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Source: Mountain Research and Development, 30(3) : 232-243

Published By: International Mountain Society

URL: https://doi.org/10.1659/MRD-JOURNAL-D-10-00031.1

Mountain Research and Development (MRD)
An international, peer-reviewed open access journal
published by the International Mountain Society (IMS)
www.mrd-journal.org

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Restoration of Former Grazing Lands in the Highlands of Laos Using Direct Seeding of Four Native Tree Species

Seedling Establishment and Growth Performance

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*Direct seeding has recently regained favor as an alternative method to conventional planting for restoration of degraded and/or abandoned sites. This study reports the establishment and growth performance of 2 pioneer (*Pinus kesiya *and* Schima wallichii*) and 2 later-successional (*Keteleeria evelyniana *and* Quercus serrata*) native trees broadcasted or buried on 14 former grazing lands in Laos. Seedling establishment was assessed 9 months after sowing; height, diameter growth, and mortality were measured 1, 3, and 5 years after direct seeding and subjected to analysis of variance. Significant interspecies and intersite variations were detected for most of the measured parameters ($P < .05$). Seedling establishment success was better for buried seeds of* Q. serrata *(49–65%) and* K. evelyniana *(20–59%) than for broadcasted seeds of* P. kesiya *(13–50%),* S. wallichii *(3–34%), and* K. evelyniana *(6–22%). Intersite variation might be related to topography-induced microhabitat conditions. The annual rate of mortality, averaged over all sites, was significantly ($P < .0001$) high for* S. wallichii *(38 ± 1%) followed by* P. kesiya *(30 ± 2.0%),* Q. serrata *(29 ± 2%), and* K. evelyniana *(22 ± 4%). The 2 pioneer species achieved better diameter and height growth than the later-successional species. We conclude that direct seeding seems to be possible for rehabilitation of abandoned sites, provided that the seeds are buried to avoid the risk of seed desiccation and predation; the seeding rate of pioneer species is reduced to avoid a high mortality rate, and species-site matching is well defined to minimize topography-induced changes in a microhabitat.*

Keywords: *Reforestation; seedling emergence; seedling survival;* Pinus kesiya*;* Schima wallichii*;* Keteleeria evelyniana*;* Quercus serrata*; Laos.*

Peer-reviewed: *May 2010* ***Accepted:*** *June 2010*

Introduction

Tropical forests in southeast Asia have the highest relative rate of net forest loss (0.71%) and degradation (0.42%) in the humid tropics (Achard et al 2002) and could lose up to three quarters of their original forests and almost half their species by the year 2100 (Brook et al 2003). In Lao People's Democratic Republic alone, it has been estimated that 6.5 million ha of forests are affected by swidden agriculture (Messerli et al 2009), and industrial logging may become a more serious threat in the future as timber companies look for new sources of raw material (Thapa 1998). Laos is one of the biologically richest countries in the region, because it sits on the boundaries of the Himalayan, Indo-Malayan, and Chinese regions, and ongoing deforestation has made numerous flora and fauna vulnerable and even extinct (Myers 1992). Because three fourths of the total area is mountainous, deforestation and shifting cultivation have accelerated the pace of soil erosion, land degradation, and siltation (Lao–ADB 1995). The Lao government has planned to increase the national forest cover to 70% by the year 2020 through establishment of plantations and natural regeneration of degraded areas, including fallow forests, as stipulated in the Forestry Strategy 2020 document.

Restoration of forests can be achieved through passive (native recolonization) or active (reforestation) mechanisms. There is ample evidence that, if left alone, abandoned agricultural land will develop into secondary forest (Aide et al 2000; Finegan and Delgado 2000; Castro Marin et al 2009; Sovu et al 2009), but the recovery may take up to several decades to develop a closed canopy (Holl 2007), and it could result in species composition that fails to meet management objectives (Brown and Lugo 1990; Aide et al 2000; Hooper et al 2005). Successful establishment of later successional forest species in deforested areas has proven difficult throughout the tropical world because of the short-lived nature of tropical forest seeds and the

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inability to form viable seed banks (Teketay and Granstrom 1997; Gonzalez-Rivas et al 2009). Thus, availability of propagules is often the major factor limiting forest recovery in abandoned areas, particularly for later-successional species (Guariguata and Pinard 1998; Holl et al 2000; Zimmerman et al 2000; Gonzalez-Rivas et al 2009). In this case, planting seeds or seedlings (active restoration) of these target species is essential to ensure their presence and to expedite the recovery process (Martinez-Garza and Howe 2003; Bonilla-Moheno and Holl 2009).

Direct seeding for reforestation is an age-old practice that has recently regained favor because of the high costs of raising seedlings in nurseries (Hardwick et al 1997; Woods and Elliott 2004). It is an easier, simpler, and less-expensive technique than planting seedlings and has increasingly being adopted in restoration of degraded tropical lands (Hardwick et al 1997; Engel and Parrotta 2001; Cabin et al 2002; Camargo et al 2002; Woods and Elliott 2004; Garcia-Orth and Martinez-Ramos 2008). Despite its potential as a less-expensive method of restoration, direct seeding is often considered to be less reliable (Brown and Lugo 1990) and also challenging. Seed germination and seedling establishment are precarious stages in the life cycle of plants (Vieira and Scariot 2006), and mortality at each stage can be caused by different factors, such as seed predation by granivores, herbivores, competition, and abiotic factors (extreme temperatures, frost, drought, and sun scorch). These drawbacks can be circumvented by choosing species suitable for direct seeding (Engel and Parrotta 2001), seeding method (Woods and Elliott 2004), timing of seeding (Vieira et al 2008), seed treatments that prevent seed predation (Birkedal 2010) and desiccation (Woods and Elliott 2004), and by a combination of these approaches.

