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Seed storage behaviour of 101 woody species from the tropical rainforest of southern China: a test of the seed-coat ratio–seed mass (SCR–SM) model for determination of desiccation sensitivity

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Abstract. The Xishuangbanna tropical rainforest in Yunnan Province is the greatest biodiversity hotspot in China. However, the biodiversity of this region is under threat, making seed conservation through seed and/or germplasm banking particularly urgent and crucial. Seed desiccation sensitivity limits the possibility of seed banking of 47% of tropical rainforest species. Thus, knowing if a species has desiccation-sensitive seeds is an important first step in seed banking; however, often resources are limited, making it difficult to determine storage behaviour for all the species in a region. Prediction of seed sensitivity using the SCR–SM model based on seed-coat ratio (SCR) and seed dry mass (SM) might be an alternative for determining desiccation sensitivity of seeds of each species. Here, seed-desiccation sensitivity of 101 woody species from the Xishuangbanna tropical forest were analysed using this model, and physiological determinations were made for a total of 25 species. Seed storage behaviour for 59 species was used for model validation, and storage behaviour of 88% of these species was successfully predicted. Seed storage behaviour of 83% of the 59 species was successfully predicted using the 1000-seed weigth–moisture content (TSW–MC) criteria, which include seeds with 1000-seed weight >500 g and seed moisture content at shedding of 30 –70%. The two predictive methods were subsequently used to predict seed desiccation sensitivity for another 42 species from Xishuangbanna whose storage behaviour was uncertain. Our results indicated that ~50% of the species in Xishuangbanna are likely to have desiccation-sensitive seeds.

Additional keywords: predictive model, recalcitrant seeds, Yunnan Province.

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Introduction

The Xishuangbanna tropical rainforest in southern Yunnan Province is the greatest biodiversity hotspot in China, containing ~7500 vascular plants, including ~6000 native species (~24% of China's total) (Xu 1987). However, the biodiversity of this region is under threat from loss of habitat as a result of logging and planting of economic plants, thus making seed conservation through seed/germplasm banking of these species particularly urgent and crucial. One of the difficulties involved in placing seeds of many tropical species into gene banks is that their seeds are recalcitrant (desiccation-sensitive, Roberts 1973). In contrast to orthodox seeds that can tolerate desiccation to a moisture content (MC) of <7% with little negative effect on viability (Roberts 1973), recalcitrant seeds are killed by drying to a MC as high as 20–30% (Pritchard 2004). Therefore, they cannot survive the drying and low temperature (−20°C) conditions of the seed bank (Li and Pritchard 2009; Walters *et al.* 2013).

Woody species account for a high percentage of species with recalcitrant seeds, and in tropical evergreen rainforests, the frequency of species with recalcitrant seeds is ~47% (Tweddle *et al.* 2003). Thus, seed banking of tropical woody species without identifying the seed storage behaviour is particularly risky because there is a high probability that the seeds will be desiccation-sensitive and, thus, will die when dried for storage. However, seed storage behaviour of <3% species of the world's seed plants has been identified, and information for Xishuangbanna tropical species is especially sparse.

Although high-throughput methods are available to determine seed storage behaviour, i.e. 100-seed test (Pritchard

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et al. 2004*b*), limited human resources and a shortage of germplasm of some species prohibits the testing of seeds of all woody species from the Xishuangbanna region. However, information on storage behaviour is critical for successful storage of seeds. Thus, we need to find a way to use seed traits to accurately predict if seeds are desiccation-sensitive.

Seed size, seed MC at shedding and seed-coat ratio (SCR) may correlate with seed-desiccation sensitivity. According to Chin *et al.* (1984) and Hong and Ellis (1996), desiccation-sensitive seeds usually have a 1000-seed weight (TSW) exceeding 500 g and a MC ranging from 30% to 70%. During the past two decades, these criteria (hereafter referred to as the TSW–MC criteria) have been used by Xishuangbanna Germplasm Bank as a decision-making tool in the handling of species with unknown seed desiccation sensitivity. In 2006, Daws *et al.* proposed a predictive model in which SCR and seed dry mass (SCR–SM model) was used to predict seed sensitivity. This model was developed using binary logistic regression on seed trait data for 104 species from 37 families from a tropical forest in Panama, and it was validated with European temperate and African tropical dryland tree species. In the model, seeds with relatively thin seed coats, (i.e. a small SCR) were combined with larger seed mass to predict desiccation sensitivity.

Since seed traits (e.g. seed mass and desiccation sensitivity) are usually habitat-associated (Tweddle *et al.* 2003; Daws *et al.* 2005; Li and Pritchard 2009; Walters *et al.* 2013), a test of the efficiency of the SCR–SM model on typical vegetation is required before a broad usage of this model can be adopted to guide seed banking of Xishuangbanna tropical rainforest species.

