New Forests (2012) 43:319–333
DOI 10.1007/s11056-011-9283-7

Effects of seed traits on the success of direct seeding for restoring southern Thailand's lowland evergreen forest ecosystem

Panitnard Tunjai · Stephen Elliott

Received: 16 March 2011 / Accepted: 9 August 2011 / Published online: 18 August 2011

Abstract The success of direct seeding, as a low-cost approach to forest restoration, varies with tree species and seed characteristics. A system to predict which tree species are likely to be suitable for direct seeding would therefore be useful for improving forest restoration projects. Therefore, this study aimed to determine the effects of seed traits on the success of direct seeding to restore tropical forest in southern Thailand. Seeds of 19 indigenous lowland tropical forest tree species were collected, from both the east and west sides of the Thailand peninsular and the following parameters measured: seed size, shape, coat thickness and moisture content. Field trials were established to determine seed germination rates and to calculate a "direct seeding suitability score" for each species, which combined seedling establishment and growth rates. Seed size, shape and moisture content were associated with germination percentage. Species with higher seedling survival tended to have large or intermediate-sized seeds, round or oval seeds and seeds with low or medium moisture content. Only seed coat thickness was significantly correlated with the suitability score ($r = 0.65$, $p < 0.01$). Seed coat thickness >0.4 mm coincided with higher rank suitability score. These conditions successfully predicted the success or failure of direct seeding for 15 out of 19 species tested. Eight tree species are recommended as suitable for restoring lowland evergreen forest ecosystems in southern Thailand, by direct seeding.

Keywords Direct sowing · Seed characteristics · Forest restoration · Reforestation · Tropical forest

P. Tunjai (✉)
Ecology and Biodiversity Program, School of Science, Walailak University, Nakhon Si Thammarat 80160, Thailand
e-mail: ptunjai@yahoo.com

S. Elliott
Forest Restoration Research Unit, Department of Biology, Faculty of Science, Chiang Mai University, Chiang Mai 50200, Thailand
e-mail: stephen_elliott1@yahoo.com

Introduction

Growing concerns over global biodiversity loss (Laurance et al. 2011) and climate change (Harris et al. 2006) have generated a recent surge in interest in the potential to restore tropical forest ecosystems, both for wildlife conservation and carbon storage (Hall et al. 2011). Most forest restoration techniques involve tree planting, which is both expensive and time consuming, since growing trees to a plantable size (50–60 cm) (FORRU 2006) in nurseries takes at least 1 year and is labour-intensive. Direct seeding (sowing forest tree seeds directly into deforested areas) could drastically reduce the costs of forest restoration (since nursery costs are eliminated) (Engel and Parrotta 2001; Lamb and Gilmour 2003; Doust et al. 2006; Cole et al. 2011), provided that it can be implemented effectively. Direct seeding has not been widely used in the tropics (Lamb 2011); however trials have been successful in South America (Parrotta and Knowles 1999; Engel and Parrotta 2001; Bonilla-Moheno and Holl 2010). Although direct seeding may be a useful technique for ecological restoration, it can be limited by seed predation (Hau 1997), low seed viability (Lamb 2011), lack of favourable micro-sites (De Steven 1991), weed competition and unsuitable seed types (Doust et al. 2008). The severity of these limitations varies with micro-site conditions. For example, little predation (<10%) was found in direct seeded trials in northern Thailand (Woods and Elliott 2004) and northern Ethiopia (Aerts et al. 2006), while an average of 74% seed loss due to predation was recorded in degraded grassland and shrublands in Hong Kong (Hau 1997).

Species choice is critical to the success of direct seeding. Tropical forests are home to many thousands of tree species. Collecting seeds of them all and testing them for germination and seedling establishment in deforested areas would be very time consuming. Therefore, this paper explores the concept that success of direct seeding may be predictable from seed traits that are already known to affect seed germination, dormancy and early seedling establishment, such as seed size, seed coat thickness, shape and moisture content.

Of these traits, seed size has been studied the most (Shankar 2006). Large seeds carry with them greater food reserves giving very young seedlings a greater chance of survival, but the effects of seed size on success of direct seeding appears to be variable. For example, in Australia, Doust et al. (2006) showed that, for buried seeds, large ones had higher germination and seedling growth rates than small or intermediate sized seeds. Within species, for example, *Prosopis cineraria* (L.) MacBride, larger seeds (seed width range 3.27–4.74 mm) are recommended for use in afforestation programs, because they have higher germination per cent, both in the laboratory (30–100%) and in the field (7–90%) (Manga and Sen 1995). Studies, suggesting that direct seeding is a promising restoration strategy for larger-seeded tree species, include those of Carmago et al. (2002), Doust et al. (2006) and Hardwick (1999), although the results vary among habitats. Despite this evidence, small-seeded pioneer species have more commonly been used to restore forest ecosystems, because they occur naturally at the early stages of succession (Sun et al. 1995; Engel and Parrotta 2001; Garcia-Orth and Martínez-Ramos 2008; Balandier et al. 2009). Successful results have also been achieved with some species that have moist, intermediate-sized seeds (Tunjai 2005).

Large seeds, with thick seed coats, are less susceptible to predation (Nepstad et al. 1996; Hau 1997), but thick seed coats can delay germination (Tunjai 2005). For example, legumes are often excellent candidate species for direct seeding, especially due to their nitrogen fixing capabilities (Engel and Parrotta 2001), but pre-sowing seed treatments are often necessary to reduce dormancy resulting from their hard seed coats (Cervantes et al. 1996). Seeds with thin seed coats can be more easily penetrated by water, which can trigger rapid germination (Bewley and Black 1985). However, Badek et al. (2006) showed no relationship between seed coat thickness and seed germination percentage.

