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Ecology of seed germination of eight non-pioneer tree species from a tropical seasonal rain forest in southwest China

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Abstract We compared various aspects of the seed biology of eight non-pioneer tree species from a tropical seasonal rain forest in Xishuangbanna, SW China, that differ in time of dispersal, size and fresh seed moisture content (MC). Seeds were tested for germination under laboratory conditions after dehydration to different moisture levels and under 3.5, 10 and 30% solar irradiances in neutral-shade houses. For six species, germination was also compared in forest understory (3.5% light) and center of a forest gap (32.5% light). Under continuous dehydration over activated silica gel, 100% of seeds of four species had lost the ability to germinate after 48 h, and those of all species except *Castanopsis hystrix* (decreased from >90 to 30% germination) had lost the ability to germinate after 120 h. Four species did not differ in final germination percentages at the three irradiances (i.e. uniform germination). However, final germination percentages of *Horsfieldia pandurifolia* and *Litsea pierrei* var. *szemaois* were significantly lower in 30% than in 10 or 3.5% light, and seeds of *Antiaris toxicaria* and *C. hystrix* germinated to higher percentages in 30 and 10% than in 3.5% light. Mean time to germination (MTG) of the eight species (forest and shade house data combined) ranged from 5–5 days for *Pometia tomentosa* to 72–207days for *L. pierrei*; MTG for four species was ≤21 days. There was no obvious relationship between relative desiccation resistance and either time of dispersal, MTG or uniformity of germination at the three light levels, or between seed size and MC or MTG. However, the relationship between seed MC at maturity (25–60% fresh mass basis) and MC at 50% loss of seed viability (12.4–42.5%) was significant. Seven of the species fit Garwood's (Ecol Monogr 53:159–181, 1983) rapid-rainy germination syndrome and one, *L. pierrei*, either her delayed-rainy or intermediate-dry germination syndrome. However, fresh, non-dehydrated seeds of all eight species germinated in ≤30 days at constant 30°C in light.

Keywords Desiccation-sensitive seeds · Forest gap · Forest understory · Fresh seed moisture content · Seed dispersal · Seed germination · Seed light response · Seed size

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Introduction

With regard to their desiccation tolerance and storage behavior, seeds of most species can be placed into one of two categories: orthodox or recalcitrant. Orthodox (desiccation-tolerant) seeds can be dried to a very low moisture content (MC) (around 2–5% MC or to as low as –350 MPa) and stored at sub-zero temperatures (optimum, –18°C) and low relative humidity for long periods of time without loss of viability (Roberts 1973; Roberts and Ellis 1989). Recalcitrant (desiccation-sensitive) seeds, on the other hand, lose viability when their MC falls below about 20–30% (or to $<$ about –1 to –3 MPa), and of course with such high water content, they cannot tolerate sub-zero temperatures because of ice formation. Further, recalcitrant seeds of tropical species are chilling-sensitive, and thus they may be injured at temperatures as high as 10–15°C (Farrant et al. 1988; Roberts and Ellis 1989; Pritchard et al. 2004).

The storage behavior of seeds of a relatively few species do not fit into either the orthodox or recalcitrant category (Farrant et al. 1988). Thus, a third category, termed intermediate, was created to accommodate them (Ellis et al. 1990, 1991a, b, c). Seeds with intermediate storage behavior are less tolerant of drying (about 6–12% MC, or to as low as –250 MPa) than orthodox seeds, and their optimum storage temperature is >0°C (optimally, 15°C) (Ellis et al. 1990, 1991a, b, c; Hong and Ellis 1995; Pammenter and Berjak 1999; Berjak and Pammenter 2001, 2002; Dickie and Pritchard 2002). Further, it is becoming more and more apparent that the storage behaviors of seeds fit multiple points along a continuum rather than into discrete categories, and this is particularly true for desiccation-sensitive seeds (Farrant et al. 1988; Berjak and Pammenter 1994, 2002, 2004; Pammenter and Berjak 1999).

Seeds of a very high percentage of both angiosperms and gymnosperms are desiccation-tolerant (orthodox), and thus the ability to tolerate drying is a major adaptation for their dispersal and survival (Dickie and Pritchard 2002; Tweddle et al. 2003). Although desiccation-sensitive (non-orthodox) seeds are produced by nearly half of the tree species in broadleaf evergreen tropical rain forests, they are much less frequent in the seasonal tropics and in temperate-zone habitats (Pammenter and Berjak 2000; Tweddle et al 2003; Pritchard et al. 2004; Daws et al. 2005). Their presence in seasonal habitats appears, at least in part, to be related to the coordinated timing of seed maturity/dispersal and the rainy season. Thus, Pritchard et al. (2004) reported that desiccation-sensitive seeds of nine of 80 African tree species were shed in months with >60 mm rainfall, whereas the orthodox seeds of the other 71 species were shed in months with 0–>200 mm rainfall. Seeds of >50% of the 71 species were shed in months with <60 mm of rainfall and >30% in months with <25 mm of rainfall. In a study of the effects of desiccation on seeds of 225 species in a tropical seasonal forest in Panama, Daws et al. (2005) reported that seeds of 32 species were desiccation-sensitive and 183 desiccation-tolerant. Seeds of the desiccation-sensitive species were much more likely to be dispersed (Chi-square highly significant) in the wet season, whereas those of the desiccation-tolerant species were more likely to be dispersed in the dry season.

However, not all non-orthodox seeds are shed in the rainy season in tropical seasonal forests. Dussert et al. (2000) did a simulation study of the reproductive cycle and seed desiccation tolerance of nine species of *Coffea* native to African seasonal tropical forests in which length of the dry season varied considerably. Plants of all nine species flowered at the beginning of the rainy season and matured and dispersed fruits at the end of the rainy season. Thus, seeds of the nine species had to withstand drought periods of different lengths before soil moisture conditions became suitable for germination. Their study suggests that seed desiccation tolerance, based on water content at which half of the initial viability was lost, WC_{50} [g H_20 (gdw) $^{-1}$], and corresponding water activity (aw_{50}), was significantly negatively correlated with length of the dry season. That is, seeds shed at the beginning of a long dry season were more desiccation-tolerant than those shed at the beginning of a short dry season.

Once seeds are dispersed, then the habitat, through its various physical and biotic characteristics, act as a selective force in determining which species will germinate and become established in it (Bazzaz 1991). In tropical forests, light is one of the most important abiotic resources, and it can control germination of seeds in the field (Bazzaz and Pickett 1991; Swaine and Whitmore 1988; Whitmore 1989, 1998; Vazquez-Yanes and Orozco-Segovia 1994). Raich and Khoon (1990) monitored germination of seeds of 43 non-pioneers and gap species sown in trays and placed in a forest understory (96% canopy cover), artificial gap (50%) and/or large opening (2%) in a lowland rain forest in West Malaysia with a 1–3 month dry season. Using this as a criterion ≥10% germination in at least one of the two light environments between which comparisons were made, their results can be summarized as follows: (1) non-pioneer species germinated in both forest and gap; (2) gap species germinated in gap but not in forest; (3) a non-pioneer species was more likely to germinate in forest than in large opening; (4) a gap species was more likely to germinate in large opening than in forest, (5) a non-pioneer species was more likely to germinate in gap than in large opening and (6) a gap species was more likely to germinate in gap than in large opening.

