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Survival and germination of an experimental seed bank population of two species of Lauraceae in a tropical montane forest in Thailand

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Abstract The survival and germination traits of two tropical species of Lauraceae, *Lindera metcalfiana* and *Litsea cubeba*, were investigated in a 2-year burial experiment and subsequent germination tests of sequentially excavated seeds. Fresh seeds extracted from fruit were packed in aluminum mesh bags and buried 5 cm deep in a mature montane forest in northern Thailand (1700 m altitude). No seed mortality was recorded for *Litsea*, but *Lindera* experienced 26%–48% mortality after being buried for 122 days. These seeds did not germinate in the forest soil during the 2-year experimental period. We found that fresh seeds of these two species did not germinate even under open conditions, suggesting that the seeds are initially deeply dormant after dispersal. In contrast, 29%–60% of excavated *Lindera* seeds germinated under open conditions after being buried for 30–753 days, and excavated *Litsea* seeds began to germinate after being buried for 408 days. These findings suggest that seeds enter a state of enforced dormancy. The ratio of germinable seeds peaked 184 days after burial in *Lindera* (33%) and 930 days after burial in *Litsea* (91%). The longer period of deep dormancy in *Litsea* prior to enforced dormancy is concordant with the fact that for regeneration *Litsea* requires larger-scale disturbance than *Lindera*.

Key words Dormancy · Experimental burying · Germination test · *Lindera metcalfiana* · *Litsea cubeba* · Soil seed bank

Introduction

The seeds of forest trees vary widely in their patterns of germination and longevity. Although most tropical rainforest species have recalcitrant seeds that germinate immediately (Ng 1978; Maury-Lechon et al. 1981; Yap 1981; Vasquez-Yanes and Orozco-Segovia 1993), many pioneer species produce small, orthodox seeds. Pioneer species tend to have longer-lived seeds with dormancy, which allows them to survive on the forest floor until conditions become suitable for germination (Gomez-Pompa and Vasquez-Yanes 1974). The germination of these seeds is frequently triggered by specific conditions of light and/or temperature (Vasquez-Yanes and Smith 1982; Vasquez-Yanes and Orozco-Segovia 1990; Washitani and Takenaka 1986, 1987). This strategy is linked with long-lasting, dormant seeds in the soil (Whitmore 1983) and is referred to as the buried-seed strategy (Harper 1977; Vasquez-Yanes and Orozco-Segovia 1984).

To assess their longevity, seeds are often buried experimentally (Teketay and Granstrom 1997; Perez-Nasser and Vasquez-Yanes 1986). Such experiments have been conducted on a number of species in many regions, e.g., tropical lowland forest in northeastern Australia (50 species; Hopkins and Graham 1987), tropical rainforest in the Pasoh Forest Reserve, western Malaysia (45 species; Kanzaki et al. 1997), and Afromontane forest in Gara Ades in the eastern highlands of Ethiopia (eight species; Teketay and Granstrom 1997). However, data from tropical montane forests are still lacking.

In a series of ecological studies on the Lauraceae in Doi Inthanon National Park, North Thailand, we observed seed fall and germination of four tree species. Among the four examined species, the seeds of *Lindera metcalfiana* and *Litsea cubeba* never germinated in plots established under

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their parent trees (Sri-ngernyuang 2003). Thus, the seeds of *Lindera metcalfiana* and *Litsea cubeba* appear to be orthodox and to require light to germinate. In this paper, we discuss the effects of experimental burial on seed viability and the germination of *Lindera metcalfiana* and *Litsea cubeba*. Hereafter, we refer to these two species simply as *Lindera* and *Litsea*.

A tree census in a 7.5-ha research plot established in a lower montane forest of Doi Inthanon National Park revealed that *Lindera* inhabits mature forest (128 trees >1.0cm stem diameter per ha) and attains a maximum size of 56.5cm in diameter, although large individuals are relatively rare (Sri-ngernyuang 2003). In contrast, *Litsea* seldom occurs in mature forests (2 trees/ha) and frequently forms pure stands following shifting cultivation in montane forests (Storrs and Storrs 1990; Forest Restoration Research Unit 2000). Thus *Lindera* may be regarded as a gap-dependent tree species in mature montane forests, whereas *Litsea* is a secondary species that mainly colonizes large disturbed patches. In this study, we focus on the seed germination traits of these two pioneer species that have contrasting habitat preferences.