Apart from seed size, few studies from the humid tropics have attempted to identify other seed characteristics that could potentially be used to predict which tree species could be used successfully for direct seeding (Knowles and Parrotta 1995; Hooper et al. 2002; Doust et al. 2008). Seed shape is also functionally important (Campbell et al. 1999). In combination with seed mass, seed shape appears to affect the probability of seed predation, persistence in the seed bank, dispersal ability, seed production, and establishment success (Liu et al. 2007). Round seeds could penetrate easily into the soil, persist longer before germination and consequently they are often dominant in the seed bank (Yu et al. 2007). In contrast, many small-, elongated- or conically-shaped seeds germinate immediately after collection (Grime et al. 1981) because shorter distances between the embryo and seed surface reduce the barrier to moisture and oxygen penetration into the embryo. Moreover, round, large seeds present handling difficulties to seed predators (Cole et al. 2011).

Seed moisture content is major factor affecting seed quality and longevity. Moisture content and longevity are negatively correlated, except at very low moisture levels (Ellis et al. 1988). Moist seeds usually germinate rapidly after sowing in open areas, which is a useful characteristic for candidate species of direct seeding (Tunjai 2005). However seed moisture content was not correlated with any of the germination variables in the study in Panama (Sautu et al. 2006).

The objectives of the present study were to (1) determine the effects of seed traits (size, shape, seed coat thickness and moisture content) on germination, seedling survival, establishment, and early growth in the harsh conditions prevalent in deforested sites and (2) to develop a system for species selection for direct seeding on degraded areas in southern Thailand. This study therefore tested the hypothesis that certain seed traits can be used to predict the suitability of native forest trees for inclusion in forest restoration projects by direct seeding.

Materials and methods

Study sites

Experiments were carried out in two southern Thailand Provinces. The Krabi (KB) site was situated next to an oil palm plantation at about 80 m elevation at the base of a hill slope and was dominated by the grass *Imperata cylindrica* (L.) P. Beauv. (Gramineae). The mean temperature was 26.9°C, with monthly averages ranging from 26.3°C in December to 27.9°C in April. Mean annual precipitation (1989–2006) was 1,772 (±61.30) mm, most of which falls between May and October.

The Nakhon Si Thammarat (NST) site was on an abandoned area, close to secondary forest, at about 100 m elevation. The site was dominated by the grass *Chrysopogon aciculatus* (Retz.) Trin. (Gramineae), a native in the tropical parts of Asia including Thailand. The mean temperature was 27.5°C, with monthly averages ranging from 25.8°C in December to 28.5°C in May. Mean annual precipitation (1989–2008) was 1,941 (±87.28) mm, mostly between October and December.

Seed collection

Seeds of 19 indigenous lowland evergreen forest tree species were collected, at most, 2 months prior to sowing at each study site. Most seeds were collected from the ground and

Table 1 List of study species, collection and storage methods in both sites

Site[a]	Species[b]	Family	Collection method[c]	Storage methods (days storage)
KB	*Archidendron clyperia* (Jack) Niels.	Leguminosae	G	Open air, 27°C (9)
	Artocarpus dadah Miq.	Moraceae	G	Open air, 27°C (2)
	Callerya atropurpurea (Wall.) Schot	Leguminosae	G	Open air, 27°C (21)
	Cinnamomum iners Reinw. ex Bl.	Lauraceae	G	Refrigerator, 10°C (3)
	Garcinia hombroniana Pierre	Guttiferae	G	Open air, 27°C (4)
	Garcinia merguensis Wight	Guttiferae	G	Open air, 27°C (3)
	Lepisanthes rubiginosa (Roxb.) Leenh.	Sapindaceae	C	Refrigerator, 10°C (29)
	Litsea grandis (Wall. ex Nees) Hk.f.	Lauraceae	G	Refrigerator, 10°C (9)
	Pajanelia longifolia (Willd.) K. Sch.	Bignoniaceae	C	Open air, 27°C (60)
	Palaquium obovatum (Griff.) Engl.	Sapotaceae	G	Open air, 27°C (4)
	Scolopia spinosa (Roxb.) Warb.	Flacourtiaceae	G	Open air, 27°C (2)
NST	*Callerya atropurpurea* (Wall.) Schot	Leguminosae	G	Open air, 28°C (20)
	Diospyros oblonga Wall. ex G. Don	Ebenaceae	G	Open air, 28°C (4)
	Diospyros pilosanthera Blanco	Ebenaceae	G	Open air, 28°C (12)
	Garcinia cowa Roxb.	Guttiferae	G	Open air, 27°C (18)
	Microcos paniculata L.	Tiliaceae	G,C	Open air, 28°C (10)
	Morinda elliptica (Hk.f.) Ridl.	Rubiaceae	G,C	Open air, 28°C (56)
	Peltophorum pterocarpum (DC.) Back. ex K. Hey.	Leguminosae	C	Open air, 28°C (17)
	Sandoricum koetjape (Burm.f.) Merr.	Meliaceae	G	Refrigerator, 10°C (56)
	Vitex pinnata L.	Verbenaceae	C	Open air, 28°C (18)

[a] Site were sown: KB, Krabi; NST, Nakhon Si Thammarat

[b] Voucher specimens stored at CMU Herbarium, Chiang Mai University

[c] Collection methods: (G) from the ground; (C) from the crown

stored in the open containers at room temperature (Table 1). Seeds of only 4 species were stored in the refrigerator at 10°C, to extend their viability until sowing time (Table 1). Seeds were sown only near the sites where they were collected.

Seed traits

The seed traits tested in this study were size, shape, coat thickness and moisture content, since previous studies showed that these traits are likely to affect germination and dormancy and therefore contribute significantly towards seedling establishment (Bewley and Black 1985; Grime et al. 1981; Doust et al. 2006; Liu et al. 2007; Yu et al. 2007).