Seeds of 19 species from a tropical seasonal forest in Ghana were tested for germination in a shade house in 30% light vs. dark and 17 species in 5% neutral shade vs. 5% green shade (green-filtered light, red/far-red ratio (R/FR) = 0.43). Further, 11 species were tested in forest understory (2% irradiance), canopy gaps of different sizes (and thus different irradiances) and in 100% irradiance outside the forest (Kyereh et al. 1999; also see Swaine et al. 1997). Germination of three (of seven) pioneer species, *Musanga cecropioides*, *Nauclea diderrichii* and *Milicia excelsa* was very low (0–7%) in the dark, but they germinated to 33% in both 5 and 30% irradiance. Of these three species, only germination of *N. diderrichii* differed significantly between 5% green light and 5% neutral shade (i.e. lower in green shade). For 16 (of 19) species, including four pioneers, there was no significant difference in percentage germination between 30% light vs. dark, and for 16 (of 17) species, including six pioneers, germination did not differ significantly between 5% neutral shade and 5% green shade. Germination rate (speed) generally was higher in dark than in 30% light. Only germination of seeds of *Terminalia ivorensis* (a pioneer) was noticeably lower in forest understory than in a forest gap with 30% irradiance. Germination in all but two of the 11 species tested was inhibited by 100% irradiance. For a semideciduous tropical forest in Brazil, Souza and Válio (2001) reported that seeds of only two (*Cecropia polystachya* and *Ficus guaranitica*) of 15 species with ≥30% germination in light and/or dark were light-stimulated.

Few studies have been done on germination of seeds of native species in the tropical seasonal rain forest in Xishuangbanna, SW China. This study presents information about the whole-seed biology of eight non-pioneer tree species in this forest that differ in time of dispersal and in size and MC at maturity. Given the wide variation in seed traits among the eight species, we hypothesized that there are considerable differences among the species in desiccation tolerance and in germination characteristics. We further hypothesized that there are ecologically meaningful relationships among the traits. Thus, we asked the following questions: (1) What is the effect of dehydration on germination? (2) Do percentage and rate of germination differ under different light levels in neutral-shade and/or between forest gap and forest understory? (3) What are the relationships between the various aspects of the seed biology of the eight species?

Methods

Study site

Xishuangbanna (21°09′–22°33′N, 99°58′–101°50′E) is located in the southwest of China, bordering Laos and Myanmar on the upper course of the Mekong River. The region is dominated by a typical tropical monsoon climate characterized by distinct wet and dry seasons. Mean annual air temperature is 21.7°C, and mean annual rainfall is approximately 1500 mm, more than 80% of which occurs in the rainy season (May–October). Mean monthly rainfall ranges from 18.6 mm in January to 316.6 mm in July, mean maximum monthly temperatures from 24.1°C in December to 33.1 °C in April and mean minimum monthly temperatures from 12°C in January to 22.6°C in June and July (Fig. 1). Altitude varies from 420 to 2400 m, and the local climate changes conspicuously with altitude (Cao et al. 2006).

Due to its unique geographical location and climatic features, this area supports an evergreen tropical rain forest, which is confined to wet ravines, lowlands and low hills with good water supply. There is a small proportion of deciduous trees within the rain forest. The seasonal rain forest in Xishuangbanna

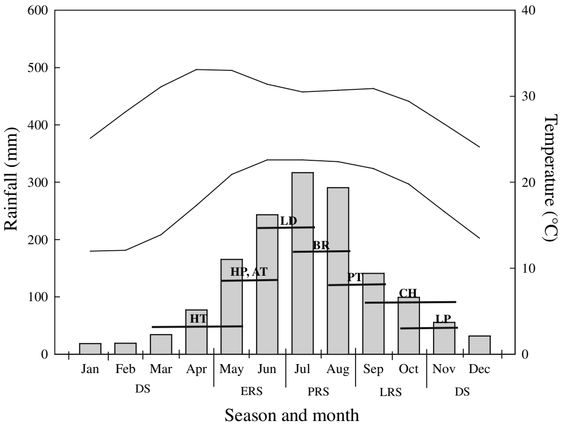

Fig. 1 Mean monthly rainfall (bars), mean monthly maximum (upper line) and minimum (lower line) temperatures and dispersal times (horizontal bars) for the eight species (initials). Rainfall and temperature data are 40-year averages (1959–1998) in Xishuangbanna, Yunnan Province, China. AT, *A. toxicaria*; BR, *B. ramiflora*; CH, *C. hystrix*; HP, *H. pandurifolia*; HT, *H. tetratepala*; LD, *L. dilleniifolia*; LP, *L. pierrei*; PT, *P. tomentosa*; DS, dry season; ERS, early rainy season; PRS, peak rainy season; LRS, late rainy season

usually occurs at altitudes ranging from 500 to 900 m. However, on south-facing slopes of large mountains this forest can extend to an elevation of about 1100 m along valleys (Wu 1980). The physical geography and forest vegetation of this area was described in Zhang and Cao (1995). Our forest experiment was done in a 1-ha permanent plot (750 m a.s.l.) described by Cao et al. (1996) and in a 116 m^2 forest gap near the 1-ha permanent plot described by Dou et al. (2001).

Study species

Seeds of eight non-pioneer (or climax) (sensu Swaine and Whitmore 1988; Whitmore 1989), tree species (Zhang and Cao 1995; Cao et al. 1996; Cao and Zhang 1997; Zhu 1997, 2006) that differ in dispersal time, size and fresh seed MC (Table 1) were chosen for a dehydration/germination experiment and for a shade house experiment, and six of the species were used to compare germination in a forest understory and in a forest gap. *Pometia tomentosa, Baccaurea ramiflora, Horsfieldia pandurifolia* and *Litsea dilleniifolia* were listed among the 10 species with the highest importance values in a plot in the tropical seasonal rain forest in Xishuangbanna (Zhang and

Table 1 Information about the eight tree species from a tropical seasonal rain forest in Xishuangbanna, SW China, investigated in this study

Species	Family	Dispersal period (months)	Mean seed size (mm) length × width	Seed fresh mass[a] (g/seed)	Fresh seed moisture content[b](%)	Forest stratum
Horsfieldia tetratepala	Myristicaceae	III–V	40.6 × 23.9	10.57 ± 1.69	31 ± 1	ST
Horsfieldia pandurifolia	Myristicaceae	V–VI	33.2 × 19.2	5.91 ± 0.73	25 ± 2	ST
Litsea dilleniifolia	Lauraceae	VI–VII	19.0 × 14.4	3.12 ± 0.32	47 ± 2	ST
Litsea pierrei var. *szemaois*	Lauraceae	X–XI	18.0 × 13.4	2.65 ± 0.09	51 ± 1	ST
Antiaris toxicaria	Moraceae	V–VI	18.1 × 13.9	2.03 ± 0.23	44 ± 1	CT/ST
Pometia tomentosa	Sapindaceae	VIII–IX	20.0 × 14.0	1.82 ± 0.29	46 ± 1	CT/ST
Castanopsis hystrix	Fagaceae	IX–XI	15.6 × 14.3	0.66 ± 0.02	32 ± 1	CT
Baccaurea ramiflora	Euphorbiaceae	VII–VIII	12.6 × 12.0	0.39 ± 0.04	60 ± 2	UT/ST

