

Traits of recalcitrant seeds in a semi-deciduous tropical forest in Panamá: some ecological implications

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Summary

1. We used cross-species and phylogenetic analyses to compare seed traits of 36 species with desiccation-sensitive and 189 with desiccation-tolerant seeds from a semi-deciduous forest in Panamá.

2. When correcting for phylogenetic dependence between taxa, the desiccation-sensitive seeds were significantly larger than desiccation-tolerant seeds (3383 vs 283 mg) and typically shed during the wet (as opposed to dry) season. Both traits presumably reduce the rate of seed drying and hence the risk of desiccation-induced mortality for the desiccation-sensitive species.

3. Growing-house germination trials in simulated understorey and canopy gap environments revealed that the desiccation-sensitive species germinated most rapidly. Additionally, on a proportion basis, the desiccation-sensitive seeds allocated significantly less resources to seed physical defences (endocarp and/or testa) which may partially facilitate rapid germination. Both relationships were significant when correcting for phylogenetic dependence and seed mass.

4. Our results suggest that, for large-seeded species which will dry slowly, desiccation sensitivity may be advantageous. Rapid germination may reduce the duration of seed exposure to predation, and the low investment in physical defence means that, per unit mass, desiccation-sensitive seeds are a more efficient use of resources in seed provisioning.

Key-words: Barro Colorado Island, germination, Panamá, recalcitrant seed, seed mass

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Introduction

Based on their response to desiccation, seeds can be divided into two broad categories: orthodox and recalcitrant. Orthodox (hereafter termed desiccation-tolerant) seeds can be dried to low water contents (<7%) with little effect on viability (Roberts 1973). In contrast, recalcitrant (hereafter termed desiccation-sensitive) seeds are killed by drying to water contents as high as 20–30% (Pritchard 2004). Because desiccation-sensitive seeds progress towards germination when stored wet, they are difficult to store for anything other than the short term. Thus their use in reforestation and *ex situ* conservation programmes is problematic.

A range of studies have attempted to predict seed responses to desiccation from seed, plant and habitat

variables (Tompsett 1984, 1987; Hong & Ellis 1997, 1998; Dickie & Pritchard 2002; Pritchard *et al.* 2004). Desiccation-sensitive seeds have been reported to be, on average, larger than desiccation-tolerant seeds, a feature that will reduce the rate of seed drying. For example, Dickie & Pritchard (2002) reported the mean seed mass of 205 desiccation-sensitive tree and shrub species to be 3958 mg compared with 329 mg for 839 desiccation-tolerant species. However, a potential problem with this analysis is that it treats species as independent when, in fact, closely related species share evolutionary history and therefore are not independent. This can result in spurious significances if a suite of closely related species share some unrelated traits (Harvey & Pagel 2000). Instead, branching events in the phylogenetic tree involving a change in seed storage behaviour, and the associated change in seed mass (or other traits), should be identified and used as independent data points. Only a single study appears to have investigated whether seed mass is associated with desiccation tolerance while correcting for phylogenetic dependence

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between taxa (Gleiser *et al.* 2004). This study compared the seed mass of just two desiccation-sensitive and 22 desiccation-tolerant *Acer* species and reported that the desiccation-sensitive species had larger seeds. However, as this study included only two desiccation-sensitive species, one of which has recently been re-evaluated and found to be desiccation-tolerant, this conclusion is tentative (Daws *et al.*, in press).

In a study of 886 tree and shrub species, Tweddle *et al.* (2003) reported that desiccation-sensitive seeds are most common in tropical rainforests, where they contribute $\approx 47\%$ of species and are infrequent in drier environments such as savanna ($\approx 12\%$ of species). Even within dry environments, species with desiccation-sensitive seeds can minimize the risk of seed desiccation by timing seed shed to the period of maximum rainfall (Pritchard *et al.* 2004). An alternative strategy has been reported for nine species in the genus *Coffea*, where the level of desiccation tolerance is related to the duration of the dry period after seed shed: species shed before a prolonged dry spell were more desiccation-tolerant than those shed prior to a short dry spell (Dussert *et al.* 2000).

It has been suggested that desiccation tolerance is the ancestral state in seeds and has subsequently been lost in species with desiccation-sensitive seeds (Farnsworth 2000; Oliver, Tuba & Mishler 2000; Dickie & Pritchard 2002). The ability to tolerate desiccation is clearly advantageous, and enables seed persistence both through time and in relatively arid environments (Pammenter & Berjak 2000). While having large, round seeds shed to coincide with the peak in annual rainfall may minimize the risk of desiccation for desiccation-sensitive seeds, it is not yet clear whether seed desiccation sensitivity is a neutral trait, or whether there are selection benefits associated with desiccation sensitivity (Pammenter & Berjak 2000).

One potential advantage of seed desiccation sensitivity may be rapid germination. Desiccation-sensitive seeds are shed at high water contents, are metabolically active, and in some cases are actively progressing towards germination (Berjak *et al.* 1984). Consequently, limited or no imbibition is required for germination to progress rapidly following dispersal. This proposition has been tested for a limited number of African dryland trees by Pritchard *et al.* (2004) who found that, at a constant temperature of 25 °C, three taxa with desiccation-sensitive seeds germinated more rapidly than six desiccation-tolerant taxa.

Mast fruiting and rapid germination of dipterocarp seeds (Curran & Webb 2000), the vast majority of which are desiccation-sensitive (Tompsett & Kemp 1996), is thought to result from selection pressure from vertebrate seed predators. Similarly, Pammenter & Berjak (2000) have proposed that for climax species in tropical forests, many of which have desiccation-sensitive seeds, the formation of a seedling bank will reduce seed predation by fungi. Consequently, rapid germination of desiccation-sensitive seeds may minimize both the risk of seed drying and the duration

of exposure to predation. Consequently there may be reduced selection for investing resources in seed physical defences, in terms of both reducing predation risk and the mechanical restraint to germination. In the study by Pritchard *et al.* (2004), an average of 15% of the dispersal unit was endocarp/testa for three desiccation-sensitive species compared with 46% for seven desiccation-tolerant species. Pritchard *et al.* (2004) hypothesized that desiccation-tolerant species require greater defences because dispersal may occur in the dry season or during short dry spells, and seeds may be exposed to predation in the soil seed bank for extended periods. However, the wider applicability of the findings of Pritchard *et al.* (2004) is unclear, particularly given the small data set involved (10 species).

Seed mass can vary over 10 orders of magnitude, and for tropical tree seeds may be correlated with germination rate: for 179 Malaysian tree species Foster (1986) reported a significant positive correlation between seed mass and time to first germination. Seed mass may also be positively related to the proportion of seed resources allocated to physical defences (e.g. within a family; Fenner 1983; Schütz 2000). Consequently, to address more fully the implications of desiccation sensitivity for seed mass, germination rates and seed defences, analyses that account for phylogenetic relationships and/or seed mass are also required.

In this paper we examine these propositions for a data set of 225 tree and shrub taxa from a semi-deciduous tropical forest in Central Panamá, including 36 with desiccation-sensitive seeds. Specifically, we use cross-species analyses and account for phylogenetic relationships to address the following questions: (1) Are desiccation-sensitive seeds larger than desiccation-tolerant seeds? (2) Do desiccation-sensitive seeds germinate more rapidly than desiccation-tolerant seeds, and does this relationship hold when accounting for seed mass? (3) Do desiccation-sensitive seeds have a lesser investment in physical defences than desiccation-tolerant seeds, and is this true when accounting for seed mass? In addition, using cross-species analyses we test whether desiccation-sensitive seeds are dispersed when water is most available (when the risk of drying is minimal), while desiccation-tolerant seeds may be shed in wet or dry periods. The results are discussed in the context of the ecological costs/benefits of seed desiccation sensitivity.