Seeds were classified according to their mean dry mass as small (<0.01–0.099 g), intermediate (0.1–4.99 g) or large (>5 g) (Doust et al. 2006). Thirty seeds of each species were randomly selected and measured for length, width and thickness. The shape of diaspores was determined by the variance of three dimensions, i.e. length, width and height following Thompson et al. (1993) and Moles et al. (2000). Variance of three dimensions was grouped into three categories: round (<0.06), oval (0.06–0.09) and flat (>0.09). The seed coat thickness of thirty randomly selected seeds of each species was then measured at 3 or 4 points, depending on the seed shape, using a stereo microscope (Leica Application

Table 2 Seed traits of species used in the study

Species	Regeneration guild[a]	Size[b]	Shape[c]	Coat[d]	%MC[e]
Archidendron clyperia	Pioneer of stem exclusion	I	R	Tn	M
Artocarpus dadah	Late-successional non-dominants	I	R	M	M
Callerya atropurpurea	Late-successional non-dominants	L	R	Tk	M
Cinnamomum iners	Late-successional non-dominants	I	R	Tn	L
Diospyros oblonga	Late-successional non-dominants	I	O	M	L
Diospyros pilosanthera	Late-successional non-dominants	I	O	M	L
Garcinia cowa	Late-successional subcanopy	I	O	M	M
Garcinia hombroniana	Late-successional subcanopy	I	O	Tk	M
Garcinia merguensis	Late-successional subcanopy	I	O	M	L
Lepisanthes rubiginosa	Late-successional subcanopy	I	R	M	H
Litsea grandis	Late-successional subcanopy	I	R	M	M
Microcos paniculata	Pioneer of stem exclusion	I	R	Tk	L
Morinda elliptica	Pioneer of stem exclusion	S	F	M	M
Pajanelia longifolia	Pioneer of stem exclusion	S	F	Tn	H
Palaquium obovatum	Late-successional subcanopy	I	O	M	M
Peltophorum pterocarpum	Pioneer of stem exclusion	S	F	M	L
Scolopia spinosa	Late-successional subcanopy	S	R	Tn	M
Sandoricum koetjape	Late-successional non-dominants	I	R	Tk	M
Vitex pinnata	Late-successional subcanopy	I	R	Tk	L

[a] Regeneration guild (following criteria of Ashton et al. 2001)

[b] Seed size category based on seed weight: *S* small (<0.01–0.099 g); *I* intermediate (0.1–4.99 g); *L* Large (>5.0 g) (seed size category determined from mean of a random sample of no less than 20 seeds per species) (Doust et al. 2006)

[c] Seed shape: *R* round (variance < 0.06); O = Oval (variance = 0.06–0.09); *F* flat (variance > 0.09)

[d] Seed coat thickness: *Tn* Thin (< 0.01–0.099 mm); *M* moderate (0.1–0.49 mm); *Tk* Thick (>0.5 mm)

[e] %Moisture content: *L* low (0–35); *M* medium (36–70); *H* high (71–100)

Suite LAS ES version 1.4.0). Seed coats were classified as thin (mean < 0.01–0.099 mm), moderate (mean 0.1–0.49 mm) or thick (mean > 0.5 mm). Moisture content was determined for four replicates of 10–15 seeds (approx 5 g before drying) placed in an oven for 17 ± 1 h at 103 ± 3°C. The samples were then placed in a desiccator to cool for about 20 min before weighing. The moisture content was calculated using the ISTA formula (ISTA 2006; Schmidt 2007). Seed moisture contents were classified as low (mean 0–35%), medium (mean 36–70%) or high (mean 71–100%). All seed traits were presented in Table 2.

Experimental design and data collection

Direct seeding experiments were established in 2009 at the beginning of the wet seasons at both sites i.e. May at KB and September at NST. Weeds were cleared by tractor (without removing the roots of grasses and herbaceous) and four replicates of 40 seeds of each species (totally 160 seeds per species) were sown, with 11 species tested at KB (except *Callerya atropurpurea*, 5 replicates were sown) and 9 species at NST (except *Sandoricum koetjape*, 8 replicates were sown) (Table 1) in May and September, respectively.

Individual seeds spaced about 60 cm apart. Seeds were buried to an approximate depth of 3–45 mm depending on seed size, since reports show that burying results in higher establishment rates (Doust et al. 2006). No protective measures were put in place to prevent seed predation and seedling predation because seed exclusion had no effect on germination and median length of dormancy at both sites (Tunjai 2011). Therefore, seeds counted as not germinated also included those removed by seed and seedling predators.

Germination (defined as radical emergence and seed germination) was monitored weekly until 4 weeks had elapsed without any further seeds germinating, after a clear peak had occurred. Germination percentage and median length of dormancy (MLD) were calculated for each species. MLD was defined as the length of time between sowing and germination of half the seeds, which eventually germinated (FORRU 2008), for each replicate. The numbers of surviving seedlings at both sites were recorded, 1 year after sowing. In addition, height, root collar diameter (RCD), and crown width of surviving seedlings were measured. In this study, establishment is defined as the number of seedlings alive after 1 year expressed as a percentage of the number of seeds sown. Survival is defined as the number of seedlings alive after 1 year, expressed as a percentage of the number of seeds which germinated.

Statistical analysis

Pearson's product-moment correlation was first carried out, to detect any relationships among the various measured parameters; germination, MLD, seedling survival and establishment (Crawley 2007). Subsequently, a generalized linear model (GLM) was used to identify the impact of seed traits on each significant parameter and identify which seed traits most influenced. GLM was used because variances in proportion and count data are not constant (Crawley 2007). In addition, ANOVA was used to detect the influence of seed traits on growth (height, RCD and crown width) at 1 year after sowing. Post-hoc analyses for pair-wise comparisons of means were undertaken using Tukey's HSD test. Seed traits were used as explanatory variables and growth data were used as response variables.

The suitability of a species for direct seeding was viewed as a combination of both establishment and growth. Raw suitability scores were calculated from the mean establishment percentage of each species multiplied by mean sapling height after 1 year. Each raw score value was divided by the highest raw value and multiplied by 100 to get a rank suitability score. Pearson's product-moment correlation was carried out to detect relationships between the suitability score and seed traits.

