

Full Paper

Seed production and dispersal of four Lauraceae species in a tropical lower montane forest, Northern Thailand

Kriangsak Sri-Ngernyuang^{1*}, Mamoru Kanzaki², Akira Itoh³

¹Faculty of Architecture and Environmental Design, Maejo University, Chiang Mai 50290, Thailand.

E-mail : kriangsa@mju.ac.th

²Tropical Forest Resources and Environments, Graduate School of Agriculture, Kyoto University, Kyoto, Japan.

³Laboratory of Plant Ecology, Graduate School of Science, Osaka City University, Osaka 558-8585, Japan.

*Author to whom correspondence should be addressed.

Received: 13 February 2007; in revised form : 20 February 2007 / Accepted: 16 May 2007 /

Published: 17 May 2007

Abstract: Seed production and dispersal of two pioneer species (*Litsea cubeba* and *Lindera metcalifiana*) and two shade-tolerant species (*Cinnamomum soeengii* and *Cryptocarya densiflora*) of Lauraceae were studied at a tropical lower montane forest in Doi Inthanon National Park, northern Thailand. Mature seed fall was monitored weekly to monthly using seed traps or belt transects for 1-3 trees per species. During the two-year study period (1998-2000), we observed only one fruiting episode for each of ten sample trees. Fruiting period was synchronized within each species, while there was no overlap in fruiting among the species. The seed fall periods were relatively short in *Litsea cubeba* (16-54 days), *Lindera metcalifiana* (25-65 days) and *Cinnamomum soeengii* (69 days), while quite long in *Cryptocarya densiflora* (159-187 days). The seed dispersal distance was short for all the species (less than 12 m), and the density of seed dispersal had a mode at 0-2 m from mother tree. The total seed production of each tree was estimated by a Weibull seed dispersal model as 93-6029, 985-3977, 1035-8910 and 6331 for *Lindera metcalifiana*, *Litsea cubeba*, *Cryptocarya densiflora* and *Cinnamomum soeengii*, respectively. Total fruit dry weight of each tree was estimated to be comparable to the leaf dry weight for the shade-tolerant species, while less than 3% of the leaf dry weight for the pioneer species. The studied

method should be applied for other species in order to gain more ecological knowledge to maintain the montane forest.

Key words: Doi Inthanon National Park, Lauraceae, seed dispersal, seed production, tropical montane forest

Introduction

Lauraceae is an important family in many tropical montane forests. For example, Lauraceae occupied 14% (1st in rank) and 15% (2nd after Fagaceae) of all trees more than 1 cm dbh in individual number and basal area, respectively, at a 15-ha plot established in a montane forest in Thailand (Kanzaki *et al.* 2004) [1]. In addition, Lauraceae is the most species rich family in the same plot, including 25 species [1].

This study is a part of ecological studies on Lauraceae trees in an Asian tropical montane forest [2,3]. In this paper, seed production and dispersal of Lauraceae species will be described. Studies of seed production and dispersal have substantial consequences for forest conservation because the production and dispersal of seeds are important stages in the life-cycle of many plants [4].

On any given plant, seed production may be limited by various factors such as the amount of nutrients and photosynthate available for allocation to fruits and seeds, the presence of pre-dispersal predators and diseases [5], and annual variation in climate [6,7]. It is well known that Asian tropical rain forests flower and fruit at irregular super-annual intervals [8]. However, the phenology of flowering and fruiting are uncertain for tropical montane forests in Asia.

Successful regeneration of plants depends largely on the dispersal of their seeds into the good locations that provide the optimum capability for seed germination and seedling survival. The distance and location of dispersal could have significant impact on the seed germination [9]. Attaining suitable sites for germination is considered to be a crucial factor affecting seedling establishment and hence the regeneration and maintenance of plant species population [10]. Recruitment of a species at a certain site within a forest is often limited merely by lack of seed input due to the limited seed dispersal, which is called 'dispersal limitation' [11,12]. Not surprisingly, recruitment of trees with short dispersal is also limited in the disturbed forests where no seed source trees remain within and around the focal forests.

There have been a considerable number of field studies on the phenology and seed dispersal of Lauraceae species in the neotropics [7,13-17], but none, to our knowledge, have been conducted in Asia. More specifically, no research has been carried out on the seed production and dispersal of tropical montane forest trees in Thailand. Therefore, the purpose of this study was to clarify the phenology of seed fall, seed dispersal and total seed production of Lauraceae species in a montane forest in order to gather more knowledge for the ecological characters and their conservation of montane forests in Thailand.

