

SPECIAL FEATURE

Listen to the voices of local beech forests: An ecological and evolutionary conception of beech under phylogenetic and environmental constraints

Characteristics of beech mixed forest distributed at low elevations on Mt. Toishi, northern Kyushu, in the upper warm-temperate zone of Japan

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Abstract

The aim of this study was to clarify the structure and regeneration status of mixed beech (*Fagus crenata*) forest on Mt. Toishi in the Sangun mountain range in northern Kyushu, a relatively low-latitude region in Japan, with emphasis on forests at lower elevations. We focused on a mixed beech forest at a low elevation of Mt. Toishi and compared the forest structure of the target stands, including tree species and size, with the forest structure near the peaks of Mt. Toishi and Mt. Sangun. Deciduous broad-leaf trees were dominant near the peaks, while evergreen broad-leaf trees dominated at lower elevations, whereas the relative dominance of beech trees was not significantly different. Near the peaks, the number of large-diameter beech trees forming the canopy decreased, and small-diameter trees were present. The proportion of small-sized trees was lower in the low-elevation forest area than in the forest area near the peak. Even at lower elevations, juvenile beech trees grew in limited areas on steep slopes along forest roads. These sites suggested that regeneration of beech populations is possible even at low elevation.

KEYWORDS

beech mixed forest, elevational distribution, regeneration, stand structure, upper warm-temperate zone

1 | INTRODUCTION

Japanese beech (*Fagus crenata* Blume) is distributed throughout Japan from the southern limit of the Takakuma mountain range of Kagoshima Prefecture to the Kuromatsunai lowland of Hokkaido (Hukushima & Iwase, 2005). Japanese beech (hereinafter simply referred to as beech) is the dominant tree species in the cool-temperate zone of Japan. It is crucial to preserve beech

forests for their water retention function as well as for conservation of genetic diversity (Yoshii & Tamai, 1994), ecosystem diversity, and various forest resources, which are specific to cool-temperate forests. However, under the policy of expanding forestation of the 1950s, beech forests were clear-cut over large areas (Murai et al., 1991). In Kyushu region, beech forests are fragmented, and there are concerns about the declining seed quality due to inbreeding weakness and unsuccessful regeneration.

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Furthermore, it is predicted that the distribution area of beech in Japan will change in the future owing to an increase in average temperatures caused by global climate change (Matsui et al., 2004a). If the air temperature continues to rise from the present day into the future, the Kyushu region, which is located at the lowest latitude of Japan's main islands, would be the first to be affected and the distribution area of beech trees would change.

Matsui et al. (2006) reported the following specific adaptation measures for beech conservation: suppression of invasion by evergreen broad-leaf tree species in beech forests in western Japan, where the lower elevation limit borders an evergreen broad-leaf forest; securing beech migration routes through ecological corridors in areas where mountain ranges connect central to northern Honshu; and beech invasion into *Quercus crispula* forests and conifer-hardwood forests north of the northern limit of beech forests in Hokkaido. All of the conservation plans have to be adapted to suit local conditions. To conserve pure or mixed forests of beech, it is first important to understand the characteristics of the target forest area. However, there is a paucity of studies on beech forests in Kyushu compared with other regions of Japan, and insufficient information is available to draw a firm conclusion on their current status.

Sangun mountain range, in the northern part of Kyushu, is an area where beech and evergreen broad-leaf trees grow in mixed forest, and beech is common on the neighboring

mountain peaks (Figure 1). A comparison of field survey results around the peak of Mt. Sangun (935.9 m above sea level [a. s. l.]) showed that in 2000 the total number of trees was 121, of which 55 were beech trees within an 800 m² survey plot (Inoue & Yamanobe, 2000), whereas in 2019 in the same plot size, the total number of trees was 309, but the number of beech trees was 15 (Itabashi et al., 2019). Thus, the total number of trees in the study area had increased during the 20-year period, while the number of beech trees had declined. This is because many of the adult beech trees have died, and regeneration by juveniles and seedlings has been largely unsuccessful. The factors that have contributed to this significant decline in the adult beech population and the lack of new seedlings are not well understood. Assessing the current status of mixed beech forests and clarifying the causes of population decline are considered to be important for the conservation of beech forests in Kyushu, which are predicted to disappear in the future.

