



Sowing time and direct seeding success of native tree species for restoring tropical forest ecosystems in northern Thailand

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Abstract

Direct seeding (sowing seeds directly into ground) is potentially a cost-effective method of forest restoration that could replace or complement conventional tree planting, under certain conditions. However, the effects of timing on both the success and practicability of direct seeding has received little attention. Therefore, this study determined the effect of seed sowing time on direct seeding efficiency in terms of yield (number of established seedlings per 10 seeds sown) and seedling growth. We tested the hypothesis that seeds, stored and sown at the start of the rainy season, have higher and more rapid germination and that the resultant seedlings perform better, compared with those sown immediately after seed collection. Seeds of 17 native tree species, typical of seasonally-dry, upland, evergreen forest, were collected. Triplicates (50 seeds per replicate) were sown directly into degraded land, shortly after collection and compared with the same for stored seeds, sown at the start of the rainy season. Control seed batches were also germinated in a nursery for comparison. Seed germination was recorded weekly and growth and survival of resultant seedlings were recorded periodically. Our results did not support the above hypothesis. Differences in mean yield (number of seedlings established per 100 seeds sown) and growth between the two sowing times were not significant. Germination percentage and median length of dormancy (MLD) did not differ significantly between the sowing times, except for *Artocarpus lacucha* and *Horsfieldia amygdalina*, whose seeds germinated better immediately after seed collection than after storage ($p < 0.01$). Storage shortened median length of dormancy of *Hovenia dulcis*, *Melia azedarach*, *Phyllanthus emblica*, *Prunus cerasoides* and *Spondias pinnata* seeds ($p < 0.01$). Seedling growth of a few species rivalled reported values of planted saplings (*P. cerasoides*, *M. azedarach* and *B. variegata*), regardless of sowing time. Timing of the direct seeding did not appear to be critical. This provides forest restoration project managers with flexibility in their use of this technique as a restoration tool. The advantages and disadvantages of direct seeding, immediately after seed collection or at the start of the rainy were compared with those of conventional tree planting. We conclude that species selection matters more than timing, when direct-seeding in forest restoration projects (except for recalcitrant species, which can only be direct seeded soon after seed collection). From this study, *Adenanthera microsperma*, *Bauhinia variegata*, *Melia azedarach*, *Phyllanthus emblica* and *Prunus cerasoides* are recommended, for direct seeding, to restore seasonally dry upland evergreen forest ecosystems in northern Thailand and at other sites within their natural species ranges.

Keywords Direct seeding · Seedling establishment · Framework tree species · Seed germination · Dormancy · Seedling growth

Introduction

The concept of tropical forest ecosystem restoration has undergone a dramatic transition over recent decades, from being the dream of a handful of ecologists 30 years ago (Goosem and Tucker 1995), to the global commitment that it has become today (UN Climate Summit 2014). Forest restoration practices vary greatly, depending on the initial degree of degradation, the target forest type, climatic conditions and surrounding landscape factors. However, restoration is possible, even under the harshest of conditions, such as those on mine sites (e.g. Fields-Johnson et al. 2012). Restoration techniques vary across a spectrum from reliance on natural regeneration (Chazdon 2014) and/or assisted (or accelerated) natural regeneration (ANR; Shono et al. 2007) to intensive land preparation, followed by densely planting large numbers of tree species (Miyawaki 1993). The framework species method lies midway along the restoration spectrum. It involves planting seedlings of a few (20–30) tree species, which are characteristic of the target forest ecosystem and can foster natural regeneration. Indigenous tree species are selected, based on high field performance, ability to shade out weeds and the provision of resources that attract seed-dispersing animals (Elliott et al. 2013) at a young age. Such trees thus promote rapid diversification of the understory.

Where natural regeneration is not dense enough to achieve restoration goals, forest restoration involves planting tree seedlings. Production of planting stock in nurseries is costly, in terms of labour, time, equipment, etc. Hence, re-establishing forests from seeds may reduce costs and allow sites that are not near a tree nursery to be restored (Schmidt 2008).

Although, direct seeding could potentially improve the cost-effectiveness of forest restoration, it does not work for all desired species. Seed size often affects seedling establishment in open degraded areas, with larger seeds tending to have higher establishment rates than smaller seeds (Doust et al. 2006; Tunjai and Elliott 2012). Genetics and seed source also play critical roles in determining seed germination and dormancy and ultimately restoration success (Evert et al. 2014).

In the seasonally dry tropics, the optimum seeding time is assumed to be the start of the rainy season, since this allows maximum time for root system development before onset of the dry season. However, only a small percentage of tree species produce seeds at that time (around 13% for northern Thailand (CMU-B Herbarium Database). Consequently, species that fruit outside the optimum direct seeding period have not been widely tested. Direct seeding could have wider applications if seeds produced at other times of the year could be stored until the optimum direct seeding time, or if the method could be implemented at other times of the year with good results. Few studies have investigated the effects of different seed sowing times on seedling establishment (but see Doust et al. 2008) and no study has been performed in seasonally dry forests of northern Thailand, where seasonal variation in weed growth is considerable. Therefore, the objective of the research, described here, was to determine the effects of seed sowing time on direct seeding efficiency in terms of yield (number of established seedlings per 10 seeds sown) and seedling growth. We tested the hypothesis that seeds, stored and sown at the start of the rainy season, have higher and more rapid germination and that the resultant seedlings perform better, compared with seeds sown immediately after seed collection.

