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Stem Growth and Interspecific Competition in a Broadleaved Secondary Forest, Central Japan

– Implications for Managing Stands to Maintain Mixture of Species –

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Abstract

Secondary forests are now becoming one of the most important habitats for wildlife species, because primary forests have been declined in recent decades. A management of secondary forests, which includes a certain structure and species composition to more accurately mimic primary forest ecosystems, has been increasingly accepted. My special concern in this study is with the practices for maintaining and/ or enhancing diversity of canopy tree species in secondary forests in central Japan. Because co-existing mechanisms of canopy trees with different light requirement are not still be cleared, I focus on competitive interactions among species as well as on growth characteristics of each component species.

The results indicated that the observed patterns could be explained by species-specific characteristics of photosynthetic light use and competitive interactions among species. Less shade-tolerant species showed greater sensitivity to the neighbors. In contrast, shade-tolerant species produced most pronounced shading effects to the neighbors, probably because of their own ability to maintain deep crowns. These were clearly consistent with the conventional model of successional dynamics: dominance tends to shift to shade-tolerant species. I also revealed that growth rates of less-tolerant species were further enhanced by intensive crown release, compared with those of tolerant species. The significance of canopy disturbance on maintaining less-tolerant species in mixed-species composition is confirmed. I concluded crown thinning should be conducted to enhance growth of less shade-tolerant species for maintaining mixture of species. According to the management objectives, species-specific growth characteristics and the general trends of competition should be taken into account for managing secondary forests, which enables multiple purpose forest utilization.

Key Words: coppice forest, forest stand dynamics, Interspecific competition; shade-tolerance; thinning.

Chapter 1

General Introduction

A general definition of forestry is the practice and science of managing trees to meet defined objectives, usually to produce wood or timber (Mitchell and Kirby 1989). In recent decades, most of forestry in Japan has been under the extensive clear cutting and replant system. Although the system has many profitable aspects for timber production, it minimizes many of natural features associated with old-growth forests (DeBell *et al.* 1997, Franklin *et al.* 1997). Forestry policy has changed recently towards much more evaluation of non-monetary outputs. In particular, in the aspects of nature conservation, forests have received greater emphasis as places where any rare species or all native species populations are aimed to enhance or maintain. In general, secondary forests regenerated after a major

disturbance contains less complex structure and composition than old-growth forests (Mitchell and Kirby 1989, Evans and Barkham 1992). Nevertheless, since old-growth forests have been markedly and rapidly declined in recent decades (cf. Nagaike and Kamitani 1997), secondary forests are now becoming one of the most important habitats for wildlife species (Mitchell 1992, Peterken 1992). The conversion management (after Matthews 1989, Garfitt 1995) of secondary forests, which introduce structural and compositional complexity to more accurately mimic primary forest ecosystems in the region, has been increasingly accepted (Franklin *et al.* 1997, Smith *et al.* 1997).

The final objective of the current study is to provide ecologically based implications for management practices to maintain mixture of canopy tree species in secondary broadleaved forests in

central Japan. Co-existence of canopy tree species causes heterogeneous environment in forests (Canham *et al.* 1994), and thereby provide wide variation in natural resource level and habitats needed for increasing ecological diversity (Runkle 1985); it also may provide additional advantages to show higher tolerance to biotic and abiotic damages (Burkhart and Tham 1992, Kerr *et al.* 1992). The conventional model of stand dynamics suggests that dominance progressively shift from less-tolerant species to more-tolerant species in developmental process of even-aged stands (Harper and White 1974, Horn 1974, Marks 1974, Aber 1979, Bormann and Likens 1979, Oliver 1981, Burrows 1990). Since secondary succession is considered as a result of interspecific competition with any plant- by plant replacement process (Horn 1974), we should investigate competitive interactions among component species to predict successional trends. In general, mixture of species is considered to be maintained by species-specific differences in response to environmental resources, especially to light (Ricklefs 1977, Denslow 1980, Poulson and Platt 1989, Yamamoto 1989). However co-existing mechanisms of canopy trees with different light requirement are not still be cleared.

I here try to clarify successional trends of mixed secondary forests with special reference to species-specific growth characteristics. I will evaluate interspecific competition for light and response to disturbance as ecological factors affecting stem growth of each component species. Chapter 3, 4, and 5 focus on competitive interactions and shifts in dominance among canopy tree species in mixed forests with different combinations of species (Yoshida and Kamitani 1997, 1999, 2000). In Chapter 6, I investigate changes in stem growth following different levels of crown release, and make comparisons among species (Yoshida and Kamitani 1998). The results will enable us to understand detailed process of interspecific competition and its consequences on successional dynamics in secondary forests. In the final chapter, I offer implications for managing secondary forests to maintain mixture of species. It does not accomplish the whole process of such a management regime, but possible to add significant knowledge of ecological processes and greatly improve practices for the future benefits.

Chapter 2

Site Descriptions

I set a target on secondary forests in the *Fagus crenata* (Siebold's beech) forest region (cf. Miyawaki 1985, Hukushima *et al.* 1995) of the Japan-Sea side of central Japan. In this region, many forests had been traditionally utilized for production of small round wood, fuelwood and charcoal by repetitive cutting (Kamitani 1993), known as 'coppicing' (after Evans 1992). However these forests have mostly been ceased regular cutting since 1960s, because

many traditional products were superseded by chemical products during the 'fuel evolution'. Some forests were cleared for agriculture, and others abandoned from management for decades; large areas of the former coppice forests have been left unmanaged (Kamitani 1993).

The study site was in a snow-rich mountain region, Kamikawa Village, located at the northern side of the Echigo Mountains, in Niigata Prefecture, central Japan. The Takigashira Research Forest (37°33'N, 139°31'E) covers an area of approximately 38 ha, at elevations between 400 and 450 m. The terrain consists of flat to steep sloping (below 35°) and slightly dissected by small streams. The bedrock of the forest is the basalt; the forest soils are predominantly volcanic brown forest soil (Kamikawa Village 1992). Precipitation on the closest meteorological station (Tsugawa: 250 m elevation, 15 km distant from the study site) averages 2,177 mm year⁻¹ and is somewhat winter-biased. The mean annual temperature is 10.5°C and the warmth-index (WI) is 83.3 (estimated from the station's records). The climate is classified as Japan-Sea type with heavy snowfall in winter; snow often lasts from early December to April and snow depth up to 4 m (Kamikawa Village, 1992). The structure and floristic composition of the original vegetation type (beech forest) in this region has been reported in Maruyama *et al.* (1989).

The forest had been utilized for producing energy materials (fuelwood and charcoal) for centuries. The compartments of ca. 0.1- 0.3 ha of the forest were periodically clear-logged in turn, with the rotation of 10- 25 years (K. Watanabe, personal communications). Some of the logged stands were converted into Japanese cedar (*Cryptomeria japonica*) plantations, but most of them were maintained as coppice stands through sprouting from the cutting stumps. The regular logging in the forest, however, had been ceased since 1960s. The stands regenerated following the last cutting had been stored since then. Currently, most of these stands are dominated by tall-tree species with height over 10 m. The deciduous broad-leaved tree species, such as Siebold's beech (*Fagus crenata* Blume) and Japanese oak (*Quercus crispula* Blume), dominate the forest over many other associated species (Table 2-1). It has been revealed that species composition of these secondary forests is affected by intensity and frequency of past logging (e.g. Kamitani 1993) as well as site factors. Although Siebold's beech dominate many of the stands, the stand without any Siebold's beech was also one of the major vegetation type in this forest, likely to be caused by the difference in the rotation period of coppice management (Kamitani 1993). In this study I investigated many types of stands, include the two, according to the objectives described fully in each chapter.

The common names of species used in this study

are listed in Table 2-1. The Latin names are followed by Ohwi and Kitagawa (1983).

Chapter 3

Stand dynamics of a mixed forest of shade-tolerant and intermediate tolerant species *

3.1 Introduction

Extensive studies have been carried out on stand development of secondary forest after clear-cutting (Aber 1979, Bormann and Likens 1979, Oliver 1981, Burrows 1990). Shift in dominance among species is most essential change in the stand dynamics, and is closely related to shade-tolerance which itself is linked with other characteristics such as growth rates and life span (Harper and White 1974, Bormann and Likens 1979). In general shade-intolerant species dominate in early stages, and intermediate and tolerant species become dominant thereafter (Marks 1974, Bicknell 1982). Furthermore it has been predicted that dominance of shade-tolerant species will gradually increase over that of intermediate tolerant species as stand mature (Bormann and Likens 1979). This prediction is supported by long-term studies in which less tolerant species decline in number in the absence of large-scale disturbance (Harcombe and Marks 1983, Whitney 1984, Pickett and White 1985, Nakashizuka *et al.* 1992, Masaki *et al.* 1992, Namikawa 1996). The shift in dominance is also closely connected with development of stand structure (Bormann and Likens 1979, Burrows 1990). Since growth rates are generally related to the amount of radiation absorbed by their crowns (e.g. Waring 1983, West and Osler 1995), aboveground competition for light between species is important. Hence inter-specific comparison of crown size may indicate their competitive condition and so help to describe the dynamics of the shift in dominance. In a mixed forest, when less tolerant species are in more favorable crown condition than that of tolerant species, they will have a competitive advantage because of their higher photosynthetic ability under high light intensity (Bazzaz 1979). On the other hand, when less tolerant species have less favorable crowns, their dominance will further decrease with declining growth.

In this chapter, I investigate two species; Siebold's beech (*Fagus crenata* Blume) and Japanese oak (*Quercus crispula* Blume), which are representatives of cool-temperate forests in Japan. In general, Siebold's beech is considered as the shade-tolerant, while Japanese oak is the intermediate shade-tolerant species judged by their photosynthetic performance (Koike 1988). Japanese oak has a comparable long life span to Siebold's beech (e.g. Higo and Teramoto 1989). These two species often co-occur in coppice

stands where fuelwood or charcoal had been produced. Kamitani (1993) summarized regeneration dynamics of the coppice stands after clear-cutting: during initial 10-15 years, several pioneer shrub species, and also small- and medium-size tree species originated from stump sprouts have a competitive advantage because of their rapid growth in height. Thereafter, their growth tend to be decrease and Siebold's beech and Japanese oak establish dominance after about 20 years. This corresponds to the conventional model of stand dynamics in secondary stands. However very little is known about the dominance relation between the two species in subsequent stage.

The objectives of this chapter were (1) to determine shift in dominance of these two species in stand dynamics, and (2) to explain the shift in dominance in connection with their growth rates and crown conditions. I first inspected changes in tree size, mainly crown size, as stand mature. I also examined growth rates of the two species in a 55 years stand, and investigated possible limiting factors that control the growth rates. Finally, crown conditions that might maintain a mixture of the two species through the stand development are discussed (Yoshida and Kamitani 1997).

3.2 Materials and methods

Five stands that had canopies dominated by Siebold's beech and Japanese oak were selected to include a range of canopy-stem densities from 420 to 1320 ha⁻¹. These stands had been logged for charcoal production before 1960 and are being neglected. Stand age were estimated from average number of year rings at base of the stem. Cores were chosen from five canopy stems randomly sampled in each of the stands. The estimates were ranged from 37 to 62 years and same in order of height of the density. Within each stand, a rectangular plot of 0.10 ha (0.12 ha at No.3) was laid out (Table 3-1). All five plots have Siebold's beech as the first dominant and Japanese oak as the second dominant species. Ratios of the two species were similar (i.e. 30-40 to 25-35 %; in stem number) among the plots except for Plot 1. Here, I regarded a sprout grown out below the breast height (1.3m) as a 'stem'. The term 'clump' refers to the multiple-stem structure of sprouts all of which come from one rootstock. In these plots, more stems per clump on average were found in Japanese oak than in Siebold's beech except for Plot 1. Only canopy stems were examined in this chapter, even when a clump had some overtopped or dead stems.

I recorded diameter at breast height (DBH), height (H) and canopy depth (CD: the distance between the top and bottom of the crown) of all the canopy stems in the five plots, while only DBH (≥10cm) were measured for the overtopped and the dead stems still with bark. DBH was transformed into basal area (BA) in the clump-basis analysis. To clarify if DBH of the two species is allometrically related to their H

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and CD in the five plots, regression analysis were conducted. Crown projection diagrams were made and projected exposed-crown area (ECA) was measured. The exposed-crown is defined as the portion of the total crown not overtopped by any other crowns (Hix and Lorimer 1990). Relative height (RH) was calculated by dividing height by the average height of neighboring stems (Hix and Lorimer 1990) whose crowns were in contact with the subject's crown. I compared these tree size variables of the two species. Since stem- and clump-basis analysis may lead to another results of the inter-specific comparison, the data were treated both as per stem and as per clump.

Plot 3 had been thinned in autumn of 1994. Growth rates of the two species were investigated in this plot in terms of BA growth. I sampled a disk from the thinned stems and a core from the residual stems at breast height. On the disk, annual radial increments were measured to the nearest 0.01mm on two randomly selected radii using a slide caliper, and then averaged. Measurements on the cores were taken only for the most recent 5 years (i.e.1989-1993). The number of stems measured was 27 (disk 17, core 10) for Siebold's beech and 26 (disk 22, core 4) for Japanese oak. Mean annual basal-area increments (BAI, $\text{cm}^2 \text{ year}^{-1}$) were calculated and used in the analysis. These data were also treated both as per stem and as per clump.

Regression analysis was used to examine the limiting factors controlling the mean annual basal-area increments (BAI) of the two species. I fitted the data to a multiple regression formula:

$$\text{BAI} = a + b \times \text{ECA} + c \times \text{RH} \quad [\text{Eq. 3-1}]$$

where a , b and c are regression coefficients. I used two crown condition variables: ECA as the representative of crown-size and RH as that of crown-position variable that indicate degree of suppression by neighboring trees.

3.3 Results

Table 3-2 shows mean basal area (BA), exposed-crown area (ECA), crown depth (CD), height (H) and relative height (RH) of Siebold's beech and Japanese oak in the five plots. The results were shown both as per stem (Table 3-2a) and as per clump (Table 3-2b). The mean BA, ECA and H generally increased with decreasing density. Siebold's beech had significantly larger mean BA and ECA per stem than Japanese oak in the three lower density plots, (plot 3,4 and 5: $P < 0.05$, Table 3-2a). However using the clump-basis analysis (Table 3-2b), the differences in mean BA and ECA were not significant for any of the plots. Mean crown depth (CD) of Siebold's beech was larger in lower density plots, while that of Japanese oak substantially decreased on average in the two lower density plots (plot 4 and 5). In these plots, differences in mean CD

between the two species were significant ($P < 0.05$: also in plot 3 as per stem). Change in the mean RH with density was not clear. Differences in mean H and RH between the two species were not significant in any of the plots both as per stem and as per clump ($P > 0.05$).

