Niche Differentiation and Sympatric Coexistence of Fagaceae Tree Species in a Tropical Montane Forest in Northern Thailand

（北タイの熱帯山地林におけるブナ科樹種のニッチ分化と同所的共存）

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Hideyuki Noguchi
（野口 英之）
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ACKNOWLEDGEMENT

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CHAPTER 1. INTRODUCTION

Tropical montane forest is one of the most complex and species rich ecosystems on the earth. It is located in the altitude higher than ca 1000m in tropical regions including Asia, Africa and Latin America and differ from the tropical lowland forests in physiognomy, flora, and fauna (Richards 1952). On most tropical mountains there is distinct ‘cloud belt’ or persistent fog (mist), which has important effect on the vegetation (e.g. Richards 1952; Grubb 1977a; Ohsawa 1995). Physical conditions in montane zone are quite different from those in lowlands in temperature, precipitation, atmospheric humidity, soil characteristics, solar radiation and wind velocity (e.g. Grubb 1977a; Kapos & Tanner 1985; Stadtmuller 1987; Bruijnzeel & Veneklaas 1998). As montane forest is isolated in high altitude, surrounded by different vegetation types, speciation of biota is promoted by this isolation (Gentry 1992), and tropical montane forests have become hotspots of species diversity, which harbor a high proportion of endemic species (Aldrich et al. 1997; Myers et al. 2000; Brooks et al. 2002; Sodhi et al. 2004).

Montane forests at different localities are classified into lower and upper montane forests (Richards 1952; Whitmore 1975; Grubb 1977a; Santisuk 1988; Ohsawa 1991; Ohsawa 1995) by temperature and physiognomic differences of the forest. Though the boundary line between these two vegetations is not always distinct, this transition occurs at a temperature sum of 85 ºC·month (Ohsawa 1991). Lower montane forests are usually located below the prevailing mist belt (Santisuk 1988) where the physiological conditions are usually more favorable for plant growth than in the upper montane forests (Ohsawa 1995). Canopy of tropical lower montane forest is higher than that of upper montane forest, and emergent trees, which are higher than the surrounding canopy trees appear in the lower montane forest (Ohsawa 1991). Fagaceae tree species, which consists of 8 genera, and c.a. 1000 species in temperate and tropical forests around the world (Heywood 1993), are the main components of tropical lower montane forest in South-east Asia, along with evergreen trees of Lauraceae, Theaceae, and other families (Santisuk 1988; Ohsawa 1993). The vegetation of this type of forest has close affinity to the temperate evergreen forest of East Asia (Kira 1991; Ohsawa 1991; Tagawa 1995), which is also called as “temperate rain forest” (Schimper 1903), “subtropical evergreen broad-leaved forest” (Hou et al. 1956), “lucidophyll forest” (Kira 1991), or “oak-laurel forest” (Tagawa 1995).

In South-east Asia, studies of tropical montane forest have been conducted on mountains in Philippines (Buat & Okitsu 1998), Indonesia (Yamada 1977; Ohsawa et al. 1985), Malaysia (Procotor
et al. 1988; Kitayama 1992; Nakashizuka et al. 1992), Brunei (Pendry & Proctor 1997), and Thailand (Ogawa & Saito 1965; Robbins & Smitinand 1966; Santisuk 1988; Maxwell et al. 1997; Maxwell & Elliot 2001; Maxwell 2007). However, most of the conventional studies put on focuses only on floral compositions (Richards 1952), zonation along elevations (Richards 1952; Ogawa et al. 1961; Kitayama 1992). Physiological traits of plants (Kitayama 1995) and habitat associations of species (Aiba et al. 2004) are studied in Mt. Kinabalu, east Malaysia, but demography and regeneration process of the component species had never studied with a large-scale permanent plot (Condit 1995; Yamakura et al. 1995; Ashton 1998; Bunyavejhewin et al. 1998) in the tropical montane forest in Asia before the establishment of the 15-ha study plot in Mt. Inthanon in northern Thailand (Hara et al. 2002; Sri-ngernyuang 2003; Sri-ngernyuang et al. 2003b; Kanzaki et al. 2004), which was the study site of this research.

Tropical montane forests of northern Thailand occur in the altitude higher than 1000m asl (Smitinand 1989). The transitional zone between lower and upper montane forest is ca 1800m asl in this region (Santisuk 1988). I have selected a forest in an upper limit of a tropical lower montane forest of Mt. Inthanon (ca 1700m asl) as a study site because the forest of Mt. Inthanon has unique and diverse flora consists of several plant geographical elements; India-Malesian, India-South China-Indochina, East Himalayan, in addition to endemic ones (Hara et al. 1996) and tree species diversity in Mt. Inthanon is highest around this altitude (Teejuntuk et al. 2002) The ecological traits of the component species, which contribute to maintain this species diversity of this forest, are almost unknown except Lauraceae tree species, which were studied thoroughly in the preceding thesis by Sri-ngernyuang (2003).

Fagaceae is one of the most dominant families in this forest along with Lauraceae, and eight species of this family is found in the study forest in the preliminary survey, but their ecological traits to enable this sympatric coexistence is not yet revealed. The main objective of this thesis is to examine how the habitat differentiation along the topographic gradients, and the difference of regeneration traits of the Fagaceae tree species contribute to enable their sympatric coexistence in a tropical lower montane forest in northern Thailand. This thesis consists of four chapters including this. In Chapter 2, habitat differentiation of the species was examined using torus randomization techniques. In Chapter 3, seed dispersal of two species of genus *Quercus* is analyzed using the regression of the seed density along distance from the mother trees by a Weibul function model based on the field data. In Chapter 4,
difference of demographic process of seeds and seedlings of two *Quercus* species were uncovered by the repeated observations.

**Description of the study site**

This study was conducted at the upper limit of a lower montane forest (ca 1700m asl) at Doi Inthanon National Park in northern Thailand (18°31′N, 98°30′E). Mt. Inthanon, which is in the park, is the highest mountain in Thailand (altitude 2565 m). This mountain is a part of the Thanon Thongchai Range, a southern extension of the Shan hills of Myanmar.

The mother rock of the study site is Pre-Cambrian gneissic, and the soil is coarse sandy loam (Pendleton 1962; Kanzaki *et al.* 2004). The annual mean rainfall and the mean monthly minimum and maximum temperatures at the Royal Project Doi Inthanon Station (1300m asl, 1993–1999) were 1908 mm, 16.1 °C, and 25.1 °C, respectively. The climate, strongly influenced by the monsoon, has three distinct seasons: the rainy season (June–October), the cool and dry season (November–February), and the hot and dry season (March–May). The lowest and highest monthly rainfall was 3.4mm in January and 371.3mm in September, respectively.

Fagaceae and Lauraceae trees are the main components of the study forest, and most of the species of both families reaches to the canopy layer. Species diversity of Fagaceae trees is quite high in Mt. Inthanon, and 30 species of 3 genera are recorded (Hara, pers. comm.). Flora of Mt. Inthanon including the forest outside the plot is documented by Hara *et al.* (2002) and vegetation of tropical upper montane forest in higher altitude than the study site is documented by Khamyong *et al.* (2004).
CHAPTER 2. HABITAT DIVERGENCE IN SYMPATRIC FAGACEAE TREE SPECIES OF A TROPICAL MONTANE FOREST IN NORTHERN THAILAND

INTRODUCTION

There is an ongoing debate on the questions of whether tropical trees are specialized to species-specific habitats, or whether their spatial distributions are random in local plant communities (Wong & Whitmore 1970; Ashton 1976; Hubbell 2001). The recent development of statistical methods utilizing randomization techniques (Legendre 1993; Plotkin et al. 2000; Harms et al. 2001; Itoh et al. 2003) has provided evidence that tree distributions are non-random, and that they are related to habitat differences, even on a local scale, in various types of tropical forests (Clark et al. 1998; Harms et al. 2001; Itoh et al. 2003; swamp forests: Miyamoto et al. 2003; montane forests: Sri-ngernyuang et al. 2003b; lowland rain forests: Cannon & Leighton 2004; Potts et al. 2004). These findings suggest that the majority of tropical trees are habitat specialists and that habitat specialization may contribute to the maintenance of species diversity in tropical tree communities.

There are varying views on the contribution of habitat specialization to the coexistence of species in tropical tree communities. Harms et al. (2001) reported that 64% of 171 tree species in a Panamanian forest were habitat specialists, but argued that habitat specialization may not contribute significantly to their coexistence because many of the species showed similar habitat associations. Valencia et al. (2004) reported a similar conclusion for an Amazonian rain forest. In contrast, some reports have suggested that habitat specialization contributes significantly to the coexistence of local species in various types of tropical forest (Clark et al. 1998; Webb & Peart 2000; Potts et al. 2004).

However, habitat specialization does not always explain the coexistence of species because species specializing to the same habitat cannot coexist by way of habitat specialization. Habitats of specialist species must be divergent from each other for coexistence. In this research, I distinguish explicitly between ‘habitat specialization’ and ‘habitat divergence’. I use ‘habitat specialization’ when a species shows skewed distribution to any habitat. ‘Habitat divergence’ is used when a pair of species specializes in different habitats. I also refer to ‘habitat convergence’ when two species specialize in the same habitat.

Most of the previous studies on habitat specialization have lacked a quantitative analysis of habitat
divergence. To evaluate the importance of habitat specialization to the coexistence of species, and the degree of habitat divergence, quantitative analysis of the relationships between the habitats of the different species is needed.

In the present study, I analyzed habitat specialization and habitat divergence for eight sympatric Fagaceae species along topographic gradients in a tropical montane forest in northern Thailand. Topography is widely recognized as one of the major factors that create diverse habitat conditions and promote local species diversity in tropical forests (Harms et al. 2001; Potts et al. 2004). I selected the Fagaceae because they are one of the most dominant and diverse families of canopy trees in Asian tropical montane forests (Ohsawa 1991; Kitayama 1992; Tagawa 1995), including the study site (Robbins & Smitinand 1966; Santisuk 1988; Hara et al. 2002; Teejuntuk et al. 2002; Sri-ngernyuang et al. 2003b; Kanzaki et al. 2004).

The specific hypotheses addressed in this chapter were: (1) The sympatric Fagaceae species are habitat specialists in relation to topography. (2) Their habitats are divergent from each other along the topographic gradients. Firstly, habitat associations of each species were examined statistically using randomization tests. Then, I tested whether the overlaps of species-specific habitats were significantly smaller than expected by chance.

**METHODS**

*Plot establishment*

This study was conducted at the upper limit of a lower montane forest (c. 1700m asl) at Doi Inthanon National Park in northern Thailand (18°31’N, 98°30’E). A permanent plot of 300×500m was established at the study site. The plot was divided into 1500 squares of 10×10 m. The relative elevations at all corner posts of each square were measured using a surveying instrument with a compass and level meter (LS-25, Ushikata Co. Ltd., Japan). All of the self-standing shrubs and trees of at least 1 cm dbh (stem diameter at 140 cm above the ground) in each square were labeled, mapped, dbh measured, and species identified (Hara et al. 2002; Sri-ngernyuang et al. 2003b; Kanzaki et al. 2004). Eight and 30 Fagaceae species were present in the plot and the entire national park, respectively (Hara, pers. obs.).

The voucher specimens were stored in the Herbarium of the Natural History Museum and Institute,
Chiba in Japan, and duplicate specimens were sent to the Royal Forest Department of Thailand and Chiang Mai University.

**Habitat association of each species**

To test the significance of the relationship between habitat and tree distribution for each species, I adopted a chi-square test combined with a Monte Carlo simulation. I selected four topographic variables as indices of habitat conditions: relative elevation, slope inclination, aspect and index of convexity (IC), following the method of Yamakura et al. (1995). Those four indices were calculated or regressed for each square based on the relative elevations at the four corners of each. IC indicates the difference between the mean altitude of the focal square and that of the surrounding 12 corners; a positive value for the IC indicates convex local landforms and a negative value indicates a concave slope. The IC was calculated for only 1344 of the 1500 squares as the squares on the outer margin of the plot could not be calculated according to the definition (Yamakura et al. 1995). The aspect value was ordered from west (0°) to east (180°), ignoring the south–north direction. This order was chosen because the frequency of the wind direction was highly skewed to the west, except during the cool and dry season (November–February; pers. obs.).

Thus, in this study, the west and east aspects stand for the windward and leeward slopes, respectively. For details of the calculation of the topographic indices, see Itoh et al. (2003) and Yamakura et al. (1995).

In the study plot, elevation was positively related to the IC (Pearson’s correlation coefficient, $r=0.477$, $P<0.01$) and the slope aspect ($r=0.100$, $P<0.01$). Thus, more convex and westward slopes were distributed at higher elevations in the plot. Slope inclination and aspect were negatively correlated ($r=-0.275$, $P<0.01$), indicating that westward slopes tended to be steeper than eastward ones. The correlations of the other pairs were not significant ($P>0.05$).

A chi-square test with a Monte Carlo simulation (Plotkin et al. 2000) was conducted to test the significance of habitat specialization. For this analysis, I sorted the 10×10-m squares into four classes of each topographic variable, so that the total area of each class was the same. I calculated the following value for each species and each topographic variable:
\[ \chi^2 = \sum_{i=1}^{n} \frac{(E_i - O_i)^2}{E_i}, \]  
(Eq. 2-1)

where \( n \) is the total number of topographic classes (four in this study) and \( E_i \) and \( O_i \) are the expected and observed number of trees in the \( i \)th topographic class, respectively. The \( E_i \) was the same for all habitat classes, as the total area of each class was the same. If spatial distributions of species and topographic variables were spatially clumped, the assumption of the conventional chi-square test must have been violated and \( \chi^2 \) could not follow the chi-square distribution (Legendre 1993). Thus, I conducted a torus random shift to obtain significance levels (Lotwick & Silverman 1982; Harms et al. 2001). The original tree map of each species was randomly shifted along the two rectangular coordinates about a two-dimensional torus, in which the opposite edges of the study plot were adjoined so that shifted trees were not located outside the study plot. The torus shift maintains the spatial aggregation of trees but changes the relationship between the tree distribution and topographic variables. The torus shift has been used in many studies on habitat association in tropical forests, including Harms et al. (2001), Itoh et al. (2003), Potts et al. (2004), and Sri-ngernyuang et al. (2003b). The torus shift was repeated 9999 times for each species, and the \( \chi^2 \) was calculated for each topographic variable in each simulation. A species was considered significantly nonrandom in relation to the habitat when the proportion of simulated \( \chi^2 \) values which exceeds the observed one was smaller than 0.05.