Materials and methods

Study site

Direct seeding was carried out on a degraded upland site at Mon Cham, Mae Rim District, Chiang Mai (N 18°56', E 98°49', elevation 1343 masl). Mean annual rainfall from 2014 to 2016 was 1324 mm. The rainy season usually starts in early May and continues into October. The highest rainfall occurs in August. Average temperature was 21.5 °C. January was the coldest month 17.3 °C. The study site was previously used for strawberry cultivation, but was subsequently allocated for forest restoration. The part of the site, used for direct seeding experiments, was dominated by herbaceous weeds, such as *Pteridium aquilinum*, *Paspalum atratum* and *Imperata cylindrica*. Nursery experiments were carried out at the research nursery of Chiang Mai University's Forest Restoration Research Unit (FORRU-CMU).

Study species and seed collection

Large batches of mature seeds, pooled from at least 5 trees of each species, were collected in nearby primary forest. The seed collection schedule was planned using FORRU-CMU's extensive database (FORRU 2016). Species included in the study are listed in Table 1. All are native forest trees of evergreen forest in northern Thailand. The species were of proven high performance as framework tree species for restoring forest of this region (Elliott et al. 2003). Fruits were collected from tree crowns (using a pole) in remnant forest or from the ground as available and the seeds extracted following well-established protocols (FORRU 2006; Schmidt 2007). The first species was collected in October 2014 and last species was collected in July 2015. Sub-batches of seeds were then sown in the nursery and in the field, both shortly after collection and at the optimum sowing time, following storage. In addition, the seeds of *Adenanthera microsperma* and *Acrocarpus fraxinifolius* were scarified prior to germination trials using a nail clipper, a standard procedure adopted by FORRU nursery staff to shorten seed dormancy, due to the tough seed coat of these species (FORRU 2016).

In this paper, the word "seed" is used to include pyrenes that comprise one or more seeds contained with the inner fruit wall (endocarp). Five of the species studied were dispersed as pyrenes. *Prunus cerasoides* produces single-seeded pyrenes ("cherry stones"), *Gmelina arborea* produces 1–4 seeded pyrenes, *Alangium kurzii* produces two-seeded pyrenes whilst *Choerospondias axillaris* and *Spondias pinnata* produce pyrenes, containing up to a maximum of five seeds (Table 1).

Nursery trials

Sub-batches of seeds were sown in the nursery immediately after collection (hereafter referred to as the IN treatment (immediate +nursery)) and after storage until the beginning of rainy season [12th June 2015, hereafter referred to as the SN treatment (stored +nursery)]. Three replicates of 50 seeds each were sown using FORRU's standard nursery protocol (FORRU 2016), buried about one centimetre in 100% forest soil in plastic modular trays, diameter 4 cm and depth 4.5 cm and watered daily. The number of germinated seeds was recorded weekly. Germination was defined as emergence of a plumule or radical through the testa. The test was ended when no seeds had germinated for at least 30 days

Table 1 List of study species

Species	Abbreviation used in this paper	Family	Seed collection date	Propagule use in this study	Storage behaviour ^f	Storage method and duration (days)	Species distribution—elevation range and countries ^d
<i>Acrocarpus fraxinifolius</i> Arn.	AF	Leguminosae	11/04/15	Seed ^a	Orthodox	5% MC, Refrigerator (62)	1000–1200 m. China, Bangladesh, Bhutan, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, Sri Lanka, Thailand; introduced to Tanzania, Uganda
<i>Adenanthera microsperma</i> Teijsm. and Binn.	AM	Leguminosae	20/02/15	Seed ^a	Orthodox	5% MC, Refrigerator (112)	1000 m. China, Cambodia, Indonesia, Laos, Malaysia, Myanmar, Thailand, Vietnam
<i>Alangium kurzii</i> Craib	AK	Cornaceae	10/07/15	Pyrene ^a	Orthodox	–	600–1600 m. China, Indonesia, Laos, Malaysia, Myanmar, Philippines, Thailand, Vietnam
<i>Artocarpus lacucha</i> Buch.-Ham.	AL	Moraceae	01/06/15	Seed ^a	Recalcitrant	Initial MC, Refrigerator (11)	100–1300 (–1800) m. China, India, Indonesia, Laos, Myanmar, Nepal, Sikkim, Thailand, Vietnam
<i>Bauhinia variegata</i> L.	BV	Leguminosae	15/05/15	Seed ^a	Orthodox	5% MC, Refrigerator (28)	1000–1500 m. China Cambodia, Laos, Myanmar, Thailand, Vietnam
<i>Choerospondias axillaris</i> (Roxb.) B.L. Burtt and A.W. Hill	CA	Anacardiaceae	12/07/15	Pyrene ^a	Orthodox	–	300–2000 m. China Cambodia, India, Japan, Laos, Thailand, Vietnam

Table 1 (continued)

Species	Abbreviation used in this paper	Family	Seed collection date	Propagule use in this study	Storage behaviour ^c	Storage method and duration (days)	Species distribution—elevation range and countries ^d
<i>Dimocarpus longan</i> Lour.	DL	Sapindaceae	01/10/14	Seed ^a	Recalcitrant	5% MC, Refrigerator (254)	500–1300 m. China, Cambodia, India, Indonesia, Laos, Malaysia, Myanmar, New Guinea, Philippines, Sri Lanka, Thailand, Vietnam
<i>Diospyros glandulosa</i> Lace	DG	Ebenaceae	15/11/14	Seed ^a	Intermediate	5% MC, Refrigerator (209)	
<i>Gmelina arborea</i> Roxb.	GA	Lamiaceae	21/05/15	Pyrene ^a	Orthodox	5% MC, Refrigerator (22)	Below 1500 m. China, Bangladesh, Bhutan, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, Philippines, Sri Lanka, Thailand, Vietnam
<i>Horsfieldia amygdalina</i> (Wall.) Warb.	HA	Myristicaceae	19/05/15	Seed ^a	Recalcitrant	Initial MC, Refrigerator (24)	100–1200 m. China, Bangladesh, India, Laos, Myanmar, Thailand, Vietnam
<i>Hovenia dulcis</i> Thunb.	HD	Rhamnaceae	20/02/15	Seed ^b	Orthodox	5% MC, Refrigerator (112)	200–1400 m. China, Japan, Korea, Thailand
<i>Manglitia garrettii</i> Craib	MG	Magnoliaceae	19/10/14	Seed ^a	Orthodox	5% MC, Refrigerator (236)	1300–1900 m. S China, Thailand, Vietnam