Material and Methods

Study site

All studies were carried out in the tropical lower montane forest at Doi Inthanon National Park (18° 24' N to 18° 40' N latitude, and 98° 24' E to 98° 42' E longitude), Chiang Mai Province, Northern Thailand. The national park is characterized by the hilly and mountainous terrain (*ca.* 400-2,565 m a.s.l.), and approximately 40 % of the area is covered with montane forest [18]. The average annual rainfall is 2,279 mm (1982-1999), measured at a radar base of the Royal Thai Air Force on the summit of Doi Inthanon (2,565 m a.s.l.). Three distinct seasons are recognizable: a rainy season from June to October, a cool and dry season from November to February, and a hot and dry season from March to May.

A 15-ha Forest Dynamics Plot was established in a lower montane forest located about 7 km south of the summit of Doi Inthanon at an altitude of *ca.* 1700 m. All trees more than 1 cm diameter at breast height (dbh) in the plot were tagged, mapped, identified into species, and their dbhs measured [1,19].

Studied species

The two pioneer and two climax species of Lauraceae were selected, which flowered in the studied forest during the two-year study period (1998-2000): (1) *Lindera metcalfiana* Allen, (2) *Litsea cubeba* Pers., (3) *Cryptocarya densiflora* Bl. and (4) *Cinnamomum soegengii* Kostermans. The former two are pioneer, and the latter were climax species. The description of these selected species will refer only the genus name hereafter.

Lindera is a large evergreen tree, which reaches to 31 m height in the studied plot, though most species of the genus *Lindera* are shrubs or small to medium sized trees. This species seems to be a pioneer in lower montane forests in northern Thailand, occurring on the disturbed sites. *Litsea* is a small to moderate sized evergreen tree, growing to *ca.* 15-20 m tall; the maximum height in the plot was 16 m. *Litsea* is also a pioneer species which often forms monospecific patches in the disturbed sites. In Nepal, this species is found mainly between 1500 and 2400 m in altitude [20]. *Cryptocarya* and *Cinnamomum* are both large, evergreen trees with the maximum heights of 31 m and 38 m in the studied plot, respectively. *Cryptocarya* has the largest total basal area (2.2 m²/ha) in the 15-ha studied plot. *Cryptocarya* shows a peculiar characteristic of vigorous forking of the stems.

The fruits of all the species are one-seeded berries, which seem to be dispersed by vertebrates including birds, and they have no special characteristic for wind dispersal. The sizes and weights of fruits and seeds of each species are shown in Table 1. The fruits and seeds of *Lindera* and *Litsea* are smaller than those of *Cryptocarya* and *Cinnamomum* (Table 1). The seeds of *Lindera* and *Litsea* are dormant at the time of dispersal and require a period of burial in the soil for their germination [3]. In contrast, the seeds of *Cryptocarya* and *Cinnamomum* have no dormancy character and germinate promptly after falling [2].

Table 1. Size and weight of a fruit and seed (Mean±SD) of the four Lauraceae species studied.

Species	Fruit					Seed				
	width (mm)	length (mm)	fresh weight (g)	dry weight (g)	n	width (mm)	length (mm)	fresh weight (g)	dry weight (g)	n
<i>Lindera metcalfeana</i>	7.2±0.36	6.4±0.35	0.176	0.060	50	5.9±0.21	5.0±0.15	0.108	0.046	20
<i>Litsea cubeba</i>	6.7±0.22	7.7±0.32	0.194	0.046	50	5.1±0.12	5.5±0.17	0.080	0.027	20
<i>Cryptocarya densiflora</i>	20.7±2.15	19.6±1.92	4.890	2.470	170	17.6±1.62	17.5±1.58	2.622	1.085	50
<i>Cinnamomum soegengii</i>	16.7±1.25	24.4±2.37	5.850	2.540	212	14.5±0.59	22.1±0.98	2.890	1.760	71

n: sample size

Seed fall study

Three isolated fruiting trees of each species, except for *Cinnamomum* ($n = 1$), were selected in the studied forest. For each sample tree, diameter at breast height (DBH) was measured with diameter tape, and height (H) was estimated from the DBH using the following equation, which is obtained from DBHs and heights of sample trees in the 15-ha plot including various species.