In this study, we identify and report the seed storage behaviour of 25 woody species from Xishuangbanna. Data for these 25 species were combined with information from the literature on seed storage behaviour for a total of 59 dominant and common species (in 41 families) in the Xishuangbanna region. Then, we used these 59 species to test the ability of the SCR–SM model (Daws *et al.* 2006) to predict the seed storage behaviour. The seed storage behaviour of these 59 species was also predicted using the TSW–MC criteria (Chin *et al.* 1984; Hong and Ellis 1996) to compare the efficiency of the two predictive methods (i.e. the SCR–SM model and the TSW–MC criteria). Further, we used both the SCR-SM model and the TSW–MC criteria to predict storage behaviour for 42 additional Xishuangbanna species. A comparison also was made between seed traits (mass and SCR) of the tropical rainforests of Xishuangbanna and of Panama (see details in Daws *et al.* 2006) and those of species from a mixture of several types of rainforests in eastern Australian (Hamilton *et al.* 2013).

Materials and methods

Study site and seed materials

Seeds or fruits (hereafter referred to as seeds) were collected at the time of natural dispersal from native forests in the Xishuangbanna Tropical Botanical Garden and mountains nearby (21°55′N, 101°15′E 570 m a.s.l.) in southern Yunnan Province, China, from 2010 to 2012. Also, seeds of 26 cultivated species were included in the study. Generally, Xishuangbanna is cooler and has less rainfall than the typical equatorial rainforests. The monthly temperatures of Xishuangbanna range between 15.5°C (January) and 25.3°C (June), with an annual mean of 21.7°C. The climate in Xishuangbanna is dominated by a south-west monsoon, with most of the rain (85%) falling between May and October. Annual precipitation is 1221 mm; however, foggy days during the dry season increase the humidity, which help compensate for the low rainfall (Zhang and Cao 1995).

Seeds were packed in polyethylene bags and taken to the laboratory on the same day of collection. On receipt, seeds were visually checked and any infested by fungi or insects were discarded. The fresh seeds were air-dried at room temperatures (18–24°C) for 1 day, and all experiments commenced within 2 days after receipt.

Initial MC, SCR and seed storage behaviour

Five replicates of 5–25 seeds each of each species were dissected into their component parts (embryonic axis, cotyledons, endosperm and seed coat/pericarp) for gravimetric determination of MC and dry mass by drying in an oven at 103°C for 17 h (ISTA 2007). MC was expressed on a fresh weight basis.

SCR, which is the ratio of endocarp and testa mass to dispersal unit mass (Pritchard *et al.* 2004*a*; Daws *et al.* 2006), was determined using the method described by Grubb and Burslem (1998) and Pritchard *et al.* (2004*a*). The TSW of each species was determined using four replicates of 1000 fresh seeds each. The width and length of 20 seeds were measured using a vernier caliper, and from these data seed volume of each species was calculated.

Seed storage behaviour of 25 species (including 23 wild species and two cultivated species) was identified using the 100-seed test as described in Pritchard *et al.* (2004*b*). For each species, seed germination before and after desiccation by silica gel was tested. Seeds with a loss of total viability at MC of ~10% were considered to be desiccation-sensitive. Seed storage behaviour of other 34 species (including 18 wild and 16 cultivated species) was obtained from other literature (see Table 1 for details).

Statistical analyses

The SCR–SM model for identification

The likelihood of desiccation sensitivity (P(D-S)) for seeds of each species was estimated using the following equation (Daws *et al.* 2006),

$$P(\mathrm{D}-\mathrm{S}) = \frac{e^{3.269-9.974a+2.156b}}{1+e^{3.269-9.974a+2.156b}},$$

where a is SCR and b is $\log_{10}$ (seed mass) in g. For estimation of P(D-S), seed mass should range between 0.01 mg and 24 g, and SCR between 0 and 1. When $P(\text{D-S}) > 0.5$, seeds are likely to be desiccation-sensitive, and when $P(\text{D-S}) < 0.5$ seeds are likely to be desiccation-tolerant.

The TSW–MC criteria for identification

According to the TSW–MC criteria (Chin *et al.* 1984; Hong and Ellis 1996), seeds with a TSW of >500 g and MC of >30% are desiccation-sensitive. In our study, seed storage behaviour of