Table 1 (continued)

Species	Abbreviation used in this paper	Family	Seed collection date	Propagule use in this study	Storage behaviour ^c	Storage method and duration (days)	Species distribution—elevation range and countries ^d
<i>Melia azedarach</i> L.	MA	Meliaceae	04/01/15	Seed ^a	Orthodox	5% MC, Refrigerator (159)	500–2100 m. China, Bhutan, India, Indonesia, Laos, Nepal, Papua New Guinea, Philippines, Sri Lanka, Thailand, Vietnam; tropical Australia, Pacific island
<i>Phyllanthus emblica</i> L.	PE	Phyllanthaceae	28/12/14	Seed ^a	Orthodox	5% MC, Refrigerator (166)	200–2300 m. China, Bhutan, Cambodia, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, Philippines, Sri Lanka, Thailand; South America (cultivated)
<i>Prunus cerasoides</i> Buch.-Ham. ex D. Don	PC	Rosaceae	11/04/15	Pyrene ^a	Orthodox	5% MC, Refrigerator (62)	700–3700 m. N. Thailand, China, Bhutan, N India, Kashmir, N Laos, Myanmar, Nepal, Sikkim, N Vietnam
<i>Spondias pinnata</i> (L. f.) Kurz	SP	Anacardiaceae	25/03/15	Pyrene ^a	Orthodox	Initial MC, Refrigerator (79)	300–1200 m. S China, Bhutan, Cambodia, India, Indonesia, Laos, Malaysia (peninsular), Myanmar, Nepal, Philippines, Singapore, Thailand, Vietnam
<i>Syzygium albiflorum</i> (Duthie ex Kurz) Bahadur and R.C. Gaur	SA	Myrtaceae	02/06/15	Seed ^a	Recalcitrant	Initial MC, Refrigerator (10)	800–1525 m Myanmar, Thailand

^aGardner et al. (2000), ^bKopachon et al. (1996), ^cMC seed moisture content, ^dWaiboonya (2017), ^eeFloras (2008)

after the germination peak. Mean germination percentage and median length of dormancy (MLD) were then calculated. MLD was defined as the time from sowing to germination of half the number of seeds that finally germinated (Elliott et al. 2013).

Direct seeding

After collection seeds were divided into two batches. The first was sown directly into the field site one day after seed collection (hereafter referred to as the IF treatment (immediate + field), whilst the second batch was stored until the beginning of the rainy season (12th June 2015, hereafter referred to as the SF treatment (stored + field)). In the field trial, seeds were positioned 50 cm apart and buried—three replicates of 50 seeds each, with replicates spaced at least 20 m apart. The seeds were buried about 5 cm deep or until soil fully covered the seeds. A PVC pipe was placed around every seed sown, to prevent movement and to make the seeds easier to find for subsequent measurements. Stored seeds were sown beside immediately-sown seeds at the beginning of the rainy season (12th June 2015). Seeds of *A. kurzii* (29th July 2015) and *C. axillaris* (15th July 2015) were sown later, because they fruited during the rainy season. Seed germination was monitored weekly until no seeds had germinated for a period of at least 30 days following the germination peak. Height and root collar diameter (RCD) of surviving seedlings were measured at the beginning of the first rainy season (July 2015), after the first rainy season (December 2015) and at the beginning of the second rainy season (July 2016). Weeds around the germination sites were slashed at the beginning of the rainy season (summer) and at the end of the rainy season (cool season). Fertilizer was applied to seedlings following the recommendations of FORRU (2006).

Seedling relative growth rate (RGR, %/year) was calculated using the following equation:

$$\text{RGR} = \frac{(\ln \text{FS} - \ln \text{IS}) \times 365 \text{ days}}{\text{No. days between measurements}} \times 100$$

where $\ln \text{FS}$ is the natural logarithm of final sapling size and $\ln \text{IS}$ is the natural logarithm of the initial seedling size (Elliott et al. 2013). RGR based on height (RGR-H) and root collar diameter (RGR-RCD) are presented in this paper.

Statistical analyses

Data were analysed using the standard statistical procedures for nursery and field trials, established for forest restoration experiments in manual by Elliott et al. (2008). Binomial data, such as percent germination and survival, were arcsine-transformed before analysis (Elliott et al. 2013). *t* tests were performed separately for each species for pair-wise comparison: (1) mean percent seed germination and MLD (days) between the field and nursery (3 replicates) and (2) mean seedling/sapling survival, yield and relative growth parameters between the two sowing times. Species were ranked according to mean percent germination for the most effective (immediate or stored) treatment for each species in the field. Subsequently, the presence of significant differences in both mean germination and relative growth rate among species was determined by analyses of variance (ANOVA). Since there were no significant differences in relative growth rates between the two sowing times, values from both treatments were pooled ($N=6$) and an ANOVA was performed with species

as the main effect and growth parameters (height and RCD) as the dependent variables. Post hoc analyses for pair-wise comparisons of means were undertaken using Tukey test ($p=0.05$). All statistical analyses were performed by PAST version 3.22 (Hammer et al. 2001).

Results

Seed germination

For all but three species, seed storage had no significant effect on germination in the field (Fig. 1). The exceptions were *H. amygdalina*, whose seeds germinated only when sown immediately after collection and *A. lacucha*, whose immediately-sown seeds germinated significantly more than its stored seeds did (t test, $p<0.01$), whilst *A. fraxinifolius* was the only species whose stored seeds germinated better than did those sown at collection time (t test, $p<0.01$).

