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Dispersal and germination syndromes of tree seeds in a seasonal evergreen monsoon rainforest on Hainan Island, China

Wenjie Yang[1,2], Fude Liu[1,3], Shiting Zhang[1] and Shuqing An[1]*

[1]Laboratory of Forest Ecology and Global Changes, School of Life Science, Nanjing University, 22 Hankou Road, Nanjing, China; [2]College of Horticulture and Forestry Science, Huazhong Agricultural University, Wuhan, China; [3]Key Laboratory of Water Resources and Environment of Shandong Province, Water Resources Research Institute of Shandong Province, Jinan 250013, China

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Abstract

This paper examines the dispersal–germination strategy of seeds of 66 native tree species from a seasonal evergreen monsoon rainforest on Hainan Island, China, and assesses correlations among seed germination and phylogeny, dispersal mode and dispersal season. Seeds of 15, 7, 25 and 19 species were dispersed during the warm dry (March–May), rainy (June–September), late rainy (October–November) and cool dry (December–February) seasons, respectively. Berries (16 species), drupes (14 species) and capsules (12 species) were common and represented about 64% of the species. Zoochory was the most common dispersal mode (69.7%) followed by anemochory (16.7%) and autochory (13.6%). More than 65% of species had dormant seeds. Based on germination speed and synchrony, six patterns were recognized: rapid and synchronous germination (13 species), intermediate and synchronous germination (3 species), intermediate and intermediately synchronous germination (24 species), intermediate and asynchronous germination (2 species), slow and intermediately synchronous germination (5 species), and slow and asynchronous germination (19 species). One-way ANOVAs revealed that the variance in germination percentages among species was largely dependent upon phylogeny. The mean and median length of germination (MLG) were largely dependent upon phylogeny, dispersal mode and dispersal season. Anemochorous seeds germinated faster than autochorous and zoochorous seeds. Seeds dispersed in the late dry or early rainy season (March–May) tended to germinate quickly, whereas those dispersed towards the end of the rainy season and into the cool dry season are likely to have a much longer length of dormancy. Correlation analyses indicated that larger seeds germinated faster and had higher germination percentages.

Keywords: dispersal strategy, germination time, phylogeny, seed dormancy, seed mass

Introduction

Seed dispersal and germination are critical periods of a plant's life cycle (Harper, 1977; Swaine, 1996). The timing of seed dispersal and germination plays a key role, not only in individual plant fitness but also in plant population dynamics, which may ultimately affect floristic diversity (Baskin and Baskin, 1998; Fenner and Thompson, 2005). In temporally and spatially variable natural environments, unfavourable conditions for germination may occur unpredictably (Venable and Brown, 1988). Species therefore have evolved different strategies to offset these fluctuations in habitat suitability (Fenner and Thompson, 2005). Tropical tree seeds exhibit a variety of dispersal and dormancy characteristics. The timing of dispersal is often the way by which species synchronize germination timing with favourable conditions for seedling establishment (Frankie *et al.*, 1974). Dormancy is a strategic alternative to dispersal (Harper, 1977), regulating the timing of germination in the field (Baskin and Baskin, 1998; Fenner and Thompson, 2005). Species also exhibit different germination characteristics or syndromes (Angevine and Chabot, 1979; Salazar *et al.*, 2011; Silveira *et al.*, 2012); for example, tropical forest plants display a wide array of germination strategies, some species germinate just after dispersal or may even germinate before dispersal, whereas other species can stay in the soil seed bank for several years before germination occurs (Garwood, 1983; Vázquez-Yañez and Orozco-Segovia, 1993).

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*Correspondence
Email: anshq@nju.edu.cn

Species exhibit considerable variation in germination time. It is selectively advantageous to maintain high variability in this trait (Vázquez-Yañez and Orozco-Segovia, 1993; Baskin and Baskin, 1998; Norden *et al.*, 2009). Rapid germination may allow seedlings to grow larger (Black and Wilkinson, 1963), and maintain competitive dominance over seedlings from seeds that germinate later (Ross and Harper, 1972). On the other hand, fast-germinating species may result in the entire seedling cohort suffering from high mortality in unpredictable environments. In this case natural selection may favour slow germination (Daws *et al.*, 2007).

Seed germination among species is not only related to environmental factors, such as temperature, rainfall, light and altitude (Baskin and Baskin, 1998; Kyereh *et al.*, 1999; Gutterman, 2000), but also to life-history attributes, such as seed mass (Garwood, 1983; Leishman *et al.*, 2000), dispersal strategy (Willson and Traveset, 2000) and phylogeny (Figueroa, 2003; Bu *et al.*, 2008; Wang *et al.*, 2009). Therefore, to assess the role of natural selection on seed germination at the community level, it is necessary to take into account phylogeny and various biological and ecological factors when measuring the effect of any single variable.

The montane region of Hainan Island, China, with its high species richness, represents a key biodiversity hotspot (Jiang and Lu, 1991; Li, 2002). Demands for reforestation and restoration of Hainan Island are increasing following extensive deforestation and long-term intensive agricultural land use (Jiang and Lu, 1991; Li, 2002). Propagation of native Hainan species from seeds is important in the conservation of rare species and in production of plants needed for restoration projects. However, studies on seed traits, especially seed mass, germination and dormancy of native species in Hainan Island of China are limited so far. This study, at a regional scale, presents information about various aspects of the whole-seed biology of 66 tree species native to the Hainan Island, China. Given the wide variation in seed traits among these species, we tested differences in seed mass and germination patterns among different fruit types and species with different germination syndromes. The objective was also to determine to what extent dispersal and dormancy characteristics of seeds of various species fit into the overall strategy of survival in this biome, and to assess whether differences in seed germination among species from the same community are related to phylogeny, dispersal mode and dispersal season.

Materials and methods

Study site

Our study was carried out in the tropical rainforest of Jianfengling National Natural Reserve (636.84 km^2 area; 18°20′–18°57′N, 108°41′–109°12′E), located to the south-west of Hainan Island, China. The tropical evergreen monsoon forest occurs at 300–700 m altitude. The soil type of this region is latosol, the mean annual temperature and annual rainfall are 22°C and 2000 mm, respectively (Fig. 1). Rainy and dry seasons are clearly demarcated, with the dry season occurring from December to April and the rainy season from May to October. The vegetation is dominated by species of Dipterocarpaceae (*Hopea hainanensis* and *Vatica mangachapoi*), Lauraceae, Euphorbiaceae, Annonceae and Myrtaceae (Jiang and Lu, 1991; Li, 2002).