Table 1. Tree species (and family) from Xishuangbanna tropical rainforests used for validation of the seed-coat ratio–seed mass (SCR–SM) model
Seed storage behaviour of 41 wild and 18 cultivated species as determined using the SCR–SM model and the 1000-seed weigth–moisture content (TSW–MC) criteria. W/C, wild species/cultivated species; MC, moisture content (% fr.wt); SM, seed dry mass; *P*(D-S), the likelihood that a species is desiccation-sensitive; DS/DT, desiccation-sensitive/desiccation-tolerant; Source, source for seed storage behaviour determination. *P*(D-S) was estimated based on SM and SCR using the SCR–SM model (Daws *et al.* 2006). Seed storage behaviour of 23 wild species and two cultivated species was assessed using the 100-seed test (Pritchard *et al.* 2004*b*). For the other 18 wild and 16 cultivated species, seed storage behaviour was obtained from the literature. Desiccation-sensitive (DS) species are shown in bold type font. Source: 1, this study; 2, Cheng and Song (2008); 3, Shao *et al.* (2006); 4, Liu *et al.* (2008); 5, Yang *et al.* (2005); 6, Hoffman and Steiner (1989); 7, Liu *et al.* (2005);8, Deng *et al.* (2008); 9, Wen (2009); 10, Yang *et al.* (2001); 11, Mai-Hong *et al.* (2006); 12, Jiao *et al.* (2011); 13, Daws *et al.* (2006); 14, Chien *et al.* (2009)

