

**Doctoral dissertation**

**REGENERATION OF *FAGUS CRENATA* IN AN OLD GROWTH  
BEECH FOREST WITH CO-DOMINANT SPECIES IN THE  
CANOPY LAYER**

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## Abstract

Beech forests in the temperate zone are important and valuable for biodiversity and environmental conservation. The beech, *Fagus crenata*, is dominant species and one of the symbolic species for natural ecosystems in Japan. However, the beech forests have been diminished and isolated because of human's activities like expansion of artificial forests in Japan. Accordingly, conservation of remaining beech forests is important, and for the conservation, mechanisms of the dynamics and regeneration of beech forests should be researched and demonstrated. The dynamics and regeneration in beech forests have been well studied, and the previous researches have told us that advance regeneration, canopy gaps by fallen trees, and seasonal canopy gap by mixed structure in the canopy layer are key points for regeneration and maintenance mechanisms of beech forests. To precisely confirm the knowledge and obtain the new knowledge, long term ecological researches are more necessary. Therefore, this study aimed (1) to detect relations between dynamics of *Fagus crenata* understory trees and canopy tree species for a long term, (2) to determine relations between establishment of canopy trees and disturbance history, and then (3) to discussed regeneration of *F. crenata* in an old-growth beech forest. For the purpose, I conducted the researches in an old growth beech forests with codominant species in canopy layer by long term ecological research and dendrochronological methods.

The present study was conducted in an old-growth beech forest in a forest reserve of Okayama Prefecture in western Japan (35°14' N, 134°23' E; 1050 m a.s.l.). This forest is located in the cool temperate zone, the annual average temperature is 8°C, and annual precipitation is 2400 mm. Maximum snow depth 1.8 m. The canopy layer was mixed with *F. crenata* and other codominant species, and dominance of *F. crenata* and *Magnolia Obovata* was prominent in the

canopy layer. In the old growth beech forest, a study plot of 50m x 240m was set in the north-facing slope.

Firstly, tree census was conducted in 1992 and in 2011. In the tree census, tree individuals with diameter at breast height (DBH)  $\geq 4$  cm were numbered, the species were identified, the DBHs were measured, and the positions were recorded. This study defined understory trees as the measured trees growing under canopy layer. These understory trees were taller than dwarf bamboo community in the forest floor, and probably it is not necessary to consider effects of dwarf bamboo coverage on the understory trees. For estimating light conditions in the understory, leaf unfolding and shedding of canopy trees was observed with automatic phenology cameras, and light intensity in the understory were measured from the beginning of leaf unfolding till the end of leaf shedding with color acetate films degrading the color according to light intensity. From the data obtained in the field work, I analyzed relations between dynamics of *F. crenata* understory trees and the canopy tree species between 1992 and 2011. In most of species including *F. crenata*, density of understory trees decreased from 1992 to 2011, and mortality of *F. crenata* understory trees was much higher than that of recruitment rate probably because of a little gap formation. In the spatial distribution correlations, *F. crenata* understory trees changed spatial correlation to *F. crenata* canopy trees from independent relation to dissociated relation. On the other hand, *F. crenata* understory trees constantly had associated relation to *M. obovata* canopy trees that are codominant species in the forest. Survival and diameter rates of *F. crenata* understory trees were significantly higher under *M. obovata* canopy trees than under *F. crenata* canopy trees. Accordingly, I intended to explain the reason from viewpoints of the light conditions in the understory. Leaf unfolding was later and leaf shedding was earlier in the canopy trees of *M. obovata* than *F. crenata*. In this season, light intensity was significantly

higher under *M. obovata* canopy trees than under *F. crenata* canopy trees. The results demonstrated the existence of seasonal gaps under *M. obovata* canopy trees. Moreover, the light intensity in the understory was higher under *M. obovata* canopy trees than canopy trees of *F. crenata* even in the growing season between the completion of leaf unfolding and the beginning of leaf shedding. Therefore, it is likely that the population size of *F. crenata* understory trees tends to be more maintained and stable under *M. obovata* than under *F. crenata* because of differences of light conditions.

Secondly, increment cores were taken for tree ring analysis from the trunk of all canopy trees in the area of 50 m x 130 m within the study plot. In the tree ring analysis, tree ring widths were measured at the unit of 0.01mm with a microscope, and then ages of trees were estimated, growing patterns were determined, and radial growth release criteria were developed to identify significant growth releases and estimate occurrence of disturbance. From those data, I analyzed dynamics of canopy trees by dendrochronological methods. Age structure of canopy trees indicated continuous establishment by *F. crenata* canopy trees and simultaneous establishment by *M. obovata* canopy trees. Next, canopy trees were classified into gap-origin and non-gap-origin trees by analysis of growth rates and patterns in the initial growing stage, and then spatial distributions of canopy trees were analyzed. *F. crenata* canopy trees had both gap-origin canopy trees and non-gap-origin canopy trees abundantly, and gap-origin canopy trees of *F. crenata* showed random distribution. On the other hand, Most of *M. obovata* canopy trees were gap-origin individuals, and those gap-origin canopy trees of *M. obovata* showed aggregated distribution patterns. Additionally, the aggregated *M. obovata* canopy trees occupied considerably large areas. From growth release analysis, a few and small growth releases were observed in the canopy trees for around 150 years after the estimated establishment period of *M.*

*obovate* canopy trees, therefore, it was estimated that a few and low intensity disturbances occurred but prominently intensive disturbances did not occur for a long time. These results suggested that *F. crenata* canopy trees gradually and constantly regenerated before and after both large and small scale disturbances, whereas canopy trees of *M. obovata* simultaneously regenerated after large scale disturbances which are estimated to rarely occur.

Finally, I discussed the regeneration of *F. crenata* from these results. Dynamics of *F. crenata* understory trees suggested that advance regeneration by these understory trees has been facilitated under the canopy trees of *M. obovate*. It is probably the reason that *M. obovata* canopy trees provided *F. crenata* understory trees with light conditions sufficient for maintaining the understory trees by seasonal gap in spring and autumn and higher light intensity in the other growing season as well. The canopy trees of *M. obovate* originally regenerated after rare and large scale disturbances and then attained to canopy layer. Therefore, this study suggested that the large scale disturbances are important factor to facilitate regeneration of *F. crenata* through the coexistence of *M. obovata* in the canopy layer. It will be stated that large scale disturbances in old beech forests contribute to sustainably maintaining structure of forest as well as species diversity.

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## Chapter 1

### GENERAL INTRODUCTION

#### *1.1. Climate features and distribution of beech forest*

Beech forests mainly occur in temperate zones of the north hemisphere, and are distributed in isolated regions of East Asia, Euro-Asia, and North America (Figure 1-1). The dominant species *Fagus crenata* Blume is one of the native and climax species in cool temperate deciduous forests of Japan (Peters 1997). The beech forests are mainly classified into Japan Sea (JS) side type that is characterized by prominent dominance of *F. crenata* in the canopy layer and *Sasa kurilensis* var. *lasiochlamys* Koidz in the understory (commonly referred to as the Japan Sea type), and Pacific Ocean (PO) side that consists of the other broad-leaved tree species including *Magnolia obovata* Thunb., *Betula grossa* Siebold & Zucc. and *Quercus mongolica* Fisch. in canopy layer (commonly referred as the Pacific Ocean type) (Fukushima et al. 1995; Shimano 1999). The difference between these two types is observed also in amounts of snowfall that are much deeper in JS type than PO type (Shimano and Okitsu 1993, 1994).

Thermal and moisture regimes are important factors to limit distributional range of beech forest (Matsui et al. 2004; Fang and Lechowicz 2006; Shen et al. 2015). The much snowfall amounts are effective to protect seeds from predation by rodents regionally (Shimano and Matsuzawa 1998; Homma et al. 1999). Therefore, distributions of beech forests might be changed due to climate changes. Matsui et al. (2004) modeled and predicted climate (temperature and precipitation) changes for future and pointed out that the rises of temperature and precipitation may cause retreating distribution of beech forests from southwest to northeast in Japan (Figure 1-2), because Ohsawa (1990) suggested that the coldest month temperature highly corresponds to northern distributional boundary of plant species.

The beech forests are valuable forests, which serve us environmental conservation function and provide us with biodiversity. However, the beech forests of Japan were intensively affected by human's activities during the years from 1950s to 1980s (Forestry agency, 2009). Many of beech forests were displaced by artificial forests. Consequently, the antropogenic disturbances diminished and isolated primary beech forests and there are a few primary beech forests remaining in mountainous region in Japan (Yamamoto and Numata 1995; Torimaru et al. 2009). Only 4 percent of total forested area (Figure 1-3) is covered with beech forest (Forestry agency, 2009) even though it is widely distributed in cool temperate zone from Kyushu to Hokkaido in Japan (Figure 1-4). Therefore, remaining beech forests are important and the conservation of beech forests should be implemented. For the purpose of the conservation, mechanisms of the dynamics and regeneration should be researched and demonstrated.

## **1.2.Gap and regeneration dynamics of beech forest**

Beech forests have been well studied and documented from the aspect of regeneration and gap dynamics in Japan (Nakashizuka and Numata 1982a, b; Nakashizuka 1983, 1984; Ohkubo et al 1996; Yamamoto and Nishimura 1999, Yamamoto 1996, 2000; Abe et al 2001, 2002, 2005; Shimano 2002; Henbo et al. 2004). Gaps are generally formed by a single and multiple canopy trees fall in forest community (Whitmore 1978; Runkle 1982; Yamamoto 1996, 2000). Consequently, gap formation increases the light intensity on the forest floor. The light conditions are important for the invasion, growth, survival and existence of understory plant species because of different light utilization and photosynthetic ability by species (Bazzaz 1979; Koike 1985). Therefore, gap size is a key factor for species coexistence by species with different shade tolerances (Abe et al. 1995). In temperate old growth forests, gaps are smaller because they are caused mostly by single tree falls (Runkle 1982, Yamamoto and Numata 1995). Small gaps are

often filled by branch expansion of neighboring canopy trees and also facilitating growth and survival of shade tolerant understory trees (Yamamoto 1989, Busing 1994, Canham 1988a), saplings and seedlings from the advance growth (Nakashizuka 1983), which survive with reduced growth under closed canopy, then response to gap formation and grow well (Nakashizuka 1983, Canham 1989). *Fagus crenata* is described as the typical gap regeneration species recruited from seedlings and saplings before gap formation (Nakashizuka and Numata 1982b; Nakashizuka 1983; Yamamoto 1989). However, even if canopy gaps are created, there are a few beech trees can survive and regenerate (Nakashizuka 1984, 1987, 1988) because their seedling and saplings are prevented from surviving and growing by dense cover of dwarf bamboo even in gaps (Veblen 1985; Taylor et al. 1995). Dwarf bamboo in understory is an ecological filter for regeneration of beech forests (Ito and Hino 2007). On the other hand, simultaneous withering of dwarf bamboo facilitates the regeneration by advance growth of shade-tolerant species including beech species (Taylor et al. 1995; Schnitzer et al. 2000) and it provides suitable condition for regeneration of intermediate and less shade-tolerant species as well (Abe et al. 2002).

On the other hand, large disturbances have played an important role in regulating structure, species composition and dynamics of forest communities (Pickett and White 1985). In Japan, beech forests are often receive frequent and intense typhoon effect (Henbo et al. 2004). Many studies have pointed the importance of intensive disturbance event (Peterson and Pickett 1995, Masaki et al. 1999) for tree regeneration (Yamamoto et al. 1995, Kobayashi and Kamitani 2000) and for species diversity in the forests. Diverse canopy layer in beech forests is probably associated with large gap formation. Large gaps are formed by multiple tree falls with and without destruction of forest floor and soil (Runkle 1982, Nakashizuka 1987, Yamamoto

1989). Shade-tolerant species are sparse in environmental conditions of larger gaps (Abe et al 1995), but the large canopy opening enables shade-intolerant pioneers and intermediate tolerant species to primarily regenerate at the initial stage, and facilitate an increase of species diversity in a forest community (Yamamoto 2000). Therefore, relationships between large disturbances and regeneration strategy by seedlings and saplings (Harrington and Bluhm 2001) of beech trees are important for continuous regeneration of beech forests as well.

### **1.3. Phenological gap**

Light Condition is one of the major factors determining dynamics of understory tree population in forests (Canham 1988; Pacala et al 1994). Mixed stands might have less light condition on understory than pure-species stands because the combined arrangement of different crown shapes of canopy tree species (Pretzsch 2014) such as wide-shallow and narrow-deep crown shape (Kikuzawa and Umeki 1996). The closed forest intercepts regeneration and growth of shade-intolerant and reduces growth of shade-tolerant species seedling and saplings. However, in some cases, canopy heterogeneity facilitates establishment, growth and survival of understory individuals because of a variety of phenological gaps by the canopy tree species and different light penetration on forest floor. The narrower openings among leaves, branches, and twigs of canopy trees and shorter duration of openings by species specific leaf phenology are observed in closed diverse canopy (Komiya et al. 2001; Augspurger and Bartlett 2003; Matsui and Koike 2006; Augspurger 2008; Lopez et al 2008). Consequently, under the closed canopy, growth and survival of understory trees differed according to varied light condition in the understory by canopy tree species, and mixed canopy layer affects understory tree abundance and the replacement pattern (Jolly et al. 2004). The phenological gap has been often observed in mixed beech (*Fagus crenata*) forests in the cool temperate zone because of different timing for

unfolding of leaves by canopy species (Kikuzawa 1983; Lechowicz 1984; Seiwa 1998; Tomita and Seiwa 2004). The canopy layer is often dominated by *F. crenata* and the other tree species, and typically co-existing species are *Q. mongolica* and *M. obovata* (Koike 1985; Hashizume 1987; Peters 1997; Yoshida and Kamitani 1998; Sugita 2009). These two species tend to unfold leaves later than *F. crenata*, which phenologically forms canopy gap between leaf unfolding of *F. crenata* and that of other species in the canopy layer (Hashizume 1982; Kikuzawa 1983). Consequently, it has been pointed out that seedlings and saplings of *F. crenata* are contagiously distributed and the density is higher under canopy trees of *M. obovata* and *Q. mongolica*, which has suggested higher survival and growth rates under canopy trees of *M. obovata* and *Q. mongolica* (Komita and Seiwa 2004). At the same time, however, the phenological canopy gaps also accelerate the growth of the evergreen dwarf bamboos, which often dominate the understory of these beech forests with dense coverage and reduce regeneration of seedlings and saplings. Therefore, it is necessary to consider the effects of phenological gaps on the seedlings and saplings through the filter effects of bamboo coverage that should be affected by phenological gaps as well.

#### ***1.4. Study objectives and contribution***

These previous researches have told us that advance growth, gap dynamics, mixed structure in canopy layer and phenological gap are important for regeneration and maintenance of Beech forests. The previous studies revealed that many forests have been intensively and frequently disturbed mainly by typhoons and strong storms and these disturbances initiate regeneration. Many of previous studies surveyed and investigated establishment, growth, and regeneration processes of beech forests in Japan from the viewpoints of effects of dwarf bamboo and gap formation (Nakashizuka and Numata 1982 a,b; Nakashizuka 1983; Ohkubo et al. 1996;

Yamamoto et al. 1995; Yamamoto and Nishimura 1999, Yamamoto 2000; Abe et al. 2001, 2002, 2005; Shimano 2002;). However, these outcomes need to be more examined by long term researches and longer term researches than the previous researches. Although a dendrochronological study is effective for long term researches, there are few dendrochronological studies in beech forests (Cao and Ohkubo 1999). Additionally, phenological gaps and the effects on the density and growth of seedlings and saplings have been well demonstrated (Peters and Platt 1996; Kikuzawa 1983; Lechowicz 1984; Seiwa 1998; Tomita and Seiwa 2004), however, these studies have not examined temporal changes and dynamics of seedlings and saplings. Therefore, it is necessary to conduct long term ecological researches also for detecting the effects of phenological gaps on the dynamics of understory individuals.

Accordingly, I researched on the understory tree dynamics in an old growth beech forest with co-dominant species in canopy layer by long term ecological researches and dendrochronological analysis from the viewpoints of effects of heterogeneity in canopy layer and dynamics of the canopy layer. Firstly, this study aimed to examine the effects of the heterogeneity in the canopy layer, especially phenological gaps, on the dynamics of understory beech tree population by the long term ecological research for 19 years in an old-growth beech forest. In this analysis, I observed *F. crenata* understory trees that are taller than dwarf bamboo communities to avoid the coverage effects by dwarf bamboos. Secondly, this study aimed to determine relations between establishment of canopy trees and disturbance history, based on dendrochronological method. Finally, I discussed regeneration of *F. crenata* and beech forest dynamics from the above two aspects.