For all statistical results presented below, "significance" was considered to be at $\alpha = 0.05$. All statistical analyses were performed using the statistical software R 2.11.1 (R Development Core Team 2010).

Results

Germination percentage, averaged across all species, differed significantly between the two study sites (47 and 59% at KB and NST, respectively) but survival percentage did not (23 and 32%). Seeds of all 19 species germinated but only 16 species established seedlings in the field, 1 year after seed sowing. Among species, establishment rates ranged from less than 10% to more than 40% (Fig. 1).

In general, species with higher establishment rates had large or intermediate-sized seeds, round or oval seeds and seeds with medium or low seed moisture content (Fig. 2).

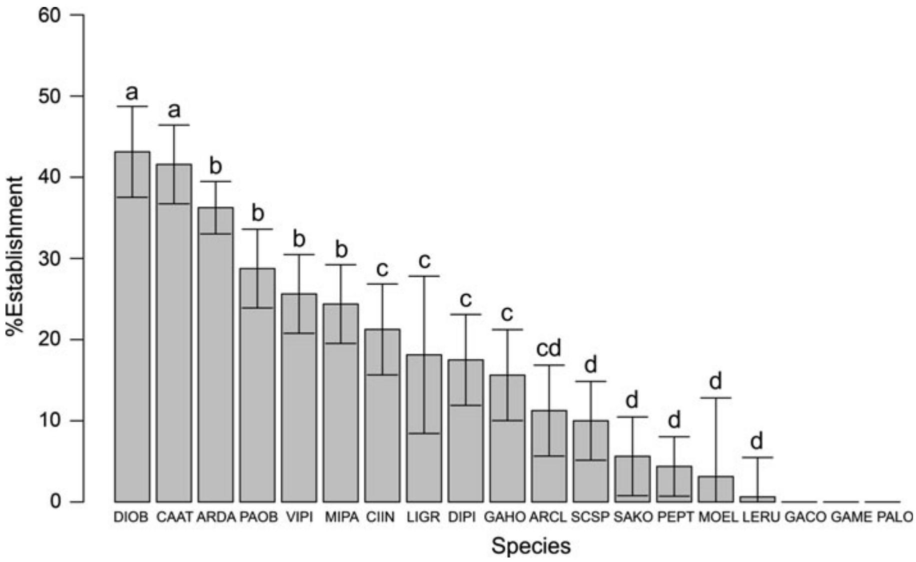

Fig. 1 Mean seedling establishment of 19 species; ARCL = *A. clyperia*, ARDA = *A. dadah*, CAAT = *C. atropurpurea*, CIIN = *C. iners*, DIOB = *D. oblonga*, DIPI = *D. pilosanthera*, GACO = *G. cowa*, GAHO = *G. hombroniana*, GAME = *G. merguensis*, LERU = *L. rubiginosa*, LIGR = *L. grandis*, MIPA = *M. paniculata*, MOEL = *M. elliptica*, PALO = *P. longifolia*, PAOB = *P. obovatum*, PEPT = *P. pterocarpum*, SAKO = *S. koetjape*, SCSP = *S. spinosa*, and VIPI = *V. pinnata*; vertical bars represent S.E. (n = 85)

The species could be divided into 4 clear groups (Table 3): (1) EF (establishment failure)–species that germinated but did not survive after 1 year; (2) LE (low establishment)–species with less than 10% establishment; (3) ME (moderate establishment)–species with establishment of 10–40% and (4) HE (high establishment)–species with establishment rates exceeding 40%. Species in the EF and LE groups were seemed unsuitable for direct seeding.

Impact of seed traits on the components of early success

Both seed germination and early seedling survival contribute to the early success of direct seeding, as determined by establishment percentage (defined above). Not surprisingly, therefore, germination was positively but weakly correlated with seedling establishment percentage ($r = 0.39$, $p < 0.001$, n = 85), and survival was positively and strongly correlated with seedling establishment percentage ($r = 0.84$, $p < 0.001$, n = 85), while no significant correlation was found between MLD and seedling establishment.

Seed traits that were associated with significantly higher germination were intermediate and large seed size, round shape, with low to medium moisture content. These seed traits were also associated with seedling survival, along with moderate to thick seed coat, and consequently affected the establishment of seedlings (Table 4).

Seeds of late-successional forest tree species tended to have two of the traits which were most strongly associated with high germination and survival, namely intermediate to large seed size and round seed shape, although moisture content and seed coat thickness was high variable. This contributed to the mean percentage establishment of such species being significantly double that of pioneer species (27 and 13%, respectively).

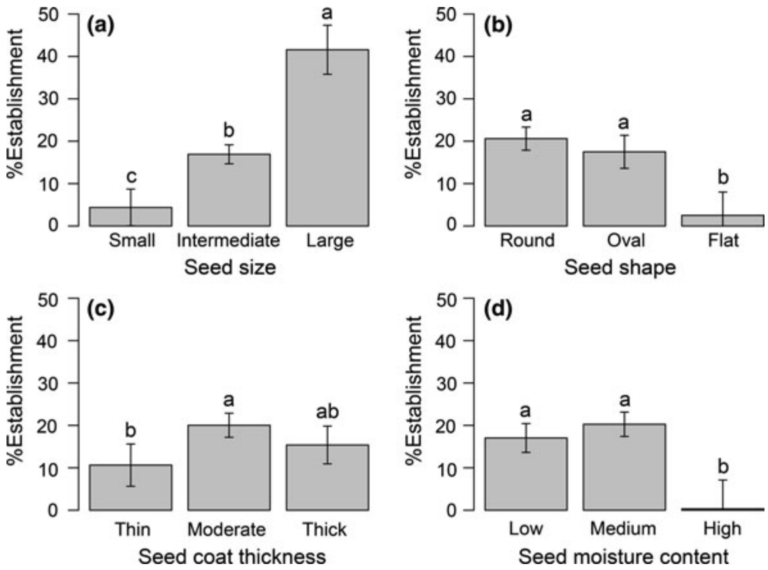

Fig. 2 Mean seedling establishment influenced by **a** seed size; **b** seed shape; **c** seed coat thickness; and **d** seed moisture content; vertical bars represent S.E. (n = 85)