To date, the major approach to forest restoration in Laos has been based on planting nursery-grown seedlings, which is labor and capital intensive, because it requires a substantial input from seed collection and from raising seedlings in the nursery to planting and maintaining planted seedlings until they can establish and grow independently (Hardwick et al 1997; Woods and Elliott 2004). Thus, seedling planting is not appealing to small landholders. Direct seeding, as a cost-saving approach for forest restoration, has not been tested in Laos. Therefore, a study was designed to evaluate seedling establishment and subsequent growth of 4 native species, *Schima wallichii* Choisy, *Quercus serrata* Thunb., *Pinus kesiya* Royle ex Gordon, and *Keteleeria evelyniana* Beissn, directly seeded on 14 former grazing lands in Xieng Khouang Province in the north-central plateau of Laos.

The species tested in this study are economically valuable as sources of timber and pulp and ecologically important species in the mountain forests of southeast Asia (Lehmann et al 2003; Costa e Silva and Graudal 2008). Seeds were sown by using 2 direct seeding methods: broadcast (even distribution of seeds over the whole area without covering with soil) and burial of seeds. Seeds of *P. kesiya* and *S. wallichii* were directly broadcasted on ploughed fields to mimic the process of natural seed dispersal by wind and because of the light requirement for germination of these pioneer species. Seeds of *K. evelyniana* were sown by using both methods, because the small-winged seeds are dispersed by wind, but seedlings thrive best in semishade conditions. Seeds of *Q. serrata* were buried because of their sensitivity to desiccation and seed predation by mice. Planting sites were selected in cooperation with the villagers and varied in terms of slope, proximity to the remaining forest fragments and microclimate, and land-use history, which are expected to influence seedling establishment and growth directly or indirectly. Assessment was carried out 9 months after direct seeding for seedling establishment, for stem density 1, 3, and 5 years after sowing, and for height and diameter after 3 and 5 years.

Material and methods

Study area

The study area is located in Xieng Khouang Province, most commonly known as the intriguing "Plain of Jars," in north-central Laos (19°06′28″–19°55′58″N; 102°39′00″–103°11′00″E), about 173 km from Vientiane, the capital (Figure 1). It is characterized by mountainous topography, with altitudes that vary between 1000 and 1100 m above sea level. The area has a typical tropical monsoon climate, with distinct rainy (May to October) and dry (November to April) seasons. Based on data collected by the Department of Meteorology in Xieng Khouang Province from 2002 to 2006, the mean (± SE) annual rainfall was 1467.96 ± 137.63 mm. Mean daily temperature during this period was 20.40°C ± 0.16. The relative humidity varied between seasons and was about 71 ± 0.63%. The mean annual wind speed at the site was 3.12 ± 0.16 m/s and was the highest encountered at the country level.

The geological formations consist mainly of a yellow-red lateritic loamy soil derived from quartz with pH varying between 3 and 5. The hills around the plain consist mainly of sandstone, granite, and schist, with medium-rich loams. Xieng Khouang Province offers the awesome beauty of elevated green mountains, luxuriant valleys, and rugged karst formations. The major natural forest types are pine forests (Lehmann et al 2003), mixed conifer–broadleaved forests, moist evergreen forests of Fagaceae and Lauraceae, dry evergreen hill forests, riverine forests, swamp forests, and dry deciduous forests. The main pine species are *P. kesiya*, *Pinus merkusii* Jungh. & de Vriese, and *K. evelyniana*. The main broadleaved species are *S. wallichii*, *Alstonia rostrata* Fischer, and *Q. serrata*.

Species description

The species investigated in the present study, *S. wallichii*, *Q. serrata*, *P. kesiya*, and *K. evelyniana*, were all selected

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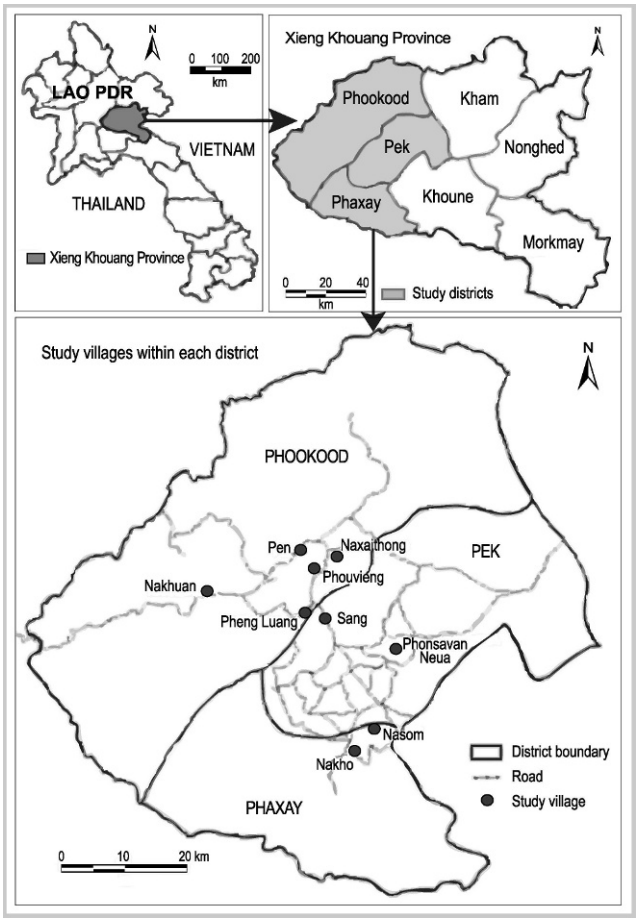
FIGURE 1 Location of the study sites. (Map by Issa Ouedraogo)



based on their economic and ecological values as well as availability of seeds during the period before trial establishment. Only tree species were used, because the study was primarily concerned with establishing species for initial site capture and accelerating tree colonization. The species have a diversity of ecological attributes, including a range of seed sizes and dispersal mechanisms, and represent both early pioneers (*P. kesiya* and *S. wallichii*) and later-successional species (*K. evelyniana* and *Q. serrata*). The species used in the present study are also highly esteemed for their high-quality timber and non-timber products (Table 1).