DBH-class distributions of the two species in the five plots are shown in Figure 3-1. The distributions seemed to be similar between Siebold's beech and Japanese oak in the two higher density plots. On the other hand, the modal class was different between the two species in the two lower density plots. In plots 4 and 5, Siebold's beech had a peak in the smallest class as a result of the abundance of the overtopped stems, while Japanese oak had a unimodal distribution with fewer overtopped stems. In these plots, the proportion of overtopped stems was significantly lower in Japanese oak than in Siebold's beech (χ^2 -test, $P < 0.05$) with no overtopped stems at all for Japanese oak in plot 5. Japanese oak had some dead stems in the smallest class in the five plots, but no dead stems were found of Siebold's beech.

Table 3-3 summarizes DBH-H and DBH-CD relations for stems only in the five plots. Parameters of linear regression formula are shown. Positive correlation was found on the DBH-H relations of the two species in all the plots ($P < 0.05$, Table 3-3a). Siebold's beech also shown significant correlation in the DBH-CD relationship in the five plots ($P < 0.05$). However this relation was not significant ($P > 0.05$) for Japanese oak except for plot 1 (Table 3-3b).

Figure 3-2 shows a 50-year sequence of mean annual basal-area increments (BAI, $\text{cm}^2 \text{ year}^{-1}$) for the canopy stems of Siebold's beech and Japanese oak in the plot 3 (estimated stand age: 55 years). On the stem-basis (Figure 3-2a), curves of the two species were similar in earlier 20 years, after that Siebold's beech grew steadily, while the curve of Japanese oak declined. Because canopy stems, which had been already deceased or overtopped, were not included in the clump-basis curves (Figure 3-2b), I could not detect change in relative growth dominance in clump-basis. However in the last 10 years, the BA increments of Japanese oak per clump also started to decrease, while that of Siebold's beech steadily increased. The growth differences between the two species were significant for the final 5 years (Table 3-4); Siebold's beech had significantly higher BAI ($\text{cm}^2 \text{ year}^{-1}$) than Japanese oak both as per stem and as per clump ($P < 0.001$).

To determine the most critical variable influencing the BAI, I fitted the data for the two species with a multiple regression [Eq. 3-1]. Only the stem-basis results are shown although similar results were obtained in the clump-basis analysis. The regressions were significant for both species ($P < 0.01$, Table 3-5). For Siebold's beech, the partial regression coefficients (β) were significant for crown-size variable; ECA ($P < 0.05$), but not for RH ($P > 0.05$). Whereas, β was significant for crown-position

variable; RH ($P < 0.001$), but not for ECA ($P > 0.05$) in Japanese oak.

3.4 Discussion

The conventional model of stand dynamics suggests that dominance eventually shift to shade-tolerant species in secondary succession (Bormann and Likens 1979). In this mixed forest, I also predict that dominance of Siebold's beech will gradually increase over that of Japanese oak as stand mature. The first reason for this is the difference in the abundance of smaller stems between the two species in the lower density plots (Figure 3-1). DBH-class distributions of less shade-tolerant species tend to shift to the right with time (McCune and Cottam 1985). Such unimodal distributions in Japanese oak were also reported by other studies (Kikuzawa and Asai 1979, Higo and Teramoto 1989). It seems that Japanese oak, which has intermediate shade-tolerance, cannot long survive in the overtopped condition (cf. Lorimer and Krug 1983). The proportion of Siebold's beech will increase over time, because abundance of sub-canopy stems result in higher potential for replacement following death of the upper stems (Bormann and Likens 1979).

The results of the interspecific comparisons shows that Siebold's beech have growth advantage over Japanese oak in this mixed forest: stems and clumps of Siebold's beech had significantly higher growth rates than those of Japanese oak (Table 3-4). Such growth differences will lead to differences not only in BA but also in ECA. The differences between the two species in the mean BA and ECA per stem have been expanding in the five plots (Table 3-2a). At present, the size differences are not significant per clump (Table 3-2b), because Japanese oak has more canopy stems on average in a clump (Table 3-1). Nevertheless if the lower growth rates of Japanese oak result in their suppression or death in the future, the size differences per clump will also become significant through decreasing number of canopy stems in a clump. Dead stems are relatively frequent in Japanese oak, while very few were found for Siebold's beech in the five plots (Figure 3-1) and surroundings. This trend is similar to that observed in other studies (Harcombe and Marks 1983, Whitney 1984, Nakashizuka *et al.* 1992, Masaki *et al.* 1992, Namikawa 1996) where less shade-tolerant species have higher mortality rates.

Why intermediate tolerant species lost their growth advantage in spite of their higher photosynthetic ability under high light intensity? The results suggest that stem growth of the two species are mainly affected by different variables: crown-size (ECA) is the most critical variable for Siebold's beech, while crown-position (RH) is that for Japanese oak (Table 3-5). In general, growth rates are size-dependent as a result of competition for light (e.g. Cannell *et al.* 1984), but the crown-size variable (ECA) were not significant in the Japanese oak's regression. I

consider that these results are related to the difference in shade-tolerance between the two species. The DBH-CD relations were significant for Siebold's beech (Table 3-3b), suggesting that their total leaf biomass increases roughly with their tree size. This capability due to their higher shade-tolerance supports themselves to have increasing BAI with increasing size. Whereas, the mean CD were smaller (Table 3-2) and the DBH-CD relations were not significant for Japanese oak in the lower density plots (Table 3-3b). I consider these to be caused by a reduced ability of Japanese oak to maintain the lower branches owing to their lower shade-tolerance. The mixture with Siebold's beech, which cast deep shade by their larger CD (cf. Canham *et al.* 1994), may result in the smaller CD of Japanese oak. On the other hand, it have founded out that relative growth rates decreased with increasing neighborhood leaf area index in mixed stands (Bi and Turvey 1996). This may be more effective on less shade-tolerant species neighboring tolerant species with larger CD. I conclude that Siebold's beech have a negative effect on stem growth of Japanese oak through encouraging death of their lower branches and increasing their neighborhood leaf biomass. Therefore BAI of Japanese oak significantly correlated with crown-position variable (RH), which indicate a degree of crown suppression.

The current results proposed that Japanese oak requires a higher RH, i.e. less crown suppression, to have the same growth rates as Siebold's beech. In the early stages, if Japanese oak had had greater relative dominance over Siebold's beech, their relative growth rates could be at higher level. However, the data showed that the mean BA increments per stem in the early stage were not different between the two species (Figure 3-2). Kamitani (1993) states that mean heights were also similar through 20 years after clear cutting. Dominance of the other species during early stage (Kamitani 1993) may restrict the initial growth rates of Japanese oak to be similar compared to Siebold's beech. I conclude therefore that Japanese oak could not entirely utilize their intermediate photosynthetic ability throughout the stand development. The decline in dominance of Japanese oak was caused not only by their less shade-tolerance but similarity of their initial growth rates to those of Siebold's beech. Throughout the stand development, Japanese oak could not have growth advantage, probably as a result of suppression in the early stage. Their lack of early advantage will accelerate the shift in dominance. The results suggest a hypothesis that less shade-tolerant species mixed with tolerant species in coppice stands can only maintain where they have much higher initial growth rates.

Chapter 4

Interspecific competition among three canopy-tree species *

4-1 Introduction

Maintaining and/ or enhancing mixture of tree species are now becoming one of the main issue for developing alternative forestry regimes to meet demand of wood production as compatible with other non-timber benefits (Mitchell and Kirby 1989, Tappeiner *et al.* 1997). Basically, mixture of species seemed to be maintained by species-specific differences in response to environmental resources, such as light, water and nutrients (e.g. Poulson and Platt 1989, Brown 1992). Supply of environmental resources is reduced by presence of neighbors (Weiner 1984, Grace and Platt 1995), so that quantifying competitive relations among neighbors is indispensable to manage forests as mixture. Recently, shading effects of neighbors on demographic functions have been studied in several forests (e.g. Hara *et al.* 1995, Kubota and Hara 1995, Nakashizuka and Kohyama 1995). However, most of these studies dealt with interaction of two species, or still obtained specific competitive attributes assuming similar responses among species. I suppose, however, that species must have their own sensitivity to suppression and also intensity of shading; differences in neighbor species would affect growth to a greater or lesser extent. I can hypothesize that 'sensitivity' must be greater in shade-intolerant species, while 'intensity' seems to be greater in shade-tolerant species. The latter is because shade-tolerant species have an ability to carry deep crowns expected to produce greater shading (Canham *et al.* 1994, Bi and Turvey 1996). Many previous studies which dealt with mixture of species with different shade-tolerance have suggested that canopy stratification, where less shade-tolerant species form an upper canopy above more tolerant species, is essential if a mixed en-aged stand is to increase in total productivity (Wierman and Oliver 1979, Kelty 1989, Marquis 1992) and also to maintain canopy species diversity (Evans 1982, Matthews 1989, Chapter 3). However few studies have made attempt to quantify competitive relations among species.

The objective of this chapter is to quantify interspecific competition among species with different shade-tolerance by determining specific competitive attributes of co-occurring species in an even-aged forest. Do shade-tolerant species actually have lesser sensitivity to suppression and greater intensity of shading? For this purpose, I examined three canopy-tree species; Siebold's beech (*Fagus crenata* Blume), Japanese oak (*Quercus crispula* Blume) and Silver magnolia (*Magnolia obovata* Thunb.), all of these are major components of

cool-temperate forests in Japan. Siebold's beech is regarded as shade-tolerant species, besides Japanese oak and Silver magnolia are designated as an intermediate tolerant class (Koike 1985). I selected six stands with different combinations of two dominant species out of the three species (i.e. Beech-Oak, Beech-Magnolia and Oak-Magnolia) in order to analyze the specific effects on particular species in relation to stem growth and crown structure. I will also examine a hypothesis that mixture with different species result in differences in stem size and growth of each species (Yoshida and Kamitani 2000).

4-2 Materials and methods

I established six study plots (0.12 -0.20 ha) containing different combinations of the dominant species; three combinations were distinguished and assigned by two plots each (Table 4-1). The plots named Beech-Oak had Siebold's beech as the first dominant and Japanese oak as the second dominant species. In the same way, Beech-Magnolia had Siebold's beech as the first and Silver magnolia as the second dominant species. The plots Oak-Magnolia had two oak species; Japanese oak (*Quercus crispula*) and *Q. serrata* Murray as the first and second dominant species, and had Silver magnolia as the third. *Q. serrata* was absent from the analysis because of their scarcity in the other plots. The top two dominant species (three in Oak-Magnolia) account for more than 50 % of the total basal area in each plots (Table 4-1). I note that these plots were adjacent, with similar slope inclination and aspect (10 -15° and north facing, respectively). The estimated stand age and stem density ranged between 48 -60 years and 811 -950 stems/ ha, respectively. The previous study (Kamitani 1993) have suggested that differences in dominant species are mainly caused by differences in disturbance regimes in the past; i.e. the differences in logging intensity and frequency which are determined by a purpose of a coppice management. They strongly affected post-logging vegetation through influencing reproductive abilities of each component species. I have already suggested that dominance of intermediate shade-tolerant Japanese oak is reduced by the presence of more shade-tolerant Siebold's beech in a stand development of a mixed-species forest (Chapter 3). Silver magnolia also has intermediate tolerance (Koike 1985), and remarkably rapid growth rates in early stages of stand development (Kamitani 1993), also occurs in the same forest type.

In the six study plots (area 0.12- 0.20ha) which assigned to the three combination types by two plots each, I measured diameter at breast height (DBH), height (H) and canopy depth (CD; the distance between the top and bottom of the crown) of all the stems with DBH ≥ 10cm. Though many individuals have a cluster of stems sprouted after logging, the results were analyzed on the basis of stems because

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very similar results were obtained in clump-based analysis. I also note that stem growth of the three species in this forest were considered to be only size- and density dependent, and not depended on whether it is from same or different root systems (unpublished data).

The forest had been started to manage again (as thinning) from the autumn of 1993. I sampled a disk from the thinned stems and two cores from the residual stems at 50cm in height. I measured annual radial increments during 1989-1993. The measurements of two radii per stem were averaged and used in analysis in terms of annual basal area increments (BAI; cm^2/year).

One of the major objective of this chapter is to detect differences in sensitivity to suppression and intensity of shading among species. For this purpose, I used an asymmetrical competition model for stem growth (Kohyama 1991, 1992, Hara *et al.* 1995, Kubota and Hara 1995, Nakashizuka and Kohyama 1995). Here, the effect of one-sided shading was expressed by cumulative basal area (B) calculated for all the stems with larger DBH than the subject stem (Kohyama 1991, 1992). I calculated B for all the neighboring stems whose crowns are in contact with the subject's crown, and divide into following four terms (cf. Nakashizuka and Kohyama 1995):

$$B = B_B + B_Q + B_M + B_{ot} \quad [\text{Eq.4-1}]$$

where B_B , B_Q , B_M and B_{ot} indicate the cumulative basal area of Siebold's beech, Japanese oak, Silver magnolia and the other species, respectively. Then, regression analysis was used to examine the shading effects of another species on basal area increments (BAI). The original model of Kohyama (1991,1992) was modified to separate shading effects by four species;

$$\text{BAI} = \text{BA} [a_0 - a_1 \ln(\text{BA}) - a_2 B_B - a_3 B_Q - a_4 B_M - a_5 B_{ot}] \quad [\text{Eq.4-2}]$$

where $a_0 - a_5$ are regression coefficients. I compared parameters of the variables among the three species. Data collected from the six plots were used together in this analysis.

I examined leaf area index (LAI) by using hemispherical photographs to show a fundamental attribute of crown structure of the three species. In the plot area, three locations where each the three species was aggregately dominated in the canopy layer were selected. Photographs were taken eight times for four points for each (set by 5 m intervals) from early May to mid December in 1995, on days with overcast cloud conditions to minimize glare from direct sunlight. Note that leaf phenology of this year was considered to be similar compared to common years (personal observation). A camera with a fisheye-lens (Nikon Co.; Nikkor 8 mm F2.8S) was positioned horizontally at a height of 1.3 m to

exclude effects of shrub layer. The photographs were computerized using a film scanner (Nikon Co.; cool-scan) with a resolution of 400×400 pixels. A threshold gray level was determined for each photographs to distinguish between sky and canopy by the same person. The LAI was then calculated by using an analyzing program HEMIPHOT (ter Steege 1993). A method used by the Li-Cor LAI-2000 Plant Canopy Analyzer (PCA) was applied to calculating LAI, where five viewing angles (7, 23, 38, 53 and 68) are considered. It has been reported that LAI estimated by the PCA generally make underestimates (Cutini *et al.* 1998), but I did not make any corrections in this chapter. I subtracted woody area (trunk and branches) on estimating LAI by comparing photographs taken during the leafy period with those during the leafless period (ter Steege 1993).

$$\text{LAI} = 2\sum [-\ln(\text{TAI}_i / \text{BAI}_i) \times W_i / S_i] \quad [\text{Eq.4-3}]$$

where i takes the five viewing angles mentioned above. TAI_i and BAI_i are gap fraction (openness) around each viewing angle of photographs taken during leafy period and leafless period (i.e. mid December), respectively. W_i takes weights to account for area correction and S_i takes the reciprocal path length corrections (ter Steege 1993).