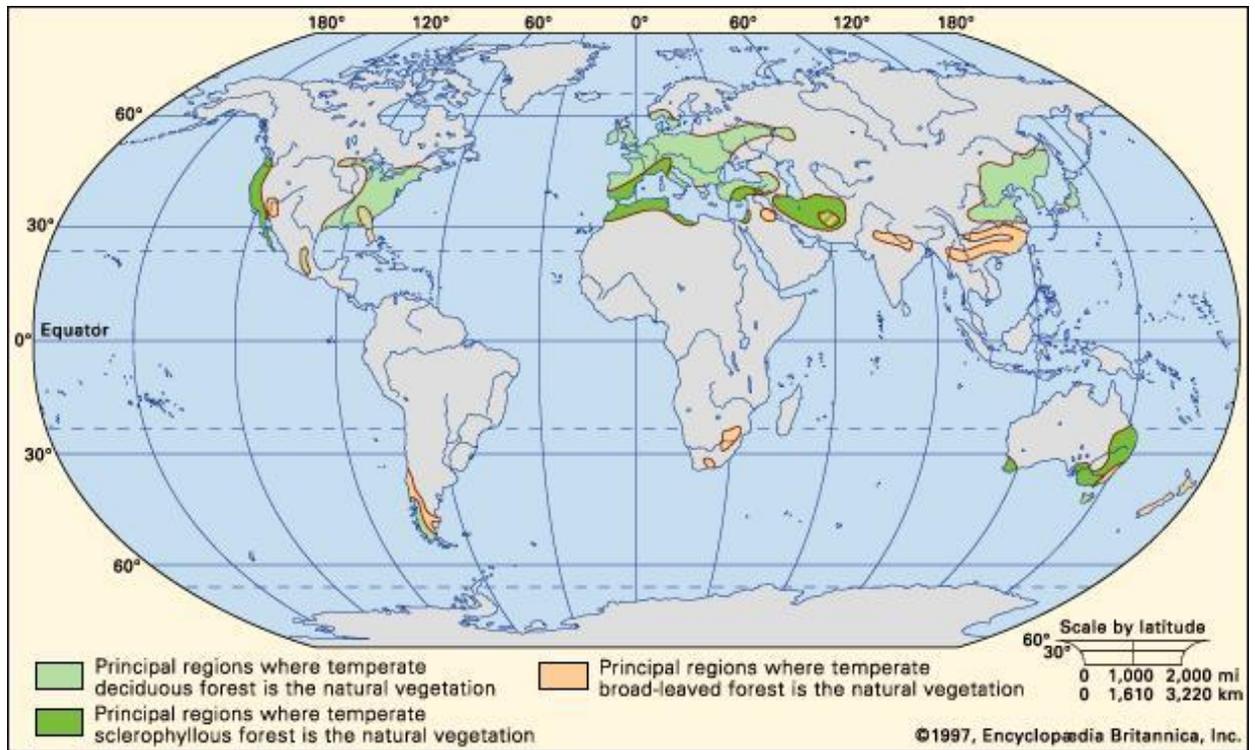


Figure 1-1. Distribution map of temperate deciduous forests.

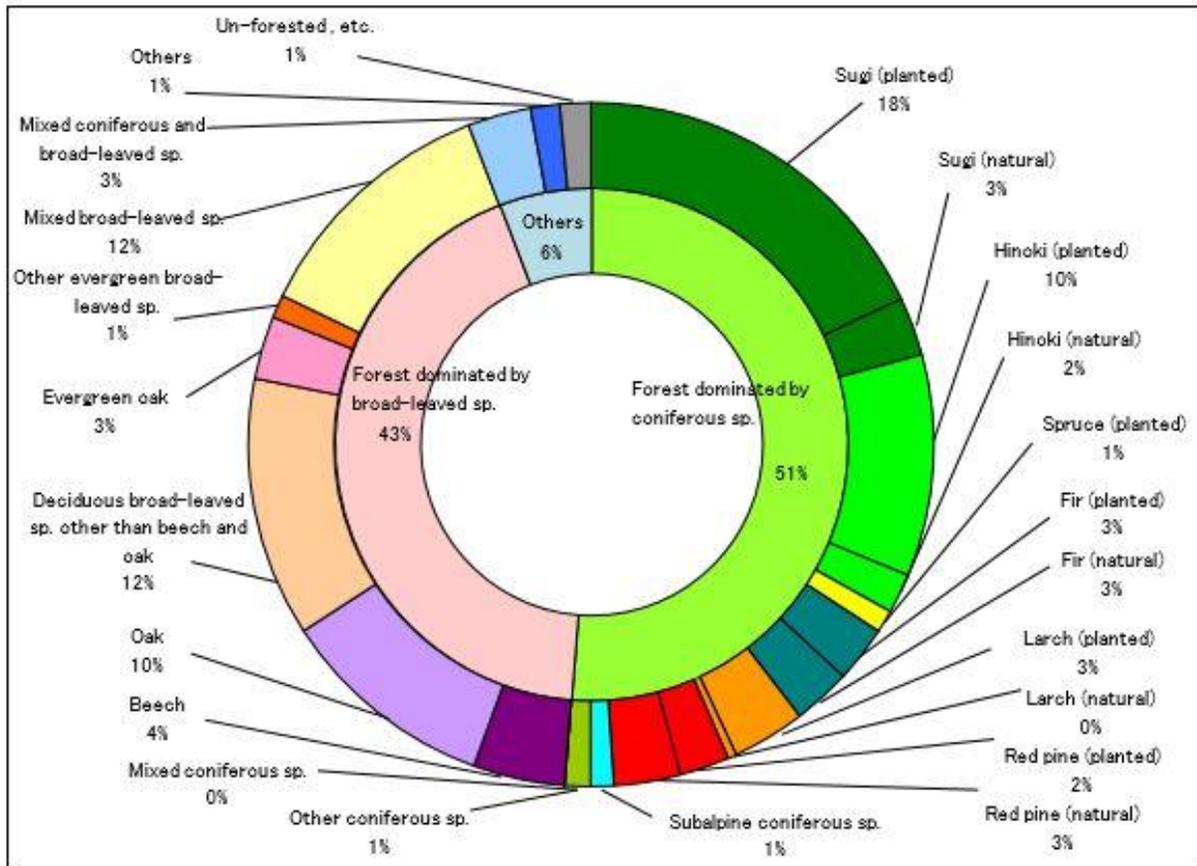


Figure 1-2. Forest species composition of Japan (Forestry agency, 2009).

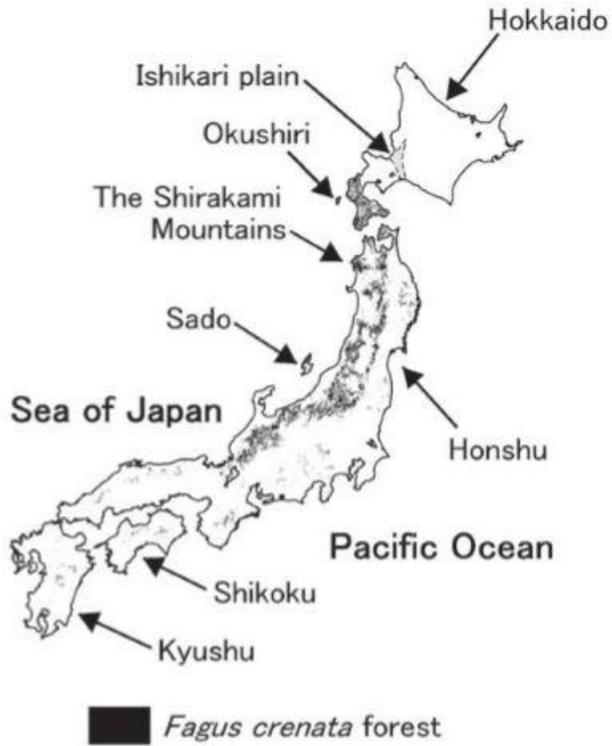
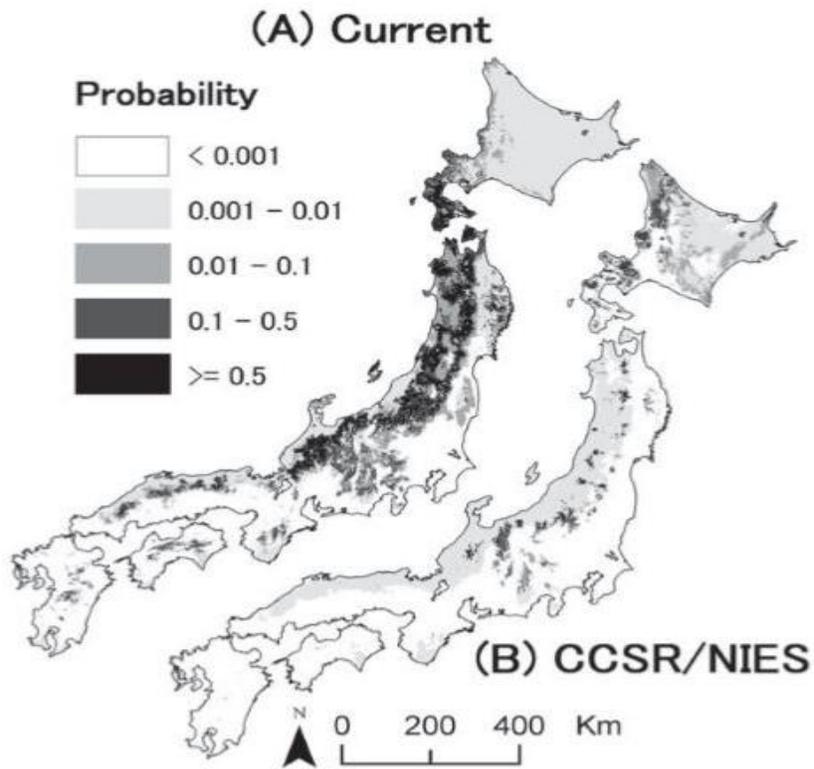


Figure 1-3. Distribution of the actual *F. crenata* forests in Japan at a spatial resolution of ca. 1 km<sup>2</sup>, based on the vegetation data from the National Survey on the Natural Environment and important geographical locations (Matsui et al. 2004).



**Figure 1-4.** Predicted probability distributions of *Fagus crenata* forests based on the ENVI model. Map A (left): under the current climate. Map B (right): under the CCSR/NIES scenario in the 2090s (Matsui et al. 2004).

## Chapter 2

# DYNAMICS OF UNDERSTORY BEECH TREES UNDER CANOPY LAYERS COMPOSED OF DIFFERENT TREE SPECIES IN AN OLD-GROWTH BEECH FOREST

### 2.1. Introduction

Light Condition is one of the major factors determining dynamics of understory tree population in forests (Nakashizuka 1987; Canham 1988; Pacala et al 1994). The light condition of understory is heterogeneous in the forests because the structure and dynamics in canopy layer causes differences of light intensity in the understory (Kikuzawa and Umeki 1996; Pretzsch 2014). The heterogeneity is often formed by fallen trees of canopy layer in the forests. These canopy gaps contribute to the invasion, establishment, and growth of tree species (Pickett and White 1985; Whitmore 1989; Busing and White 1997). On the other hand, not only these canopy gaps but canopy gaps phenologically formed by diverse canopy layer causes heterogeneity of understory light conditions in deciduous forests (Tomita & Seiwa 2004; Augspurger 2008; Lopez et al 2008). This phenological gap has been often observed in beech (*Fagus crenata*) forests in the cool temperate zone because timing for unfolding of leaves by different canopy species (Kikuzawa 1983; Lechowicz 1984; Seiwa 1998; Tomita and Seiwa 2004). The canopy layer is often dominated by *F. crenata* and other different tree species, and the typically co-existing species are *Quercus mongolica* and *Magnolia obovata* (Koike 1985; Hashizume 1987; Peters 1997; Yoshida and Kamitani 1998). These two species tend to unfold leaves later than *F. crenata*, which phenologically forms canopy gap between leaf unfolding of *F. crenata* and that of other species in the canopy layer (Hashizume 1982; Kikuzawa 1983;). Consequently, it has been pointed out that seedlings and saplings of *F. crenata* are contagiously distributed and the density

is higher under canopy trees of *M. obovata* and *Q. mongolica*, which has suggested higher survival and growth rates under canopy trees of *M. obovata* and *Q. mongolica* (Komita and Seiwa 2004).

At the same time, however, the phenological canopy gaps also accelerate the growth of the evergreen dwarf bamboos, which often dominate the understory of these beech forests with dense coverage and reduce regeneration of seedlings and saplings. Therefore, it is necessary to consider the effects of phenological gaps on the seedlings and saplings through the filter effects of bamboo coverage that should be affected by phenological gaps as well. Effects of phenological gaps the establishment of tree species would be clearly observed in the understory trees that are taller than dwarf bamboo community. Few studies, however, demonstrated the effects of phenological gaps on those understory trees. The density of those large sized understory *F. crenata* trees is higher under canopy trees of *M. obovata* and *Q. mongolica* (Tomita & Seiwa 2004) and similar result reported in America that the higher number of understory *F. grandifolia* individuals demonstrated under the canopy *M. grandifolia* individuals than under the canopy *F. grandifolia* individuals (Peters 1996). However, these studies have demonstrated the special distribution and density of those large-sized-understory trees, but not demonstrated effects of the canopy phenologicality on actual dynamics of larger-sized understory trees. Therefore, it is necessary to conduct long term ecological researches for detecting the effects of phenological gaps on the dynamics of large-sized understory trees.

This study aimed to examine the effects of the heterogeneity in the canopy layer, especially phenological gaps, on the dynamics of understory beech tree population by the long term ecological research for 19 years in an old-growth beech forest. The understory trees are individuals with diameters of more than 4 cm and taller than dwarf bamboo community. The

effects of different canopy trees on the survival and growth rates of those understory trees were analyzed. At the same time, we measured and compared the leaf unfolding and shedding timing and the phenological changes in light conditions under the different canopy trees.

## **2.2. Materials and methods**

### **2.2.1. Study site**

This study considered an old-growth beech forest (35°14' N, 134°23' E; 1050 m a.s.l.) of the Wakasugi Forest Reserve in the western part of Japan. This forest is located in the cool temperate zone, and annual average temperature is 8°C and annual precipitation is 2400 mm. Maximum snow depth 1.8 m. The soil is forest brown soil and the parent rock is granite. The dominant species were *F. crenata* and *M. obovata* while the understory was dominated by dense dwarf bamboo, *S. kurilensis*. It has been pointed out that dense coverage of the dwarf bamboo probably reduces regeneration of *F. crenata* in this forest as well (Nishimura and Yamamoto 2002).

### **2.2.2. Study plot and tree census**

A study plot of 50m x 240m was set in the north-facing slope. In the study plot, tree census was conducted in 1992 (Mizunaga et al. 1996). In the tree census, trees with diameters at breast height (DBH)  $\geq 4$  cm were sampled and numbered, the species were identified, the DBH (diameter at breast height) were measured, and the positions were recorded. For canopy layer structure, canopy tree species were identified above the centre of every 2.5m x 2.5m grid as dominant canopy tree species of the grid in 1992. We conducted the re-measurement in 2011. In the re-measurement, we repeated the same measurement, and recorded the survival of trees

measured in 1992, and recorded trees newly recruited into dbh size class of cm and more than 4 cm.

### **2.2.3. *Leaf phenology of canopy trees***

We recorded leaf phenology of canopy trees of *F. crenata*, *M. obovata*, and *B. grossa* with two automatic cameras set in the different sites of forest floor. Canopies of all the three species were taken in the image of each camera. We began taking pictures on 13<sup>th</sup> Apr. May when leaves of every canopy species have not yet been unfolded, and completed it on 22<sup>nd</sup> Nov. when all leaves of every canopy species were shed. The pictures were automatically taken at noon every day. The picture images were trimmed so that a branch of each species could be recorded without overlapping each other. In the trimmed area, Images were processed into white and black images which indicate only black parts are leaves and branches. With those imaged, percentages of the leaves and branches were calculated in the images.

