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Seed Storage Behaviour of Native Forest Tree Species of Northern Thailand

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Abstract

Storage of native forest tree seeds is essential for the development of seed-based forest restoration methods, such as direct or aerial seeding and for increasing representation of native trees in nurseries, for conventional tree planting. The study, presented here, investigated seed germination, dormancy and storage behaviour of 16 native tree species, used to restore upland evergreen forest in northern Thailand. Eleven of them, had orthodox seeds (storable at minus 20˚C and 5% moisture content): a proportion consistent with other studies of seasonally dry tropical forest: *Acrocarpus fraxinifolius, Adenanthera microsperma, Alangium kurzii, Bauhinia variegata, Choerospondias axillaris, Gmelina arborea, Hovenia dulcis, Manglietia garrettii, Melia azedarach, Phyllanthus emblica and Prunus cerasoides*. Four species had recalcitrant seeds: *Artocarpus lacucha, Dimocarpus longan, Horsfieldia amygdalina and Syzygium albiflorum*. All except *D. longan* set seed in the early rainy season and could therefore be used for direct or aerial seeding without storage. Inclusion of *D. longan and Diospyros glandulosa* (the latter classed as intermediate, with seeds that could be partially dried but not frozen) in forest restoration plantings will only be possible by nursery-based sapling production and conventional tree planting.

***Keywords**:* Tropical forest restoration; Seed storage; Germination; Dormancy

1. Introduction

In tropical forests, tree seed production at the community level, is spread among species across all months of the year. For example, in Doi Suthep-Pui National Park, northern Thailand, fruiting of wind-dispersed tree species peaks during the hot dry season (February to May), coinciding with the strongest wind gusts (Elliott *et al*., 1994). In contrast, numbers of animal-dispersed tree species in fruit gradually increase during the rainy season, peaking in September (FORRU, 2006).

Direct seeding is potentially a cost-efficient alternative to tree-planting for restoring tropical forest ecosystems, since there are no planting-stock production costs and seeds are easier and cheaper to transport than tree saplings are (Cole *et al*., 2011). The optimum time for direct seeding is the beginning of the rainy season, but at that time only about 13% of forest tree species are producing viable seeds, according to CMU Herbarium Database for trees of Doi Suthep. This limitation considerably reduces the ability of direct seeding to achieve the high tree-species richness that tree planting can, at the start of restoration projects. Therefore, efficient seed storage, from seed maturation time to the optimum direct seeding time, could play an important role in enabling more widespread adoption of direct seeding as a cost-effective forest restoration tool (Guarino and Scariot, 2014). In general, the limited seed supply of native forest tree species seriously constrains tropical forest restoration globally, regardless of the techniques employed (Jelonen *et al*., 2018). So, any increase in knowledge about storage of native forest trees is likely to be useful for achieving the ambitious, forest-restoration goals, currently being set by such global initiatives as the Bonn Challenge (Dave *et al*., 2017) etc.

According to a predictive tool, developed at the Royal Botanic Gardens, Kew, (Wyse and Dickie, 2017) only about 54% of Thailand's >2,000 native forest tree species have orthodox seeds (capable of being stored frozen at -20°C with 5±1% moisture content), whilst 46% are likely to be recalcitrant (intolerant of being dried and/or frozen) (across all forest types). Hard data are needed to confirm such predictions, at the species level.

More comprehensive knowledge of seed-storage behaviour could transform forest restoration from being based largely on tree planting to being based largely on seeding - either direct seeding or aerial seeding from planes, helicopter or drones, especially in Northern Thailand where forest covers are dramatically decrease. It would also improve management of forest genetic resources and provide a seed supply when trees fail to fruit. Hence, it is important to know how long seeds can be stored and under which conditions. (Hong and Ellis, 1996).

The study, presented here, determined the seed storage behaviour of sixteen indigenous forest tree species, currently being used to restore upland forest ecosystems in northern Thailand. The aim was to establish which species could have their seeds stored from their natural fruiting period to the optimum seeding time at the start of the rainy season (June), to prepare the way to replace labour- intensive tree planting with direct or aerial seeding.