I examined whether different species compositions would result in differences in crown structure, in terms of vertical distribution of crown foliage within a stem. Although the stratified clipping method may be more preferable for this purpose (e.g. Kikuzawa and Umeki 1996), I used a non-destructive sampling technique, as detailed below, for ease of measurement. A crown consists of many foliage tufts grown from the main stem. First, I selected major first-order branches, constituting their own foliage tuft, growing out below 12m in height. The height 12 m was selected in this chapter because it was difficult to distinguish each branch above 12 m by observations in the plots (the average height was c.a. 16 m). Second, I measured the top height of the every foliage tuft and expressed it as height class, indicating relative height of the foliage tuft to the top height of the stem (<80, 80-90, 90-100 and 100%; 100% denotes the foliage tuft compose the highest part of the whole crown). Third, I divided exposed crown (defined as a portion of total crown not overtopped by any other crowns) into several parts corresponding to the foliage tufts already distinguished, and measured each exposed crown area on crown projection diagrams. Finally, I calculated vertical distribution of the exposed crown area among the height classes (%CA), expressing a degree of stratification of the crown foliage. In the three combinations, the largest eight stems in DBH for each species were measured, and the average %CA for each height class were calculated.

Moreover, I investigated causes of differences in

crown structure among species by quantifying limiting factors controlling crown depth (CD). Though several studies have presented prediction models for crown depth as a function of stand parameters (Ward 1964, Hynynen 1995), I focused specifically on the shading effects on a stem by its neighbors. For this purpose, the data were fitted to a multiple regression formula;

$$CD = a_0 + a_1 (BA) - a_2 B_B - a_3 B_Q - a_4 B_M - a_5 B_{ot} \quad [\text{Eq.4-4}]$$

where B_B , B_Q , B_M and B_{ot} are the species-specific cumulative basal area, and $a_0 - a_5$ are regression coefficients. Data collected from the six plots were used together in this analysis.

4-3 Results

Table 4-2 shows mean DBH, height (H) and crown depth (CD) of the three species in the six study plots; the means of the two co-occurring species in each plot were compared. The results were similar between the two plots designated as the same combination type. The mean height was not significantly different between the two species in each plot (Mann-Whitney, $P > 0.05$). On the other hand, Siebold's beech had significantly larger mean DBH and crown depth than Japanese oak in Beech-Oak ($P < 0.05$). Siebold's beech has also larger mean crown depth than Silver magnolia in Beech-Magnolia ($P < 0.01$), but the difference in mean DBH was not significant. Also, mean DBH were not significantly different between Silver magnolia and Japanese oak in Oak-Magnolia.

Figure 4-1 shows mean annual basal area increments (BAI; $\text{cm}^2 / \text{year}$) over the most recent 5 years plotted against basal area (BA; cm^2) for stems of the three species. There was a significant linear relationship between the two variables for all the cases ($P < 0.05$). For Siebold's beech and Silver magnolia, there appeared to be no significant difference in BAI between the two plots (ANCOVA with the covariate BA; $P > 0.05$), whereas it was found that mean BAI of Japanese oak in Beech-Oak were significantly smaller than that in Oak-Magnolia ($P < 0.01$).

Table 4-3 summarizes the effect of size (BA) and neighbors (B) on BAI for the three species; parameters of the regression formula (2) were shown. The coefficient for B_B , indicating cumulative basal area of larger Siebold's beech, was significant for Japanese oak and Silver magnolia as positive values, suggested that presence of larger Siebold's beech as neighbors has a significant negative effect on BAI of both the two species. In the same way, the presence of larger Japanese oak (B_Q) affected BAI of Siebold's beech, significantly. On the contrary, the coefficient for B_M only showed non-significant values (rather negative), suggesting that they tended to not have any effects on BAI for their neighbors.

Figure 4-2 illustrates seasonal changes of LAI for the three species in 1995. I note again that leaf phenology of this year was considered to be similar compared to common years (personal observation). Siebold's beech had highest LAI throughout the growing season, and had longest leafy period. The LAI of Silver magnolia were lower than those of Japanese oak until leaf-fall season; the difference between the two species was greatest in spring, suggesting a delay of sprouting of Silver magnolia.

Figure 4-3 shows a result of non-destructive sampling technique for crown structure; comparison of vertical distribution of foliage tuft between the two different species-combination types were shown. The percent exposed crown areas (%CA) of Japanese oak in Beech-Oak have less stratified and extremely upper biased crown, i.e. more than 50% of exposed crown were in the height class of 100% (again note the 100% indicate the foliage tuft compose the highest part of the whole crown). In contrast, the proportion of lower height classes was higher in Oak-Magnolia, suggesting that Japanese oak have a more stratified crown in Oak-Magnolia. Also, crowns of Silver magnolia in Oak-Magnolia appeared to be more stratified than that in Beech-Magnolia. On the other hand, the distribution of Siebold's beech seemed to be similar between the two stands; Beech-Oak and Beech-Magnolia.

The factors affecting crown depth of the three species are summarized in Table 4-4, showing parameters of the regression formula [Eq.4-4]. It was found that crown depth was positively related to DBH ($P < 0.01$) for both Siebold's beech and Silver magnolia. A significant positive effects was also found in B_B for Siebold's beech ($P < 0.01$). In contrast, the crown depth of Japanese oak was not significantly related to its DBH, but was negatively affected by B_B ($P < 0.01$), suggesting that presence of larger Siebold's beech has a significant negative effect on the crown depth of Japanese oak.

4-4 Discussion

In this chapter I examined two issues: (1) effects of mixture with different species on stem size and growth, and (2) relation between shade-tolerance and competitive attributes (i.e. sensitivity to suppression and intensity of shading) of canopy tree species. First, this chapter clearly indicates that mixture with different species may result in concomitant differences in stem size and growth of each species, as seen notably in Japanese oak. Mean DBH of Japanese oak was significantly smaller than Siebold's beech in Beech-Oak, whereas similar to Silver magnolia in Oak-Magnolia (Table 4-2). In spite of the similarity of mean height between the two species-combinations, mean DBH in Oak-Magnolia was considerably larger than that in Beech-Oak (Table 4-2). Also, presence of shade-tolerant Siebold's beech led to considerably reduced stem growth of Japanese oak (Figure 4-1). I could not, of

course, directly compare means of these variables among the species-combinations, because stand ages and stem densities were different among the plots. Nevertheless, I could recognize that the differences were not so distinct for the comparison in this chapter. I believe that only such differences in ages and densities (in the case of Japanese oak, the range of the age and density were 48-55 years and 844-950 stems/ ha, respectively: Table 4-1) could not explain the crucial differences in stem size and growth observed; differences in species composition should strongly affect the current results.

On the contrary to Japanese oak, stem size and growth of Siebold's beech and Silver magnolia appeared to be less influenced by differences in canopy composition. The greater shade-tolerance of Siebold's beech seemed to be the main reason accounting for similar stem growth between the two plots (Beech-Oak and Beech-Magnolia) irrespective of difference in species composition (Figure 4-1). Although, Siebold's beech is also affected by the neighbors as shown in Table 4-3, it may be less influenced by neighbors (non-*Fagus* species) because the opposite effects (i.e., effects of Siebold's beech on the other species) were more intensive (Table 4-3). Its ability to use low light intensity seemed to protect it from competition by other canopy species.

The results of Silver magnolia were considerably different from that of Japanese oak, in spite of their similarity in shade-tolerant class. Though the shading effect of Siebold's beech was also negative on Silver magnolia, the stem growth of Silver magnolia seemed to mainly determined by its stem size (i.e. large parameter value of 'constant'; Table 4-3). Even in the stand of mixture with Siebold's beech (Beech-Magnolia), they have similar mean DBH compared to Siebold's beech (Table 4-2). I suppose that rapid growth ability in the early stage of stand development enables Silver magnolia to maintain its growth to similar between the two species-combinations. It had been revealed that Silver magnolia had the greatest initial height growth rates among regenerated species in a coppice stand after clear logging (Kamitani 1993). This must result in making fully developed crowns in early stage under initial high light intensity. In contrast, Japanese oak has lower initial growth rates and thus is suppressed by several pioneer shrubs and small- and medium size tree species (Kamitani 1993), resulting in an early check to its growth (Chapter 3).

Second, this study revealed that shade-tolerance of species seemed to decide their intensity of shading, as similar to the sensitivity to suppression. Shade-tolerant species had greater intensity of shading and lesser sensitivity to suppression. I suppose that such specific competitive attributes are probably related to their crown structure. Shade-tolerant Siebold's beech had deeper crown depth and higher LAI compared to Japanese oak (Table 4-2, Figure 4-2, 4-3). Canham *et al.*(1994)

documented a relationship between shade-tolerance and light extinction characteristics, showing shade-tolerant species cast deep shade because of their ability to maintain deep crowns. In fact, light transmission through Siebold's beech dominate canopy was considerably less than through Japanese oak and Silver magnolia dominate canopy in this forest (unpublished data). The neighbor Siebold's beech, which casts deep shade by virtue of its deeper crown depth and higher LAI, must therefore contribute to higher shading effects. In contrast, less-tolerant species could not have higher intensity (Table 4-3), probably because of their poorer crown structure. The shading effect, especially from shade-tolerant species, should contribute the death of lower branches of less-tolerant species, resulting in less stratified and upper biased crown structure (e.g. Japanese oak in Beech-Oak; Figure 4-2). The fact that crown depth of Japanese oak was not significantly influenced by its stem size (Table 4-4) is considered to be come from its lower sensitivity to suppression and strong shading by neighbors (probably, mainly by Siebold's beech). Although shallow crowns may increase growth efficiency of the stem (e.g. Gilmore and Seymour 1996), actual size growth of Japanese oak was considerably decreased in Beech-Oak (Figure 4-1). Shallow crowns should reduce its ability to intercept light and, notably, its shading ability to neighbors. I note that cumulative basal area of larger Silver magnolia had non-significant negative effects on its neighbors (expressed as rather positive values in the parameter: Table 4-3). This should be also resulted from shallower crown depth and lower LAI, and its shorter duration of leafy period (especially in spring to early summer; Figure 4-2, also cf. Maruyama 1978), may be partly related.

These results indicate the marked advantage of shade-tolerant species in interspecific competition in mixed-species stands. I consider stem growth must be considerably affected by the presence of shade-tolerant species as its neighbors. Therefore, differences in initial species composition, often resulted from a special kind of disturbance (e.g. Kamitani 1993, Fajvan and Wood 1996), will lead each species component having a different degree of dominance in stand development (cf. Nowak 1996). When shade-tolerant species are absent in mixture, less shade-tolerant species could maintain their dominance for a long period. In contrast, mixture with tolerant species would reduce the dominance of less-tolerant species, unless they had growth advantage in early stage in development (such like Silver magnolia in this chapter). Because the effect of neighbors on tolerant species are relatively weak, tolerant species could maintain, and probably increase the dominance through the decline of less-tolerant species.

Chapter 5 Growth of a shade-intolerant tree species as a component of a mixed-species forest *

5-1 Introduction

It is widely recognized that shade-intolerant species gradually lose their dominance as part of the developmental process of even-aged stands (Harper and White 1974, Horn 1974, Bormann and Likens 1979, Oliver 1981, Burrows 1990). Such a trend seems to be true not only for intolerant herbaceous and shrub species (e.g. Marks 1974, Ash and Barkham 1976, Bicknell 1982, Mitchell and Kirby 1989) but for intolerant tall-tree species with relatively long life spans (Horn 1974, Bormann and Likens 1979). The decline can be attributed to two major factors: a decrease in recruitment, and an increase in mortality. Numerous studies have reported that shade-intolerant species often show unimodal age distributions as a result of reduced survival ability of their seedlings and saplings under closed canopy conditions (Hubbel 1979, Lorimer and Krug 1983, Masaki *et al.* 1992, Namikawa 1996). Because shade-intolerant species tend to regenerate in intensively disturbed sites (Bormann and Likens 1979, Brokaw 1987, Whitmore 1989, Yamamoto 1989), their opportunities for successful recruitment seem to be quite limited in younger even-aged stands, where larger scale disturbances are scarce (Oliver 1981, Mitchell and Kirby 1989).

Furthermore, many long-term studies have shown that shade-intolerant components of mixed-species forests are generally decreased in number through increased mortality of upper-story trees (Whitney 1984, Nakashizuka *et al.* 1992, Leak and Smith 1996, Namikawa 1996). Although causes of death vary with species (e.g. Harcombe and Marks 1983), it is recognized that tree mortality is often size-dependent: smaller trees tend to have higher mortality (Harcombe and Marks 1983, Platt *et al.* 1988, Nakashizuka 1991), indicating that death of trees would be increased if they were being under suppressed condition. In particular, trees that have a smaller tolerance for shading may have an increased mortality risk due to their increased sensitivity to suppression. In chapter 4, I have shown that growth of intermediate shade-tolerant species is more sensitive to suppression than that of tolerant species, resulting in decline in dominance of the former in mixed-species stands. However comparisons among species with various tolerant classes have not been made yet; further evidence are needed to prove the possible relationship between shade-tolerance and the sensitivity to suppression.

In this chapter, I examined a shade-intolerant

tall-tree species Amur cork-tree (*Phellodendron amurense* Rupr.), the photosynthetic performance of which evidently indicates an enhanced capacity for utilization of light under light-rich conditions (i.e. higher light compensation-, and light saturation-point, and the dark respiration rate, in conjunction with a light-saturation curve with a lower initial slope; Koike 1985). The potential life span of the species appears to reach more than 90 years (Komiyama 1989), a duration that probably approximates the turnover time of temperate old-growth forests (i.e., 100-200 years, Runkle 1985, Nakashizuka 1987, Yamamoto 1989). They rarely form pure stands; they frequently occur in both even-aged secondary or natural stands as a component of mixed-species forests in cool temperate regions (Tanimoto 1990). Hence the competitive interactions among the other component species are considered to be important for the population dynamics of Amur cork-tree.