### **2.2.4. *Light conditions of understory***

Light intensity measured at three points under each of three canopy trees of each canopy tree species, under three canopy gaps, and under an open site with color acetate films (R-3D and Y-1W, Taisei Chemical Industries, Tokyo, Japan). The color of the acetate films is degraded by sun light. Therefore, accumulative light amount can be estimated from the degradation degree of the color which can be read with a reading instrument (D-meter RYO-470, Taisei Chemical Industries, Tokyo, Japan). Two kinds of acetate color films used for this study, R-3D and Y-1W that have different degrading velocity between them. The acetate films were set in the slide film mounts, and they were put on the small woody table set with poles at the height of 1.3m in each measuring point. Films changed once for 3 to 10 days from 7<sup>th</sup> May to 22<sup>nd</sup> Nov and the

degradation degree measured. PPFD (photosynthetic active photon flux density) estimated from the relations between the color degradation degree and PPFD with temperature correction. To estimation, color degradation degrees and PPFDs were calibrated in the different temperature conditions in advance. The calibrated relation was obtained by setting the color acetate films and photon sensor in the experimental field of Okayama University. The calibration curves constructed based on method by Kawamura et al. (2005).

### **2.2.5. Analysis**

Spatial distribution correlations analysis conducted between canopy trees and *F. crenata* understory trees by pair correlation function with the position data. The analysis used L12 function that was modified from K12 function (Ripley 1977) with the data in 1992 and 2011. This function can be expressed from the ratio of the density of other category in a circle having the centre at the position of a randomly selected individual to the average density of other category. Categories in our analysis are *F. crenata* understory trees and canopy tree species, and we used *F. crenata* understory trees in 1992, those in 2011 that existed in 1992 and survived in 2011, and excluded newly recruited understory trees between 1992 and 2011. Significance of the correlation was evaluated in the confidence limit which was calculated from Monte Carlo simulation by randomizing the distribution of other category points.

Survival rates and DBH increments of the *F. crenata* understory trees were analyzed for 19 years (1992-2011), and intended to detect limiting factors limiting by GLMM, the general linear mixed model. When the independent variable was survival rates, we used binomial distribution and logic link function. When the independent variable was DBH increments, we used logarithmic normal distribution and log function. The explanatory variables were coverage of

dwarf bamboos and slope gradient in 5m x 5m grids where the *F. crenata* understory trees were located, canopy tree species above the *F. crenata* understory trees, and diameters of the *F. crenata* understory trees in 1992. Percentages of covering area in 5m x 5m grids were used for coverage of dwarf bamboo. Slope gradient in each 5m x 5m grid was calculated from the differences in the level of four corners of 5m x 5m grid, according to Yamakura et al. (1995). The canopy tree species above the understory trees meant dominant canopy tree species of 2.5m x 2.5m grids where the *F. crenata* understory trees were located. As the dominant canopy tree species, we gave value 0 to *F. crenata* and value 1 to other species, for observing relative effects of other species to *F. crenata*. Because of the way to give those values for other species, we constructed one model for each combination between *F. crenata* and *M. obovata* and between *F. crenata* and *B. grossa*. In any model analysis, model selection was based on AIC (Akaike's Information Criterion).

The PPFD values in the understory under several canopy types statistically compared by multivariate comparison method, with Tukey's HSD test. The PPFD values in every measurement time were tested in the leaf unfolding season and the shedding season. Cumulative values of PPFD were also tested through growing season as well as in the growing season after completion of leaf unfolding before beginning of leaf shedding (Kawamura et al. 2005).

### **2.3. Results**

*Fagus crenata*, *M. obovata*, and *B. grossa* occupied more than 10 % in BA and are likely to be dominant species in the studied forest in both 1992 and 2011 (Table 2-1). *Quercus mongolica* and *Kalopanax septemlobus* Koidz. occurred in the canopy layer, but their dominance was much lower than *F. crenata*, *M. obovata*, and *B. grossa*. Thirty-one species occurred in 1992, but the species number decreased into twenty-six species, and the stem density decreased from 1992 to

2011 in most of species although total basal area increased. *F. crenata* understory trees also decreased in the number of individuals from 1992 to 2011 (Table 2-2). The mortality was much higher than recruitment rate.

As the change of population size was observed in *F. crenata* understory trees, changes of spatial distribution pattern analyzed from 1992 to 2011 by comparing spatial distribution correlations with different canopy tree species (Figure 2-1). *Fagus crenata* understory trees had independent relation to *F. crenata* canopy trees in 1992, but dissociated relation to *F. crenata* canopy trees in 2011. *F. crenata* understory trees had associated relation to *M. obovata* canopy trees in 1992, and the tendency became clearer in 2011. *F. crenata* understory trees had associated relation to *B. grossa* canopy trees in 1992, but the tendency was similar with that in 2011. Therefore, it is likely that density of *F. crenata* understory trees decreased more under the *F. crenata* canopy trees than under *M. obovata* canopy trees and *B. grossa* canopy trees.

GLMM analysis also demonstrated that survival rate of *F. crenata* understory trees was higher under *M. obovata* canopy trees than under *F. crenata* canopy trees (Table 2-3). But, there was no difference between under *B. grossa* canopy trees under *F. crenata* canopy trees (Table 2-4). Diameter growth rate of *F. crenata* understory trees was higher under *M. obovata* canopy trees than *F. crenata* canopy trees. Additionally, in this analysis, an increase of dwarf bamboo coverage tended to increase the growth rate. Growth rate of *F. crenata* understory trees under *B. grossa* canopy trees was not likely to differ from that under *F. crenata* canopy trees (Table 2-6).

Among the canopy tree species, leaf unfolding timing and leaf shedding timing were different (Figure 2-2). In spring leaves unfolded in the canopy layer in the order of *F. crenata*, *B. grossa*, and *M. obovata*. In autumn leaves were shed in the order of *M. obovata*, *B. grossa*, and *F.*

*crenata*. In the change of PPFD (Figure 2-3), PPFD was significantly higher under *M. obovata* canopy trees than *F. crenata* and *B. grossa* canopy trees in the leaf unfolding season and leaf shedding season. Cumulative value of PPFD was significantly higher under *M. obovata* canopy trees than under *F. crenata* canopy trees through growing season as well as (Table 2-3).

Therefore, we detected the existence of phenological gaps under *M. obovata* canopy trees in both leaf unfolding and leaf shedding season. Moreover, we observed that light intensity is higher under *M. obovata* canopy trees than canopy trees of other species even in the growing season between the completion of leaf unfolding and the beginning of leaf shedding.

## **2.4. Discussion**

### **2.4.1. Effects of light conditions**

In beech forests of Japan, there are two types, i.e. Japan Sea side type and Pacific Sea side type. Canopy layer tends to be homogeneous due to the prominent dominance of *F. crenata* in Japan Sea side type, and canopy layer tends to be heterogeneous because of codominance with several species in Pacific Sea side type (Koike 1985; Hashizume 1987; Shimano and Okitsu 1993, 1994; Peters 1997; Yoshida and Kamitani 1998). The canopy layer in the studied beech forest is thought to belong to the Pacific Sea side type. Accordingly, it is hypothesized that light conditions in the understory are heterogeneous and the heterogeneity will have large effects on the dynamics of the understory tree population. It has already been pointed out that phenological gaps in the spring by *M. obovata* facilitate regeneration of *F. crenata* seedlings and saplings (Komiya 2001; Tomita and Seiwa 2004). In north America, the density of understory *F. grandifolia* trees was higher beneath *M. grandifolia* canopy trees than beneath *F. grandifolia* canopy trees (Peters and Platt 1996). Long term ecological research in this study enabled us to

examine and confirm that it is true for *F. crenata* understory trees. In deciduous broad-leaved forests, leaf unfolding of understory trees is earlier than that of canopy trees (Kikuzawa 1984), which indicates that light conditions before leaf unfolding of canopy trees determine the primary production of understory trees (Hashimoto and Aoki 1996). Harrington et al. (1989) has reported that understory trees gain 27% to 35% to annual amount in carbon base before leaf unfolding of canopy trees in the spring. *Fagus crenata* is flush type species in unfolding leaves, and determines large amounts of annual production in the initial period of growing season (Kikuzawa 1983). Therefore, phenological gaps in the early spring will probably has large contribution to their annual production.

Besides phenological gaps in the early spring, this study demonstrated that PPFD in the understory higher under *M. obovata* canopy trees than under *F. crenata* canopy trees in leafy season, i.e. after unfolding of leaves and before shedding of leaves in canopy trees, and that phenological gaps work in the autumn as well. The higher PPFD under *M. obovata* will probably cause the higher survival rate and growth rate of *F. crenata* understory trees. The relative values of PPFD were 7.49 % in leafy season and 8.63 % through growing season under *F. crenata* canopy trees and 11.98 % in leafy season and 13.32 % thorough growing season under *M. obovata* canopy trees. As for relationships between light conditions and survival and growth, it has been pointed out that the survival rates of *F. crenata* saplings is more than 90% in the light intensity of more than 15%, and the survival rates ranges from 15% to 33% in the light intensity of less than 5% (Hashizume 1982), on the other hand even more than 5 % is not suitable for the survival (Koyama et al. 2007; Tomita and Seiwa 2004). Accordingly, it is likely that survival rate of *F. crenata* understory trees may be drastically changeable in the range of 5 % to 15 %.

Relative values of PPFD under *M. obovata* is higher than that under *F. crenata* in this range of relative light intensity, which might cause the differences of survival rates between them.

#### **2.4.2. Janzen –Connel hypothesis**

These relationships between understory trees and canopy tree species should be examined also by other factor as well as light conditions. It has been hypothesized and well-known that con-species of canopy trees have a negative effect on the survival of seedlings and saplings (Peters 1996; Akashi 1996). The Janzen-Connel hypothesis has been researched and observed also in beech forests. It has been suggested that survival of *F. crenata* seedlings and saplings decreases under canopy trees of con-species and *F. crenata* seedlings and saplings have dissociated special distribution with con-species canopy trees (Akashi 1996). Seedlings and saplings are likely to be infected by fungi specific for con-species canopy trees or mother trees (Masaki et al 2005). However we examined survival rate of larger understory trees with DBH > 4 cm in this study. Therefore, it is likely these effects on the survival of *F. crenata* are small in this study.

#### **2.4.3. Effect of dwarf bamboo**

It has been pointed out that coverage of dwarf bamboos reduce establishment and growth of seedlings and saplings due to filter effect (Ito and Hino 2007) and slow decomposition rate of litter (Dolezal et al. 2009). On the other hand, it is necessary to consider competition in the underground (Abe et al. 2002) because studied understory trees are taller than dwarf bamboos. However, the coverage of dwarf bamboos has a positive effect on growth of *F. crenata* understory trees. Growth of the dwarf bamboo is facilitated by the stable and thick soil on the steep slope (Noguchi & Yoshida 2005). Higher coverage of dwarf bamboos might indicate the

habitats have stable and thick soil on the steep slopes, which might cause the higher growth rates of understory trees. Once understory trees emerge from dwarf bamboo community, soil conditions allowing dense dwarf bamboos might be more suitable for the growth of *F. crenata* understory trees.

#### **2.4.4. Regeneration of *F. crenata***

Regeneration of *F. crenata* is facilitated by gap formation in beech forests (Nakashizuka and Numata 1983; Hara 1983; Nakashizuka 1987; Yamamoto and Nishimura 1995). After the gap formation, *F. crenata* will be established as new individuals and as individuals by advance regeneration (Nakashizuka 1983; Akashi 1996). Besides the seedling bank and sapling bank, understory trees will contribute to the regeneration of the species. *F. crenata* understory trees are likely to wait for gap formation, and abundance of understory population will probably determine the speed of regeneration in beech forests (Nakashizuka 1983). However, gap formation with suitable magnitude disturbance for the regeneration does not always occur constantly and frequently (Nakashizuka 1987). There are periods without those disturbances in beech forests, and *F. crenata* understory tree population tends to be reduced and decrease (Yamamoto and Nishimura 1999; Shimano 2002). Also in the study beech forest, population size of *F. crenata* understory trees tends to decrease. The clumped distribution of *M. obovata* might be more important for regeneration of understory *F. crenata* tree, because random distribution of canopy tree species might create low light penetration on understory. Mixed-species stands might have less light condition on understory than pure-species stands because the combined arrangement of different crown shapes of canopy tree species (Pretzsch 2014) such as wide-shallow and narrow-deep crown shape (Kikuzawa and Umeki 1996). Therefore, co-existence of *M. obovata* in the canopy layer with clumped distribution is important to the regeneration by

understory trees of *F. crenata* in beech forests. After gap formation by *M. obovata* canopy trees, smooth and early regeneration by *F. crenata* understory trees will probably be achieved.

Accordingly, species diversity will probably contribute to maintaining the regeneration of *F. crenata* as well. Additionally, aggregation of *M. obovata* canopy trees is suitable for maintenance of *F. crenata* understory trees and the aggregation requires large openings for their regeneration. Therefore, large magnitude disturbance is necessary through forming *M. obovata* canopy trees for the maintenance of *F. crenata* population.

Table 2-1. Species composition in 1992 and 2011. Basal area, stem density and the relative values are given by species.

Species	1992				2011			
	Basal area, BA ( $\text{m}^2 \cdot \text{ha}^{-1}$ )	Relative values of BA (%)	Stem density ( $\text{ha}^{-1}$ )	Relative stem density (%)	Basal area, BA ( $\text{m}^2 \cdot \text{ha}^{-1}$ )	Relative values of BA (%)	Stem density ( $\text{ha}^{-1}$ )	Relative stem density (%)
<i>Fagus crenata</i>	13.7	43.1	161.7	29.8	14.1	43.8	131.7	33.5
<i>Magnolia obovata</i>	9.5	29.8	75.8	14.0	10.7	33.2	65.0	16.6
<i>Betula grossa</i>	3.6	11.4	24.2	4.5	3.8	11.9	22.5	5.7
<i>Quercus mongolica</i>	1.2	3.6	5.8	1.1	0.6	1.7	3.3	0.8
<i>Kalopanax septemlobus</i>	0.6	1.8	2.5	0.5	0.3	1.0	1.7	0.4
<i>Acer shirasawanum</i>	0.5	1.7	20.8	3.8	0.6	1.8	25.0	6.4
<i>Pterocarya rhoifolia</i>	0.5	1.6	4.2	0.8	0.7	2.0	9.2	2.3
<i>Viburnum furcatum</i>	0.4	1.2	150.0	27.7	0.2	0.7	82.5	21.0
<i>Magnolia salicifolia</i>	0.2	0.7	5.0	0.9	0.1	0.3	1.7	0.4
<i>Acer japonica</i>	0.2	0.6	18.3	3.4	0.2	0.5	15.8	4.0
<i>Acer Mono</i> subsp. <i>marmoratum</i>	0.2	0.6	0.8	0.2	0.2	0.6	0.8	0.2
<i>Acer sieboldianum</i>	0.2	0.6	1.7	0.3	0.1	0.4	0.8	0.2
<i>Stewartia pseudocamellia</i>	0.2	0.5	4.2	0.8	0.2	0.5	4.2	1.1
<i>Acer micranthum</i>	0.1	0.4	12.5	2.3	0.0	0.0	2.5	0.6
<i>Acanthopanax sciadophylloides</i>	0.1	0.4	5.8	1.1	0.1	0.4	1.7	0.4
<i>Sorbus commixta</i>	0.1	0.3	5.0	0.9	0.0	0.1	1.7	0.4
<i>Fraxinus lanuginosa</i> f. <i>serata</i>	0.1	0.3	10.8	2.0	0.0	0.1	4.2	1.1
<i>Criptomeria japonica</i>	0.1	0.3	4.2	0.8	0.1	0.4	3.3	0.8
<i>Sorbus alinifolia</i>	0.1	0.3	3.3	0.6	0.1	0.3	2.5	0.6
<i>Clethra barbinervis</i>	0.1	0.3	8.3	1.5	0.0	0.1	4.2	1.1
<i>Acer rufinerve</i>	0.0	0.1	1.7	0.3	0.0	0.1	0.8	0.2
<i>Euonymus oxyphyllus</i>	0.0	0.1	3.3	0.6	0.0	0.0	1.7	0.4
<i>Acer argutum</i>	0.0	0.0	1.7	0.3	0.0	0.0	1.7	0.4
<i>Styrax shirasawana</i>	0.0	0.0	4.2	0.8	0.0	0.0	2.5	0.6
<i>Symplocos coreana</i>	0.0	0.0	0.8	0.2	0.0	0.0	0.8	0.2
<i>Cornus macrophylla</i>	0.0	0.0	0.8	0.2	-	-	-	-
<i>Symplocos chinensis</i>	0.0	0.0	0.8	0.2	-	-	-	-
<i>Viburnum wrightii</i>	0.0	0.0	0.8	0.2	-	-	-	-
<i>Cornus controversa</i>	0.0	0.0	0.8	0.2	-	-	-	-
<i>Rhus trichocarpa</i>	0.0	0.0	0.8	0.2	-	-	-	-
<i>Ilex macropada</i>	0.0	0.0	0.8	0.2	-	-	-	-
<i>Padus grayana</i>	-	-	-	-	0.0	0.0	0.8	0.2
<b>Total</b>	<b>31.9</b>	<b>100.0</b>	<b>566.7</b>	<b>100.0</b>	<b>32.3</b>	<b>100.0</b>	<b>414.2</b>	<b>100.0</b>

Table 2-2. number of individuals, recruitment rate and mortality in the understory trees of

*F. crenata*. Value in parentheses indicate 95% confidence interval

Number of individuals		Recruitment (% yr <sup>-1</sup> )	Mortality (% yr <sup>-1</sup> )
1992	2011		
108	74	0.52 (0.15-0.83)	2.28 (1.60-3.10)

Table 2-3. factors limiting survival of understory trees of *Fagus crenata*. GLMM was adopted. Zero was given for *f. crenata* and one was given for *M. obovata* in the variable of canopy tree species. The model explained by only canopy tree species was selected based on AIC value.