Materials and methods

STUDY SITE AND SPECIES

This study was conducted on the Barro Colorado Nature Monument (BCNM), Republic of Panamá (9°10' N, 79°51' W). Vegetation on the BCNM consists of semi-deciduous tropical forest, and has been described in detail elsewhere (Leigh, Rand & Windsor 1982): nomenclature follows the *Flora of Panama Checklist* (D'Arcy 1987). Rainfall on the BCNM averages

2600 mm year⁻¹, with a pronounced dry season between January and April (Dietrich, Windsor & Dunne 1982).

Ripe fruits/seeds, at the point of natural dispersal, were collected from 226 tree, liana and shrub species (see Appendix 1) between 1985 and 1989. Fleshy fruits were cleaned by removing the fleshy pulp within 2 days of collection: no cleaning was necessary for wind-dispersed seeds and those in dry, dehiscent pods. For each species the month of seed collection was recorded and seed dry mass was determined by drying c. 10 cleaned seeds per species (with fruit tissue removed) at 60 °C for 3 days.

Data on seed desiccation tolerance was collated from Release 6 of the Royal Botanic Gardens Kew's online Seed Information Database (SID; Flynn, Turner & Dickie 2004). Seed responses to desiccation are divided into three categories in SID: orthodox (desiccation-tolerant); recalcitrant (desiccation-sensitive); and intermediate. Intermediate seeds have seed storage characteristics that are intermediate between those of orthodox and recalcitrant taxa and account for only ≈2% of SID. Species in the data set were assigned to these seed storage categories, resulting in 189 orthodox, 36 recalcitrant and 0 intermediate taxa.

GERMINATION EXPERIMENTS

Where seed numbers allowed, germination tests were conducted on each seed collection within the growing house in the laboratory clearing on Barro Colorado Island (BCI; part of the BCNM). Following collection, seeds were stored at 25 °C and sown within 2 days. For germination experiments, seeds were sown in plastic or fibre (peat) pots containing unsterilized soil collected from within the forest. The number of seeds sown per pot was determined primarily by seed size, and ranged from one per pot in the case of the larger-seeded species (e.g. *Prioria copaifera*) to 200 for the smallest seeded species (e.g. *Conostegia* spp.). For each species between 20 and 200 seeds were planted. Seeds were sown on the soil surface in an attempt to mimic natural dispersal by wind, being dropped by animals or deposited in faeces. However, a few of the larger-seeded species are actively buried by scatter-hoarding rodents; we did not take this into account. As a number of the species in this study can be classified as pioneers (*sensu* Swaine & Whitmore 1988) and require high-light conditions for germination (Daws *et al.* 2002a), pots were split between the upper and lower shelves in the growing house to mimic conditions within canopy gaps (upper shelf) and closed understorey sites (lower shelf) (Garwood 1983; Molofsky & Augspurger 1992). On the upper shelf, irradiance levels averaged 18.5 ± 0.7% (±1 SE) full sunlight vs 2.3 ± 0.2% on the lower shelf. These values are typical of medium-sized gaps and intact understorey sites, respectively, on BCI (Daws *et al.* 2002a; Pearson *et al.* 2002).

Pots were watered daily or as required (Garwood 1983), and germination was scored at weekly intervals until either (1) all seeds had germinated; (2) all remaining seeds were badly damaged or had disappeared from

the pots (restricted to larger-seeded species); or (3) >3 months had passed with no further germination since the last germination event. Consequently, many germination tests extended up to 3 years. Germination was scored as visible seedling emergence.

For each taxa, the mean time to germination (MTG) on both upper and lower shelves of the growing house was calculated using the following equation:

$$\text{MTG} = \sum (n \times d) / N \quad \text{eqn 1}$$

where n is the number of seeds germinated between scoring intervals; d the incubation period in days at that time point; and N the total number of seeds germinated in the treatment (Tompsett & Pritchard 1998).

DETERMINATION OF RESOURCE ALLOCATION TO DEFENCE

For each species, a minimum of eight individual seeds (dispersal unit) were dissected into their component parts: endocarp/testa and embryo/endosperm. These component parts were subsequently dried at 103 °C for 17 h (ISTA 2004) followed by mass determinations. To calculate the allocation to defence (seed-coat ratio, SCR), the ratio of the mass of covering structures (endocarp and testa) to the mass of the total dispersal unit was determined (Grubb & Burslem 1998; Pritchard *et al.* 2004).

STATISTICAL ANALYSIS

One-way ANOVA implemented in MINITAB 13 (Minitab Inc., State College, PA, USA) was used to test for a relationship between desiccation sensitivity and seed mass, MTG or SCR. In all analyses, seed mass was logarithmically and SCR arc-sine transformed to ensure homoscedasticity. For both cross-species and phylogenetic analyses involving MTG, two separate analyses were performed using MTG in the shade (MTGS; lower shelf) and in the light (MTGL; upper shelf). MTG was transformed using a Box-Cox transformation with the optimum value of λ determined using MINITAB 13. This resulted in λ values of -0.224 and -0.225 for MTGS and MTGL, respectively. The effect of either MTG or SCR on desiccation sensitivity while removing the effect of seed mass was tested using ANCOVA in MINITAB 13. In addition, sign tests were used to test the null hypothesis, for desiccation-sensitive and desiccation-tolerant species separately, of no difference between MTG in light and in shade.

For each species the timing of dispersal was classified as dry or wet season. This classification was based on whether dispersal occurred in January to April, inclusive (dry season) or May to December (wet season) (Daws *et al.* 2005). Subsequently, for desiccation-tolerant and desiccation-sensitive species, a χ^2 test of association was used to test the null hypothesis of no association between response to drying and timing of dispersal.

Table 1. Results of statistical analyses investigating the effect of desiccation tolerance/sensitivity on the relationship between seed mass, seed-coat ratio and mean time to germination in shade (MTGS) or light (MTGL)

Independent variable	Covariate	-Phylogeny		+Phylogeny	
		df	<i>F</i>	+ve contrasts	-ve contrasts
Seed mass	–	1, 212	68.6***	19	1**
Seed coat ratio	–	1, 106	38.5***	2	17**
Seed coat ratio	Seed mass	1, 101	28.0***	4	13*
MTGS	–	1, 194	10.8**	3	15*
MTGS	Seed mass	1, 193	11.0***	1	17**
MTGL	–	1, 201	3.6 ns	3	15*
MTGL	Seed mass	1, 194	7.3**	1	17**

Analyses either assumed that species were statistically independent data points (-phylogeny), or accounted for phylogenetic relatedness between species (+phylogeny).