Table 3 Groups of tested species by establishment success at 1 year after sowing

EF[a]	LE[b]	ME[c]	HE[d]
G. cowa	*L. rubiginosa*	*A. clyperia*	*C. atropurpurea*
G. merguensis	*M. elliptica*	*A. dadah*	*D. oblonga*
P. longifolia	*P. pterocarpum*	*C. iners*	
	S. spinosa	*D. pilosanthera*	
	S. koetjape	*G. hombroniana*	
		L. grandis	
		M. paniculata	
		P. obovatum	
		V. pinnata	

[a] *EF* Establishment failure, none of the seedlings survived

[b] *LE* Low establishment, establishment <10%

[c] *ME* Moderate establishment, establishment 10–40%

[d] *HE* High establishment, establishment >40%

Influence of seed traits on seedling growth

By the end of the study, seedlings germinated from seeds with thin seed coats had significantly larger RCD than those germinated from seeds with moderate or thick coats. Small seeds tended to give rise to seedlings with broader crowns, whereas flat seeds tended to produce taller seedlings with broader crowns (Fig. 3).

There was no relationship between MLD and the growth of direct-seeded seedlings 1 year after sowing. In general, seeds with shorter dormancy tended to be smaller, with thinner seed coats and higher moisture content than seeds with longer dormancy (Table 5).

Table 4 Means of germination and survival percentage affected by seed traits

Component	Seed traits	Classes (No. of species in each classes)	Mean[a] (SE)
%Germination	Size	Small (4)	40.0b (5.6)
		Intermediate (14)	54.9a (3.3)
		Large (1)	62.1a (3.4)
	Shape	Round (10)	57.4a (2.8)
		Oval (6)	51.2ab (6.6)
		Flat (3)	37.5b (6.3)
	Moisture content	Low (7)	48.4ab (5.4)
		Medium (10)	59.1a (2.8)
		High (2)	35.6b (6.5)
%Survival[b]	Size	Small (4)	10.3c (4.3)
		Intermediate (14)	26.1b (3.4)
		Large (1)	65.4a (6.0)
	Shape	Round (10)	32.4a (4.2)
		Oval (6)	24.7a (5.3)
		Flat (3)	11.4b (5.3)
	Coat	Thin (4)	12.0b (4.0)
		Moderate (10)	31.2a (4.2)
		Thick (5)	29.9a (6.4)
	Moisture content	Low (7)	30.1a (4.9)
		Medium (10)	30.0a (4.2)
		High (2)	0.9b (0.9)

[a] Means followed by the same letter do not differ ($\alpha = 0.05$)

[b] Survival is based on percentage of germinants, not seed sown

Using seed traits for species selection

Suitability scores were calculated for the 16 species that could survive 1 year after sowing (Table 6). Only seed coat thickness was significantly correlated with the suitability score ($r = 0.65$, $p < 0.01$, n = 15).

Discussion

Tree species with high suitability for direct seeding have seeds with high germination rates (small numbers of seeds would need to be sown); rapid germination (reduces the time available for seed predation and maximizes seedling growth period before dry season) and high seedling survival (Lamb 2011). Although some seed traits tested in this study were associated with high germination percentage and/or shorter dormancy, they did not guarantee successful seedling establishment.

In addition to high seedling recruitment, fast-growth is also needed for successful direct seeding, in order for the seedlings to out-compete surrounding vegetation (Engel and Parrotta 2001; Doust et al. 2008). Therefore both parameters were combined to calculate the suitability score. Seed coat thickness was significantly correlated with suitability score,

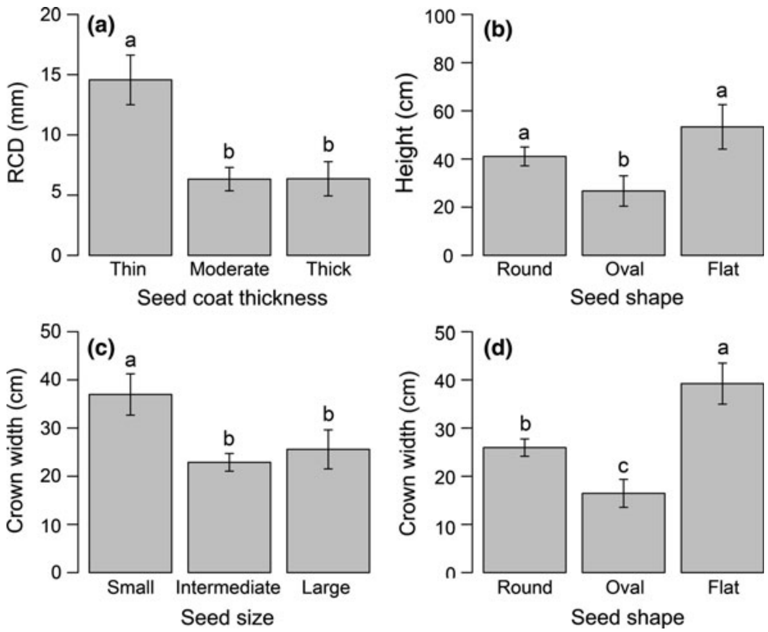

Fig. 3 Effects of seed traits on seedling growth and development **a** effects of seed coat thickness on final RCD; **b** effects of seed shape on final height; **c** effects of seed size on mean crown width; and **d** effects of seed shape on crown width; *vertical bars* represent S.E. (n = 61)