Explanatory variable#1	Explanatory variable#2	AIC	Intercept	Coefficient	Coefficient
Null		92.52	0.519±0.253		
Canopy tree species		91.20	0.111±0.334	0.9448±0.529	
DBH		94.35	0.318±0.551	0.0218±0.054	
Coverage of dwarf bamboo		94.25	0.338±0.426	0.4137±0.796	
Slope gradient		94.52	0.529±0.972	-0.0005±0.040	
Canopy tree species	+DBH	92.89	-0.718±0.618	0.971±0.533	0.030±0.054
Canopy tree species	+Coverage of dwarf bamboo	92.42	-0.251±0.531	1.041±0.546	0.735±0.836
Canopy tree species	+Slope gradient	93.10	-0.200±1.062	0.974±0.538	0.013±0.041

Table 2-4. Factors limiting survival of understory trees of *F. crenata*. GLMM was adopted. Zero was given *F. crenata* and one was given for *B. grossa* in the variable of canopy tree species. Null model was selected based on AIC value.

Explanatory variable	AIC	Intercept	Coefficient
Null	86.57	0.365±0.260	
Canopy tree species	87.14	0.111±0.334	0.643±0.543
DBH	88.55	0.294±0.570	0.007±0.053
Coverage of dwarf bamboo	88.54	0.435±0.489	-0.151±0.882
Slope gradient	87.14	-0.811±1.024	0.048±0.041

Table 2-5. Factors limiting diameter growth rates of understory tree of *F. crenata*. GLMM was adopted. Zero was given *F. crenata* and one was given for *M. obovata* in the variable of canopy tree species. the model explained by coverage of dwarf bamboo and canopy tree species was selected based on the AIC value.

Explanatory variable#1	Explanatory variable#2	AIC	Intercept	Coefficient	Coefficient
Null		107.00	-0.166±0.288	Not selected	
Canopy tree species		106.10	-0.586±0.564	0.720±0.648	
DBH		108.90	0.009±0.718	-0.023±0.069	
Coverage of dwarf bamboo		76.43	-2.104±0.483	2.609±0.626	
Slope gradient		80.59	8.177±2.853	-0.587±0.172	
Canopy tree species	+DBH	74.65	-2.842±0.778	2.540±0.594	1.419±0.741
Canopy tree species	+Coverage of dwarf bamboo	77.51	-2.763±0.941	2.751±0.633	0.062±0.071
Canopy tree species	+Slope gradient	76.63	1.445±1.876	2.153±0.902	-0.174±0.094

**Table 2-6.** Factors limiting diameter growth rates of understory tree of *F. crenata*. GLMM was adopted. Zero was given for *F. crenata* and one was given for *B. grossa* in the variable of canopy tree species. Null model was selected based on the AIC value.

Explanatory variable	AIC	Intercept	Coefficient
Null	31.81	-0.104±0.157	
Canopy tree species	32.03	-0.370±0.271	0.497±0.323
DBH	33.71	-0.214±0.389	0.011±0.035
Coverage of dwarf bamboo	33.66	0.012±0.300	-0.254±0.597
Slope gradient	33.21	-0.725±1.700	0.024±0.025

Table 2-7. Cumulative values of PPFD (photosynthetic photon flux density) under the canopy trees of different species. Values with the same letters are not significantly different.

Species of canopy trees	Cumulative value of PPFD (mol m <sup>-2</sup> )	
	Total through observation	Leafy season
<i>Fagus crenata</i>	8.63±1.50b	7.49±2.89b
<i>Magnolia obovata</i>	13.32±2.97b	11.98±1.44a
<i>Betula grossa</i>	11.57±2.87ab	10.31±3.00ab

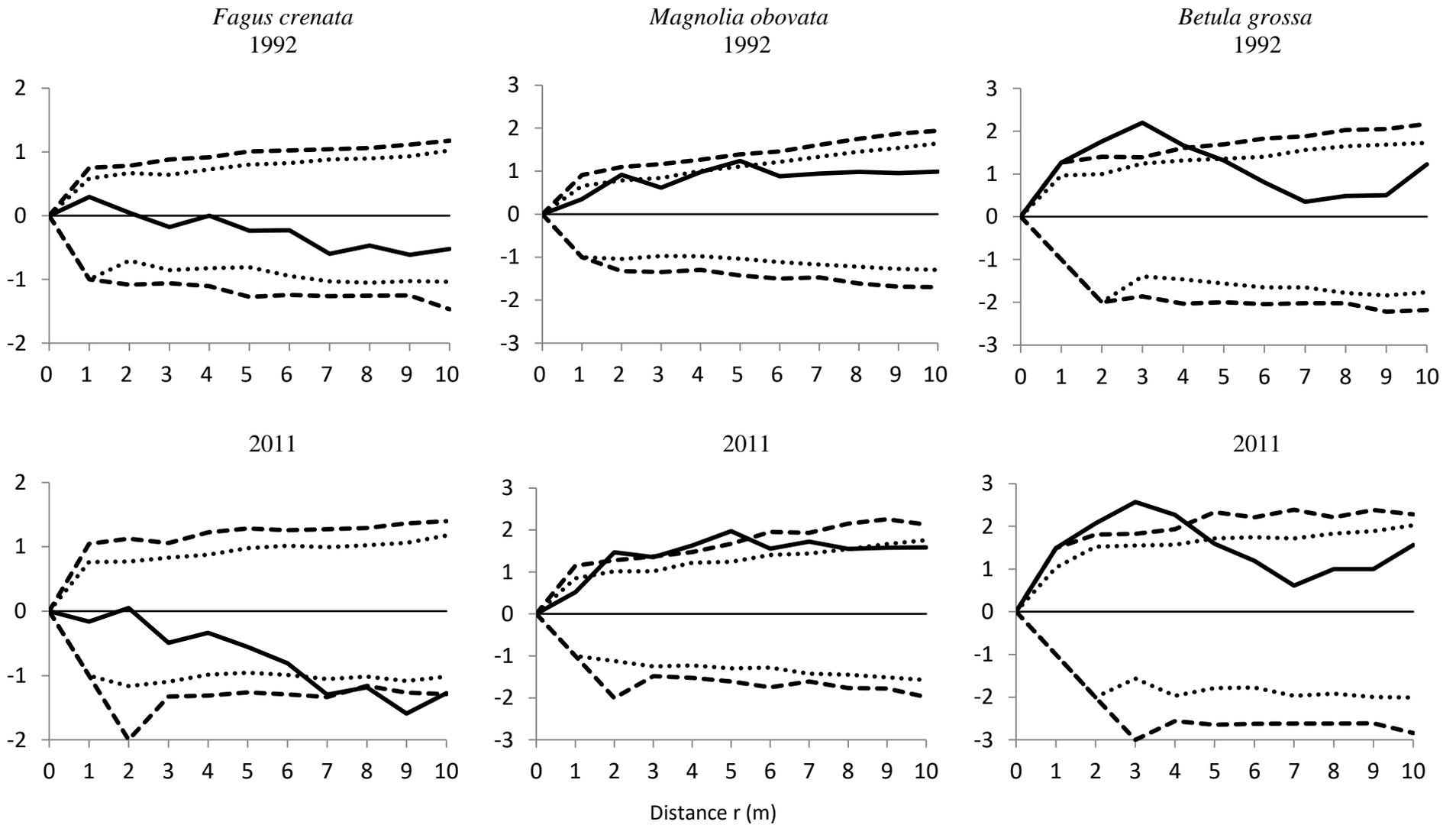


Figure 2-1. Spatial distribution correlation between *F. crenata* understory trees and canopy trees in 1992 and 2011 by bi-variable analysis of L-function. Range enclosed by dotted lines and broken lines indicate 95% and 99% confidence interval, respectively.

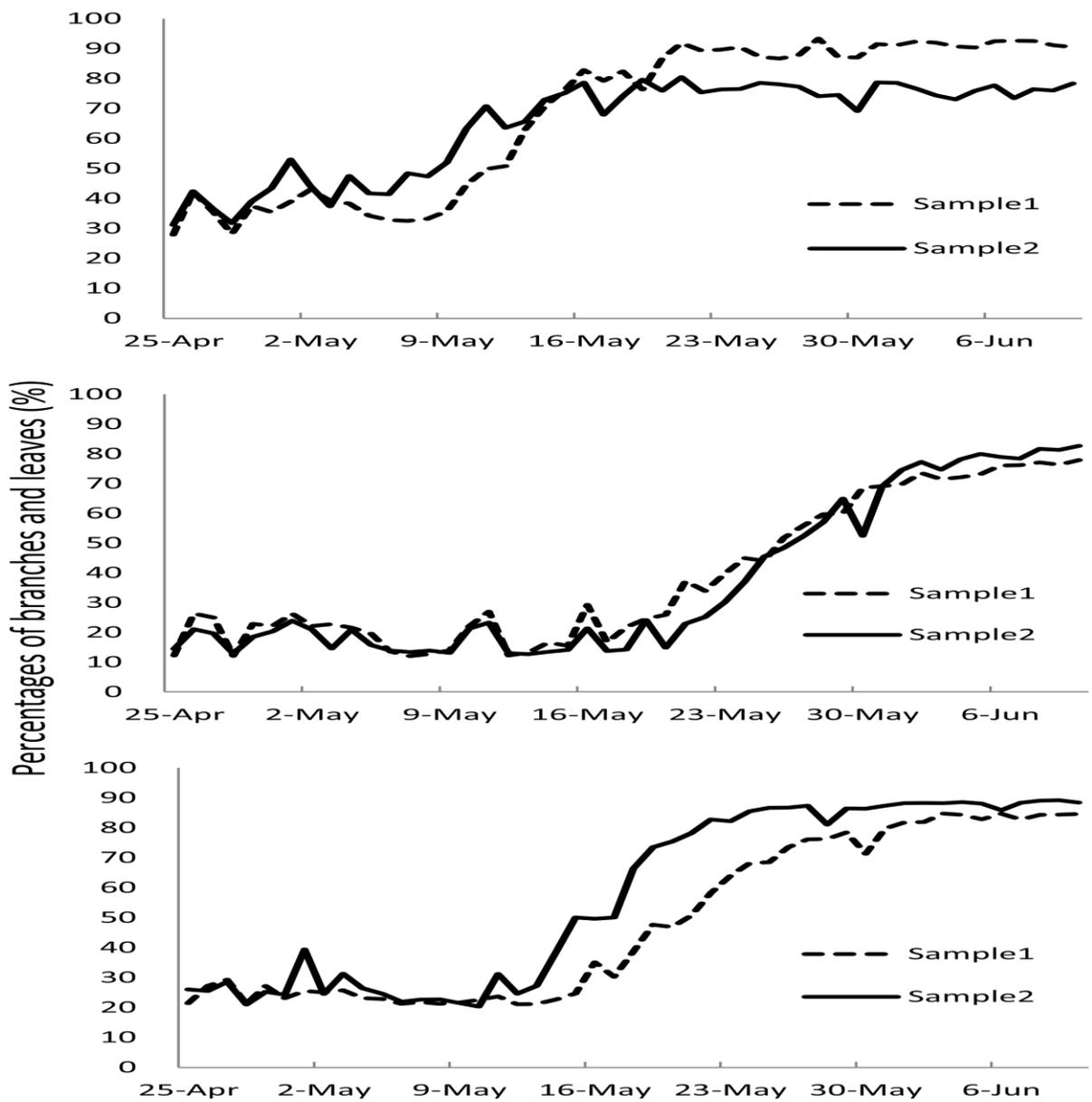


Figure 2-2. Leaf unfolding processes in the beginning of growing season by species of canopy trees. Changes in percentages of leaves and branches are shown by species from the image data with photo-cameras.

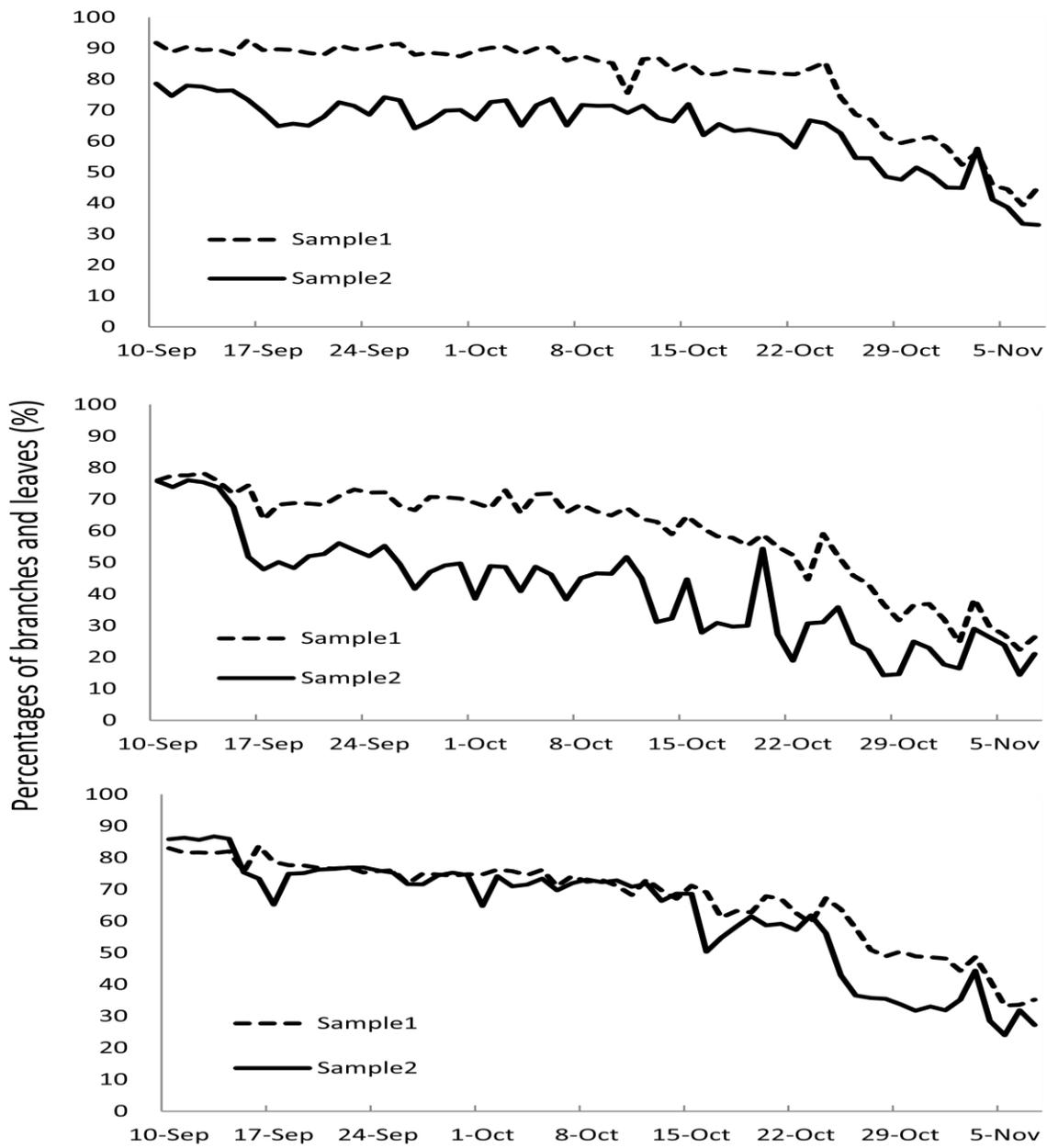


Figure 2-3. Leaf shedding processes in the end of growing season by species of canopy trees. Changes in percentages of leaves and branches are shown by species from the image data with photo-camera.