$$\frac{1}{H} = \frac{1}{1.42DBH} + \frac{1}{51.72}. \quad (1)$$

Two belt transects were established from the base of each sample tree of *Cryptocarya* and *Cinnamomum*. The directions of the two transects of each sample tree were selected to keep them straight and to minimize the slope inclination along the transects. The 1-m-width transects were used for *Cryptocarya* and the 2-m-width transects for *Cinnamomum* because the density of fallen seeds was lower for *Cinnamomum*. The lengths of the transects varied depending on the dispersal ranges of the sample trees. The transects were terminated when no seeds were found on the ground further from the sample trees. The transects were divided into 1 m x 1 m quadrats for two sample trees of *Cryptocarya*, 1 m x 1.5 m for the other tree of *Cryptocarya*, and 2 m x 2 m for the sample tree of *Cinnamomum*. All mature seeds falling in each quadrat were checked and labeled by numbered flags. Observations were made at irregular intervals of one week to one month during the periods January-September 1999 for *Cryptocarya* and June 1998 - February 1999 for *Cinnamomum*, which included the seed dispersal periods of all sample trees.

Seed traps were used to monitor seed production and dispersal of *Lindera* and *Litsea* because their seeds were too small to observe on the ground. Seed traps of various sizes (0.5 m x 1 m - 1.5 m x 1.5 m) depending on the seed rain density of the sample trees were established continuously from the base of each sample tree. The seed traps were set in two directions until no dispersed seeds were found on the forest floor for each tree (7-9 m) in the same way as for belt transects. Mature seeds in each seed trap were collected and the seed number was counted at irregular intervals of two weeks to one month during the period May 1999 to February 2000, which included the seed dispersal periods of all sample trees.

Analysis of seed fall phenology

Phenological patterns of seed fall were analyzed assuming that the probability of seed fall dates followed the Weibull distribution for each sample tree. Then, the cumulative number of fallen seeds at a date d is given by the equation,

$$F(d) = N \left\{ 1 - \exp \left[- \left(\frac{d - \xi}{a} \right)^m \right] \right\}, \quad (2)$$

where N is the total number of fallen seeds in the transect/traps during the study period, a is a scaling parameter, m is the shape parameter and ξ is the first date of mature seed fall. The value of ξ for each tree was determined as one day before the date when the first mature seed fall was observed under the canopy of the tree. For some sample trees, the first seed-fall dates pre-dated the establishment of the transects or traps. The coefficients of the Weibull distribution were estimated by non-linear regression with DeltaGraph ver. 4.0J (SPSS Inc, USA). In order to compare the lengths of seed fall periods, the period during which 90% of the total seeds (excluding the earliest 5% and the latest 5%) fell to the ground was estimated for each sample tree using equation (2). The period in days is given by $d_1 - d_2$, where

$$\begin{cases} F(d_1) = 0.95N \\ F(d_2) = 0.05N \end{cases}$$

of equation (2).

Analysis of seed dispersal

The seed dispersal of each sample tree was analyzed using the Weibull distribution seed dispersal model [21]. We assumed that seed density at x meters from the center of the canopy [$\rho(x)$ (seed m^{-2})] follows the Weibull distribution expressed by the equation,

$$\rho(x) = N \frac{m}{a^m} x^{m-1} \exp \left[- \left(\frac{x}{a} \right)^m \right], \quad (2)$$

where N is the total number of seeds in the 1-m-wide transect ($x = 0$ to infinity), a is the scaling parameter, and m is the shape parameter. The center of the canopy was chosen so that the seed dispersal curves would be symmetrical in both directions of the transects. Therefore, the center of the canopy was not necessarily identical to the base of the sample tree. The values of the coefficients were estimated by non-linear regression using SYSTAT ver. 5 (SPSS Inc, USA). Then, the total number of dispersed seeds or the total seed production (N^*) was estimated by the equation,

$$N^* = 2\pi \int_0^{\infty} x \rho(x) dx = 2\pi N E(x), \quad (3)$$

where $E(x)$ is the mean value of the Weibull distribution. $E(x)$ is expressed by the equation,

$$E(x) = a\Gamma\left(\frac{1}{m} + 1\right), \quad (4)$$

where $\Gamma(-)$ is the gamma function. The values of $E(x)$ were also used to compare the seed dispersal ability among sample trees.

Results and Discussion

Phenology of seed fall

During the two-year study period, only one episode of fruiting was observed for each sample tree (Fig. 1). This result, as well as additional field observations on fruiting in the study site [22], suggests that individual trees of many Lauraceae species would not produce seeds every year at the studied forest. It is also suggested that different species may fruit at different times or different years because no overlap in seed fall was observed among the four studied species, though seed fall periods were synchronized within each species (Fig. 1).