Species	Family	W/C	TSW (g)	MC (%)	SM (mg)	SCR	*P*(D-S)	DS or DT?	Source
Adenanthera pavonina L. var. *microsperma* (Teijsm. & Binn.) I.C. Nielsen	Leguminosae	W	135	14.71	63	0.512	0.024	DT	1
Antiaris toxicaria Lesch.	**Moraceae**	**W**	**1715**	**45.25**	**1114**	**0.081**	**0.951**	**DS**	**2**
Archontophoenix alexandrae (F.Muell.) H.	**Palmae**	**C**	**765**	**28.14**	**511**	**0.089**	**0.872**	**DS**$^{\mathrm{C}}$	**3**
Ardisia crenata Sims var. _bicolor_ (Walker) C.Y.Wuet C.Chen (_A.bicolor_ Walker)	**Myrsinaceae**	**W**	**105**	**47.63**	**98**	**0.050**	**0.661**	**DS**$^{\mathrm{C}}$	**1**
Ardisia arborescens Wall. ex A.DC.	Myrsinaceae	W	106	11.62	50	0.152	0.422	DT	1
Ardisia brunnescens E.Walker	Myrsinaceae	W	77	36.74	171	0.113	0.451	DT	1
Ardisia squamulosa C.Presl	Myrsinaceae	W	21	11.63	33	0.239	0.072	DT	1
Ardisia virens Kurz var. _annamensis_ Pit.	**Myrsinaceae**	**W**	**177**	**40.93**	**110**	**0.063**	**0.734**	**DS**$^{\mathrm{C}}$	**1**
Areca catechu L.	**Palmae**	**C**	**6290**	**43.33**	**3228**	**0.067**	**0.985**	**DS**	**4**
Areca triandra Roxb.	**Palmae**	**C**	**1234**	**36.94**	**811**	**0.259**	**0.707**	**DS**	**5**
Artocarpus heterophyllus Lam	**Moraceae**	**C**	**5844**	**56.65**	**2507**	**0.030**	**0.990**	**DS**	**4**
Baccaurea ramiflora Lour.	**Euphorbiaceae**	**W**	**251**	**58.00**	**129**	**0.136**	**0.642**	**DS**$^{\mathrm{C}}$	**1**
Calophyllum inophyllum L.	**Guttiferae**	**W**	**11 870**	**50.95**	**7582**	**0.093**	**0.991**	**DS**	**1**
Camellia sinensis (L.) Kuntze	**Theaceae**	**W**	**1353**	**37.71**	**1177**	**0.300**	**0.671**	**DS**	**6**
Carica papaya L.	Caricaceae	C	15	11.48	27	0.592	0.001	DT	6
Cassia fistula L.	Leguminosae	W	194	10.75	176	0.788	0.002	DT	1
Cassia grandis	Leguminosae	C	310	10.97	299	0.886	0.001	DT	1
Castanea henryi (Skan) Rehd. & E.H.Wils.	Fagaceae	W	473	25.28	302	0.300	0.395	DT	7
Chrysalidocarpus lutescens H.Wendl.	**Palmae**	**W**	**712**	**46.12**	**464**	**0.058**	**0.925**	**DS**	**6**
Chrysophyllum cainito L.	Sapotaceae	C	346	13.51	248	0.440	0.107	DT	13
Citrus maxima (Burm.) Merr.	**Rutaceae**	**C**	**340**	**42.18**	**275**	**0.440**	**0.106**$^{\mathrm{A}}$	**DS**$^{\mathrm{C}}$	**6**
Cleidiocarpon cavaleriei (H. Lév.) Airy-Shaw	**Euphorbiaceae**	**W**	**6334**	**42.77**	**2870**	**0.354**	**0.804**	**DS**	**1**
Coffea arabica L.	Rubiaceae	C	219	45.70	75	0.150	0.587$^{\mathrm{B}}$	DT	6
*Delonix regi*a (Hook.) Raf	Leguminosae	C	540	16.22	466	0.741	0.009	DT	4
Dimocarpus longan Lour.	**Sapindaceae**	**W**	**1568**	**38.84**	**116**	**0.083**	**0.942**	**DS**	**6**
Dipterocarpus alatus	Dipterocarpaceae	C	4600	18.93	3647	0.720	0.077	DT	4
Dipterocarpus retusus Blume	**Dipterocarpaceae**	**W**	**5177**	**73.36**	**1267**	**0.674**	**0.129**$^{\mathrm{A}}$	**DS**	**4**
Dipterocarpus turbinatus Gaertn.	**Dipterocarpaceae**	**W**	**4597**	**51.55**	**2260**	**0.322**	**0.818**	**DS**	**4**
Elaeocarpus braceanus Watt ex C.B.Clarke	Elaeocarpaceae	W	5094	14.20	5088	0.941	0.010	DT	1
Elaeocarpus prunifolioides Hu	Elaeocarpaceae	W	1740	18.08	422	0.846	0.002	DT	1
Eugenia uniflora L.	**Myrtaceae**	**C**	**669**	**53.00**	**528**	**0.038**	**0.927**	**DS**	**6**
Garcinia cowa Roxb.	**Guttiferae**	**W**	**2211**	**55.15**	**1038**	**0.305**	**0.721**	**DS**	**7**
Garcinia paucinervis Chun & How	**Guttiferae**	**W**	**7190**	**39.80**	**4828**	**0.021**	**0.994**	**DS**	**1**
Garcinia xanthochymus Hook.f. ex	**Guttiferae**	**W**	**4291**	**45.00**	**2531**	**0.064**	**0.982**	**DS**	**1**
Gomphandra tetrandra (Wall.) Sleumer	**Icacinaceae**	**W**	**979**	**49.73**	**537**	**0.130**	**0.876**	**DS**	**1**
Gustavia gracillima Miers	**Lecythidaceae**	**W**	**1080**	**36.65**	**885**	**0.113**	**0.897**	**DS**	**1**
Helicia cochinchinensis Lour.	**Proteaceae**	**C**	**594**	**43.57**	**403**	**0.021**	**0.930**	**DS**	**1**
Hevea brasiliensis (Willd. ex A.Juss.) Müll. Arg.	**Euphorbiaceae**	**C**	**3123**	**23.77**	**2302**	**0.422**	**0.538**	**DS**$^{\mathrm{C}}$	**4**
Jatropha curcas L.	Euphorbiaceae	W	818	24.37	508	0.333	0.442	DT	8
Livistona chinensis (Jacq.) R.Br.	**Palmae**	**W**	**885**	**37.42**	**573**	**0.123**	**0.869**	**DS**	**6,9**
Livistona saribus (Lour.) Merr. ex A.Chev.	**Palmae**	**W**	**4389**	**40.00**	**1843**	**0.181**	**0.944**	**DS**	**1**
Macadamia ternifolia F.Muell.	**Proteaceae**	**W**	**3981**	**23.73**	**3022**	**0.711**	**0.081**$^{\mathrm{A}}$	**DS**$^{\mathrm{C}}$	**6**
Mangifera indica L.	**Anacardiaceae**	**W**	**17 942**	**39.00**	**11 022**	**0.273**	**0.962**	**DS**	**4**
Mangifera sylvatica Roxb.	**Anacardiaceae**	**W**	**5265**	**37.21**	**573**	**0.274**	**0.890**	**DS**	**1**
Manilkara zapota van Royen	Sapotaceae	W	551	17.68	392	0.546	0.061	DT	4
Mesua ferrea L.	**Guttiferae**	**W**	**1983**	**25.25**	**1100**	**0.353**	**0.589**	**DS**$^{\mathrm{C}}$	**1**
Micromelum integerrimum (Buch.-Ham.) Roem.	**Rutaceae**	**W**	**76**	**60.23**	**82**	**0.102**	**0.521**	**DS**$^{\mathrm{C}}$	**10**
Mimusops elengi L.	Sapotaceae	C	765	39.15	492	0.403	0.267	DT$^{\mathrm{D}}$	11

(*continued next page*)

Table 1. (*continued*)