2. Materials and methods

2.1 Study site and species

Seeds of sixteen native tree species were collected, as they became available throughout the year (Table 1). All species were native to upland, evergreen forest of northern Thailand (>1,000 m elevation), with average annual temperature of 21-22˚C, and annual rainfall of 1,000-1,500 mm and a distinct dry season from November to April (monsoonal climate). Seed germination were tested at FORRU-CMU nursery and seed storage were carry at Department of Biology, Faculty of Sciences Chiang Mai University.

2.2 Baseline Germination

A standard nursery germination test was carried out. Three replicates of 50 seeds were prepared in modular plastic trays, diameter 4 cm and depth 4.5 cm with 100% forest soil. The seeds were buried about 1 cm in the media. The numbers of germinated seeds and seedlings (surviving and dead) were counted every 7 d. Germination was defined as emergence of a plumule or radical through the testa. Graphs were plotted of time vs. the cumulative numbers of seeds that germinated. Mean and variability of germination percentage and median length of dormancy (MLD = the time taken for germination of half of the total number of seeds that germinated) were calculated. Germination tests were monitored until 30 d after the last germination had been recorded. *A. fraxinifolius* and *A. microsperma* seeds were subjected to an additional experiment to trial the effects of seed scarification; a treatment known to accelerate germination.

2.3 Moisture Content

Moisture content (MC) was determined using the standard ISTA protocol (ISTA, 2006). Three replicates of 10 to 15 seeds were randomly selected and weighed with a digital scale, accurate to 1/10,000 th of a gram. The seeds were then dried in a hot air oven at 103 ±3°C for 17 ±1 h. Seed moisture content was calculated on a fresh weight basis (Schmidt, 2007), as following equation;

$$\text{Moisture content (\%)} = \frac{\text{(Wet weight – Dry weight) x 100}}{\text{Wet weight}}$$

2.4 Seed Storage Behaviour testing

Seed storage behaviour was tested, following the protocol of Hong and Ellis (1996). Seeds were dried to 10% moisture content and their germination tested. Seeds were then further dried to 5% moisture content and stored at room temperature or -20°C for 1 month and germination was tested again (three replicates of 50 seeds each).

2.5 Statistical Analysis

Differences in mean percent seed germination and MLD (days) among storage treatments and species were tested with ANOVA, followed by pair-wise t-tests, when indicated. Binomial data, such as percent germination, were arcsine-transformed, before analysis to ensure homogeneity of variance (Elliott *et al*., 2013).

3. Results

3.1 Seed germination and median length of dormancy

The mean (±SE) germination percentage across species was 44.7 ±3.6%, ranging from 6% (*G. arborea* ±1.2%) to 92% (*A. lacucha* ±2.0%) (Table 2). Species could be divided into 3 groups, according their germination percentage: 1) low germination (<30%): *D. longan, D. glandulosa and G. arborea,* 2) intermediate germination (30-60%): *A. fraxinifolius, A. kurzii, C. axillaris, H. dulcis, M. garrettii, M. azedarach, P. emblica and S. albiflorum* and 3) high germination (>60%): *A. microsperma, A. lacucha, B. variegata, H. amygdalina and P. cerasoides*. Average MLD across species was 69.4 ±8.2 d, ranging from 8 d (*B. variegata* ±0.1) to 244 (*C. axillaris* ±14.1). The species tested could be divided into 3 groups, based on MLD: 1) a short-dormancy group (MLD <30 days): *A. microsperma, A. lacucha, B. variegata, D. longan and G. arborea;* 2) an intermediate-dormancy group (MLD 30-100 d): *A. kurzii, H. amygdalina, H. dulcis, M. azedarach, P. cerasoides and S. albiflorum* and 3) a prolonged-dormancy group (MLD >100 d): *A. fraxinifolius, C. axillaris, D. glandulosa, M. garrettii and P. emblica* (Table 2).

The scarification treatment significantly reduced MLD of both species. For *A. fraxinifolius* the reduction averaged 99 days, (from 118.3 ±6.7 d (control) to 9.0 ±0.0 d (scarified) (t-test, $p<0.01$)), whilst for *A. microsperma*, it averaged 14 days (from 23.3 ±2.0 d (control) to 9.0 ±1.0 d (scarified) (t-test, $p< 0.01$)). Scarification also significantly and substantially increased germination percentage of *A. fraxinifolius* seeds by 45% (from 43.3 ±8.7% (control) to 88.9 ±2.9% (scarified) (t-test, $p<0.01$)), whereas it had no significant effect on germination percentage of *A. microsperma* seeds (68.7 ±4.4% (control), 59.3 ±1.8% (scarified) (t-test, $p=0.12$)).