Rehabilitation trials

In May 2001, 29.8 ha of rehabilitation plots were established by using direct seeding by the Namgum Watershed Cooperation Project (NAWACOP) on former grazing lands in Xieng Khouang province in Phookood, Pek, and Phaxay districts at 14 sites distributed within 9 villages (Figure 1). Seeds of *K. evelyniana* were sown at all the sites, *P. kesiya* and *S. wallichii* at 10 sites, and *Q. serrata* at 5 sites (Table 2), because of the limitations of local seed sources. A soil survey carried out to estimate pH and nitrogen, phosphorus, and potassium content indicated no significant difference between the sites. However, the sites differ in terms of microclimate, land-use history and slope. The reforested area of Jar2, with a slope of 15% and located close to the village, was more intensively used for pasture than the sites at Nahi and Nakhuan. The reforested area at Nahi has a slope of 25% and is surrounded by more trees and forest. At Nakhuan, the reforested plots were nearly flat (0–10%) and located close to the village and the remaining forest fragment. The sites at Nasom village are flat and located far away from the road and villages, whereas Sui (flat) and Nongnam (foot of the mountain) are close to the road. Demo, Nayum, and Khangyum are located close to rivers on flat terrain, whereas School lies in the valley.

Seeds for the rehabilitation trial were collected by hand from several mother trees in natural forests in close proximity to the experimental sites to ensure that seed stocks were of local provenance. Seeds were collected in 2000 for *K. evelyniana* and *Q. serrata*, and, in 2001, for *P. kesiya* and *S. wallichii*. The seed bulk was cleaned to remove dehiscent capsules and fleshy parts and was stored at ambient conditions for 6 months. Before sowing, the open plots were ploughed to prepare a tilt suitable for sowing and to remove existing vegetation, thereby reducing competition and seed predation by granivores. Seeds were sown by using 2 direct seeding techniques, namely even-handed broadcasting (BC) for *P. kesiya*, *S. wallichii*, and *K. evelyniana*, and sowing with loose soil cover (seed burial) to a maximum depth of 0.5 cm (SB) for *K. evelyniana* and *Q. serrata*. Seeds of *Q. serrata* were only sown with SB to prevent predation by rodents because of the high nutritious value of the seeds and also to preserve seed moisture content because of high seed weight (350 seeds/kg). In SB methods, seeds were sown along the furrows at intervals of 30 cm.

For examining seedling establishment, 1 kg of seeds from each species was seeded on an area of 0.25 ha at each site. Seeds of the 4 species were sown mixed. The remaining area at each site was sown with varying amounts of seeds per species (Table 2). The number of seeds sown at each site was not uniform because of the limited availability of seeds from each species in the close-by natural forest stands.

Data collection

Nine months after sowing (February 2002), 4 sample plots (4 × 4 m) were established to count the number of seedlings that emerged. First, each 0.25-ha site was divided into 4 plots (25 × 25 m) and then 4 × 4-m sampling plots were established in the middle of the plots to avoid edge effects. Seedling emergence was calculated as the proportion of the number of seedlings emerged to the number of viable seeds sown per kilogram. Before

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TABLE 1 Growth habit, ecological attributes, economic importance, and distribution of the species examined in the study. (Source: Lehmann et al 2003)

Species	Common/local name	Family	Leaf phenology	Seed size
S. wallichii	Needle wood; *mee*	Theaceae	Evergreen	Small (< 0.01g)
Q. serrata	Oak; *ko khae*	Fagaceae	Deciduous	Medium (0.1–5.0 g)
P. kesiya	Yellow pine; *peak sam bai*	Pinaceae	Evergreen	Small (< 0.01 g)
K. evelyniana	Fir; *hing*	Pinaceae	Evergreen	Small (< 0.01 g)

TABLE 1 Extended.

Species	Dispersal vector[a)]	Structural characteristics	Wood uses	Ecological distribution
S. wallichii	Wd	Medium to large tree growing to 47 m in height; bole cylindrical, branchless, Dbh up to 1 m	Heavy hard wood used for construction, pulp, firewood	Pioneer species supporting wide range of climates, habitats and soils; altitude: up to 2400 m; mean annual temperature: from 0–5° to 37–45°C; mean annual rainfall: 1400–5000 mm
Q. serrata	M	Oak tree growing to 15 m in height and 1 m Dbh	Very hard wood, strong, red-brown in color. Used for construction	Later-successional species, deciduous forests below 100–2000 m; grows in wet yellow-red ferralitic, rich loamy and calcareous soil in semishade (light woodland) or no shade
P. kesiya	Wt, Wd	Coniferous tree 40 m tall and 1 m Dbh with straight, cylindrical bole	Soft and light timber used for construction, paper pulp	Pioneer species, wet climate, temperature 19–20°C, subtropical, with a distinct dry and rainy season; altitude: 1000–1500 m; high light demand and drought tolerance
K. evelyniana	Wt, Wd, M, B	Coniferous tree up to 40 m height and 1 m Dbh	Hard wood used in construction, railroad ties, mine timbering	Later successional species, wet climate, subtropical, with a distinct dry and rainy season, grows at elevations above 600 m and is shade intolerant, prefers neutral or limestone soils

[a)] Dispersal vector: Wd, wind; M, mammals; Wt, water; B, birds.

sowing, the number of seeds per kilogram was estimated at 35,000, 250,000, 7000, and 350 for *P. kesiya*, *S. wallichii*, *K. evelyniana*, and *Q. serrata*, respectively. Subsequent assessment of growth performance of the species was carried out at 3 sites only (Jar2, Nakhuan, and Nahi), because these sites were well protected from disturbances by livestock grazing and well managed compared with the other sites. Height and root collar diameter of seedlings were measured after 3 years, whereas sapling height and diameter at breast height (Dbh) were measured after 5 years on 10 plots established randomly at each site by using graduated pole and caliper. To do this, first each rehabilitation site was gridded (5 × 5 m) and numbered, and then 10 plots were randomly selected for growth assessment over time. Stem density was also counted 1, 3 and 5 years after sowing on these sample plots.

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TABLE 2 Amount of seeds (kg/ha) of 4 native species directly seeded in different sites and villages of Xieng Khuang plateau, Laos.