The purpose of this study was to survey the current status of mixed beech forests in the Sangun mountain range in northern Kyushu, which is within the upper warm-temperate zone of Japan's climate classification. Specifically, the aim was to clarify the stand structure of mixed beech forests at the peak and at lower elevations, and to consider the environmental conditions necessary for successful seedling regeneration based on the site conditions of the seedling safe sites.

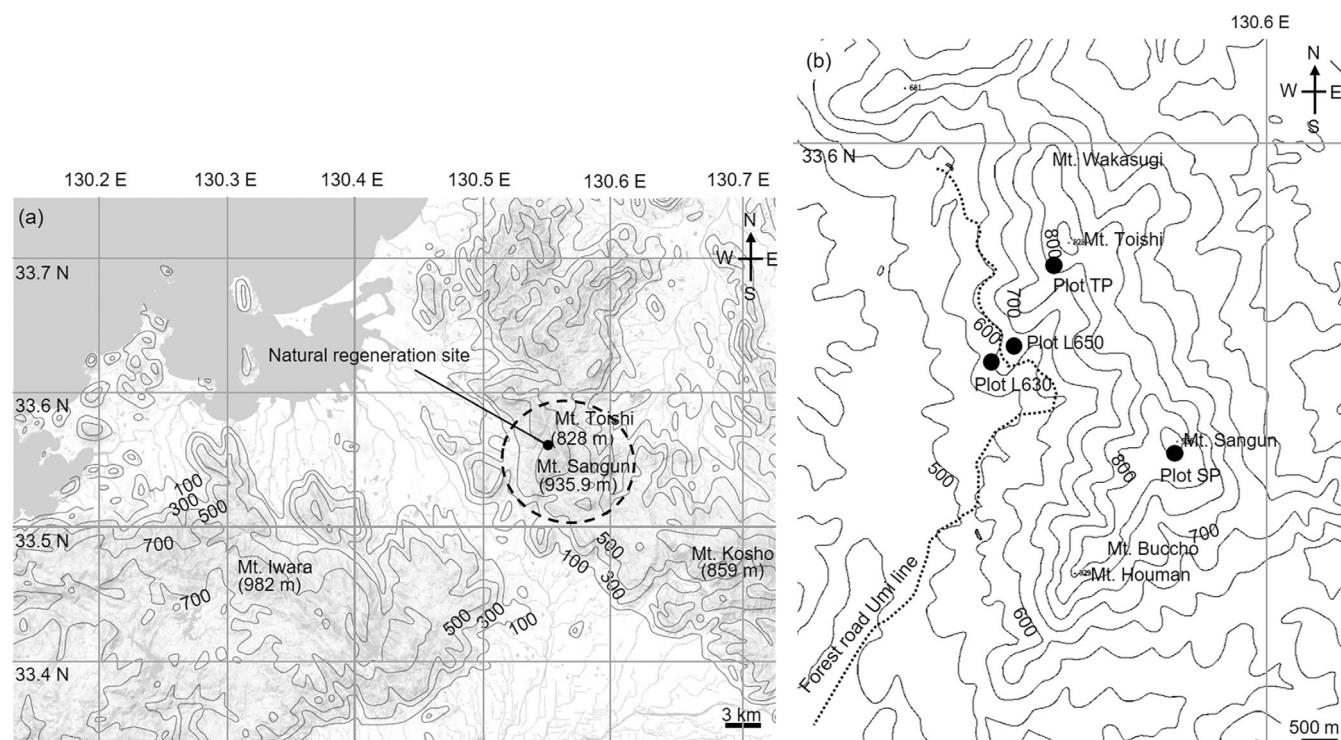


FIGURE 1 Map of suburbs of Fukuoka city and location of Sangun mountain range (enclosed by dashed line) (a), the locations of survey plots (filled circle) (b) in this study. This map was created by the Geospatial Information Authority of Japan website (<https://maps.gsi.go.jp/vector/>) and partially altered by the authors.