Materials and methods

Materials

Mature seeds of *Lindera* and *Litsea* were collected from one parent tree of each species in a primary lower montane forest. To avoid contamination of the seeds by other conspecifics, we chose isolated parent trees and collected mature seeds from the forest floor during the seed-dispersal period. The fruiting periods of *Lindera* and *Litsea* are from July to October and from late August to November, respectively; fresh seeds of *Lindera* and *Litsea* were therefore collected in September and October 1999, respectively. Seeds were extracted from the fruits and floated in tap water to identify and eliminate empty seeds. The fruits of these two species are one-seeded berries, and the seeds of *Lindera* are slightly larger (5.45mm diameter and 0.108g fresh weight in *Lindera*; 5.28mm and 0.080g in *Litsea*: $P < 0.001$ for seed diameter). The fruits of both species have an oily mesocarp and are dispersed by birds, and the seeds have a thin, ligneous, hard seed coat. Whole fruits and seeds of both species have a strong odor, and local people use the seeds of *Litsea* as a spice.

Seed-burial experiment

Sound seeds of each species were placed into bags made of aluminum netting (2-mm mesh). Each bag held 50 seeds, and 12 bags were prepared for each species. These bags were buried 5cm below the soil surface in a 7.5-ha research plot established in a primary lower montane forest of the Doi Inthanon National Park, North Thailand, approximately 1700m a.s.l. (Sri-ngernyuang et al. 2003) on September 16, 1999 (*Lindera*), and October 16, 1999 (*Litsea*).

The burial site was mid-slope under a closed canopy dominated by Fagaceae, Lauraceae, *Mastixia euonymoides*, and *Manglietia garrettii* (Hara et al. 2002). A plastic stick (20cm long) was planted in the soil to mark the position of each buried bag. Three bags of each species were excavated 1 month, 4 months, 14 months (13 months for *Litsea*), and 25 months (24 months for *Litsea*) after interment. Germinated seeds were counted and isolated, and the condition of ungerminated seeds was checked by floating them in tap water and crushing them by hand. Sampled seeds were subsequently classified into three categories: (1) germinated (2) ungerminated-dead, and (3) ungerminated-intact.

The surface soil temperature was monitored twice at the burial sites, in November 1999 and in February 2000, using stem thermometers. Soil temperatures at the site ranged from 12.5° to 16°C during the monitoring period.

Germination test in the nursery

Ungerminated-intact seeds (category 3) extracted from the seed bags were planted shortly after each sampling to test their ability to germinate. In addition to these excavated seeds, 150 fresh seeds of each species were also planted in this test. Seeds were planted in polyethylene seed pots (15cm wide × 45cm long × 15cm deep) filled with fine river sand. Seeds were placed at a depth of about 1cm in the germination bed, with a seed density of 50 seeds/225cm². The seed pots were sent to the nursery of the 60th Anniversary of Queen Sirikit Botanical Garden, in Chiang Mai City (360m altitude), within 1 week of planting. The pots were placed in a sunny location and covered with a transparent plastic sheet. To avoid desiccation, the pots were watered by mist-spraying twice a day at 8:00 a.m. and 4:30 p.m. Seedlings that emerged were counted every week until germination ceased. All germinated seedlings were transplanted within several weeks after germination.

Soil temperature in the pots was measured at a depth of 1 cm, once a week, from November 1999 to February 2002. The soil temperature fluctuated from 23° to 38°C in the hot season (April) and from 15° to 32°C in the cold season (January).

Germination and survival model

We used the Weibull function to fit observed survival and germination data and attempted to quantify these processes. This function provides a close fit to a wide range of observed seed survival and germination data (Kanzaki et al. 1997; Brown and Mayer 1988).

The probability of survival of an ungerminated-intact seed $S(t)$ can be expressed by the equation

$$S(t) = 1 \quad [t \leq k]$$

$$S(t) = e^{-\left(\frac{t-k}{a}\right)^m} \quad [t > k] \quad (1)$$

where t denotes the time in days since seed burial, k is the lag-time between seed burial and timing of first mortality, and a and m denote a scaling parameter and a shape parameter that are specific to each species. We used a nonlinear least-squares method to fit the model of Eq. 1 to our observed data. The mean life span (MLS) of buried seeds was calculated from the coefficients m , a , and k as

$$\text{MLS} = a\Gamma\left(\frac{1}{m} + 1\right) + k$$

where Γ denotes the gamma function.