ns, Not significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

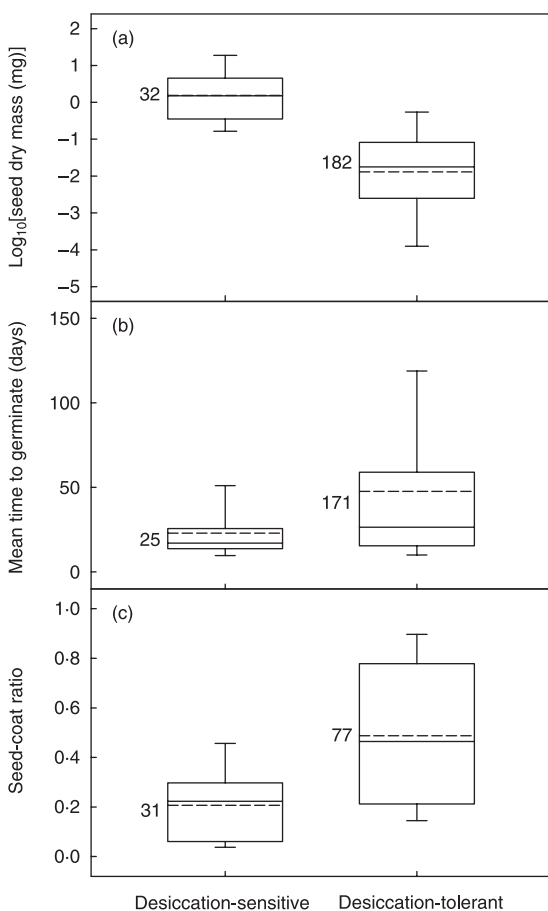


Fig. 1. Box plots comparing (a) seed dry mass; (b) mean time to germinate in the shade; and (c) seed-coat ratio for desiccation-sensitive and desiccation-tolerant seeded species. Numbers adjacent to boxes refer to number of species included in the comparison. Boxes span the 25th to 75th percentiles; whiskers span the 5th to 95th percentiles. Dashed and solid lines across boxes show mean and median, respectively.

Phylogenetically independent contrasts (Felsenstein 1985; Pagel 1992) were used to analyse the relationship between desiccation sensitivity and seed mass, MTG and SCR. This approach is based on the logic of comparing pairs of species within a phylogeny that share an immediate common ancestor. The null hypothesis is

that there is no correlation between changes in traits at the nodes. The package CAIC (Purvis & Rambaut 1995) was used to generate contrasts. Within the phylogeny we assumed that all branch lengths were the same: analyses of simulated data sets suggest that equal branch lengths may perform better than estimated branch lengths (Purvis, Gittleman & Luh 1994). For these analyses, the Branch procedure, designed for discrete predictor variables, was used (Purvis & Rambaut 1995).

For analyses testing whether the transition from desiccation-tolerant to desiccation-sensitive seeds is associated with changes in either MTG or SCR while holding the effect of seed mass constant, contrasts between mass and MTG or SCR were calculated using the Crunch procedure in CAIC, designed for continuous data (Purvis & Rambaut 1995). Subsequently a linear regression, forced through the origin, was fitted to the contrasts. A linear regression with the same slope was then fitted to the raw data for mass and MTG and for mass and SCR, and the contrasts from the line recorded. Changes in these contrasts associated with seed desiccation tolerance were subsequently analysed using the Branch procedure. All contrasts were analysed using a sign test (Purvis & Rambaut 1995). In all phylogenetic analyses, the latest phylogeny available to (sub-) family level from the Angiosperm Phylogeny Group was used (APG II 2003). However, due to the wide range of families and the lack of complete phylogenies to genus level for many families, a series of polytomies were created. Exceptions (classification source given in parentheses) were the Anacardiaceae (Aguilar-Ortigoza & Sosa 2004), Arecaceae (Uhl & Dransfield 1987), Clusiaceae (Gustafsson, Bittrich & Stevens 2002), Fabaceae (Polhill 1994), Lauraceae (Li *et al.* 2004), and Meliaceae (Muellner *et al.* 2003).

Results

SEED MASS AND SEED-COAT RATIO

Taxa with desiccation-sensitive seeds had a significantly greater seed mass than taxa with desiccation-tolerant seeds (3383 vs 283 mg, $P < 0.05$; Table 1, Fig. 1). When

Table 2. Contingency table for observed number of species with desiccation-sensitive and desiccation-tolerant seeds dispersed in either the dry or wet season on Barro Colorado Island

Seed type	Timing of seed dispersal	
	Dry season	Wet season
Desiccation-sensitive	5 (13.5)	27 (18.5)
Desiccation-tolerant	86 (77.5)	97 (105.5)

Values in parentheses are the expected number of species assuming a 2×2 contingency table.

correcting for phylogenetic relatedness, this relationship was still significant ($P < 0.05$; Table 1), indicating that the transition from desiccation-tolerant to desiccation-sensitive seeds is significantly correlated with an increase in seed mass.

The SCR for desiccation-sensitive seeds was significantly lower than for desiccation-tolerant seeds (0.212 vs 0.512, $P < 0.05$; Table 1, Fig. 1): this relationship was still significant when controlling for both effects of seed mass and phylogenetic relationships ($P < 0.05$; Table 1).

MEAN TIME TO GERMINATION

In the shade treatment, the desiccation-sensitive seeds germinated more rapidly than desiccation-tolerant seeds (MTG 23.3 vs 47.7 days, $P < 0.05$; Table 1); the relationship was marginally non-significant in the light treatment ($P = 0.061$; Table 1). Taking into account the effect of seed mass, germination occurred significantly more rapidly for desiccation-sensitive seeds in both light and shade environments (Table 1). In addition, these relationships were phylogenetically robust (Table 1).

The desiccation-sensitive species were significantly more likely to germinate rapidly in the shade than in the higher-light treatment (sign test, 22 species where $MTGS < MTGL$; three species where $MTGS > MTGL$, $P < 0.001$). However, for the desiccation-tolerant species there was no significant bias to either rapid germination in the shade or higher-light treatments (sign test, 86 species where $MTGS < MTGL$; 84 species where $MTGS > MTGL$, $P > 0.05$).

Across species, there was a highly significant ($P < 0.001$) relationship between MTG and the spread of germination times (difference between the first and last days on which germination occurred) (Spearman's rank correlation, $r_s = 0.70$, $df = 194$; $r_s = 0.72$, $df = 201$, for germination in the shade and light, respectively). Thus with an increasing MTG, species had an increasing spread of germination times.

TIMING OF SEED DISPERSAL

The distribution of seed dispersal times in relation to the wet and dry seasons was non-random (Table 2;

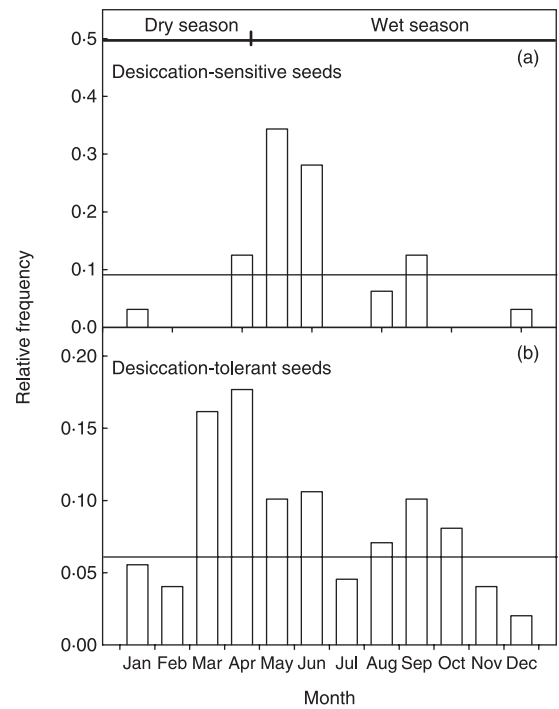


Fig. 2. Frequency distribution of the timing of dispersal for (a) 32 desiccation-sensitive; and (b) 183 desiccation-tolerant species in relation to the wet and dry seasons on Barro Colorado Island. The frequency of dispersal in each month is standardized by the number of species in the comparison. Horizontal lines indicate an even distribution of dispersal throughout the year.