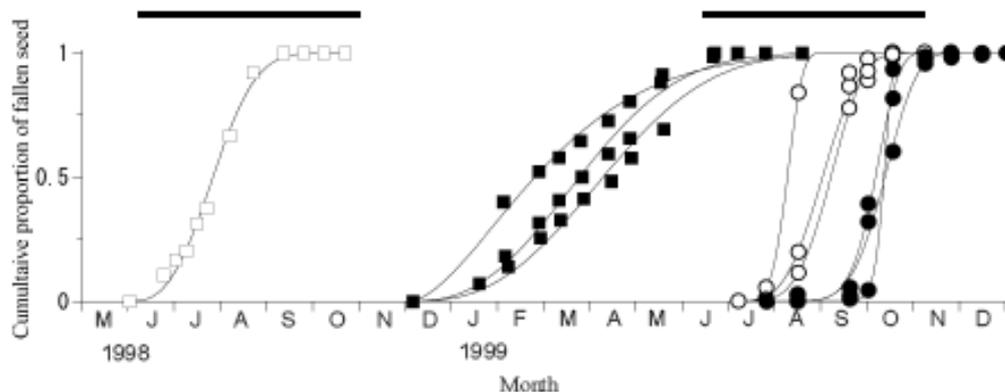


Fig. 1. Time courses of mature seed fall of four Lauraceae species. Changes in cumulative proportion of the seed fall are plotted for each sample tree. Open squares: *Cinnamomum soegengii*, closed squares: *Cryptocarya densiflora*, open circles: *Lindera metcalfiana*, closed circles: *Litsea cubeba*. The curves estimated by the Weibull distribution models (see Table 2) are also shown for each tree (see text for the details of the model). The solid bars stand for the rainy seasons.

At a Costa Rican tropical montane forest, similar fruiting phenology of Lauraceae was reported [7]: few individual trees of 22 Lauraceae species fruited every year during a 7-year study, and fruiting years of individuals were not completely synchronized even among the same species [7]. Although fruiting periods of conspecific individuals were synchronized in our study, this may possibly be because we selected only fruiting trees during the study period. We do not know whether these individuals will fruit synchronously again in the next fruiting time. Wheelwright [7] reported that

fruiting of Lauraceae as a whole showed three mast years followed by 1-2 poor fruiting years during the 7-year period. It is not clear whether the Lauraceae of our studied forest also have mast years at the community level because the period of our observations had been too short so far. Long-term observations are definitely required to know the fruiting intervals of each individuals and species. We are continuing the phenological observations of flowering and fruiting of Lauraceae species in the studied forest.

The duration of mature seed fall differed among the studied species (Table 2). The periods during which 90% of the seeds fell were relatively short for *Litsea* (16-54 days), *Lindera* (26-61 days) and *Cinnamomum* (69 days), while very long for *Cryptocarya* (159-187 days). The estimated seed fall date probability by the Weibull distribution model (Fig. 2) clearly showed that *Lindera*, *Litsea* and *Cinnamomum* showed a clear peak in seed fall rate, while *Cryptocarya* fell seeds constantly during the six-month seed fall period.

Table 2. Estimated coefficients of the Weibull distribution of seed fall date for *Lindera metcalifiana* (LNM), *Litsea cubeba*, *Cryptocarya densiflora* (CRD), and *Cinnamomum soegengii* (CIS). a: the scaling parameter, m: the shape parameter of the Weibull distribution. Zero stands for the starting date of mature seed fall. Seed fall period is the period during which 90% of the total seed fell.

Mother tree	Zero date	<i>a</i>	<i>m</i>	Seed fall period (days)
LNM1	02-Jul-99	61.9	3.34	60.5
LNM2	02-Jul-99	35.2	4.69	25.8
LNM3	02-Jul-99	66.5	4.08	54.9
LTC1	20-Jul-99	75.9	6.60	41.2
LTC2	09-Aug-99	73.5	4.66	54.2
LTC3	20-Jul-99	78.7	18.88	16.2
CRD1	01-Dec-98	143.6	2.64	171.0
CRD2	01-Dec-98	127.0	2.49	158.8
CRD3	01-Dec-98	101.7	1.59	187.1
CIS	01-Jun-98	62.8	2.90	69.1