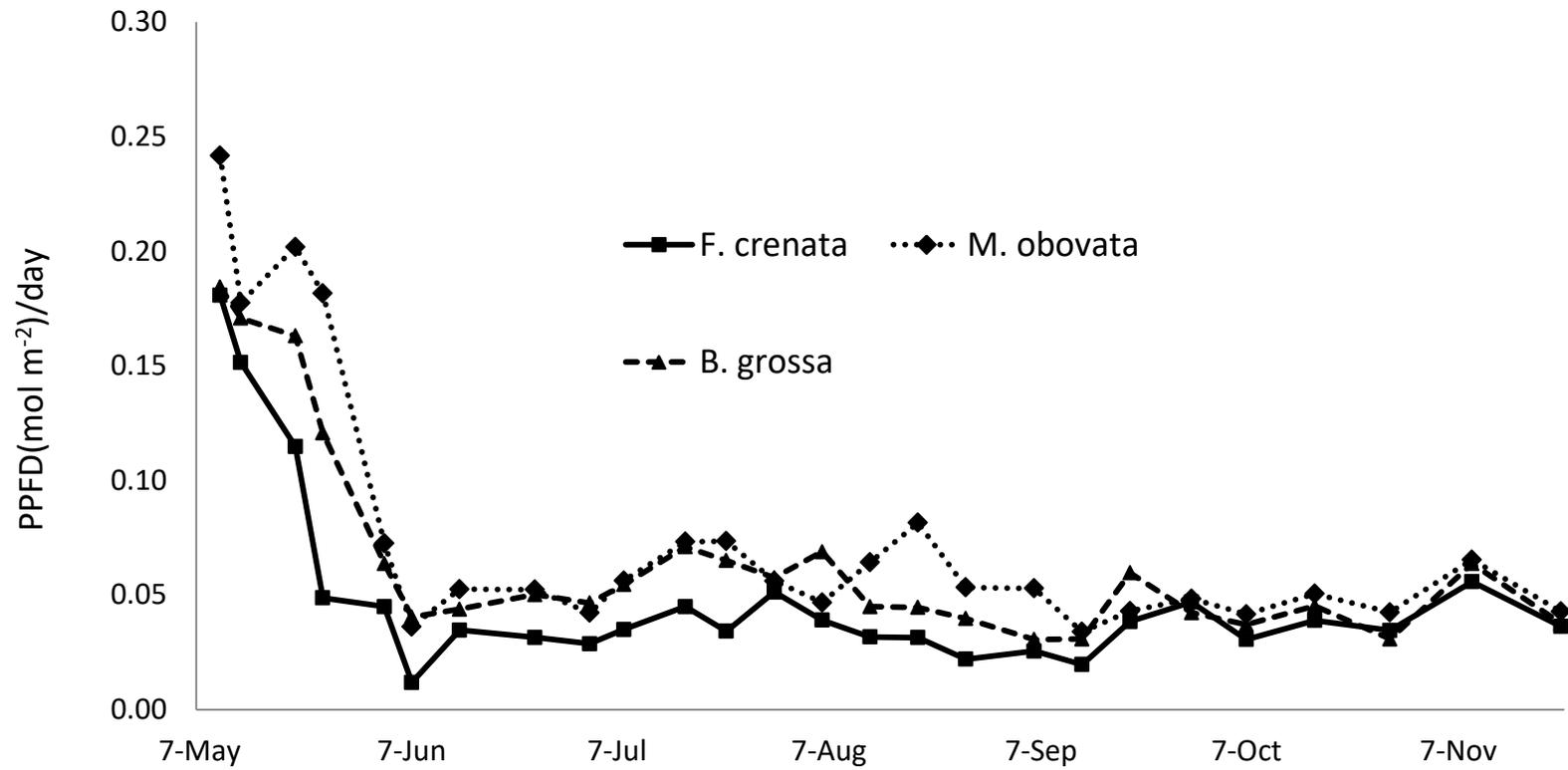


Figure 2-4. Changes in PPFD (Photosynthetic Photon Flux Density) under the canopy trees of different species.

## Chapter 3

# TEMPORAL AND SPATIAL DYNAMICS OF AN OLD-GROWTH BEECH FOREST

### 3.1. Introduction

Canopy trees that establish and grow into the canopy layer are affected by a variety of environmental conditions. The magnitude, intensity and frequency of disturbance regimes determine regeneration patterns of canopy tree species (Nakashizuka 1984; Yamamoto 1989). Disturbance and competitive interactions among individuals and species are factors that determine the structure and species composition of the canopy layer. Therefore, describing how the present canopy trees were established and attained the canopy layer is valuable for understanding the underlying drivers of forest stand dynamics. Although estimates of canopy tree dynamics have been derived from long-term ecological research in large study plots (Fujita et al. 2003; Henbo et al. 2004; Anderson-Teixeira et al. 2014), few of these plots have been observed for a period of time sufficient to detect the processes influencing individual canopy trees from the time of establishment until they attain the canopy. As such, historical variation in growth patterns as recorded in tree rings can be an effective tool for estimating long-term canopy tree dynamics, the occurrence of past forest disturbance, and growth processes (Foster 1988; Lorimer and Frelic 1989; Nowacki and Abrams 1997; Frelich 2002).

Dendrochronological techniques have been successfully developed to estimate establishment patterns using establishment dates (Lorimer et al. 1988) and responses to disturbances using patterns of radial growth to identify suppressions and releases (Canham 1985; Orwig and Abrams 1994). Such method provide unique information on past disturbances, historical stand dynamics, interspecific variability in the timing and nature of recruitment (Fritts and Swetnam 1989; Nowacki and Abrams 1994) and, in some cases, the influence of climate variability (Henry and Swan 1974; Oliver and Stephens 1977; Foster 1988; Abrams and Orwig 1995; Abrams et al.

1995; Druckenbrod 2005). Busing and Brokaw (2002) observed that forest canopy recruitment processes are very complex and are mostly related to competition and spatial structure in gap-phase regeneration.

Accordingly, we applied dendroecological methods to analyze establishment and growth patterns and processes of canopy trees in an old-growth beech forest in Japan. Cao and Ohkubo (1999) conducted a dendroecological analysis to examine the difference in shade tolerance and the suppression and release histories during canopy recruitment of *F. crenata* and *Acer mono Maxim.* in two old-growth beech forests. However, various species co-exist in the canopy layer of beech forests and, owing to the lack of dendroecological studies in these forests, the underlying variability in canopy dynamics, which is inherently high in mixed species forests, is poorly understood. Thus, this study provides novel insights into the canopy tree dynamics of a species-rich temperate forest.

The beech forest selected for the present study is located within the cool-temperate zone in the Chugoku Mountains in western Japan. Fukushima et al. (1995) and Shimano (1999) have pointed out that beech forests of Japan are typically divided into pure beech forest, characterized by much snowfall and *Sasa kurilensis* present in the understory (commonly referred to as the Japan Sea type), and multi-species, layered-canopy beech forest (commonly referred as the Pacific Ocean type). The selected beech forest has the characteristics of frequent snowfall and presence of *S. kurilensis* Makino & Shibata in common with the Japan Sea type (Mizunaga et al., 1996), but additionally has a multi-species canopy layer characteristic of the Pacific Ocean type (Yamamoto and Nishimura 1995). In this forest the dominance of other canopy species mixed with beech is higher in the forest type. These characteristics are probably associated with gap formation, which is often observed in old-growth forest. The objective of this study was to identify the factors that have enabled the co-dominant canopy species to co-exist in the canopy layer of the selected old-growth beech forest. We used a dendroecological approach to clarify the

processes involved in canopy layer and stand dynamics of the forest. This study aimed to elucidate patterns of establishment and growth among the co-dominant canopy species that have led to their establishment in the canopy layer in an old-growth beech forest.

### **3.2. Materials and methods**

The study was conducted in an old-growth beech forest (35°14'N, 134°23'E, 1048 m a.s.l.) in the eastern Chugoku Mountains, western Japan. The parent rock is granite. The soil type is a deep brown forest soil. The area is located within the cool-temperate zone. The mean temperature is about 8.2 °C, mean annual precipitation is 2400 mm, and maximum snow depth is 1.8 m (Mizunaga et al. 1996). In this old-growth beech forest, the canopy layer is dominated by *F. crenata* and *M. obovata*, and *B. grossa*. The understory is characterized by dense coverage of dwarf bamboo (*S. kurilensis*).

We established a permanent plot of 50 m × 130 m on a north-facing slope. A tree census in the plot was conducted in 2011. The species, diameter and location of each individual tree in the canopy layer were measured within the plot. The canopy trees were defined as trees in which the upper portion of the crowns formed the upper surface of the canopy layer. Tree core samples were collected from the three dominant canopy tree species (*F. crenata*, *M. obovata* and *B. grossa*) in the summer of 2012. Two increment cores were extracted from parallel to the slope contour direction in each individual to avoid sampling of tension wood. The sampling height of the increment cores was 0.5 m above ground level, but ranged from 0.5 to 1.2 m above ground level when it was impossible to extract a sample at 0.5 m height.

The tree core samples were air dried, mounted on a wood base, and sanded with sandpapers of successively finer grits from 180 to 800 grit to reveal the cellular structure of the wood (Orvis and Grissino-Mayer 2002), prior to observation with a stereo microscope. Each core was visually cross-dated using key rings and then tree-ring widths were measured on a digital measuring stage with resolution of 0.01 mm. Core samples that had broken or were rotten were excluded from

subsequent analyses. The cross-dating was verified by the quality-control program COFECHA, which uses segmented time-series correlation analyses to confirm correct dating of all tree rings (Holmes 1983; Grissino-Mayer 2001). The numbers of missed pith rings were calculated using Duncan's (1989) geometric method based on the average of the five innermost ring width measurements to estimate the establishment age of the individual tree for construction of age-class distributions.

Trees were considered to have a gap origin if the mean annual growth rate of the innermost five rings was greater than a threshold value for rapid growth for the species. The 75th percentile growth rate was calculated from all tree ring measurements for each species. Individuals that showed higher or lower values in the initial phase of establishment than the 75th percentile growth rate were classified as gap-origin and non-gap-origin trees, respectively. For the analysis, we used all of the samples, including the cores that did not reach the pith. Baker and Bunyavejchewin (2006) excluded core samples in which the innermost rings were >5 cm from the pith. Among our samples, 77% of *F. crenata* (maximum 5.1 cm), 73% of *M. obovata* (maximum 6.7 cm), and 23% of *B. grossa* (maximum 9.0 cm) samples satisfied this criterion. Therefore, in this study, estimations can be considered very rough, especially for *B. grossa*.

Determination of growth release from suppression of each species was based on percentage growth change (%GC) using the following formula proposed by Nowacki and Abrams (1997):  $\%GC = [(M_2 - M_1) / M_1] * 100$ , where  $M_1$  and  $M_2$  are the mean growth in the preceding 10 years (including the present year) and in the subsequent 10 years, respectively. As %GC tends to be higher in the low prior growth, release was estimated for each species by plotting %GC against prior growth for every growth increment of every tree as follows. The prior growth was quantified as the average of 10-years prior growth to a given growth increment. A boundary line was constructed from the relations between prior growth and the 10 highest %GC in every 0.5-mm-range class of prior growth. Species-specific boundary lines were fitted by linear, power, logarithmic and exponential curves. The most suitable function was selected based on the highest

value of  $R^2$  (Black and Abrams 2003). We defined a release as a growth increase of more than 100%GC.

Based on the initial growth rate and occurrence of release, we divided individuals into four categories of canopy accession as 1) gap origin followed by release, 2) gap origin followed by non-release, 3) non-gap origin followed by release, and 4) non-gap origin followed non-release (Baker and Bunyavejchewin 2006).

We used L- and intertype  $L_{12}$ -functions modified from Ripley's K- and  $K_{12}$ -functions (Ripley 1981; Lotwick and Silverman 1982; Goreaud and Pelissier 2003; Lancaster and Downes 2004) to characterize the spatial distribution pattern of univariate and bivariate patterns. The L-function was used to characterize the spatial distribution pattern of the three dominant species by gap-origin category. The  $L_{12}$ -function characterized the spatial correlation pattern of gap-origin species in the same group and the spatial correlation pattern of groups in the same species. A Monte Carlo simulation method was used to estimate a 95% confidence range for both spatial distribution and spatial correlation analysis. All analyses were conducted with R software version 2.15.2 using the ads package to implement the L- and  $L_{12}$ -functions (R Core Team 2012).

### **3.3. Results**

Thirteen tree species were recorded in the canopy layer of the study plot (Table 3-1). *Fagus crenata*, *M. obovata* and *B. grossa* each exceeded 10% in both relative density and relative basal area, and thus dominated the canopy layer. *Fagus crenata* showed the highest mean diameter at the breast height and the widest range of dbh values.

The oldest age classes were 1820s, 1840s and 1850s for *F. crenata*, *M. obovata* and *B. grossa*, respectively (Figure 3-1). *Fagus crenata* showed evidence of continuous recruitment over the past 200 years; it showed the widest range of age classes. The age-class distribution of *M. obovata* showed a clear peak in the 1840s class. *Betula grossa* did not show a clear peak but showed a narrower range of age-classes than that of *F. crenata*. These age-class distributions indicated that *F. crenata* showed continuous establishment, *B. grossa* also showed continuous

establishment but for a shorter period than *F. crenata*, and *M. obovata* showed simultaneous establishment.

Figure 3- 2 shows all of the individual tree-ring series after establishment and the mean growth increment for each dominant study species. Growth increment of *F. crenata* showed wide fluctuation among individuals with a constant annual mean. Growth increment of *M. obovata* and *B. grossa* also showed wide fluctuation among individuals, but the annual means were decreased. These differences were indicative of disparity in the establishment patterns of the species. *Fagus crenata* showed various initial growth patterns, which suggested that individuals of this species were established under a variety of environmental conditions. However, both *M. obovata* and *B. grossa* showed a high growth rate in the initial phase of establishment, which suggested that these species were more likely to have established in open sites, such as canopy gaps.

To explore these differences further, we compared initial increments amongst species. First, we compared fluctuations in annual increment of the three species (Figure 3-3). No significant difference in the mean annual increment was observed among the species. We then defined the 75th percentile as the threshold for a rapid growth rate. The rapid growth thresholds for the three species were 2.28 mm in *F. crenata*, 2.08 mm in *M. obovata* and 2.21 mm in *B. grossa*. We compared these threshold growth rates with individuals' growth rates in the initial phase of establishment (the first 5 years) to classify each individual as either gap-origin or non-gap-origin types (Table 3-2). The number of non-gap-origin individuals exceeded that of gap-origin individuals in *F. crenata*, whereas gap-origin individuals were most frequent in *M. obovata* and *B. grossa*. No individuals of non-gap-origin were identified in *B. grossa*.

To identify spatial patterns in temporal establishment pattern of the species, the spatial distributions of individuals in different groups with different establishment periods conducted to analyses. For the analysis, we divided individuals into several groups with a comparatively wide range of age-class distribution to avoid low sample sizes as much as possible (Figure 3-4). Three

consecutive groups selected and focused on analyses. The highest peaks in the age-class distributions occurred in the period 1840–1900, particularly for gap-origin individuals. These age-class distributions indicated that most individuals of *M. obovata* and *B. grossa* established during this period. Non-gap-origin individuals showed a wide range of ages with no specific peak in both *F. crenata* and *M. obovata* within the period 1840–1900. Then selected three groups with establishment periods of 1841–1860, 1861–1880 and 1881–1900, considered as the first (I), second (II) and third (III) group, respectively, to conduct a spatial analysis and to understand further species establishment characteristics.

Figure 3-5 shows the spatial distribution patterns of the three dominant species for gap-origin and non-gap-origin individuals. We observed a random spatial pattern in gap-origin individuals of *F. crenata*, but aggregated spatial patterns in gap-origin individuals of *M. obovata* and *B. grossa*. The opposite patterns were observed in trees that did not originate in gaps: *F. crenata* was aggregated and *M. obovata* was random. Non-gap-origin individuals were not identified in *B. grossa*.