3.2 Seed Mass and Seed Moisture Content

The propagules (or "dispersal units") that are dispersed by forest trees may be seeds or pyrenes. The latter include the inner fruit wall (endocarp) surrounding one or several seeds. Pyrenes were the dispersed propagules of 5 of the species studied: *P. cerasoides* (1 seed/pyrene), *A. kurzii* (2 seeds/pyrene), *G. arborea* (up to 4 seeds/pyrene) and *C. axillaris* (up to 5 seeds/pyrene) (Gardner *et al*., 2000).

H. amygdalina produced the heaviest propagules (mean dry seed mass 3.800±0.124 g), whilst *H. dulcis* produced the lightest (0.023 ±0.001 g, Table 4.1). The propagules of 5 species were categorized as small (0.01-0.099 g) (following the protocol of Doust *et al*., (2006)): *A. fraxinifolius, H. dulcis, M. garrettii, M. azedarach and P. emblica*. Most of the studied species (11 of 16) had propagules of intermediate size (0.1-4.99 g): *A. microsperma, A. kurzii, A. lacucha, B. variegata, C. axillaris, D. longan, D. glandulosa, G. arborea, H. amygdalina, P. cerasoides and S. albiflorum.*

Propagule moisture content (MC), at collection time, varied from 7 to 46.6% (Table 1). Propagules of 2 of the studied species had very low MC: *A. microsperma* (7.1 ± 0.2%) and

Table 1. List of study species. C=Climax (late successional, shade-tolerant) & P=pioneer (early successional, light loving) species and diaspore classification follow Gardner *et al.* (2000).

Species	Family	Seed collection date	Diaspore used	Successional Status
1. *Acrocarpus fraxinifolius* Arn.	Leguminosae	11/04/15	Seed	C
2. *Adenanthera microsperma* Teijsm. & Binn.	Leguminosae	20/02/15	Seed	P
3. *Alangium kurzii* Craib	Cornaceae	10/07/15	Pyrene	P
4. *Artocarpus lacucha* Buch.-Ham.	Moraceae	01/06/15	Seed	P
5. *Bauhinia variegata* L.	Leguminosae	15/05/15	Seed	P
6. *Choerospondias axillaris* (Roxb.) B.L.Burtt & A.W.Hill	Anacardiaceae	12/07/15	Pyrene	C
7. *Dimocarpus longan* Lour.	Sapindaceae	01/10/14	Seed	C
8. *Diospyros glandulosa* Lace	Ebenaceae	15/11/14	Seed	C
9. *Gmelina arborea* Roxb.	Lamiaceae	21/05/15	Pyrene	P
10. *Horsfieldia amygdalina* (Wall.) Warb.	Myristicaceae	19/05/15	Seed	C
11. *Hovenia dulcis* Thunb.	Rhamnaceae	20/02/15	Seed	C
12. *Manglietia garrettii* Craib	Magnoliaceae	19/10/14	Seed	C
13. *Melia azedarach* L.	Meliaceae	04/01/15	Seed	P
14. *Phyllanthus emblica* L.	Phyllanthaceae	28/12/14	Seed	P
15. *Prunus cerasoides* Buch. -Ham. ex D.Don	Rosaceae	11/04/15	Pyrene	P
16. *Syzygium albiflorum* (Duthie ex Kurz) Bahadur & R.C. Gaur	Myrtaceae	02/06/15	Seed	C

Table 2. Percentage of germination, median length of dormancy (MLD) (Mean±SE), initial moisture content (MC) and propagule mass of native tree species, northern Thailand.