The objective of this chapter is to explain the process of decline of shade-intolerant species from the viewpoint of competitive relations among neighborhood trees. To this end, I use a regression model of tree growth incorporating the asymmetrical effects of shading (Kohyama 1991, 1992), which in this case consist of several dominant tree species of varying shade tolerances. Based on the results, I discuss some definitive factors affecting the general trend of the decline of shade-intolerant species across the development of mixed-species even-aged forests (Yoshida and Kamitani 1999).

5-2 Materials and methods

In 38 ha area of the Takigashira Research Forest, there were 45 stems of Amur cork-tree having a DBH (diameter at breast height) greater than 10 cm (1.18 stems ha⁻¹); 18 stems were located on hill-slopes and 27 stems along streams (streamside, defined as within 5 m from a stream; all trees not designated as streamside were designated as hill-slope). The distribution of Amur cork-tree is therefore biased toward riparian areas (cf. Ishizuka and Sugawara 1989, Tanimoto 1990).

In 1997, I marked all the 45 stems of Amur cork-tree and established circular plots within a 5 m radius of each. Although Amur cork-tree is dioecious (cf. Mizui and Kikuzawa 1991), I did not divide male and female trees in analysis because the dividing was difficult for unflowering trees. For each circular plot I recorded species name, DBH, height (H) and crown ratio (CR: the ratio of length of foliage crown to total height) of Amur cork-tree and the other all stems with a DBH \geq 10 cm (called 'neighbors' hereinafter). I sampled two increment cores at a height of 50 cm (upper and opposite sides of the slope) from all Amur cork-tree and also from the other two greatest DBH stems (called 'neighborhood dominants') in each plot.

The circular plots were dominated by Japanese oak, Silver magnolia, and Siebold's beech, irrespective of

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their locations, i.e., hill-slope or streamside (Table 5-1); species preferring riparian locations, such as Japanese wingnut (*Pterocarya rhoifolia* Sieb. et Zucc.), Japanese walnut (*Juglans mandshurica* Maxim. var. *sachalinensis* (Miyabe et Kudo) Kitamura), and Japanese horse chestnut (*Aesculus turbinata* Blume), shared lower rates even in the streamside. The sites suited for these riparian species seemed to be limited because of narrow width of streams in this forest. Since most of the results did not differ substantially between the two locations, the data were combined, except in the case of the stem-age analysis.

I measured stem age and mean annual basal area increments for the previous 5 years (1989-1993, BAI: $\text{cm}^2 \text{ year}^{-1}$) from the increment cores of Amur cork-tree. The measurements of two cores were averaged. To eliminate the effects of the thinning operations, the period of 1994-1997 was excluded from the measurements for the BAI. I also estimated past diameters at 20 and 40 years-of-age, in order to clarify temporal changes in the diameter growth. The reason of selecting tree age of 20 years was that tall-tree species in coppice forests in this region achieve dominance over shrub species at this period of time (Kamitani 1993). Since most of Amur cork-tree (37 out of 45 stems) had been over 40 years at 1993, the age of 40 years was selected for comparison. The stem age and the BAI were also measured for the two neighborhood dominants; the past diameters were measured for the year corresponding to the ages of 20 and 40 years of Amur cork-tree (D_{20} and D_{40} , respectively).

In order to estimate relative dominance, relative stem sizes were calculated by dividing the stem size (DBH, H, and CR) of Amur cork-tree by the mean of those of the neighbors (RDBH, RH, and RCR, respectively). In the same way, relative past diameters (RD_{20} and RD_{40}) were calculated by dividing the D_{20} and D_{40} of Amur cork-tree by the mean of those of the two neighborhood dominants; the RD_{20} was then plotted against the RD_{40} . Furthermore, I compared the BAI of Amur cork-tree and the neighborhood dominants, by using the analysis of covariance with basal area as a covariate. I used multiple regression analysis, same as chapter 4, to examine the shading effects on basal area growth of Amur cork-tree. The effect is expressed by cumulative basal area (B) calculated for all the stems with greater DBH than the subject stem in the circular plot

5-3 Results

The stem ages of Amur cork-tree, determined by numbering the annual rings on the sampled cores, ranged between 33 and 60 years. I calculated the difference in stem-age between Amur cork-tree and the two neighborhood dominants in each circular plot in order to estimate the length of the established period of Amur cork-tree. The frequency

distributions of the difference at the two locations (hill-slope and streamside) are shown separately in Figure 5-1. The distributions were significantly different between the two locations ($P < 0.05$). On the hill-slope, the established period was relatively narrow with maximum differences of +12 years (Amur cork-tree was younger). Conversely, the period in the streamside was wider with maximum differences of +20 years. Furthermore the length of the established period seemed to be affected by the neighborhood species; the values of the difference were markedly greater in Silver magnolia- than Siebold's beech- dominate plots at the two locations.

Table 5-2 shows the mean DBH, H, and CR of Amur cork-tree, and their relative values (RDBH, RH, and RCR). The mean RDBH and RH were about 80% and significantly lower than 100% ($P < 0.05$); that is, Amur cork-tree tended to have smaller DBH and H values compared with its neighbors. The mean CR was about 25%, and its relative values (RCR) were also significantly lower than 100% (ca. 60%: $P < 0.05$).

In order to clarify temporal changes in the relative size of Amur cork-tree, I plotted each RD_{20} against the corresponding RD_{40} (Figure 5-2). The result showed that most of the RD_{20} s were smaller than 100% (34 out of 37 stems) and the maximum RD_{20} was below 130%, indicating that most of Amur cork-tree had already been under a suppressed condition at 20 years-of-age. On the other hand, there was only one stem of Amur cork-tree that had an RD_{40} greater than 100%; that is, most Amur cork-tree did not have the greatest diameter in the circular plot at present. Most of the plotted points on the figures were below the equivalent lines between RD_{20} and RD_{40} (26 out of 37 stems), indicating that the relative size of Amur cork-tree had decreased over the 20 years ($P < 0.05$).

Table 5-3 shows the mean annual basal area increments over the prior 5 years (BAI $\text{cm}^2 \text{ year}^{-1}$) of Amur cork-tree and the average of the two neighborhood dominants in the circular plot. The result of the analysis of covariance (with the basal area specified as a covariate) revealed that the mean BAI of Amur cork-tree was significantly lower than that of the two neighborhood dominants ($P < 0.05$).

Table 5-4 summarizes the effect of size (BA) and the shading (in terms of the cumulative basal area: B) on the BAI of the canopy stems of Amur cork-tree; the parameters in the regression (2) are shown. For comparison, results for the three dominant species in the same forest are also shown (Siebold's beech, Japanese oak, and Silver magnolia: after chapter 4). In the regression for Amur cork-tree, all the coefficients except for B_M (cumulative basal area of Silver magnolia) were significant ($P < 0.001$). The terms of the shading effects (B) in the regression for Amur cork-tree were mostly higher than those for the other three species, suggesting that Amur cork-tree is more sensitive to the shading. From the regressions

shown in Table 5-4, I calculated the BAI of Amur cork-tree and the other three species for the case without any suppression (i.e. all the $B = 0$). The result (Figure 5-3) indicated that Amur cork-tree would have a greater BAI than the other three species under a non-suppressed condition.

5-4 Discussion

The recruitment of Amur cork-tree, especially in the hill-slope, seemed to be restricted during a relatively short period following the major disturbance (Figure 5-1). Whereas coppice forestry seems to be suited for reproduction of shrub species with greater sprouting ability (Kamitani 1993), it is also characterized by a minimal number of larger- and soil-disturbed sites needed for regeneration of most of shade-intolerant species (Bormann and Likens 1979, Brokaw 1987, Whitmore 1989, Yamamoto 1989), including Amur cork-tree (Ishizuka and Sugawara 1986, Higo 1994). Such the sites seem to be quite limited until the forest reaches the old-growth stages (which takes at least 100 years: cf. Oliver 1981, Mitchell and Kirby 1989). Nevertheless the establishment period was slightly longer in the streamside (Figure 5-1), suggesting that disturbances are more frequent in the riparian area. The existence of broader streams, which should be expected to cause larger and more frequent disturbances, may be important for the stable occurrence of shade-intolerant species.

Most of Amur cork-tree in this coppice forest had smaller means of stem sizes (DBH, H, and CR) than their neighbors (Table 5-2). In general, trees with smaller size (especially in height) have distinct disadvantages in competition for light (Hara 1988, Weiner 1990), and the disadvantages are expected to be amplified in shade-intolerant species, which are strongly adapted to light-rich conditions (Bazzaz 1979). In the growth model, in fact, Amur cork-tree generally had higher coefficients for the shading effects (B) than those of the other three species (Table 5-4), indicating its greater sensitivity to suppression. Amur cork-tree could grow faster when not suppressed (Figure 5-3), however their actual growth rates in the research forest were significantly lower than those of their neighborhood dominants (Table 5-3). These results were consistent with the theoretical prediction, and with the previous studies conducted for northern American tree species (Loach 1970, Marks 1975, Bazzaz 1979, Hix and Lorimer 1990).

Furthermore the result indicated that the intensity of the shading vary considerably with species (Table 5-4). This seems to be as a result of the species-specific crown structures (cf. Horn 1971); the light transmission through deep crowns is expected to be less than that through shallow crowns (cf. Canham *et al.* 1994) and thus should produce stronger shading effects (Bi and Turvey 1996). In fact, Siebold's beech and Japanese oak, which develop deeper crowns

(Chapter 4), had a greater effect on the stem growth of Amur cork-tree, whereas Silver magnolia, which has shallower crown depth, had a lesser effect (Table 5-4). Such the differences seemed to also cause the difference in the length of the established period of Amur cork-tree between Siebold's beech- and Silver magnolia-dominate plot (Figure 5-1).

I conclude that the fate of individuals of Amur cork-tree varies considerably according to the surrounding components. In a mixed-species forest consisting mainly of species with shallower crowns, Amur cork-tree might be expected to have greater growth rates and lesser mortality. The species composition in a mixed-species stand, which is determined by several biotic and/or abiotic factors (Connell and Statyer 1977, Oliver 1981), plays a definitive role in the population dynamics of Amur cork-tree, and probably in that of many shade-intolerant species.

It has been pointed out that secondary forests are potentially dominated by entirely different communities depending on the past management regimes (Runkle 1985, Evans and Barkham 1992; Kamitani 1993). I consider that the declining trend of Amur cork-tree was closely related to the distinctive regeneration process of coppice forests. In heavy snowfall regions in central Japan, repetitive clear logging of trees, which is associated with coppice forestry, causes an increasing in the dominance of shrub species with greater ability of sprouting (Kamitani 1993). These species can rapidly regrow and share dominance (Kamitani 1993), promoting intensified competition in the initial stage following the logging. Essentially, shade-intolerant tree species should also show higher growth rates in the early stage, due to their ability to exploit light-rich conditions (cf. Bazzaz 1979). Nevertheless, the results showed that most of Amur cork-tree in this forest had already been suppressed at 20 years-of-age (i.e., $RD_{20} < 100\%$: Figure 5-2). I consider that they could not entirely utilize their sun-adopted photosynthetic ability in this forest, because of the dominance of the shrub species in the early stage of development. The lack of initial competitive advantages should cause a further decline in growth ('negative feedback loop': Hix and Lorimer 1990), and would result in further decreases in the relative tree size compared with their neighborhoods in the subsequent stages (Table 5-2, Figure 5-2).

This chapter revealed two important factors on the process of decline of shade-intolerant species: the relative growth rates in the initial stage, and species composition in the following stage. Some general features of coppice forests were closely associated with these factors, although the latter factor may be somewhat accidental. It would appear that the probability of extinction of shade-intolerant species increases in cases where these species lack early competitive advantages, and where their stands are dominated by species with deeper crown depths, as

seen here in the study forest. Whereas the decline may be compensated by its early seed-bearing (ca. 10 years: Mori 1991) with long-life seeds (more than 10 years: Mori 1991), increases in suppressed trees (and naturally, in dead trees) should reduce the production of seeds and supply for the seed-banks, and thereby adversely affect its stable reproduction. Because Amur cork-tree is dioecious and it tends to occur in forests as an occasional associate, existence of a mature stem should greatly influence its population dynamics (cf. Mizui and Kikuzawa 1990). Moreover, wide-ranging neglect of coppice forests, such as has been common in recent decades in Japan (cf. Nagaike and Kamitani 1997), may further the extinction process by causing a severe scarcity of sites for establishment. The installation of artificial disturbances (e.g., canopy gaps: Runkle 1985, Lorimer 1989) in forests is considered one means of encouraging the stable occurrence of shade-intolerant species.

Chapter 6

Effects of crown release on stem growth of species with different shade-tolerance *

6-1 Introduction

Many studies have suggested that competition for light is often one-sided; taller plants can limit the growth of smaller ones but not *vice versa* (e.g. Hara 1988, Weiner 1990). If neighbor crowns with taller or similar height were removed, a crown of a residual stem could receive a larger amount of radiation, which would then be available for photosynthesis. It is widely recognized that such a crown release (like a 'crown thinning': Smith *et al.* 1997) increases the growth of residual stems for many coniferous (Brix 1982, Lavigne 1988, Ginn *et al.* 1991) and broad-leaved tree species (Clark 1967, West and Osler 1995, Kerr 1996). However, most of the studies have been conducted in an even-aged monoculture and/or for the most dominant species in a forest; few studies have compared growth responses among species (Marquis and Ernst 1991). I consider that same intensity of crown release should have considerably different effects among species; less shade-tolerant species might have a stronger response to the intensive release than more shade-tolerant species because of its ability to use the high light intensity (cf. Marks 1975, Bazzaz 1979).

In this chapter, I compare three or four year effects of crown release on stem growth among four broad-leaved tree species: Siebold's beech (*Fagus crenata* Blume), Japanese oak (*Quercus crispula* Blume), Silver magnolia (*Magnolia obovata* Thumb.) and Painted maple (*Acer mono* Maxim.). All of these species are representative of secondary forests in

heavy snowfall regions in central Japan. The light utilization patterns differs among the four species, judging from their photosynthetic performance (Koike 1985). Japanese oak and Silver magnolia, which are regarded as intermediate shade-tolerant species, seemed to be able to use the high light intensity more effectively than the more shade-tolerant Siebold's beech and Painted maple.

Are the differences in growth responses among the species consistent with the theoretical consideration? I first examined if the crown release resulted in improvements in growth rates for the four species. I then inspected whether or not the intensity of crown release would affect the growth rates and the differences in growth responses among the four species (Yoshida and Kamitani 1998).