**Habitat overlap between species**

To quantify the degree of habitat overlap between the species, I employed the following index of Whittaker & Fairbanks (1958):

\[ C_{ij} = 1 - 0.5 \sum_{k=1}^{n} |p_{ik} - p_{jk}| \]  
(Eq. 2-2)

where \( n \) is the total number of topographic classes (four in this study) and \( p_{ik} \) and \( p_{jk} \) are the relative abundances of the species \( i \) and \( j \) in the \( k \)th topographic class, respectively. The relative abundance is the total number of individuals in the focal topographic class divided by the total number of each species in the entire plot. \( C_{ij} \) takes values from 0 (no overlap) to 1 (complete overlap), depending on the degree of overlap. I calculated the \( C_{ij} \) for all pairs of the eight study species (28 pairs) for each of the four topographic variables.
To test the significance of the empirical $C_{ij}$, I conducted a Monte Carlo simulation as follows. Torus random shifts were conducted independently for the original tree maps of the eight study species. The $C_{ij}$ was calculated for all possible species pairs (28 pairs) based on the shifted tree maps and each of the four topographic maps, which were as the original. In this procedure, the spatial association between the species and that between the species and the topography were randomized, but the spatial aggregation of each species was kept as per the original. The torus shift was repeated 9999 times, and the overlap between each species pair was considered significantly smaller or larger than expected when the proportion of simulated $C_{ij}$ values not exceeding the observed one ($Prop.$) was smaller than 0.025 or larger than 0.975, respectively. Significantly smaller and larger overlaps indicate divergence and convergence of two species along a focal topographic gradient, respectively. To determine the total habitat divergence among the eight species, the mean $C_{ij}$ of the 28 species pairs was also tested for each topographic variable using the same simulation procedure. Different numbers of topographic classes (four to twelve classes) were tried, and there were no critical differences in the results of either the habitat association or the overlap of the species. To examine the effect of abrupt changes of habitat at the edges of the original plots in torus shifted maps, I have tried the similar analyses using another kind of randomization, i.e. random shifting of plots in expanded topographic maps obtained by mirror image reflection at boundary edges (Cannon & Leighton 2004). The differences of the results between those randomizations were negligible; therefore, I will refer only the results of torus shift randomizations.

RESULTS

Fagaceae trees in the plot

There were 73 655 trees of 111 genera and 162 species in the plot, including three genera and eight species of the Fagaceae (Table 1, Figure 2.1). The Fagaceae were the most dominant and the second-most-abundant family, occupying 20.2% and 13.1% of trees $\geq$ 1 cm dbh in basal area and number, respectively (Table 1). The second-dominant and the most abundant family was the Lauraceae (14.7% in basal area and 14.6% in number, with 25 species). The family with the third-largest basal area was the Cornaceae (11.9%, with one species). At the species level, none of the Fagaceae species was exceptionally abundant. Their rank in total basal area ranged from second
(Quercus eumorpha, 8.5%) to 44th (C. accuminatissima, 0.5%). For more details on the floristic composition of this study plot, refer to Hara et al. (2002).

**Habitat association of each species**

All of the study species showed significantly non-random distributions in at least one of the four topographic variables, indicating that they were all habitat specialists (Table 2.2). The IC had the largest effect; all of the study species except L. echinops had significantly biased distributions in relation to the IC. There were no distinct species groups with similar habitat association for any topographic variable (Figure 2.2). Rather, the habitat association of each species changed along each topographic gradient. Although C. acuminatissima, C. calathiformis, Q. eumorpha and L. aggregatus were the most abundant in the largest IC class, the degree of skewness varied (Figure 2.2). Quercus brevicalyx, C. purpurea and L. vestitus were positively associated to the second smallest IC class. Two Castanopsis species, C. calathiformis and C. purpurea, had skewed distributions toward the highest and lowest elevation classes, respectively, although the latter was not statistically significant. All of the Lithocarpus species were significantly biased in distribution, and most abundant in the steepest slope class. Quercus eumorpha and C. acuminatissima were more abundant in the westward slopes, although the latter was not statistically significant.

**Habitat overlap**

Out of the 112 possible combinations of species pairs and topographic variables, 18 pairs (16%) showed significantly smaller overlaps than expected, indicating habitat divergence (Table 2.3). However, two combinations (1.8%) had significantly larger overlaps, which indicate habitat convergence (Table 2.3). The most important variable in habitat divergence was the IC, along which ten species pairs (36%) had divergent distributions (Table 2.3). For relative elevation, four species pairs had divergent habitats (Table 2.3). There was no divergent pair in slope inclination, although two pairs had convergent distribution in this gradient (Table 2.3). There were four and one species pairs with significantly smaller and larger overlaps, respectively, in slope aspect (Table 2.3). All of the divergent pairs in this gradient contained either C. acuminatissima or Q. eumorpha, the distributions of which were highly biased toward convex and westward slopes (Table 2.3).
The mean overlap value for all 28 pairs was significantly smaller than expected in the IC (0.764, Prop.=0.002), marginally but not significantly smaller in the elevation (0.716, Prop.=0.026), and not statistically different in slope inclination (0.869, Prop.=0.745) and aspect (0.793, Prop.=0.107), respectively.

**DISCUSSION**

**Habitat divergence of the Fagaceae**

The results of the current study indicate that all eight Fagaceae species are specialized to certain topographic habitats within the local scale studied (15 ha). However, habitat specialization does not always result in the coexistence of species with similar specialties. The importance of habitat specialization in the coexistence of species depends on how their habitats are related to each other (Harms *et al.* 2001; Itoh *et al.* 2003).

For simplicity, I assume here three typical patterns of relationships among habitat-specialist species (Figure 2.3). First, their habitats are significantly divergent from each other (Figure 2.3a). Second, the species can be classified into a few groups of multiple species by the similarities in their habitats (Figure 2.3b). Third, their habitats shift gradually along the habitat axis, with large overlaps with neighboring species (Figure 2.3c). In the last case, I cannot distinguish clear species groups with the same habitat, as is possible with the second case. Of course, these patterns are not mutually exclusive, and mixtures of these patterns might be found within a local tree community. However, for simplicity, here I will consider each pattern independently.

The predicted patterns of occurrence of convergent and divergent species pairs in the three habitat patterns differ.

For the first pattern, I expect only habitat divergence for most (or all) species pairs. The second pattern may be supported when I find habitat convergence between species in the same habitat groups and divergence between pairs belonging to different groups. For the third pattern, no habitat convergence is expected, and divergence would be observed between species with more distantly located habitats. In the last case, the divergence might be undetectable between pairs with relatively similar habitats because of the larger overlaps.

The current results suggest that the third habitat pattern is applicable to the Fagaceae species along
the topographic habitat axis, especially with slope convexity (IC). A large number of species pairs showed insignificant differences in habitat overlap (Table 2.2), suggesting that not all of the species were divergent from each other. I found only two cases of convergence out of 112 possible species and topography combinations, a result that rejects the second pattern. The relatively large overlaps between species distributed in neighboring habitats, and the divergence between species associated with contrasting habitats on the topographic gradients support the third pattern. The gradual changes in tree frequency along the IC axis (Figure 2.2) also support this conclusion.

The gradual shift of habitat makes it difficult and inappropriate to classify the species into a few distinct topographic habitat groups, such as valley or ridge species. This might be true not only for topography but also for other continuous habitat variables, such as water and light conditions and soil nutrients. Therefore, it may be less informative and possibly misleading in habitat studies to make distinct habitats depend on continuous gradients, unless I have good reasons to define proper thresholds.

There have been several studies that have analyzed habitat specialization with continuous gradient variables (Miyamoto et al. 2003; Potts et al. 2004). However, none of them analyzed quantitatively the relationship between species-specific habitats. There are no standard statistical methods for such an analysis. The development of proper analytical methods using continuous habitat variables is needed for detailed analyses of habitat divergence.

The significantly smaller mean overlaps than predicted in the IC and the altitude confirmed the existence of habitat divergence among the sympatric Fagaceae trees. Therefore, habitat specialization should contribute at least partly to their coexistence in the study forest. However, because their habitats were not highly divergent from each other, shifting gradually, rather, with large overlaps between neighboring species, habitat divergence in relation to topography cannot explain the total species richness of the Fagaceae trees in the study plot. Further studies with proper analytical methods for continuous habitat variables will be required to evaluate the extent of the contribution of the observed habitat specialization and divergence to the coexistence of these species.

**Factors in the habitat divergence of the Fagaceae**

The results of this study indicate that the most important topographic gradient for the distribution of the Fagaceae trees was slope convexity. A similar result was obtained for the Lauraceae, the most
species-rich family in our study plot (Sri-ngernyuang et al. 2003a). Takyu et al. (2002) also reported differences in the vegetation between ridges and valleys in a Bornean montane forest. The position on a slope is therefore important for tree distribution in Asian tropical montane forests as well as in lowland tropical forests, in which many studies have revealed that microtopography has significant effects (Yamada et al. 1997; Yamada et al. 2000; seasonal forests: Bunyavejchewin et al. 2003; subtropical evergreen forests: Enoki 2003; Itoh et al. 2003; swamp forests: Miyamoto et al. 2003; lowland rain forests: Gunatilleke et al. 2006).

Microtopography and slope convexity are generally related to small-scale spatial variations in soil water conditions and nutrient status (Becker et al. 1988; Daws et al. 2002). Studies on the effects of topography in tropical lowland forests have suggested that either the soil water or the soil nutrient conditions, or both, affect tree distributions (Hirai et al. 1997; Clark et al. 1998; Itoh et al. 2003; Palmiotto et al. 2004). However, in a Bornean montane forest, Takyu et al. (2002) found no soil water deficit, even on ridges, throughout a 2.5-y study period, including a severe El Niño drought, possibly due to more frequent fog and rainfall than in lowland forests. The authors concluded that the soils were continuously wet in the montane forest and that the effects of topography were mediated not by the soil water conditions but by differences in the nutrient status related to the topography.

In contrast to the results of Takyu et al. (2002), some of my data and field observations suggest that soil water conditions have significant effects on tree regeneration in this study forest. Of all newly established seedlings, 32% of Quercus eumorpha seedlings and 28% of Q. brevicalyx seedlings were killed by water stress during the first dry season (pers. obs.). In the same site, more than 70% of the established seedlings of a common Lauraceae species, Cinnamomum cf. soenggii Kosterman, were also killed by water stress (Sri-ngernyuang et al. 2003). These observations suggest that water stress is a cause of the habitat associations, at least for these species. The differences in soil water conditions between the current study and that of Takyu et al. (2002) were probably due to the current study site being located in a strong seasonal climate. A distinct annual dry period occurs in northern Thailand, in contrast to the continuous wet weather in Borneo. The relationship between the microtopography and soil moisture in tropical montane forests may be different to those in aseasonal and seasonal climates. More studies on the relationship between microtopography, soil moisture and nutrient status, especially in the seasonal tropics, are needed to determine the relative importance of soil moisture and nutrients in local vegetation differences in tropical montane forests.
My results also suggest that wind has some effect on the tree distributions in the study forest. The west and east slopes in the study forest correspond to the windward and leeward aspects, respectively. Although the mean overlap was not smaller than expected by chance along the gradient of slope aspect, *Q. eumorpha* and *C. acuminatissima* showed strong associations with westward slopes. The spatial distributions of the two species skewed to higher elevations and larger IC values (Figure 2), where the wind should be stronger. Other species that were distributed at lower elevations showed no relationship to the aspect gradient. Therefore, the effects of wind may only be significant on ridges.

As is common in montane forests, the wind speed was high at the study site. The daily maximum wind speeds at the summit of Mt. Inthanon (altitude 2565 m) were >5 ms\(^{-1}\) almost every day, except during the cool dry season (November-February, from 1996 to 1997).

Although I do not have data for the wind at the study plot (altitude 1700 m), winds strong enough to affect the canopy trees were often observed in the plot (pers. obs.).

Strong wind may affect tree distributions through two possible mechanisms: mechanical stress (Grace 1977; Lawton 1982), and limitations in soil moisture, nutrients and/or light (Sun et al. 1996). At present, I have no information suggesting which mechanism is more important in the study forest. Monitoring of the wind in the study plot and studies of the effects of wind on tree growth will be necessary to reveal the mechanisms of the effects of wind on the habitat divergence of the study species.
Figure 2.1. Spatial distribution of Fagaceae trees with dbh ≥ 1 cm in a 15-ha study plot in a tropical montane forest at Doi Inthanon National Park, northern Thailand. Contour lines in the figures are drawn at 10-m intervals of the relative elevation.
Figure 2.2. Relative frequencies of eight Fagaceae species in four topographic gradients in a 15-ha study plot in a tropical montane forest at Doi Inthanon National Park, northern Thailand. Asterisks beside the species abbreviations indicate that the species distributions were significantly non-random in relation to the topographic gradients, judged by chi-square tests combined with Monte Carlo simulations. The species are sorted by the mean values of their topographic variances. See Table 1 for abbreviations of the species names.
Figure 2.3. Schematic examples of habitat structures of habitat-specialist species. Three patterns of specialisation along the topographic gradients are shown. The habitats of the species are completely divergent from each other (a). Species can be classified into a few groups of several species based on their habitat similarities (b). Habitats of species shift gradually along the habitat axis, with large overlaps with neighbouring species (c).
Table 2.1. Status of eight Fagaceae species in a 15-ha study plot in a tropical montane forest at Doi Inthanon National Park, northern Thailand. The species are presented in alphabetical order. Individuals with dbh larger than 1 cm were enumerated. Measurements of multiple trunks were included in the calculation of the basal area.