Species	Family	W/C	TSW (g)	MC (%)	SM (mg)	SCR	*P*(D-S)	DS or DT?	Source
Murraya exotica L.	Rutaceae	W	369	4.66	42	0.285	0.084	DT	6
***Nephelium lappaceum* L.**	**Sapindaceae**	**W**	**2027**	**32.52**	**1240**	**0.077**	**0.958**	**DS**	**6**
***Pachira macrocarpa* (Schltdl. & Cham.) Walp§**	**Bombacaeae**	**W**	**2126**	**31.85**	**1633**	**0.207**	**0.872**	**DS**	**1**
Plukenetia volubilis L.	Euphorbiaceae	C	1371	7.95	1238	0.341	0.541^{B}	DT	12
***Podocarpus nagi* (Thunb.) Zoll. & Mor. ex Zoll.**	**Podocarpaceae**	**W**	**529**	**35.31**	**299**	**0.575**	**0.024^{A}**	**DS**	**4**
***Pometia tomentosa* (Bl.) Teysm. & Binn**	**Sapindaceae**	**W**	**2420**	**30.40**	**1669**	**0.089**	**0.961**	**DS**	**1**
***Sterculia lanceolata* Cav.**	**Sterculinaceae**	**W**	**512**	**75.60**	**129**	**0.063**	**0.880**	**DS**	**1**
Strychnos nux-vomica L.	Loganiaceae	C	1571	27.56	1197	0.149	0.904^{B}	DT	4
Swietenia mahagoni (L.) Jacq.	Meliaceae	W	163	10.71	158	0.326	0.163	DT	14
***Theobroma cacao* L.**	**Sterculiaceae**	**C**	**944**	**40.52**	**646**	**0.051**	**0.937**	**DS**	**4**
Trewia nudiflora L.	Euphorbiaceae	W	207	18.13	151	0.825	0.001	DT	1

[A] Desiccation-sensitive species incorrectly assigned by the SCR–SM model.
[B] Desiccation-tolerant species incorrectly assigned by the SCR–SM model.
[C] Desiccation-sensitive species incorrectly assigned by the TSW–MC criteria.
[D] Desiccation-tolerant species incorrectly assigned by the TSW–MC criteria.

all the species from Xishuangbanna was predicted using the TSW–MC criteria.

Comparisons of seed traits

SCR and seed dry mass of seeds of species with different seed storage behaviours from Xishuangbanna, Panama and eastern Australia were compared using a one-way ANOVA with Fisher's l.s.d. *post hoc* analysis (Dytham 2003).

Results

TSW, seed MC at shedding, SCR and seed dry mass for the 101 tree species from Xishuangbanna and the probability of seeds of being desiccation-sensitive (P (D–S)) as determined using the SCR–SM model based on SCR and seed dry mass are shown in Tables 1 and 2. The TSW–MC criteria used to classify seed storage behaviour of all the species also are shown in Tables 1 and 2. Seed storage behaviour for 25 species from 13 families was determined; 16 species that did not survive drying were recorded as 'desiccation-sensitive' (Table 1).

Fifty-nine species with known storage behaviour were used for model validation. The SCR–SM model and the TSW–MC criteria correctly predicted the seed desiccation sensitivity for 52 and 49 of the 59 species, respectively (i.e. a success rate of 88% and 83%, respectively; Table 1).

Seed traits for 42 species whose seed storage behaviour is not known are shown in Table 2. The TSW–MC criteria and the SCR–SM model generated consistent results for 33 species (Table 2). Using the SCR–SM model, 16 species were predicted to be desiccation-sensitive with a *P*(D-S) value of >0.5. However, seeds of eight species were small (TSW < 500 g, seed volume ranging from 32 to 148 mm^2) or had a low MC (7.4 – 20.3%), and were classified as 'desiccation-tolerant' on the basis of the TSW–MC criteria (Table 2). Seeds of *Pyrularia edulis* were large and had a high MC and thus were identified as desiccation-sensitive on the basis of the TSW–MC criteria. However, these seeds had a high SCR (0.49), and the *P*(D-S) as determined by the SCR–SM model was 0.39 (Table 2).

Among the wild species with known seed storage behaviour (Table 1), seed dry mass ranged from 82 mg to 11 022 mg for the 26 species with desiccation-sensitive seeds and from 33 mg to 5088 mg for the 12 species with desiccation-tolerant seeds. Mean SCR of desiccation-sensitive seeds of wild species was 0.21 (range 0.06 – 0.71) (Table 1, Fig. 1) compared with a mean of 0.47 (range 0.51– 0.94) (Table 1, Fig. 1) for desiccation-tolerant seeds ($P < 0.003$, one-way ANOVA). Most desiccation-sensitive species had an MC of ≥24% (range 24 –76%) at shedding. MC of desiccation-tolerant species ranged from 5% to 46% (Table 1).

Patterns for seed dry mass and SCR of wild species from Xishuangbanna, Panama and eastern Australia were similar in that seed dry mass was higher and SCR lower for the desiccation-sensitive seeds (Fig. 1). Mean seed dry mass for Panama desiccation-sensitive seeds was higher than that for Xishuangbanna and eastern Australian desiccation-sensitive seeds (Fig. 1). Variations in seed dry mass of Xishuangbanna desiccation-tolerant seeds were greater than those of Panama and eastern Australia desiccation-tolerant seeds. However, within each seed storage behaviour category, ranges of seed dry mass and of SCR overlapped (Fig. 1). To increase the sample size, the wild species in Table 2 with *P*(D-S) value of >0.5 and *P*(D-S) value of <0.5 treated as the desiccation-sensitive and desiccation-tolerant species, respectively, were added into the comparison. Increase of sample size did not change the patterns (Fig. 1, inset graphs).