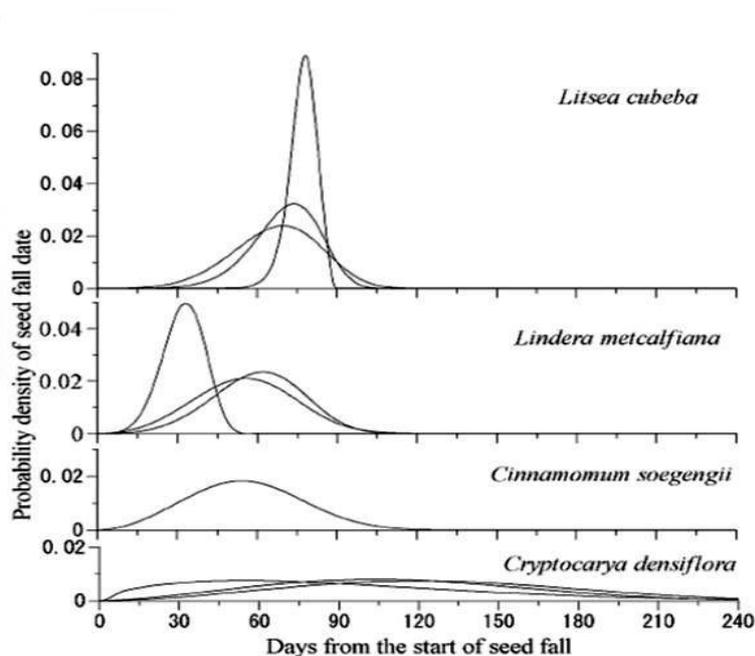


Fig. 2. Simulated probability densities of fruit fall dates for ten sample trees of four Lauraceae species by the Weibull distribution models (see text for the model). Actual dates of the start of seed fall varied among the trees (see Table 2 for the model coefficients for each tree).

The season of seed fall was also unique for *Cryptocarya* in that it fell seeds from the midst of the dry season until the beginning of the rainy season (Fig. 1). The other three species fell seeds at the midst of the rainy season (Fig. 1). The typical seed fall season was the rainy period in Costa Rican Lauraceae [7]. Lauraceae species which disperse fruits in the dry season as *Cryptocarya* are generally rare [7].

The unique phenology in fruit fall in *Cryptocarya*, viz the long and constant seed fall starting from the dry season, is worth studying further. Although the reason of this unique phenology is unclear, it might be related to the seed dispersal mechanisms of this species. While seeds of the other three species are dispersed mainly by birds, the seeds of *Cryptocarya* are likely to be dispersed by some ground vertebrates after seed fall [22]. A long and gradual seed fall might enhance the possibility of seed dispersal if the dispersers are rare and relatively inactive compared to birds.

Seed dispersal

The Weibull distribution model fitted satisfactorily the seed dispersal data of each sample tree ($r^2 = 0.93-0.99$; Fig. 3, Table 3). Seed dispersal distance was rather short for all species; the fallen seed density had a peak at 0-2 m from the center of the mother tree and no seeds were dispersed further than 12 m. The mean seed dispersal distance, $E(x)$, was positively correlated with tree height within each species (Fig. 4). There was no evidence that small-seeded pioneers gained greater dispersal distances than large-seeded climax species because values of $E(x)$ of *Litsea* and *Lindera* were not larger than the other two species, which were taller than the former two species (Fig. 4). *Litsea* had larger $E(x)$ values than those of *Lindera* trees even though their height and fruit size were similar. Thus, tree height

seems more important than fruit size in seed dispersal at least in the Lauraceae species studied. The short dispersal distances observed in the four species suggested a strong dispersal limitation [11] on their recruitment at the sites away from mother trees. Therefore, remaining seed source trees are an important strategy for conservation of the studied species.