[a] Mean ± SE of 50 seeds for each species. [b]Mean ± SE of five lots of 10 seeds of each species. Plant nomenclature, taxonomy, forest stratum of species occurrence and dispersal period from Wu (1980). CT: canopy tree, ST: subcanopy tree, UT: understory tree

Cao 1995), *P. tomentosa* and *Antiaris toxicaria* as "representative tree species" of this forest and *Litsea pierrei* var. *szemaois* as a "representative species" of the tropical montane rain forest in Xishuangbanna (Cao and Zhang 1997). *A. toxicaria, B. ramiflora, H. pandurifolia, H. tetratepala, L. dilleniifolia* and *P. tomentosa* were important to somewhat important species in one or more of Zhu's (2006) sample plots in the tropical seasonal rain forest in Xishuangbanna. *P. tomentosa* had the highest importance value in the *P. tomentosa–Terminalia myriocarpa* forest "association" and *A. toxicaria* in the *A. toxicaria–Pouteria grandiflora* association. *Castanopsis hystrix* was a somewhat important species in one of Zhu's plots in the tropical seasonal moist forest. In the tropical montane evergreen broad-leaved forest, *C. hystrix* had the second highest importance value in the *Schima wallichii–Castanopsis hystix* forest association and the sixth highest [of a total of 26 species (>5 cm DBH)] in the *Schima wallichii–Lithocarpus fahaiensis* forest association (Zhu 2006).

Selection of species was based on their abundance in the forest, seed availability and tree stratum of occurrence, i.e. canopy, subcanopy and understory. Fruits of each species were collected from 10 to 12 trees with a pole, mixed and the seeds separated from fleshy fruit material under water and washed, except for *C. hystrix* in which the fruit is a nut. Seeds were collected from August 2003 to August 2004 due to differences in time of fruit maturity among the species (Table 1). Therefore, seeds of each of the study species were not sown simultaneously in our experiments. Fresh seeds were not stored for any period of time between collection and initiation of experiments.

Of the eight species investigated in this study, *H. tetratepala*, *H. pandurifolia*, *L. dilleniifolia* and *L. pierrei* var. *szemaois* (hereafter *L. pierrei*) occur only in countries bordering China and in Southern Yunnan, where they are restricted to fragments of tropical rain forest. *A. toxicaria* and *P. tomentosa* are widely distributed in the tropical forest of southeast Asia (Wu 1980). However, the present tropical rain forest in Xishuangbanna is at the altitudinal and latitudinal limits of tropical rain forests in the northern hemisphere, and its distribution is fragmented (Zhu et al. 2006). Thus, these six species are endangered in China (Fu 1989). *C. hystrix* and *B. ramiflora* are common and widely distributed in Southern China and Southeast Asia (Wu 1980).

Seed size and moisture content

Seed length and seed width of 50 randomly chosen seeds of each species were measured with a digital caliper (0.01 mm, Guanglu Digital Caliper Manufacturer Co., Ltd, China), and fresh and dry mass of these seeds were determined using an analytical balance (0.0001 g, Mettler-Toledo Inc., Switzerland). Fresh seed MC was calculated using the following formula:

$$\%\ \text{MC} = [(\text{fresh mass} - \text{dry mass}) / \text{dry mass}] \times 100$$

Dry mass was determined after drying the seeds at 103°C for 17 h (ISTA 1999).

Dehydration/germination experiment

Sixty seeds per desiccation treatment of each species were placed in a glass desiccator over activated silica gel and dehydrated for 0, 6, 12, 24, 48, 72, 96 and 120 h. After each treatment, seed MC was determined as described above for each of 30 seeds per species. Seeds larger than 1 cm were cut into smaller pieces for drying. Of the remaining seeds, three replicates of 10 seeds each were used to test germination. Seeds of seven species were sown in Petri dishes on a layer of 1.0% agar gel. Because of their small size, seeds of *B. ramiflora* were germinated on top of two layers of Whatman No. 1 filter paper. Germination tests were conducted in an incubator (MGC-300H, Stron light incubators, Shanghai Yiheng Technology Co. Ltd., China) with a 14 h daily photoperiod (30 μmol m^{-2} s^{-1}, cool white fluorescent light tubes) at 30°C. We chose a constant day/night temperature of 30°C based on the results of Yang et al. (2001), who showed that this was the optimal temperature for germination of tree species in the Xishuangbanna tropical forest. Seeds were watered daily or as required to keep the filter paper moist. Germination was monitored daily until all seeds had germinated, all ungerminated seeds were badly damaged by fungi or no additional seeds germinated for at least 1 month.

Shade house experiment

Light treatments were carried out in Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (XTBG) in nine (8 m × 8 m × 2.5 m in height) shade houses (three replicates for each of three light treatments). The neutral-density light levels were obtained using different numbers of layers of black plastic mesh to cover the tops of the shade houses and also the sides to within 15 cm of the ground. The ground surface of the shade houses was covered with forest topsoil.

Ten seeds of each of the eight species were planted in plastic pots (30 cm diameter, 15 cm in height) filled with a mixture of river sand and forest topsoil (2:1 v/v). Fifteen pots (three replicates of five pots each per species) were placed in each of the nine shade houses. This gave a total of 1350 seeds (10 seeds × 5 pots × 3 replicates × 3 shade houses × 3 light levels = 1350) for each species used in the shade house experiment. To avoid exposing seeds of the eight species to different microenvironments inside each shade house, we changed the position of the pots at two-day intervals. Soil in the pots was watered as needed to keep it moist, and daily monitoring of germination was continued until no additional seeds germinated for at least 1 month. At this time, all ungerminated seeds appeared to have decayed, except those of *L. pierrei*, which were still alive; thus, germination of this species was monitored for 9 months.

Daily maximum and daily minimum air temperatures were recorded by a maximum/minimum thermometer in each shade house during the experiment, September 2003–November 2004. Average daily maximum and average daily minimum air temperatures for this period were 31.2 and 21.5°C, respectively. Photosynthetic photon flux density (PPFD) was recorded once each minute at three random points in each light treatment from 8 a.m. to 6 p.m. for three consecutive days in January 2004 and in July 2004, using quantum sensors (LI-190-SA, LI-COR, Lincoln, Nebraska, USA) connected to a LI-1400 DataLogger (LI-COR, Lincoln, Nebraska, USA). Light levels in the shade houses were 3.5 ± 0.2% (three layers of shade cloth), 10 ± 1.2% (two layers) and 30 ± 1.1% (one layer) of full sunlight, simulating solar irradiance in the forest understory, edge of gap and center of gap, respectively.