Discussion

This study tested the applicability of the SCR–SM model for determining seed desiccation sensitivity for 101 woody plant species from the tropical rainforest in Xishuangbanna. For the 59 species with known seed storage behaviours, the SCR–SM model successfully predicted the seed response to desiccation for 52 (88%) of 59 species, which is similar to the success rate (87%) achieved using this model for 104 Panamanian woody species (Daws *et al.* 2006). The similarity of the success rates achieved for species from these two sites suggested that the SCR–SM model is a reliable predictive method for Xishuangbanna species. Four of the desiccation-sensitive species that were incorrectly assigned in our study had a high SCR (between

Table 2. Seed traits of the 42 species from Xishuangbanna with unknown seed storage behaviour

Seed storage behaviour of 34 wild and 8 cultivated species as determined using the seed-coat ratio–seed mass (SCR–SM) model and the 1000-seed weight–moisture content (TSW–MC) criteria. W/C, wild species/cultivated species; SS, seed size; MC, seed moisture content at shedding; SM, seed dry mass; SCR, seed-coat ratio and *P*(D-S), the likelihood of desiccation sensitivity of species are shown. *P*(D-S) was estimated using the SCR–SM model. Species with *P*(D-S) values > 0.5 (desiccation-sensitive) are shown in bold type font

Species	Family	W/C	TSW (g)	SS (mm^2)	MC (%)	SM (mg)	SCR	*P*(D-S)
***Actinodaphne obvata* Bl.**	**Lauraceae**	**W**	**3412**	**413**	**34.1**	**1609**	**0.215**	**0.904**
Aegle marmelos (L.) Correa	Rutaceae	C	135	44	42.3	93	0.261	0.230
***Amoora ouangliensis* (Lév.) C.Y.Wu**	**Meliaceae**	**W**	**4508**	**454**	**54.9**	**2517**	**0.072**	**0.979**
Anneslea fragrans Wall.	Theaceae	W	67	52	5.5	506	0.442	0.024
***Ardisia villosa* Roxb.**	**Myrsinaceae**	**W**	**114**	**32**	**45.4**	**59**	**0.035**	**0.675**[A]
***Aphanamixis polystachya* (Wall.) R.Parker**	**Meliaceae**	**W**	**1106**	**143**	**20.3**	**884**	**0.148**	**0.870**[A]
Azadirachta indica A.Juss	Meliaceae	W	400	93	12.6	327	0.883	0.002
Bauhinia monandra Kurz	Leguminosae	C	202	88	19.0	105	0.678	0.007
Bridelia insulana Hance	Euphorbiaceae	W	97	41	12.9	88	0.382	0.061
Bruinsmia polysperma (C.B.Clarke) von Steenis	Styracaceae	W	147	52	6.1	164	0.816	0.001
Caesalpinia minax Hance	Leguminosae	W	1473	211	13.5	164	0.511	0.188
Caesalpinia pulcherrima (L.) Sw.	Leguminasae	C	138	76	27.1	139	0.672	0.005
Canthium horridum Bl.	Rubiaceae	W	399	131	14.5	290	0.626	0.021
Clerodendrum colebrookianum Walp.	Verbenaceae	W	38	66	10.7	25	0.473	0.011
***Cryptocarya chinensis* (Hance) Hemsl.**	**Lauraceae**	**W**	**386**	**86**	**62.9**	**122**	**0.243**	**0.523**[A]
Daphniphyllum longeracemosum K.Rosenthal	Daphniphyllaceae	W	224	85	32.0	104	0.309	0.225
Desmos chinensis Lour.	Annonaceae	W	80	34	45.6	654	0.118	0.437
Embelia sessiliflora Kurz	Myrsinaceae	W	124	43	7.9	158	0.179	0.398
Enterolobium cyclocarpum (Jacq.) Griseb.	Leguminasae	C	539	164	18.6	605	0.531	0.080
***Erycibe obtusifolia* Benth.**	**Convolvulaceae**	**W**	**4205**	**355**	**43.2**	**2104**	**0.067**	**0.980**
Gmelina arborea Roxb. ex Sm.	Verbebaceae	W	393	98	23.4	170	0.889	0.002
***Hydnocarpus kurzii* (King) Warb.**	**Flacourtiaceae**	**C**	**490**	**148**	**7.4**	**538**	**0.115**	**0.836**[A]
Iodes cirrhosa Turcz.	Icacinaceae	W	706	179	11.2	715	0.513	0.096
Ixora chinensis Lam.	Rubiaceae	W	59	27	19.9	61	0.285	0.094
Jatropha podagrica Hook.	Euphorbiaceae	C	172	86	19.9	126	0.307	0.176
Kadsura ananosma Kerr	Magnoliaceae	W	497	224	12.1	474	0.368	0.258
Linociera ramiflora (Roxb.) Wall. ex G.Don	Oleaceae	W	432	144	10.0	418	0.621	0.025
***Litsea baviensis* Lecomte**	**Lauraceae**	**W**	**2620**	**333**	**43.6**	**1525**	**0.028**	**0.981**
***Lucuma nervosa* A.DC.**	**Sapotaceae**	**C**	**9935**	**874**	**44.1**	**5498**	**0.142**	**0.981**
Mallotus barbatus (Wall.) Muell. Arg.	Euphorbiaceae	W	58	23	7.6	51	0.596	0.005
Memecylon polyanthum H.L.Li	Melastomataceae	W	60	22	15.1	44	0.262	0.129
***Neolitsea levinei* Merr.**	**Lauraceae**	**W**	**601**	**128**	**16.2**	**473**	**0.200**	**0.676**[A]
***Ochna integerrima* (Lour.) Merr.**	**Ochnaceae**	C	**176**	**45**	**36.6**	**98**	**0.126**	**0.586**[A]
***Ormosia yunnanensis* Prain**	**Leguminosae**	**W**	**317**	**92**	**12.1**	**312**	**0.185**	**0.618**[A]
Parakmeria yunnanensis Hu	Magnoliaceae	W	189	107	12.8	184	0.754	0.003
***Pithecellobium clypearia* (Jack) Benth.**	**Leguminosae**	**W**	**1016**	**159**	**58.4**	**463**	**0.051**	**0.946**
Polyalthia suberosa (Roxb.) Thw.	Annonaceae	W	86	22	32.2	43	0.105	0.415
***Pothos kerrii* Buchet ex Gagn.**	**Araceae**	**W**	**473**	**111**	**55.3**	**268**	**0.115**	**0.832**[A]
Pygeum wilsonii Koehne	Rosaceae	W	278	61	36.1	181	0.305	0.252
Pyrularia edulis (Wall.) A.DC.	Santalaceae	W	3534	375	39.0	1964	0.489	0.385[A]
***Saraca griffithiana* Prain**	**Leguminosae**	**W**	**8836**	**1312**	**49.8**	**2989**	**0.045**	**0.992**
***Ziziphus attopensis* Pierre**	**Rhamnaceae**	**W**	**1208**	**201**	**39.8**	**712**	**0.273**	**0.672**