Seed dispersal, maturation and germination

Seeds of 66 endemic species, belonging to 29 families and 49 genera, were collected from 1–5 parent trees when fruits were mature and ripe, between December 2006 and December 2007. All species were selected because of their commercial and ecological importance, as well as availability of mature seeds during the period of the experiment. All species are planted in, or considered feasible for, restoration and timber species plantations within the tropical rainforest of Hainan Island, China (Zhou, 2000).

Fruits were cut from branches or collected from the ground only if they were ‘fresh’ and not decayed. Species (as reported by Chun, 1964, 1965; Guangdong Institute of Botany, 1974), their life-form, family, seed mass, maturation time, possible mode of dispersal and extraction method from fruits were recorded. The seed extraction method, depending on the type of fruit, followed the protocol of Thapliyal and Phartyal (2005): (1) a single/double/multiple indehiscent fruit, described as ‘seed’ in the functional sense, required only drying; (2) dry fruits were split open, followed by drying in the sun (30–35°C) for 2 d and seeds were then extracted by shaking, tumbling, flowing, threshing, etc.; (3) the seeds from dry indehiscent fruits were extracted by rubbing them dry on a wire-net cloth and gently pounding with wooden clubs or hammering; (4) fleshy fruits, sometimes with bony

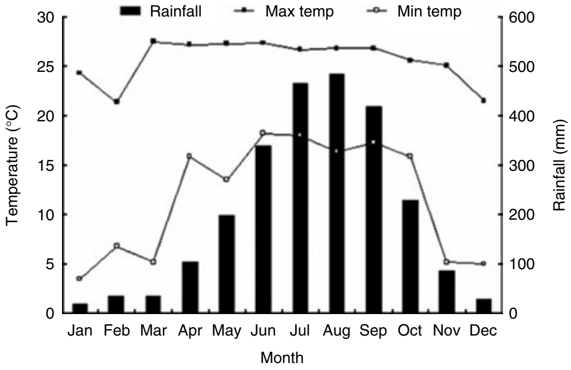

Figure 1. Monthly rainfall and temperature in the seasonal evergreen monsoon forest of Hainan Island, China.

endocarp, burst open or required extraction methods as above; (5) seeds from pulpy fruits were extracted by heaping the fruits in shade or by soaking to make the pulp soft and then macerating by hand or on a tray on wire-net cloth with constant washing in running tap water.

Following extraction and cleaning, seeds were dried in the laboratory under a fan or in the sun. Usually seeds derived from fruits that dry as they mature were dried in the sun, while those from fruits that are pulpy at maturity were dried in the shade.

Four replicates of 100 seeds were sown on sand in plastic trays under 50% of full sunlight. Large seeds were pushed into the sand for one-half of their diameter. Small seeds were covered by 1–3 mm of sand, if seeds were uncovered after watering they were covered with sand again. Due to shortage of seeds from *Acmena acuminatissima*, *Calophyllum inophyllum*, *Quercus patelliformis*, *Sindora glabra* and *Drypetes perreticulata*, we sowed four replicates of 50 seeds. Conditions in the nursery were similar to those of the natural environment. Average monthly rainfall and temperature (outdoor) data for the past 25 years in the study area, recorded by the Jianfengling Experimental Station (Research Institute of Tropical Forestry, Chinese Academy of Forestry), are presented in Fig. 1.

Germination was defined as emergence of any part of the shoot, since roots were buried in the sand, and was monitored every day, based upon interspecific differences until 1 month without any germination. The days to first germination and last germination of each species were recorded. The median length of germination time (the median value of all the times to germination, MLG) and the mean length of germination time (the mean value of all the times to germination, mean LG) were calculated (pooling individuals of each species from the four replicate batches) from the germination times of all seeds that germinated. Median lengths of germination time (MLG) for all the seeds that germinated were calculated as measures of dormancy. Seeds with a MLG ≤ 30 d were considered to be non-dormant, while those with MLG > 30 d were considered to be dormant (Baskin and Baskin, 2004).

For the purposes of nursery production, germination was defined as rapid if the MLG was ≤ 21 d, and slow if the MLG was ≥ 84 d. For tree production in the nursery, germination was defined as synchronous if all seedlings of a given species emerged within 21 d, and highly asynchronous if this occurred over a period of more than 84 d (Blakesley *et al.*, 2002).

Following Blakesley *et al.* (2002), we calculated the month of peak germination for each species, taking into consideration month of collection and MLG. For example, seeds collected in November with an MLG of 62 d will have a peak of germination in January. Then we plotted the number of species that had their peak of germination for each month.

Statistical analyses

One-way ANOVAs were used to determine the effects of phylogeny, dispersal mode and dispersal season on germination percentage, days to first germination, MLG, mean LG and days to last germination.

(1) Phylogenetic group: to evaluate phylogenetic effect on germination, each of the 65 angiosperm species was assigned to an Order according to Angiosperm Phylogeny Group III (2009): Ericales, Fabales, Fagales, Gentianales, Gunnerales, Lamiales, Laurales, Magnoliales, Malpighiales, Malvales, Myrtales, Oxalidales, Rosales, Sapindales, Saxifragales.

(2) Dispersal mode: each species was assigned to a dispersal category – anemochorous seeds with wings, hairs or a pappus; autochorous seeds having no obvious morphological structure for dispersal; zoochorous seeds with an aril or flesh.

(3) Dispersal season: according to rainfall and temperature (Fig. 1), dispersal mode was assigned to a dispersal season category – March–May, June–September, October–November, December–February.

Pearson correlation analysis was used to determine the correlation between all variables for germination studies. Data of germination were checked for normality and homogeneity of variances, and were log-transformed when necessary to correct deviations from these assumptions. All statistical methods were performed using SPPS Base 15 for Windows (SPSS, Inc., Chicago, Illinois, USA).

Results

Pattern of seed dispersal syndromes

Overall, berries (16 species), drupes (14 species) and capsules (12 species) were common and represented about 64% of the species, followed by legumes (7 species), nuts (7 species), figs (4 species) and follicles (4 species). Pomes and samaras were represented by only one species each. Zoochory was the most common dispersal mode (69.7%), followed by anemochory and autochory (16.7 and 13.6%, respectively). Seeds of 15, 7, 25 and 19 species were dispersed during the warm dry (March–May), rainy (June–September), late rainy (October–November) and cool dry (December–next February) seasons, respectively (see Appendix).