<table>
<thead>
<tr>
<th>Species</th>
<th>Abbreviation</th>
<th>No. of Individuals in 15 ha</th>
<th>Basal area (m² ha⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Castanopsis acuminatissima</em> (Blume) A. DC.</td>
<td>Ca</td>
<td>77</td>
<td>0.22</td>
</tr>
<tr>
<td><em>Castanopsis calathiformis</em> Kurz</td>
<td>Cc</td>
<td>3992</td>
<td>0.87</td>
</tr>
<tr>
<td><em>Castanopsis purpurea</em> Barnett</td>
<td>Cp</td>
<td>1411</td>
<td>0.57</td>
</tr>
<tr>
<td><em>Lithocarpus aggregatus</em> Barnett</td>
<td>La</td>
<td>467</td>
<td>0.49</td>
</tr>
<tr>
<td><em>Lithocarpus echinops</em> Hjelmq.</td>
<td>Le</td>
<td>428</td>
<td>0.35</td>
</tr>
<tr>
<td><em>Lithocarpus vestitus</em> (Hickel &amp; A. Camus) A. Camus</td>
<td>Lv</td>
<td>1246</td>
<td>0.65</td>
</tr>
<tr>
<td><em>Quercus brevicalyx</em> A. Camus</td>
<td>Qb</td>
<td>884</td>
<td>1.57</td>
</tr>
<tr>
<td><em>Quercus eumorpha</em> Kurz</td>
<td>Qe</td>
<td>1168</td>
<td>3.45</td>
</tr>
<tr>
<td>Total of Fagaceae</td>
<td></td>
<td>9673</td>
<td>8.17</td>
</tr>
<tr>
<td>Total of all species</td>
<td></td>
<td>73655</td>
<td>40.7</td>
</tr>
<tr>
<td>Dominance of Fagaceae (Total of Fagaceae / Total of all spp.)</td>
<td></td>
<td>(13.1%)</td>
<td>(20.1%)</td>
</tr>
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</table>
Table 2.2. Results of a test of habitat preference for eight Fagaceae species in a 15-ha study plot in a tropical montane forest at Doi Inthanon National Park, northern Thailand. The significance of their distributional bias along each topographic variable was judged by chi-square tests combined with Monte Carlo simulations. Proportions of simulated $\chi^2$ values obtained from 9999 torus shifts, which exceeds the observed one were indicated. Proportion values are indicated in bold letters when they are smaller than 0.05. See Table 2.1 for abbreviations of species names.

<table>
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<tr>
<th>Species</th>
<th>Relative elevation (m)</th>
<th>Slope inclination (°)</th>
<th>Slope aspect (°)</th>
<th>Index of Convexity (m)</th>
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</thead>
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<tr>
<td></td>
<td>Mean ± SD</td>
<td>Proportion</td>
<td>Mean ± SD</td>
<td>Proportion</td>
</tr>
<tr>
<td>Ca</td>
<td>-3.6 ± 11.8</td>
<td>0.100</td>
<td>26.6 ± 7.9</td>
<td>0.757</td>
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<tr>
<td>Cc</td>
<td>-4.8 ± 15.3</td>
<td><strong>&lt; 0.001</strong></td>
<td>21.0 ± 7.5</td>
<td>0.588</td>
</tr>
<tr>
<td>Cp</td>
<td>-28.4 ± 18.0</td>
<td>0.053</td>
<td>24.6 ± 8.9</td>
<td>0.358</td>
</tr>
<tr>
<td>La</td>
<td>-20.1 ± 17.1</td>
<td>0.424</td>
<td>26.6 ± 8.4</td>
<td><strong>0.004</strong></td>
</tr>
<tr>
<td>Le</td>
<td>-24.9 ± 17.7</td>
<td>0.215</td>
<td>26.8 ± 8.9</td>
<td><strong>&lt; 0.001</strong></td>
</tr>
<tr>
<td>Lv</td>
<td>-28.4 ± 17.6</td>
<td>0.157</td>
<td>25.7 ± 9.2</td>
<td><strong>0.002</strong></td>
</tr>
<tr>
<td>Qb</td>
<td>-28.4 ± 16.1</td>
<td>0.127</td>
<td>25.5 ± 8.5</td>
<td>0.161</td>
</tr>
<tr>
<td>Qe</td>
<td>-21.9 ± 18.7</td>
<td>0.891</td>
<td>26.8 ± 8.0</td>
<td>0.051</td>
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Table 2.3. Matrices for relative distributional overlaps along four topographic variables for eight Fagaceae species in a 15-ha study plot in a tropical montane forest at Doi Inthanon National Park, northern Thailand. The values above the diagonals are observed values of the overlap indices (Whittaker & Fairbanks 1958) of the focal species pairs, and those below the diagonals are the proportion of simulated $C_{ij}$ values obtained from 9999 torus shifts, which do not exceed the observed one. Species pairs with the proportion value less than 0.025 or more than 0.975 were indicated in bold or italic letters, respectively. The species are presented in alphabetical order. See Table 2.1 for abbreviations of species names.

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<th>Ca</th>
<th>Cc</th>
<th>Cp</th>
<th>La</th>
<th>Le</th>
<th>Lv</th>
<th>Qb</th>
<th>Qe</th>
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<tr>
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<td>0.85</td>
<td>0.44</td>
<td>0.63</td>
<td>0.52</td>
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<td>0.43</td>
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<tr>
<td>Cc</td>
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<tr>
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<td>0.89</td>
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<tr>
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<td>0.80</td>
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<tr>
<td>Le</td>
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<td>0.89</td>
<td>0.88</td>
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<td>0.932</td>
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<td>0.279</td>
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<td>0.143</td>
<td>0.384</td>
<td>0.663</td>
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<tr>
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<td>0.145</td>
<td>0.499</td>
<td>0.944</td>
<td>0.770</td>
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<th>Le</th>
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<td>0.89</td>
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<th>Le</th>
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<th>Qe</th>
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<td>0.59</td>
<td><strong>0.50</strong></td>
<td>0.54</td>
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<tr>
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<td>0.95</td>
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<tr>
<td>Lv</td>
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<td>0.909</td>
<td><strong>0.018</strong></td>
<td>0.205</td>
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<td>0.185</td>
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CHAPTER 3. SEED DISPERSAL OF TWO QUERCUS SPECIES

INTRODUCTION

Seed production and dispersal (Howe & Smallwood 1982; Nakashizuka et al. 1995; Clark et al. 1999; Willson & Traveset 2000; Vander Wall 2001) have important effect on the spatial distribution of individual trees (e.g. Vander Wall 2001), population dynamics of a given species, and community dynamics of the forest as a whole (e.g. Nathan & Muller-Landau 2000). If mature trees are characterized either by the spatially crowded or scattered distribution, their distribution patterns are partially the reflection of seed dispersal. For example, the long distance seed dispersal, including secondary dispersal by animals, enhances the survival chance of seeds, sending seeds to the better habitats for the seedling establishment (Howe & Smallwood 1982). The long distance seed dispersal is also effective for avoiding the resource competition between siblings and escaping the high risk of mortality due to disease fungi, insects and frugivores (e.g. Augspurger 1983, 1984; Forget et al. 1994; Forget et al. 1999; Hammond et al. 1999), which often occur around mother trees (Janzen 1970; Connell 1971).

The fate of dispersed seeds is affected not only by the physical environmental factors such as soil moisture but also by the fruiting behavior of other tree species. For seeds with higher palatability, the feeding behavior of animals is also crucial. Abundant seeds may saturate the demand of frugivores (Silvertown 1980), such as rodents and insects, and increase the number of uneaten seeds, while fungal pathogens may severely decrease the chance of seed and seedling survivals under canopies of their mother trees, where pathogen density is quite high. However, little is known about seeds’ circumstances because of difficulties in counting the per tree’s total number of dispersed seeds in short research periods, although the number of dispersed seeds is indispensable for describing the fate of dispersed seeds and sprouting seedlings.

Since the quantity of seeds, which are produced by mother trees, is too large to count directly, it is estimated by several hypothetical methods resting on some presumptions, such as the uniform spatial distribution of dispersed seeds within crown area (Greenberg 2000), mechanistic process of long distance seed dispersals (Nathan & Muller-Landau 2000; Clark et al. 2001). The statistical model of Weibul distribution is also reported to well represent the seed density around individual mother trees in
tropical (Rokujo 1998; Sri-ngernyuang 2003; Itoh et al. 2004) and temperate (Hirayama et al. 2004; Hirayama et al. 2008) forests. When a seed dispersal pattern is expressed by a statistical distribution function, seed production and dispersed seeds are easily estimable (Itoh et al. 2004). Variation of the seed production between mother trees can also be estimated by the statistical distribution.

In this study, I have investigated the seed dispersal of two tree species of genus Quercus, i.e., Quercus eumorpha Kurz and Quercus aff. brevicalyx A. Camus in the half area (7.5 ha) of the 15-ha plot in tropical lower montane forest of Doi Inthanon National park. The two species produced substantial amount of seeds at least for two years (1998-1999), providing the sufficient number of seeds for detailed analysis. Two species had outstanding biomass stocks among Fagaceae species and the whole species of the plot. Furthermore, they had contrasting spatial distribution along topography factors and their habitats represented an insignificant overlap. One species densely occurred at ridge terraces and upper western slopes, while the other had dispersed spatial distribution among the whole plot avoiding the domains of the former species (see Chapter 2).

Since the focal Quercus seeds do not have any specialized structure suitable for wind and mechanistic dispersal, the most of them fall beneath the crown of the mother trees. Seeds are foraged by rodents, birds, and insects. They are also heavily infected by fungal pathogens in humid forest floors. In temperate forest, the secondary seed dispersal by rodents and birds are reported for trees of the genus Quercus (e.g. Forget 1992, 1994, Yasuda 2000, Xiao 2005) If secondary dispersal plays important role in the population dynamics in this forest, many seedlings and saplings should be observed outside the boundary of possible primary dispersal.

Considerable number of seed might deserve to be foraged by animals and fungi in the monitoring duration of seed dynamics. Since the species of Quercus have inedible hard cupules, the number of cupules per tree was also counted for the better estimation of produced seeds. In this chapter, I have focused on the following three ecological aspects of seed dispersal and compared the analytical results between two species, in order to clarify the impact of seed production on post-seed-dispersal processes, which are related with species demography; i.e.

1) distribution density functions of seed dispersal for a) determining seed fecundity per tree and b) describing seed shadows in individual tree levels and population levels,

2) differences of seed dispersal within and between species, and

3) possible pass ways leading to secondary seed dispersal by animals.
METHODS

Seed dispersal in mature trees

Transect inventory of per tree seed-fall in eight sample trees

Focal 7.5-ha area

In a lower montane forest of Mt. Inthanon in northern Thailand (c. 1700m asl, 18°31’N, 98°30’E), a 15-ha permanent plot (300 × 500m) was established. All of the self-standing shrubs and trees with dbhs ≥ 1.0 cm in the plot were labeled, mapped, measured by dbh, and identified to species, as already described (See chapter 1 and 2 for the details). In the northern half area (7.5ha; 300 × 250m) of the plot, the seed dispersal study of selected mature trees was carried out by using transects for the inventory of fallen seeds. Transects were first established in 1998, when any forest inventory work was not performed in the other southern half area of the plot, although the plot demarcation had been completed. Hence, my study of seed dispersal was regretfully confined to the northern half area of the plot.

Mature trees

Fruiting did not occur in young small trees. It was highly correlative with tree size, suggesting the effect of tree maturity on fruiting. In my observation of seed fall, mature trees were discerned by the minimal dbh of fruited trees observed in 1998 and 1999. It was 27.9cm found in 64 fruited Q. eumorpha trees and 32.4cm in 39 Q. brevicalyx trees. It followed that the trees were considered to be mature, when Q. eumorpha and Q. brevicalyx trees had their dbhs ≥ 27.9 cm and ≥ 32.4 cm, respectively.

Eight transects for eight selected trees

The 1.0-m wide belt-transects with different lengths were established below the crowns of eight selected trees belonging to two species. The eight trees were isolated enough to exclude the contamination of seeds from other conspecific fruiting trees and their crown shapes were rather round and not irregular. The number of transects per species was four. The length of respective transects depended on the crown size of selected trees. All the transects had their starting points corresponding to the projected positions of the center of the crowns of selected trees and were extended to two opposite directions so as to include the change of seed density with respect to seed dispersal distance. Transects were subdivided into 1.0 m ×1.0-m quadrats for easily counting seeds and cupules (Table 3.1).

Handling of seeds and cupules occurred in transects

All seeds and current year cupules in each
1.0 m × 1.0-m quadrats were counted at every 8 to 30 day intervals during two observation periods from August 1998 to April 2000, and on 19 June 2000 and 10 December 2000 (30 times in total). To avoid errors in counting seeds, numbered plastic tapes with steel wires were placed besides every seeds, while current year cupules were removed from transects after counting. Current year cupules were easily distinguished from old cupules by the degree of decomposition.

**Supplementary inventory of per tree see-fall in 103 mature trees**

A set of three 1.0 m × 1.0-m quadrats was established under the canopies of respective 103 mature trees belonging to two species in the 7.5-ha plot. Fallen cupules in the respective quadrats were counted in August and September in 1999 for *Q. brevicalyx*, and July and August 1999 for *Q. eumorpha*. The number of examined trees was 64 in *Q. eumorpha* and 39 in *Q. brevicalyx*. The counted cupule data were used for estimating the coefficients of the seed dispersal model.

**Seed dispersal model applied to eight selected trees**

Use of cupule data Since the per tree number of cupules was larger than that of seeds in my observation, I used the number of cupules per 1.0 m × 1.0-m quadrat for the calculation of seed density along transects. Therefore, the total number of dispersed seeds per tree was calculated from cupule density. In two species, most of cupules fell down from mother trees together with seeds and were separated from seeds after falling on the ground.

Weibul distribution The change of seed density with respect to dispersal distance along transects was approximated by the Weibul distribution. In this study, the density of cupules (or seeds) per square meter at a given distance *x* (m) from the seed dispersal center was also approximated by Weibul distribution, which is written in the form,

\[
\rho_i(x) = N_i \cdot \frac{m_i}{a_i^{m_i}} x^{m_i-1} \exp\left(-\left(\frac{x}{a_i}\right)^{m_i}\right),
\]

Eq. (3-1)

where the symbol of \(\rho_i(x)\) represents the cupule density at *x* in a given mother tree with an identification number *i*, \(a_i\) (m) and \(m_i\) (m\(^{-2}\)) are the coefficients of Weibul distribution, \(N_i\) is the expected total number of seeds per transect in the *i*th mother tree. Out of the three coefficients, \(a_i\) and \(m_i\) are designated as a scale parameter and a shape parameter, respectively, as can be seen in their functional forms. Eq. (3-1) gives an exponential distribution of *x*, when \(m_i = 1.0\). When \(m_i \geq 1.0\),
Eq. (3-1) represents $x$ vs. $\rho_i(x)$ relations having the peak cupule density ($\rho_{i,\text{max}}$) at $x = a_i \left(1 - 1/m_i\right)^{1/m_i}$. The $\rho_{i,\text{max}}$ is expressed in the form,

$$
\rho_{i,\text{max}} = \frac{N_i m_i}{a_i} \left(1 - \frac{1}{m_i}\right)^{-\frac{1}{m_i}} \exp \left[-\left(1 - \frac{1}{m_i}\right)\right] 
$$

Eq. (3-2)

The above equation of $\rho_{i,\text{max}}$ leads to a numerical techniques to estimate $N_i$ when $a_i$, $m_i$, and $\rho_{i,\text{max}}$ are concretely given, i.e.

$$
N_i = \rho_{i,\text{max}} \frac{a_i}{m_i} \left(1 - \frac{1}{m_i}\right)^{-\frac{1}{m_i}} \exp \left[-\left(1 - \frac{1}{m_i}\right)\right] 
$$

Eq. (3-3)

The per tree total number of dispersed seeds of $i$th tree ($N^*_i$) is given by the arc-wise integration of Eq. (3.1), i.e

$$
N^*_i = 2\pi \int_0^\infty x\rho_i(x)dx = 2\pi a_i N_i \Gamma \left(\frac{1}{m_i}+1\right),
$$

Eq. (3-4)

where the symbol $\Gamma$ is the gamma function.

