast germinating species, sowing this type of seeds only when rains are constant seems to be a positive strategy for increasing establishment. A long-term field experiment is necessary to verify the best environment, if it exists, for the development of these species, and whether in fact seedling growth affects survival. For example, higher growth could increase survival after herbivory or fire, or in competition with grass. Survival of virtually all plants during the dry season is an unexpected result, as mortality during the dry season is a major limiting factor for the regeneration of seasonal forest trees (Lieberman and Li, 1992; Cabin et al., 2002; Marod et al., 2002; McLaren and McDonald, 2003; Marod et al., 2004; Russell-Smith and Setterfield, 2006), even for deciduous seedlings (McLaren and McDonald, 2003; Vieira et al., 2007). Factors found in the forest but not in the greenhouse can contribute to mortality of deciduous seedlings, for example root predation by termites (D.L.M. Vieira; pers. obs.).

The high mortality for half of the species at the onset of the rainy season was unexpected. We could not determine if mortality was caused by pathogens or if seedlings were stressed after passing through the dry season and could not sprout when rains started, and then pathogens attacked them. More studies are necessary to understand the sprouting process and its limiting factors, including dry season stress and microorganism activity at the onset of the rainy season. We did not find this type of research in literature. Our results are not able to contribute to this question, as we did not take physiological measures of seedlings and biological attributes of soil were certainly affected in the greenhouse.

#### 4.4. Ecological traits of dry forest seedlings

Our results contribute to the discussion about the ecological traits of dry forest seedlings. Comparing nine vicariant species, Hoffmann and Franco (2003) found that 150-day-old seedlings from gallery forests of Central Brazil have a root/shoot ratio equal to 1.26, while seedlings from Cerrado (Brazilian savannas) have a root/shoot ratio equal to 2.31. Open and woodland savanna seedlings (150-day-old) from 10 tree species had an average root/shoot ratio of 2.2, varying from 0.6 to 4.5 among species (Moreira and Klink, 2000). It is argued that light is more abundant in Cerrado (Kanegae et al., 2000), but water and nutrients are limiting factors, causing high investment in roots. Large roots would serve as a reserve for resprouting after fire (Moreira and Klink, 2000; Hoffmann and Franco, 2003). In gallery forests light is the limiting factor, ranging from 0.3% to 11% of transmittance in the understory (Felfili and de Abreu, 1999), which induces shoot growth (Hoffmann and Franco, 2003). In a dry forest environment, seedlings are highly limited by water during the dry period. On the other hand, in the rainy season the large amount of litter accumulated during the dry season is rapidly decomposed, liberating high levels of nutrients (Roy and Singh, 1995; Campo et al., 1998). Seedlings of deciduous species, like those studied here, should grow fast during the rainy season and accumulate biomass in the roots and stem, which have storage functions (Wurth et al., 2005), in order to resprout at the onset of the rainy

season. In fact, seedlings of *Amburana*, *Anadenanthera*, *Sterculia* and *Tabebuia* had tuberous roots. Seedlings are not expected to invest in water acquisition because seedlings are deciduous and soils from dry forests are frequently shallow on calcareous outcrops, where there is no water during the dry season. Light is not a limiting factor as it is in moister forests because the canopy is on average 10% open (Vieira and Scariot, 2008), much higher than the 2% average of moister forests (Nicotra et al., 1999; Poorter and Arets, 2003). Furthermore, during the first rains, the canopy is not completely closed because many species have not yet produced leaves. Thus, contrary to savanna seedlings, the roots should not necessarily be large because the stem can store starch. But leaf biomass ratio should be similar to savanna seedlings because light is not too limiting and seedlings need to invest in reserve tissues to resprout. The root/shoot ratio of seedlings that were approximately 150 days old was extremely variable among species (seedlings in partial shade and delayed dispersal: *Cavanillesia*, *Aspidosperma*, *Myracrodruon*, *Cedrela*, *Anadenanthera*, *Amburana*, *Tabebuia* and *Sterculia* had ratios of 0.3, 0.6, 0.6, 0.7, 1.1, 1.2, 2.0 and 2.4, respectively). But, in fact, the mean value among species (1.13) was similar to gallery forest seedlings (Hoffmann and Franco, 2003; see similar values for older seedlings in Felfili et al., 2001). Leaf biomass ratio for *Cavanillesia*, *Aspidosperma*, *Myracrodruon*, *Cedrela*, *Anadenanthera*, *Amburana*, *Tabebuia* and *Sterculia* was 0.22, 0.30, 0.41, 0.25, 0.26, 0.17, 0.24, 0.14, respectively; mean = 0.24, similar to savanna seedlings, which had mean = 0.22 (Hoffmann and Franco, 2003).

## 5. Conclusions and recommendations

Although the dry season is the better time for seed dispersal, it is certainly not for germination. Seeds have to be quiescent until the first rains and to remain dormant a little while after that. The species studied had variable dormancy, from fast germinating species, *Anadenanthera* and *Cavanillesia*, to species that germinated after constant rains, *Amburana* and *Tabebuia*. Thus, delayed dispersal can be advantageous for fast germinating species, but irrelevant or even worse for those with a short dormancy, because in this time pathogens and competitors are more abundant, attacking seeds soon after imbibition. Future research should evaluate variability among species for (i) dormancy on a fine time scale (days), with different water potentials; (ii) desiccation after imbibition/germination with different water potentials; and (iii) duration and synchrony of seed dispersal. Given the erratic pattern of rains and its impact on dry forest regeneration, natural selection must act to favor high variability in the regeneration mechanisms within species. This research can promote an understanding of regeneration strategies of each species and contribute to improved management plans.

## Acknowledgements

We thank Antonieta N. Salomão for lab and greenhouse facilities at Embrapa Recursos Genéticos e Biotecnologia. Nilton F. Barbosa, Juarez P. do Amaral, Vanessa Martins, Marcos P.R. da Silva, Junio O. da Silva, Hélder N. Consolaro, Aline Z.M. Simões, Ângela Rossi and Lourdiane M.G. Nogueira for helping with data collection. Ernestino S. Guarino, Maurício B. Sampaio and Alexandre B. Sampaio for helping with experimental design and criticizing the early phases of the manuscript. Lisa Mandle for English editing. Part of this study was funded by FNMA/MMA (Ministry of Environment), through the Conservação e Reintrodução de Espécies Ameaçadas de Extinção edital. D.L.M. Vieira had a doctorate fellowship from CAPES and CNPq.

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