Dormancy and germination synchrony categories

The MLG ranged from 7 to 272 d, and mean LG ranged from 10 to 353 d (Table 1). Based on the MLG and 30 d

Table 1. Germination data of seeds of 66 species from a seasonal evergreen monsoon forest in Hainan Island, China. Species are divided into six germination and synchrony categories

Type/species	Germination percentage (%)	Days to first germination	Days to last germination	MLG (d)	Mean LG(d)
Rapid germination and synchrony (RG/S)					
Altingia obovata	60.5	10	25	16	18
Homalium hainanense	24.6	12	33	18	21.5
Sterculia lanceolata	93.2	4	15	7	9.5
Aquilaria sinensis	71.5	9	28	15	16.5
Winchia calophylla	65.3	7	27	11	12.5
Dolichandrone caudafelina	86.7	12	24	21	20
Radermachera hainanensis	43.6	6	24	11	13.5
Hopea hainanensis	95.5	4	19	7	9
Vatica mangachapoi	94.5	4	19	8	9
Castanopsis fissa	77.5	10	31	16	18
Bischofia javanica	82.1	15	30	20	22.5
Syzygium araiocladum	85.5	12	47	20	22
Nephelium topengii	90.4	12	27	15	17.5
Intermediate germination and synchrony (IG/S)					
Castanopsis hystrix	77.3	19	40	24	25.5
Beilschmiedia roxburghiana	93.3	20	34	26	27
Madhuca hainanensis	92.3	37	58	26	29.5
Intermediate germination and intermediate synchrony (IG/IS)					
Pithecellobium clypearia	90.5	26	56	40	41
Pterospermum heterophyllum	86.1	32	62	41	43.5
Polyspora balansae	42.3	31	112	71	71.5
Schima superba	52.5	18	58	31	34
Dalbergia hainanensis	65.3	25	46	35	37
Castanopsis hainanensis	75.2	21	46	33	33.5
Tarrietia parvifolia	80.8	25	50	35	36
Canarium album	86.5	20	65	35	37.5
Canarium pimela	86.2	25	71	41	43.5
Bridelia balansae	88.4	26	56	36	40
Endospermum chinense	73.3	22	64	20	24
Cinnamomum burmanni	80.8	12	42	27	27
Cryptocarya chinensis	77.6	40	118	65	70
Cryptocarya concinna	72.1	40	121	80	80.5
Machilus chinensis	83.5	27	50	35	36.5
Machilus salicina	85.2	30	54	35	38
Aglaia tsangii	87.3	22	86	54	54
Ficus altissima	12.1	15	51	29	29
Ficus benjamina	15.8	12	48	29	29
Syzygium cumini	80.4	21	41	30	33.5
Syzygium bullockii	80.5	20	43	25	27.5
Syzygium odoratum	83.1	20	55	29	32
Eriobotrya deflexa	91.5	28	63	40	42.5
Tutcheria multisepala	46.6	24	63	44	43.5
Intermediate germination and asynchrony (IG/AS)					
Castanopsis formosana	76.2	32	128	80	80
Cyclobalanopsis patelliformis	63.6	32	121	77	76.5
Slow germination and intermediate synchrony (SG/IS)					
Euodia meliaefolia	36.9	120	162	142	141
Mitrephora thorelii	56.9	278	310	290	294
Garcinia oblongifolia	81.5	180	224	200	202
Microcos chungii	25.2	164	190	177	177
Ardisa densilepidotula	28.6	182	212	197	197
Slow germination and asynchrony (SG/AS)					
Sapium discolor	82.4	80	196	138	138
Ormosia balansae	76.2	150	346	248	248

Table 1. *Continued*

Type/species	Germination percentage (%)	Days to first germination	Days to last germination	MLG (d)	Mean LG(d)
Ormosia pinnata	73.6	35	229	132	132
Ormosia semicastrata f. litchiifolia	86.8	150	387	266	269
Magnolia lotungensis	48.5	36	183	109	110
Manglietia hainanensis	49.4	35	160	97	97.5
Michelia balansae	45.3	85	215	150	150
Gleditsia microcarpa	87.8	45	60	90	90
Sindora glabra	80.6	40	55	86	86
Dillenia turbinata	55.6	54	235	144	145
Elaeocarpus sylvestris	3.5	185	441	313	313
Hydnocarpus hainanensis	75.8	50	268	159	159
Garcinia multiflora	80.5	180	360	270	270
Artocarpus styracifolius	78.6	55	159	107	107
Artocarpus nitidus ssp. lingnanensis	93.1	30	152	91	91
Acmena acuminatissima	73.3	90	245	110	128
Syzygium championii	50.2	45	183	114	114
Syzygium chunianum	75.4	39	262	150	151
Symplocos lancifolia	30.6	68	180	124	124