$\chi^2 = 11.0$, $df = 1$, $P < 0.001$), with desiccation-sensitive seeds more likely to be dispersed in the wet than in the dry season (Fig. 2a). However there were exceptions, such as *Viola sebeifera* for which seed dispersal occurred at the beginning of the dry season (January; Fig. 2a). In contrast, desiccation-tolerant seeds were more likely to be shed in the dry than in the wet season (Fig. 2b).

Discussion

TIMING OF DISPERSAL AND SEED DESICCATION SENSITIVITY

For species with desiccation-sensitive seeds, dispersal occurred predominantly in the wet, as opposed to the dry season, with the pattern reversed for desiccation-tolerant species. Similar results have been demonstrated by Pritchard *et al.* (2004) for African dryland trees, where the desiccation-sensitive species timed seed dispersal to the wettest month(s) of the year, while desiccation-tolerant seeds were dispersed in either wet or dry months. For desiccation-sensitive seeds, wet-season dispersal has the advantage of minimizing the likelihood of seed desiccation and consequent death. However, for desiccation-tolerant seeds, dry-season dispersal has the advantage of allowing a seasonal seed bank to accumulate prior to the onset of significant rains, when the (pre-)existence of a seed bank may facilitate site pre-emption in advance of species

without a seed bank (Garwood 1983; Daws *et al.* 2005). However, there were exceptions among desiccation-sensitive species. For example, *V. sebeifera* was dispersed primarily early in the dry season (January). Interestingly, the distribution of this species on BCI is significantly biased towards slope sites (Harms *et al.* 2001), which maintain a higher level of water availability throughout the dry season. On slope sites, even in the dry season, the matric potential at the soil surface rarely falls below levels that are likely to inhibit germination (approximately -1.5 MPa) (Daws *et al.* 2002a, 2002b). Consequently, the specialization of this species to wet microsites may circumvent selection for wet-season seed dispersal. This reinforces the hypothesis that desiccation-sensitive seeds are shed to coincide with high water availability, albeit in this case related to spatial rather than temporal patterns.

GERMINATION AND DESICCATION SENSITIVITY

In our study the desiccation-sensitive species germinated more rapidly than the desiccation-tolerant species, independently of seed mass and phylogeny. This supports our hypothesis that, based on their high water content (which will minimize the period of imbibition) and metabolic activity at dispersal, desiccation-sensitive seeds will germinate rapidly. Although the observed differences in mean germination times between desiccation-sensitive and desiccation-tolerant species (≈ 38 days) may seem considerable, imbibition in some large, non-hard-seeded species can be protracted. For example, complete imbibition of dry seeds of *Hyophorbe lagenicaulis* (Arecaceae) has been reported to take 20 days (Wood & Pritchard 2003). Rapid germination of desiccation-sensitive seeds post-dispersal may enable rapid access to soil water, thereby minimizing the risks of desiccation-induced mortality in short wet-season dry spells.

For desiccation-tolerant species, less rapid germination and a greater spread of germination times may be advantageous. For example, in environments of unpredictable rainfall, such as the start of the wet season on BCI (Garwood 1983), less rapid germination, which is dispersed in time, may reduce the risk of drought or desiccation-induced mortality once seeds have either started to germinate or are at the early seedling stage (Doussi & Thanos 2002). However, this may not be a viable strategy for desiccation-sensitive species, for which slow germination and a prolonged dry spell following seed dispersal could potentially result in mortality of an entire annual cohort of seeds.

For 179 Malaysian tree and shrub species, Foster (1986) reported a positive relationship between seed size and germination rate, which was likely to result from reduced seed–soil contact with increasing seed size. However, the relationship between MTG and desiccation sensitivity that we observed was still significant when controlling for seed mass. While the number of desiccation-sensitive species in the data set used by

Foster (1986) is unclear, our findings suggest that the high water content of desiccation-sensitive seeds at shedding and their metabolic activity result in rapid germination, irrespective of seed–soil contact.

In a cross-species analysis, the desiccation-sensitive species were more likely to germinate rapidly in the shade than in the light. In higher-light conditions, there may be a negative impact on large-seeded species as a result of water loss and the consequent decrease in vigour associated with desiccation damage (Pamenter & Berjak 2000). In support of this proposition, Molofsky & Augspurger (1992) reported that in gaps on BCI, seeds of the desiccation-sensitive species *Gustavia superba* (see Appendix 1) germinate to a higher level when buried under leaf litter than when exposed on the soil surface, presumably because of water loss. However, in the shade, litter had no effect on germination. Similarly, burial can have a beneficial effect on the germination and survival of desiccation-sensitive *Quercus rubra* seeds (Garcia, Banuelos & Houle 2002). These findings highlight the potential importance of burial by seed predators or burial beneath leaf litter for successful establishment of species with desiccation-sensitive seeds. However, the desiccation-tolerant species were equally likely to germinate rapidly in the shade (lower-shelf) or light (upper-shelf) treatments. For the generally small-seeded desiccation-tolerant species, germination in the higher-light environment may be less inhibited as a result of a greater level of seed–soil contact. Additionally, a number of desiccation-tolerant species have been classified as ‘pioneers’ (*sensu* Swaine & Whitmore 1988), for example *Ochroma pyramidale* and *Miconia argentea* (Pearson *et al.* 2002). These species rely on the occurrence of open (high-light) microsites for successful germination and seedling establishment, and have seedlings with a physiological requirement for high-light conditions.

SEED MASS, SEED-COAT RATIO AND DESICCATION SENSITIVITY

Desiccation-sensitive species in this study had large seeds which will presumably reduce the rate of seed desiccation. Interestingly, our values for average seed mass for desiccation-sensitive and desiccation-tolerant species were similar to values presented by Dickie & Pritchard (2002), who included values from a wide range of both tropical and temperate vegetation types. Our observed trend of desiccation-sensitive seeds being large was phylogenetically robust, leading us to suggest that the loss of desiccation tolerance during evolution has been associated with an increase in seed mass. However large seed size *per se* does not result in desiccation sensitivity. For example, there are a number of large-seeded desiccation-tolerant species in the data set, including *Astrocaryum standleyanum* and *Dipteryx panamensis*, both of which have a seed mass >6 g.

In addition to being metabolically active at seed shed, the thin seed coat of desiccation-sensitive species

may also contribute to rapid germination by providing less of a mechanical restraint to germination. Our results for MTG and SCR are consistent with the hypothesis of Pritchard *et al.* (2004) that rapid germination of desiccation-sensitive seeds may reduce the duration of seed exposure to predation (cf. dipterocarps; Curran & Webb 2000), the corollary being reduced selection for a large investment in seed physical defences. Consequently, per unit mass, desiccation-sensitive seeds appear to be a more efficient use of resources in seed provisioning than desiccation-tolerant seeds.

For some groups of species it has been demonstrated that larger seeds may invest proportionally more resources in defence (e.g. Asteraceae; Fenner 1983). However, the differences in SCR we observed were independent of mass. There is also limited evidence for a negative relationship between seed mass and post-dispersal seed predation (Hulme 1998). Viewed in the light of these two relationships, the generally large-seeded desiccation-sensitive species have a surprisingly low investment in physical defences, which presumably reflects the limited time span of seed exposure to predators. Grubb *et al.* (1998) demonstrated a positive relationship between both seed physical defences and seed nitrate content for a range of tropical tree seeds. Consequently, it is also possible that a low allocation to defence in desiccation-sensitive species may be related to their being of low nutritional value. Investigations into the chemical composition of desiccation-sensitive and desiccation-tolerant species may be worth pursuing to clarify this issue.