Species	Germination (%)	MLD (days)	Propagule MC (%)	Dry propagule mass (g)
Acrocarpus fraxinifolius	43.3±8.7	118.3±6.7	10.3±0.1	0.034±0.001
Adenanthera microsperma	68.7±4.4	23.3±2.0	7.1 ±0.2	0.102±0.003
Alangium kurzii	52.0±6.1	53.0±0.0	16.1 ±0.2	0.148±0.016
Artocarpus lacucha	92.0±2.0	24.8±5.3	46.4 ±1.2	0.353±0.017
Bauhinia variegata	85.3±3.7	7.8±0.1	10.7 ±0.1	0.275±0.012
Choerospondias axillaris	46.7±6.8	244.3±8.1	20.6 ±1.0	1.700±0.080
Dimocarpus longan	8.7±0.7	17.0±2.3	43.4 ±1.3	0.378±0.026
Diospyros glandulosa	8.7±3.5	128.3±1.8	44.2 ±0.3	0.149±0.005
Gmelina arborea	6.0±1.2	23.3±2.0	13.3 ±0.1	0.432±0.032
Horsfieldia amygdalina	63.3±3.7	35.0±0.4	18.0 ±1.0	3.800±0.124
Hovenia dulcis	34.7±7.9	73.0±2.9	7.9 ±0.2	0.023±0.001
Manglietia garrettii	49.3±5.3	106.7±6.3	15.2 ±0.6	0.052±0.001
Melia azedarach	31.3±3.5	79.2±2.3	10.6 ±0.2	0.048±0.001
Phyllanthus emblica	38.7±5.9	107.0±5.5	10.8 ±0.1	0.024±0.001
Prunus cerasoides	64.0±1.2	46.3±21.4	19.5 ±0.3	0.229±0.007
Syzygium albiflorum	49.3±2.7	66.3±2.4	35.7 ±0.8	1.636±0.060

H. dulcis (7.9 ±0.2 %) and may require little or no further drying before storage. In contrast, *A. lacucha* (46.4 ±1.2 %) seeds had the highest moisture content (Table 2).

3.2 Seed Storage Behaviour

Seed viability of 10 species: *A. microsperma, A. kurzii, B. variegata, C. axillaris, G. arborea, H. dulcis, M. garrettii, M. azedarach, P. emblica and P. cerasoides* was not significantly reduced after storage at 5% MC and minus 20°C for a month. This group was classified as orthodox. Although, *A. fraxinifolius* significantly lost viability, when the seeds were dried to 5% MC and stored at -20°C (ANOVA, p=0.02, Table 3), the germination rate was still high. Therefore, it was added to the orthodox group, bringing the total number of orthodox species to 11. Seeds of four species; *A. lacucha, D. longan, H. amygdalina and S. albiflorum* were very sensitive to drying and freezing, completely losing viability when dried to 10% and 5% MC. These species were classified as recalcitrant (Table 3). *D. glandulosa* was the only species whose seeds were classed as intermediate in storage behaviour. Its seeds could be dried to 10% MC, but they totally lost viability when dried to 5% MC and stored at -20°C.

The MLDs of *D. glandulosa, G. arborea and P. cerasoides* were not significantly affected by the storage treatments (ANOVA, p=0.18, 0.08 and 0.24 respectively, Table 4). However, drying significantly shortened dormancy of *B. variegata, C. axillaris, H. dulcis, M. garrettii, M. azedarach and P. emblica* seeds (Table 4). *A. fraxinifolius* was the only species for which storage significantly lengthened dormancy (ANOVA, p<0.01, Table 4).

4. Discussion

Eleven of the 16 species tested, had orthodox seeds (Table 3), which could potentially be stored dry in freezers for years. Effective storage would enable their use for direct seeding or aerial seeding, at the optimal time of year (mid-June in northern Thailand) and would enable seed-distribution to nurseries for planting-stock production. Such basic information is essential for the development of national or regional seed-supply systems that would for the scaling-up of restoration projects. However, several of the orthodox species had naturally low germination rates, unrelated to storage treatments (e.g. *G. arborea* (6%) and *M. azedarach* (31%) (Table 2). Use of such species would require collecting large numbers of seeds, to compensate for their low germination rates or developing treatments to increase germination percentage, such as the scarification treatment for *A. fraxinifolius*, described above.