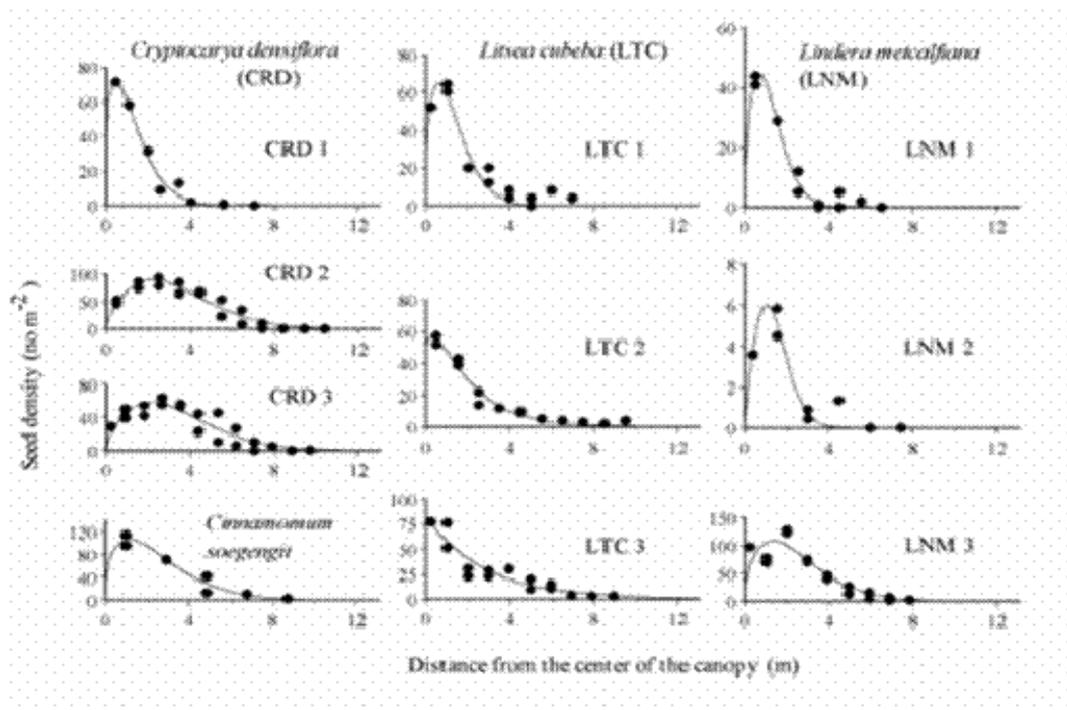


Fig. 3. Seed dispersal curves for ten sample trees of four Lauraceae species. Solid lines represent regression lines based on the Weibull-distribution seed dispersal model (see text for details, see also Table 2 for the coefficients of the model). Note that scales of y-axis are standardized to make the total area below the lines of the same magnitude using the regressed Weibull-distribution models in order to show the differences in dispersal patterns clearly.

Table 3. Coefficients of the Weibull distribution seed dispersal model for trees of four Lauraceae species; *Lindera metcalfiana* (LNM), *Litsea cubeba*, *Cryptocarya densiflora* (CRD), and *Cinnamomum soegengii* (CIS). Mean distance stands for the mean value of the Weibull distribution, $E(x)$. See text for details of the model.

Mother tree	DBH (cm)	Height (m)	Coefficients			Mean distance (m)	Total seed production (No./tree)
			N	a	m		
LNM1	20.6	18.7	76.2	1.305	1.585	1.2	560
LNM2	26.7	21.9	11.0	1.525	1.895	1.4	93
LNM3	30.2	23.4	391.4	2.718	1.506	2.5	6029
LTC1	13.4	13.9	123.0	1.404	1.427	1.3	985
LTC2	16.0	15.8	142.6	1.981	1.121	1.9	1701
LTC3	23.6	20.3	229.2	2.762	1.000	2.8	3977
CRD1	24.2	20.7	132.0	1.355	1.316	1.2	1035
CRD2	37.5	26.2	425.5	3.736	1.701	3.3	8910
CRD3	46.1	28.9	278.3	3.688	1.673	3.3	5759
CIS	40.9	27.4	398.8	2.773	1.402	2.5	6331