Conclusions

There are a number of advantages associated with large seed size, including a higher probability of seedling survival under low light (Leishman & Westoby 1994a) and drought conditions (Leishman & Westoby 1994b), and an ability to resprout following herbivory (Harms & Dalling 1997). However, large and hydrated seeds can be very attractive to both fungal and vertebrate seed predators. In habitats of benign, uniform climate that are continuously conducive to germination and seedling establishment, there may be little selection driving the evolution or maintenance of desiccation tolerance, particularly for large seeds that will dry slowly (Pammenter & Berjak 2000). Our results for germination rate and seed resource allocation support the hypothesis of Pammenter & Berjak (2000) that, in this habitat, desiccation sensitivity may not necessarily be a neutral trait, and may be related to the risk of predation. Thus desiccation sensitivity may be advantageous by minimizing predation through rapid germination, with the consequent low investment in defence resulting in these seeds being a more efficient use of resources in seed provisioning.

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Appendix 1. Details of species used in the study: classification to family level [following APG (2003)], seed dry mass, seed-coat ratio, and timing of dispersal relative to wet season (W) and dry season (D) on Barro Colorado Island (species with desiccation-sensitive seeds in bold type)

Species	Clade	Order	Family	DWT (mg)	Seed-coat ratio	Dispersal period
<i>Abarema macradenium</i> Pittier	Eurosids I	Fabales	Fabaceae	90	0.153	W
<i>Abuta racemosa</i> (Thunb.) Triana & Planch	Eudicots	Ranunculales	Menispermaceae	579		D
<i>Adelia triloba</i> (Müll. Arg.) Hemsle	Eurosids I	Malpighiales	Euphorbiaceae	26	0.354	D
<i>Adenopodia polystachya</i> (L.) J.R. Dixon ex Croat	Eurosids I	Fabales	Fabaceae	298	0.942	D
<i>Aegiphila elata</i> Sw.	Euasterids I	Lamiales	Verbenaceae	60		W
<i>Albizia guachapele</i> (H.B. & K.) Dugand	Eurosids I	Fabales	Fabaceae	32	0.433	W
<i>Alchornea costaricensis</i> Pax & K. Hoffm.	Eurosids I	Malpighiales	Euphorbiaceae	34	0.799	W
<i>Alibertia edulis</i> (Rich.) A. Rich. ex DC.	Euasterids I	Gentianales	Rubiaceae	15	0.114	D
<i>Alseis blackiana</i> Hemsl.	Euasterids I	Gentianales	Rubiaceae	0.2		D
<i>Anacardium excelsum</i> (Bertero & Balb. Ex Kunth) Skeels	Eurosids II	Sapindales	Anacardiaceae	1507	0.433	D
<i>Andira inermis</i> (Sw.) Kunth	Eurosids I	Fabales	Fabaceae	792	0.297	W
<i>Annona acuminata</i> Saff.	Magnoliids	Magnoliales	Annonaceae	36		D
<i>Annona glabra</i> L.	Magnoliids	Magnoliales	Annonaceae	229	0.358	W
<i>Annona hayesii</i> Saff. In Standl.	Magnoliids	Magnoliales	Annonaceae	62		W
<i>Annona muricata</i> L.	Magnoliids	Magnoliales	Annonaceae	322	0.706	W
<i>Annona purpurea</i> Moç. & Sessé ex Dunal	Magnoliids	Magnoliales	Annonaceae	897		W
<i>Annona spraguei</i> Safford	Magnoliids	Magnoliales	Annonaceae	34		W
<i>Anthodon panamense</i> A.C. Sm.	Eurosids I	Celastrales	Celastraceae	81	0.438	D
<i>Antirhea trichantha</i> (Griseb.) Hemsl.	Euasterids I	Gentianales	Rubiaceae	10		W
<i>Apeiba membranacea</i> Spruce ex Benth.	Eurosids II	Malvales	Malvaceae	69	0.776	W
<i>Apeiba tibourbou</i> Aubl.	Eurosids II	Malvales	Malvaceae	17	0.584	W
<i>Aristolochia chapmaniana</i> Standl.	Magnoliids	Piperales	Aristolochiaceae	6		W
<i>Arrabidaea candicans</i> (Rich.) DC.	Euasterids I	Lamiales	Bignoniaceae	19		W
<i>Arrabidaea patellifera</i> (Schltdl.) Sandwith	Euasterids I	Lamiales	Bignoniaceae	17		D
<i>Artocarpus altilis</i> (Parkinson) Fosberg	Eurosids I	Rosales	Moraceae	5898		W
<i>Aspidosperma cruenta</i> Woodson	Euasterids I	Gentianales	Apocynaceae	565		W
<i>Aspidosperma megalocarpon</i> Müll. Arg	Euasterids I	Gentianales	Apocynaceae			D
<i>Astrocaryum standleyanum</i> L.H. Bailey	Commelinids	Arecales	Areaceae	7598		W
<i>Astronium graveolens</i> Jacq.	Eurosids II	Sapindales	Anacardiaceae	30	0.368	D
<i>Bactris gasipaes</i> Kunth	Commelinids	Arecales	Areaceae	1680	0.303	W
<i>Beilschmiedia pendula</i> (Sw.) Hemsl.	Magnoliids	Laurales	Lauraceae	3987	0.100	W
<i>Bertiera guianensis</i> Aubl.	Euasterids I	Gentianales	Rubiaceae	1		W
<i>Bixa orellana</i> L.	Eurosids II	Malvales	Bixaceae	25		D
<i>Brosimum alicastrum</i> Sw.	Eurosids I	Rosales	Moraceae	712	0.045	W
<i>Bursera simaruba</i> (L.) Sarg.	Eurosids II	Sapindales	Burseraceae	82		D
<i>Byrsonima spicata</i> (Cav.) Kunth	Eurosids I	Malpighiales	Malpighiaceae	108	0.953	W
<i>Callichlamys latifolia</i> (Rich.) K. Schum.	Euasterids I	Lamiales	Bignoniaceae	134	0.328	D
<i>Calophyllum longifolium</i> Willd.	Eurosids I	Malpighiales	Clusiaceae	4532	0.266	D
<i>Capparis flexuosa</i> L.	Eurosids II	Brassicales	Brassicaceae			W
<i>Capparis frondosa</i> Jacq.	Eurosids II	Brassicales	Brassicaceae	97	0.262	W
<i>Capsicum annuum</i> L.	Euasterids I	Solanales	Solanaceae	3		D
<i>Carica papaya</i> L.	Eurosids II	Brassicales	Caricaceae	12	0.459	W
<i>Casearia sylvestris</i> Sw.	Eurosids I	Malpighiales	Salicaceae	1		D
<i>Castilla elastica</i> Sessé	Eurosids I	Rosales	Moraceae			W
<i>Cavanillesia platanifolia</i> (Bonpl. in Humb. & Bonpl.) Kunth	Eurosids II	Malvales	Malvaceae	1751		D
<i>Cecropia insignis</i> Liebm.	Eurosids I	Rosales	Moraceae	0.5		D
<i>Cecropia longipes</i> Pittier	Eurosids I	Rosales	Moraceae	0.7		W
<i>Cecropia obtusifolia</i> Bertol.	Eurosids I	Rosales	Moraceae	0.5	0.878	W
<i>Cecropia peltata</i> L.	Eurosids I	Rosales	Moraceae	0.6		D
<i>Cedrela odorata</i> L.	Eurosids II	Sapindales	Meliaceae	11		W
<i>Ceiba pentandra</i> (L.) Gaertn.	Eurosids II	Malvales	Malvaceae	55	0.309	D
<i>Celtis iguanaea</i> (Jacq.) Sarq.	Eurosids I	Rosales	Celtidaceae	106		W
<i>Cespedezia macrophylla</i> Seem.	Eurosids I	Malpighiales	Ochnaceae	0.2		D
<i>Chamaedorea tepejilote</i> Liebm.	Commelinids	Arecales	Areaceae	150	0.053	W
<i>Chloroleucon mangense</i> (Jacq.) J.F. Macbr.	Eurosids I	Fabales	Fabaceae	45		W
<i>Chromolaena odorata</i> (L.) R.M. King & H. Rob.	Euasterid II	Asterales	Asteraceae	0.2		D
<i>Chrysophyllum cainito</i> L.	Asterids	Ericales	Sapotaceae	210	0.562	D
<i>Cissus sicyoides</i> L.	Rosids		Vitaceae	22		D
<i>Citrus aurantifolia</i> L.	Eurosids II	Sapindales	Rutaceae			W
<i>Clidemia capitella</i> var. <i>neglecta</i> (D. Don) L.O. Williams	Rosids	Myrtales	Melastomataceae	0.02		W
<i>Clidemia capitellata</i> (Bonpl.) D. Don	Rosids	Myrtales	Melastomataceae			D
<i>Clidemia dentata</i> D. Don	Rosids	Myrtales	Melastomataceae	0.02		W
<i>Clidemia octona</i> (Bonpl.) L.O. Williams	Rosids	Myrtales	Melastomataceae	0.01	0.250	W