[A] Species were given inconsistent prediction of the seed desiccation sensitivity by the SCR–SM model and the TSW–MC criteria.

0.44 and 0.71), although their seed dry mass ranged from 248 mg to 3022 mg. A high SCR seems to have biased the results for these desiccation-sensitive species.

The thin seed coat (low SCR) of desiccation-sensitive species is usually associated with rapid germination (Pritchard *et al*. 2004*a*; Daws *et al*. 2005). A thin seed coat may be an advantageous for rapid water uptake and germination, and it minimises the 'investment' of the mother plant in covering structures for defensive purposes (Pritchard *et al*. 2004*a*; Daws *et al*. 2005). However, different ecological factors and evolutionary drivers may result in exceptions. For example, the covering structure (pericarp) of desiccation-sensitive seeds of *Quercus schottkyana* and *Q. franchetii* minimises the rate of water loss, which reduces the risk of mortality during post-dispersal dry spells (Xia *et al*. 2012*a*, 2012*b*). The thick seed coat of the five desiccation-sensitive species in our study may reduce the rate of seed water loss; however, this has not been investigated.

Based on TSW and MC, the TSW–MC criteria predicted a lower success rate (83%) than that (88%) predicted by the SCR–SM model. The TSW–MC criteria correctly assigned 95% of the desiccation-tolerant species but only 76% of the