Germination in forest gap and in forest understory

The forest experiment was run concurrently with the shade house experiment and with the same lots of seeds. *A. toxicaria*, *H. pandurifolia*, *L. pierrei*, *P. tomentosa*, *B. ramiflora* and *C. hystrix* were used for the forest experiment, based on seed availability. Five 1 m × 1 m germination "beds" were established in the center of a forest gap and in the forest understory in the 1-ha plot. Light levels in the forest understory and in the center of the forest gap were measured in the same way as they were in the shade house, and PPFD was 3 ± 0.8 and 32.5 ± 1.8% of full sunlight, respectively.

Freshly matured seeds were pushed to half their length into the soil and allowed to germinate naturally. Number of seeds used for each germination "bed" (five replicates for each species) was 24 for *A. toxicaria*, 20 for *H. pandurifolia*, 15 for *L. pierrei*, 25 for *P. tomentosa*, 15 for *B. ramiflora* and 12 for *C. hystrix*. These seed densities are similar to those collected near mature trees in five 1 m × 1 m seed traps (unpublished data). Thus, a total of 240 seeds of *A. toxicaria*, 200 of *H. pandurifolia*, 150 of *L. pierrei*, 250 of *P. tomentosa*, 150 of *B. ramiflora* and 120 of *C. hystrix* were used in the forest gap and forest understory germination experiments. Species were not tested concurrently because of differences in dispersal time. Seedling emergence was monitored daily until all seeds germinated, all ungerminated seeds were badly damaged by fungi or no additional seedlings emerged for at least 1 month. No additional water was supplied to seeds sown in forest understory or in forest gap.

Data analysis

Final germination percentage, mean time to germination (MTG = $\sum(Dn)/\sum n$) and rate of germination ($\sum n/D$) were calculated (Saxena et al. 1996; Tompsett and Pritchard 1998; Daws et al. 2005), where n is the number of seeds that germinate on day D and D the number of days from beginning of germination experiment.

We used the complete randomized design in laboratory and forest experiments. Randomized complete block design was used in shade house experiment, and light was the main factor. Analyses were performed on the means of individuals from each replicate, and all means quoted in the text are derived from mean values per treatment. The germination variables of each species in each treatment were analyzed using two-way ANOVA and Tukey's test. All analyses were carried out with SPSS 12.0 (SPSS Inc., Chicago, USA).

A linear regression analysis of percent initial MC (fresh seeds) vs. percent water content of seeds when 50% of them had lost viability, i.e. did not germinate, was performed using the GLM procedure in SAS (SAS Institute Inc. 2002).

Results

Seed size and moisture content

Seeds of the eight species are dispersed from March to November, i.e. from the late dry/early rainy season to the late rainy/early dry season (Fig. 1, Table 1). Fresh seeds exhibited a wide range of values in size, mass and MC. Seed size (area one side, l × w) ranged from 151 to 970 mm^2, mass of the largest seed was 27 × that of the smallest one and MC ranged from 25 to 60%.

Dehydration/germination experiment

Resistance to water loss (dehydration) varied considerably among the eight species (Fig. 2). Seed MC decreased rapidly during the first 6–24 h of the dehydration experiment for *H. tetratepala*, *H. pandurifolia*, *P. tomentosa*, *B. ramiflora* and *L. dilleniifolia* and much more slowly for *L. pierrei*, *C. hystrix* and *A. toxicaria*. Only after 24 h of dehydration, the five species with an initial high rate of water loss reached a lower MC than the three species with an initial slow rate of water loss (Fig. 2). After 120 h of dehydration, water content of seeds of *H. tetratepala*, *H. pandurifolia*, *P. tomentosa*, *B. ramiflora* and *L. dilleniifolia* still was considerably lower than that of seeds of *L. pierrei*, *C. hystrix* and *A. toxicaria*. Thus, seeds of *A. toxicaria*, *C. hystrix* and *L. pierrei* were more resistant to water loss than those of the other five species. For example, seed MC of *L. pierrei* had decreased only about 15% (i.e. 51%–ca. 35%) after 120 h, whereas that of *B. ramiflora* had decreased by >40% (i.e. 60 to <20%) after 24 h.

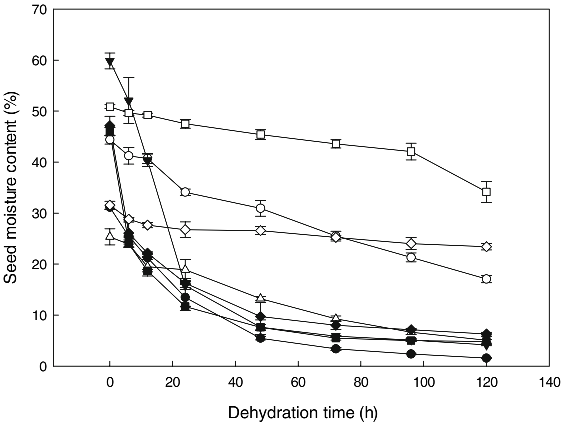

Fig. 2 Dehydration curves for seeds of eight tree species from a tropical seasonal rain forest in Xishuangabanna, SW China. Data are mean ± SE of three lots of 10 seeds each for each species. –●– *H. tetratepala*; –□– *L. pierrei*; –■– *P. tomentosa*; –◇– *C. hystrix*; –Δ– *H. Pandurifolia*; –▼– *B. ramiflora*; –○– *A. toxicaria*; –♦– *L. dilleniifolia*

Dehydration had a strong effect on germination (Fig. 3), and percentage MC at which 50% of the seeds lost the ability to germinate (WC_{50}) ranged from 12.4% in *H. pandurifolia* to 42.5% in *L. pierrei*. There was a highly significant relationship between initial MC and WC_{50} for seeds of the eight species ($R^2 = 0.83$, $p = 0.0043$). The regression model is: $y = 0.634\ (\pm 0.12) \times -0.903\ (\pm 5.4)$, where $y = WC_{50}$ and x = initial water content; CV = 15.16 and MSE = 3.78. Four species (*H. tetratepala*, *B. ramiflora*, *C. hystrix* and *L. pierrei*) showed a significant increase in final germination after short-term dehydration compared with untreated seeds (i.e. 0 h dehydration). After 48 h of dehydration, 97% of the seeds of *C. hystrix* germinated, but germination in the other three species was much lower following dehydration. Germination of *P. tomentosa* was reduced to zero after only 12 h of dehydration, and this was associated with a decrease in seed MC from 46% to 18%.