All but one of the orthodox species in this study were also predicted to be orthodox by the Kew model (Wyse and Dickie, 2017). The exception was *M. garrettii*, which the Kew model predicted to be recalcitrant (probability 0.72, from family-level data). In the present study, storage of this species reduced mean germination percentage, but not significantly, and all storage treatments significantly accelerated germination.

Even though the number of species in this study was quite small (16), the percentage that were orthodox (69%) was close to that reported by Tweddle *et al*. (2003) (75%, of 68 species) for "semi-evergreen rain forest" (seasonally dry): the ecological zone of the present study. This suggests that a figure of three out of four species being orthodox in the seasonally dry tropical forests of northern Thailand (and neighboring countries) is a useful guideline. Since 1,100-1,200 tree species are native to the region (Gardner *et al*., 2000), about 800-900 are likely to be storable. A regional seed bank, with a capacity to store 10,000 seeds of each of 800-900 tree species would therefore be more than enough to i) ensure the long-term conservation of all of northern Thailand's bankable tree species and support ii) forest research and iii) restoration projects throughout the region.

The four species that this study classified as recalcitrant were also predicted to be recalcitrant by the Kew model (Wyse and Dickie, 2017). Obviously, use of such species in forest restoration projects by direct or aerial seeding is limited to the immediate sowing of fresh seeds. Although cryopreservation of such seeds may become technically possible, it would most likely be prohibitively expensive and is not necessary for those species that set seed at the optimum time for direct or aerial seeding. In our study, three out the four recalcitrant species did so and they could therefore be used for direct or aerial seeding without the need for storage. Viable *H. amygdalina* seeds can be collected in mid-May (Table 1), when rainfall is intermittent and variable, but they germinate fairly rapidly (MLD 35 d) and with acceptable percentage (63%) (Table 2). Viable seeds of *A. lacucha* and *S. albiflorum* can be collected in very early June (Table 1), also with reasonably rapid and high germination (MLD 25 d, 92% and 66 d, 49%, respectively, Table 2). Seedlings of all these species would emerge over June-July and would

Table 3. Effects of drying and freezing on initial germination of native tree species, northern Thailand (Mean±SE)

Species	Germination (%)			
	Initial	Dried 10% MC	Dried 5% MC	Dried 5% MC, stored at -20°C
Orthodox				
Acrocarpus fraxinifolius	88.9 ± 2.9^{a}	-	56.7 ± 6.9^{b}	60 ± 8.8^{b}
Adenanthera microsperma	59.3 ± 1.8^{b}	-	47.8 ± 8.0^{ab}	76.7 ± 1.9^{a}
Alangium kurzii	52.0 ± 6.1^{a}	50.0 ± 3.3^{a}	15.6 ± 1.1^{b}	37.8 ± 2.9^{a}
Bauhinia variegata	85.3 ± 3.7^{a}	-	62.2 ± 4.8^{b}	76.7 ± 1.9^{ab}
Choerospondias axillaris	46.7 ± 6.8^{ns}		-	33.3 ± 5.1^{ns}
Gmelina arborea	6.0 ± 1.2^{ns}	-	7.8 ± 1.1^{ns}	3.3 ± 1.9^{ns}
Hovenia dulcis	34.7 ± 7.9^{ab}	-	50.0 ± 3.3^{a}	21.1 ± 2.2^{b}
Manglietia garrettii	49.3 ± 5.3^{ab}	68.9 ± 6.8^{a}	43.3 ± 3.8^{ab}	32.2 ± 7.8^{b}
Melia azedarach	31.3 ± 3.5^{ns}	-	28.9 ± 3.9^{ns}	11.1 ± 5.9^{ns}
Phyllanthus emblica	38.7 ± 5.9^{a}	-	13.3 ± 1.9^{b}	25.6 ± 6.8^{ab}
Prunus cerasoides	64.0 ± 1.2^{ab}	54.4 ± 9.7^{b}	82.2 ± 2.2^{a}	81.1 ± 2.2^{a}
Intermediate				
Diospyros glandulosa	8.7 ± 0.3^{a}	16.7 ± 1.9^{a}	0^{b}	0^{b}
Recalcitrant				
Artocarpus lacucha	92.0 ± 1.2^{a}	0^{b}	0^{b}	0^{b}
Dimocarpus longan	8.7 ± 1.3^{a}	0^{b}	0^{b}	0^{b}
Horsfieldia amygdalina	63.3 ± 1.0^{a}	0^{b}	0^{b}	0^{b}
Syzygium albiflorum	49.3 ± 0.8^{a}	0^{b}	0^{b}	0^{b}

Values not sharing the same superscripts, a and b, (within species, rows) indicate significant difference among storage treatments ($p<0.05$), ns indicate non-significant differences.