Germination environment (IN vs. IF) also had no significant effect on germination of all but 3 species at seed-collection time. The exceptions were *A. fraxinifolius*, *A. lacucha* and *C. axillaris*, which all germinated significantly better in the nursery (IN > IF, by 42%, 32% and 25%, respectively, t test, $p<0.05$, Fig. 2a). A similarly insignificant result was obtained for seed that had been stored (SN vs. SF). After seed storage, the exceptions were *M. azedarach*, *M. garrettii* and *P. emblica* which, in contrast to the earlier results, germinated significantly better in the field than in the nursery (SF > SN by 36%, 16% and 25%, respectively, t test, $p<0.05$, Fig. 2b).

The species were ranked according to highest mean percentage emergence, regardless of sowing time (immediately sown vs. stored), (Fig. 3). *B. variegata* exhibited the highest percent germination ($88.7 \pm 1.3\%$), from immediate sowing at collection time (IF), followed by stored seeds of *A. microsperma* and *P. cerasoides* sown at the start of the rainy season ($71.3.0 \pm 6.8\%$ and $64.0 \pm 4.7\%$, respectively). In contrast, *D. glandulosa* (SF)

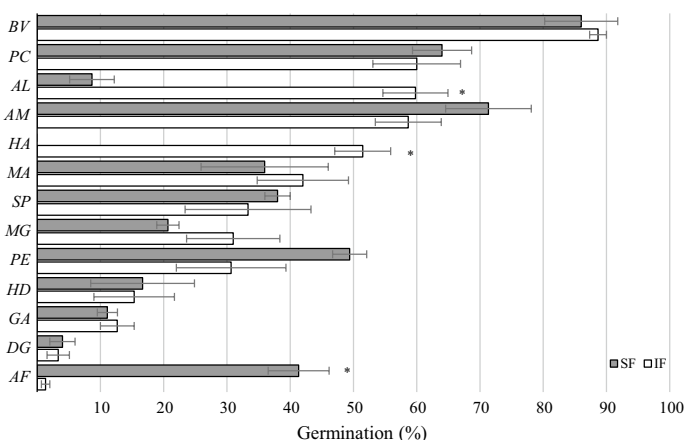


Fig. 1 Mean (\pm SE) percent seed germination of 13 tree species, sown in the field at collection time (IF) and at the beginning of rainy season after storage (SF). Three replicates of 50 seeds. *A. microsperma* and *A. fraxinifolius* seeds were scarified for the SF treatment. Asterisks indicate significant differences between the two bars within each species (t test, $p<0.05$). For species abbreviations please see Table 1

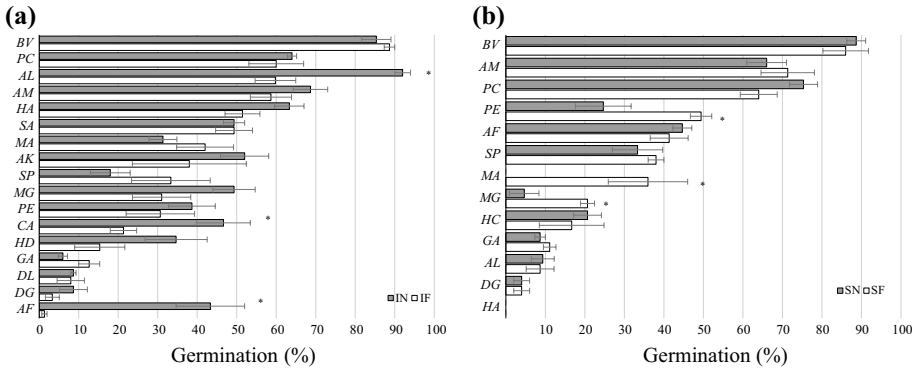


Fig. 2 Mean (\pm SE) percent seed germination of 17 tree species between nursery and field conditions for **a** 17 species of seeds sown at collection time (IF vs. IN) and **b** 13 species after storage (SN vs. SF). Three replicates of 50 seeds. Asterisks indicate significant difference between the two bars within each species (*t* test, $p < 0.05$). For species abbreviations please see Table 1

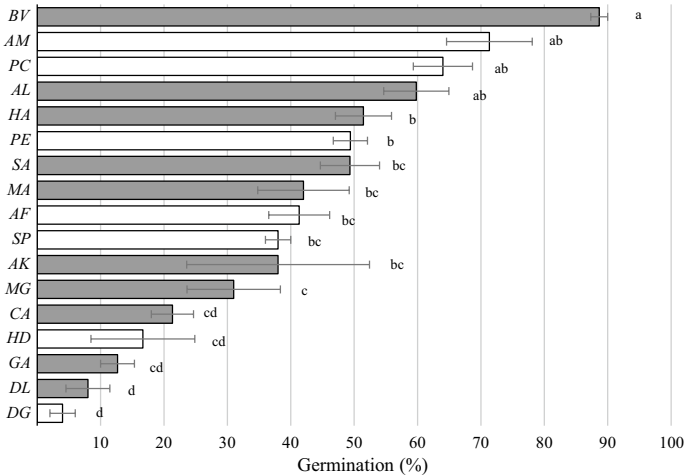


Fig. 3 Species ranked in declining order of highest mean germination (\pm SE) under the most effective treatment in the field. Gray bars indicate seed sown at collection times, whilst white bars indicate those sown at the beginning of rainy season after storage ($N = 3$). Bars not sharing the same superscripts indicate significant differences among species. (mean differentiation, using Tukey, $\alpha = 0.05$). For species abbreviations please see Table 1

germinated the least (only $4.0 \pm 2.0\%$). A similar result was obtained with *D. longan* (IF) (only $8.1 \pm 3.5\%$, Fig. 3).