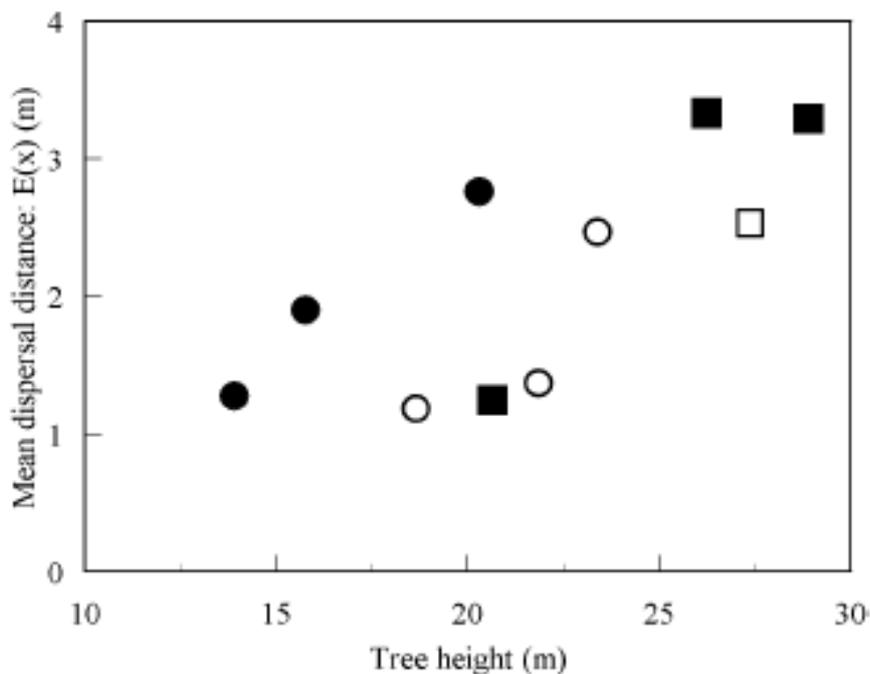


Fig. 4. Relationship between tree height and the mean of Weibull distribution, $E(x)$, which is an index of mean seed dispersal distance (see text for the model). Open squares: *Cinnamomum soegengii*, closed squares: *Cryptocarya densiflora*, open circles: *Lindera metcalfiana*, closed circles: *Litsea cubeba*.

It should be noted that the estimated seed dispersal in this study might be considerably underestimated especially for *Litsea* and *Lindera* because their seeds are dispersed mainly by birds. Turner [23] reviewed seed dispersal patterns of zoochorous tropical trees and found that at least half of

any seed crop falls beneath the parent crown but that the tail of the distribution is generally long. In our study, we observed that some of the fruits in the traps and transects had endocarps from which exocarps and mesocarps had been removed, suggesting bird-dissemination [24]. However, the proportion of bird-disseminated seeds was unclear. The proportion of bird-disseminated seeds was reported to be highly varied even among conspecific trees in a forest. The proportions of fruits removed by birds were 0-100% with a mean value of 46.2% for 29 *Ocote tenera* trees, a small tree species of Lauraceae at a Costa Rican tropical montane forest [7]. Only 17% of mature fruits were dispersed by birds for a temperate deciduous canopy tree species of Lauracea, *Cornus controversa*, in Japan [24]. Since bird-disseminated seeds are generally dispersed farther than directly fallen seeds [24], our method possibly missed long-dispersed seeds. Therefore, we should conclude that the dispersal distance of all studied species was very limited (less than 12 m) but that some seeds were possibly dispersed further by birds especially for *Lindera* and *Litsea*. Quantitative studies on bird dispersal are necessary to understand fully the seed dispersal of bird-dispersed species, though they are generally very difficult [24].

Seed production

Estimated total seed production differed among species and the sample trees within the same species (Table 3). Figure 5 shows the relationship between the leaf dry weight and fruit dry weight of each sample tree. The leaf dry weight of each tree was estimated from its diameter and height using the allometric equations of Yamakura *et al.* [25]. Each sample tree of the two shade-tolerant canopy species, *Cinnamomum* and *Cryptocarya*, produced a comparable weight of fruit to its total leaf dry weight. Rokujo [26] reported that the fruit weights of four shade-tolerant species were similar to their leaf weights in a Bornean tropical rain forest during a mast fruiting year. It is noteworthy that climax species produced a similar mass of fruit on a dry matter base during a single fruiting event regardless of species and in both a tropical rain forest and a tropical montane forest. We cannot conclude whether similar relationships between leaf mass and fruit production would be found more generally in other species and forests, because there are no other quantitative studies on fruit production and leaf mass of individual trees, as far as we know. We need to accumulate more data on fruit production of individual trees.

In contrast to the shade tolerant species, the two pioneer species, *Litsea* and *Lindera*, produced less than 3% of the total leaf weight in most sample trees (Fig. 5). This seems inconsistent with the general idea that pioneers make more effort in reproduction and produce larger number of smaller seeds comparing to the climax species [27]. However, in spite of the relatively small allocation to the fruit mass, *Litsea* and *Lindera* produced a comparable or rather larger number of seeds than *Cryptocarya* and *Cinnamomum* did when similar-sized trees were compared (Table 3). This is because the fruits and seeds of the two pioneers were much smaller (Table 1). Thus, the larger number of seeds produced by pioneers does not necessarily indicate the larger allocation to reproductive organs. It is yet to be studied whether pioneers generally allocate less to seeds and fruits than climax species, as was shown in this study. Do pioneers produce much larger number of seeds merely by making their fruits and seeds small? Or, do they allocate more to reproduction as well? The reproductive allocation of the

tropical trees need to be further studied and long-term ecological research should be done to conclude this.