2 | MATERIALS AND METHODS

2.1 | Study area and field survey plots

The study area was located at low elevations and near the peaks of the Sangun mountain range in Fukuoka Prefecture, Japan. In the Sangun mountain range (Figure 1), a traverse route connects Mt. Wakasugi (681 m a. s. l.), Shokegoe (500 m a. s. l.), Mt. Toishi (828 m a. s. l.), Mt. Sangun (935.9 m a. s. l.), Mt. Buccho (868 m a. s. l.), and Mt. Houman (829 m a. s. l.) [Correction added on 22 November 2023, after first online publication: in the preceding sentence, the value ‘826 m a. s. l.’ has been corrected to ‘828 m a. s. l.’]. The entire Sangun mountain range is formed of granite, with crystalline schists termed Sangun metamorphic rocks in the northern portion of the range (Environment Agency, 1980). In selecting the survey plots for this study, we traversed the major trails in the Sangun mountain range and recorded the locations of mature beech trees using a handheld GPS (GPSMAP 64sc J, Garmin, Schaffhausen, Switzerland) (Itabashi et al., 2020).

The location and outlines of the plots surveyed for forest structure in this study are summarized in Table 1. The total area of each plot was 800 m², with direct comparison with the data reported by Inoue and Yamanobe (2000) in mind (however, the lowest-elevation plot L630 was smaller than 800 m²). The plots were situated in mixed beech forest with a closed canopy. The survey plot near the peak of Mt. Toishi (TP) was established in April 2019. The individual subplots were 20 m × 20 m, sited on north- and south-facing slopes straddling one ridge

near the peak (TP-S and TP-N, respectively). To assess the stand structure of mixed beech forests near the lowest elevation in Kyushu, one plot (L650) was established in September 2020 at a low elevation (650 m) on Mt. Toishi. One 20 m × 20 m subplot was established on each of the north- and west-facing slopes (referred to as L650-N and L650-W, respectively); the combined data from these subplots were used in the analysis for L650. Furthermore, another plot (L630) was established in September 2021 on a north-facing slope at an elevation of 630 m, which was considered to be the lowest elevation of mixed beech forests on Mt. Toishi. At this lowest-elevation point, the goal was to have the largest possible area, resulting in a combined plot of 12 m × 15 m and 13 m × 22 m (466 m²).

In all survey plots, the tree species and circumference at breast height (1.3 m above the ground) were recorded for all individual trees (stems) with a diameter at breast height (DBH) of at least 5 cm. In addition to these data, the data from the survey plots near the peak of Mt. Sangun from the report by Itabashi et al. (2019) were recalculated and included in the present analysis as plot SP.

The breast-height cross-sectional area of each stem was determined from the DBH, and the total breast-height cross-sectional area and number of stems were used to determine the relative dominance of each tree species in each survey plot using the following formula:

$$RD (\%) = \left(\frac{BA_{Sp}}{BA} + \frac{\text{Number of stems by tree species}}{\text{Total number of stems}} \right) \times 100 \div 2,$$

TABLE 1 Outline of each plot in this study.