Table 5 Means of MLD (days) influenced by seed traits

Seed traits	Classes (No. of species in each classes)	Mean[a] (SE)
Size	Small (4)	46.1a (16.5)
	Intermediate (14)	38.4ab (3.8)
	Large (1)	131.2b (6.7)
Shape	Round (10)	44.4a (6.3)
	Oval (6)	56.6a (7.7)
	Flat (3)	57.4a (21.2)
Coat	Thin (4)	10.8a (0.7)
	Moderate (10)	66.3b (7.9)
	Thick (5)	40.2b (2.4)
Moisture content	Low (7)	60.4b (9.3)
	Medium (10)	48.9b (6.6)
	High (2)	11.0a (1.00)

[a] Means followed by the same letter do not differ ($\alpha = 0.05$)

and thus could be used to predict suitability of other species for direct seeding. All tested species with the seed coat thickness >0.40 mm tended to achieve the rank suitability score above 20 except 3 species; *A. dadah*, *C. iners* and *D. oblonga*.

Seeds with moderate and thick seed coats had significantly higher seedling survival and establishment percentage after the first year. Soil moisture content is an important factor

Table 6 Suitability score of studied species at 1 year after sowing

Species	Seed coat thickness (mm)	Establishment (%)	Height (cm)	Raw suitability score[a]	Rank suitability score (0–100)
A. dadah	0.13	36.25	83.03	3009.76	100.00
C. atropurpurea	1.34	41.57	28.97	1204.30	40.01
V. pinnata	0.57	25.63	44.29	1134.97	37.71
P. obovatum	0.43	28.75	34.95	1004.73	33.38
D. oblonga	0.31	43.13	20.57	887.13	29.47
M. paniculata	1.04	24.38	30.30	738.45	24.54
C. iners	0.08	21.25	31.16	662.13	22.00
G. hombroniana	0.52	15.63	40.90	639.06	21.23
L. grandis	0.13	18.13	30.34	549.95	18.27
A. clyperia	0.07	11.25	46.14	519.06	17.25
D. pilosanthera	0.29	17.50	14.03	245.47	8.16
S. koetjape	0.34	5.63	42.98	241.74	8.03
S. spinosa	0.09	10.00	24.06	240.63	7.99
P. pterocarpum	0.13	4.38	35.83	156.77	5.21
M. elliptica	0.15	3.13	45.44	142.01	4.72
L. rubiginosa	0.15	0.63	15.00	9.38	0.31

[a] Raw suitability score means establishment percentage multiply by height

affecting the success of seedling recruitment in degraded forest lands (Fenner and Thompson 2005), species with thin seed coat are therefore more susceptible to desiccation and contributed to less success on establishment.

Although seed size was not significantly associated to the suitability score, it was another component of establishment success along with seedling survival. Seed size is an important life history trait influencing regeneration success (Turnbull et al. 1999) through survival and growth (Moles et al. 2005; Lamb 2011). In this study, seeds with intermediate to large size and round shape showed excellent establishment. The key advantage of large seeds appears to be their tolerance of stresses since higher resources can be allocated to tolerate particular stresses such drought or shade, however this advantage does not appear uniformly under all conditions (Coomes and Grubb 2003; Muller-Landau 2010) or each stage of life cycle (Kleijn 2003). Seed size influences early after germination, for cotyledon-stage seedlings, survival is influenced mostly by stored reserves and by initial seedling size (Leishman and Westoby 1994; Saverimuttu and Westoby 1996) while later on, growth and survival are largely determined by seedling morphology and physiology (Grubb and Metcalfe 1996; Saverimuttu and Westoby 1996).

Remarkably, although they varied in seed size and seed coat thickness, all three Legume species (*A. clyperia*, *C. atropurpurea* and *P. pterocarpum*); that successfully established in the degraded sites showed excellent growth. This was probably due to their ability to fix atmospheric nitrogen by bacteria in their root nodules (Engel and Parrotta 2001).

Of the 14 species with intermediate-sized seeds, tested in this study, all had round seeds and high establishment percentages (e.g. *A. dadah*, *L. grandis* and *V. pinnata*). In addition, round intermediate-sized seeds are the common traits in this study and they tended to produce robust seedlings with relative high rates of survival and establishment. In contrast, flat- and small-seeded tend to have high fecundity but low stress-tolerance (Moles and

Westoby 2006; Muller-Landau 2010). These traits usually represent pioneer species with less probability of survival and establishment compared to late successional species which invest in few large offspring (Fenner and Thompson 2005).

Elongated or flattened seeded species tended to germinate immediately after collection and had high germination in a desertified grassland in northeastern Mongolia, China (Liu et al. 2007) while oval and round seeds had significantly higher germination and survival in this study. Compact and round seeds can easily penetrate cracks in the soil, and thus escape post-dispersal predation (Yu et al. 2007). They are less susceptible to seed desiccation, and therefore possibly contributed to the germination and establishment success. Liu et al. 2007 demonstrated that species with rounder and larger seeds tended to be superior colonist on bare areas.

Seed moisture content was not significantly related to the suitability score, however it had been mentioned as an indicator of seed maturity in several species (Edwards 1980; Shah et al. 2010; Tewari et al. 2011), for example, germination and moisture content of seeds were negatively correlated in Wild Cherry (*Prunus cerasoides* D. Don.) in lesser Himalayan zone (Tewari et al. 2011).

In addition, seed size, coat thickness and shape all influenced seedling growth. Seed traits that were negatively correlated with establishment tended to be positively correlated with growth. A positive effect plus a negative effect result in no net effect. So when calculating the suitability score these effects cancelled each other out. Species with small seeds created bigger crowns, whereas thin-coated seeds gave rise to seedlings with larger RCD's. Flat-seeded species showed bigger crowns and taller seedlings. Nevertheless, the rapid growth is known to be a habit of pioneer species that are less of stresses-tolerant (Muller-Landau 2010). Although there was no relationship between MLD and the growth of direct-seeded seedling, the species with small seeds tended to become dependent on external resources very quickly, and their priority may therefore be to photosynthesize as soon as possible (Van Ulft 2004). This enables them to develop roots quickly and so gain access to external sources of minerals and subsequently express better growth. Large amount of seeds will be needed if the species with these traits are selected to be sown.