Dormancy

Storage generally shortened MLD of most species. In the field, seeds of most species sown at collection time (IF) had significantly longer MLD than those stored and sown at beginning of the rainy season (SF): *A. microsperma* (IF > SF by 46 days, seeds stored 112 days, *t* test, $p < 0.01$), *H. amygdalina* (IF > SF by 62 days, seeds stored 24 days, *t*

test, $p < 0.01$), *H. dulcis* (IF > SF by 78 days, seeds stored 112 days, t test, $p = 0.01$), *M. azedarach* (IF > SF by 97 days, seeds stored 159 days, t test, $p < 0.01$), *P. emblica* (IF > SF by 93 days, seeds stored 166 days, t test, $p < 0.01$) *P. cerasoides* (IF > SF by 57 days, seeds stored 62 days, t test, $p < 0.01$) and *S. pinnata* (IF > SF by 76 days, seeds stored 79 days, t test, $p < 0.01$, Fig. 4). *B. variegata* seeds were the only ones with longer dormancy when stored and sown at the start of the rainy season (SF, 28 days' storage), compared with IF. The difference was only 4 days, although it was statistically significant (t test, $p < 0.01$, Fig. 4).

For seeds sown in the field at collection time (IF), most germinated just before the start of the rainy season (median date of germination). The exceptions were *D. longan*, *D. glandulosa* and *M. garrettii* whose median germination dates fell in October, December and March respectively. For seeds sown after storage (sowing date 12/06/16), all species had median germination dates within the rainy season (June to August 2015).

When mean dormancy was compared between seeds sown in the nursery and field at seed collection time (IN and IF), six species took significantly longer to germinate in the field than in the nursery: *A. lacucha* (IF > IN 22 days, t test, $p = 0.01$), *A. microsperma* (IF > IN 50 days, t test, $p < 0.01$), *H. amygdalina* (IF > IN 26 days, t test, $p = 0.02$), *M. azedarach* (IF > IN 38 days, t test, $p < 0.01$), *S. pinnata* (IF > IN 79 days, t test, $p < 0.01$) and *S. albiflorum* (IF > IN 10 days, t test, $p = 0.01$), whilst three took significantly longer to germinate in the nursery than in the field: *A. fraxinifolius* (IF < IN 90 days, t test, $p = 0.04$), *B. variegata* (IF < IN 5 days, t test, $p < 0.01$) and *C. axillaris* (IF < IN 157 days, t test, $p < 0.01$, Fig. 5). Comparing MLD after seed storage, between the nursery experiments and the field trials, five species had longer mean MLD in the field than in the nursery; *A. microsperma* (SF > SN 10 days, t test, $p < 0.01$), *B. variegata* (SF > SN 3 days, t test, $p = 0.01$), *M. azedarach* (SF > SN 20 days, t test, $p < 0.01$), *P. cerasoides* (SF > SN 3 days, t test, $p = 0.01$) and *S. pinnata* (SF > SN 10 days, t test, $p < 0.01$, Fig. 5b).

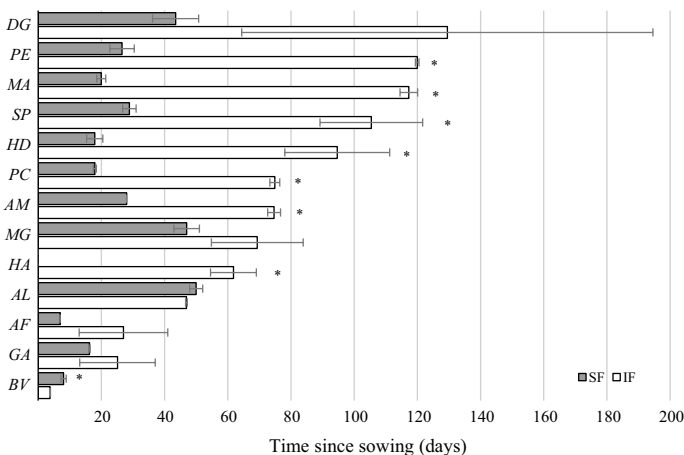


Fig. 4 Mean (\pm SE) median length of dormancy (MLD) of 13 tree species compared between two sowing times in the field: at collection time (IF) and at the beginning of the rainy season after storage (SF), (N = 3). Asterisks indicate significant differences between the two bars within each species (t test, $p < 0.05$). For species abbreviations please see Table 1

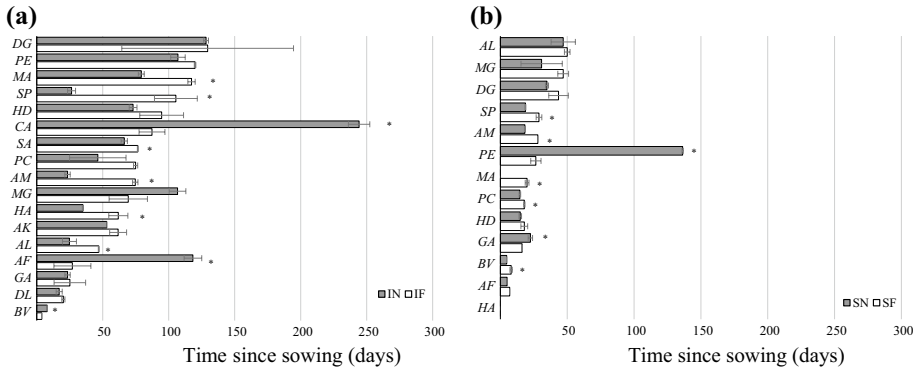


Fig. 5 Mean (\pm SE) MLD's of 17 tree species, seeds sown in the field (IF) and in the nursery (IN) (N=3) at **a** collection time and **b** after storage. Asterisks indicate significant differences between the two bars within each species (*t* test, $p < 0.05$). For species abbreviations please see Table 1