Villages	Sites	Area (ha)	Sowing method	*P. kesiya*	*S. wallichii*	*K. evelyniana*	*Q. serrata*
Nakho	Jar2	3	BC	2.9	1.2	20	–
		2	SB	–	–	22.8	230
Nakhuan	Sui	1	BC	3	3	54	240
Nakhuan	Nakhuan	3	BC	5.7	1.8	24	163
Nasom	Nagam1	1	BC	3	1.5	40	–
Nasom	Nagam2	1	BC	3	1.5	30	–
Nasom	Nagam3	1	BC	3	1.5	40	–
Nasom	Nagam4	0.6	SB	–	–	50	–
Naxaithong	Nayum	0.5	SB	–	–	90	–
Naxaithong	Khangyum	0.5	SB	–	–	90	–
Pen	School	2	BC	5	1.25	42.5	143
Phengluang	Junction	1	SB	–	–	63	–
Phonsavan N.	Nongnam	10	BC	2.5	2.2	31	–
Phouvieng	Nahi	2.5	BC	8	2.1	26	287
Sang	Demo	0.7	BC	5.7	2	20	–

Data analysis

Seedling establishment, stem density (number of individuals/ha), and height and diameter increment for each species were computed for each plot. The annual rate of mortality was calculated by using the following formula:

$$m_i\,\% = \left[\frac{(\mathrm{N}_0 - \mathrm{N}_\mathrm{t})}{\mathrm{N}_0 \times \Delta t}\right] \times 100$$

where m_i represents annual mortality rates; N_0 and N_t, the total number of individuals 1 (t_0) and 5 (t_i) years after sowing, respectively; and Δt, the number of years between 2 sampling dates, t_0 and t_i.

Two-way analysis of variance (ANOVA) was performed to examine differences among species and sites. Before the analysis, variables expressed as a percentage (seedling establishment) were transformed by an arcsine function to ensure normality. Descriptive statistics presented are of original untransformed data. Because the species × site interaction was significant, 1-way ANOVA was performed separately for each species. The results of the statistical analyses were considered significant if $P < .05$. Significant differences were further compared by using Tukey Honestly Significant Difference multiple comparisons test. For *K. evelyniana*, which was sown by using broadcasting and seed burial methods, a pairwise *t*-test was performed to examine the effect of direct seeding methods on the studied parameters. The same test was used to compare seedling establishment of *K. evelyniana* and *Q. serrata*, which were sown by using seed burial as a direct seeding method. All statistical analyses were performed by using the SPSS 15 software package (SPSS 15 for Windows, Release 2006 Chicago: SPSS Inc).

Results

Seedling establishment

The 2-way between-groups analysis of variance indicated that, 9 months after direct seeding, there was a significant difference between species ($P < .001$) for seedling establishment by using the BC seeding method. Seedling establishment was better for *P. kesiya* (38%) than for *S. wallichii* (14%) and *K. evelyniana* (13%), which were similar. For all species, there was a conspicuous difference in seedling establishment between sites ($P < .001$). Compared with other sites, School (32%), Nagam2 (29%), Nahi (27%), Nagam3 (25%), Nongnam (22%), and Sui (22%) recorded the best seedling establishment, whereas the worst seedling establishment success was recorded at Nagam1 (9%). The interaction between species and sites was also significant ($P = .046$). For *K. evelyniana*, seedling establishment success was higher at Nagam2 (21%), Nagam3 (22%), and Nahi

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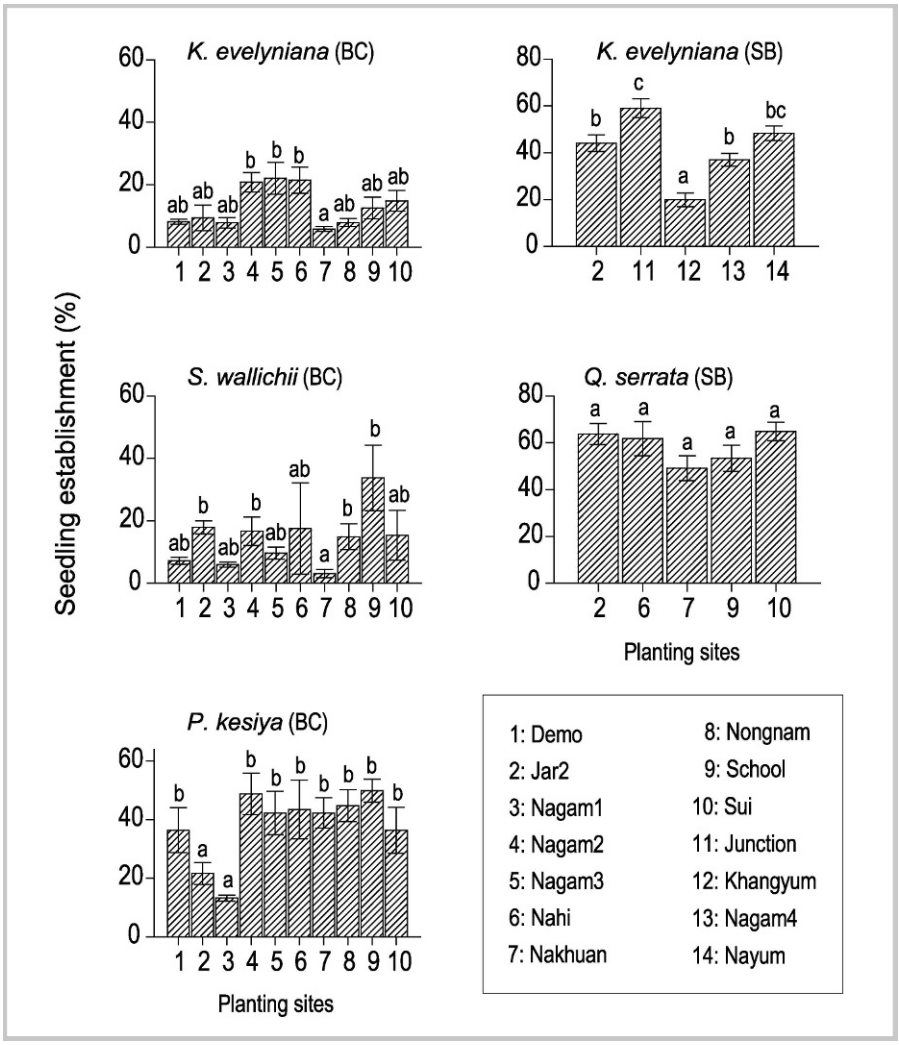
FIGURE 2 Seedling establishment success (in %) of 4 native tree species 9 months after direct seeding (mean ± SE). Bars with different letter(s) are significantly different.