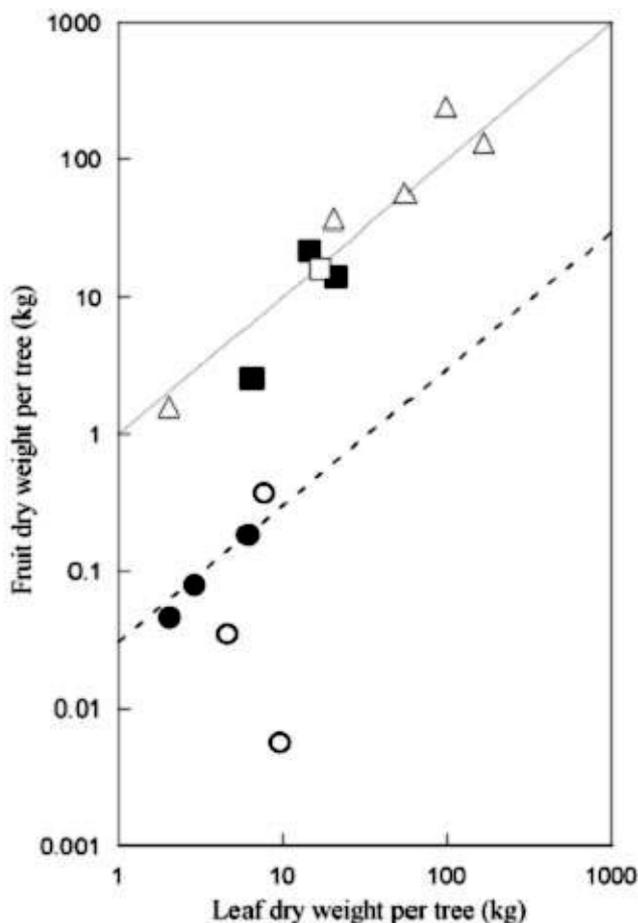


Fig. 5. Relationship between leaf dry weight and fruit dry weight of individual trees for four Lauraceae species in a montane forest of Thailand (this study) and four species of a tropical rain forest in Sarawak, Malaysia [26]. Open square: *Cinnamomum soegengii*, closed squares: *Cryptocarya densiflora*, open circles: *Lindera metcalfiana*, closed circles: *Litsea cubeba*, open triangles: Bornean rain forest species, i.e. *Dryobalanops aromatica* (Dipterocarpaceae), *Dryobalanops lanceolata* (Dipterocarpaceae), *Shorea xanthophylla* (Dipterocarpaceae), *Drypetes xanthophylloides* (Euphorbiaceae). The solid and dotted lines stand for $y = x$ and $y = 0.03x$, respectively.

Conclusion

This study, which covers a period of 2 years, shows firstly that the fruiting of the four studied Lauraceae species do not occur annually in a tropical montane forest in Thailand, though there are relatively distinct seasons in the climate there. Secondly, it was found that tree height seems likely more important than fruit size in seed dispersal, at least in the Lauraceae species studied. The short dispersal distances observed in the four species suggest a strong dispersal limitation. Furthermore, for

shade-tolerant species in this study, i.e. *Cinnamomum soegengii* and *Cryptocarya densiflora*, there was no difference between the percentage of seed germination and seed survival away from the mother tree. For the two pioneer species, i.e. *Litsea cubeba* and *Lindera metcalifiana*, germination was not observed during the two-year study period. So, relationship between seed production and germination from mother tree could not be clarified. The very limited seed dispersal of all the species suggests the possibility of ‘seed limitation’, and thus, the importance of seed sources for their conservation. Though this study obtains some interesting information on seed production of Lauracea species, further long term studies are required on phenology of Asian tropical montane forests. This study also suggests that more data are needed to understand fully the ecology of reproduction of Lauraceae, though there is a considerable number of studies on the phenology and the reproduction in the neotropics. The most recommendable subjects of future researches are 1) proportion and distance of bird-dispersed seeds, and 2) allocation to reproductive and vegetative organs by individual trees.

Acknowledgements

This study was conducted with the permission of the Royal Forest Department and the National Research Council of Thailand. This study was supported by Grants-in-Aid from the Ministry of Education, Sciences, Sports, and Culture of Japan (Nos. 08041155 and 11691194). We thank Mr. A. Mathavararug, superintendent of Doi Inthanon National Park, and his staff for their kind support. We also thank Dr. T. Santisuk and staff of the Forest Herbarium, Royal Forest Department, Dr. J. F. Maxwell (Faculty of Science, Chiang Mai University), Dr. W. Nanakorn (The Botanical Garden Organization, Prime Minister’s Offices) and Dr. M. Hara (Natural History Museum and Institute, Chiba, Japan.) for their kind support in identification of species. Many people have contributed to the success of the 15-ha Forest Dynamics Plot; to all of them we are deeply grateful.

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