Figure 3-6 shows the spatial distribution patterns of gap-origin individuals in each group. Individuals of *M. obovata* showed an aggregated distribution pattern in each group, which suggested that every group was established by groups in gaps. A random spatial distribution was observed in the third (III) group of *F. crenata* and in the second (II) group of *B. grossa*. However, the third (III) group of *B. grossa* was spatially aggregated. Therefore, it is likely that individuals of *F. crenata* were established randomly in small gaps. *Betula grossa* individuals may have established in groups in gaps. *Fagus crenata* in first (I) and second (II) groups, and *B. grossa* in first (I) group were not analyzed because of the paucity of individuals ( $n = 1$  in each group and species).

In *M. obovata*, associated correlations were detected between the first (I) and second (II) group, and between first (I) group plus second (II) group and third (III) group. However, an

independent correlation was observed between the second (II) and third (III) groups (Figure 3-7b). The associated correlations suggested that establishment of *M. obovata* continued in the same gaps or around the gaps during these periods. Groups of *F. crenata* were not spatially correlated with each other, suggesting that establishment of *F. crenata* was not linked to large gaps. In *B. grossa*, independent correlations were detected between the second (II) and third (III) groups. The paucity of individuals limited the spatial correlation analysis for *F. crenata* (all cases in Figure 3-7b) and *B. grossa* (Figure 3-7b: except group II & III)

Spatial correlation analysis of gap-origin individuals between species did not detect significant associated and disassociated correlations within the same group (Figure 3-8). Such independent establishment patterns between the species within a group were due to situations where some gap-origin individuals used the same gap and other gap-origin individuals used different gaps between species.

Each of the three study species showed evidence for growth releases. The number of releases differed between species in the study plot (Figure 3-9). In *Fagus crenata*, releases occurred over a wider range of years and frequencies of releases were lower compared with *M. obovata* and *B. grossa* over the time series. *Magnolia obovata* also showed a wide range of releases, but the release frequency was lower in the several decades following individual establishment before the 1900s and releases frequently occurred after 1900s. Few growth releases occurred in *B. grossa*. Dates of recorded disturbances near the study plot did not always coincide with the timing of growth releases.

Table 3-3 shows the number of individuals in each canopy accession type for each species. *Magnolia obovata* individuals were classified into all canopy accession types. The proportion of individuals that established in a gap and grew to the canopy layer with one or more release events was highest in *M. obovata*, low in *B. grossa* and absent in *F. crenata*. The proportion of individuals that were classified as non-gap-origin without a release event was lowest in *M. obovata* and highest in *F. crenata*.

### 3.4. Discussion

The beech forest in the present study contained a diverse canopy layer dominated by the species *F. crenata*, *M. obovata* and *B. grossa*. This codominance by several species can be explained in terms of each species' characteristics for regeneration, growth and canopy recruitment according to the disturbance regime in the studied forest (Masaki et al. 1999; Kobayashi and Kamitani 2000). The initial species composition may determine the dominance of a species in canopy development (Yoshida and Kamitani 2000). The present dendroecological study demonstrated that most *F. crenata* canopy individuals, few canopy individuals of *M. obovata*, and no *B. grossa* canopy individuals established as advance regeneration (Figure 3-4, Table 3-3). Seedlings, saplings and juvenile individuals established in these patterns can be recruited into the canopy layer. These patterns can be explained in terms of the species' shade tolerance, *i.e.* *F. crenata* is shade-tolerant, *B. grossa* is shade-intolerant, and *M. obovata* shows intermediate shade tolerance (Koike 1985; Masaki et al. 1992). These results support previous research indicating that *F. crenata* canopy individuals can establish after gap formation from advance regeneration or as newly established seedlings, whereas advance regeneration is uncommon in *M. obovata* and *B. grossa* (Yamamoto 1989; Yamamoto et al. 1995; Yoshida and Kamitani 1998; Abe et al. 2005). Regarding advance regeneration, a sprouting bank has been observed in *M. obovata* (Yamamoto 1989) and *M. fraseri* (Runkle 1981; Palmer 1987). Thus, *M. obovata* canopy trees established by advance regeneration might show sprouting origins in mature soil (Yamamoto et al. 1995).

Analyses of spatial distribution patterns and spatial correlations among groups with a different establishment period suggest that it is likely that *M. obovata* canopy trees were derived from individuals establishing simultaneously in gaps and that the other individuals of *M. obovata* continuously established in the same gaps or established around the gaps in subsequent decades. Such an establishment pattern for *M. obovata* might be facilitated by gap enlargement after gap

formation. A long-term study of gap dynamics has shown that gaps expand over time (Henbo et al. 2004). However, it is likely that *F. crenata* canopy trees were derived from a continuous inflow of establishing individuals and were less concentrated in large openings. Such gap replacement by a tree species depends on the magnitude and frequency of disturbance (Nakashizuka 1987; Yamamoto 1989; Hara et al. 1995; Hiura 1995; Masaki et al. 1999; Kobayashi and Kamitani 2000; Yamashita et al. 2002). Small gaps are often filled by suppressed shade-tolerant seedlings and saplings through advance regeneration (Brewer and Merritt 1978) or by sprouts (Runkle 1982). This pattern is likely to apply to *F. crenata* in the forest that we studied. Large openings are created by large-magnitude disturbances at low frequencies, which also allow shade-intolerant and intermediate species to invade the openings (Runkle 1981; Yamamoto 1989). This pattern is probably applicable for *M. obovata* canopy trees in the present study. *Betula grossa* is shade-intolerant; however, some individuals were established in groups in a gap, whereas other individuals were sparsely established in the same gap in which *M. obovata* was established. The spatial distribution of *B. grossa* may suggest the following two patterns for its establishment and existence in this forest. First, *B. grossa* established simultaneously in the same large gap as *M. obovata*, but most *B. grossa* individuals disappeared as the forest developed because of competition and a shorter life-span than *M. obovata*. This pattern may be defined by species-specific characteristics of forest development. Whitmore (1989) reviewed gap replacement and forest cycling characteristics supported by studies on different characteristics of shade tolerance and life-span between pioneer, transitional and late-successional species during forest development. He suggested that pioneer species show faster growth and shorter life-spans than transitional and late-successional species. *Betula grossa* might show shorter longevity than *M. obovata* because, in the present study, the oldest individuals of *B. grossa* were the youngest among the three species (Figure 3-1). Second, *B. grossa* might establish in different gaps, as shown in third group (Figure 3-8), because of the different soil conditions between gaps. Such an establishment pattern has been evoked in previous studies, which have pointed out that *F.*

*crenata* and *M. obovata* are established in undisturbed soil, whereas *B. grossa* preferentially establishes in disturbed soil (Nakashizuka 1989; Yamamoto et al. 1995). Yamamoto and Numata (1995) have reported that seed germination of *B. grossa* tends to be highest in disturbed soil on the tip-up mounds of uprooted trees. Therefore, canopy trees of *B. grossa* probably established in disturbed soil in severely disturbed sites.

After establishment, some of the gap-origin trees experience releases. This release implies that the individuals were suppressed and then released during their growth into the canopy layer. Competition among established individuals and density-dependent thinning occur in gaps (Yamamoto 1989). In the present study, density-dependent thinning probably occurred among *M. obovata* trees during their growth from saplings to recruitment into the canopy layer because of their simultaneous establishment in large openings. In addition, canopy trees surrounding a gap suppress the trees growing within the gap (Yoshida and Kamitani 1999), and it is possible that release occurs after the death of these surrounding trees.

Large-magnitude disturbances or large gaps probably allow *F. crenata*, *M. obovata* and *B. grossa* to co-dominate in the canopy layer. *Fagus crenata* individuals may be established and grow to the canopy layer in small openings, or even under the closed canopy, whereas individuals of the other two species can be established and be recruited into the canopy layer in large openings or in disturbed sites. However, it is premature to discuss the establishment characteristics and role in co-existence of *B. grossa* in this old-growth forest because of the comparatively few individuals of this species in the canopy layer and the number of missed rings during initial part of core sample might have been higher for *B. grossa* than for *F. crenata* and *M. obovata*. The co-existence mechanisms in the canopy layer support relationships between the disturbance regimes and regeneration properties of species reported for other old-growth forests (Henbo et al. 2004). Although in other beech forests seedlings or saplings of *M. obovata* also occur in small openings (Yamamoto 1989), the present results indicated that *M. obovata* canopy

trees appeared to be derived from regeneration in large openings. It is possible that seedlings or saplings of *M. obovata* growing in small openings may be unable to attain the canopy layer.

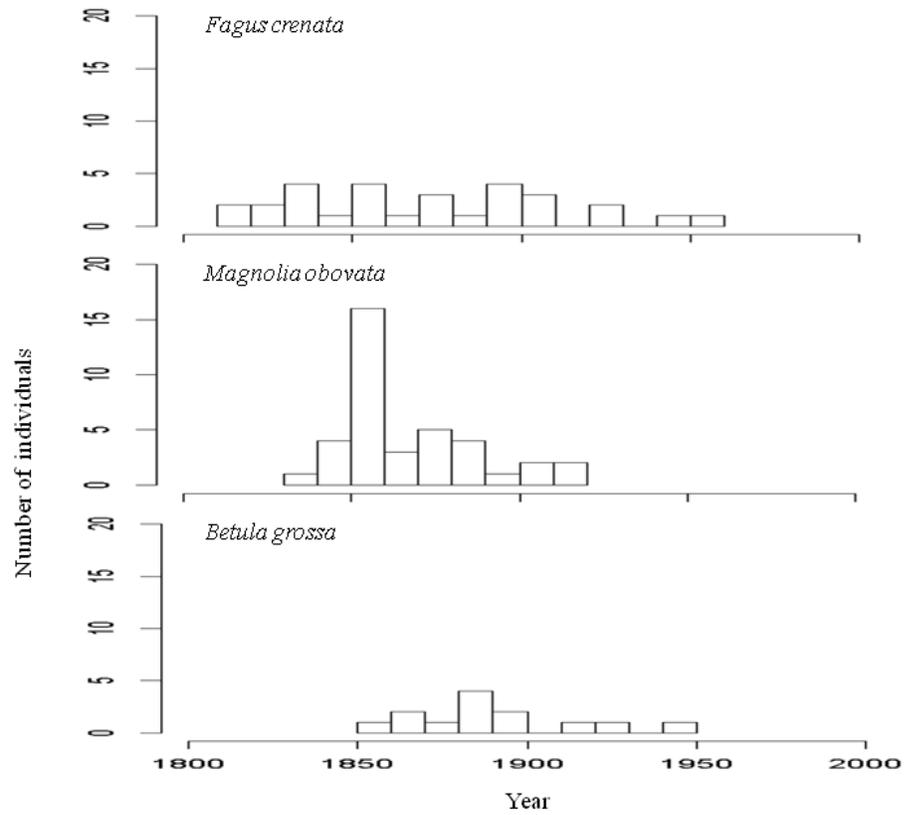
In the case of non-gap-origin canopy trees, release is probably caused by gap formation in the canopy layer above their crown, disturbance in the surrounding canopy layer, or natural thinning among established individuals. Such release was observed in *F. crenata* and *M. obovata*. In contrast, it is likely that some *F. crenata* canopy trees were recruited into the canopy layer gradually without release because of their shade tolerance. In such cases, release is less frequently observed once when trees attain to the canopy layer (Nowacki and Abrams 1997). The majority of non-gap-origin canopy trees of *M. obovata* are unlikely to attain the canopy layer.

We found no evidence for discrete periods characterized by many release events. For all three species the frequency of release was low and relatively consistent over the past 100 years. Notably, there was no obvious association of release events with historical records of storms (1915, 1923, 1931 and 1934) and typhoons (1857, 1870, 1941, 1960, 1970 and 2004) recorded in local government documents (Nishiawakura-Son 1977). Single tree falls are caused by density-dependent thinning and diseases. Gap formation by a single tree fall may also generate growth release pulses of surrounding individuals without disturbance from typhoons and storms, which may be the reason that release did not coincide with historical records. Therefore, limited disturbance by single tree falls rather than high-magnitude and large-areal disturbances may have affected the growth and recruitment of canopy trees over the past 100 years in the study forest.

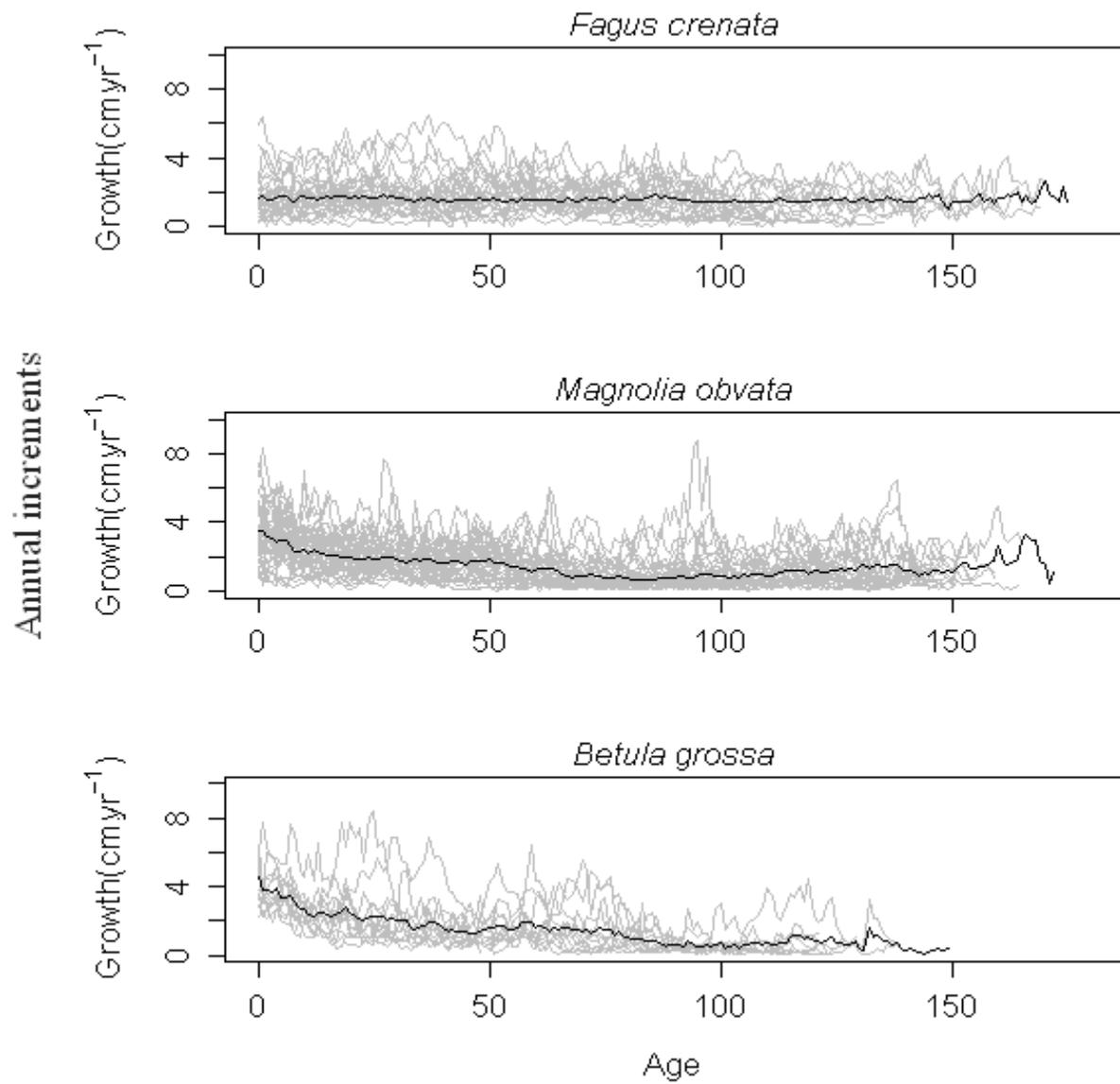
Old-growth forest is maintained by gap formation. Gaps frequently occur in the studied beech forest (Fig. 9) and are mostly filled by regeneration of *F. crenata* after establishment of *M. obovata* and *B. grossa*. However, the occurrence of rare, high-intensity disturbance events, such as typhoons, facilitates establishment of certain species (e.g., *M. obovata*), thereby enhancing the species diversity of the canopy layer in the beech forest.