Plot Subplot	L630	L650		TP		SP	
		L650-N	L650-W	TP-N	TP-S	SP-N	SP-S
Area (m ²)	466	400	400	400	400	400	400
North latitude	33.573	33.574	33.573	33.579	33.578	33.555	33.554
East longitude	130.562	130.565	130.564	130.567	130.567	130.583	130.584
Elevation (m)	635	657	647	780	770	905	905
Slope direction	North	North	West	North	South	North	South
Slope gradient	15°	30°	15°	22°	26°	32°	30°
Number of stems	171	216		290		336	
Number of species	19	22		20		24+	
Stem density per 100 m ²	36.7	27.0		36.3		42.0	
Density of species per 100 m ²	4.1	2.8		2.5		3.0+	
Max DBH (cm) and its species	56.1 <i>Fc</i>	49.8 <i>Fc</i>		69.7 <i>Fc</i>		34.1 <i>Fc</i>	
Mean DBH and SD (cm)	14.3 ± 9.9	14.5 ± 11.6		11.3 ± 9.3		9.2 ± 4.6	

Note: TP and SP represent “Toishi peak” and “Sangun peak,” respectively. Letters following the hyphen indicate slope direction in the Sub plot column. Character “+” in the SP row means seven trees with uncertain. *Fc* means *Fagus crenata*. DBH and SD means diameter at breast height and standard deviation, respectively.

where RD is relative dominance, BA_{sp} is total breast-height cross-sectional area of one tree species, and BA is total breast-height cross-sectional area of all tree species.

2.2 | Natural regeneration site at low elevation

At the lower-elevation sites (L650 and L630), small juvenile beech trees were lacking in the survey plots, but were plentiful at a specific site (along a forest road) outside the plots. Thus, we conducted a survey of the population and environmental factors at the regeneration site. This low-elevation natural regeneration site on Mt. Toishi was located at an elevation of 630–640 m along a forest road established in 1990 (Figure 1). The site was situated on a northwest-facing slope. The surrounding forest contained mature beech trees as well as *Quercus acuta*, *Carpinus tschonoskii*, and *Camellia japonica*. Juvenile beech trees were distributed unevenly only on the cut slope of the forest road and were not observed in the surrounding forest containing adult beech trees.

The number and size of juvenile beech trees were recorded in August 2019 at the natural regeneration site along the forest road. Owing to the relatively wide range of tree sizes, to confirm the age of the trees, in November and December 2019, one each of the juvenile beech trees with a main-axis length of 1–2 m, 2–3 m, and 3–4 m was selected and, felled at the base.

Juvenile beech trees at the natural regeneration site were only present on the cut slope along the forest road and not in the surrounding forest. To investigate the factors responsible for the uneven distribution of juvenile beech trees, we measured the light environment and depth of the soil litter layer (A_0 layer) on the slope along the forest road where juvenile beech trees were distributed and in the surrounding mixed forest of beech trees. In estimating the light environment, whole-sky images were captured with a digital camera (COOLPIX 4500, Nikon, Tokyo, Japan) in combination with a fish-eye converter (FC-E8, Nikon) at eight sites on the slope along the forest road and in the forest, respectively, on a cloudy day in November 2019. The intensity of direct and scattered light at the forest floor was estimated from the obtained whole-sky images using LIA32 free software (Yamamoto, 2013). Additionally, the slope angle and depth of the litter layer (A_0 layer) were measured at three points in December 2019 at a site where juvenile beech seedlings were growing and on small ridges, gentle slopes, and steep slopes in the surrounding forest.

3 | RESULTS

3.1 | Stand structure

The number of stems and species in each survey plot, as well as the size of the trees are summarized in Table 1. The number of stems per 100 m² was highest in SP (42 stems/100 m²) and stem density was lowest in L650 (27 trees/100 m²). The number of species per 100 m² was highest in L630 (4.1 species/100 m²) and the lowest species density was recorded in TP (2.5 species/100 m²). The mean DBH of stems within each survey plot was highest in L630 (14.3 ± 9.9 cm) and lowest in SP (9.2 ± 4.6 cm). The mean DBH tended to be smaller at higher elevations. The tree species with the highest DBH was beech in all plots. However, the maximum stem size at the highest elevation (in SP) was much smaller (34.1 cm) than those in the other three survey plots (approximately 50 cm or more).