(21%) than at Nakhuan (6%); that of *S. wallichii* was higher at School (34%) than at Nakhuan (3%); and that of *P. kesiya* was more than 40% at all sites except Jar2 (22%); whereas, the buried seeds *K. evelyniana* had higher seedling establishment success at Junction (59%) than at Khangyum (20%); *Q. serrata* established well (49–65%) at all sites (Figure 2). Pairwise *t*-tests ($t = -4.06$, df = 36, $P = .0002$) indicated that buried seeds of *K. evelyniana* recorded higher seedling establishment (42 ± 3%) than broadcasted seeds (13 ± 1%). For species established with the seed burial method, seedling establishment was significantly ($t = 11.87$, df = 19, $P < .0001$) higher for *Q. serrata* (59 ± 3%) than for *K. evelyniana* (42 ± 3%).

Nine months after sowing, seedling height differed significantly with respect to sites ($P < .001$), species ($P < .001$), and their interaction ($P < .001$). For *K. evelyniana* established by broadcasting, the mean height (± SE) was higher at Demo (7.5 ± 0.5 cm) than at Nahi (4.8 ± 0.9 cm) and Nongnam (4.8 ± 0.3), whereas that established by the seed burial method was similar, ranging from 7.3 ± 0.3 cm to 8.0 ± 0.6 cm (Figure 3). Seedling height was more than double at Nahi (16.8 ± 1.4 cm) than at School (7.3 ± 0.5 cm) for *P. kesiya*, at Sui (23.5 ± 0.7 cm) than at Nongnam (10.3 ± 0.6 cm) and School (10.5 ± 0.7 cm) for *S. wallichii*, whereas *Q. serrata* had similar seedling height across all sites (Figure 3).

Mortality

The stem density (stem/ha) of the 4 species used in a mixed direct seeding decreased with increasing ages (Figure 4). The stem density ha^{-1} (mean ± SE) across all sites was 24,373 ± 1553; 9493 ± 616; and 5733 ± 289 after 1, 3 and 5 years of sowing, for *P. kesiya*; 46,040 ± 1815;

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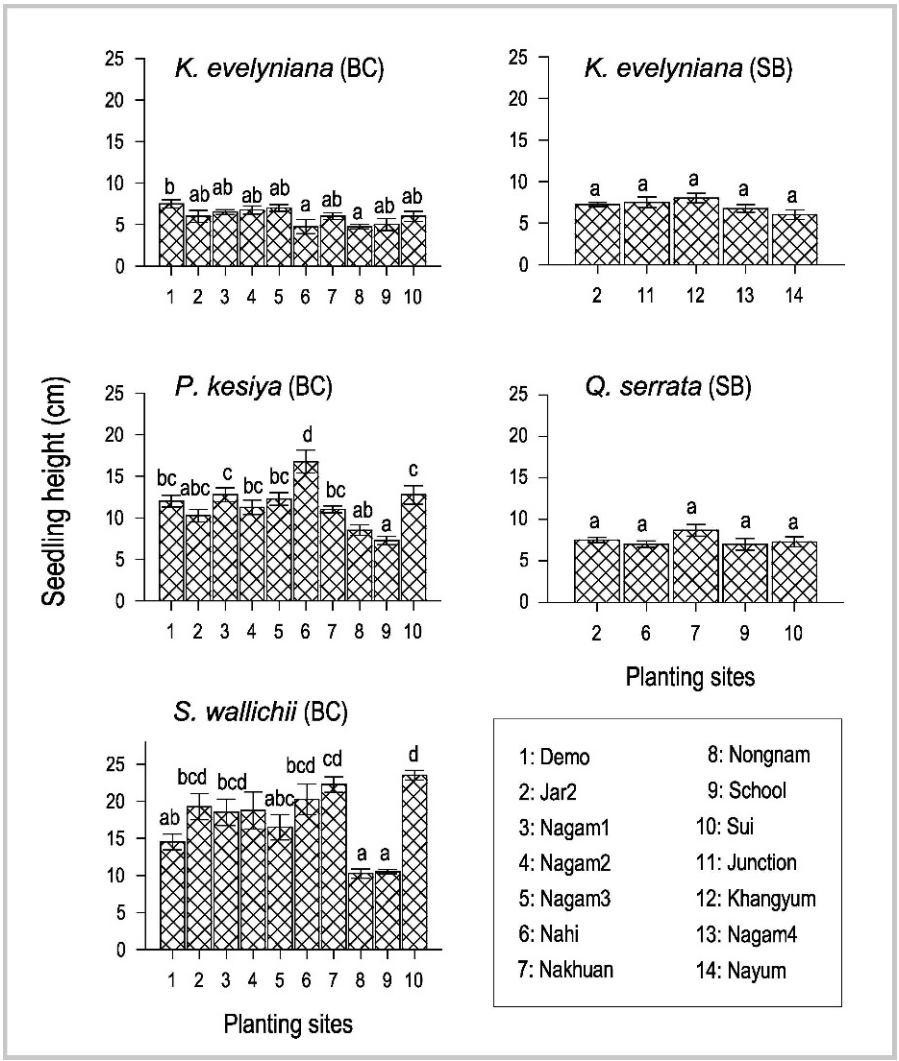
FIGURE 3 Seedling height (in cm) of 4 native tree species 9 months after direct seeding (mean ± SE). Bars with different letter(s) are significantly different.