**Dependency of model coefficients on tree size**

The coefficient of $a_i$ in Eq. (3-1) and Eq. (3-2) is designated as the scale parameter of $x$ because it can adjusts the modal position of $x$ ($x = a_i \left(1 - 1/m_i\right)^{1/m_i}$), as already described. Therefore, $a_i$ appeared to be expressible by the exponential function of tree height, if a micro-meteorological rule with respect to wind was applicable to seed dispersal. The rule describes the exponential increase of wind speed with the increase of aboveground height, which is analogous to tree height. If seeds were blown by strong wind, seed should be sent far away from mother trees, resulting in large values of the coefficient $a_i$ of Eq. (3-1). Hence the focal meteorological rule of wind suggests the long distance seed dispersal in tall trees and the exponential increase of $a_i$ with respect to tree height. Following these considerations, the dependency of model coefficients on tree size, such as dbh and tree height, was examined. If the coefficients, $a_i$, $m_i$ and $N_i$ are expressible by the empirical or theoretical functions of tree size, the functions should offer me useful tools for the numerical simulation of seed dispersal. The allometric relations between different size dimensions led to an available numerical approach to estimate the tree size values of two Quercus species.

**Allometric relations**

Tree height values were calculated from dbhs using a height curve model describing the dbh vs. tree height relations. The height curve model was determined by observed data
of dbh and tree height. Tree height was measured in 15, 10 m × 10-m squares that were randomly selected in the 15-ha plot and covered the wide range of topography features. In tree height measurements, ten trees including largest and smallest individuals were selected in each sampling square. The dbh vs. tree height relation in each square was approximated well by the ‘generalized allometric equation’ model proposed by Ogawa et al. (1965), i.e.

\[
\frac{1}{H} = \frac{1}{A_k D} + \frac{1}{H^*_k}, \quad \text{Eq. (3-5)}
\]

where \(H\) is tree height in m, \(D\) is dbh in cm, \(A_k\) and \(H^*_k\) are the coefficients specific to a given 10 m × 10-m square marked by identification number \(k\). The coefficients, \(A_k\) and \(H^*_k\), were expressed by the topography indices, which have been introduced in Chapter 2, i.e.

\[
A_k = 0.0117 I_k + 1.690, \quad \text{Eq. (3-6)}
\]

\[
H^*_k = -0.4570 I_k - 2.786 C_k + 48.14, \quad \text{Eq. (3-7)}
\]

where \(I_k\) is the slope inclination, and \(C_k\) is the index of convexity of \(k\)-th square. These relationships were adopted to estimate tree height values in any one of squares (Kanzaki, pers. comm., Noguchi 1998). Since in the particular squares adjacent to the outer margin of the plot did not have \(C_k\) values, the average value of \(C_k\) (0.013) in other 10 m × 10-m squares was used for the substitution.

The above ground plant mass of individual trees was estimated by the following equations that were introduced by Ogawa and Saito (1965; referred from Naka 1982) in several temperate evergreen oak-laurel forests in Japan, i.e.

\[
w_S = 0.0396(D^2H)^0.9326, \quad \text{(kg, cm}^2\text{m)} \quad \text{Eq. (3-8)}
\]

\[
w_B = 0.00602(D^2H)^1.027, \quad \text{(kg, cm}^2\text{m)} \quad \text{Eq. (3-9)}
\]

\[
\frac{1}{w_L} = \frac{26}{w_S + w_B} + 0.02, \quad \text{(kg, kg)} \quad \text{Eq. (3-10)}
\]

where \(w_S\), \(w_B\) and \(w_L\) are dry weight dimensions of the stems, branches and leaves of individual trees, respectively, and \(D\) and \(H\) are dbh and tree height, respectively.

**RESULTS**

**Seed dispersal in an individual tree unit**

The seed-fall was observed for four *Q. eumorpha* trees and four *Q. brevicalyx* trees using survey
transects, as already described. Most of the seeds of *Q. brevicalyx* were dispersed in three months from May to July 1999, while *Q. eumorpha* trees dispersed their seeds in other months from March to May 1999 (for further details, see Chapter 4). The seed-fall data were fitted well to the seed dispersal model of Eq. (3-1), of which estimated coefficients for individual trees are listed in Table 3.1, together with other related variables. However, a data set of *x* vs. *ρ*(_i_(*x*)) relations from the particular one fruited tree of *Q. brevicalyx* was not covered by Eq. (3-1) because of the scarcity of dispersed seeds and cupules within the survey transect. Coefficients, *a*_i and *m*_i of Eq. (3.1), were estimated by the non-linear least squares method and their dependency on tree size was examined, as shown in Fig. 3.1. The coefficient *a*_i increased with an increase in tree height and could be approximated by an exponential equation, i.e.

\[
a_i = 2.04 \exp (0.0248 \cdot H_i), \quad (r^2 = 0.4998) \quad \text{Eq. (3-11)}
\]

where *H*_i is the height of the fruited tree. The estimates of *a*_i from seven fruited trees belonging to two species were combined together in the determination of Eq. (3-11) (Figure 3.1, Table 3.1). In contrast to *a*_i, the coefficient estimates of *m*_i appeared to be constant with respect to tree height, as shown in Fig. 3.1. Therefore, the seven observed *m*_i values were lumped together and their average was calculated and resulted in *m*_i = 1.36 (Table 3.1).

**Seed dispersal in a population unit**

The total number of mature trees was 64 in *Q. eumorpha* and 39 in *Q. brevicalyx* trees in the 7.5 ha area. Concerning these mature trees, three 1.0 m × 1.0-m quadrats for cupule enumeration were established under the respective crowns of all 113 trees. The cupules were counted in each quadrat and their quantity per quadrat was assumed to be equal to the quantity of seeds. Out of three records of the number of cupules per quadrat per tree, the largest observed record (*ρ*_i, maxjobs) was hypothetically considered to correspond to the quantity of *ρ*_i, max in Eq. (3-2) and Eq. (3-3). Substituting *ρ*_i, maxjobs into Eq. (3-3), we got the tentative estimates of *N*_i for all 113 trees. By combining the estimates of *N*_i with estimates of *a*_i calculated by Eq. (3-11) and constant *m*_i = 1.36 for all trees, and by using the model of Eq. (3-1), the seed dispersal was simulated for respective mature trees. Using the simulated results of *x* vs. *ρ*_i(*x*) relations, the total number of dispersed seeds per tree (*N*_i*) in Eq. (3-4) was calculated for respective trees. The mean *N*_i* was 3618.1 (± 6540.1 SD) in *Q. brevicalyx* and 2841.1 (±6199.1 SD) in *Q. eumorpha*. Variations of *N*_i* values were quite large in two species;
i.e. \( CV = 16769.5 \) in \( Q. \ brevicalyx \) and \( CV = 9686.1 \) in \( Q. \ eumorpha \). Hence, the total number of dispersed seeds per species population in 7.5 ha (\( Y_{seeds} \)) was given by multiplying mean \( N_i \) with the number of mature trees in the following way, i.e. \( Y_{seeds} = 141105.9/7.5 \) ha for \( Q. \ brevicalyx \) and 181833.4/7.5 ha for \( Q. \ eumorpha \).

In two species, a few number of mature trees with middle-sized dbhs had disproportionately high seed production, while most of the other trees dispersed the intermediate amount of seeds (Fig 3.2a and Fig. 3.2b). The 23.1% and 10.9% of mature trees of \( Q. \ brevicalyx \) and \( Q. \ eumorpha \), respectively, did not produce any seeds in 1999. Large individuals, possibly senescent trees, dispersed rather small quantities of seeds. The contribution of each mature tree to the total seed dispersal (or production) in a population unit (\( Y_{seeds} \)) was quite uneven among trees in two species (Figure 3.3). One tree with the largest seed production contributed 20.3 % in \( Q. \ brevicalyx \) and 19.3 % in \( Q. \ eumorpha \). Furthermore, the 50 % of \( Y_{seeds} \) was contributed to only four nature individuals in respective species (Figure 3.3).

**Spatial patterns of seed rain in two populations**

The aforementioned simulated seed dispersal patterns for 39 \( Q. \ brevicalyx \) and 64 \( Q. \ eumorpha \) trees were mapped together to visualize the variation of seed-fall density within the 7.5 ha area, as shown in Fig. 3.4. The spatial positions of mature trees as seed suppliers had strong influence on the spatial distribution of dispersed seeds. Most of the dispersed seeds concentrated below and around the crowns of mature trees. The overall mean densities of dispersed seeds per square meter were higher in \( Q. \ eumorpha \) (2.40 ± 12.0) than in \( Q. \ brevicalyx \) (1.78 ± 9.35; Wilcoxon rank sum test, \( W = 5297546, P < 0.001; \) Table 3.2). The proportions of areas, where more than one seed per square meter was expected, were 14.7% in \( Q. \ brevicalyx \ eumorpha \) and 17.1% for \( Q. \ eumorpha \), respectively. The slight difference between two proportion values was statistically significant (Table 3.2; chi-square test, \( \chi^2 = 6.10, P = 0.0135 \)). On the other hand, the proportion of areas, where more than 0.001 seed per square meter was expected, were significantly higher in the former species (54.3% in \( Q. \ brevicalyx \) and 42.7% in \( Q. \ eumorpha \); chi-square test, \( \chi^2 = 80.3, P < 0.001 \)).

The estimated dry weight of dispersed seeds per mature tree was smaller than that of the foliage per tree, but few mother trees produced much more seeds whose dry weight was far greater than leaf dry weight (Figure 3.5). The largest ratios of seed weight per tree to foliage weight per tree were 2.57 for \( Q. \ eumorpha \), and 5.30 for \( Q. \ brevicalyx \), respectively. These ratios were used for the estimation of

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hypothesized proposed “maximal seed rain,” in which produced seed weight per tree is 2.57 times heavy than per tree leaf weight in *Q. eumorpha* and 5.30 times heavy than per tree leaf weight in *Q. brevicalyx*.

**Proposed maximal seed rain**

In the proposed “maximal seed rain,” 14.9 (± 41.8 SD) and 38.67 (± 97.5 SD) seeds per square meter were expected for *Q. brevicalyx* and *Q. eumorpha*, respectively (Figure 3.6). The area with more than 1 seed per square meter was also larger (chi-square test, $\chi^2 = 6.10, P = 0.0135$; Table 3.3) in *Q. eumorpha* (37.2%) than in *Q. brevicalyx* (33.3%; Table 3.3), while the area with more than 0.001 seeds per square meter was larger (chi-square test, $\chi^2 = 80.3, P < 0.001$; Table 3.3) in *Q. brevicalyx* (54.3%) than in *Q. eumorpha* (42.7%). The significant fraction of saplings (1cm ≤ dbh < 3 cm) of *Q. eumorpha* (6.2%) were spatially located at the outside of the area < 0.001 in seed density, while up to 19.9% of the saplings of *Q. brevicalyx* distributed outside the area < 0.001 in seed density (chi-square test, $\chi^2 = 80.3, P < 0.001$; Figure 3.6, Table 3.3).

**DISCUSSION**

**Seed production of mature trees**

The change of seed density with respect to the change of dispersal distance from mature trees was successfully expressed by the Weibul distribution function in two *Quercus* species, as confirmed in other tropical (Rokujo 1998; Sri-ngernyuang 2003; Itoh *et al.* 2004) and temperate (Hirayama *et al.* 2004; Hirayama *et al.* 2008) forest. The mathematical relationships between seed density and dispersal distance led to numerical estimation of the total seed dispersal per mature tree, using belt transects. Furthermore, by extrapolating the relationships to other fruiting trees, fair estimation of the seed dispersal pattern in tree populations became possible. The estimated numbers of dispersed seeds were not always dependent on tree size such as dbh. It was difficult to find a simple relationship between the number of seeds and the diameter of the mother tree (Fig 3.2a and b). In two species, the maximum number of dispersed seeds per tree peaked in the middle-sized individuals (60cm < dbh < 80cm in *Q. eumorpha* and 50cm < dbh < 70 cm in *Q. eumorpha*) and decreased in the large-sized individuals. This tendency was more prominent in *Q. brevicalyx* than in
Q. eumorpha. Similar decrease in seed production in larger trees has observed in other oak species in temperate forest (Downs & McQuillen 1944). The senescence of trees might cause the reduction of seed production especially in Q. brevicalyx.

The total number of dispersed seeds was larger in Q. eumorpha than in Q. brevicalyx, while the total mass of seeds were larger in Q. brevicalyx than in Q. eumorpha. In two species, the most of dispersed seeds were from only few mother trees. A few number of mature trees dispersed disproportionately large number of seeds than other individuals (Figure 3.3). I had only single-year data of seed dispersals, but if this tendency was consistent between years, the fitness of each mature tree and gene flow of the population must be highly biased. Environmental factors such as canopy exposure to sunlight, soil water availability, soil nutrients, and biotic factor such as pollen availability, and genetic differences may cause the variation of seed production and the amount of dispersals. Year to year variation of the seed production is also commonly seen in Fagaceae species (Hirayama et al. 2008, Downs, 1944). Trade-offs between vegetative growth and investments to reproductive organs (Hirayama et al. 2008) may also cause this variation. Temporal variation of seed dispersal and genetic structure of each species need to be carefully examined.

Proposed maximal seed rain and possible secondary seed dispersal in the 7.5 ha area

The spatial distribution of dispersed seeds was strongly influenced by the positions of mature trees in two Quercus species. The density of dispersed seeds decreased rapidly with the increase of distance from mature trees. Long distance dispersal was not observed. Long distance dispersal, which mitigates the overcrowding, was not found by observed seed dispersal.