Appendix I. Continued

Species	Clade	Order	Family	DWT (mg)	Seed-coat ratio	Dispersal period
<i>Clidemia septuplinervia</i> Coqn.	Rosids	Myrtales	Melastomataceae	0-02		W
<i>Clitoria javitensis</i> var. <i>portobellensis</i> (Beurl.) Fantz	Eurosids I	Fabales	Fabaceae	483		D
<i>Cochlospermum vitifolium</i> (willd.) Spreng.	Eurosids II	Malvales	Cochlospermaceae	26	0-741	D
<i>Connarus panamensis</i>	Eurosids I	Oxalidales	Connaraceae	294		W
<i>Connarus turczaninowii</i> Triana & Planch.	Eurosids I	Oxalidales	Connaraceae	405	0-214	W
<i>Conostegia cinnamomea</i> (Beurl.) Wurdack.	Rosids	Myrtales	Melastomataceae			W
<i>Conostegia speciosa</i> Naudin	Rosids	Myrtales	Melastomataceae	0-1		W
<i>Cordia alliodora</i> (Ruiz & Pav.) Oken	Euasterids I		Boraginaceae	6		W
<i>Cordia panamensis</i> L. Riley	Euasterids I		Boraginaceae	59	0-720	W
<i>Cordia spinescens</i> L.	Euasterids I		Boraginaceae	11		D
<i>Couroupita guianensis</i> Aubl.	Asterids	Ericales	Lecythidaceae	5		D
<i>Coussapoa asperifolia</i> ssp. <i>magnifolia</i> (Trécul) Akkermans & C.C. Berq.	Eurosids I	Rosales	Moraceae	2		D
<i>Coutarea hexandra</i> (Jacq.) K. Schum	Euasterids I	Gentianales	Rubiaceae	5		D
<i>Crotalaria cajanifolia</i> Kunth	Eurosids I	Fabales	Fabaceae	13		D
<i>Cupania cinerea</i> Poepp.	Eurosids II	Sapindales	Sapindaceae	510	0-254	W
<i>Cydista aequinoctalis</i> (L.) Miers.	Euasterids I	Lamiales	Bignoniaceae	112	0-547	D
<i>Dalbergia retusa</i> Hamsl.	Eurosids I	Fabales	Fabaceae	130	0-792	D
<i>Dalechampia tiliifolia</i> Lam.	Eurosids I	Malpighiales	Euphorbiaceae	21		D
<i>Davilla aspera</i> (Aubl.) Benoist	Core Eudicots		Dilleniaceae	24	0-337	W
<i>Dendropanax arboreus</i> (L.) Decne. & Planch.	Euasterid II	Apiales	Araliaceae	8	0-790	W
<i>Desmoncus isthmius</i> L.H. Bailey	Commelinids	Arecales	Arecaceae	314	0-261	W
<i>Didymopanax morototoni</i> (Aubl.)	Euasterid II	Apiales	Araliaceae	14	0-642	D
<i>Dioclea guianensis</i> Benth.	Eurosids I	Fabales	Fabaceae	72		D
<i>Dioclea reflexa</i> Hook. f.	Eurosids I	Fabales	Fabaceae	4013	0-672	W
<i>Dipteryx panamensis</i> (Pittier) Record & mell	Eurosids I	Fabales	Fabaceae	6127	0-870	D
<i>Elaeis oleifera</i> (Kunth) Cortés	Commelinids	Arecales	Arecaceae	2507	0-694	W
<i>Enterolobium cyclocarpum</i> (Jacq.) Griseb.	Eurosids I	Fabales	Fabaceae	545	0-470	W
<i>Erythrina costaricensis</i> Micheli	Eurosids I	Fabales	Fabaceae			W
<i>Eugenia uniflora</i> L.	Rosids	Myrtales	Myrtaceae		0-141	
<i>Ficus citrifolia</i> Mill.	Eurosids I	Rosales	Moraceae	0-9		W
<i>Ficus dugandii</i> Standl.	Eurosids I	Rosales	Moraceae	0-1		W
<i>Ficus insipida</i> Willd.	Eurosids I	Rosales	Moraceae	1		W
<i>Ficus obtusifolia</i> Kunth	Eurosids I	Rosales	Moraceae	1	0-635	W
<i>Ficus popenoei</i> Standl.	Eurosids I	Rosales	Moraceae	0-5		W
<i>Garcinia mangostana</i> L.	Eurosids I	Malpighiales	Clusiaceae	748	0-281	W
<i>Genipa americana</i> L.	Euasterids I	Gentianales	Rubiaceae	123		W
<i>Guarea guidonia</i> (L.) Sleumer	Eurosids II	Sapindales	Meliaceae	153	0-267	W
<i>Guazuma ulmifolia</i> Lam.	Eurosids II	Malvales	Malvaceae	4	0-488	D
<i>Gustavia superba</i> (Kunth.) O. Berq.	Asterids	Ericales	Lecythidaceae	2815	0-061	W
<i>Hamelia patens</i> Jacq.	Euasterids I	Gentianales	Rubiaceae	0-05		W
<i>Hampea appendiculata</i> (Donn. Sm.) Standl.	Eurosids II	Malvales	Malvaceae	60	0-187	D
<i>Henriettea succosa</i> (Aubl.) DC.	Rosids	Myrtales	Melastomataceae	0-09		W
<i>Henriettea fascicularis</i> Triana	Rosids	Myrtales	Melastomataceae	0-02		W
<i>Herrania purpurea</i> (Pittier) R.E. Schult	Eurosids II	Malvales	Malvaceae	217	0-296	D
<i>Hevea brasiliense</i> Müll. Arg	Eurosids I	Malpighiales	Euphorbiaceae	3630	0-525	W
<i>Hippobroma longiflora</i> (L.) G. Don	Euasterids II	Asterales	Campanulaceae	0-07		W
<i>Hura crepitans</i> L.	Eurosids I	Malpighiales	Euphorbiaceae	845	0-327	W
<i>Hybanthus prunifolius</i> (Humb. & Bonpl. Ex Roem. & Schult.) Schulze-Menz	Eurosids I	Malpighiales	Violaceae	12	0-268	W
<i>Hyeronima laxiflora</i> (Tul.) Müll. Arg	Eurosids I	Malpighiales	Euphorbiaceae	7	0-699	D
<i>Hylенаea praecelsa</i> (Miers) A.C. Sm.	Eurosids I	Celastrales	Celastraceae	2027	0-670	D
<i>Hymenaea courbaril</i> L.	Eurosids I	Fabales	Fabaceae	5418		D
<i>Inga minutula</i> (Schery) T.S. Elias.	Eurosids I	Fabales	Fabaceae	380	0-141	W
<i>Inga punctata</i> Willd.	Eurosids I	Fabales	Fabaceae			W
<i>Jacaranda copaia</i> (Aubl.) D. Don.	Euasterids I	Lamiales	Bignoniaceae	5		W
<i>Laetia procera</i> (Poepp.) Eichler	Eurosids I	Malpighiales	Salicaceae	5	0-762	D
<i>Lafoensia punicifolia</i> DC.	Rosids	Myrtales	Lythraceae	36	0-516	D
<i>Lantana camara</i> L.	Euasterids I	Lamiales	Verbenaceae	9		W
<i>Leandra dichotoma</i> (D. Don) Coqn.	Rosids	Myrtales	Melastomataceae	0-008		W
<i>Lonchocarpus pentaphyllus</i> (Poir.) Kunth	Eurosids I	Fabales	Fabaceae	161	0-156	W
<i>Luehea seemannii</i> Triana & Planch.	Eurosids II	Malvales	Malvaceae	3	0-784	D
<i>Macfadyena unguis-cati</i> (L.) A.H. Gentry	Euasterids I	Lamiales	Bignoniaceae	29	0-633	D
<i>Mangifera indica</i> L.	Eurosids II	Sapindales	Anacardiaceae	4500	0-381	W
<i>Margaritaria nobilis</i> L.f.	Eurosids I	Malpighiales	Euphorbiaceae	8	0-756	W