10,653 ± 401; and 5920 ± 281 for *S. wallichii*; 4620 ± 164; 2440 ± 166 and 1573 ± 178 for *K. evelyniana*, whereas that of *Q. serrata* was 9960 ± 456; 4000 ± 178 and 2200 ± 183 after 1, 3, and 5 years of sowing, respectively. During the first 3 years after sowing, the annual rate of mortality, averaged over all sites, was significantly ($P < .0001$) high for *S. wallichii* (38 ± 1%) followed by *P. kesiya* (30 ± 2.0%), *Q. serrata* (29 ± 2%), and *K. evelyniana* (22 ± 4%).

When examining each species separately, the annual rate of mortality during the same period did not vary significantly ($P = .235$) among sites for *P. kesiya*, whereas, a significant difference was observed for *S. wallichii* ($P = .008$), *K. evelyniana* ($P = .013$), and *Q. serrata* ($P = .017$). Mortality was lower at Jar2 (35 ± 1%) than at Nakhuan (40 ± 1%) and Nahi (39 ± 1%) for *S. wallichii* (Figure 5). Similarly, mortality was lower at Jar2 (12 ± 5%) than at Nakhuan (26 ± 4%) and Nahi (28 ± 3%) for *K. evelyniana*, whereas mortality was lower at Nakhuan (23 ± 3%) than at Nahi (34 ± 1%) for *Q. serrata* (Figure 5). During the subsequent assessment period (3–5 years after sowing), the variation in the annual rate of mortality among sites was significant ($P = .011$) for *P. kesiya* only, and it was lower at Jar2 (13 ± 3%) and Nakhuan (14 ± 3%) than at Nahi (25 ± 2%). There was a decreasing tendency for mortality with increasing time for all species (Figure 5).

Growth performance

Assessment of seedling growth performance after 3 years of sowing revealed significant differences among sites and species and their interaction in root collar diameter and shoot height ($P < .0001$ for both seedling traits). Among restoration sites, seedling growth was better at Nakhuan

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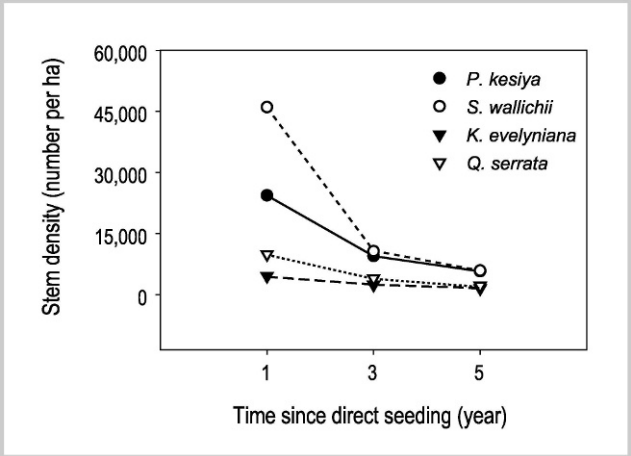
FIGURE 4 Mean stem density (number/ha), averaged overall sites, of 4 native tree species 1, 3, and 5 years after direct seeding.



than at Nahi and Jar2. *K. evelyniana* and *Q. serrata* recorded the lowest values for both root collar diameter and shoot height, whereas *P. kesiya* and *S. wallichii* had the highest root collar diameter, and *S. wallichii* had the longest seedlings compared with other species (Figure 6A). Further assessment of growth at the age of 5 years showed that diameter at breast height of saplings differed significantly among species, sites, and their interaction ($P < .0001$). Sapling diameter was the biggest for *P. kesiya* and at Nakhuan and Nahi, whereas the lowest value was recorded for *K. evelyniana* and at Jar2 (Figure 6B). Total height at the age of 5 years was also significantly higher for *P. kesiya* and *S. wallichii* than for the other species, but no significant difference was observed among rehabilitation sites.

Discussion

Species tested in the present rehabilitation trial showed a striking difference in seedling establishment success where buried seeds of *Q. serrata* and *K. evelyniana* had better establishment success than broadcasted seeds of *P. kesiya*, *S. wallichii*, and *K. evelyniana*. The success of direct seeding hinges on several factors. First, open sites are often characterized by higher light intensity, lower surface soil moisture, and fluctuation in diurnal temperature regime (Bullock 2000). Thus, the full sunlight in open pastures increases soil temperature and results in seed desiccation during dry spells in the wet season. Seeds of *K. davidiana* (franchet) beissner var. formosana, a close relative of the species investigated in our study, are desiccation sensitive and lose their viability when the moisture content decreases to 10–12% (Yang et al 2006). In their study of direct seeding on abandoned agricultural land in northern Thailand, Woods and Elliott (2004) found that seed burial prevents desiccation of seeds and

FIGURE 5 Annual mortality rate (%) of 4 native tree species sown at three sites (mean ± SE). Bars with different letter(s) are significantly different.