Data from a single cohort does not permit the analysis of inter-annual variations in seed production and seed dispersal. However, I supposed the year-to-year variation of seed production in an individual tree level and a population level and introduced the hypothetical “maximal seed rain”, in which all mature trees are expected to produce seeds in their maximum ability, which was empirically measured by leaf mass per tree. Although the “maximal seed rain” hypothetically rested on the unusually heavy seed production, it was supposed to evaluate whether the predicted seed dispersal, which followed the Weibul distribution, could explain the spatial distribution of the saplings that really occurred in the 7.5 ha area. In the simulation of the “maximal seed rain”, many of actually observed seedlings (1 ≤ dbh < 3cm) were located within the spatial range of predicted seed dispersal area having predicted
seed density $> 0.001/m^2$. Here, the areas having predicted seed density $> 0.001/m^2$ is tentatively designated as the “maximal seed rain range.” The introduced focal “range” was greater in *Q. brevicalyx* (5.055 ha/7.5 ha) than in *Q. eumorpha* (4.395 ha/7.5 ha). The ratio of the number of seedlings occurring outside the “maximal seed rain range” to that of seedlings occurring inside the “maximal seed rain range” was significantly larger in *Q. brevicalyx* than in *Q. eumorpha*, despite the greater “maximal seed rain range”, greater seed volume and greater seed weight in the former species. Thus, the seedling establishment beyond the “maximal seed rain range” should be repeated in *Q. brevicalyx* than in *Q. eumorpha*.

The possible explanations for locations of actually living seedlings in the 7.5 ha area are the seed dispersal by unusual strong wind, secondary dispersal by animals, and presence of dead mother trees in the past. It is unlikely that larger and heavier seeds of *Q. brevicalyx* can be carried long by weak wind often occurred in the study plot. The last explanation, the presence of disappeared mature trees in the past cannot be examined. As already observed in many other temperate and tropical forests (e.g. Forget 1992, 1994, Yasuda 2000, Xiao 2005), caching of seeds by rodents or other frugivores may act as secondary dispersal in this study forest. The high rate of disappearance of seeds from the belt-transects without any scars of herbivory suggested the occurrences of the translocation and caching activities by unobserved animals. Although the direct observation of foraging and caching activities of frugivores is necessary, the secondary seed dispersal by animals is highly expectable in this forest.
Table 3.1. Summary of the regression of dispersed seed density of *Quercus brevicalyx* and *Q. eumorpha* along distance from the mother trees by Weibul distribution function in a tropical montane forest at Doi Inthanon National Park, northern Thailand. Coefficients $N_i$, $m_i$, and $a_i$ are the total number of dispersed seed per belt-transect, shape parameter, and scaling parameter of $i$th mother tree, respectively. $N^*_i$ is the total number of dispersed seeds per selected tree.

<table>
<thead>
<tr>
<th>Dbh (cm)</th>
<th>Height (m)</th>
<th>Number of 1.0 × 1.0-m quadrats</th>
<th>Total number of observed cupules</th>
<th>Coefficients</th>
<th>$r^2$</th>
<th>$N^*_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$N_i$</td>
<td>$m_i$</td>
<td>$a_i$</td>
</tr>
<tr>
<td><em>Q. brevicalyx</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>99.1</td>
<td>39.8</td>
<td>31</td>
<td>739</td>
<td>328.5</td>
<td>1.303</td>
<td>6.12</td>
</tr>
<tr>
<td>99.5</td>
<td>35.4</td>
<td>28</td>
<td>288</td>
<td>224.7</td>
<td>1.087</td>
<td>3.829</td>
</tr>
<tr>
<td>63.5</td>
<td>29.7</td>
<td>27</td>
<td>2162</td>
<td>1143.3</td>
<td>1.235</td>
<td>3.966</td>
</tr>
<tr>
<td>46.2</td>
<td>29.4</td>
<td>25</td>
<td>1278</td>
<td>696.6</td>
<td>1.661</td>
<td>4.228</td>
</tr>
<tr>
<td><em>Q. eumorpha</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>65.2</td>
<td>27.5</td>
<td>27</td>
<td>2240</td>
<td>1405.5</td>
<td>1.276</td>
<td>4.281</td>
</tr>
<tr>
<td>69.9</td>
<td>27.9</td>
<td>21</td>
<td>280</td>
<td>155.8</td>
<td>1.089</td>
<td>4.445</td>
</tr>
<tr>
<td>50.6</td>
<td>25.7</td>
<td>14</td>
<td>71</td>
<td>32.6</td>
<td>1.877</td>
<td>3.932</td>
</tr>
<tr>
<td>†36.4</td>
<td>24.1</td>
<td>12</td>
<td>34</td>
<td>8.0</td>
<td>2.351</td>
<td>2.209</td>
</tr>
</tbody>
</table>

†: Coefficients of this tree were not used for the following analyses because of the small number of observed cupules.
Figure 3.1. Relationships between estimated coefficients $a_i$ (upper) and $m_i$ (lower) of the regression of seed dispersal of seven selected trees of *Quercus brevicalyx* (solid circles) and *Q. eumorpha* (open circles) by Weibul distribution function, in a tropical montane forest at Doi Inthanon National Park, northern Thailand. Vertical bars on the circles indicate 95% confidence limits of the regressed coefficients. The estimates of $a_i$ from seven fruited trees were approximated by an exponential equation as $a_i = 2.04 \exp (0.0248 H_i)$ ($r^2 = 0.4998$; solid line in the upper figure), where $H_i$ was the tree height of the $ith$ mother tree. Coefficient $m_i$ appeared to be constant with tree height, and their average was 1.36 (solid line in the lower figure).
Figure 3.2a. Estimated number of dispersed seeds per mature tree (dbh ≥ 27.9, N = 64) of *Quercus eumorpha* in 1999 in the 7.5-ha area of a 15-ha study plot in a tropical montane forest at Doi Inthanon National Park, northern Thailand. Number of seeds of each tree was regressed by a Weibull distribution model of seed dispersal along distance from its mother tree.
Figure 3.2b. Estimated number of dispersed seeds per mature tree (dbh ≥ 32.4, N = 39) of *Quercus brevicalyx* in 1999 in the 7.5-ha area of a 15-ha study plot in a tropical montane forest at Doi Inthanon National Park, northern Thailand. Number of seeds of each tree was regressed by a Weibul distribution model of seed dispersal along distance from its mother tree.
Figure 3.3. Relative contribution of each mature tree to the total number of dispersed seeds of *Quercus brevicalyx* and *Q. eumorpha* in 1999, in the 7.5-ha area of a 15-ha study plot in a tropical montane forest at Doi Inthanon National Park, northern Thailand. Solid circles with solid lines, and open circles with dashed lines indicate the accumulated ratio of the number of dispersed seeds of *Q. brevicalyx* and in *Q. eumorpha*, respectively, along the rank of mature trees by the number of dispersed seeds.
Figure 3.4. Estimated density of dispersed seeds of *Quercus brevicalyx* (left) and *Q. eumorpha* (right) in 1999 in the 7.5-ha area of a 15-ha study plot in a tropical montane forest at Doi Inthanon National Park, northern Thailand. Numbers on contour lines indicate estimated densities of dispersed seeds of each species per square meter. Open circles indicate the position of mature trees of each species (dbh ≥ 32.4cm in *Q. brevicalyx*; dbh ≥ 32.4cm in *Q. eumorpha*).
Table 3.2. Summary of the estimated seed rain of *Quercus brevicalyx* and *Q. eumorpha* in 1999 in the 7.5-ha area of a 15-ha study plot in a tropical montane forest at Doi Inthanon National Park, northern Thailand.

<table>
<thead>
<tr>
<th>Species</th>
<th><em>Q. brevicalyx</em></th>
<th><em>Q. eumorpha</em></th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of mature trees* in 7.5-ha sub-plot</td>
<td>39</td>
<td>64</td>
<td></td>
</tr>
<tr>
<td>Estimated mean seed density per square meter (no m$^{-2}$ ± SD)</td>
<td>1.78 ± 9.35</td>
<td>2.40 ± 12.01</td>
<td>&lt;0.0001 †1</td>
</tr>
<tr>
<td>Proportion of the area in which more than 1 seed per square was expected (%)</td>
<td>14.7</td>
<td>17.1</td>
<td>0.0135 †2</td>
</tr>
<tr>
<td>Proportion of the area in which more than 0.001 seed per square was expected (%)</td>
<td>54.3</td>
<td>42.7</td>
<td>&lt;0.0001 †3</td>
</tr>
</tbody>
</table>

*: Dbh ≥ 32.4cm in *Q. brevicalyx*; dbh ≥ 32.4cm in *Q. eumorpha*

†1: Wilcoxon rank sum test, $W = 5297546$

†2: Chi-squared test, $\chi^2 = 6.1021$

†3: Chi-squared test, $\chi^2 = 80.3482$
Figure 3.5. Relationships between the estimated mass of leaves and dispersed seeds in *Quercus brevicalyx* (upper) and *Q. eumorpha* (lower) in the 7.5-ha area of a 15-ha study plot in a tropical montane forest at Doi Inthanon National Park, northern Thailand. Solid lines indicate the highest ratio of seed mass per tree ($W_{SD}$) against leaf mass per tree ($W_L$), which were determined as $W_{SD} = 5.30\cdot W_L$ in *Q. brevicalyx* and $W_{SD} = 2.57\cdot W_L$ in *Q. eumorpha*. Dotted lines indicate the equal biomass of leaves and seeds ($W_{SD} = W_L$). See text for the details of the methods of the estimation of the mass of leaves and dispersed seeds.
Figure 3.6. Estimated density of dispersed seeds of Quercus brevicalyx (left) and Q. eumorpha (right) in proposed “maximal seed rain”, in which all mature trees (dbh ≥ 32.4cm in Q. brevicalyx; dbh ≥ 32.4cm in Q. eumorpha) are expected to produce seeds in their maximum ability, in the 7.5-ha area of a 15-ha study plot in a tropical montane forest at Doi Inthanon National Park, northern Thailand. Numbers on contour lines indicate estimated density of dispersed seeds per square meter. Open circles and plus symbols indicate the position of mature trees and saplings (1cm ≤ dbh < 3 cm), of each species respectively.
Table 3.3. Comparison of the abundance of saplings (1 cm ≤ dbh < 3 cm) and estimated density of dispersed seeds in “maximal seed rain” of *Quercus brevicalyx* and *Q. eumorpha* in the 7.5-ha area of a 15-ha study plot in a tropical montane forest at Doi Inthanon National Park, northern Thailand.

<table>
<thead>
<tr>
<th>Species</th>
<th><em>Q. brevicalyx</em></th>
<th><em>Q. eumorpha</em></th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of saplings in 7.5-ha sub-plot</td>
<td>251</td>
<td>194</td>
<td></td>
</tr>
<tr>
<td>Sapling density (no. m⁻²)</td>
<td>0.00335</td>
<td>0.00259</td>
<td></td>
</tr>
<tr>
<td>Number of saplings per conspecific mature tree*</td>
<td>6.44</td>
<td>3.03</td>
<td></td>
</tr>
<tr>
<td>Proportion of saplings located outside the range in which more than 1 seed per square was expected in maximal seed rain (%)</td>
<td>53.4</td>
<td>12.9</td>
<td>&lt;0.0001 †1</td>
</tr>
<tr>
<td>Proportion of saplings located outside “maximal seed rain range” in which more than 0.001 seed per square was expected in maximal seed rain (%)</td>
<td>19.9</td>
<td>6.2</td>
<td>&lt;0.0001 †2</td>
</tr>
<tr>
<td>Estimated mean seed density per square meter (no. m⁻² ± SD)</td>
<td>14.9 ± 41.8</td>
<td>38.7 ± 97.5</td>
<td>&lt;0.0001 †3</td>
</tr>
<tr>
<td>Proportion of the area in which more than 1 seed per square was expected in maximal seed rain (%)</td>
<td>33.3</td>
<td>37.2</td>
<td>0.0135 †4</td>
</tr>
<tr>
<td>Proportion of the area in which more than 0.001 seed per square was expected in maximal seed rain (%)</td>
<td>67.4</td>
<td>58.6</td>
<td>&lt;0.0001 †5</td>
</tr>
</tbody>
</table>

*: Dbh ≥ 32.4 cm in *Q. brevicalyx*; dbh ≥ 32.4 cm in *Q. eumorpha*

†1: Chi-squared test, $\chi^2 = 76.4054$

†2: Chi-squared test, $\chi^2 = 16.0879$

†3: Wilcoxon rank sum test, $W = 6136748$

†4: Chi-squared test, $\chi^2 = 6.1021$

†5: Chi-squared test, $\chi^2 = 80.3482$
CHAPTER 4. DEMOGRAPHY AND TRAITS OF SEEDS AND SEEDLINGS OF TWO QUERCUS SPECIES

INTRODUCTION

Demography of seeds and seedlings is important to determine population dynamics. Grubb (1977b) emphasized the importance of regeneration niche for the coexistence of plant species, which compete for common resources, e.g. light, water and mineral nutrients. Difference in ecological traits on regeneration processes is the key to determine the spatial distribution of the species.

Many vertebrates and invertebrates species feed on the seeds of Fagaceae species (Crawley 1992). Fagaceae seeds are heavily attacked by them and/or fungal pathogens. Therefore, the number of seeds decreases rapidly on the forest floor after seed dispersal. If the mortality rates of seeds and seedlings are disproportionately high around mother trees, more regeneration is expected away from the mother trees (Janzen 1970; Connell 1971). This process is caused by density-dependent mortality by seed and/or seedling predators and pathogens, and has been observed for many tropical trees (Wills et al. 1997; Harms et al. 2000). As well as biotic factors, environmental factors, such as canopy openness (Schupp et al. 1989; Ashton & Larson 1996), soil moisture (Long & Jones 1996; Germaine & McPherson 1998), litter depth (Molofsky & Augspurger 1992; Green 1999) can be affecting the growth and the mortality of seeds and seedlings (Harper et al. 1965; Collins & Good 1987). Thus, ecological traits of seedlings relating to environmental conditions strongly affect the spatial distributions of species. Regeneration of some species is dependent upon periodic or unpredictable disturbances for their regeneration (Grubb 1988; Vetaas 2000). The optimal light intensity for seedling growth may differ among species. Tolerance to desiccation may important for survival of seedlings. Seedlings of some species may have an ability to make forked stems to maintain seedling banks in unfavorable conditions or after physical damages.