**Table 3-1.** Species composition of canopy trees in the study plot.

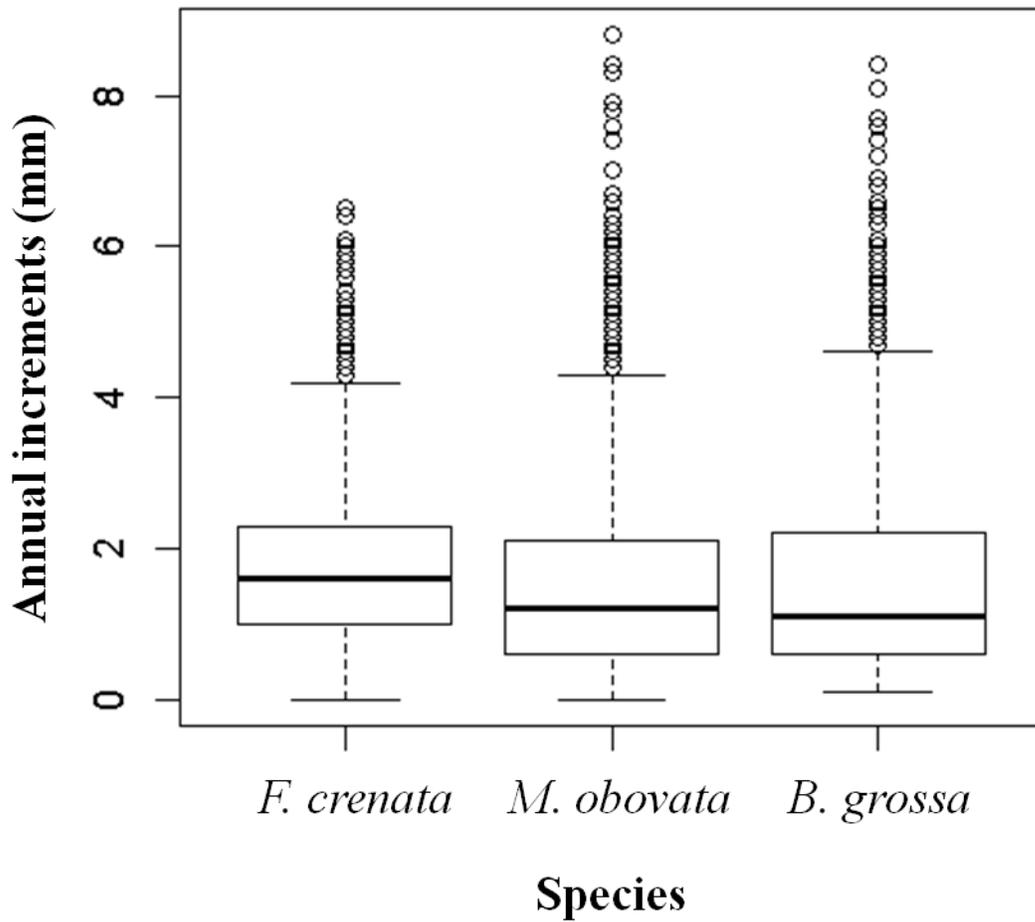
Species	DBH			Density (ha <sup>-1</sup> )	Relative Density(%)	B.A. (m <sup>2</sup> ha <sup>-1</sup> )	Relative B.A. (%)
	Mean±SD	Min	Max				
<i>Magnolia obovata</i>	47.1±12.5	20.9	79.5	58.5	40.1	12.6	44.1
<i>Fagus creanata</i>	44.5±19.5	10.2	99.0	44.6	30.5	8.8	30.9
<i>Betula grossa</i>	44.4±13.9	20.1	63.9	20.0	13.7	3.6	12.8
<i>Pterocarya rhoifolia</i>	48.8±8.7	41.1	60.0	4.6	3.2	1.2	4.1
<i>Kalopanax septemlobus</i>	49.7±4.4	46.6	52.8	3.1	2.1	0.6	2.1
<i>Quercus mongolica</i>	46.7±1.3	45.7	47.6	3.1	2.1	0.5	1.8
<i>Stewartia pseudocamellia</i>	25.3±7.9	20.5	34.4	3.1	2.1	0.2	0.9
<i>Sorbus alnifolia</i>	23.4±11.8	15.0	31.7	3.1	2.1	0.1	0.5
<i>Acer Mono</i> subsp. <i>marmoratum</i>	55.3	55.3	55.3	1.5	1.0	0.4	1.3
<i>Acanthopanax sciadophylloides</i>	40.9	40.9	40.9	1.5	1.0	0.2	0.7
<i>Acer shirasawanum</i>	30.5	30.5	30.5	1.5	1.0	0.1	0.4
<i>Acer japonica</i>	22.0	22.0	22.0	1.5	1.0	0.1	0.2
<i>Fraxinus lanuginosa f.serata</i>	21.5	21.5	21.5	1.5	1.0	0.1	0.2
Total				146.0	100.0	28.5	100.0



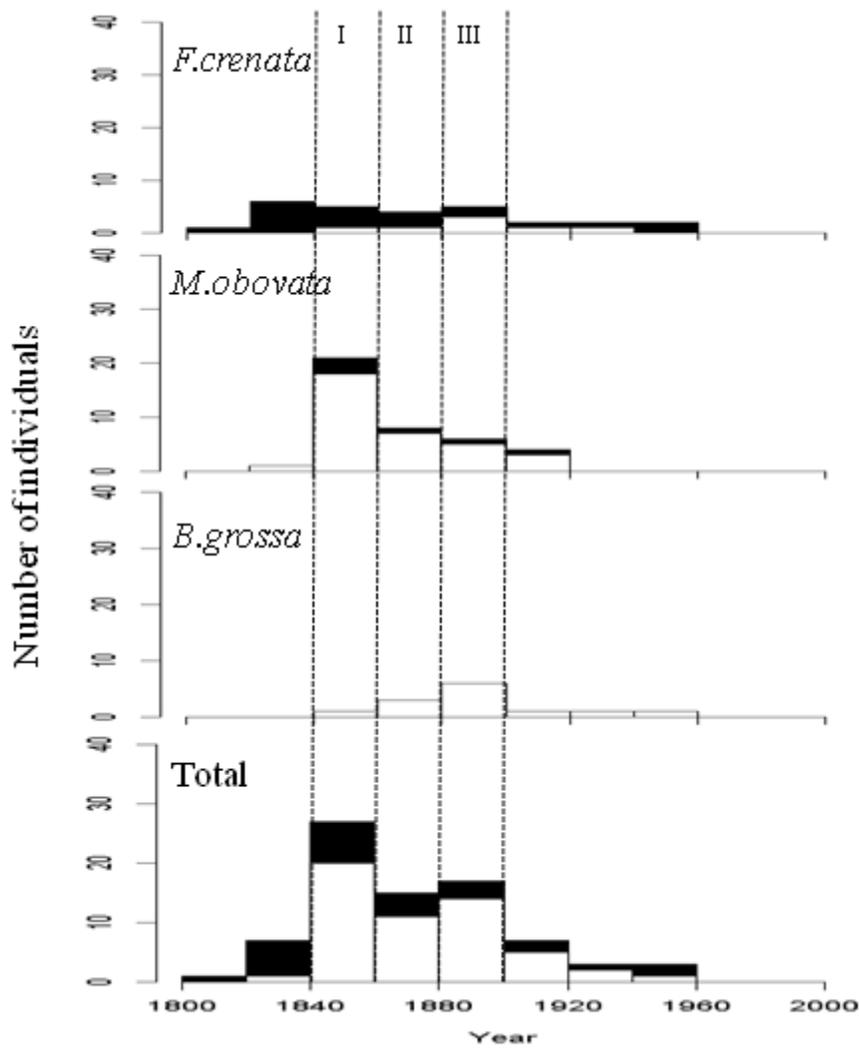
**Fig. 3-1.** Age structure of the dominant tree species in the study plot (0.65 ha). Frequencies are presented as the number of individuals.



**Fig. 3-2.** Changes in annual increment of the dominant tree species. Gray lines: individual changes in annual increment; black lines: changes in average increment. Age was determined from the length of the tree-ring series, which started from the innermost ring.



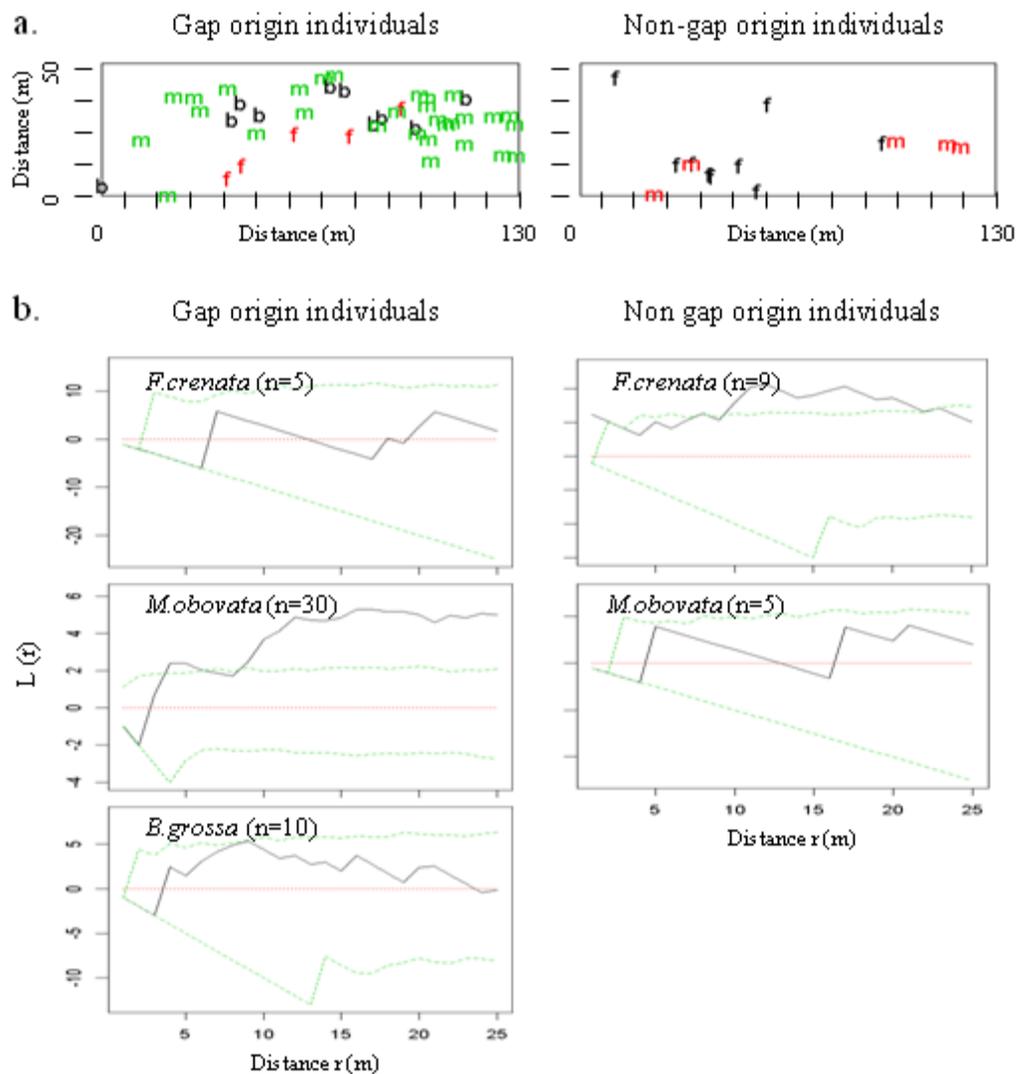
**Fig. 3-3.** Annual tree-ring widths for the dominant tree species. The lower and upper box boundaries represent the 25th and 75th percentiles, respectively. The horizontal line within the box indicates the median value. The lower and upper whiskers indicate the 90th and 10th percentiles, respectively. Hollow circles indicate values that exceed the 90th percentile.



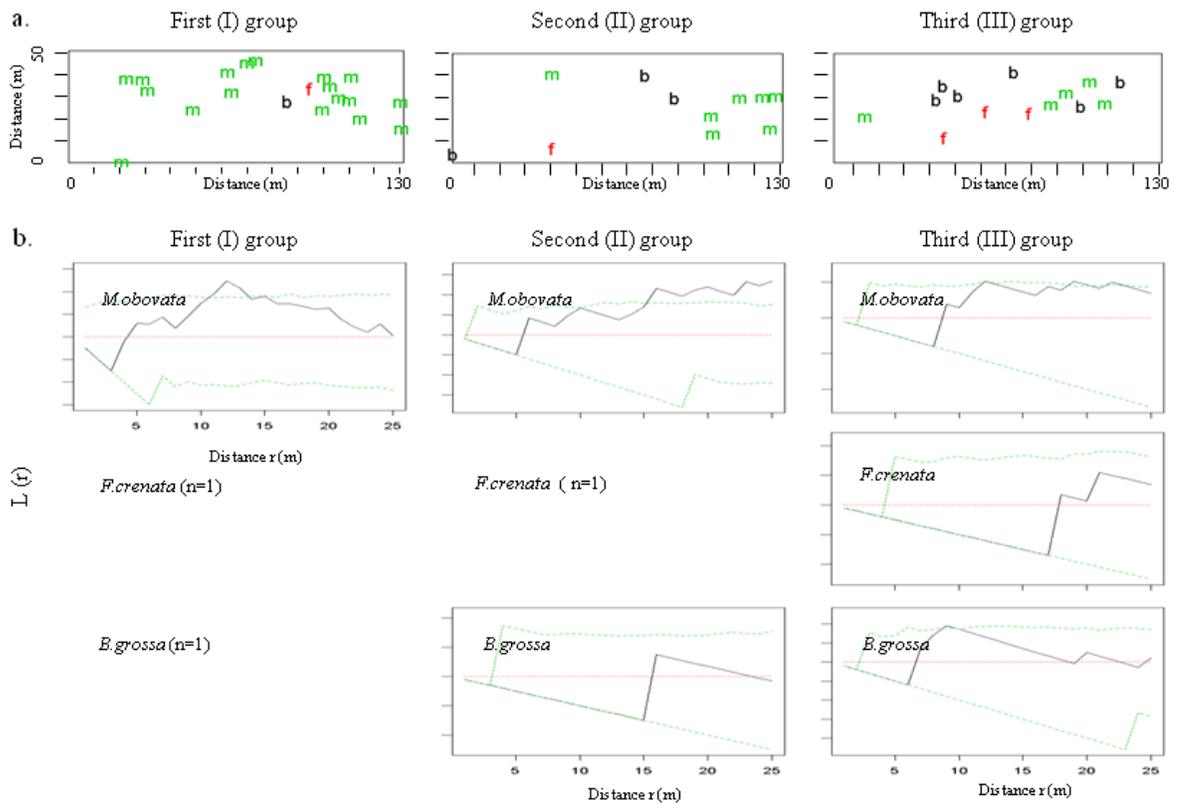
**Fig.3- 4.** Age distribution and division into groups of the dominant tree species. White columns: gap-origin individuals; black columns: non-gap-origin individuals. First (I) group: 1841–1860; second (II) group: 1861–1880; third (III) group: 1881–1900.

**Table 3-2.** Number of fast- and slow-growth individuals in the study plot. Individuals of gap and non-gap origin were identified by species-specific radial growth thresholds.