6-2 Materials and methods

During the autumn of 1992 and 1993, part of the study forest (area 1.5 ha: Table 6-1) was thinned and 26 artificial canopy gaps were created. The projected area of the canopy gaps (GAPA) ranged from 5.4 to 376.8 m² and was used as an indicator of the intensity of crown release. I selected 31-47 stems both neighboring and not neighboring these canopy gaps (defined as 'released stems' and 'non-released stems', respectively) for each of the four species (Table 6-2). The mean diameter at breast height (DBH) was not significantly different between the released and non-released stems for all of the species ($P > 0.05$, Mann-Whitney's U-test). The data were analyzed on the basis of a stem, which was defined as a stool grown out below the breast height. Because light intensity around a gap has a directional gradient (i.e. it should decrease from north to south in the northern hemisphere, c.f. Canham 1988), directional differences may lead to significant effects on stem growth of the four species. However, the preliminary analysis have appeared that the directional differences have no impact on the current results, so I did not address the effects in the following analysis.

I sampled two cores from a stem at a height of 50 cm and measured the annual radial increments during the period from 1990 to 1996. The two radii measurements were averaged and used for analysis in terms of relative growth rates for basal area ($RGR_{BA} \% \text{ year}^{-1}$). The period was divided into two parts: 'before the release' (1990-1992 or 1990-1993) and 'after the release' (1993-1996 or 1994-1996) according to the crown release year. The annual RGR_{BA} was averaged for each range of the period; I believe that the difference in length of the averaging period (i.e., three or four years) will have a relatively minor effect on the results, because changes in the annual RGR_{BA} were generally gradual in each period (Figure 6-1). Furthermore, I calculated the rate of increase in RGR_{BA} by dividing the mean RGR_{BA} after the release by that before the release.

In order to clarify if the intensity of the crown release would influence the stem growth, the rate of

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increase in RGR_{BA} were compared among the three GAPA-classes (i.e. $0 < GAPA \leq 50 \text{ m}^2$, $50 < GAPA \leq 150 \text{ m}^2$, $150 \text{ m}^2 < GAPA$). I also calculated the standardized partial correlation coefficients of the GAPA in relation to the RGR_{BA} . Differences in the growth responses among species were investigated by comparing the relation between the RGR_{BA} and the basal area in the same level of the GAPA-class, with the analysis of covariance (ANCOVA).

6-3 Results

Figure 6-1 shows the 8-year sequences (4 years both before and after the crown release) of the mean annual RGR_{BA} (% year⁻¹) of the four species. The mean RGR_{BA} during the years before and after the crown release are shown in Table 6-3. For the non-released stems, the mean annual RGR_{BA} of Siebold's beech, Japanese oak and Painted maple decreased gradually with time, while those of Silver magnolia remained stable; the decreases of the former three species were significant (Table 6-3: $P < 0.01$, Wilcoxon's matched-pairs signed-ranks test). For the released stems, it appeared that the mean annual RGR_{BA} had been improved for the four species, however only Silver magnolia showed a significant increase after the crown release (Table 6-3, $P < 0.001$).

I investigated whether or not the intensity of the crown release would relate to the stem growth of the four species. Figure 6-2 shows scatterplots of the rate of increase in RGR_{BA} in relation to the basal area for the released stems in each GAPA-class. There were not any significant correlation between the two ($P > 0.05$), suggesting that the rates of increase were not influenced by stem size. For Japanese oak and Silver magnolia, differences in the rate of increase among the GAPA-classes were significant ($P < 0.05$, Kruskal-Wallis test); stems neighboring larger gaps tended to have higher growth rates. In contrast, the differences among the GAPA-classes were not significant for Siebold's beech and Painted maple ($P > 0.05$).

Table 6-4 shows the standardized partial regression coefficients (β) of the GAPA in relation to the mean RGR_{BA} after the release (with an independent variable, basal area) for the four species. The correlation was significant for Japanese oak and Silver magnolia with positive β values ($P < 0.05$), indicating that stems with larger GAPA had a higher RGR_{BA} . In contrast, the RGR_{BA} of Siebold's beech and Painted maple did not significantly correlate with the GAPA, with a positive but low β value in Painted maple ($P > 0.05$), and a rather negative value in Siebold's beech ($P > 0.05$); these results indicate that the intensity of the crown release did not affect the RGR_{BA} for the latter two species.

Figure 6-3 shows the relationships between the mean RGR_{BA} after the release and the basal area of the released stems of the four species at the three different GAPA-classes. At $GAPA \leq 50 \text{ m}^2$, Japanese

oak had a significantly lower RGR_{BA} than Siebold's beech and Silver magnolia ($P < 0.05$, ANCOVA). This lower RGR_{BA} for Japanese oak, however, did not occur in the larger GAPA-classes (i.e. $GAPA > 50 \text{ m}^2$). On the other hand, the RGR_{BA} of Silver magnolia was significantly higher than those of Siebold's beech and Painted maple at the level of $150 \text{ m}^2 < GAPA$ ($P < 0.05$).

6-4 Discussion

As has been shown in many previous studies (e.g. Clark 1967, Marquis and Ernst 1991, West and Osler 1995, Kerr 1996), crown release enhanced stem growth for the four study species (Figure 6-1, Table 6-3). However, my results revealed that the effects of intensive crown release were different among the species; the RGR_{BA} of Japanese oak and Silver magnolia tended to increase with increases in the GAPA, while that of Siebold's beech and Painted maple were not related to the GAPA (Figure 6-2, Table 6-4). I consider differences among species are closely related to the characteristics of their photosynthetic light use. Obviously, intensive crown release increases total amount of sunlight available for the residual crowns, especially in direct sunlight. Both the light saturation and light compensation points were quite low in Siebold's beech and Painted maple, but were relatively high in Japanese oak and Silver magnolia (Koike 1985), suggesting that the latter two species can use high light intensity more effectively than the former two species (cf. Marks 1975, Bazzaz 1979). It has been showed that growth of shade-tolerant species approaches an asymptote with increases in exposed crown area, whereas that of intolerant species does not (Hix and Lorimer 1990). These results are consistent with both their theory and data. It appears that less shade-tolerant species exhibit greater growth rates relative to the intensity of crown release than tolerant species. Although this was not investigated in this chapter, more intolerant 'pioneer' species with a higher light saturation point should be also suitable for growth rate in intensive crown release.

The current results reveal that an intensive thinning to improve stem growth rates is effective for less shade-tolerant species (Japanese oak and Silver magnolia), but not as much for shade-tolerant species (Siebold's beech and Painted maple). The differences in intensity of thinning might result in a difference in the species with higher growth rates in a mixed-species forest; an intensive crown release could make stem growth of less tolerant species to be similar to or at a higher level than that of tolerant species (Figure 6-3).

Chapter 7

General Discussion

The observed stem growth patterns in a mixed secondary forest were decided by species-specific characteristics of photosynthetic light use (i.e.

shade-tolerance) and competitive interactions among species. The interspecific competition was asymmetry; shade-tolerant species was superior to less-tolerant species. Clearly, shade-tolerant species would be resistible to suppression, whereas less tolerant species would not. In fact, shade-intolerant Amur cork-tree was most responsive to asymmetric competition (Yoshida and Kamitani 1999, Chapter 5) in this study. On the other hand, shade-tolerant Siebold's beech produced most pronounced shading effect (Yoshida and Kamitani 1997, 2000, Chapter 3, 4), seemed to be caused by its own ability to maintain deep crowns. In contrast, Silver magnolia (with relatively shallower crown) did not offer the effect on the any other species (Yoshida and Kamitani 2000, Chapter 4). Species characteristics of shade-tolerance might effect its own arrangement of the foliage crown (Horn 1971), and thereby closely related to its species-specific intensity of shading effects to neighbors. Since less-tolerant species tend to naturally decrease their crown through death of lower branches, they might gradually lessen the effect (Yoshida and Kamitani 1997, Chapter 3). The tendency would be further accelerated by suppression from neighbors.

On the basis of competitive interactions among species, I can explain the conventional model of stand dynamics in which dominance eventually shifts to shade-tolerant species in stand development (Bormann and Likens 1979, Burrows 1990). The analyses of Beech-Oak mixed stands (Yoshida and Kamitani 1997, Chapter 3) clearly indicate that shade-tolerant Siebold's beech eventually increase its dominance as stand mature against Japanese oak. In a similar way, a shade-intolerant Amur cork-tree, would be declined and may be excluded from the secondary forest, because of its higher sensitiveness to suppression (Yoshida and Kamitani 1999, Chapter 5). Since mixture with different species may result in concomitant differences in size and growth of each species, it have been strongly indicated that different combinations of mixture may lead each component species to have a different degree of dominance in secondary succession (cf. Nowak 1996). Mixture with tolerant species would reduce the dominance of less-tolerant species, unless the latter had growth advantage in early stage of stand development (as seen in Silver magnolia; Yoshida and Kamitani 2000, Chapter 4). In contrast, less-tolerant species could maintain dominance if they were in mixture with another less-tolerant species (Yoshida and Kamitani 2000, Chapter 4).

On the other hand, crown release or thinning obviously increases total amount of available sunlight, and usually enhance growth of residual trees (e.g. Clark 1967, Marquis and Ernst 1991, West and Osler 1995, Kerr 1996). This is true for the species concerned in this study, however effects of intensity of the release were different among species; the differences were consistent with theoretical

prediction that derived from their photosynthetic characteristics of light-use (Yoshida and Kamitani 1998, Chapter 6). Stem growth of less shade-tolerant species, Japanese oak and *Silver magnolia*, increased with cutting intensity (in terms of the neighbor gap area), whereas those of shade-tolerant species, Siebold's beech and Painted maple, were not related to the intensity.

Implications for managing stands as mixture

Many articles have suggested that thinning would be appropriate for maintaining or enhancing mixture (Hart 1995, Smith *et al.* 1997, Tappeiner *et al.* 1997). However, very few attention were received for thinning with such objectives. The selection criteria for residual trees in thinning have been conventionally on the point of view of timber production i.e., quality and vigor of trees (cf. Yanagisawa 1981, Evans 1992, Nyland 1996). Although they are fundamentally important, I here propose two substantial criteria for maintaining or enhancing complexity in forests. The first, intensity of thinning should be changed by the target (i.e. residual) species; their characteristics of photosynthetic light use should be taken into account. To maintain mixture of species, thinning should be conducted to enhance growth of less-tolerant species in the stand. Wide-ranging neglect of secondary forests, such as has been common in recent decades in Japan (cf. Nagaike and Kamitani 1997), may further the extinction process of intolerant species in mixed stands. The installation of artificial disturbances (e.g., canopy gaps: Runkle 1985, Lorimer 1989) is considered one means of encouraging the stable occurrence of shade-intolerant species. Since responses to disturbances were stronger in less-tolerant species (Yoshida and Kamitani 1998, Chapter 6), we should introduce crown release thinning (Singer and Lorimer 1997) to enhance growth of less-tolerant species. The attention is to ensure high light intensity for less-tolerant species through maintaining crown stratification, so that less-tolerant species forming an upper canopy to prevent tolerant species throughout the stand development (cf. Evans 1982 Matthews 1989). In Europe, where mixture of *Fagus* and *Quercus* are common, to prevent *Fagus* becoming dominant over *Quercus* is empirically recommended to maintain mixture (Evans 1982, Matthews 1989). The second, intensity of thinning should be changed according to the surrounding components; shade-tolerant species adjacent to the target less-tolerant species should be removed (Yoshida and Kamitani 1999, 2000, Chapter 4 and 5). When less-tolerant species is aimed to manage, 'free-growth' where trees grow without overlapping any other neighboring crowns by repetitive thinning may be also recommended (Jobling and Pearce 1977). In addition, thinning at an early stage is essential; it should be begun before the suppression effect of shade-tolerant species become

apparently (at about 20 years-old in the study forest: Chapter 4). The delay of thinning may diminish thinning effects for less-tolerant species, because their crowns tend to be decreased as stand development (Yoshida and Kamitani 2000, Chapter 4).

I note again that these thinning should open the canopy (i.e. crown thinning) to favor the crown development of residual trees so that they can obtain higher light intensity (crown thinning; Evans 1984, Nyland 1996). Unless intensive cutting (which bring about more diverse light condition) is introduced, developments of forests toward irregular and stratified structure would not be accelerated (DeBell *et al.* 1997). Low thinning, which has been mainly adopted in practice in Japan, is thus less profitable for the objective (cf. Marquis and Ernst 1991, Miguchi 1996). I believe that thinning on the basis of such criteria would accelerate the development of secondary stands toward more complex structure, and desirable for the multi-purpose forestry.

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* The title is tentatively translated in English by the author.

Table 2-1. Density and basal area of stems with DBH \geq 10 cm for the major component species in the study plots (total 2.0 ha).

Species	Common name	Density (ha ⁻¹)	BA (m ² ha ⁻¹)
<i>Fagus crenata</i>	Siebold's beech	353	10.87
<i>Quercus crispula</i>	Japanese oak	269	8.58
<i>Magnolia obovata</i>	Silver magnolia	104	4.78
<i>Quercus serrata</i>	Konara oak*	110	4.11
<i>Acer mono</i>	Painted maple	85	2.30
<i>Aesculus turbinata</i>	Japanese horse chestnut	5	0.45
<i>Acanthopanax sciadophylloides</i>	Koshiabura*	23	0.45
<i>Prunus sargentii</i>	Sargent cherry	13	0.36
<i>Castanea crenata</i>	Japanese chestnut	5	0.28
<i>Kalopanax pictus</i>	Prickly castor-oil tree	2	0.26
<i>Betula grossa</i>	Japanese cherry birch	4	0.24
<i>Tilia maximowicziana</i>	Ohba-bodaijyu linden*	5	0.23
<i>Acer japonicum</i>	Downy Japanese maple	17	0.17
<i>Pterocarya rhoifolia</i>	Japanese wingnut	4	0.15
<i>Juglans mandshurica</i>	Japanese walnut	3	0.14
<i>Phellodendron amurense.</i>	Amur cork-tree	5	0.12
Total		1026	33.66

The Latin names are followed by Ohwi and Kitagawa (1983).

* not found an appropriate common name.

Table 3-1. Descriptions of the study plots.

Plot No.		1	2	3	4	5
Estimated age:	yr.	37	43	55	61	62
Plot area:	ha	0.10	0.10	0.12	0.10	0.10
Mean DBH:	cm	16.0	18.6	24.0	25.9	26.8
Stem density:	ha ⁻¹	1320	1060	642	590	420
Siebold's beech	%	59.8 (1.49)	38.7 (1.17)	37.7 (1.21)	35.6 (1.31)	31.1 (1.08)
Japanese oak	%	30.3 (1.25)	32.1 (1.38)	33.8 (1.49)	27.1 (1.78)	26.2 (1.43)
Clump density	ha ⁻¹	980	810	480	410	320
Siebold's beech	%	54.1	44.4	40.0	39.0	37.5
Japanese oak	%	32.7	32.1	30.4	22.0	21.9

Only canopy stems were examined. The term stem means a sprout grown out below breast height, clumps are groups of stems that arise from the same individual root (see text). Mean DBH were calculated by stem data. Figures in parentheses are mean number of stems per clump.