The objective of this chapter is to examine differences in seed and seedling demography between two sympatric Fagaceae species, *Quercus brevicalyx* and *Q. eumorpha*. I studied differences in 1) densities and spatial distributions, 2) survival rates, 3) causes and timing of mortality, 4) the optimum light intensity for growth, and 5) forking ability. I also analyzed whether sibling density, distance from mother tree, litter depth, and canopy openness affect the mortality of seeds and seedlings to discuss the
factors facilitating the coexistence of *Q. brevicalyx* and *Q. eumorpha*. Density, distribution, and forking traits of seedlings of genus *Castanopsis* and *Lithocarpus* were also studied for comparison among Fagaceae species.

**METHODS**

**Census of trees and seedlings**

In a lower montane forest of Mt. Inthanon in northern Thailand (c. 1700 m asl, 18°31'N, 98°30'E), a 15-ha permanent plot (300 × 500 m) was established. All stems of self-standing shrubs and trees of at least 1 cm dbh (stem diameter at 140 cm above the ground) in the plot were labeled, mapped, dbh measured, and identified to species (See chapter 1 and 2 for the details).

Seedlings of all Fagaceae tree species (dbh < 1 cm) were tagged by numbering tapes within a subplot (5 × 5 m) at each 10 m × 10-m square in a 3-ha area (300 × 100 m) of the 15-ha plot (*N* = 300). Current year seedlings were excluded from this census. For evaluating forking ability, number of forked stems was counted for each seedling. Stems being connected at lower than one thirds of the height of a seedling were defined as forked stems of the individual.

**Germination test**

A germination test was conducted under conditions that all predators were excluded. Intact seeds without any apparent damage were gathered with collecting nets set on the forest floor. The nets were set under the crowns of three mother trees for each species. Periods of seed collection were from May to June 1999 for *Q. brevicalyx*, and April to May 1999 for *Q. eumorpha*, respectively. The collected seeds were placed on germination beds, which were filled with sterilized river sand. The germination beds were covered by black shading nets; the mean relative light intensity inside was ca 50%. Dry weights of the seeds from the same samples (*N* = 75 in *Q. brevicalyx* and *N* = 16 in *Q. eumorpha*) were measured after oven dried at 70°C for more than two days to constant weights. Weights of acorns, pericarps and cotyledons were measured separately.

**Shading experiment**

A shading experiment with shading cages (1.0 × 2.0 × 1.2-m height) was conducted at a nursery in
Doi Inthanon National Park (ca 1700m asl) from December 1999 to December 2000. Irradiances inside the shading cages were adjusted by different number of black nylon shading nets. The mean relative light intensities (RLI) of the five treatments were 3.4%, 10%, 31%, 51%, and 100% (open control). Three replicate cages and controls were prepared for each treatment. Seedlings obtained by the germination test were used ($N = 148$ for $Q. \textit{brevicalyx}$ and $N = 42$ for $Q. \textit{eumorpha}$). Seedlings were planted to the plastic pots (18 cm in diameter; 30 cm tall) filled with paddy field soil and rice husk with a ratio of 4:1 from 10 to 12 December 1999. The seedlings were well watered twice a day at 0700h and 1600h throughout the experiment, except on rainy days.

All living seedlings were harvested on 2 December 2000 (24 moths after planting). Dry weight of each seedling was measured after oven dried to constant weight at 70ºC for two days. The optimum relative light intensity (RLI) for the growth of seedlings was calculated for each species using the optimum growth model proposed by Hozumi \textit{et al.} (1960) as:

$$\frac{1}{w} = \frac{A_1}{f} + A_2 f + B,$$  \hspace{1cm} (Eq. 4.1)

where $w$ is the mean dry weight of seedlings, $f$ is the amount of growth factor, i.e. RLI (%) in this study, and $A_1$, $A_2$ and $B$ are coefficients specific to species, the period of growth, and other conditions. The optimum RLI ($f_{\text{opt}}$) for each species was calculated as:

$$f_{\text{opt}} = \frac{A_1}{\sqrt{A_2}}.$$  \hspace{1cm} (Eq. 4.2)

Values of the coefficients of the model were estimated using a function of a nonlinear least-square estimation (nls) on R version 2.62 (R Development Core Team 2008).

**Field observation of seeds and seedlings**

I selected four fruiting trees having well shaped crowns for each species. Each mother tree was isolated from other conspecific fruiting trees so that its seed shadow had no overlap with those of other conspecific trees. A belt-transect of 1.0-m wide was established for each mother tree. The transect was set from the projected position of the center of the crown to two opposite directions in order to include all dispersed seeds. Each transect was subdivided into $1.0 \times 1.0$-m quadrats. The number of quadrats was different among the mother trees depending on their crown sizes (Table 3.1). All seeds in the transects were tagged with numbered plastic tags with steel wires. Mortality and its causes were
recorded every 8 to 30 days from August 1998 to April 2000 (28 times in total) and on 19 June 2000 and 10 December 2000. Seeds that were dead at the first observation were not tagged but the causes of mortality were recorded. Counts of the seeds and seedlings in each quadrats of the belt-transects were weighed by the area of concentric rings from the projected position of the center of the crown of each mother tree.

Seeds were regarded as “germinated” when their cotyledons expanded and their radicles extended more than 5-mm long. Seedlings were recorded as “established” when their hypocotyls penetrated into the soil and epicotyls were longer than 5-mm.

Mortality causes of seeds were classified into four categories as follows. 1) “Insect”: a seed having emergence holes of insects or insects themselves on the surface and/or inside the pericarp; 2) “frugivore”: a seed having scars by gnawing on the seed; 3) “disappeared”: a seed that has disappeared between the observation intervals, possibly eaten in situ or removed by frugivores; 4) “pathogen”: a seed being rotten without scars by gnawing, insect holes, nor insects themselves; 5) establishment failure: a seed that has not established as seedling after germination in spite of no apparent physical damage.

Mortality causes of seedlings were divided into three categories as follows. 1) “Cut or eaten”: a dead seedling of which shoot and/or root were broken or damaged, possibly by insects or herbivores; 2) “wilted”: a seedling being killed by water stress and/or attack of fungal pathogens; 3) “disappeared”: a seedling that has disappeared between the observation intervals.

**Measurement of canopy openness and litter depth**

Hemispherical photographs were taken at 60 cm above ground at the center of each 1.0 × 1.0-m quadrats of the belt-transects using a camera (Nikon, FM2) with fish eye lens (Nikkor, 8mm) from 1 January to 29 April 2000. Percentages of canopy openness were calculated from the hemispherical images using Winphot 5.0 (ter Steege 1996). Litter depth on the ground was also measured at the center of each quadrat.

**Statistical analyses**

The onset and end of the seed dispersal period of each species were defined as the date when 5% and 95% of total seeds were dispersed, respectively. For the calculation of seed dispersal period, data
of the four mother trees were pooled in each species. Difference in mortality of seeds and seedlings were examined by the log-rank test between species and mother trees within species. Difference in proportion of mortality factors was examined by the chi-square tests between species and among mother trees of each species. Relationship between seed/seedling mortality and environmental factors, i.e. distance from the center of the crown of a mother tree, initial density of seeds or seedlings, canopy openness, litter depth, was analyzed by logistic regression using SPSS 11.0J. Counts of seeds and seedlings were not weighed according to their locations for this regression. Other statistical tests were conducted by R version 2.62 (R Development Core Team 2008).

RESULTS

Size distributions of Fagaceae trees

All of the eight Fagaceae species showed typical L-shaped size distributions (Figure 4.1). *Quercus eumorpha* had higher proportions of middle-sized trees between 20-60 cm in dbh compared with other species. Size distributions of *Q. eumorpha* and *Castanopsis accuminatissima* showed weak bimodality (Figure 4.1).

Abundance and spatial distributions of Fagaceae seedlings

Most of *Q. eumorpha* seedlings (dbh < 1cm) were distributed on the ridge and the upper part of the western slope in the study area (3 ha). In contrast, seedlings of *Q. brevicalyx* were distributed mostly in the middle to lower part of the slopes (Figure 4.2). Most of the seedlings of the two *Quercus* species and *Castanopsis calathiformis* were located near conspecific mature trees, while seedlings of *Castanopsis purpurea* and three *Lithocarpus* species were found even at the areas away from conspecific adults (Figure 4.2). There were high-density patches (maximum: 10.3 seedlings per square meter; Figure 4.1, Table 4.1) around highly prolific mother trees of *Q. eumorpha*. For *Q. brevicalyx*, a large and continuous area with high seedling densities (2.20-0.04 seedlings per square meter) was observed on the ridge, where many mature *Q. brevicalyx* trees were located.

Mean seedling density was highest in *Q. brevicalyx* (0.12 seedlings per square meter), followed by *C. calathiformis* (0.08 seedlings per square meter) and *Q. eumorpha* (0.07 seedlings per square meter) (Table 4.1). The mean seedling density of *Q. brevicalyx* was twice higher than that of
Q. eumorpha. Seedling densities of Castanopsis and Lithocarpus species were relatively low compared with Quercus species except for C. calathiformis. Seedling density was extremely low in C. acuminahtissima, possibly reflecting the small population of mature trees.

Number of seedlings per mature tree (dbh > 25 cm) was larger in C. calathiformis (16.6 seedlings per tree) and Q. brevicalyx (12.8 seedlings per tree) than other species. The value of Q. brevicalyx was more than four times larger than that of congeneric Q. eumorpha (2.9 seedlings per tree). Commonness of seedlings, in terms of the proportion of squares where seedlings were presented to the total number of squares in the study area, was significantly different among species (Chi-square test, \( P < 0.001 \)), being highest in Q. brevicalyx (34.7%), followed by C. calathiformis (30.3%) (Table 4.1).

**Forking traits of Fagaceae seedlings**

Forking traits of seedlings were various among the species. The ratio of forking individuals and mean number of stems per individual were significantly different among the eight study species (Kruskal-Wallis test, \( P < 0.001 \); Table 4.1, Figure 4.3). Average number of stems per individual was highest in C. calathiformis (2.83 stems), followed by C. purpurea (1.43 stems), L. echinops (1.33 stems) and L. vestitus (1.23). The maximum numbers of stems per seedling were 11 and 6 in C. calathiformis and C. acuminatissima, respectively. In the genus Quercus, Q. eumorpha had a significantly larger mean number of stems per individual (1.13) than Q. brevicalyx (1.03; Kruskal-Wallis test, \( \chi^2 = 52.9067, P = 3.498e-13 \)).

**Seed traits of Quercus**

Seeds of Q. brevicalyx and Q. eumorpha had similar morphology without any organs for dispersal. Mean dry weights of a seed were 7.04 ± 2.50 g (SD) and 2.58 ± 0.82 g for Q. brevicalyx and Q. eumorpha, respectively. The former value was significantly larger than the latter (SD; t-test, \( P < 0.001 \); Table 4.1). Pericarp of a Q. brevicalyx seed was thicker than that of Q. eumorpha, and the ratio of pericarp weight to the total seed weight was significantly larger in Q. brevicalyx than Q. eumorpha (Kruskal-Wallis test, \( P < 0.005 \); Table 4.2).
Germination of seeds in forest and experiment

Germination rates of intact seeds of the two Quercus species were almost same in Q. brevicalyx (75.6%) and Q. eumorpha (72.0%) in the experimental condition, in which all predators and fungal pathogens in the soil were excluded (Table 4.2). In belt transects on the forest floor of the study forest, germination rates were much lower in both species. The germination rate of Q. brevicalyx (39.0%) was larger than that of Q. eumorpha (14.0%), which was severely damaged by insects, frugivores and fungal pathogens at the forest floor.

Optimal illumination for growth of seedlings

Mean weights of seedlings grown for 24 months in the shade houses were larger in Q. brevicalyx than Q. eumorpha at all light conditions (Figure 4.4). Relationship between mean dry weight and RLI fitted well the Hozumi’s optimum growth model in both species ($r^2 = 0.682$ and 0.926 for Q. brevicalyx and Q. eumorpha, respectively) (Fig. 4.4). The estimated values of $A_1$, $A_2$ and $B$ were 0.2057, 0.001792 and 0.1420, respectively, for Q. brevicalyx, and 3.315, 0.03638 and -0.1381, respectively, for Q. eumorpha. The optimum RLI was only slightly higher in Q. brevicalyx (10.71%) than in Q. eumorpha (9.54%).

Demography of seeds and seedlings

The seed dispersal periods in 1999 (the period that 90% of the seeds were dispersed) were from 13 May to 22 July in Q. brevicalyx (71 days) and from 22 March to 18 May in Q. eumorpha (77 days) (Figures 4.5a and 4.5b). The onset of seed fall was just after the beginning of the rainy season in Q. brevicalyx, and about one month before the start of rainy season in Q. eumorpha. No seed dormancy was observed in both species. Average periods from seed fall to seedling establishment were significantly longer in Q. brevicalyx (69.3 ± 24.0 SD) than in Q. eumorpha (40.9 ± 15.8) (t-test: $t = 11.64, P < 2.2e-16$; Figures 4.5a and 4.5b).

The median periods between dispersal and mortality were significantly shorter in Q. eumorpha (41 days) than Q. brevicalyx (81 days) (Log-rank test: $\chi^2 = 1083, P < 0.001$; Figures 4.5a and 4.5b, Table 4.3). Establishment rates, the proportion of seeds that successfully established as seedlings, were significantly higher in Q. brevicalyx (23.1%) than in Q. eumorpha (7.8%) (chi-square test, $P < 2.2e-16$; Table 4.3). Survival rates of seeds were significantly different among four mother trees in
Q. brevicalyx (Chi-square test: $P < 2.2\text{e-16}$), but not significantly different in Q. eumorpha (Table 4.3). The highest survival rate in Q. eumorpha was observed for the mother tree that fell the largest number of seeds.

Seeds of Q. brevicalyx grew into seedlings during the period from the middle to the end of the rainy season (21 July - 20 September, 1999), while those of Q. eumorpha did earlier from the beginning to the middle of the rainy season (29 April - 15 July, 1999). The median dates of seedling establishment were 4 September in Q. brevicalyx and 30 May in Q. eumorpha (Figures 4.5a and 4.5b).

Mortality of established seedlings were concentrated at the end of the rainy season in Q. brevicalyx, and in the middle of the rainy season in Q. eumorpha. Median period from establishment to mortality were significantly shorter in Q. eumorpha (59 days, $N = 101$) than Q. brevicalyx (129 days, $N = 1151$) (Log-rank test, $\chi^2 = 69.8$, $P <0.001$). The final survivorship of seedlings was significantly higher in Q. brevicalyx (5.8%) than in Q. eumorpha (0.29%) (Chi-square test: $P < 2.2\text{e-16}$; Table 4.3). All seedlings were killed by December 2000 in Q. brevicalyx except for a mother tree that produced the largest number of seeds (Table 4.3).