Conclusions

Since the tree species richness of tropical forests is so high, the selection of tree species to include in forest restoration projects can be a bewildering process. The young stages trees (i.e. seeds and small seedlings) are much more vulnerable to environmental stress than containerized saplings, more usually planted for forest restoration projects. So direct seeding has a higher failure rate than conventional tree planting. A process to screen out those species most likely to fail in direct seeding trials, based on easily measured parameters, would therefore speed up the process of achieving effective forest restoration strategies, whether by direct seeding alone or by combining the technique with accelerated natural regeneration (ANR) or conventional tree planting (Lamb 2011). This paper shows that tree species with certain seed coat (>0.40 mm) have an acceptability high probability of being suitable for direct seeding than species selected at random. The native forest tree species, identified is being particularly suitable for direct seeding in S. Thailand were: *A. dadah*, *C. atropurpurea*, *V. pinnata*, *P. obovatum*, *D. oblonga*, *M. paniculata*, *C. iners* and *G. hombroniana*.

Acknowledgments The authors thank Suwit Somechue and Theerasak Konghor for help with field works. We are grateful for institutional support provided by Walailak University, especially the Ecology and

Biodiversity Program, School of Science and Chiang Mai University Herbarium and the Forest Restoration Research Unit (FORRU) at Biology Department, Faculty of Science. This work was financially supported by the TRF/BIOTEC Special Program for Biodiversity Research and Training grant BRT T-351014 and the Walailak University Fund. We also thank the Khlong Thom Nuea Sub-district Administration Organization and the Farm University, Walailak University for granting permission to establish experiments in their areas.

References

Aerts R, Maes W, November E, Negussie A, Hermy M, Muys B (2006) Restoring dry Afromontane forest using bird and nurse plant effects: direct sowing of *Olea europaea* ssp. *cuspidata* seeds. For Ecol Manag 230:23–31

Ashton MS, Gunatilleke CVS, Singhakumara BMP, Gunatilleke IAUN (2001) Restoration pathways for rain forest in southwest Sri Lanka: a review of concepts and models. For Ecol Manag 154:409–430

Badek B, Duijn Bv, Grzesik M (2006) Effects of water supply methods and seed moisture content on germination of China aster (*Callistephus chinensis*) and tomato (*Lycopersicon esculentun* Mill.) seeds. Eur J Agron 24:45–51

Balandier P, Frochot H, Sourisseau A (2009) Improvement of direct tree seeding with cover crops in afforestation: microclimate and resource availability induced by vegetation composition. For Ecol Manag 257:1716–1724

Bewley JD, Black M (1985) Physiology of development and germination in: seeds. Plenum Press, New York

Bonilla-Moheno M, Holl KD (2010) Direct seeding to restore tropical mature-forest species in areas of slash-and-burn agriculture. Restor Ecol 18:438–445

Campbell BD, Stafford DM, Ash AJ (1999) A rule-based model for the functional analysis of vegetation change in Australasian grasslands. J Veg Sci 10:723–730

Carmago JLC, Ferraz IDK, Imakawa AM (2002) Rehabilitation of degraded areas of central Amazonia using direct sowing of forest tree seeds. Restor Ecol 10:636–644

Cervantes V, Carabias J, Vazques-Yanes C (1996) Seed germination of woody legumes from deciduous tropical forest of southern Mexico. For Ecol Manag 82:171–184

Cole RJ, Holl KD, Keene CL, Zahawi RA (2011) Direct seeding of late-successional trees to restore tropical montane forest. For Ecol Manag 261:1590–1597

Coomes DA, Grubb PJ (2003) Colonization, tolerance, competition and seed-size variation within functional groups. Trends Ecol Evol 18:283–291

Crawley MJ (2007) The R book. Wiley, West Sussex

De Steven D (1991) Experiments on mechanisms of tree establishment in old-field succession: seedling emergence. Ecology 72:1066–1075

Doust SJ, Erskine PD, Lamb D (2006) Direct seeding to restore rainforest species: microsite effects on the early establishment and growth of rainforest tree seedlings on degraded land in the wet tropics of Australia. For Ecol Manag 234:333–343

Doust SJ, Erskine PD, Lamb D (2008) Restoring rainforest species by direct seeding: tree seedlings establishment and growth performance on degraded land in the wet tropics of Australia. For Ecol Manag 256:1178–1188

Edwards DGW (1980) Maturity and quality of tree seeds: a state-of-the-art review. Seed Sci Technol 28:625–657

Ellis RH, Hong TD, Roberts EH (1988) A low-moisture-content limit to logarithmic relations between seed moisture content and longevity. Ann Bot 61:405–408

Engel VL, Parrotta JA (2001) An evaluation of direct seeding for reforestation of degraded lands in central Sao Paulo state, Brazil. For Ecol Manag 152:169–181

Fenner M, Thompson K (2005) The ecology of seeds. Cambridge University Press, New York

FORRU (2006) Planting trees. In: Elliott S, Blakesley D, Maxwell JF, Doust S, Suwannaratana S (eds) How to plant a forest: the principles and practices of restoring tropical forests. Biology Department, Science Faculty, Chiang Mai University, Chiang Mai, pp 103–132

FORRU (2008) Propagating and identifying candidates framework. In: Elliott S, Blakesley D, Chairuangsri S (eds) Research for restoring tropical forest ecosystems: a practical guide. Biology Department, Chiang Mai, p 144

Garcia-Orth X, Martínez-Ramos M (2008) Seed dynamics of early and late successional tree species in tropical abandoned pasture: seed burial as a way of evading predation. Restor Ecol 16:435–443