Seedling survival and seedling yield

In general, seed storage had no significant effect on seedling survival in the field (defined as the number of surviving seedlings, expressed as a percentage of the seeds that germinated after 12 months). *B. variegata* achieved the highest percent survival ($69.7 \pm 9.1\%$), followed by *P. emblica* ($51.1 \pm 10.2\%$). *A. fraxinifolius*, *G. arborea* and *H. dulcis* had low survival percentages in the field ($1.1 \pm 1.1\%$, $3.3 \pm 2.2\%$ and $3.3 \pm 3.3\%$, respectively). No seedlings survived of *A. fraxinifolius* from immediate sowing and of *G. arborea* from stored seeds (Fig. 6a).

Seedling yield (the number of seedlings that survived to reach 1-year-old, expressed as a percent of the number of seeds sown) was also not significantly affected by seed storage for all species except for *A. lacucha*—the only species for which percent yield of immediately sown seeds was significantly higher (22%) than that of stored seeds (*t* test, $p = 0.04$, Fig. 6b). *B. variegata* achieved the highest yield in the field ($60.7 \pm 8.7\%$),

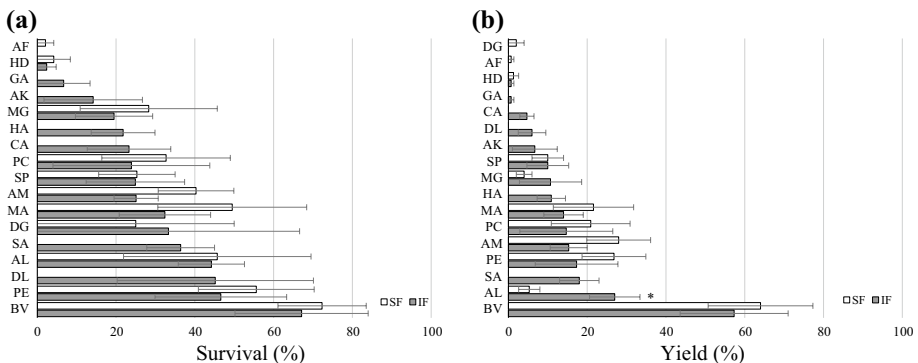


Fig. 6 Mean (\pm SE) **a** seedling survival and **b** seedling yield, in the field over one year of direct-seeded seedlings from two sowing periods, Gray bars IF=sown at collection time. White bars SF=seeds stored and sown at the beginning of rainy season (N=3). Asterisk indicates significant difference between IF and SF ($p < 0.05$). For species abbreviations please see Table 1

whereas most other species had yields of less than 20 percent. All seedlings of *A. fraxinifolius* from immediate sowing died in the field. *A. fraxinifolius* and *H. dulcis* had the lowest yields: only $0.3 \pm 0.3\%$.

Seedling growth

All growth measures of 1-year-old seedlings were not significantly affected by seed sowing time, both within each species and for data pooled across species (*t* test, RGR-H, $p=0.83$, and RGR-RCD, $p=0.92$) (Fig. 7).

Differences in growth rates between the species tested were significant (ANOVA, $p<0.01$). *P. cerasoides* seedlings grew the fastest (RGR-H ($171.7 \pm 37.9\%/year$), followed by *M. azedarach* ($127.3 \pm 27.9\%/year$). Conversely, *G. arborea*, *S. pinnata* and *H. dulcis* grew the slowest, with RGR-H values of just 15.6 ± 15.6 , 17.6 ± 12.1 and $17.7 \pm 17.7\%/year$, respectively, Fig. 8a). *P. cerasoides* also achieved highest RGR-RCD (ANOVA, $p<0.01$, $121.1 \pm 28.1\%/year$), followed by *M. azedarach* and *P. emblica* ($119.0 \pm 14.2\%/year$ and $109.2 \pm 20.6\%/year$, respectively). In contrast, RGR-RCD of *S. pinnata*, *H. amygdalina* and *C. axillaris* seedlings was low ($21.7 \pm 11.7\%/year$, $22.2 \pm 12.3\%/year$ and $24.2 \pm 61.8\%/year$, respectively, Fig. 8b).

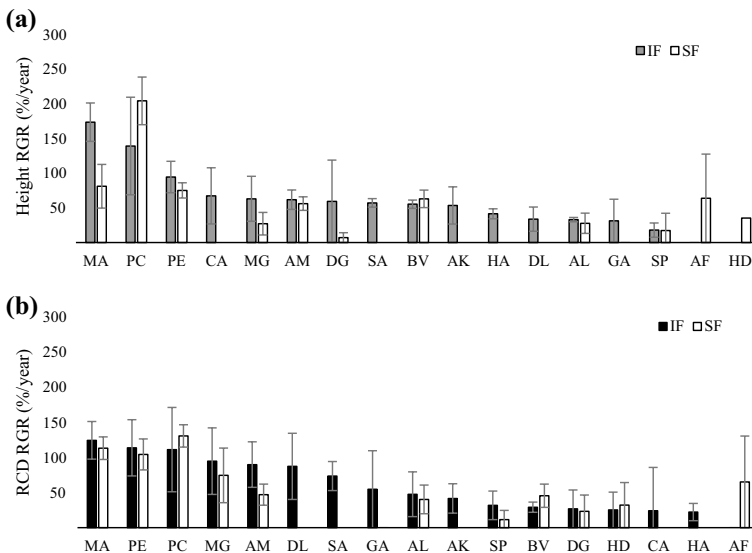


Fig. 7 Mean (\pm SE) relative growth rates (RGR) for **a** height and **b** root collar diameter over 1 year of direct-seeded seedlings in the field, by species, between two sowing periods, IF=sown at collection time, SF=Stored and sown at the beginning of rainy season (N=3). No significant differences between treatments for every species ($p<0.05$) Species abbreviations see Table 1