as the time-line, more than 65% (43 of 66) species had dormant seeds. Based on germination time and synchrony categories exhibited, six patterns could be distinguished (Table 1). The first group is characterized by rapid and synchronous germination (RG/S), e.g. *Winchia calophylla, Dolichandrone caudafelina, Radermachera hainanensis, Hopea hainanensis, Vatica mangachapoi, Bischofia javanica, Castanopsis fissa, Altingia obovata, Syzygium araiocladum, Homalium hainanense, Nephelium topengii, Sterculia lanceolata* and *Aquilaria sinensis.* The second group is characterized by intermediate but synchronous germination (IG/S), e.g. *Castanopsis hystrix, Beilschmiedia roxburghiana* and *Madhuca hainanensis.* The third group, intermediate and intermediately synchronous germination (IG/IS), includes *Canarium album, Canarium pimela, Bridelia balansae, Endospermum chinense, Pithecellobium clypearia, Dalbergia hainanensis, Castanopsis hainanensis, Cinnamomum burmanni, Cryptocarya chinensis, Cryptocarya concinna, Machilus chinensis, Machilus salicina, Aglaia tsangii, Ficus altissima, Ficus benjamina, Syzygium cumini, Syzygium bullockii, Syzygium odoratum, Eriobotrya deflexa, Pterospermum heterophyllum, Tarrietia parvifolia, Polyspora balansae, Schima superba* and *Tutcheria multisepala.* The fourth group is characterized by intermediate but asynchronous germination (IG/AS), e.g. *Castanopsis formosana* and *Cyclobalanopsis patelliformis.* The fifth group, slow and intermediately synchronous germination (SG/IS), e.g. *Mitrephora thorelii, Garcinia oblongifolia, Microcos chungii, Ardisia densilepidotula* and *Euodia meliaefolia.* The sixth group was characterized by slow and asynchronous germination (SG/AS), e.g. *Dillenia turbinata, Elaeocaepus sylvestris, Sapium discolor, Gleditsia microcarpa, Sindora glabra, Ormosia balansae, Ormosia pinnata, Ormosia semicastrata f. litchiifolia, Hydnocarpus hainanensis, Garcinia multiflora, Magnolia lotungensis, Manglietia hainanensis, Michelia balansae, Artocarpus styracifolius, Artocarpus nitidus* ssp. *lingnanensis, Acmena acuminatissima, Syzygium championii, Syzygium chunianum* and *Symplocos lancifolia*. Germination percentages among species with the six patterns were not significantly different ($F = 1.916$, $P > 0.05$) but the differences in seed mass among the six patterns were significant ($F = 3.055$, $P = 0.016$). Seeds characterized by intermediate but asynchronous germination (IG/AS) were the largest, followed by seeds characterized by IG/S, IG/IS, SG/AS and SG/IS, whereas seeds characterized by rapid and synchronous germination (RG/S) were the smallest.

Correlation between germination and phylogeny, dispersal mode and dispersal season

One-way ANOVAs showed that phylogenetic group had statistically significant effects on germination percentages of the 66 species; dispersal season and dispersal mode had statistically significant effects on days to first germination; phylogenetic group, dispersal season and dispersal mode had statistically significant effects on MLG, mean LG and days to last germination (Table 2).

Species in the Laurales presented the highest germination percentage (81%), and species in the Ericales presented the lowest germination percentage (48%) (Fig. 2a); the days to first germination were not significantly different among phylogenetic groups; the MLG and mean LG displayed a significant difference among phylogenetic groups, species in the

Table 2. One-way ANOVAs showing effect of phylogeny, dispersal mode and dispersal season on germination variables among species

	Phylogenetic group				Dispersal mode				Dispersal season			
Source of variation	df	*F*	Sig.	R^2	df	*F*	Sig.	R^2	df	*F*	Sig.	R^2
Germination percentage	14	5.03	***	0.58	2	0.54	ns	0.02	3	0.16	ns	0.01
Days to first germination	14	2.13	ns	0.11	2	7.08	**	0.18	3	2.85	*	0.12
MLG	14	2.7	**	0.43	2	7.95	**	0.21	3	2.91	*	0.12
Mean LG	14	2.61	**	0.42	2	7.05	**	0.19	3	3.52	*	0.15
Days to last germination	14	2.85	**	0.44	2	7.59	**	0.19	3	3.62	*	0.15

MLG, median value of all the times to germination; mean LG, mean value of all the times to germination.
ns, Not statistically significant. Significance (Sig.) at *, $P \le 0.05$; **, $P \le 0.01$; *** $P \le 0.001$.

Magnoliales presented the longest MLG and mean LG (44 and 45 d, respectively), species in the Laurales presented shortest MLG and mean LG (13 and 12 d, respectively) (Fig. 2b).

Germination percentage of seeds did not differ among dispersal mode (Fig. 3a). The days to first germination and days to last germination were significantly different among dispersal mode: anemochorous seeds presented shortest days to first germination and days to last germination (16 and 44 d, respectively), and autochorous seeds presented longest days to first germination and days to last germination (71 and 184 d, respectively). MLG and mean LG showed significant differences among dispersal mode: autochorous seeds presented the longest MLG and mean LG (both 115 d) whereas species with anemochorous seeds displayed shortest MLG and mean LG (26 and 30 d, respectively) (Fig. 3b).

Germination percentage of seeds did not differ among dispersal season (Fig. 4a). The days to first germination and days to last germination were significantly different among dispersal season: seeds dispersed in March–May presented shortest days to first germination and days to last germination (16 and 38 d, respectively); seeds dispersed in October–November presented longest days to first germination and days to last germination (58 and 145 d, respectively). MLG and mean LG showed significant differences among dispersal season: seeds dispersed in March–May presented shortest MLG and mean LG (26 and 27 d, respectively) and seeds dispersed in October–November presented longest MLG and mean LG (both 102 d) (Fig. 4b).

Seed mass and germination of species

Correlation analyses showed that seed mass was positively correlated with germination percentage, days to first germination, MLG and mean LG. Germination percentage was negatively correlated with days to first germination, MLG and mean LG (Table 3).

Month of peak seed maturation and germination

The number of species with a germination peak in each month is shown in Fig. 5. Fruits of five species matured in the hot, dry months (March–April), 36 matured during the rainy season (May–October) and 25 matured during the cool season (November–

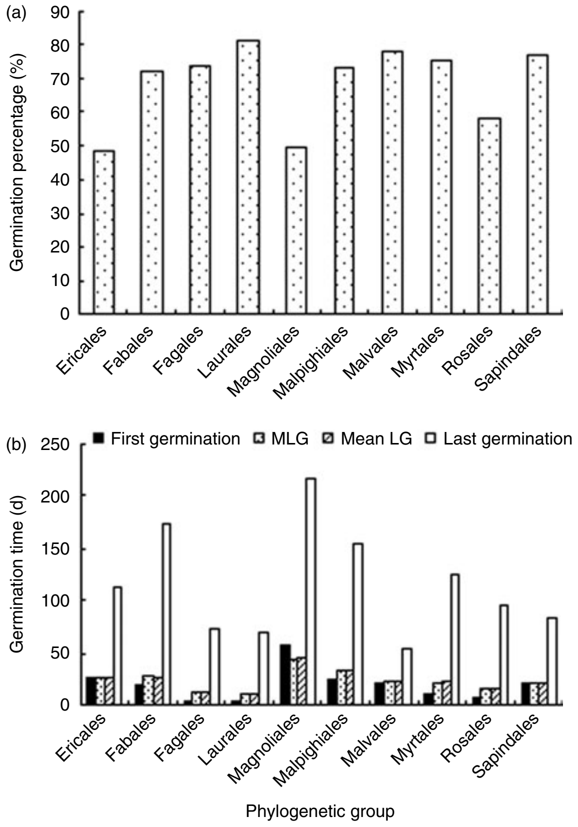

Figure 2. Differences in (a) mean germination percentage and (b) germination time among phylogenetic groups (five orders – Gentianales, Gunnerales, Lamiales, Oxalidales and Saxifragales – with a low number of species were excluded). MLG, median value of all the times to germination; mean LG, mean value of all the times to germination.