Table 4. Effects of drying and freezing on median length of seed dormancy (MLD) of native tree species in northern Thailand (Mean±SE)

Species	MLD (days)			
	Initial	Dried 10% MC	Dried 5% MC	Dried 5% MC, stored at -20°C
Orthodox				
Acrocarpus fraxinifolius	9.0 ± 0.0^{b}	-	5.0 ± 0.0^{c}	16.7 ± 0.3^{a}
Adenanthera microsperma	$9.0\pm^{a}1.0^{b}$	-	12.1 ± 0.4^{a}	8.0 ± 0.6^{b}
Alangium kurzii	53.0 ± 0.0^{ab}	33.9 ± 4.0^{b}	61.0 ± 13.7^{ab}	73.8 ± 3.9^{a}
Bauhinia variegata	7.8 ± 0.1^{a}	-	5.0 ± 0.2^{b}	4.6 ± 0.1^{b}
Choerospondias axillaris	$244.3\pm8.2^{*}$	-	-	46.0 ± 23.0
Gmelina arborea	23.3 ± 2.0^{ns}	-	6.0 ± 1.5^{ns}	14.7 ± 7.3^{ns}
Hovenia dulcis	73.0 ± 1.9^{a}	-	15.7 ± 0.6^{b}	16.5 ± 2.5^{b}
Manglietia garrettii	106.7 ± 6.3^{a}	66.1 ± 10.2^{b}	30.4 ± 0.7^{c}	30.5 ± 0.5^{c}
Melia azedarach	79.2 ± 2.3^{a}	-	38.3 ± 4.9^{ab}	31.9 ± 16.0^{b}
Phyllanthus emblica	107.0 ± 5.5^{a}	-	62.2 ± 2.8^{b}	57.9 ± 0.3^{b}
Prunus cerasoides	46.3 ± 21.4^{ns}	35.6 ± 14.7^{ns}	13.3 ± 0.3^{ns}	11.4 ± 0.6^{ns}
Intermediate				
Diospyros glandulosa	128.3 ± 1.8^{ns}	122.1 ± 5.8^{ns}	-	-
Recalcitrant				
Artocarpus lacucha	24.8±9.2	-	-	-
Dimocarpus longan	17.0±2.3	-	-	-
Horsfieldia amygdalina	35.5±0.4	-	-	-
Syzygium albiflorum	66.3±2.4	-	-	-

Values not sharing the same superscripts, a and b, (within species, rows) indicate significant difference among storage treatments ($p<0.05$), ns indicate non-significant differences therefore have 4-5 months of rains, during which to grow a root system, deep enough to tap into soil moisture during the subsequent hot, dry season, the following February to April. In contrast *D. longan* seeds were produced in early October (Table 1). Although germination was rapid (MLD 17 d) the germination rate was very low (9%) (Table 2). It is unlikely that this species will be suitable for direct or aerial seeding. The most effective strategy for including it in forest restoration projects would be to use seeds collected in October to raise planting stock in a nursery. The same goes for *D. glandulosa*, the only intermediate species in the study, which produces seed in mid-November, with long dormancy and very low percent germination (128 d, 9% germination, Table 2). Similarly, for other recalcitrant or intermediate species, whose seeds mature outside the optimal period of May-June, their inclusion in forest restoration project will continue to depend on the production of nursery-raised saplings.

5. Conclusions

This study has shown that seed storage is a valuable tool that could potentially make forest restoration more feasible over larger areas, by enabling direct or aerial seeding and by supplying seeds of a broader range of native forest tree species to nurseries for conventional planting-stock production. Inclusion of tree species with recalcitrant seeds in forest restoration projects by direct or aerial seeding is likely to be restricted to those that set seed shortly before or during the start of the rainy season. Others will have to be grown nurseries for conventional tree planting.

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