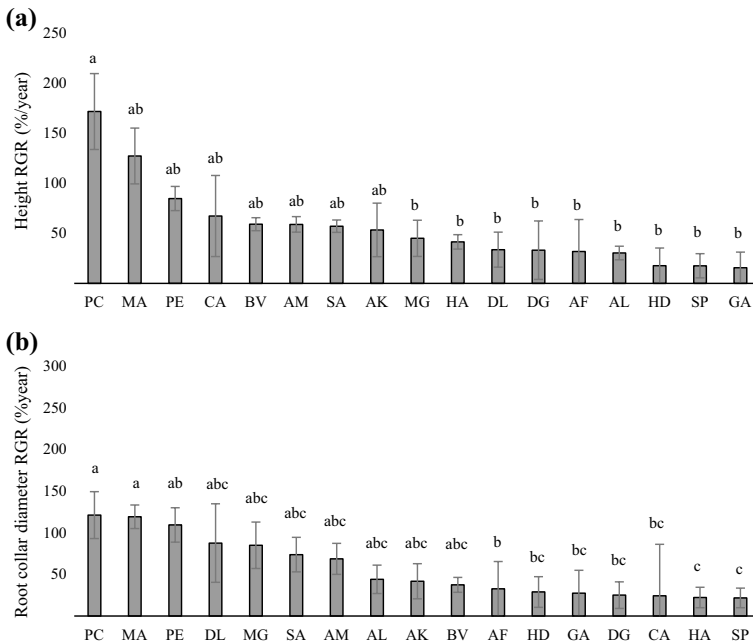


Fig. 8 Mean (\pm SE) relative growth rate (RGR), averaged across sowing times, of **a** height RGR and **b** root collar diameter RGR, over 1 year of direct-seeded seedlings in the field, by species, IF=sown at collection time, SF=Stored and sown at the beginning of rainy season (N=3). Species abbreviations see Table 1. Columns not sharing the same superscripts indicate significant differences among species (Turkey, $\alpha=0.05$)

Discussion

With the current surge in forest restoration programs globally, particularly for climate change mitigation (Dave et al. 2017), interest in developing direct seeding, as a more cost effective alternative to conventional tree planting, has never been greater. Its advantages for tropical regions, such as no requirement for a tree nursery, ease of transport and the ability to restore remote sites, have been well reviewed (Schmidt 2008), but mortality of seeds, and the tiny seedlings that emerge from them, is usually much higher than for conventionally planted tree saplings, due to their higher vulnerability to weed competition, pests and diseases and sudden changes in environmental conditions. So, the efficiency of direct seeding must be increased, if it is to become a viable alternative to conventional tree planting on a broad scale.

The most effective timing of direct seeding is debatable, both in terms of its likely effects on the outcome of restoration and for practical reasons. We reasoned that the optimal direct seeding time would be the beginning of the rainy season, since tree seed germination (in terms of species numbers) naturally peaks then. In the seasonally dry tropical forests of northern Thailand, the median seed germination dates of more than three quarters of tree species are in the late dry or early rainy seasons (75.8% of 262 species studied (FORRU 2006, p. 44). This allows maximum time for roots to grow deep enough to access sufficient soil moisture to survive the dry season; desiccation being a major cause of tree seedling mortality in exposed deforested sites during the first dry season (Elliott et al.

2003). Consequently, we hypothesized that, compared with seeds sown immediately after seed collection, those stored and sown at the start of the rainy season would have higher yield (number of seedlings established from 100 seeds sown) and growth.

However, the results, presented above, did not support this hypothesis, there being no significant differences between the two sowing times in both yield (Fig. 6b) and growth rates (Fig. 7) of all species tested, except for yield of *A. lacucha*. This implies that the timing of the direct seeding is not as critical as we first thought it to be. This provides forest restoration project managers with flexibility in their use of the technique as a restoration tool. For practical purposes, it still makes sense to sow the seeds of as many species as possible in a single operation at the start of the rainy season. This strategy would require a small local seed bank to be established, with staff to maintain it, and it would exclude tree species whose seeds rapidly become non-viable during storage (recalcitrant species) and which also fruit more than a few weeks before the planned mass-sowing event. In this study, seeds of only two species (*H. amygdalina* and *A. lacucha*) were sensitive to desiccation and totally or substantially lost viability, when stored even for very short periods. They were, therefore, classed as recalcitrant (Waiboonya 2017). However, recalcitrant species, in general, tend to disperse their seeds in the rainy season (Daws et al. 2005). In this study, only one of three recalcitrant species fruited outside the start of the rainy season (*Dimocarpus longan*, November). So, seeds of many recalcitrant species are likely to be available for multi-species, mass, direct-seeding operations at the start of the rainy season, without storage being necessary.

Yields, in terms of the number of trees established per 100 seeds sown, were generally lower than could be expected from conventional tree planting (except for *B. variegata*) (Elliott et al. 2003), but that is to be expected, since in nature, only a minuscule proportion of the seeds dispersed into deforested sites germinate to become trees. Of the 17 species tested, eight had first-year yields of less than 10%, four of 10–20%, 4 of 20–30% and one of >60%; certainly higher than for naturally dispersed seeds in a similar environment (Hardwick et al. 1997). In contrast, Elliott et al. (2003) reported that in restoration trials that tested conventional tree-planting in a nearby site, more than half (51%) of species tested ($n=37$) achieved survival rates of >70% over 2 rainy seasons. The lower yields of direct seeding, compared with conventional tree planting, could be compensated for by collecting and sowing larger numbers of seeds. This in turn raises the issue of the need to develop and scale up efficient regional tree seed collection and distribution programs, to achieve economies of scale, if direct seeding is to be practiced on a wide scale.