**Causes of seed and seedling mortality**

Proportions of causes of seed mortality were significantly different between Q. brevicalyx and Q. eumorpha (Chi-square test, $\chi^2 = 13973$, $P < 2.2\text{e-16}$) (Figure 4.6). For Q. brevicalyx, the most important cause was “disappeared” (37.0%), followed by “insect” (31.2%). Twenty three percent of the dispersed seeds survived to grow into seedlings. For Q. eumorpha, “insect” was the most important mortality cause (49.8%), followed by “disappeared” (20.2%) and “frugivore” (19.9%). Proportions of the seeds that were killed by “pathogen” were small for both species (3.75% and 1.09% in Q. brevicalyx and Q. eumorpha, respectively). However, most of the seeds that were killed by insects and/or nibbled by frugivores were infected by fungal pathogens and decayed on the forest floor afterward. Only a few seeds were uprooted and dead immediately after germination (3.03% and 1.18% in Q. brevicalyx and Q. eumorpha, respectively).

Proportions of causes of seedling mortality were also significantly different between species (Chi-square test, $\chi^2 = 13973$, $P < 2.2\text{e-16}$) (Figure 4.7). The most important mortality cause was “wilted” (37.4%) for Q. brevicalyx seedlings; the second one was “cut or eaten” (27.2%). Only 22.4% of seedlings survived until December 2000 in Q. brevicalyx. For Q. brevicalyx, “cut or eaten” was the
largest mortality cause (47.8%), followed by “wilted” (35.6%).

Figure 4.8 shows the temporal shift of mortality causes of seeds. In *Q. brevicalyx*, “pathogen” killed only a small fraction of the dispersed seeds, having a small peak in the beginning of April when the rainy season just started. Mortality by “insect” was consistently high throughout the rainy season, from April to October. “Disappeared” was also high through the rainy season, showing a peak at the end of July. In *Q. eumorpha*, mortality by “frugivore” was high from February till June 1999. Mortality by “insects” and “disappeared” increased from March and continued till September having a peak in June.

Figure 4.9 shows the temporal shift of mortality causes of seedlings. For *Q. brevicalyx*, mortality by “wilted” was the most important mortality cause of seedlings. “Wilted” started after the onset of dry season, and showed a peak at the end of November. “Cut or eaten”, and “disappeared” peaked in October, the end of the rainy season. In *Q. eumorpha*, “cut or eaten”, “wilted” and “disappeared” had peaks in May, the middle of the rainy season. “Wilted” increased after the onset of the dry season in November. “Wilted” had two peaks: one in the rainy season probably due to fungal pathogens and the other in the dry season due to water stress.

**Environmental effects on seed and seedling mortality**

Logistic regression analyses showed that the environmental factors studied affected significantly the survivorship of seeds and seedlings of the two *Quercus* species (Table 4.4a). Distance from mother tree, initial seed density, canopy openness, and litter depth showed significant positive effects on the survival of *Q. brevicalyx* seeds (Table 4.4b). For *Q. eumorpha*, only initial seed density had a significant negative effect on the seed survival. Distance from mother tree and canopy openness had significant positive effects on the survival of *Q. brevicalyx* seedlings (Table 4.4c). There were no significant factors for the seedling survival of *Q. eumorpha* possibly due to the small sample size.

**DISCUSSION**

**Abundance of seedlings**

Abundance of seedlings was different among the eight Fagaceae species (Figure 4.2, Table 4.1). For the two *Quercus* species, the mean number of seedlings per adult was more than four times larger in
than Q. eumorpha (Table 4.1). The difference in seedling density is consistent with the results of seed and seedling demography observed during the study period.

Estimated mean number of seeds produced by each mature tree in 1999 was larger in Q. brevicalyx (3,618) than in Q. eumorpha (2,635) (see Chapter 3). Although this study observed only one fruiting time, the lower productivity of Q. eumorpha observed at the population level might be a reason for the lower seedling to adult ratio. In addition, the lower germination and survival rates of Q. eumorpha seeds (Table 4.3) are possible causes for the low seedling density of this species.

Nevertheless, we cannot conclude why Q. eumorpha had less seedlings than Q. brevicalyx in the study site only from this study that covered only one fruiting episode. It is known that many Fagaceae species showed the mast seeding habit; hence degree of seed production fluctuates largely from year to year (e.g. Downs & McQuillen 1944; Koenig et al. 1996). Estimation of seed production of each adult tree (Chapter 3) suggests the study year was not a mast year. It is yet to be studied the larger seed production of Q. brevicalyx than that of Q. eumorpha is consistent in mast years and over longer periods. Moreover, demography of seeds and seedlings might be different between heavily and lightly fruiting years. In mast years, seed survival is generally improved because seed predators would be saturated. It is not clear whether survivorship of Q. eumorpha seeds is worse than Q. brevicalyx even in mast years. We need to accumulate demographic data in longer time scales to include several mast and no-mast years.

**Seed mortality**

There were significant differences in the causes of seed mortality between the two Quercus species. The most important mortality cause of seeds was “disappeared” for Q. brevicalyx and “insect” for Q. eumorpha (Figure 4.6). Based on the spatial distributions of seed dispersal and juveniles in Chapter 3, secondary dispersal of seeds by rodents or frugivores are likely to be occurred especially for Q. brevicalyx. Thus, “disappeared” seeds may include secondary dispersal, and the survival rate of Q. brevicalyx seeds might be underestimated.

Disappeared seeds were also recorded in Q. eumorpha, but the proportion of seed that were eaten by frugivores under the canopy of mother trees was much higher in this species than Q. brevicalyx (Figure 4.6). Generally, larger seeds are more likely to be removed and then cached, rather than eaten in situ (Vander Wall, 1995, 2003, Forget et al., 1998). Seeds with thick pericaps are also likely to be
removed rather than be consumed in situ, to avoid the risk of predation while the frugivores treat the seeds. The mean seed weight of *Q. brevicalyx* was more than two times heavier than that of *Q. eumorpha*, and the pericarp was thicker in *Q. brevicalyx* (Table 4.2). It is possible that *Q. brevicalyx* seeds are more likely to be removed by frugivores than consumed in situ. The morphological and demographic data obtained by this study suggest that secondary dispersal is more frequent in *Q. brevicalyx* than in *Q. eumorpha* resulting in more scattered tree distributions of *Q. brevicalyx* in the study forest.

The higher mortality by “insect” in *Q. eumorpha* than *Q. brevicalyx* may be related at least partly to the difference in seed morphology between the two species. The thinner pericarp of *Q. eumorpha* might be one reason for the high mortality by “insect”. Damage to cotyledons by insects is more likely to be fatal in *Q. eumorpha* because of its smaller reserve in cotyledon (Bonfil 1998; Dalling & Harms 1999). In addition to the seed morphology, contents of secondary metabolites in seeds, such as tannin, might affect the demographic pattern of seeds (e.g. Smallwood & Peters 1986; Weckerly et al. 1989; ChungMacCoubrey et al. 1997; Xiao et al. 2006), though they were not examined in this study.

The phenology of seed dispersal may relate to the difference in the seed demography of the two species. Seed dispersal started about two months earlier in *Q. eumorpha* than in *Q. brevicalyx* (Figures 4.6a and 4.6b). Seeds of *Q. eumorpha* were dispersed shortly before the rainy season and rapidly germinate and established to seedlings. The rapid growth trait of *Q. eumorpha* seeds is presumably to escape mortality by insects and/or frugivores (Hammond et al. 1999), which were important mortality causes of this species. In contrast, *Q. brevicalyx* seeds were dispersed in the rainy season, and its seeds took longer time for germination and establishment to seedlings. Seed predation of *Q. brevicalyx* by frugivores increased only after the time when *Q. eumorpha* seeds were killed or established to seedlings. This suggests a possibility that frugivores prefer *Q. eumorpha* seeds to *Q. brevicalyx* ones.

**Seedling mortality**

As well as seed mortality, seedling mortality was also higher in *Q. eumorpha* than in *Q. brevicalyx*. This was largely due to the higher mortality by “cut or eaten” in *Q. eumorpha* (Figure 4.7). Nearly half of the *Q. eumorpha* seedlings were killed by this factor. Frugivores may have eaten cotyledons of seedlings during the early seedling stage when cotyledons were still attached to the seedlings. Frugivores may prefer *Q. eumorpha* cotyledons to those of *Q. brevicalyx* just like the case
of seeds.

“Wilted” killed many seedlings both in *Q. brevicalyx* and *Q. eumorpha* (Figure 4.7). “Wilted” occurred mainly in the dry season (Figure 4.9), suggesting that water stress may have been casually related to wilting of seedlings. There is a distinct seasonality in rainfall in the study site. Thus, water stress during the dry season may be a crucial mortality factor of *Quercus* seedlings at the study forest. However, wilted seedlings were observed in the rainy season as well as the dry season in *Q. eumorpha* (Figure 4.9). The cause of wilting in the rainy season is not clear but it might be attributed to fungal pathogens. Seedlings of *Q. eumorpha* were smaller than those of *Q. brevicalyx* at the early seedling stage due to their smaller seed sizes, and they seemed to be more susceptible to pathogens.

In summary, the results showed that demography of the two *Quercus* seedlings were affected both by biotic (frugivores) and abiotic (water stress) factors. Relative importance of these two factors differed between the species.

**Effects of environment on seed and seedling mortality**

Distance form mother tree was positively related to seed and seedling survival in *Q. brevicalyx* but not in *Q. eumorpha* (Table 4.3). This result indicates that seed and seedling mortality is higher in the vicinity of conspecific adults, as is predicted by the Janzen-Connell hypothesis (Janzen 1970; Connell 1971), only in *Q. brevicalyx*. It is however in conflict with the Janzen-Connell hypothesis that initial seed density had a positive effect on seed survival of *Q. brevicalyx*. This conflict might be because I analyzed the data of four mother trees at once. If seed predators forage seeds in the vicinity of fruiting trees but saturated when the seed density is very high, morality would be lower for seeds of heavily fruiting trees than those of poorly fruiting ones. Thus, we can expect the observed results, the positive distance and density effects on seed survival. In fact, seed mortality was lower in mother trees with larger seed production (Table 4.3).

Initial seed density showed a negative effect on seed survival in *Q. eumorpha* (Table 4.4b), suggesting a density-dependent mortality. In contrast to *Q. brevicalyx*, predators of *Q. eumorpha* may have foraged more on the sites with dense seedling populations and may not have been saturated even at the densest seedling population.

Abiotic factors, i.e., canopy openness and litter depth, had significant effects on seed and/or
seedling mortality only in *Q. brevicalyx*. Thus, abiotic factors may be less important than biotic factors in seed and seedling demography of *Q. eumorpha*, while both factors are important for *Q. brevicalyx*. This result is consistent with the results of the analysis of mortality factors that proportions of biotic factors were larger in *Q. eumorpha* (Figures 4.6 and 4.7).

**Habitat divergence and seedling traits**

Habitats of *Q. eumorpha* and *Q. brevicalyx* were different in the study plot (see Chapter 2). *Q. eumorpha* is distributed on the upper western slopes to ridges, while *Q. brevicalyx* on lower slopes. At the larger spatial scale, *Q. eumorpha* is more common at the upper montane forest, where wind is stronger than the study forest (a lower montane forest), in Doi Inthanon (Khamyong *et al.* 2004). More canopy gaps were located on the upper western slopes to ridges possibly due to the strong western wind in the plot (Noguchi 1998). Therefore, it is possible that *Q. eumorpha* is more light demanding than *Q. brevicalyx*. However, the optimum light intensity for the seedlings was very similar for both species (Figure 4.4). Thus, the divergent distribution of these two species may not be accounted for the difference of light conditions between their habitats.

Rather than light condition, disturbance seems more important for the habitat divergence. The windward western ridges suffered from constant and strong western wind throughout rainy seasons, and tree mortality was higher in this habitat than others (Sri-ngernyuang, pers. comm.). Therefore, disturbance is more frequent, and seedlings would suffer from more physical damage, in the western ridges. The higher ratio of forking seedlings of *Q. eumorpha* (11.1 %) than that of *Q. brevicalyx* (2.1 %) (Table. 4.1) suggests that *Q. eumorpha* seedlings produce more forking stems after physical damage. The ability of sprouting is known as an adaptive trait for woody plants in frequently disturbed habitats (Bond & Midgley 2001). *Q. eumorpha* may be able to maintain seedling populations by this high sprouting ability even in frequently disturbed habitats, such as the western ridges.

Difference in soil moisture between ridges and lower slopes is alternative cause for the habitat divergence between the two *Quercus* species. Because water stress was suggested to be an important mortality factor of *Quercus* seedlings, *Q. eumorpha* would be more common if it is more tolerant to water stress than *Q. brevicalyx*. However, no data on drought tolerance were obtained in this study.

This study clearly showed that the two sympatric *Quercus* species differ in various aspects of seed and seedling traits. The results obtained here support that niche divergence plays an important role in their
coexistence, though we still need to clarify the detailed mechanism that promotes their coexistence.
Figure 4.1. Size distribution of Fagaceae tree species in a 15-ha study plot in a tropical montane forest at Doi Inthanon National Park, northern Thailand. See table 2.1 for abbreviations of the species names.
Figure 4.2. Seedling density of Fagaceae tree species in a 3-ha area of a 15-ha study plot in a tropical montane forest at Doi Inthanon National Park, northern Thailand. Density of the seedlings per square meter is shown in the grey scale as in the legend. Contour lines in the figures are drawn at 10-m intervals of the relative elevation. See Table 2.1 for abbreviations of the species names.
Table 4.1. Abundance and forking traits of seedlings of Fagaceae tree species in a 3-ha area of a 15-ha study plot in a tropical montane forest at Doi Inthanon National Park, northern Thailand. Seedlings (dbh < 1cm) of all Fagaceae tree species within a subplot (5 × 5 m) at each 10 m × 10-m square in a 3-ha area (300 × 100 m) of the 15-ha plot were sampled. Current year seedlings were excluded from this census. See Table 2.1 for abbreviations of the species names.