Germination curves for the eight species following the dehydration period that gave the highest germination percentage are shown in Fig. 4. Germination rates (speed) were higher for *L. dilleniifolia*, *P. tomentosa*, *C. hystrix*, *L. pierrei* and *B. ramiflora* than they were for *H. pandurifolia*, *H. tetratepala* and *A. toxicaria*. In all of the species, however, final

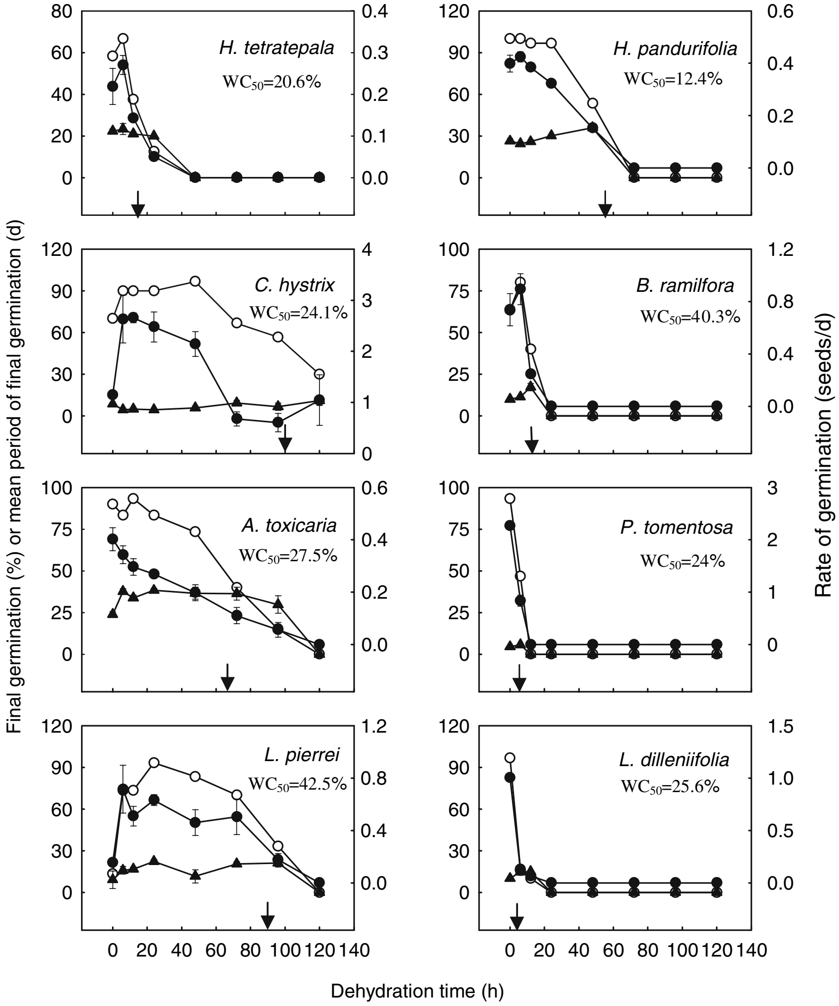

Fig. 3 Final germination (–○–), MTG (–▲–) and rate of germination (–•–) of seeds of eight tree species from a tropical seasonal rain forest in Xishuangabanna, SW China, in the laboratory after dehydration for 0–120 h. Data are mean ± SE. WC$_{50}$, seed water content when germinability (viability) had decreased 50%. Arrows indicate drying time when germinability (viability) had decreased 50%

germination percentages were >65%, and for *H. pandurifolia*, *L. dilleniifolia*, *P. tomentosa*, *A. toxicaria* and *L. pierrei*, it was >90%. About 65–100% of seeds of all eight species that germinated did so in ≤30 days.

Shade house experiment

Of the eight species tested in the shade house experiment, there were significant differences ($P < 0.01$) in final germination percentages of *H. pandurifolia*, *L. pierrei* and *A. toxicaria* among the three light treatments (Table 2). Final germination percentages for seeds of *H. pandurifolia* and *L. pierrei* were 7.0 and 0.0%, respectively, in the 30% light treatment, but they germinated to considerably higher percentages under 10 and 3.5% light. All eight species germinated in the 10 and 3.5% light treatments, which represented light levels at edge of forest gap and in forest understory, respectively. MTG ranged from 5 days for *P. tomentosa* to 84–120 days for *H. tetratepala*, depending on light level.

Germination in forest gap and in forest understory

There was no difference in germination percentages of seeds of *P. tomentosa* or of those of *B. ramiflora* between forest gap and forest understory; final germination percentages were high for both species in the two habitats (Table 2). Germination percentages of *L. pierrei* and of *H. pandurifolia* seeds were significantly higher in forest understory than in

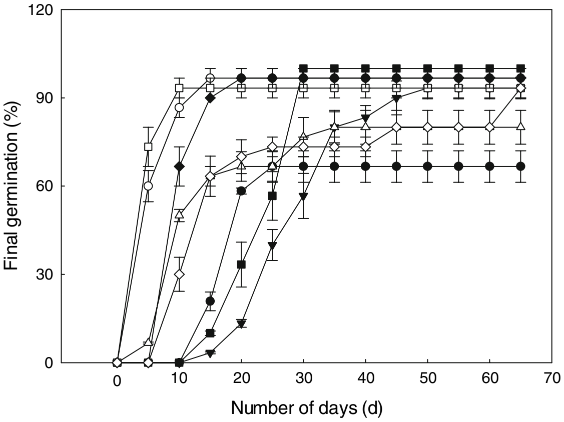

Fig. 4 Germination percentage (mean ± SE) of seeds of eight tree species dehydrated for 0 h (*H. pandurifolia*, *P. tomentosa* and *L. dilleniifolia*), 6 h (*B. ramiflora* and *H. tetratepala*), 12 h (*A. toxicaria*), 24 h (*L. pierrei*) or 48 h (*C. hystrix*) and then incubated for 65 days at 30°C and a 14 h daily photoperiod. –■– *H. pandurifolia* –◇– *L. pierrei* –▼– *A. toxicaria* –□– *P. tomentosa*; –Δ– *B. ramiflora* –●– *H. tetratepala* –○– *C. hystrix* –◆– *L. dilleniifolia*

forest gap. In contrast, germination percentages of *A. toxicaria* and of *C. hystrix* seeds were significantly higher in forest gap than in forest understory. MTG ranged from only 5 days for *P. tomentosa* to more than 200 days for *L. pierrei* (Table 2). For the other four species, MTG ranged from 16 to 34 days in canopy gap and from 6 to 32 days in forest understory.

There were no obvious differences in final germination percentages between forest understory and 3.5% light in shade houses for *A. toxicaria*, *P. tomentosa* and *C. hystrix*. However, for *B. ramiflor*a and *L. pierrei* germination percentages were higher in forest understory than in 3.5% light in shade houses, and for *H. pandurifolia*, germination percentages in forest understory was lower than in 3.5% light in shade houses. Final germination percentages of the six species were higher in center of forest gap than in 30% light in shade houses, except for *P. tomentosa*. MTG in shade houses and forest treatments was quite similar, except for *L. pierrei*, which took 207 and 206 days to complete germination in the forest gap and forest understory, respectively, but only 72 days to do so in the shade houses (Table 2). Rates of germination in the forest generally were lower than those in the shade houses, except for *P. tomentosa* and *A. toxicaria*, which germinated to a higher rate in forest gap and in forest understory.