Table 3-2. Average \pm S.D. of basal-area (BA), exposed-crown area (ECA), crown depth (CD), height (H) and relative height (RH) for Siebold's beech and Japanese oak in the five plots.

(a) per stem

Plot No.		n	BA (cm ²)	ECA (m ²)	CD (m)	H (m)	RH (%)
1	Beech	79	240 \pm 160	7.2 \pm 4.6	3.4 \pm 0.7	13.0 \pm 2.2	101.1 \pm 8.4
	Oak	40	193 \pm 122	6.1 \pm 5.1	2.9 \pm 0.6	12.7 \pm 2.1	98.8 \pm 9.7
2	Beech	41	292 \pm 147	11.9 \pm 8.2	6.3 \pm 2.0	16.3 \pm 2.5	101.6 \pm 15.5
	Oak	34	289 \pm 130	8.4 \pm 5.4	5.2 \pm 1.5	14.9 \pm 2.3	97.4 \pm 13.8
3	Beech	29	560 \pm 283	19.9 \pm 11.8	8.6 \pm 1.8	18.1 \pm 1.6	99.9 \pm 9.1
	Oak	26	350 \pm 141	11.8 \pm 7.8	7.2 \pm 2.1	17.2 \pm 1.5	98.2 \pm 9.2
4	Beech	23	821 \pm 413	22.1 \pm 15.9	9.5 \pm 1.8	18.7 \pm 2.6	99.7 \pm 10.4
	Oak	18	398 \pm 165	12.6 \pm 4.8	6.2 \pm 2.6	17.4 \pm 1.8	98.3 \pm 8.7
5	Beech	13	861 \pm 335	30.7 \pm 18.1	9.4 \pm 1.9	19.6 \pm 1.8	100.8 \pm 3.7
	Oak	10	534 \pm 233	16.7 \pm 11.0	5.3 \pm 1.1	18.8 \pm 1.3	97.3 \pm 5.7

(b) per clump

Plot No.		n	BA (cm ²)	ECA (m ²)	CD (m)	H (m)	RH (%)
1	Beech	54	351 \pm 290	10.5 \pm 7.3	3.6 \pm 0.8	13.1 \pm 2.2	101.2 \pm 9.0
	Oak	25	309 \pm 242	9.8 \pm 8.1	3.2 \pm 0.8	12.9 \pm 2.2	100.4 \pm 9.1
2	Beech	39	316 \pm 155	12.8 \pm 8.8	6.5 \pm 2.0	16.4 \pm 2.5	101.7 \pm 16.6
	Oak	23	476 \pm 300	13.1 \pm 9.9	5.6 \pm 1.6	15.7 \pm 1.7	98.4 \pm 10.4
3	Beech	24	653 \pm 317	23.4 \pm 12.6	8.9 \pm 1.8	18.4 \pm 1.5	99.3 \pm 6.8
	Oak	15	556 \pm 281	18.1 \pm 8.8	8.6 \pm 2.0	17.7 \pm 1.3	97.8 \pm 8.0
4	Beech	18	957 \pm 755	26.8 \pm 25.7	9.7 \pm 2.6	18.8 \pm 2.7	100.1 \pm 11.2
	Oak	9	707 \pm 565	22.3 \pm 14.7	7.4 \pm 3.0	17.8 \pm 1.9	98.5 \pm 9.6
5	Beech	12	940 \pm 397	33.3 \pm 22.9	9.3 \pm 2.0	19.6 \pm 1.9	101.2 \pm 5.5
	Oak	5	934 \pm 607	30.5 \pm 20.6	5.5 \pm 1.4	18.5 \pm 1.7	97.3 \pm 9.2

Asterisks indicate averages differ significantly between the two species; U-test

* $P < 0.05$, ** $P < 0.01$.

Table 3-3. Parameters of the linear regression formula ; (a) $DBH = a + b \times H$ and (b) $DBH = a + b \times CD$ for the stems of Siebold's beech and Japanese oak in the five plots.

(a) DBH-H

Plot No.	Siebold's beech					Japanese oak				
	n	a	b	R ²		n	a	b	R ²	
1	79	-2.61	1.48	0.337	***	40	2.37	1.09	0.236	**
2	41	-7.52	1.609	0.644	***	34	-5.30	1.58	0.445	***
3	29	-30.01	3.08	0.487	***	26	-6.89	1.61	0.336	**
4	23	-18.08	2.64	0.692	***	18	-9.57	1.85	0.409	*
5	13	-11.96	2.27	0.425	*	10	-40.43	3.53	0.548	*

(b) DBH-CD

Plot No.	Siebold's beech					Japanese oak				
	N	a	b	R ²		n	a	b	R ²	
1	79	4.15	3.62	0.211	***	40	7.04	2.74	0.143	*
2	41	11.42	1.15	0.202	**	34	14.86	0.74	0.065	NS
3	29	7.00	2.25	0.285	**	26	17.07	0.50	0.059	NS
4	23	11.87	2.11	0.368	**	18	18.69	0.53	0.064	NS
5	13	3.02	3.34	0.445	*	10	13.05	2.39	0.202	NS

Asterisks indicate regression is significant; F-test * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. NS refers to not significant.

Table 3-4. Mean annual relative growth rates for basal-area (RGR_{BA} , % year⁻¹) during recent 5 years for Siebold's beech and Japanese oak in plot 3.

	per stem		per clump	
Siebold's beech	3.32 ± 0.93		3.41 ± 0.92	
Japanese oak	1.99 ± 0.68	***	1.97 ± 0.59	***

Averages differ significantly between the two species; U-test *** $P < 0.001$.

Table 3-5. Standardized partial regression coefficients (β) of multiple regression formula; $RGR_{BA} = a + b \times (ECA) + c \times (RH)$ for Siebold's beech and Japanese oak in plot 3.

Parameters	Siebold's beech		Japanese oak	
	$R^2=0.48^{***}$		$R^2=0.32^{**}$	
	β	p	β	p
Exposed-crown area (ECA)	0.5094	0.03	0.1275	0.46
Relative height (RH)	0.2276	0.31	0.5346	0.00

Asterisks indicate that regression was significant; F-test ** $P < 0.01$, *** $P < 0.001$.

Table 4-1. Description of the six study plots with three combinations of dominant species.

Plot Name	Beech-Oak		Beech-Magnolia		Oak-Magnolia		
	No.	1	2	3	4	5	6
Estimated age (yr.)		55	51	60	57	52	48
Plot area (ha)		0.16	0.14	0.18	0.14	0.16	0.16
Stem density (ha ⁻¹)		844	921	811	850	888	950
Basal area (m ² ha ⁻¹)		33.7	32.7	36.2	36.3	36.7	35.2
Siebold's beech		(41.8)	(39.3)	(48.3)	(46.8)	(0.0)	(0.0)
Japanese oak		(21.4)	(21.6)	(12.5)	(1.5)	(50.9)	(48.5)
Silver magnolia		(13.4)	(10.1)	(25.7)	(29.2)	(16.8)	(17.6)

Only stems with DBH \geq 10cm were examined. Figures in parentheses are percentages of basal area for each species.

Table 4-2. Mean \pm S.D. of DBH, height (H) and crown depth (CD) of the three species in the six study plots.

Plot	No.	Spp.	n	DBH (cm)	H (m)	CD (m)
Beech-Oak	1	Beech	46	23.8 \pm 7.9 **	15.8 \pm 3.5	8.0 \pm 2.3 *
		Oak	39	18.8 \pm 5.0	15.3 \pm 3.5	7.0 \pm 2.3
	2	Beech	51	22.6 \pm 8.1 *	15.8 \pm 2.5	8.7 \pm 2.6 **
		Oak	39	18.4 \pm 4.8	15.7 \pm 2.5	7.0 \pm 1.7
Beech- Magnolia	3	Beech	67	23.0 \pm 9.4	15.8 \pm 3.2	6.9 \pm 2.4 **
		Magnolia	37	23.2 \pm 6.0	16.6 \pm 3.7	5.5 \pm 1.8
	4	Beech	50	24.3 \pm 9.3	16.3 \pm 3.3	8.3 \pm 2.9 **
		Magnolia	33	25.7 \pm 4.3	17.1 \pm 2.4	5.2 \pm 2.1
Oak- Magnolia	5	Oak	75	21.6 \pm 6.3	15.7 \pm 2.9	7.6 \pm 2.3 ***
		Magnolia	22	23.0 \pm 6.6	16.4 \pm 2.4	5.7 \pm 2.0
	6	Oak	66	21.9 \pm 6.8	16.7 \pm 2.0	7.3 \pm 2.4 *
		Magnolia	21	23.8 \pm 5.8	17.0 \pm 2.0	5.9 \pm 1.9

Asterisks indicate means differ significantly between the two species that co-occurred in each plot;

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ (Mann-Whitney's U-test)

Table 4 - 3. Parameters of the multiple regression formula;

$$BAI = BA[a_0 - a_1 \ln(BA) - a_2 B_B - a_3 B_Q - a_4 B_M - a_5 B_{ot}] \text{ for the three species.}$$

	n	R ²	Constant	ln (BA)	B _F	B _Q	B _M	B _O
Siebold's beech	54	0.799	2.890 ***	1.870 ***	0.057	0.064 *	-0.055	-0.004
Japanese oak	56	0.699	1.720 **	0.776	0.122 *	0.022	-0.020	0.163 **
Silver magnolia	52	0.866	3.138 ***	2.085 ***	0.078 **	0.005	-0.017	0.044 *

Asterisks indicate the coefficient is significant; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 4 - 4. Parameters of the multiple regression formula;

$$CD = a_0 + a_1 BA - a_2 B_B - a_3 B_Q - a_4 B_M - a_5 B_{ot} \text{ for the three species.}$$

	n	R ²	(BA)	B _F	B _Q	B _M	B _O
Siebold's beech	54	0.208	0.408 **	-0.365 **	-0.049	0.168	0.097
Japanese oak	56	0.133	0.037	0.386 **	0.107	-0.090	-0.133
Silver magnolia	52	0.230	0.579 ***	-0.062	-0.051	-0.035	-0.034

Asterisks indicate the coefficient is significant; ** $P < 0.01$, *** $P < 0.001$.

Table 5-1. The ratio of basal area of major component species in the circular plots at the two locations.

	Hill-slope	Streamside
Japanese oak	26.3	22.0
Silver magnolia	16.7	11.2
Siebold's beech	13.0	12.5
Others	44.0	54.3

Table 5-2. Mean \pm S.D. of stem sizes and the relative sizes of Amur cork-tree in the study forest.

DBH (cm)	17.6	\pm	4.3
Relative DBH (%)	83.3	\pm	30.8
	(73.9 – 93.1)		
Height (m)	11.6	\pm	2.7
Relative height (%)	81.6	\pm	18.2
	(75.3 – 87.8)		
Crown ratio (%)	26.2	\pm	7.2
Relative crown ratio (%)	58.7	\pm	24.0
	(50.4 – 66.9)		

The relative sizes were calculated by dividing the stem size of Amur cork-tree by the mean size of the neighbors in the circular plot. Numerals in parentheses are 95 % C.I. of the each relative size.

Table 5-3. Comparison of the mean annual basal-area increments (BAI: $\text{cm}^2 \text{ year}^{-1}$) between Amur cork-tree and mean of the two neighborhood dominants.

	Amur cork-tree	Dominants
Mean BAI ($\text{cm}^2 \text{ year}^{-1}$)	8.9 \pm 4.1	25.9 \pm 10.9
Mean basal area (cm^2)	261 \pm 136	745 \pm 333
ANCOVA	F = 7.31 (P = 0.008)	

Table 5 - 4. Parameters of the multiple regression formula:

$$BAI = BA[a_0 - a_1 \ln(BA) - a_2 B_B - a_3 B_Q - a_4 B_M - a_5 B_{ot}]$$

for the canopy stems of Amur cork-tree and three dominant species in the study forest.

	n	R ²	Constant	ln (BA)	B _F	B _Q	B _M	B _O
Amur cork-tree	31	0.987	2.911 ***	1.717 ***	0.131 ***	0.123 ***	0.043	0.100 ***
Siebold's beech [†]	54	0.799	2.890 ***	1.870 ***	0.057	0.064 *	-0.055	-0.004
Japanese oak [†]	56	0.699	1.720 **	0.776	0.122 *	0.022	-0.020	0.163 **
Silver magnolia [†]	52	0.866	3.138 ***	2.085 ***	0.078 **	0.005	-0.017	0.044 *

Asterisks indicate the coefficient is significant; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. [†] after Chapter 4.

Table 6 - 1. Description of the study forest.

Range of tree age	50 – 65
Mean DBH ± SD (cm)	21.3 ± 8.0
Stem density (ha ⁻¹)	969
(%) Siebold's beech	38.9
Japanese oak	22.0
Silver magnolia	13.9
Painted maple	11.8

Table 6-2. Description of stems examined in this study.

Species		<i>n</i>	Mean DBH ± SD (cm)	Range of the neighboring gap area (m ²)
Siebold's beech	released	47	27.9 ± 8.1	6.9 - 376.8
	non-released	47	28.7 ± 7.8	0.0
Japanese oak	released	44	23.2 ± 6.9	5.4 - 376.8
	non-released	44	21.8 ± 7.0	0.0
Silver magnolia	released	45	26.0 ± 5.9	8.7 - 355.2
	non-released	41	26.4 ± 5.8	0.0
Painted maple	released	31	25.2 ± 7.1	6.9 - 376.8
	non-released	31	24.2 ± 7.1	0.0

Table 6-3. Mean relative growth rates for basal area (RGR_{BA}; % year⁻¹) of (A) released, and (B) non-released stems of the four species, during the years before and after the crown release.