Germination of seeds in the nursery was also fitted to the Weibull distribution model. Probability of germination at a given time, $g(t)$, can be expressed by two equations:

$$\begin{aligned} g(t) &= 0 & [t \leq l] \\ g(t) &= G^* \frac{n}{b^n} (t-l)^{(n-1)} e^{-\left(\frac{t-l}{b}\right)^n} & [t > l] \end{aligned} \quad (2)$$

where t denotes time since planting (days), G^* represents the observed final germination ratio, and b , n , and l denote a scaling parameter, a shape parameter, and the lag-time of germination. The cumulative probability of germination $G(t)$ can then be expressed by two equations:

$$\begin{aligned} G(t) &= 0 & [t \leq l] \\ G(t) &= G^* \left(1 - e^{-\left(\frac{t-l}{b}\right)^n}\right) & [t > l] \end{aligned} \quad (3)$$

We used a nonlinear least-squares method to fit the model of Eq. 3 to our observed data. After estimating the coefficients, the mean germination time (MGT) was calculated from the coefficients n , b , and l as

$$\text{MGT} = b\Gamma\left(\frac{1}{n} + 1\right) + l$$

When $n > 1.0$, we can also define the maximum germination rate g_{\max} and time t^* that give g_{\max} as

$$\begin{aligned} t^* &= b\left(\frac{n-1}{n}\right)^{\frac{1}{n}} + l \\ g_{\max} &= g(t^*) \end{aligned}$$

Results

Survival of ungerminated seeds

The survival rates of the two species differed substantially. *Litsea* seeds showed 100% survival throughout the whole burial period, while the seeds of *Lindera* rapidly lost their viability after 30 days and only 52%–74% survived (Fig. 1). Both species showed no germination at the burial site.

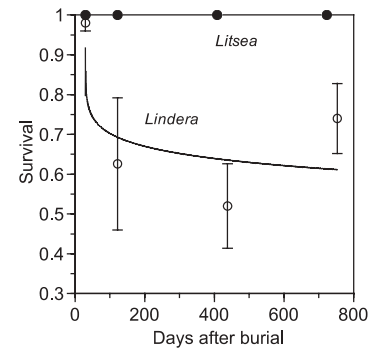


Fig. 1. Survival of seeds buried in a closed montane forest of northern Thailand at 1700m altitude. Each circle indicates the mean (\pm SD) survival ratio of seeds in three excavated bags. The survival curve of *Lindera metcalfiana* was regressed by the Weibull function shown in Eq. 1 in the text

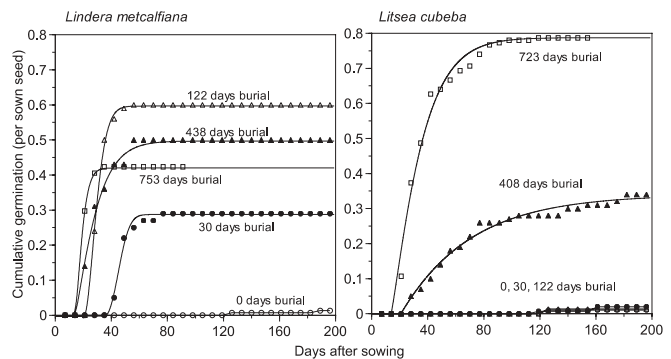


Fig. 2. Cumulative germination of seeds that had been buried for different lengths of time in forest soil plotted against time since planting. The cumulative germination curves were regressed by the Weibull model shown in Eq. 3 (see text)

The Weibull model of survival poorly fits the survival curve of *Lindera*, with a coefficient of determination of 0.69 (Fig. 1). The estimated MLS of *Lindera* seeds was >100 years. We could not apply the survival model to *Litsea* because we recorded no seed mortality.

Germination traits

Figure 2 shows cumulative germination curves for each of the excavated seeds, plotted against time since planting. All of the germination processes were regressed by the Weibull model except those with $<5\%$ final germination. Fresh seeds that were sent to the nursery without burial treatment did not germinate. However, seeds did germinate after having been buried. Exhumed viable seeds of *Lindera* had a final germination ratio of 29%–60%. This ratio peaked in seeds that had been buried for 122 days, and then decreased with increased time since burial (Fig. 2, Table 1). Viable *Litsea* seeds that were buried for less than 1 year had a fairly low final germination ratio (Fig. 2), while 34% and 78% of