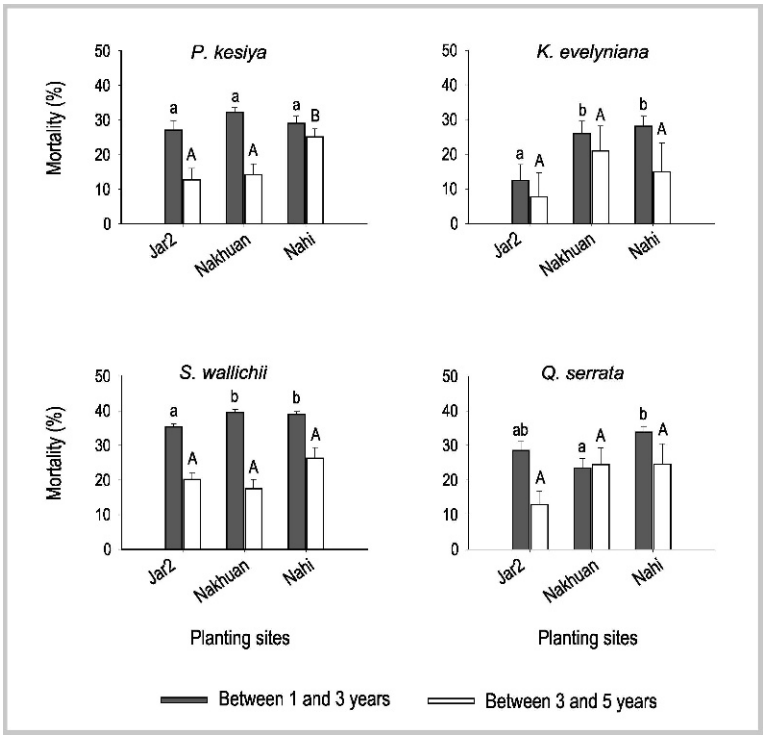


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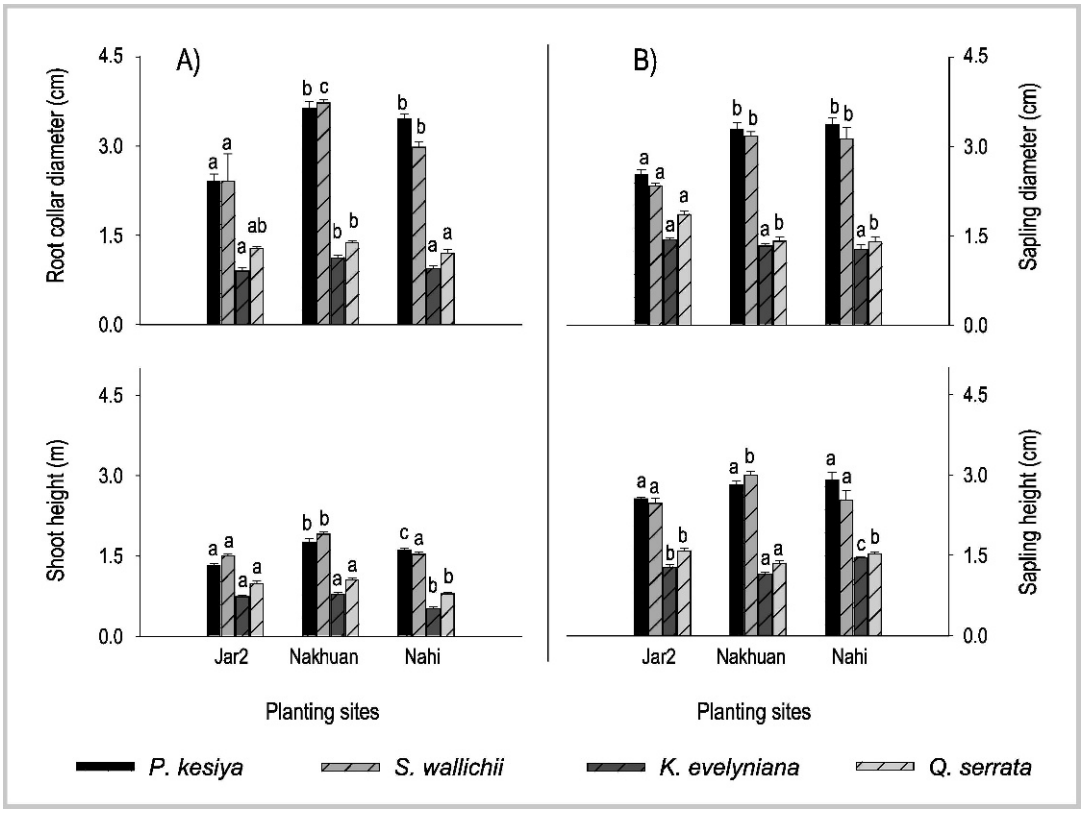
FIGURE 6 (A) Seedling growth and (B) sapling growth of 4 native tree species 3 and 4 years after direct seeding (mean ± SE). For each species, bars with different letter(s) are significantly different.



yields better germination of buried seeds. For dry forest species of central Brazil, Viera and Scariot (2006) found seed desiccation to be one of the factors that hindered seedling establishment in the pasture. Similarly, McLaren and McDonald (2003) observed increased germination with a decrease in exposure to full sun.

Second, seed predation is another bottleneck that determines the fate of sown seeds. Exposed seeds are more highly susceptible to predation than buried and excluded seeds (Holl and Lulow 1997; Notman and Gorchov 2001; Woods and Elliott 2004; Garcia-Orth and Martinez-Ramos 2008). Although we did not quantify the level of predation in our study, the relatively better establishment success of buried seeds of *Q. serrata* and *K. evelyniana* suggests a lower probability of encounter with predators than seeds broadcasted on the surface of the soil. Cheng et al (2007) found that burial significantly reduced the predation of *Q. serrata* acorns by rodents, whereas Xiao et al (2006) ascribed the high content of tannins in *Q. serrata* acorns as a deterrent against high levels of rodent predation. Early successional species are also susceptible to higher levels of seed predation rate than later-successional species (Garcia-Orth and Martinez-Ramos 2008) because of the high cost of handling large seeds of the latter species. Previous studies have shown that seed removal tends to be lower as seed size increases in some habitat types (Nepstad et al 1996; Moles et al 2003; Mendoza and Dirzo 2007) and the odds of seedling emergence increase with seed size on old fields (Zimmerman et al 2000; Camargo et al 2002; Hooper et al 2005). This partly explains the low seedling establishment success of small-seed species (*S. wallichii*) in our study.

Third, seeds of different sizes are suited to different germination strategies and establishment conditions, that is, small-seeded species show significantly greater germination in response to irradiance than in complete darkness, and their germination remains unaffected by an increasing magnitude of diel temperature fluctuation up to a species-specific threshold, whereas large-seeded species germinate equally in light and dark, and either showed a positive germination response to an increasing magnitude of temperature fluctuation or no significant response (Pearson et al 2002). We observed large numbers of seedlings of *P. kesiya* and *S. wallichii* (small-seeded species) 10 and 15 days after sowing, respectively; whereas, the large seeds of *Q. serrata* started to germinate about 4 to 6 weeks after sowing (pers. obs.). This might be a result of the greater time for water to permeate a large seed, or it might be associated with

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the higher relative growth rates of small-seeded species (Swanborough and Westoby 1996). Although rapid germination might give small-seeded species an establishment advantage under favorable germination conditions (Seiwa 1998), early emerging seedlings can succumb to high mortality because of water stress during dry spells in the wet season, herbivory, and competition (Ray and Brown 1995; Zida et al 2008). By contrast, seedlings from large-seeded species are better able to survival various establishment hazards (Moles and Westoby 2004; Doust et al 2006; Herrera and Laterra 2009), as a result of committing relatively lower resources at any given time during the early periods of seedling's growth, the so-called larger-seed-later commitment mechanism (Kidson and Westoby 2000). Evidence for this comes from the relatively small size of *Q. serrata* seedlings (the large-seeded species) compared with small-seeded species (*P. kesiya* and *S. wallichii*) in our study.