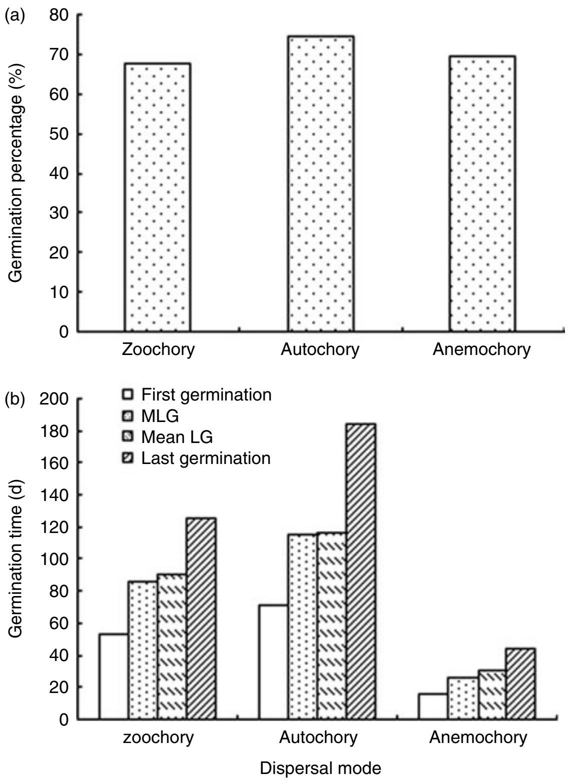

Figure 3. Differences in (a) mean germination percentage and (b) germination time among dispersal mode groups. MLG, median value of all the times to germination; mean LG, mean value of all the times to germination.

February). This seasonal variation resulted in a peak in nursery germination and seed dispersal, with the germination peak in March and October, while seed dispersal peaked in June and December (Fig. 5).

Discussion

In our study, seed dispersal occurred throughout the rainy and dry seasons. Similarly, Thapliyal and Phartyal (2005) reported that seeds of 77 studied tree species matured in the hot, dry summer months (April–June), rainy season (July–September), cold season (October–February) and late spring (March) in a monsoonal forest in northern India. Blakesley *et al.* (2002) reported that seeds of the 36 tree species they studied were dispersed throughout the wet and dry seasons in a tropical seasonal forest in Thailand. Sautu *et al.* (2006) also reported that roughly equal percentages of seeds of 95 forest tree species were dispersed during the dry, early rainy and late rainy seasons in a tropical seasonal forest in Panama.

Considerable variation in mean time to germination has been reported in tropical forests around the world. For example, for eight species in a tropical seasonal rainforest in south-west China, the mean time to germination (MTG) ranged from 5 to 207 d (Yu *et al.*, 2008). For 157 species in a tropical seasonal moist forest in Panama, the mean length of dormancy (time between sowing and germination) ranged from 2 to 370 d (Garwood, 1983). Sautu *et al.* (2006) reported that mean and median (MLG) lengths of germination period for 94 species in the same forest type in Panama were 3.7–253 d and 3–203 d, respectively. For 18 species in a Ghanaian tropical seasonal forest, MTG ranged from 16 to 79 d in forest understorey and from 15 to 100 d in a forest gap with 30% irradiance (Kyereh *et al.*, 1999). For 36 tree species in a tropical seasonal forest in Thailand, the median length of dormancy (MLD) ranged from 7 to 219 d (Blakesley *et al.*, 2002). Similarly, in the present study, the MLG ranged from 7 to 313 d and mean LG ranged from 9.5 to 353 d.

Baskin and Baskin (2005) indicated that about 60% of the seeds of tropical rainforest and about 50% of those of tropical semi-evergreen forest are non-dormant at maturity. Here, more than 65% of the 66 studied species had dormant seeds. The proportion of species with dormant seeds was much higher than has been reported in several other tropical seasonal forests. Garwood (1983) reported that about 50% of 157 species had dormant seeds, based on length of

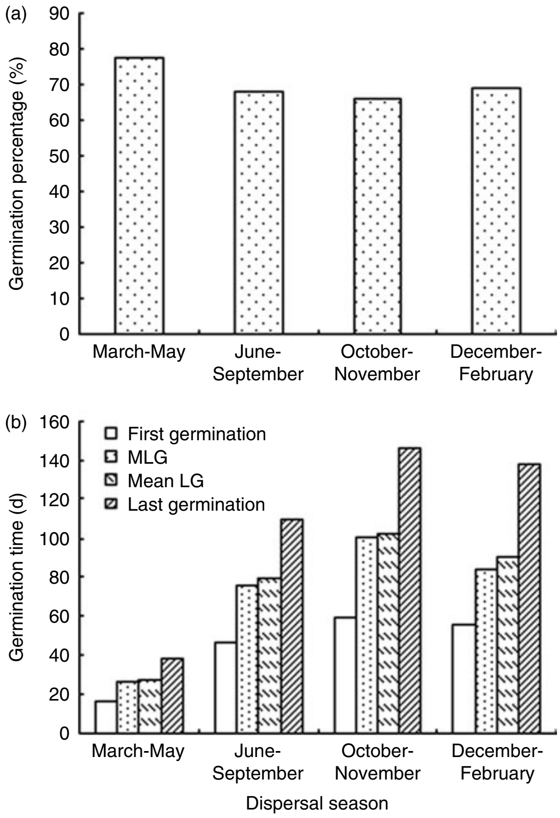

Figure 4. Differences in (a) mean germination percentage and (b) germination time among dispersal season groups. MLG, median value of all the times to germination; mean LG, mean value of all the times to germination.