<table>
<thead>
<tr>
<th>Species</th>
<th>Ca</th>
<th>Cc</th>
<th>Cp</th>
<th>La</th>
<th>Le</th>
<th>Lv</th>
<th>Qb</th>
<th>Qe</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observed number of seedlings (no. per 0.75ha)</td>
<td>6</td>
<td>664</td>
<td>97</td>
<td>39</td>
<td>54</td>
<td>114</td>
<td>921</td>
<td>496</td>
</tr>
<tr>
<td>Maximum density of seedlings (no.m⁻²)</td>
<td>0.12</td>
<td>2.04</td>
<td>0.24</td>
<td>0.12</td>
<td>0.12</td>
<td>0.24</td>
<td>10.32</td>
<td>2.20</td>
</tr>
<tr>
<td>Average density of seedlings (no.m⁻²)</td>
<td>0.0008</td>
<td>0.0885</td>
<td>0.0129</td>
<td>0.0052</td>
<td>0.0072</td>
<td>0.0152</td>
<td>0.1228</td>
<td>0.0661</td>
</tr>
<tr>
<td>Number of mature trees (dbh &gt; 25cm)</td>
<td>3</td>
<td>10</td>
<td>4</td>
<td>12</td>
<td>5</td>
<td>11</td>
<td>18</td>
<td>43</td>
</tr>
<tr>
<td>Number of seedlings per mature trees*</td>
<td>0.50</td>
<td>16.60</td>
<td>6.06</td>
<td>0.81</td>
<td>2.70</td>
<td>2.59</td>
<td>12.79</td>
<td>2.88</td>
</tr>
<tr>
<td>Ratio of the number of squares where seedlings were observed (%)†</td>
<td>1.0</td>
<td>30.3</td>
<td>23.0</td>
<td>11.3</td>
<td>15.0</td>
<td>26.7</td>
<td>34.7</td>
<td>22.3</td>
</tr>
<tr>
<td>Ratio of forking individuals (%)‡</td>
<td>66.7</td>
<td>47.3</td>
<td>34.0</td>
<td>5.1</td>
<td>25.9</td>
<td>15.8</td>
<td>2.1</td>
<td>11.1</td>
</tr>
<tr>
<td>Average number of stems per individual (no. ± SD)‡‡</td>
<td>2.83 ± 1.77</td>
<td>1.89 ± 1.29</td>
<td>1.43 ± 0.67</td>
<td>1.08 ± 0.35</td>
<td>1.33 ± 0.64</td>
<td>1.23 ± 0.61</td>
<td>1.03 ± 0.19</td>
<td>1.13 ± 0.40</td>
</tr>
</tbody>
</table>

*: Estimated numbers of seedlings per 3-ha area (observed numbers multiplied by 4) were divided by the number of mature trees in the same area.
†: Chi-square test, $\chi^2 = 154.308$, $P < 2.2e-16$
‡: Chi-square test, $\chi^2 = 556.9$, $P < 2.2e-16$; Data of C. acuminatissima were excluded from this test because of the small sample size.
‡‡: Kruskal-Wallis rank sum test, $\chi^2 = 578.5$, $P < 2.2e-16$
Figure 4.3. Forking traits of the seedlings of Fagaceae tree species sampled from 3-ha area of a 15-ha study plot in a tropical montane forest at Doi Inthanon National Park, northern Thailand. See Table 2.1 for the abbreviations.
Table 4.2. Traits of seed and forking of seedlings of *Quercus brevicalyx* and *Q. eumorpha* in a 3-ha area of a 15-ha study plot in a tropical montane forest at Doi Inthanon National Park, northern Thailand.

<table>
<thead>
<tr>
<th>Species</th>
<th><em>Q. brevicalyx</em></th>
<th><em>Q. eumorpha</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of seed (mm ± SD)*</td>
<td>21.8 ± 2.8</td>
<td>19.7 ± 2.1</td>
</tr>
<tr>
<td>Width of seed (mm ± SD)*</td>
<td>26.8 ± 3.4</td>
<td>17.4 ± 2.2</td>
</tr>
<tr>
<td>Dry weight of seed (g ± SD)*</td>
<td>7.04 ± 2.50</td>
<td>2.58 ± 0.82†</td>
</tr>
<tr>
<td>Dry weight of pericarp (g ± SD)*</td>
<td>1.85 ± 0.70</td>
<td>0.55 ± 0.13†</td>
</tr>
<tr>
<td>Pericarp ratio (ratio ± SD)‡</td>
<td>0.268 ± 0.057</td>
<td>0.227 ± 0.058</td>
</tr>
<tr>
<td>Germination rate in experimental condition (%)</td>
<td>75.6</td>
<td>72.0</td>
</tr>
<tr>
<td>Germination rate on forest floor (%)</td>
<td>39.0</td>
<td>14.0</td>
</tr>
</tbody>
</table>

*: N = 75 for *Q. brevicalyx*; N = 16 for *Q. eumorpha*  
†: t-test, P < 0.001  
‡: Kruskal-Wallis test, $\chi^2 = 10.35$, P = 0.001297
Figure 4.4. Dry weight of seedlings of *Q. brevicalyx* (solid circles) and *Q. eumorpha* (open circles) after 24-months growth under different relative light intensity at a nursery in Doi Inthanon National Park, northern Thailand. Vertical bars on the circles indicate standard error of the mean values. Solid and dashed lines indicate the regression curves of the weight of seedlings of *Q. brevicalyx* and *Q. eumorpha* by the optimum growth model proposed by Hozumi et al. (1960).
Figure 4.5a. Demography of the seeds and seedlings of *Quercus brevicalyx* in a tropical montane forest at Doi Inthanon National Park, northern Thailand. Solid line, dashed line, bold solid line, bold dashed line indicates the accumulated number of arrived seeds, dead seeds, established seedlings, and dead seedlings, respectively. Dotted line indicates the number of seeds and seedlings alive at the moment. Observed number of seeds and seedlings from the belt-transects under four mother trees were pooled after weighed by the area of concentric rings from the center of the crowns of each mother trees, respectively.
Figure 4.5b. Demography of the seeds and seedlings of *Quercus eumorpha* in a tropical montane forest at Doi Inthanon National Park, northern Thailand. Solid line, dashed line, bold solid line, bold dashed line indicates the accumulated number of arrived seeds, dead seeds, established seedlings, and dead seedlings, respectively. Dotted line indicates the number of seeds and seedlings alive at the moment. Observed number of seeds and seedlings from the belt-transects under four mother trees were pooled after weighed by the area of concentric rings from the center of the crowns of each mother trees, respectively.
Table 4.3. Demography of seeds and seedlings dispersed from eight selected mother trees of *Quercus brevicalyx* and *Q. eumorpha* in 1999 in a tropical montane forest at Doi Inthanon National Park, northern Thailand.

### *Q. brevicalyx*

<table>
<thead>
<tr>
<th>Dbh (cm)</th>
<th>Observed number of seeds</th>
<th>Weighed number of seeds</th>
<th>Survival rate (weighed) till seedling†</th>
<th>till Dec. 2000‡</th>
</tr>
</thead>
<tbody>
<tr>
<td>99.1</td>
<td>735</td>
<td>13998.9</td>
<td>0.127</td>
<td>0.0148</td>
</tr>
<tr>
<td>99.5</td>
<td>286</td>
<td>3804.5</td>
<td>0.077</td>
<td>0.0033</td>
</tr>
<tr>
<td>63.5</td>
<td>2161</td>
<td>20792.6</td>
<td>0.374</td>
<td>0.1256</td>
</tr>
<tr>
<td>46.2</td>
<td>1275</td>
<td>14124.6</td>
<td>0.165</td>
<td>0.0155</td>
</tr>
<tr>
<td>Total</td>
<td>4457</td>
<td>52720.6</td>
<td>0.231*</td>
<td>0.0579**</td>
</tr>
</tbody>
</table>

†: Chi-square test: $\chi^2 = 4093.3$, *P* < 2.2e-16
‡: Chi-square test: $\chi^2 = 2901.4$, *P* < 2.2e-16

### *Q. eumorpha*

<table>
<thead>
<tr>
<th>Dbh (cm)</th>
<th>Observed number of seeds</th>
<th>Weighed number of seeds</th>
<th>Survival rate (weighed) till seedling†</th>
<th>till Dec. 2000‡</th>
</tr>
</thead>
<tbody>
<tr>
<td>65.2</td>
<td>2233</td>
<td>25657.4</td>
<td>0.079</td>
<td>0.0033</td>
</tr>
<tr>
<td>69.9</td>
<td>272</td>
<td>3072.5</td>
<td>0.070</td>
<td>0.0000</td>
</tr>
<tr>
<td>50.6</td>
<td>62</td>
<td>636.2</td>
<td>0.091</td>
<td>0.0000</td>
</tr>
<tr>
<td>36.4</td>
<td>24</td>
<td>174.4</td>
<td>0.054</td>
<td>0.0000</td>
</tr>
<tr>
<td>Total</td>
<td>2591</td>
<td>29540.4</td>
<td>0.078*</td>
<td>0.0029**</td>
</tr>
</tbody>
</table>

†: Chi-square test: $\chi^2 = 3059.7$, *P* < 2.2e-16
‡: Chi-square test: $\chi^2 = 1560.062$, *P* < 2.2e-16
Figure 4.6. Fate of dispersed seeds of *Quercus brevicalyx* and *Q. eumorpha* from 1999 to 2000 in the 7.5-ha area of a 15-ha study plot in a tropical montane forest at Doi Inthanon National Park, northern Thailand. Primal factors of deaths and establishment as seedlings were indicated as shown in the legend. See text for the details of each factor. Numbers of the seeds from the belt-transects under the four mother trees for each species (*N* = 4457 for *Q. brevicalyx* and *N* = 2591 for *Q.eumorpha*) were pooled after weighed by the area of concentric rings from the center of the crowns of the mother trees, respectively. The fates of seeds are significantly different between the two species (Chi-square test, $\chi^2 = 13973, P < 2.2e-16$).
Figure 4.7. Fate of established seedlings of *Quercus brevicalyx* and *Q. eumorpha* from 1999 to 2000 in a tropical montane forest at Doi Inthanon National Park, northern Thailand. Factors of deaths and survivals of seedlings are indicated as shown in the legend. Solid area indicates survived seedlings. See text for the details of each factor. Numbers of the seedlings from the belt-transects under the four mother trees for each species (*N* = 1242 for *Q. brevicalyx* and *N* = 159 for *Q. eumorpha*) were pooled after weighed by the area of concentric rings from the center of the crowns of the mother trees, respectively. The fates of the seedlings were significantly different between the two species (Chi-square test, *χ²* = 13973, *P* < 2.2e-16).
Figure 4.8. Temporal shift of the causes of mortality of seeds of *Quercus brevicalyx* (upper) and *Q. eumorpha* (lower). Mortality rate of seeds was defined as the numbers of killed seeds divided by the total number of dispersed seeds and by the number of days between the observations. Numbers of seeds in the belt-transects under the four selected mother trees of each species were pooled after weighed by the area of concentric rings from the center of the crowns of the mother trees, respectively. Mortality rates were plotted at the mid-days of the observation intervals.
Figure 4.9. Temporal shift of the causes of mortality of seedlings of *Quercus brevicalyx* (upper) and *Q. eumorpha* (lower). Mortality rate of seedlings was defined as the numbers of killed seedlings divided by the total number of established seedlings and by the number of days between the observations. Numbers of seedlings in the belt-transects under the four selected mother trees of each species were pooled after weighed by the area of concentric rings from the center of the crowns of the mother trees, respectively. Mortality rates were plotted at the mid-days of the observation intervals.
Table 4.4. Indirect factors affecting the mortality of seeds and seedlings of *Quercus brevicalyx* and *Q. eumorpha* in a tropical montane forest at Doi Inthanon National Park, northern Thailand. Distance from the point just below the center of the crown of the mother trees, densities of seeds or seedlings per square meter, canopy openness (%), litter depth (mm) were used as the variables for the logistic regression. Coefficients are selected by backward elimination procedure based on the probability of the likelihood-ratio statistic on SPSS 11.0J.

a) Survival of seeds of *Q. brevicalyx* (*N* = 3876)

<table>
<thead>
<tr>
<th>Variables</th>
<th>B</th>
<th>Standard Error</th>
<th>Wald</th>
<th>d.f.</th>
<th>P</th>
<th>Exp(B)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance</td>
<td>0.0355</td>
<td>0.012</td>
<td>8.59</td>
<td>1</td>
<td>3.39E-03</td>
<td>1.036</td>
</tr>
<tr>
<td>Density of seeds</td>
<td>0.0017</td>
<td>0.001</td>
<td>7.64</td>
<td>1</td>
<td>5.69E-03</td>
<td>1.002</td>
</tr>
<tr>
<td>Canopy openness</td>
<td>0.3729</td>
<td>0.055</td>
<td>45.68</td>
<td>1</td>
<td>1.39E-11</td>
<td>1.452</td>
</tr>
<tr>
<td>Litter depth</td>
<td>0.2339</td>
<td>0.062</td>
<td>14.35</td>
<td>1</td>
<td>1.52E-04</td>
<td>1.263</td>
</tr>
<tr>
<td>Constant</td>
<td>-2.6435</td>
<td>0.132</td>
<td>402.27</td>
<td>1</td>
<td>1.76E-89</td>
<td>0.071</td>
</tr>
</tbody>
</table>

\[ r^2 = 0.0925 \]

b) Survival of seeds of *Q. eumorpha* (*N* = 1668)

<table>
<thead>
<tr>
<th>Variables</th>
<th>B</th>
<th>Standard Error</th>
<th>Wald</th>
<th>d.f.</th>
<th>P</th>
<th>Exp(B)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density of seeds</td>
<td>-0.0086</td>
<td>0.002</td>
<td>26.78</td>
<td>1</td>
<td>2.28E-07</td>
<td>0.991</td>
</tr>
<tr>
<td>Constant</td>
<td>-1.3618</td>
<td>0.156</td>
<td>76.50</td>
<td>1</td>
<td>2.20E-18</td>
<td>0.256</td>
</tr>
</tbody>
</table>

\[ r^2 = 0.0325 \]

c) Survival of seedlings of *Q. brevicalyx* (*N* = 1224)

<table>
<thead>
<tr>
<th>Variables</th>
<th>B</th>
<th>Standard Error</th>
<th>Wald</th>
<th>d.f.</th>
<th>P</th>
<th>Exp(B)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance</td>
<td>0.0411</td>
<td>0.017</td>
<td>6.10</td>
<td>1</td>
<td>1.35E-02</td>
<td>1.042</td>
</tr>
<tr>
<td>Canopy openness</td>
<td>0.4288</td>
<td>0.083</td>
<td>27.00</td>
<td>1</td>
<td>2.03E-07</td>
<td>1.535</td>
</tr>
<tr>
<td>Constant</td>
<td>-2.2169</td>
<td>0.265</td>
<td>69.96</td>
<td>1</td>
<td>6.05E-17</td>
<td>0.109</td>
</tr>
</tbody>
</table>

\[ r^2 = 0.0435 \]
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