Discussion

Seeds of all eight tree species are desiccation-sensitive, i.e. not orthodox, and thus they are either in the recalcitrant or intermediate category of seed storage behavior. It appears that *H. pandurifolia* (WC_{50} = 12.54%) may be in the intermediate seed storage category and the other seven species (WC_{50} = 20–42.5%) in the recalcitrant category (see references cited in Introduction). As a group, the eight species differ not only in time of seed dispersal, seed size and fresh seed MC, but also in desiccation resistance, $WC_{50,}$ MTG and uniformity of germination response to amount of light, thus supporting our first hypothesis that seed traits vary among the eight non-pioneer species. Differences in various aspects of seed biology also have been reported for several other tropical seasonal forests, e.g. in Ghana (Swaine et al. 1997; Kyereh et al. 1999), Panama (Garwood 1983; Daws et al. 2005; Sautu et al. 2006), Brazil (Souza and Válio 2001) and Thailand (Blakesley et al. 2002). Clearly, differences in seed biology do not prevent tree species from coexisting in Xishuangbanna or in other tropical forests.

Season of dispersal varies from the late dry/early rainy season, for *H. tetratepala*, to the late rainy/early dry season, for *L. pierrei*. All seeds of *H. pandurifolia*, *A. toxicaria*, *L. dilleniifolia*, *B. ramiflora* and *P. tomentosa* are dispersed during the rainy season (May–October), as are portions of those of *H. tetratepala*, *C. hystrix* and *L. pierrei*. For a tropical seasonal forest in Thailand, Blakesley et al. (2002) found that seeds of the 36 tree species they studied were dispersed throughout the wet and dry seasons. Marod et al. (2002) also found considerable variation in season of seed dispersal of forest trees in a tropical seasonal forest in Thailand: middle to late dry season, middle of rainy season and early rainy season. In a tropical seasonal forest in Panama, about equal percentages of seeds of 95 forest tree species were dispersed during the dry, early rainy and late rainy seasons (Sautu et al. 2006).

MTG for the six species planted in both forest gap and forest understory ranged from 5 days for *P. tomentosa* to 206–207 days for *L. pierrei*. In a study of seed dormancy of 157 species in a tropical seasonal moist forest in Panama, mean length of dormancy (time between sowing and germination) ranged from 2 to 370 days (Garwood 1983). Sautu

Table 2 Final germination percentage (mean ± SE), MTG and rate of germination of seeds of eight tree species under three light levels in shade houses and in center of canopy gap (CG) and understory of forest (UF) in a tropical seasonal rain forest in Xishuangbanna, SW China

Species	Final germination (%)					Mean time to germination (days)					Rate of germination (seeds/day)				
	Shade house			Forest		Shade house			Forest		Shade house			Forest	
	30%	10%	3.5%	CG	UF	30%	10%	3.5%	CG	UF	30%	10%	3.5%	CG	UF
HT	13 ± 3^{A}	23 ± 5^{A}	17 ± 4^{A}	–	–	120 ± 6^{A}	84 ± 2^{B}	113 ± 9^{A}	–	–	0.01 ± 0.00^{B}	0.03 ± 0.01^{A}	0.02 ± 0.00^{A}	–	–
F = 2.17, *P* = 0.85															
HP	7 ± 1^{B}	68 ± 6^{A}	62 ± 5^{A}	17 ± 4^{B}	28 ± 6^{B}	40 ± 2^{A}	33 ± 2^{B}	28 ± 2^{B}	34 ± 1^{A}	32 ± 1^{A}	0.27 ± 0.02^{B}	0.34 ± 0.05^{A}	0.36 ± 0.04^{A}	0.12 ± 0.13^{B}	0.20 ± 0.05^{A}
F = 1.96, *P* = 0.76															
LD	93 ± 4^{A}	99 ± 1^{A}	97 ± 3^{A}	–	–	21 ± 1^{A}	20 ± 1^{A}	20 ± 1^{A}	–	–	0.69 ± 0.02^{B}	0.79 ± 0.02^{A}	0.76 ± 0.03^{A}	–	–
F = 1.51, P = 0.92															
LP	0^{C}	50 ± 3^{A}	33 ± 1^{B}	21 ± 5^{B}	54 ± 5^{A}	0^{B}	72 ± 3^{A}	72 ± 3^{A}	207 ± 2^{A}	206 ± 1^{A}	0^{B}	0.11 ± 0.04^{A}	0.08 ± 0.02^{A}	0.02 ± 0.01^{B}	0.04 ± 0.01^{A}
F = 4.29, P = 0.15															
AT	56 ± 5^{A}	65 ± 4^{A}	37 ± 5^{B}	74 ± 4^{A}	40 ± 5^{B}	48 ± 2^{AB}	44 ± 1^{B}	49 ± 2^{A}	25 ± 2^{A}	19 ± 1^{A}	0.18 ± 0.02^{B}	0.23 ± 0.02^{A}	0.12 ± 0.02^{B}	0.44 ± 0.05^{B}	0.68 ± 0.02^{A}
F = 3.33, *P* = 0.47															
PT	99 ± 1^{A}	96 ± 2^{A}	97 ± 2^{A}	96 ± 2^{A}	95 ± 2^{A}	5 ± 1^{A}	5 ± 1^{A}	5 ± 1^{A}	5 ± 1^{A}	5 ± 1^{A}	2.01 ± 0.05^{A}	2.03 ± 0.08^{A}	2.01 ± 0.04^{A}	3.00 ± 0.07^{A}	3.37 ± 0.09^{A}
F = 1.42, P = 0.88															
BR	50 ± 5^{A}	59 ± 5^{A}	61 ± 3^{A}	84 ± 8^{A}	93 ± 7^{A}	12 ± 1^{A}	11 ± 1^{AB}	10 ± 1^{B}	18 ± 1^{A}	17 ± 0^{B}	0.70 ± 0.07^{B}	0.85 ± 0.05^{A}	0.91 ± 0.05^{A}	0.72 ± 0.06^{A}	0.85 ± 0.05^{A}
F = 1.87, *P* = 0.73															
CH	38 ± 6^{A}	40 ± 7^{A}	31 ± 4^{A}	59 ± 9^{A}	25 ± 7^{B}	15 ± 2^{AB}	20 ± 2^{A}	9 ± 1^{B}	16 ± 3^{A}	6 ± 1^{B}	0.79 ± 0.05^{B}	0.82 ± 0.20^{A}	1.01 ± 0.28^{A}	0.50 ± 0.09^{A}	0.51 ± 0.14^{A}
F = 2.93, *P* = 0.61															

Different uppercase letters indicate a significant difference among three light regimes in shade houses or between CG and UF for final germination percentage, MTG and rate of germination of the same species (ANOVA and Tukey's, $p < 0.05$). There were four degrees of freedom in the forest experiment and two in the shade house experiment. HP: *H. pandurifolia*; LP: *L. pierrei* var. *szemaois*; AT: *A. toxicaria*; PT: *P. tomentosa*; BR: *B. ramiflora*; CH: *C. hystrix*; HT: *H. tetratepala*; LD: *L. dilleniifolia*; "–" no data et al. (2006) reported that mean and median (MLG) length of germination period for 94 species in the same forest type in Panama were 3.7–253 and 3–203 days, respectively. For 18 species in a Ghanaian tropical seasonal forest, MTG ranged from 16 to 79 days in forest understory and from 15 to 100 days in a forest gap with 30% irradiance (Kyereh et al. 1999), and for 36 tree species in a tropical seasonal forest in Thailand median length of dormancy ranged from 7 to 219 days (Blakesley et al. 2002). Finally, germination of 65% of 180 tree species in the tropical evergreen rain forest of West Malaysia were classified as "rapid" (germination period ≤12 weeks), 7% as "intermediate" (germination period extends from <12 to >12 weeks) and 28% as "delayed" (germination period >12 weeks) germinators. Seeds of 41 of the 117 rapid germinators had a germination period ≤4 weeks (Ng 1978).