Species		<i>n</i>	Mean RGR _{BA} ± SD (% year ⁻¹)		% of stems that increased the RGR _{BA}	<i>P</i>
			Before the release	After the release		
Siebold's beech	(A)	47	2.52 ± 0.76	2.56 ± 0.71	51.1	0.254
	(B)	47	2.92 ± 1.14	2.68 ± 0.98	29.3	0.000
Japanese oak	(A)	44	2.89 ± 0.85	2.97 ± 0.70	54.8	0.305
	(B)	44	3.18 ± 1.08	2.89 ± 0.85	29.3	0.002
Silver magnolia	(A)	45	2.46 ± 0.70	2.74 ± 0.73	87.8	0.000
	(B)	41	2.61 ± 0.58	2.65 ± 0.66	51.4	0.332
Painted maple	(A)	31	2.65 ± 0.81	2.73 ± 0.63	60.7	0.254
	(B)	31	2.83 ± 0.92	2.43 ± 0.77	16.1	0.000

P values are from a Wilcoxon's matched-pairs signed-ranks test.

Table 6-4. Standardized partial regression coefficients (β) of the GAPA in relation to the RGR_{BA} after the release (with an independent variable, basal area) for the released stems of the four species.

Spp.	<i>n</i>	β	<i>P</i>
Siebold's beech	47	- 0.1056	0.1741
Japanese oak	44	0.4817	0.0017
Silver magnolia	45	0.2583	0.0358
Painted maple	31	0.1617	0.1586

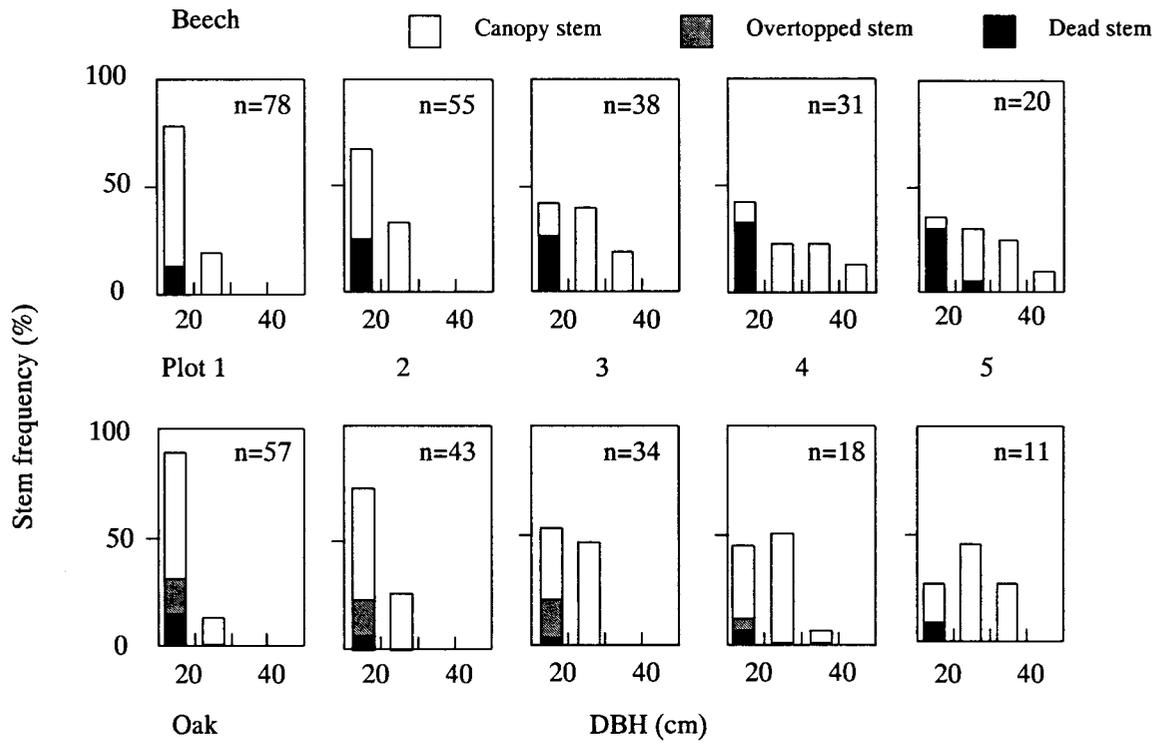


Fig. 3-1. DBH-class distribution of Siebold's beech and Japanese oak in the five plots.

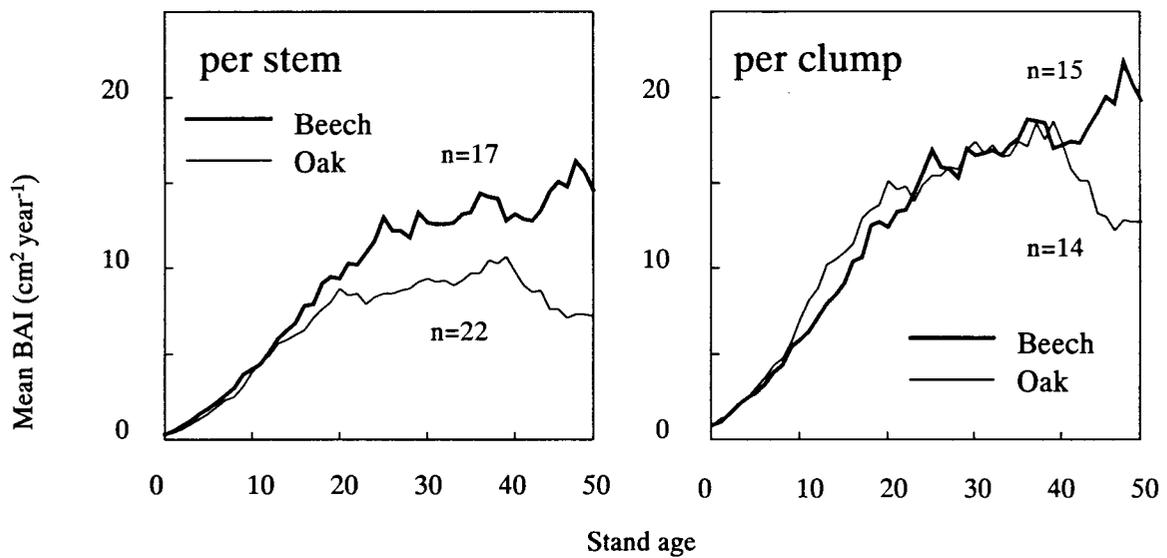


Fig. 3-2. Change in mean annual basal area increments (BAI: cm² year⁻¹) during 50 years for Siebold's beech and Japanese oak in Plot 3.

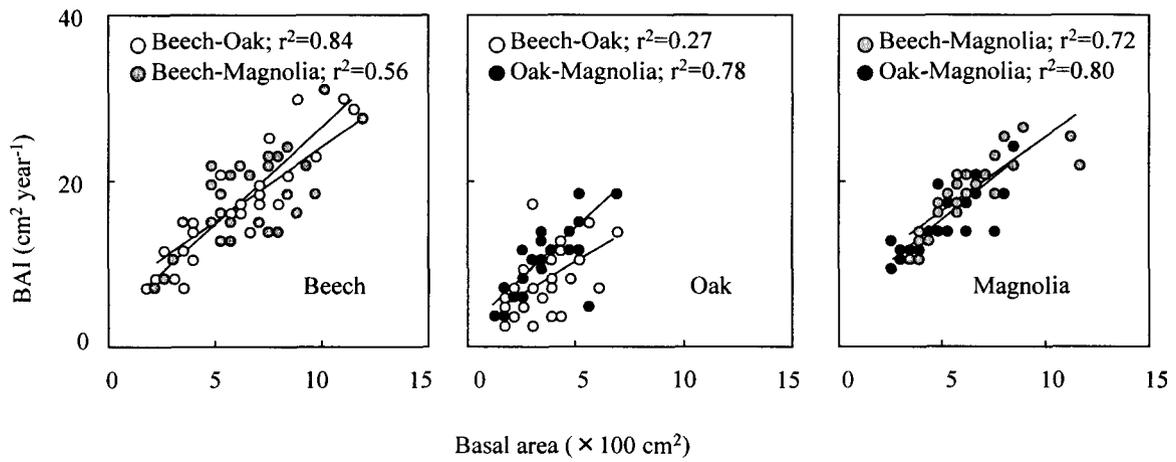


Fig. 4-1. Mean basal area increments over the most recent 5 years (BAI: cm² year⁻¹) as a function of basal area at the beginning of the period for Siebold's beech, Japanese oak and Silver magnolia in the study plots with different combinations of dominant species. The solid lines show the fit to the data.

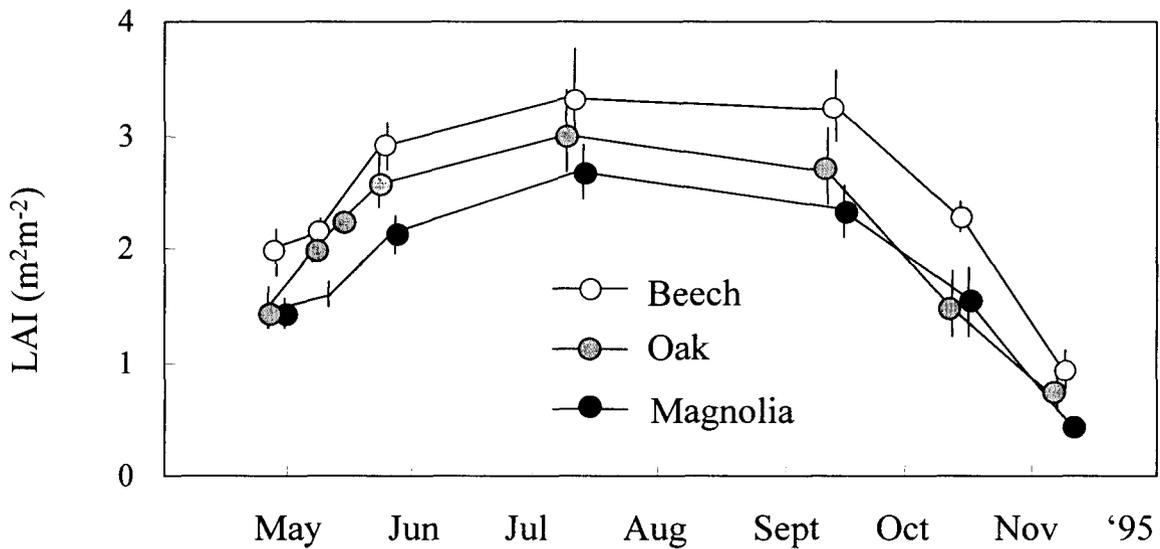


Fig. 4-2. Seasonal changes in the leaf area index (LAI), estimated by using hemispherical photographs, of Siebold's beech, Japanese oak and Silver magnolia in the study plots. Error bars are S.D of the mean.

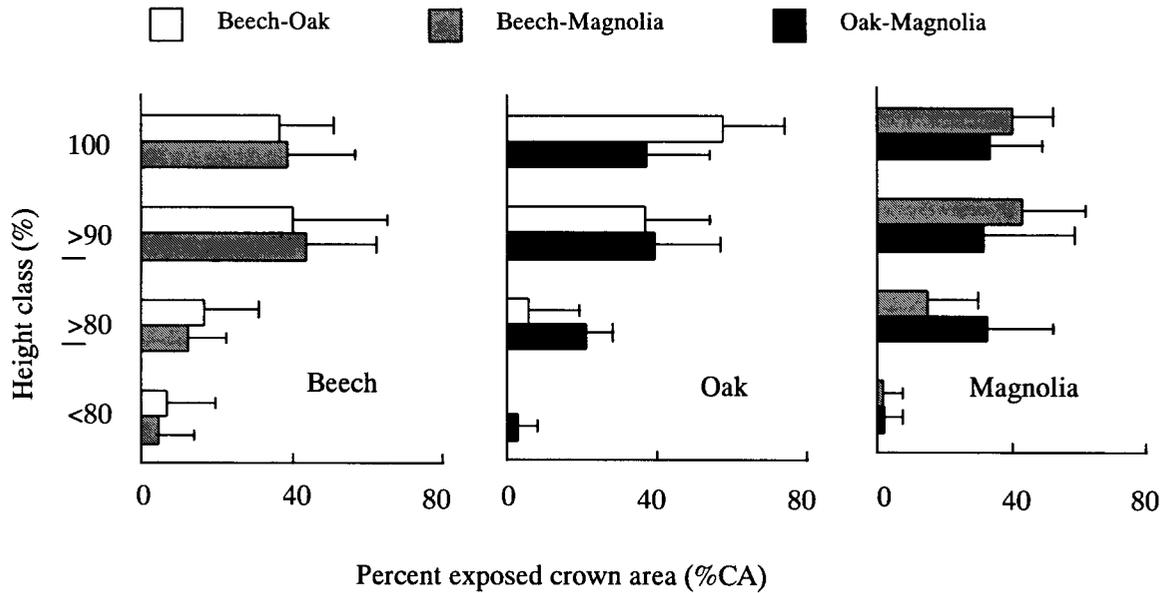


Fig. 4-3. Percent exposed crown area (%CA) of height class of branches for Siebold's beech, Japanese oak and Silver magnolia in the study plots with different combinations of dominant species. Height class indicates relative height of foliage tuft (each of which has its own exposed crown) compared to the top height of the stem. Error bars are S.D of the mean.