Appendix I. Continued

Species	Clade	Order	Family	DWT (mg)	Seed-coat ratio	Dispersal period
<i>Maripa panamensis</i> Hemsl.	Euasterids I	Solanales	Convolvulaceae	353	0-094	W
<i>Melochia lupulina</i> Sw.	Eurosids II	Malvales	Malvaceae	0-3		D
<i>Melothria trilobata</i> Coqn. In Mart.	Eurosids I	Cucurbitales	Cucurbitaceae	4		W
<i>Merremia umbellata</i> (L.) Hallier f.	Euasterids I	Solanales	Convolvulaceae	35		D
<i>Mesechites trifida</i> (Jacq.) Müll. Arg.	Euasterids I	Gentianales	Apocynaceae	3	0-429	W
<i>Miconia affinis</i> DC.	Rosids	Myrtales	Melastomataceae	0-2		W
<i>Miconia argentea</i> (Sw.) DC.	Rosids	Myrtales	Melastomataceae	0-08	0-274	D
<i>Mikania micrantha</i> Kunth	Euasterid II	Asterales	Asteraceae	0-09		D
<i>Mimosa pigra</i> L.	Eurosids I	Fabales	Fabaceae	16		W
<i>Mouriri myrtilloides</i> ssp. <i>parvifolia</i> (Benth.) Morley	Rosids	Myrtales	Melastomataceae	68	0-116	W
<i>Muntingia calabura</i> L.	Eurosids I	oxalidales	Elaeocarpaceae	0-04		D
<i>Myroxylon balsamum</i> (L.) Harms	Eurosids I	Fabales	Fabaceae	478		W
<i>Nectandra membranacea</i> (Sw.) Griseb.	Magnoliids	Laurales	Lauraceae		0-159	
<i>Ochroma pyramidale</i> (Cav. Ex Lam.) Urb.	Eurosids II	Malvales	Malvaceae	10	0-940	D
<i>Ocotea whitei</i> Woodson	Magnoliids	Laurales	Lauraceae	7300	0-013	W
<i>Odonellia hirtiflora</i> (M. Martens & Galeotti) K.R. Roberston	Euasterids I	Solanales	Convolvulaceae	27		D
<i>Odontadenia macrantha</i> (Roem. & Schutt.) Markgr.	Euasterids I	Gentianales	Apocynaceae	172	0-379	D
<i>Ormosia coccinea</i> (Aubl.) Jackson	Eurosids I	Fabales	Fabaceae	543		W
<i>Ormosia macrocalyx</i> Ducke	Eurosids I	Fabales	Fabaceae	401	0-131	W
<i>Ossaea quinquenervia</i> (Mill.) Coqn.	Rosids	Myrtales	Melastomataceae	0-01	0-207	W
<i>Pachira aquatica</i> Aubl.	Eurosids II	Malvales	Malvaceae	1730		D
<i>Pachira quinata</i> (Jacq.) Dugand	Eurosids II	Malvales	Malvaceae	40		D
<i>Pachira sessilis</i> (Benth.) Pittier.	Eurosids II	Malvales	Malvaceae	349	0-206	D
<i>Pachyrhizus erosus</i> (L.) Urb.	Eurosids I	Fabales	Fabaceae	763		D
<i>Palicourea guianensis</i> Aubl.	Euasterids I	Gentianales	Rubiaceae	14		W
<i>Passiflora ambigua</i> Hemsl.	Eurosids I	Malpighiales	Passifloraceae	34		D
<i>Passiflora biflora</i> Lam.	Eurosids I	Malpighiales	Passifloraceae	3		W
<i>Passiflora foetida</i> L.	Eurosids I	Malpighiales	Passifloraceae	8	0-650	D
<i>Persea americana</i> Mill.	Magnoliids	Laurales	Lauraceae	20670	0-037	W
<i>Petrea aspera</i> Turcz.	Euasterids I	Lamiales	Verbenaceae	35		D
<i>Phryganocydia corymbosa</i> (Vent.) Baill.	Euasterids I	Lamiales	Bignoniaceae	69		D
<i>Piper aequale</i> Vahl	Magoliids	Piperales	Piperaceae	0-06		W
<i>Piper dilatatum</i> Rich.	Magoliids	Piperales	Piperaceae	0-1		W
<i>Piper hispidum</i> Sw.	Magoliids	Piperales	Piperaceae	0-1		
<i>Piper marginatum</i> Jacq.	Magoliids	Piperales	Piperaceae	0-1	0-208	D
<i>Piper peltatum</i> L.	Magnoliids	Piperales	Piperaceae	0-04	0-147	W
<i>Pithecoctenium crucigerum</i> (L.) A.H. Gentry	Euasterids I	Lamiales	Bignoniaceae	59		D
<i>Platymiscium pinnatum</i> (Jacq.) Dugand	Eurosids I	Fabales	Fabaceae	313	0-791	D
<i>Platydiem elegans</i> Vogel	Eurosids I	Fabales	Fabaceae	1219	0-892	D
<i>Plenotoma variabilis</i> (Jacq.) Miers	Euasterids I	Lamiales	Bignoniaceae	32		D
<i>Poulsenia armata</i> (Miq.) Standl.	Eurosids I	Rosales	Moraceae	65		W
<i>Pouteria sapota</i> (Jacq.) H.E. Moore & Stearn	Asterids	Ericales	Sapotaceae	13040	0-472	W
<i>Prionostemma aspera</i> (Lam.) Miers	Eurosids I	Celastrales	Celastraceae	182	0-431	D
<i>Prioria copaiifera</i> Griseb.	Eurosids I	Fabales	Fabaceae	23840	0-366	W
<i>Protium panamense</i> (Rose) I.M. Johnst.	Eurosids II	Sapindales	Burseraceae	4800	0-256	W
<i>Protium tenuifolium</i> ssp. <i>sessiliflorum</i> (Rose) D.M. Porter	Eurosids II	Sapindales	Burseraceae	1300		W
<i>Pseudobombax septenatum</i> (Jacq.) Dugand	Eurosids II	Malvales	Malvaceae	60	0-246	D
<i>Psidium guajava</i> L.	Rosids	Myrtales	Myrtaceae	8	0-861	W
<i>Psychotria acuminata</i> Benth.	Euasterids I	Gentianales	Rubiaceae	12		W
<i>Psychotria brachybotrya</i> Müll. Arq.	Euasterids I	Gentianales	Rubiaceae	4		W
<i>Psychotria deflexa</i> DC.	Euasterids I	Gentianales	Rubiaceae	4		W
<i>Psychotria horizontalis</i> Sw.	Euasterids I	Gentianales	Rubiaceae	6		W
<i>Psychotria micrantha</i> Kunth.	Euasterids I	Gentianales	Rubiaceae	10	0-575	W
<i>Psychotria pittieri</i> Standl.	Euasterids I	Gentianales	Rubiaceae	3		W
<i>Psychotria pubescens</i> Sw.	Euasterids I	Gentianales	Rubiaceae	8		W
<i>Psychotria tomentosa</i> (Aubl.) Vahl	Euasterids I	Gentianales	Rubiaceae	9		W
<i>Quararibea pterocalyx</i> Hemsl.	Eurosids II	Malvales	Malvaceae	4040	0-356	W
<i>Randia formosa</i> (Jacq.) Schum.	Euasterids I	Gentianales	Rubiaceae	31	0-523	W
<i>Rheedia edulis</i> (Seem.) Planch.	Eurosids I	Malpighiales	Clusiaceae	289	0-252	W
<i>Rhynchosia pyramidalis</i> (Lam.) Urb.	Eurosids I	Fabales	Fabaceae	61		
<i>Roupala montana</i> Aubl.	Eudicots	Proteales	Proteaceae	19		D
<i>Serjania decapleuria</i> Croat	Eurosids II	Sapindales	Salindaceae	48		D
<i>Serjania rhombea</i> Radlk.	Eurosids II	Sapindales	Sapindaceae	11	0-829	D