Grime JP et al (1981) A comparative study of germination characteristics in a local flora. J Ecol 69:1017–1059

Grubb PJ, Metcalfe DJ (1996) Adaptation and inertia in the Australian tropical lowland rainforest flora: contradictory trends in intergeneric and intrageneric comparisons of seed size in relation to light demand. Funct Ecol 10:512–520

Hall JS, Ashton MS, Garen EJ, Jose S (2011) The ecology and ecosystem services of native trees: implications for reforestation and land restoration in Mesoamerica. For Ecol Manag 261:1553–1557

Hardwick K (1999) Tree colonization of abandoned agricultural clearings in seasonal tropical montane forest in nothern Thailand. Doctor of Philosophy. University of Wales, Bangor, p 168

Harris JA, Hobbs RJ, Higgs E, Aronson J (2006) Ecological restoration and global climate change. Restor Ecol 14:170–176

Hau CH (1997) Tree seed predation on degraded hillsides in Hong Kong. For Ecol Manag 99:215–221

Hooper E, Condit R, Legendre P (2002) Responses of 20 native tree species to reforestation strategies for abandoned farmland in Panama. Ecol Appl 12:1626–1641

ISTA (2006) International rules for seed testing, rules 2006. International Seed Testing Association, Zurich

Kleijn D (2003) Can establishment characteristics explain the poor colonization success of late successional grassland species on ex-arable land? Restor Ecol 11:131–138

Knowles OH, Parrotta JA (1995) Amazonian forest restoration: an innovative system for native species selection based on phenological data and field performance indices. Comm For Rev 74:230–243

Lamb D (2011) Ecological restoration. In: Lamb D (ed) Regreening the bare hills: tropical forest restoration in the Asia-Pacific region. Springer, New York, pp 325–355

Lamb D, Gilmour D (2003) Rehabilitation and restoration of degraded forests. IUCN, Gland, Switzerland and Cambridge, UK and WWF, Gland, Switzerland

Laurance WF et al (2011) Global warming, elevational ranges and the vulnerability of tropical biota. Biol Conserv 144:548–557

Leishman MR, Westoby M (1994) The role of large seed size in shaded conditions: experimental evidence. Funct Ecol 8:205–214

Liu Z, Yan Q, Li X, Ma J, Ling X (2007) Seed mass and shape, germination and plant abundance in a desertified grassland in northeastern Inner Mongolia, China. J Arid Environ 69:198–211

Manga VK, Sen DN (1995) Influence of seed traits on germination in *Prosopis cineraria* (L.) MacBride. J Arid Environ 31:371–375

Moles AT, Westoby M (2006) Seed size and plant strategy across the whole life cycle. Oikos 113:91–105

Moles AT, Hodson DW, Webb CJ (2000) Seed size and shape and persistence in the soil in the New Zealand flora. Okios 89:541–545

Moles AT, Ackerly DD, Webb CO, Tweddle JC, Dickie JB, Westoby M (2005) A brief history of seed size. Science 307:576–580

Muller-Landau HC (2010) The tolerance-fecundity trade-off and the maintenance of diversity in seed size. Proc Natl Acad Sci USA 107:4242–4247

Nepstad DC, Uhl C, Pereira CA, Cardosa da Silva JM (1996) A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. Oikos 76:25–39

Parrotta JA, Knowles OH (1999) Restoration of tropical moist forests on bauxite-mined lands in the Brazilian Amazon. Restor Ecol 7:103–116

R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Sautu A, Baskin JM, Baskin CC, Condit R (2006) Studies on the seed biology of 100 native species of trees in a seasonal moist tropical forest, Panama, Central America. For Ecol Manag 234:245–263

Saverimuttu T, Westoby M (1996) Seedling longevity under deep shade in relation to seed size. J Ecol 84:681–689

Schmidt L (2007) Seed testing. In: Czeschlik D (ed) Tropical forest seeds. Springer, Heidelberg, p 409

Shah S, Tewari A, Tewari B, Singh RP (2010) Seed maturity indicators in *Myrica esculenta*, Buch-Ham. Ex. D.Don.: a multipurpose tree species of subtropical-temperate Himalayan region. New Forests 40:9–18

Shankar U (2006) Seed size as a predictor of germination success and early seedling growth in 'hollong' (*Dipterocarpus macrocarpus* Vesque). New Forests 31:305–320

Sun D, Dickinson GR, Bragg AL (1995) Direct seeding of *Alphitonia petriei* (Rhamnaceae) for gully revegetation in tropical northern Australia. For Ecol Manag 73:249–257

Tewari B, Tewari A, Shah S, Pande N, Singh RP (2011) Physical attributes as indicator of seed maturity and germination enhancement in Himalayan Wild Cherry (*Prunus cerasoides* D. Don.). New Forests 41:139–146

Thompson K, Band SR, Hodgson JG (1993) Seed size and shape predict persistent in soil. Funct Ecol 7:236–241

Tunjai P (2005) Appropriate tree species and techniques for direct seeding for forest restoration in Chiang Mai and Lamphun provinces. Master of Science. Chiang Mai University, Chiang Mai, p 107

Tunjai P (2011) Direct seeding for restoring tropical lowland forest ecosystems in southern Thailand. Doctor of Philosophy. Walailak University, Nakhon Si Thammarat, p 216

Turnbull LA, Rees M, Crawley MJ (1999) Seed mass and the competition/colonization trade-off: a sowing experiment. J Ecol 87:899–912

Van Ulft LH (2004) The effect of seed mass and gap size on seed fate of tropical rain forest tree species in Guyana. Plant Biol 6:214–221

Woods K, Elliott S (2004) Direct seeding for forest restoration on abandoned agricultural land in Northern Thailand. J Trop For Sci 16(2):248–259

Yu S, Sternberg M, Kutiel P, Chen H (2007) Seed mass, shape, and persistence in the soil seed bank of Israeli coastal sand dune flora. Evol Ecol Res 9:325–340