Table 3. Pearson correlation coefficients between seed mass, germination percentage, days to first germination, MLG, mean LG and days to last germination, calculated from germination data of 66 species from a seasonal evergreen monsoon forest in Hainan Island, China

	Germination percentage (%)	Days to first germination	MLG (d)	Mean LG (d)	Days to last germination
Seed mass (g)	0.435**	0.255*	0.246*	0.248*	0.242
Germination percentage (%)		− 0.252*	− 0.258*	− 0.275*	− 0.265
Days to first germination			0.912**	0.942**	0.949**
MLG (d)				0.980**	0.988**
Mean LG (d)					0.995**

MLG, median value of all the times to germination; mean LG, mean value of all the times to germination.
*, Correlation is significant at the 0.05 level. **, Correlation is significant at the 0.01 level.

dormancy (MLD, days from sowing to germination) of 4 weeks, in her study of a seasonal tropical forest in Panama. In another example, of a seasonal moist tropical forest in Panama, Central America, Sautu *et al.* (2006) reported about 48% of 94 tree species with dormant seeds, based on the median length of germination (MLG) of 30 d as the time-line between dormancy and non-dormancy. Seed dormancy can be an important survival strategy because it prevents seeds from germinating shortly after maturation, when seedlings might be exposed to unfavourable establishment conditions (Clauss and Venable, 2000).

Our results clearly show that seed germination percentage and germination time (except days to first germination) among species was strongly related to phylogenetic group (Order). Previous studies on various communities, for example, temperate rainforests (Figueroa, 2003), alpine meadows (Bu *et al.*, 2008) and arid and semi-arid zones (Wang *et al.*, 2009, 2012), have shown that there is a phylogenetic pattern of seed germination. Our results suggest that variation in seed germination may be closely related to phylogeny, i.e. inherent characters of species may play a prominent role in evolution and phylogeny of species may play an important role in natural selection for the regulation of seed germination. Thus, germination behaviour will be similar in more closely related species, regardless of ecological factors, than in distantly related species.

Seeds of *M. hainanensis, M. lotungensis, H. hainanensis* and *M. thorelii* were dormant and began to germinate after 1–3 months of sand burial in our study. Seeds of these species belonging to the Magnoliales have physiological dormancy, requiring 2–3 months of cold stratification to break dormancy (Baskin and Baskin, 2005). These species shed their seeds in the late rainy season and must experience a period of natural low temperature and a moist environment to come out of dormancy, which might ensure that they germinate in the next rainy season.

Physical dormancy has been recorded in 15 families of angiosperms (Baskin *et al.*, 2000) and is well represented in the three subfamilies of Fabaceae (Caesalpinoideae, Mimosoideae and Papilionoideae) (Baskin and Baskin, 1998). In our study, seeds of *S. glabra, P. clypearia, D. hainanensis, O. balansae, O. pinnata* and *O. semicastrata f. litchiifolia* can be assigned to physical dormancy. Such dormancy is caused by one or more layers of palisade cells in the seed or fruit coat that are impermeable to water (Baskin *et al.*, 2000). Previous studies of species from several environments have shown that alternating temperatures between 15 and 35°C can break physical dormancy of seeds in tree species growing in gaps in a rainforest in Mexico (Vázquez-Yañes and Orozco-Segovia, 1982) and in non-climax tree species from the evergreen Atlantic forest (Paula *et al.*, 2012; Souza *et al.*, 2012). Seeds with physical dormancy in the present study were dispersed in the late rainy season and cool dry season. These seeds experience natural fluctuating temperatures before germination, resulting in synchronization of the peak of germination with high rainfall.

Seeds with different dispersal strategies have been generally viewed as showing an adaptation to avoid unfavourable conditions (i.e. natural enemies, sibling interactions, any limitation of available

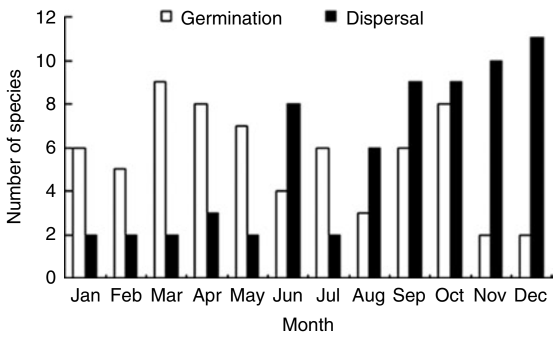

Figure 5. Number of species with seed dispersal and germination peaks in each month (calculated based on month of seed collection and median length of germination period).

resources to the parents), as well as to increase the probability of finding a suitable establishment site (Janzen, 1970; Cheplick, 1993; Willson and Traveset, 2000). In the present study, seed dispersal period had no significant effect on seed germination percentage, but did have a significant effect on time to germination and could explain independently 12–15% of the total variance in germination time in the rainforest. Garwood (1983) recognized three germination syndromes: the first is *delayed-rainy*, seeds are dispersed in the rainy season but germination is delayed until the beginning of the next rainy season. In our study, *G. oblongifolia, M. lotungensis, M. hainanensis, E. sylvestris, H. hainanensis, M. balansae, G. multiflora* and *A. densilepidotula* conformed to the delayed rainy syndrome. The second germination syndrome is *intermediate-dry*, seeds are dispersed during the dry season and germination is delayed until the beginning of the rainy season. In the present study, *O. semicastrata f. litchiifolia, M. chungii, E. meliaefolia, S. chunianum, S. championii, S. discolor, S. lancifolia, A. styracifolius, O. balansae, G. microcarpa, O. pinnata* and *C. chinensis* can be assigned to the intermediate-dry syndrome. The third syndrome is *rapid-rainy*, seeds are dispersed and germinate in the rainy season. In our study, *N. topengii, F. benjamina, S. lanceolata, R. hainanensis, S. araiocladum, B. roxburghiana, S. cumini, A. sinensis, H. hainanense, V. mangachapoi, S. superba, A. obovata* and *C. fissa* appeared to be similar to this group. It is important to link the likelihood of seedling establishment with the ‘drought avoidance syndrome’ (Angevine and Chabot, 1979).

Species exhibit considerable variation in dormancy and germination synchrony. Results of our study show that species with seeds dispersed in the late dry/early wet season (March–May) tend to germinate quickly, whereas those with seeds dispersed towards the end of the wet season and into the dry season are likely to have a much longer length of dormancy (Fig. 4), similar to results of Blakesley *et al.* (2002) in a tropical seasonal forest in Thailand. Troup (1921) also described natural regeneration in many species; seeds of most species belonging to monsoon forests germinated in nursery beds near the onset of the rainy season. It is well recognized that germination at the onset of the rainy season is 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 and increases the survival probability in the next dry season (Garwood, 1983).