Table 1. Condition of seeds excavated from the forest soil after having been buried for 0–753 days, and germination trait of viable seeds under open nursery conditions for *Lindera metcalifiana* (top) and *Litsea cubeba* (bottom). Germination tests of viable seeds were begun on the day of excavation. Seed germination was checked once a week between 23 September 1999 and 14 January 2002. All viable seeds were used for germination tests. Germination curves with final germination ratios of <5% were not regressed by the Weibull distribution model

Date of excavation (burial duration in days)	Survival of buried seeds in the forest (%)	G^* (% sown seeds)*	l (days after sowing)	t^* (days after sowing)	g_{\max} (day ⁻¹)	MGT (days)
<i>Lindera metcalifiana</i>						
16 Sep. 1999 (0)	100.0 ± 0.0	1.3	–	–	–	–
16 Oct. 1999 (30)	98.0 ± 2.0	28.6	35	45.0	0.020	46.6
16 Jan. 2000 (122)	62.6 ± 16.6	59.6	21	26.8	0.044	30.2
27 Nov. 2000 (438)	52.0 ± 20.8	50.0	14	17.8	0.023	28.7
8 Oct. 2001 (753)	74.0 ± 8.8	42.3	14	16.5	0.051	19.6
<i>Litsea cubeba</i>						
16 Oct. 1999 (0)	100.0 ± 0.0	0.0	–	–	–	–
16 Nov. 1999 (30)	100.0 ± 0.0	2.0	–	–	–	–
16 Feb. 2000 (122)	100.0 ± 0.0	3.3	–	–	–	–
27 Nov. 2000 (408)	100.0 ± 0.0	34.0	21	21.3	0.004	70.9
8 Oct. 2001 (723)	100.0 ± 0.0	78.7	14	18.6	0.026	35.5

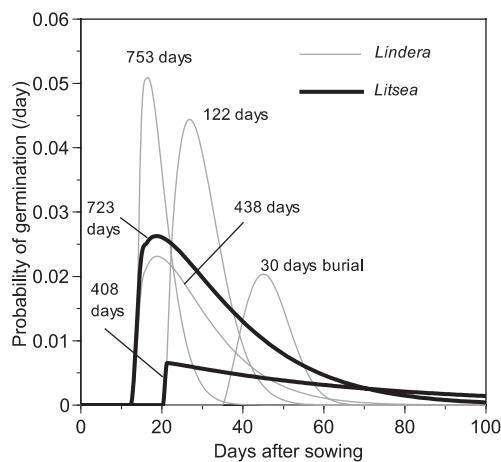


Fig. 3. Changes in the probability of germination $g(t)$. The curve was fixed by using parameters determined by the regression shown in Fig. 2

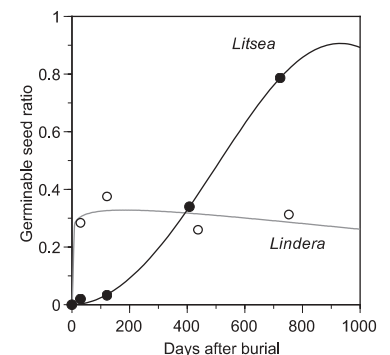
seeds that were buried for 408 and 723 days, respectively, germinated (Table 1).

The daily germination rate, $g(t)$, was fixed using parameters determined by the curve fitting for $G(t)$ (Fig. 3). In *Lindera*, the lag-time (l) decreased from 35 to 14 days with increased time since burial from 30 to 753 days (Fig. 3, Table 1). MGT and t^* also decreased with increased burial duration (Fig. 3, Table 1). Similarly, germination patterns of *Litsea* seeds also changed with length of burial. Lag-time (l) decreased from 21 to 14 days, and MGT and t^* decreased with increased burial time (Fig. 3, Table 1). Maximum germination rate, however, differed clearly between these two species, and the germination of *Litsea* was slower than *Lindera* in terms of g_{\max} (Table 1).

Germinable seed density

As a result of seed mortality in the ground and changes in germinability of buried seeds, the number of buried seeds

Fig. 4. Changes in the germinable seed ratio (number of germinable seeds/initial number of seeds buried) as a function of time since burial. The Weibull function was fitted to express these changes



that can respond quickly to alterations in site conditions changes as seeds age. These germinable seeds can contribute to the establishment of seedling populations when gaps or open sites are formed in the forest. Here, we define the germinable seed ratio as the ratio of germinable seeds to initially buried seeds ($= S(t) \cdot G^*$). In Fig. 4, this ratio was plotted against the time since burial, and time-course changes were modeled by the Weibull distribution assuming that lag-time = 0. The germinable seed ratio in *Lindera* increased rapidly with increased time since burial; it peaked at 184 days, with a maximum ratio of 33%, and then gradually decreased (Fig. 4). In contrast, the germinable seed ratio in *Litsea* constantly increased with increased time since burial and was expected to attain a maximum ratio of 91% at 930 days (Fig. 4).