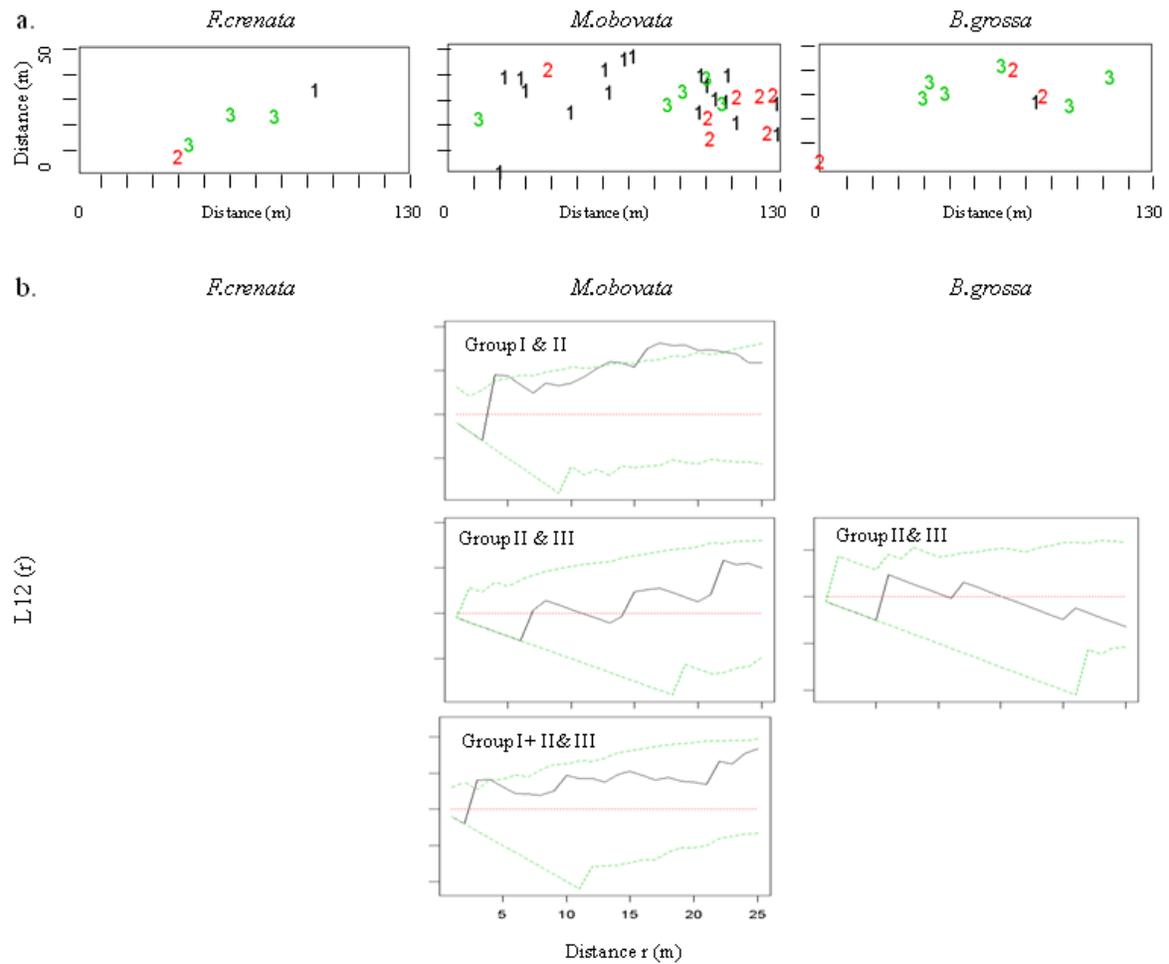
Species	Gap origin	Non-gap origin	Total
	individuals	individuals	Individuals
<i>Fagus crenata</i>	7	20	27
<i>Magnolia obovata</i>	34	6	40
<i>Betula grossa</i>	13	-	13



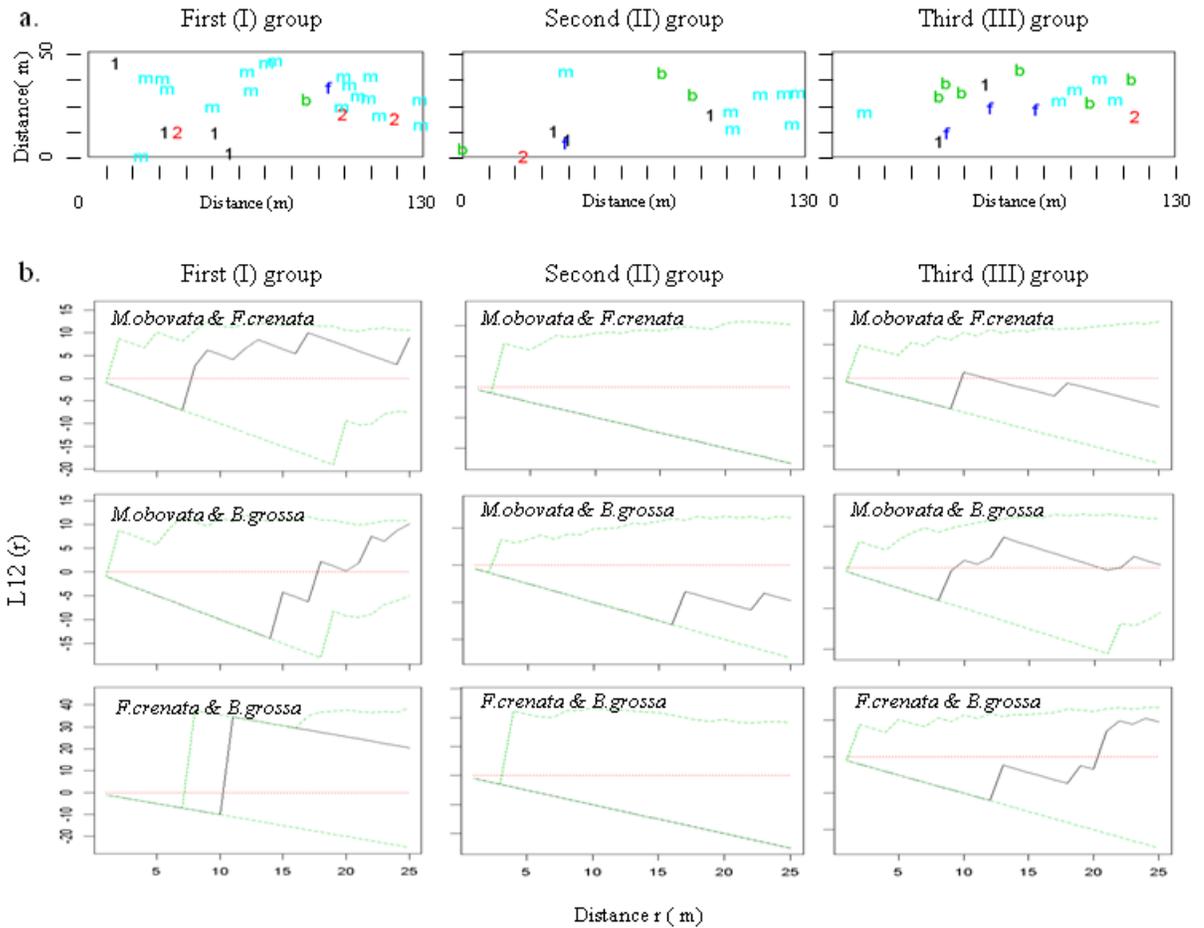
**Fig. 3-5.** Position maps of individuals in three selected cohorts in figure 5a. f: *Fagus crenata*; m: *Magnolia obovata*; b: *Betula grossa*. Univariate spatial pattern analysis of the three dominant species for gap-origin individuals (left) and non-gap-origin individuals (right) in figure 5b. Solid lines: the corresponding Ripley's L-function with 5% confidence intervals. Dashed lines: 95% confidence envelope interval.



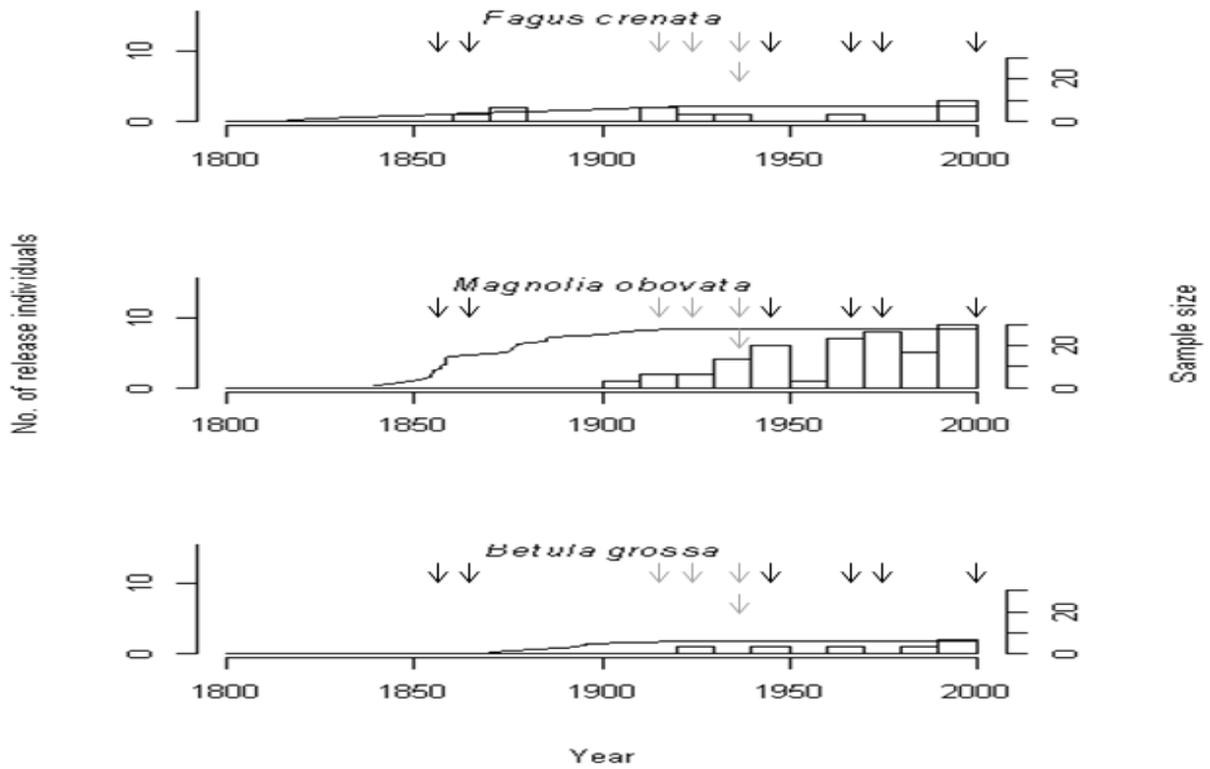
**Fig. 3-6.** Point position pattern of gap origin individuals by cohorts shown in figure 6a. f: *Fagus crenata*; m: *Magnolia obovata*; b: *Betula grossa*. Univariate spatial pattern analysis of gap-origin individuals by groups in figure 6b: first (I) group in left, second (II) group in middle, and third (III) group in right. Solid lines: the corresponding Ripley's L-function with 5% confidence intervals. Dashed lines: 95% confidence envelope interval.



**Fig. 3-7.** Point position pattern of gap-origin individuals shown in figure 7a. 1: first (I) group (1841–1860), 2: second (II) group (1861–1880), 3: third (III) group (1881–1900). Bivariate spatial correlation between groups by species shown in figure 7a. Solid lines: the corresponding Ripley's  $L_{12}$ -function with 5% confidence intervals. Dashed lines: 95% confidence envelope interval.



**Fig. 3-8.** Point position pattern of individuals shown in figure 8a. f: *Fagus crenata* (gap origin); m: *Magnolia obovata* (gap origin); b: *Betula grossa* (gap origin). 1: *F. crenata* (non-gap origin); 2: *M. obovata* (non-gap origin). Bivariate spatial pattern analysis on gap-origin individuals by groups in different establishment periods shown in figure 8b: first (I) group in left, second (II) group in middle, and third (III) group in right. Solid lines: the corresponding Ripley's  $L_{12}$ -function with 5% confidence intervals. Dashed lines: 95% confidence envelope interval.



**Fig. 3-9.** Growth release dates for the three dominant tree species. Release chronologies were based on the number of major release events per decade. Solid lines: changes in the cumulative number of samples. Black arrows: Typhoon. Gray arrows: Strong storm.

**Table 3-3.** Number of trees in canopy accession types for the three dominant species. The classification criterion is described in the text.

Species	Gap	Gap	Non-gap	Non-gap
	release	No-release	release	No-release
<i>F. crenata</i>	-	7	7	13
<i>M. obovata</i>	24	10	3	3
<i>B. grossa</i>	6	7	-	-

## Chapter 4

### GENERAL DISCUSSION AND CONCLUSION

#### 4.1. Understory Dynamics

*Fagus crenata* understory trees are likely to wait for gap formation, and abundance of understory population will probably determine the speed of regeneration in beech forests (Nakashizuka 1983). However, population size of *F. crenata* understory trees decreased in 19 years and mortality was much higher than recruitment rate. With a few disturbances in beech forests, and *F. crenata* understory tree population tends to be reduced and decrease (Yamamoto and Nishimura 1999; Shimano 2002). On the other hand, it was also suggested that *M. obovata* canopy trees provide higher light intensity and longer phenological gaps under them than *F. crenata* canopy trees. *Fagus crenata* understory trees had independent relation in 1992 and dissociated relation in 2011 to *F. crenata* canopy trees, but associated relation to *M. obovata* and *B. grossa* canopy trees in both 1992 and 2011. Survival and diameter growth rates of *F. crenata* understory trees were higher under *M. obovata* canopy trees than under *F. crenata* canopy trees, but there was no difference between under *B. grossa* and *F. crenata* canopy trees in survival rates. Light intensity during the growing season and phenological gaps under canopy trees of *M. obovata* in the early spring are probably contributes to their annual production. Above all, phenological gaps caused by the structure in canopy layer have large effects. A variety of light intensity by heterogeneity of canopy layer was beneficial for survival and growth of understory *F. crenata* trees. The result supports the research that has already been pointed out that the effects of light intensity and phenological gaps by different canopy tree species on understory tree survival and growth (Koike 1985; Yoshida and Kamitani 1998; Komiyama 2001; Tomita and Seiwa 2004). Peters and Platt (1996) reported a similar result that the existence of understory *F. grandifolia* is higher under the *M. grandifolia* canopy trees than the other under the *F. grandifolia* canopy trees in an old growth forest of northern Florida, America.

#### 4.2. Canopy Dynamics

The age structure and initial growth rate are indicating continuous establishment mostly by non-gap origin individuals of *F. crenata* and simultaneous establishment mostly by gap-origin individuals of *M. obovata*, but *B. grossa* has narrow range of age distribution and all canopy trees are gap-origin individuals. Such results are explained by their gap-regeneration characteristics (Runkle 1981; Palmer 1987; Yamamoto 1989; Yamamoto et al. 1995; Yoshida and Kamitani 1998; Abe et al. 2005) and shade-tolerance ability (Koike 1985; Masaki et al. 1992). Individuals of *M. obovata* are likely to be continuously established in the same gaps or established around the gaps in subsequent decades. Such an establishment pattern for *M. obovata* might be facilitated also by gap enlargement after gap formation. A long-term study of gap dynamics has shown that gaps expand over time (Henbo et al. 2004). On the other hand, it is likely that *F. crenata* canopy trees were derived from continuously established individuals and were less concentrated spatially in large openings. Small gaps are often filled by suppressed shade-tolerant seedlings and saplings by advance regeneration (Brewer and Merritt 1978) or by sprouts (Runkle 1982). Establishment pattern of *B. grossa* is not well explained in this study, but the pattern might be explained as follows; individuals of *B. grossa* disappeared early in the large openings due to their short longevity (Whitmore 1989), or they tended to invade disturbed soil conditions within gap (Nakashizuka 1989; Yamamoto et al. 1995). A variety of low-intensity disturbances were identified, after the 1900s but the occurrence of high-intensity catastrophic disturbance not indicated. We found no evidence for discrete periods characterized by many release events. For all three species the frequency of release was low and relatively consistent over the past 100 years. There was no obvious association between release events and historical records of storms and typhoons (Nishiawakura-Son 1977). Therefore, small-sized disturbance by single tree falls rather than high-magnitude and large-sized disturbances may have affected the growth and recruitment of canopy trees over the past 100 years in the studied forest. It has been estimated that rotation time of disturbances causing canopy gaps are ranged 100-200 years (Brokaw 1985, Runkle 1985) and the large catastrophic disturbances occurs three to five times in

1000 years (Canham and Loucks 1983) in temperate and tropical forests. Therefore it is suggested that rotation time of *F. crenata* canopy trees are short and the regeneration occurs frequently before and after both large- and small-scale disturbances, whereas rotation time of *M. obovata* and *B. grossa* canopy trees are long and the regeneration occurs rarely.

#### 4.3. *Conclusions*

Mixed structure in canopy layer facilitates survival and growth of understory *F. crenata* species by providing different light conditions in the understory. Above all, phenological gaps caused have large effects. This study presents an increase dominance of *F. crenata* in canopy layer, and a decrease population size of *F. crenata* understory trees. Therefore, existence of *M. obovata* species in the canopy layer contributes to maintenance of understory *F. crenata* population. The study result also suggests that the large scale catastrophic disturbances are important factor for establishment and existence of *M. obovata* and *B. grossa* species in this old-growth beech forest. Therefore, large-scale disturbances facilitate regeneration of *M. obovata* and *B. grossa* species, at the same time are also important to regeneration of *F. crenata*.

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