Harper (1977) suggested that germination during the rainy season may reduce mortality and increase seedling establishment. In this study, seed germination occurred not just in the rainy season, but even in the driest season, which indicates that rainfall itself is not the only factor determining germination time, as was observed in other dry forests (Garwood, 1983; Van Schaik *et al.*, 1993; Sautu *et al.*, 2006). Some biotic factors, such as seed predators and litter, may be an additional factor affecting seed germination (Molofsky and Augspurger, 1992; Vallejo-Marín *et al.*, 2006).

Seeds of desiccation-sensitive species are much more likely to be dispersed in the wet season, whereas those of desiccation-tolerant species are more likely to be dispersed in the dry season. However, in a tropical seasonal moist forest in Panama, very short-lived seeds were reported to be dispersed in the dry (DS), early rainy (ERS) and late rainy (LRS) seasons (Sautu *et al.*, 2006). Seed of some desiccation-sensitive species, for example, *V. mangachapoi, N. topengii, A. sinensis, M. hainanensis, H. hainanensis* and *S. lanceolata* in the present study were dispersed in less wet (humid) months. Seeds of these species exhibited rapid synchronous germination. These species may rely on a seedling bank rather than a seed bank to persist and respond to favourable growth conditions and, therefore, require minimal time in the germination stage when they are particularly susceptible to pests and diseases (Daws *et al.*, 2005). Rapid germination and high synchrony is an adaptation for avoidance of seed predation.

In this study, seed dispersal mode had no significant effect on the interspecific variation of germination percentage, but dispersal mode had a significant effect on germination time and could explain independently 18–21% of the germination time. Wind-dispersed seeds have faster germination than both unassisted-dispersed seeds and vertebrate-dispersed seeds. It has been suggested that in some species seed dormancy may have evolved to reduce the risk of sibling competition by spreading germination out in time (Venable and Brown, 1988). Venable and Lawlor (1980) noted that there was a strong tendency for the poorly dispersed morph to have delayed germination and the well-dispersed morphs to have rapid germination.

A majority of fleshy and pulpy fruits produced seeds that take a long time to germinate, similar to results reported by Thapliyal and Phartyal (2005) in a monsoonal forest in northern India. Seeds with fleshy and pulpy fruits exhibited slow germination and asynchronous/intermediate synchrony. A long time to germinate is possibly because of their dependence on frugivores for dispersal. Seeds that have hard, mechanically resistant coats that protect the embryo from damage during chewing or enzymatic action while passing through the gut, or depend on slow decomposition or insect action for release of seeds, can take a long time to germinate. Seeds of some species in this category take several years to germinate (Troup, 1921) and length of dormancy could be the secondary effect of a defence mechanism. The germination of vertebrate-dispersed seeds with fleshy fruit, which may be swallowed by birds or other vertebrates, is promoted by passage through the animal's digestive system (Willson and Traveset, 2000). These requirements have led to selection for delayed germination. Some seeds of fleshy and pulpy fruits ripen and are dispersed in the cold season (November or December). In this case, low temperature and/or lack of moisture may be another reason leading to slow decomposition or insect action for release of seeds; thus, they take a long time to germinate.

Theoretical models predict that small seeds are more likely to show delayed germination than large seeds (Venable and Brown, 1988; Rees, 1994; Norden *et al.*, 2009) and early emergence of large seeds can compensate for the lower number of seeds by increasing seedling survival (Westoby *et al.*, 2002). Conversely, small-seeded species may be more persistent in the soil seed bank (Venable and Brown, 1988; Rees, 1994), and delayed germination has been an important factor for the formation of a persistent soil seed bank. Swanborough and Westoby (1996) considered that large seeds take a longer time to germinate than small ones because large seeds need a longer time for water to permeate than small ones. Faster germination might give small-seeded species a survival advantage, especially if conditions for seedling establishment remain favourable for only a short time (Moles and Westoby, 2004). Seed mass was weakly correlated with MLG and mean LG in the present study (Table 3), which is similar to results by Chen *et al.* (2002) who found a weak correlation between germination and seed mass in subtropical forests in China. Seed mass was significantly positively correlated with germination percentage across species. The higher germination percentage of large seeds than small ones can compensate for the lower number of seeds by increasing seedling survival (Verdú and Traveset, 2005).

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Appendix

Fruit type, dispersal agent, seed mass, reported fruiting time, month of collection and seed extraction procedure for 66 species from a seasonal evergreen monsoon forest in Hainan Island, China. Fruiting as reported by Chun (1964, 1965), Guangdong Institute of Botany (1974) and Zhou (2000).

Family/species	Plant form	Fruit type	Dispersal mode	Seed mass (mg)	Fruiting as reported (month)	Month of collection	Extraction method
Annonaceae							
Mitrephora thorelii Pierre	Tree	Bacca	Animal	322.3	5-8	8	5
Apocynaceae							
Winchia calophylla A.DC.	Tree	Follicle	Wind	3.151	11-2	2	2
Bignoniaceae							
Dolichandrone caudafelina (Hance) Benth & Hook	Tree	Capsule	Wind	85.55	3-4	3	2
Radermachera hainanensis Merr	Tree	Capsule	Wind	1.254	4-6	6	2
Burseraceae							
Canarium album (Lour) Raeusch	Tree	Drupe	Animal	1693	9-11	11	4
Canarium pimela Leenh	Tree	Drupe	Animal	1674	9-10	10	4
Fabaceae							
Gleditsia microcarpa Metc	Tree	Legume	Gravity	91.67	11-4	1	3
Sindora glabra Merr et De Wit	Tree	Legume	Gravity	2473	7-9	8	3
Pithecellobium clypearia (Jack) Benth	Shrub or tree	Legume	Gravity	2.635	4-8	6	2
Dalbergia hainanensis Merr et Chun	Tree	Legume	Wind	75.48	11-12	12	3
Ormosia balansae Drake	Tree	Legume	Gravity	803.1	9-11	11	2
Ormosia pinnata (Lour) Merr	Tree	Legume	Gravity	490.8	11	1	2
Ormosia semicastrata f. litchiifolia How	Tree	Legume	Gravity	206.3	12-1	12	2
Dilleniaceae							
Dillenia turbinata Finet et Gagnep	Tree	Bacca	Animal	13.25	6-7	6	5
Dipterocarpaceae							
Hopea hainanensis Merr et Chun	Tree	Nut	Wind	312.1	3-4	4	1
Vatica mangachapoi Blanco	Tree	Nut	Wind	252.7	8-9	9	1
Elaeocarpaceae							
Elaeocaepus sylvestris (Lour)	Tree	Drupe	Animal	878.0	8-10	9	4
Euphorbiaceae							
Bischofia javanica Bl	Tree	Bacca	Animal	16.07	10-12	12	5
Bridelia balansae Tutch	Shrub or tree	Drupe	Animal	65.82	11	11	5
Endospermum chinense Benth	Tree	Drupe	Animal	13.22	8-9	9	5
Sapium discolor (Champ ex Benth) Muell- Arg	Tree	Capsule	Animal	43.05	5-12	11	2
Fagaceae							
Castanopsis fissa (Champ) Rehd & Wils	Tree	Nut	Animal	1346	10-12	10	1
Castanopsis formosana (Skan) Hayata	Tree	Nut	Animal	1388	9-10	10	1
Castanopsis hainanensis Merr	Tree	Nut	Animal	1714	8-10	9	1
Castanopsis hystrix A.DC	Tree	Nut	Animal	613.3	11-12	11	1
Cyclobalanopsis patelliformis (Chun)	Tree	Nut	Animal	3477	10-11	11	1
Flacourtiaceae							
Hydnocarpus hainanensis (Merr) Sleum	Tree	Bacca	Animal	1232	8-10	10	5