Appendix I. Continued

Species	Clade	Order	Family	DWT (mg)	Seed-coat ratio	Dispersal period
<i>Simarouba amara</i> Aubl.	Eurosids II	Sapindales	Simaroubaceae	105		W
<i>Siparuna guianensis</i> Aubl.	Magnoliids	Laurales	Monimiaceae	20	0.618	W
<i>Solanum hayesii</i> Fernald	Euasterids I	Solanales	Solanaceae	2	0.807	D
<i>Solanum torvum</i> Sw.	Euasterids I	Solanales	Solanaceae	1		W
<i>Souroubea sympetala</i> Gilg	Asterids	Ericales	Marcgraviaceae	3		D
<i>Spondias mombin</i> L.	Eurosids II	Sapindales	Anacardiaceae		0.957	
<i>Stizolobium pruriens</i> (L. in Stickm.) Medik.	Eurosids I	Fabales	Fabaceae	529	0.176	D
<i>Stylogyne standleyi</i> Lundell	Asterids	Ericales	Myrsinaceae	66	0.278	D
<i>Swartzia simplex</i> var. <i>ochracea</i> (Sw.) Spreng.	Eurosids I	Fabales	Fabaceae	1025	0.048	W
<i>Swietenia macrophylla</i> King	Eurosids II	Sapindales	Meliaceae	470	0.290	D
<i>Symphonia globulifera</i> L.f.	Eurosids I	Malpighiales	Clusiaceae	2334		D
<i>Synechanthus warscewiczianus</i> H. Wendl.	Commelinids	Arecales	Arecaceae	272	0.105	W
<i>Syzygium jambos</i> L.	Rosids	Myrtales	Myrtaceae	2380	0.076	
<i>Tabebuia guayacan</i> (Seem.) Hemsl.	Euasterids I	Lamiales	Bignoniaceae	26	0.204	D
<i>Tabebuia rosea</i> (Bertol.) DC.	Euasterids I	Lamiales	Bignoniaceae	25		D
<i>Tachigali versicolor</i> Standl. & L.O. Williams	Eurosids I	Fabales	Fabaceae	910	0.275	W
<i>Terminalia amazonia</i> (J.F. Gmel.) Exell	Rosids	Myrtales	Combretaceae	2		D
<i>Terminalia oblonga</i> (Ruiz & Pav.) Steud.	Rosids	Myrtales	Combretaceae	55		
<i>Tetracera portobellensis</i> Bewl.	Core Eudicots		Dilleniaceae	14		D
<i>Tetrathylacium johansenii</i> Standl.	Eurosids I	Malpighiales	Salicaceae	1		D
<i>Theobroma cacao</i> L.	Eurosids II	Malvales	Malvaceae	1771	0.275	
<i>Tournefortia hirsutissima</i> L.	Euasterids I		Boraginaceae	2		W
<i>Trema micrantha</i> (L.) Blume	Eurosids I	Rosales	Ulmaceae	2	0.682	W
<i>Trichilia tuberculata</i> C. DC.	Eurosids II	Sapindales	Meliaceae	151	0.038	W
<i>Trichospermum galeottii</i> (Turcz.) Kosterm.	Eurosids II	Malvales	Malvaceae	3	0.571	D
<i>Triplaris cumingiana</i> Fisch. & C.A. Mey. ex C.A. Mey	Core Eudicots	Caryophyllales	Polygonaceae	83		D
<i>Triumfetta bogotensis</i> DC.	Eurosids II	Malvales	Malvaceae	22		D
<i>Vernonia patens</i> Kunth	Euasterid II	Asterales	Asteraceae	0.1		D
<i>Viola sebifera</i> Aubl.	Magnoliids	Magnoliales	Myristiceae	472	0.223	D
<i>Viola surinamensis</i> (Rol.) Warb.	Magnoliids	Magnoliales	Myristiceae	1952	0.103	W
<i>Vismia macrophylla</i> Kunth	Eurosids I	Malpighiales	Clusiaceae	0.6		W
<i>Vochysia ferruginea</i> Mart.	Rosids	Myrtales	Vochysiaceae			W
<i>Zanthoxylum belizense</i> Lundell	Eurosids II	Sapindales	Rutaceae	14		D
<i>Zanthoxylum panamense</i> P. Wilson	Eurosids II	Sapindales	Rutaceae	29	0.791	D
<i>Zanthoxylum procerum</i> Don. Sm.	Eurosids II	Sapindales	Rutaceae	11		W
<i>Zanthoxylum setulosum</i> P. Wilson	Eurosids II	Sapindales	Rutaceae	10		W