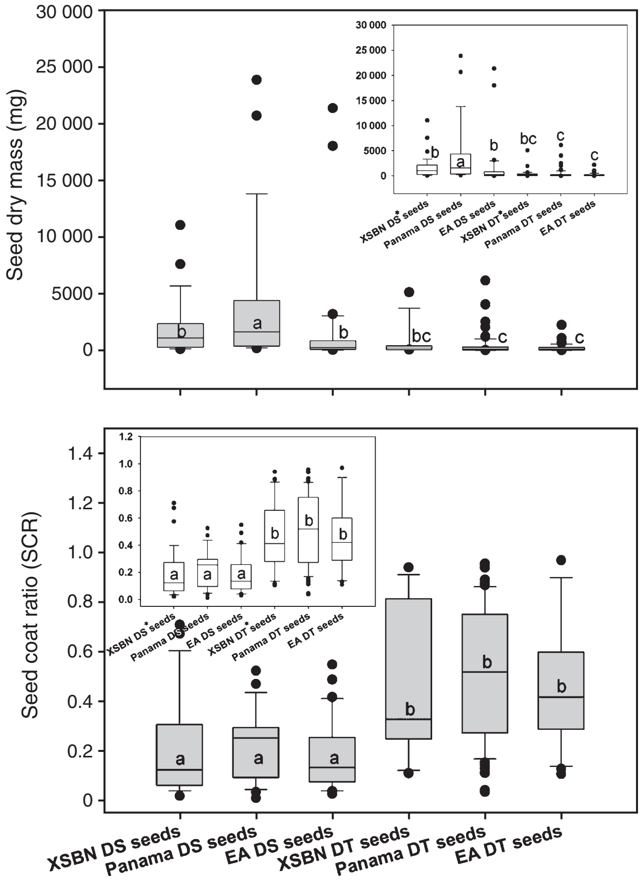

Fig. 1. Comparison of seed dry mass and seed coat ratio between woody species of Xishuangbanna (XSBN), Panama and eastern Australia (EA). Cultivated species in Xishuangbanna are not included. Data for 104 Panama woody species and 69 eastern Australian woody species were obtained from Daws *et al.* (2006) and Hamilton *et al.* (2013). Data presented in inset graphs for Xishuangbanna species include all the studied wild species and for data from Table 2, the wild species with a *P*(D-S) value >0.5 and <0.5 were treated as desiccation-sensitive and desiccation-tolerant, respectively. Seeds of *Ormosia yunnanensis* from Table 2 had a low moisture content of 12% at shedding and are unlikely to be desiccation-sensitive, are treated as desiccation-tolerant in the figure. DS seeds, desiccation-sensitive seeds of wild species from Table 1; DT seeds, desiccation-tolerant seeds of wild species from Table 1; DS* seeds, desiccation-sensitive seeds of wild species from Table 1 and seeds of wild species with a *P*(D-S) value >0.5 from Table 2; DT* seeds, desiccation-tolerant seeds of wild species from Table 1 and seeds of wild species with a *P*(D-S) value <0.5 from Table 2. Differences in seed-coat ratio and seed dry mass were tested for significance using one-way ANOVA with Fisher's l.s.d. *post hoc* analysis. Boxes with the same letters are not significantly different at $P > 0.05$.

desiccation-sensitive species. The TSW–MC criteria are problematic in predicting smaller or drier desiccation-sensitive seeds. However, ~14% or 11% of the desiccation-sensitive seeds in this study had TSW <500 g or MC <30%. Although the SCR–SM model is robust and more reliable than the TSW–MC criteria, a seed mass of 0.01 mg to 24 g is required (Daws *et al.* 2006), and in many species, data for SCR are not available. In which case, TSW–MC can be used as a practical tool to predict seed storage behaviour.

For the 42 species with uncertain seed behaviour, the predictions for nine of them were inconsistent when using the SCR–SM model versus using the TSW–MC criteria. Desiccation-sensitive seeds lack the maturation drying phase, and thus usually are shed with a high MC (Tompsett and Pritchard 1993). Although seed MC was not a useful predictor (Daws *et al.* 2006), desiccation-sensitive seeds from Xishuangbanna, Panama (Daws *et al.* 2006) and eastern Australia (Hamilton *et al.* 2013) were shed with a MC of >20%. These data are reasonable, because drying below 20% may result in desiccation-induced mortality for desiccation-sensitive seeds. Among the nine species, *Hydnocarpus kurzii*, *Neolitsea levinei* and *Ormosia yunnanensis* with a *P*(D-S) value of >0.5 are not likely to be desiccation-sensitive because of their low MC (<17%) at shedding.

Our study tested seed desiccation sensitivity and provided seed dry mass and SCR for 75 native and 26 cultivated woody species from Xishuangbanna. Consistent with previous research on tropical rainforests (Tweddle *et al.* 2003) and on eastern Australian rainforests (Hamilton *et al.* 2013), ~50% of the species from Xishuangbanna had desiccation-sensitive seeds or had seeds that are likely to be desiccation-sensitive (seeds with a *P*(D-S) value >0.5), not including *Hydnocarpus kurzii*, *Neolitsea levinei* and *Ormosia yunnanensis*. The results of our study will allow researchers to better predict which seeds may be difficult to store in the dry, cold conditions of gene banks. Desiccation-sensitive seeds from Xishuangbanna tended to be larger and have a thinner seed coat than the desiccation-tolerant seeds. While only 11 and 10 families in the Xishuangbanna dataset occur in the Panama (Daws *et al.* 2006) and eastern Australian (Hamilton *et al.* 2013) datasets, respectively, the ranges in seed dry mass and in SCR were similar for seeds of woody species from the three areas.

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