Garwood (1983) recognized three germination syndromes: delayed-rainy, seeds dispersed in rainy season but germination delayed until beginning of next rainy season; intermediate-dry, seeds dispersed during dry season and germination delayed until beginning of rainy season; and rapid-rainy, seeds dispersed and germinated in rainy season. Seven of the eight species in our study can reasonably be assigned to the rapid rainy syndrome, i.e. they are dispersed and germinated in the rainy season. *L. pierrei*, on the other hand, more appropriately can be assigned to the delayed-rainy or to the intermediate-dry syndrome, i.e. its seeds are dispersed during late rainy and early dry seasons, and germination, based on a MTG of 206–207 days in the forest experiment, would be delayed until the beginning of the next rainy season. More or less in an agreement with the long delay of germination following dispersal for seeds of *L. pierrei*, Sautu et al. (2006) reported that seeds dispersed during the late rainy season in Panama had significantly longer MLGs than those dispersed in the dry and early rainy seasons, which did not differ.

In contrast to the high rate of germination of *L. pierrei* seeds in the laboratory, germination of those planted in both forest and shade house experiments was delayed for a considerable period of time, i.e. MTG was 72–207 days. The reason for this delay in the field may have been due to low soil moisture during the long dry season, which followed seed dispersal at the end of the rainy season/beginning of the dry season. In which case, we cannot explain how these apparently recalcitrant seeds with a WC_{50} of 42.5% were able to survive the dry season and then germinate after rainfall increased at the beginning of the rainy season. However, seeds of this species lost water relatively slow when stored over silica gel. Interestingly, seeds of the two dipterocarps *Shorea siamensis* and *Dipterocarpus alatus* were dispersed in the mid to late dry season in a season tropical forest in Thailand (Marod et al. 2002). Seeds of *S. siamensis*, which were dispersed about 1 month earlier than those of *D. alatus* (Marod et al. 2002), are recalcitrant, whereas those of *D. alatus* are "orthodox with limited desiccation ability," i.e. intermediate storage category or partial tolerance to desiccation (Tompsett 1998). Further, in a tropical seasonal moist forest in Panama very short-lived seeds (very S-L) were dispersed in the dry (DS), early rainy (ERS) and late rainy (ERS) seasons. However, the proportion of species with very S-L seeds dispersed in the DS (4/31) was less than that of species with very S-L seeds dispersed in the ERS (8/29) or LRS (11/29) (Sautu et al. 2006).

Ng (1992) reported that the germination period of fresh seeds of *A. toxicaria* from the tropical evergreen rain forest in West Malaysia sown under light shade in a nursery extended from day 18 to day 89 (i.e. intermediate germination period, but almost rapid germinator, 89 vs. 84 days). Further, in our study, the MTG for *A. toxicaria* was 44–49 days in the shade houses, 19 days in the forest understory and 25 days in the forest gap. Ng (1978, 1980, 1992) also collected such phenological data on germination of seeds of the other five genera in our study: 11 species of *Baccaurea*, four of *Castanopsis*, four of *Horsfieldia*, seven of *Litsea* and one of *Pometia* from the West Malaysian rain forest, all of which had different specific epithets than the ones in our study. All but one species of *Baccaurea* had a rapid germination period (the other one intermediate). In our study, *B. ramiflora* was also a rapid germinator, with an MTG of 10–18 days. In Ng's studies, *P. pinnata* was a rapid germinator with the shortest germination period among species of all six genera (including *A. toxicaria*). Likewise, *P. tomentosa* also had the highest rate of germination in our study, with a MTG of 5 days. In Ng's studies, *Horsfieldia* and *Litsea* contained both rapid and intermediate germinators. In our study, one species of each of the two congeneric

Table 3 Summary of various aspects of the seed biology of eight tree species in a tropical seasonal rain forest, southwest China

Species	Time of dispersal	Seed size[a]	Seed MC	Desiccation resistance	WC_{50}	MTG	Final germination in light		
							3.5%	10%	30%
HT	LDS/ERS	1	6	–DR	7	84–120	+	+	+
HP	ERS	2	8	–DR	8	28–40	+	+	–
AT	ERS	6	5	+DR	3	19–49	–	+	+
LD	ERS/PRS	3	3	–DR	4	20–21	+	+	+
BR	PRS	8	1	–DR	2	10–18	+	+	+
PT	PRS/LRS	5	4	–DR	6	5–5	+	+	+
CH	LRS/EDS	7	7	+DR	5	6–20	–	+	+
LP	LRS/EDS	4	2	+DR	1	72–207	+	+	–

HP, *H. pandurifolia*; LP, *L. pierrei*; AT, *A. toxicaria*; PT, *P. tomentosa;* BR, *B. ramiflora*; CH, *C. hystrix*; HT, *H. tetratepala*; LD, *L. dilleniifolia*. EDS, early dry season; ERS, early rainy season; LDS, late dry season; LRS, late rainy season; PRS, peak rainy season; seed size, 1 (largest)–8 (smallest); moisture content of fresh seeds [MC (fmb)%]: 1 (highest)–8 (lowest); –DR, less desiccation-resistant, +DR, more desiccation-resistant; WC_{50}, seed water content when germinability (viability) had decreased 50%: 1 (highest)–8 (lowest); MTG, mean time to germination (days). Final germination (%) in light, (including forest understory as part of 3.5 % light and forest gap as part of 30% light): + + +, germination does not differ with percentage light; + + –, germination percentage lower in 30% than in 3.5% or 10% light; – + +, germination percentage lower in 3.5% than in 10% and 30% light

[a] Seed size = [(relative rank of seed length × mass) + (relative rank of seed mass)] / 2

pairs *H. tetratepala*/*H. pandurifolia* and *L. pierrei*/*L. dilleniifolia* had a high MTG and the other a low MTG. Among the four species of *Castanopsis* in Ng's study, one was an intermediate germinator and three delayed germinators. Yet, in our study MTGs for *C. hystrix* were only 6–20 days.

Combined results from shade house and forest experiments (Table 3) show that germination percentages were generally uniform in the three levels of light for four of the eight species. However, seeds of *H. pandurifolia* and *L. pierrei* germinated to significantly lower percentages in 30% light (shade houses and center of forest gap) than they did in 10% (shade house, not tested in field) and 3.5% (shade house and forest understory) light. Further, seeds of *A. toxicaria* germinated to significantly lower percentages in 3.5% light (shade house and forest understory) and those of *C. hystrix* to a significantly lower percentage in forest understory than in 10 or 30% light. Seeds of all 17 species from a tropical seasonal forest in Ghana tested at 30% and at 5% neutral shade in a shade house germinated to about equal percentages at these two solar irradiances (Kyereh et al. 1999). Further, seeds of nine of these species, as well as those of *Albizia ferruginea*, germinated about equally well in forest understory (2% irradiance) and in a forest gap with 30% irradiance. *T. ivorensis* germinated to 37% in gap but to only 12% in forest understory.