Seedling growth was similar to that reported for the same species in other nearby studies and some species exceeded growth rates reported for nursery-grown planting stock. For example, *P. cerasoides* seedlings grew the tallest (87.4 cm) of all the species tested, one year after germination and attained the highest RCD, followed by *M. azedarach* (46.9 cm tall) and *B. variegata* (30.4 cm). These heights exceeded the recommended height (30–50 cm; FORRU 2006) for planting out of nursery-grown saplings. Tunjai (2005) reported similar results for direct-sown seedlings of *P. cerasoides* (80 cm tall) and *M. azedarach* (120 cm tall). In a head-to-head paired comparison with nursery-raised saplings, she reported that, within a year, direct seeded *M. toosendan*, *P. cerasoides* and *C. axillaris* saplings grew significantly taller than did the nursery-raised saplings that they were paired with ($p<0.05$). The differences became even greater during the second year of the experiment, by which time direct seeded *G. arborea* saplings had also grown significantly taller than nursery-raised ones. She attributed this to better root system development of direct seeded trees, since containerized, nursery-grown saplings often develop root abnormalities (spiralizing) in the nursery and suffer transplantation shock when planted out (see also

Table 2 Pros and cons and relative costs of direct seeding (immediate and after seed storage) versus conventional tree planting—insights from this study with additional information from Schmidt (2008)

Task	Direct seeding		Conventional tree planting
	Single multispecies sowing event (after seed storage)	Immediate sowing after seeds of each species are collected	
Seed collection	More seeds must be collected to compensate for lower conversion rates of seed to tree in the field (higher cost)		Regular seed collection—fewer seeds need be collected (lower cost)
Seed storage	Orthodox species stored from fruiting time to direct seeding event date (higher cost)	None needed (no cost)	Optional, for fast-growing orthodox species, to streamline nursery production (optional cost)
Nursery	None needed—huge cost saving		Planting stock production relies on efficient nursery operation and trained staff (very high cost)
Transport to restoration site	Single trip—high volume (low cost)	Multiple trips—high volume per trip—but costs increase with the number of species planted and depends on relative seeding times of each species	Saplings and their containers and media are bulky therefore costly to transport to the restoration site
Planting/Sowing	No transplantation “shock” Low cost in terms of labour and materials. Could not include those recalcitrant species that fruit outside the optimal sowing period.	Higher costs due to labour required on multiple occasions. Both recalcitrant and orthodox species included.	Fewer trees planted per unit time—high labour costs. Transplantation “shock” is a risk. Both recalcitrant and orthodox species included.
Clean up	None needed (no cost)		Containers must be removed from the restoration site (small cost)
Weeding	Emerging tree seedlings are tiny—therefore weeding must be carried out frequently and with meticulous care to avoid damaging them (higher cost)		Larger saplings more resistant to weed competition—less frequent weeding needed (lower cost).
Rooting	Often better root system development than for planted saplings		Containerized saplings often develop root deformations before planting date

Table 2 (continued)

Task	Direct seeding	Conventional tree planting
Single multispecies sowing event (after seed storage)	Immediate sowing after seeds of each species are collected	
Yield (trees established per seeds sown or trees planted after one year)—highly variable among species for all methods	See Fig. 6b About half of species 10–20%, several > 20% and very rarely up to 60%	About ½ species > 75% (Elliott et al. 2003)
	Similar or slightly lower than after storage	

Schmidt 2008). The high growth rates of *M. toosendan*, *P. cerasoides*, *C. axillaris* and *G. arborea*, the fact that they flower and fruit at a young age (2–3 years) and their attractiveness to seed-dispersing animals makes them ideal framework species (FORRU 2006). If low yields are compensated for by high sowing densities, direct seeding may be a more efficient way to include these species in forest restoration projects than conventional tree planting. However, tree planting may remain the most efficient technique for slower growing species. For example, in our study, *A. fraxinifolius* seedlings grew the least—averaging only 4.3 cm tall in a year. In contrast, FORRU (2006) reported excellent results of this species with conventional tree planting (68 cm tall, RGR-H = 180 one year after planting 30-cm-tall saplings). Consequently, although direct seeding may become a more common component of forest restoration projects, it is unlikely to replace tree planting entirely. The pros and cons of conventional tree planting versus direct seeding (both multi- and single events) are summarized in Table 2.

Our study implies that species selection matters more than timing when designing forest restoration projects with a direct-seeding component (except for the recalcitrant species mentioned above, which can only be direct seeded soon after seed collection). This is in broad agreement with the only other major study known to the authors that focussed specifically on the timing of direct seeding: that by Doust et al. (2008), who investigated the effects of sowing seeds early or late in the rainy season (with minimal seed storage). That study also reported that the effects of timing were small, except for a few small-seeded species at one site only, which did appear to benefit from sowing late in the rainy season. However, the authors attributed this to weeding the site prior to late seeding, which reduced competition. Consequently, for most tree species in the seasonal dry tropics, the timing of direct seeding is unlikely to be critical to the overall success of forest restoration projects, provided species with relatively high rates of establishment and growth are selected. From this study, those species with yields > 20% and RGR-H > 50% are recommended for direct seeding to restore seasonally dry upland evergreen forest ecosystems in northern Thailand and at other sites within their species ranges, namely: *Adenantha microsperma*, *Bauhinia variegata*, *Melia azedarach*, *Phyllanthus emblica* and *Prunus cerasoides*.

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