Appendix *Continued*

Family/species	Plant form	Fruit type	Dispersal mode	Seed mass (mg)	Fruiting as reported (month)	Month of collection	Extraction method
Clusiaceae							
Garcinia multiflora Champ	Tree	Bacca	Animal	2880	10-11	10	5
Garcinia oblongifolia Champ	Tree	Bacca	Animal	801.1	8-10	9	5
Hamamelidaceae							
Altingia obovata Merr et Chun	Tree	Capsule	Wind	9.215	10	10	2
Lauraceae							
Beilschmiedia roxburghiana Nees	Tree	Drupe	Animal	872.4	5-7	6	4
Cinnamomum burmanni (Nees) Bl	Tree	Drupe	Animal	118.0	3-4	4	4
Cryptocarya chinensis (Hance) Hemsl	Tree	Drupe	Animal	406.0	8-12	2	5
Cryptocarya concinna Hance	Tree	Drupe	Animal	416.4	10	6	5
Machilus chinensis (Champ) Hemsl	Tree	Drupe	Animal	1664	2	3	4
Machilus salicina Hance	Tree	Drupe	Animal	318.8	7-8	7	4
Magnoliaceae							
Magnolia lotungensis Chun et C Ysoong	Tree	Follicle	Animal	114.4	8-10	10	2
Manglietia hainanensis Dandy	Tree	Follicle	Animal	465.2	9-11	10	2
Michelia balansae (A. DC.) Dandy	Tree	Follicle	Animal	152.1	9-10	9	2
Meliaceae							
Aglaia tsangii Merr	Tree	Bacca	Animal	2626	7-8	7	4
Moraceae							
Artocarpus styracifolius Pierre	Tree	Figs	Animal	236.3	10-11	11	5
Artocarpus nitidus ssp. lingnanensis Merr.	Tree	Figs	Animal	297.5	9-10	9	5
Ficus altissima Bl	Tree	Figs	Animal	0.2615	11-12	11	5
Ficus benjamina L	Tree	Figs	Animal	0.3833	1-12	5	5
Myrsinaceae							
Ardisia densilepidotula Merr	Tree	Bacca	Animal	113.3	8-10	10	5
Myrtaceae							
Acmena acuminatissima (Bl) Merr & Perry	Tree	Bacca	Animal	1309	12	12	5
Syzygium cumini (L) Skeels	Tree	Bacca	Animal	442.3	6	6	5
Syzygium araiocladum Merr & Perry	Tree	Bacca	Animal	50.25		6	5
Syzygium bullockii (Hance) Merr et Perry	Tree	Bacca	Animal	200.7		12	5
Syzygium championii (Benth) Merr et Perry	Tree	Bacca	Animal	279.0		11	5
Syzygium chunianum Merr et Perry	Tree	Bacca	Animal	608.8	12-1	12	5
Syzygium odoratum (Lour) DC	Shrub or tree	Bacca	Animal	120.8		12	5
Rosaceae							
Eriobotrya deflexa (Hemsl) Nakai	Tree	Pome	Animal	522.3	10	10	4
Rutaceae							
Euodia meliaefolia (Hance) Benth	Tree	Capsule	Gravity	8.533	11-12	12	2
Samydaceae							
Homalium hainanense Gagnep	Tree	Capsule	Wind	1.011	7-8	8	2
Sapindaceae							
Nephelium topengii (Merr) H S Lo	Tree	Drupe	Animal	777.1	5-6	5	5

Appendix *Continued*

Family/species	Plant form	Fruit type	Dispersal mode	Seed mass (mg)	Fruiting as reported (month)	Month of collection	Extraction method
Sapotaceae							
Madhuca hainanensis Chun & How	Tree	Bacca	Animal	882.8	3-4	4	5
Sterculiaceae							
Pterospermum heterophyllum Hance	Tree	Capsule	Wind	65.32	9-10	12	2
Sterculia lanceolata Cav	Tree	Capsule	Animal	503.5	6	6	2
Tarrietia parvifolia (Merr) Merr & Chun	Tree	Samara	Gravity	3022	8-9	8	1
Symplocaceae							
Symplocos lancifolia Sieb & Zucc	Tree	Drupe	Animal	33.51	9-10	11	5
Theaceae							
Polyspora balansae (Pitard) Hu	Tree	Capsule	Wind	9.812	7-9	8	2
Schima superba Gardn et Champ	Tree	Capsule	Wind	4.522	9-10	9	2
Tutcheria multisepala Merr et Chun	Tree	Capsule	Animal	360.5	1-12	12	4
Thymelaeaceae							
Aquilaria sinensis (Lour) Spreng	Tree	Capsule	Gravity	141.8	7-8	8	2
Tiliaceae							
Microcos chungii (Merr) Chun	Tree	Drupe	Animal	130.4	11-12	10	5