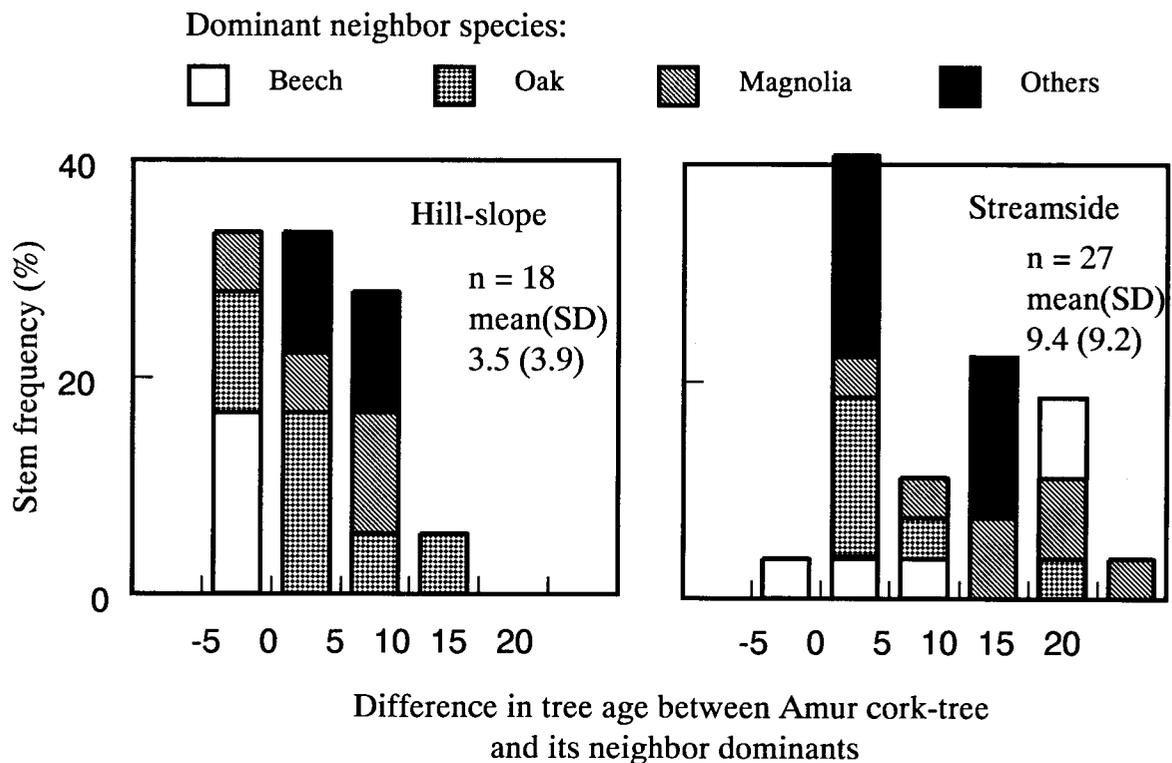


Fig. 5-1. Distributions of the difference in the estimated tree age between Amur cork-tree and the two neighborhood dominants in the two locations. The difference shown as a plus value indicates Amur cork-tree is younger. Patterns in the bars indicate the most dominant species (in terms of basal area) in the circular plot:

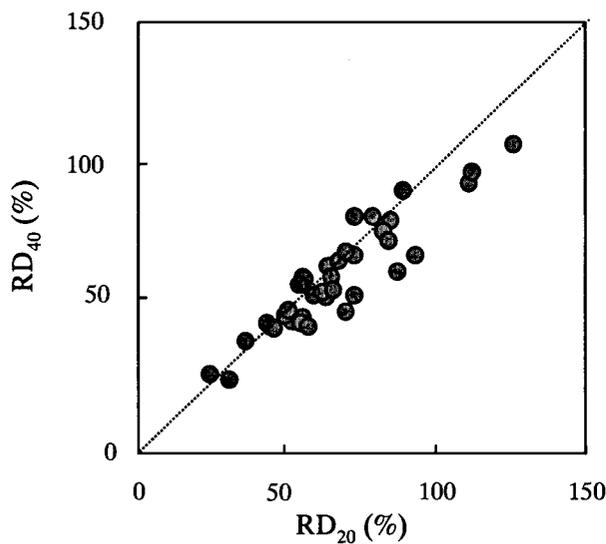


Fig. 5-2. Relations between the relative DBH (the ratio of the DBH of Amur cork-tree to the mean DBH of the two neighborhood dominants in the circular plot) at 20 (RD_{20}) and 40 years-of-age (RD_{40}). The dotted lines are the equivalent lines.

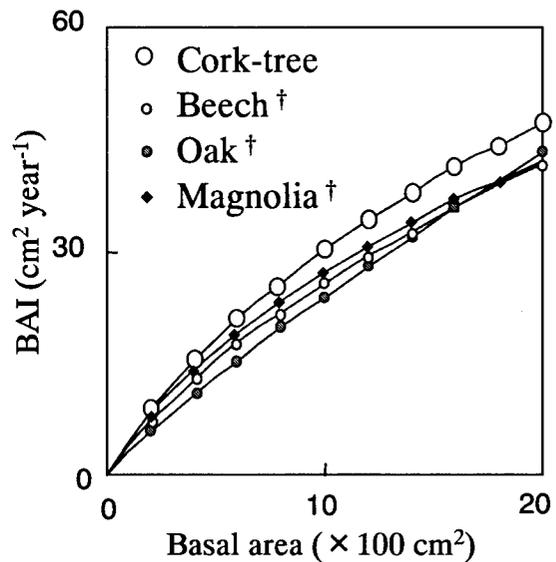


Fig. 5-3. Mean annual basal-area increments (BAI: $\text{cm}^2 \text{ year}^{-1}$) as a function of the basal area (cm^2) in the case without any suppression for canopy stems of Amur cork-tree and the three dominant species in the study forest (\dagger after Chapter 4).

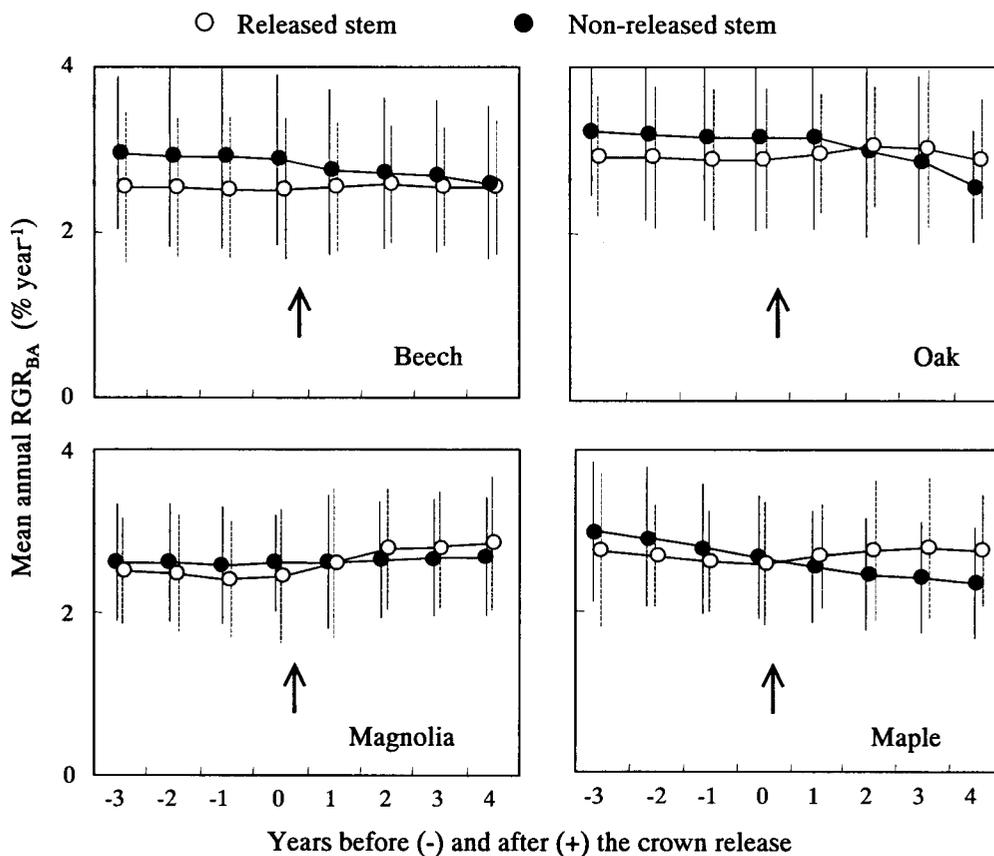


Fig. 6-1. Eight-years consequence of the mean annual RGR_{BA} of the released- (\circ) and non-released-stems (\bullet) of the four species (Siebold's beech, Japanese oak, Silver magnolia and Printed maple). Bars indicate the standard deviations.

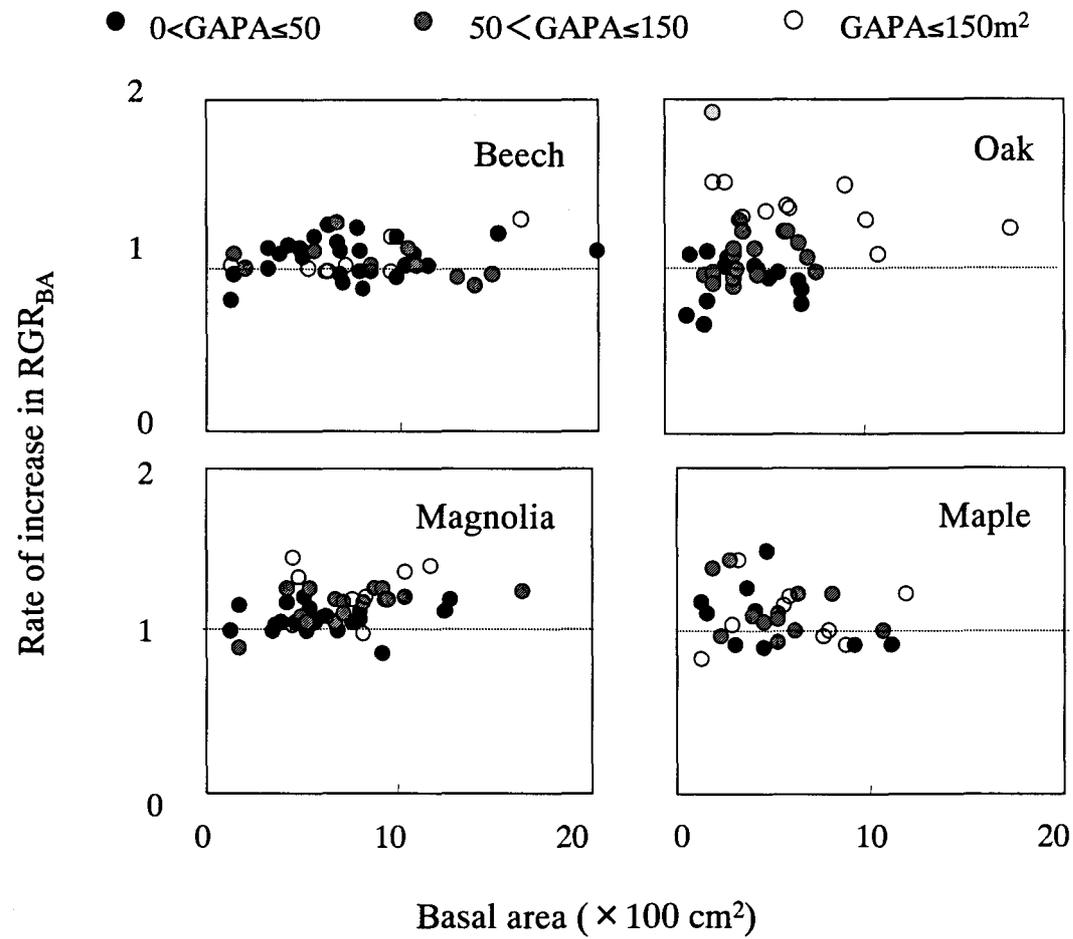


Fig. 6-2. The rate of increase in RGR_{BA} (the rate of the RGR_{BA} after the release to that before the release) in relation to the basal ea of the four species (Siebold's beech, Japanese oak, Silver magnolia and Printed maple) at the different levels of GAP.

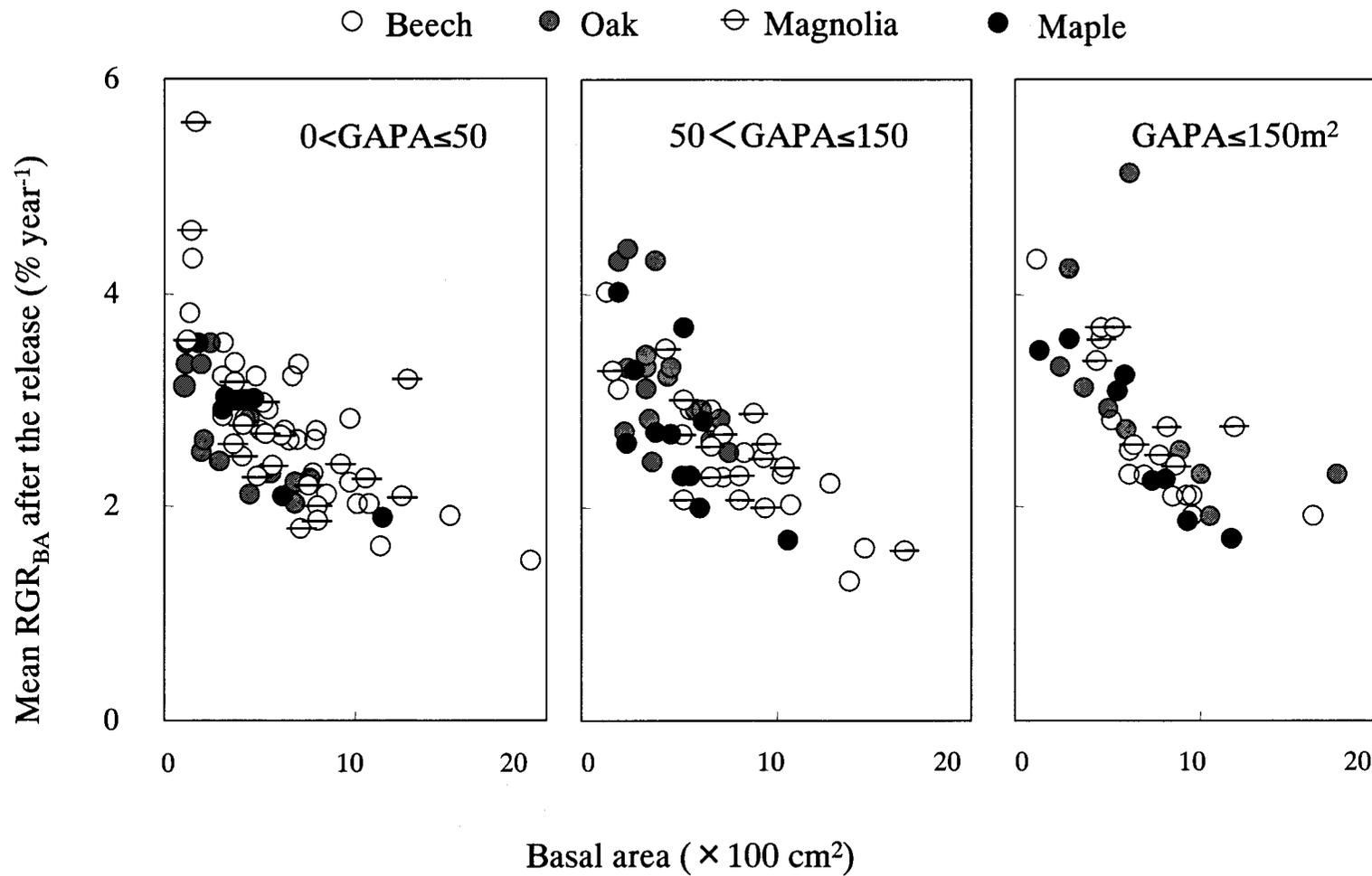


Fig. 6-3. Scatterplots of the RGR_{BA} after the release of the four species (Siebold's beech, Japanese oak, Silver magnolia and Printed maple) in relation to the basal area at the different levels of GAPAs.