3.2 | Tree size structure

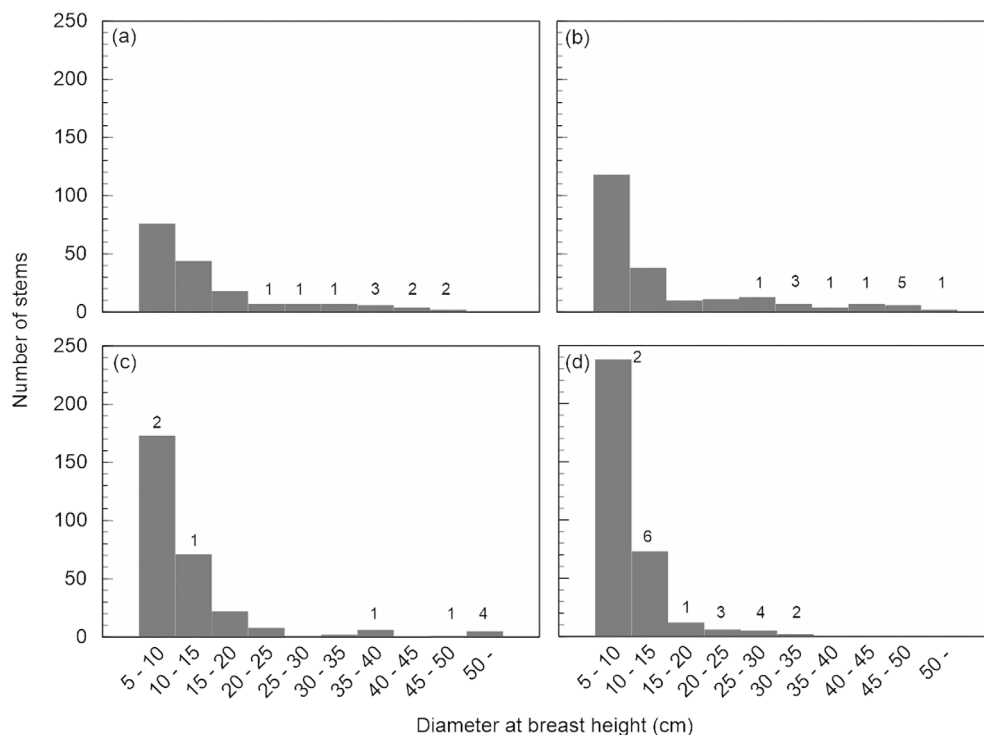
The frequency distribution of DBH in each survey plot are shown in Figure 2. At all study sites, the frequency was highest in the DBH hierarchy within the 5–10 cm DBH class and declined with increase in size class. The proportion of trees with DBH between 5 and 10 cm was lowest in L630 (44.4%) and highest in SP (70.8%), and it tended to increase with elevation.

Regarding the frequency distribution of beech, trends differed between the study sites at lower elevations (L630 and L650) and those near the peaks (TP and SP). Beech trees were only recorded in the classes above 20 cm DBH in L630 and 25 cm DBH in L650, and beech seedlings with relatively small DBH were not observed in these plots. In contrast, beech trees were present from the lowest to the highest DBH classes in TP and SP. In particular, beech trees were present in all classes from 5 to 35 cm DBH in SP.

3.3 | Tree species composition

The tree species composition of the four survey plots is summarized in Table 2 for evergreen tree species and Table 3 for deciduous broad-leaf tree species. The RD of evergreen tree species in L630 and L650 was 85.8% and 86.7%, respectively, indicating that evergreen broad-leaf tree species predominated at lower elevations of Mt. Toishi. The RD of beech was 10.5% in L630 and 10.7% in L650. The beech trees were mixed with *Distylium racemosum* and *Castanopsis*

FIGURE 2 Frequency distribution of diameter at breast height (DBH) in the survey plot of L630 (a), L650 (b), TP (c) and SP (d), respectively. The numbers in the figures indicate the number of beech trees in each stratum.



sieboldii, which are common in evergreen broad-leaf forest. In addition, evergreen broad-leaf tree species, such as *Camellia japonica* and *Cinnamomum yabunikei*, were common. Deciduous broad-leaf tree species other than beech, such as *Carpinus tschonoskii* and *Chengiopanax sciadophylloides*, were identified but in small numbers.