Only two (*H. pandurifolia*, *L. pierrei*) of the eight species in our study germinated to higher percentages in 3.5% than in 30% light in the shade house experiment, and none germinated to a higher percentage in 3.5% than in 10% light. In fact, seeds of *L. pierrei* and of *A. toxicaria* germinated to significantly lower percentages in 3.5% than in 10% light. Further, for the six species sown in the forest experiment only *L. pierrei* germinated to a significantly higher percentage in the forest understory (3.5% full sunlight), whereas *A. toxicaria* and *C. hystrix* germinated to significantly higher percentages in center of canopy gap (32.5% full sunlight) than in forest understory. Germination percentages for the other three species did not differ between forest understory and center of canopy gap.

For species in a tropical seasonal moist forest in Panama, desiccation-sensitive seeds were significantly more likely to germinate rapidly in 2.3% than in 18.5% full sunlight, which are light levels typical of intact forest understory and medium-sized gaps, respectively (Daws et al. 2005). In our study, germination rate (seeds/day) for seeds of six of the eight species sown in the shade house were significantly higher in 3.5% than in 30% light, but for none of the species was it higher in 3.5% than in 10% light. In fact, germination rate of *A. toxicaria* seeds was higher in 10% than in 3.5% light. However, for seven of the species germination rate was higher in 10% than in 30% light. For the six species sown in the forest experiment, three germinated to faster rates in forest understory, and for the other three germination rate did not differ between forest understory and canopy gap. Thus, our study partially supports the conclusion of Daws et al. (2005).

There is no clear relationship between uniformity/non-uniformity of germination in the three light levels in either time of dispersal, seed size, seed MC, desiccation resistance or MTG (Table 3). Thus, for example, seeds of *H. tetratepala*, which are dispersed in the late dry season/early rainy season and germinate uniformly in 30, 10 and 3.5% light have a MTG of 84–120 days and dry rapidly. In contrast, seeds of *B. ramiflora*, which also germinate uniformly in the three light levels, are dispersed in peak of the rainy season, have a MTG of 10–18 days and dry rapidly. Rate of water loss varied greatly among seeds of the eight species, but it was not related to seed size. Seeds of three species with the slowest drying rate, *C. hystrix*, *A. toxicaria* and *H. pandurifolia*, ranked seventh, sixth and second, respectively, in seed size. Thus, there is an obvious lack of relationships that could reasonably be expected among the seed traits, and as such our second hypothesis is not supported.

Mean PPFD in the forest understory and in center of forest gap was 3 ± 0.8 and 32.5 ± 1.8% of full sunlight, respectively. We did not measure the R/FR ratio, but based on the results of others it is likely to have been lower in the forest understory than in the gap. Unfiltered sunlight typically has a R/FR ratio of ca. 1.2, and filtering by plant leaf canopies may reduce this value to 0.2, or even lower (Vasquez-Yanes et al. 1980; Smith 1982; Lee 1987; Ballaré 1994). However, R/FR ratio of shade light in the forest understory may or may not be low enough to inhibit germination (Orozco-Segovia et al. 1987; Vasquez-Yanes and Orozco-Segovia 1990; Metcalfe 2001; Kyereh et al. 1999; Souza and Válio 2001). Thus, seeds of non-pioneers and of those of some pioneers can germinate in leaf-filtered light in forest understory (Orozco-Segovia and Vasquez-Yanes 1989; Metcalfe 2001; Kyereh et al. 1999; Souza and Válio 2001). At constant temperature, the R/FR thresholds above which germination of five neotropical pioneer species increased sharply was 0.12 for *Miconia argentea*, 0.21–0.27 for three *Cecropia* species and 0.21 for *Solanum hayesii*. At fluctuating temperatures, seeds of *S. hayesii* germinated equally well at R/FR ratios of <0.05 to >1.0 (Pearson et al. 2003). For these five species plus four *Piper* species studied by Dawes et al (2002), the R/FR threshold was positively correlated with seed mass, i.e. small seeds had a lower R/FR threshold for germination than large seeds (Pearson et al. 2003).

In three of the six species sown in our forest experiment, germination percentages did not differ significantly between forest understory and forest gap. In one species, germination percentage was significantly higher in forest understory, and in two species germination percentage was significantly lower in forest understory. Thus, it seems unlikely that low R/FR ratio had an effect on germination in our experiment. Also, a R/FR ratio of 0.43, which is low enough to inhibit seed germination of some positively photoblastic seeds (e.g. Orozco-Segovia et al. 1987, 1993; Vasquez-Yanes et al. 1990), had little or no effect on germination of seeds of tropical rain forest species in Ghana, except at the very low irradiance of 1 μmol m^{-2} s^{-1} (Swaine et al. 1997; Kyereh et al. 1999). Neither did an enrichment in FR (natural shade) have much of an effect on germination percentages of 14 species in a semi-deciduous tropical forest in Brazil. Thus, most species in forest interior (R/FR ratio 0.23–0.74) germinated as well as, and several of them better than, they did at forest edge, where R/FR ratio of full sun was 1.22–1.44 (Souza and Válio 2001). Even some small seeded tropical tree species that do not germinate in darkness may do so in low R/FR ratios similar to those in the forest understory (Drake 1993; Metcalfe 2001).

In general, it has been found that recalcitrant seeds are larger and germinate faster than orthodox seeds (Dickie and Pritchard 2002; Pritchard et al. 2004; Daws et al. 2005). The apparent ecological advantage of recalcitrant seeds, which have thin seed coats, being large is that it allows them to germinate rapidly and thus to avoid vertebrate predators (Pritchard et al. 2004; Daws et al. 2005, 2006). However, in our study, the three species (*B. ramiflora, P. tomentosa* and *C. hystrix*) with the lowest MTGs (highest germination rates) also had the smallest seed sizes (l × w) and seed masses, just the opposite of what would be expected if large recalcitrant seeds germinate faster than small recalcitrant seeds. Further, seed size and seed mass of the congeners *L. pierrei* and *L. dilleniifolia* were similar, yet MTGs were 72–207 and 20–21 days, respectively. Finally, *H. tetratepala*, which had the largest seed size and seed mass, had the second highest MTG. Thus, there is no obvious consistent relationship between MTG and seed size or seed mass for the desiccation-sensitive seeds of the eight species in our study.

The only clear relationship among the various aspects of the seed biology of the eight tree species investigated in this study was between initial seed MC (at maturity) and WC_{50}. Thus, fresh seeds with high water content had a higher WC_{50} than those with a low WC_{50}. Finch-Savage and Blake (1994) found a strong positive relationship between MC of *Quercus robur* seeds at time of shedding in different years and WC_{50}. However, for a gymnosperm and two angiosperm trees (Farrant et al. 1989), one African tree species of the Sahelian Zone and three from the Sudanian Zone (Danthu et al. 2000) and nine species of *Coffea* native to tropical seasonal forests of Africa (Dussert et al. 1999, 2000), there was no significant relationship between initial MC and WC_{50}.

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