We found relatively high annual rate of mortality for small-seeded species (eg *S. wallichii*) compared with large-seeded species (eg *Q. serrata*), which can be related to a high seeding rate (250,000 seeds/kg for *S. wallichii*, and 350 seeds/kg for *Q. serrata*), which resulted in a high rate of self-thinning because of inter- and intraspecies competition (Camargo et al 2002). Evidence for this also comes from the 4-fold decline in seedling density of *S. wallichii* against a 2-fold decline of *Q. serrata* in 3 years after direct sowing. For *Q. serrata*, we still found annual mortality as high as 29% and 21% during the first (1–3 years after sowing) and the second (3–5 years after sowing) periods of assessment, respectively. As this species is intermediately shade tolerant, exposure to full light might have induced photoinhibition, because some later-successional species are photoinhibited in high light conditions (Loik and Holl 2001). Rapid seedling growth is a desirable characteristic of plant species used in restoring degraded areas. In our study, the pioneer species achieved significant growth in height and root collar diameter compared with the later-successional species. Several studies have shown that seedling survival is lower mainly for small-seeded species, but growth is higher at more open sites, particularly for large-seeded species (Camargo et al 2002; Vieira et al 2007). The relatively low-growth performance of large-seeded species in our study could be related to delayed germination (4 to 6 weeks after sowing for *Q. serrata* versus 10 and 15 days after sowing for *P. kesiya* and *S. wallichii*, respectively), which resulted in less time for growth.

A conspicuous intersite difference for measured seedling parameters was found in the present study. Topography plays a critical role in the variation of seedling establishment among sites, causing drainage, moisture, and nutrients to vary from ridge top to valley floor (Enoki and Abe 2004). At higher positions on the slope, the groundwater level is low and hence the soil-water content is not sufficiently high, which results in low establishment success. In our study, the site at School and Junction, where seedling establishment was good, is located on the valley floor and the foot of the mountain, respectively, whereas Jar2, with a 15% slope and Nahi with a 25% slope, had poor seedling establishment, particularly for *S. wallichii*. Excessively high soil moisture levels at the lower position of the slope (flat areas) can create anoxia and poor seed germination, as can be seen from poor seedling establishment of *K. evelyniana*, and *S. wallichii* at Nakhuan (flat area) and the former species at Khongyum, which is located close to the river. Intersite variations in seedling establishment can also be related to the contribution of proximity to the remaining forest fragments to seed and seedling predation, that is, the closer a planting site is to a forest fragment, the higher the probability of seed and seedling predation. Because the nearby fragmented forest provides shelter and concealment for granivores from their own predators (Aide and Cavelier 1994; Nepstad et al 1996; Guariguata and Ostertag 2001), they can readily cross or enter the nearby open sites. Takahashi et al (2006) observed increasing dispersal of *Q. serrata* acorns (mostly consumed) by wood mouse into cutover land, provided that the risk of predation of wood mice is minimal. This might explain the low seedling establishment success of *K. evelyniana* and *S. wallichii* at Nakhuan, which is located close to the remaining forest fragment in our study.

Implications and conclusions

The results of the present study illustrate that direct seeding seems to be possible for rehabilitation of abandoned sites provided that

1. The seeds are buried to avoid the risk of seed desiccation and predation, as evidenced from better establishment success of buried seeds of *Q. serrata* and *K. evelyniana*;
2. The seeding rate, particularly for small-seeded species (*S. wallichii* and *P. kesiya*), is reduced to avoid inter- and intraspecies competition, leading to high mortality while increasing the seeding rate for large-seeded species (*Q. serrata*) to enhance seedling density; and
3. Species-site matching is well defined to minimize topography-induced changes in micro-habitat, because the species tested in this study perform relatively better at the foot of the mountains (flat areas).

To improve growth performance of shade-tolerant species, such as *Q. serrata*, 2-stage seeding, where seeds of pioneer species are sown first to capture the site is followed by planting of later-successional plants underneath these pioneer species, which in turn can serve as nurse trees. Because the current study tested only 4 species under slight topographic variation, screening of more species that can establish well across a topographic gradient is needed.

Our findings have important implications for the rehabilitation of secondary mountain forests on abandoned swidden (shifting) cultivation in Laos and

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elsewhere in southeast Asia. Since the 1980s, the stabilization of swidden cultivation has been a major policy focus of the Lao government (Kingsada 1998), and secondary forests make up the largest share of forest cover in the lower Mekong basin, with more than 80% located in Laos and Cambodia (Heinimann et al 2007). The rate of recovery of secondary forest on fallows to mature forest attributed varies greatly, and it seems that the successional stage is at the establishment phase, dominated by bamboo (Sovu et al 2009). Direct seeding can thus be used as a cost- and time-saving method to expedite the recovery process, especially in inaccessible mountainous sites where establishing a nursery to produce and maintain plants can be difficult. It also reduces the costs of transport and labor during soil preparation and sowing. Mechanical injuries and desiccation damage, which frequently occur in seedlings, can also be avoided.

ACKNOWLEDGMENTS

The study was financially supported by the Swedish International Development Agency (Sida). Khamking Khutsavanh and Kham Lanoy are acknowledged for their contribution during the field work and the Provincial Agriculture and Forestry Division for allowing us to carry out this research on the former NAWACOP sites. Thanks to Issa Ouedraogo for help in mapping the study site and proofreading the manuscript. We also thank Dr John Blackwell and Sees-editing Ltd for linguistic improvements.

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