Discussion

Seed dormancy

The germination traits of the examined species changed depending on how long their seeds had been buried. Fresh

seeds did not germinate even under open conditions and thus appeared to be in a state of deep dormancy. This dormant phase terminated within 1 month in *Lindera* and within 1 year in *Litsea*. Following the deep dormant phase, seeds apparently entered a state of enforced dormancy (Harper 1977) or quiescence (Murdoch and Ellis 2000). Under open conditions, seeds in this phase were able to germinate vigorously, whereas seeds in forest soil remained dormant continuously. Thus, seeds in the latter phase showed germination patterns typical of pioneer species (Whitmore 1989). Nursery trials to propagate *Litsea cubeba* from seed failed in Doi Suthep National Park, North Thailand (Forest Restoration Research Unit 2000); this failure was probably caused by the initial deep dormant phase that is characteristic of this species.

In general, seed dormancy is caused by mechanical impermeability of the seed coat, immaturity of the embryo, and/or physiological or chemical inhibition of germination (Tran and Cavanagh 1984). In this study, we were unable to determine the mechanisms of initial dormancy in *Lindera* and *Litsea*. Wright (1990) studied the germination response of *Lindera melissifolia* (Walt.) Blume in northeastern Arkansas. Seeds of this species rarely germinate in their natural state; however, peeling away the entire seed coat to expose the cotyledons resulted in 100% germination of this species at 29°C under sterile conditions on Petri plates. In contrast, notching the seed coat yielded a final germination of only 5%. These results suggest that the seed coat controls dormancy in this species (Wright 1990). Our study species also possess ligneous seed coats; therefore, the initial dormant phase may have been caused by the impermeability of the seed coat.

The importance of chemical inhibition was emphasized by Yagihashi et al. (2000), who found that juice extracted from the pulp of *Prunus* seeds significantly reduced germination. However, the seeds used in our burial experiments were manually extracted from the pulp layer; thus, it is unlikely that pulp juice caused the initial deep dormancy observed in our study species.

After seeds enter the phase controlled by enforced dormancy, germination is probably triggered by environmental signals associated with open conditions. The signals for our study species could include the quality and quantity of light and/or high and fluctuating temperatures, as has been reported for many pioneer tree species (Vasquez-Yanes and Smith 1982; Washitani and Takenaka 1986, 1987; Wright 1990; Vasquez-Yanes and Orozco-Segovia 1990, 1993; Teketay and Granstrom 1997). The dormancy traits of these two pioneer species may help to reduce losses of buried seeds and increase their chances of germinating in open sites.

Habitat preference and seed germination

Although both study species experienced dormancy, changes in seed mortality in the soil and the ability to germinate under open conditions were quite different. Although mortality was high in *Lindera* seeds during the first month,

they maintained a survival rate of approximately 65% after 25 months of being buried. The density of germinable *Lindera* seeds also quickly increased 1 month after burial. In contrast, *Litsea* seeds showed no mortality during the 2-year burial experiment, and the density of germinable seeds increased gradually after 1 year of being buried. These observed differences in seed behavior may be closely related to the regeneration strategy of these species. *Litsea* is infrequently observed in undisturbed montane forests and occurs mainly in open disturbed areas, such as abandoned shifting cultivation sites. *Lindera* is also a pioneer species, but it grows mainly in gaps that occur in undisturbed forests (Sri-ngernyuang 2003). The low mortality of *Litsea* and its deep and prolonged initial dormant phase seem concordant with its regeneration strategy. Regeneration sites of *Litsea* are typically in large-scale disturbed patches (Storrs and Storrs 1990; Forest Restoration Research Unit 2000), which form infrequently in natural forests. Therefore, maintaining a prolonged initial dormant phase may increase the probability of *Litsea* seeds encountering large-scale disturbances.

Seeds of these two species are dispersed by birds. In general, seeds that have passed through the guts of birds show higher germination rates than do intact seeds (Barnea et al. 1991; Traveset and Willson 1997). Future studies should therefore examine the fate of seeds dispersed by birds as compared to seeds that simply fall from the parent tree, particularly for *Litsea* seeds, which enter a long dormant period after dispersal.

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