The RD of evergreen tree species in TP was 64.8%, which was lower than that of L630 and L650, but accounted for more than half of the trees present. In contrast, the RD of evergreen tree species in SP was 6.0% and the survey plot was almost entirely composed of deciduous broad-leaf tree species. The tree species with the highest RD in TP was *Quercus acuta* (26.7%). The tree species with the highest RD in SP was *Lyonia ovalifolia* (19.4%). The RD of beech in each survey plot was 6.9% for TP and 8.3% for SP, which were lower than those at lower elevations on Mt. Toishi (L630 and L650). Thus, with increase in elevation from the lower elevations of Mt. Toishi to the peak of Mt. Toishi and the peak of Mt. Sangun, the tree species composition changed from predominantly evergreen broad-leaf tree species to predominantly deciduous broad-leaf tree species. Trees common in evergreen broad-leaf forests, such as *Distylium racemosum* and *Castanopsis sieboldii*, which were identified at the lower-elevation sites (L630 and L650), were not observed at the study sites of TP and SP. For beech, the difference in RD among the study sites was limited.

3.4 | Juvenile beech trees at the natural regeneration site

3.4.1 | Size of juvenile trees

Twenty-eight juvenile beech trees were observed along the forest road within an elevational range of 630–640 m, over a distance of approximately 300 m. The relationship between the main-axis length of these individuals and the diameter at ground level is shown in Figure 3. The maximum length of the main axis of the juvenile beech trees in the natural regeneration area was 466 cm and the maximum diameter at ground level was 4.1 cm. The minimum values were 67 and 0.9 cm, and the means were 228.9 and 2.0 cm, respectively. A significant positive correlation was observed between the main-axis length and the diameter at ground level of the juvenile beech trees ($p < 0.05$).

3.4.2 | Age of juvenile beech trees

The three juvenile trees examined in the laboratory correspond to the hollow circles (A, B, and C) in Figure 3. The main-axis length and the diameter at ground level of these three individuals were 102 and 1.7 cm for A, 256 and 1.8 cm for B, and 314 and 2.6 cm for C, respectively [Correction added on 22 November 2023, after first online publication: in the preceding sentence, the values ‘133’ and ‘360’ for hollow circles A and C have been corrected

TABLE 2 Stem density, mean diameter at breast height (DBH), and relative dominance (RD) of each evergreen tree species in the plots of this study.

Plot	L630 (466 m ²)			L650 (800 m ²)			TP (800 m ²)			SP (800 m ²)		
	Stem density (N 100 m ⁻²)	DBH (cm)	RD (%)	Stem density (N 100 m ⁻²)	DBH (cm)	RD (%)	Stem density (N 100 m ⁻²)	DBH (cm)	RD (%)	Stem density (N 100 m ⁻²)	DBH (cm)	RD (%)
<i>Quercus acuta</i>	9.7	16.6 (8.5)	28.4	4.0	28.6 (11.5)	22.1	7.8	17.0 (10.8)	26.7	0.8	15.8 (7.3)	2.4
<i>Symplocos kuroki</i>	7.7	9.7 (3.1)	17.7	0.5	10.1 (4.8)	1.6	3.1	10.3 (3.2)	8.2			
<i>Camellia japonica</i>	5.2	7.9 (3.1)	10.9	6.0	7.9 (2.4)	17.1	6.9	8.3 (3.6)	16.4	0.1	5.1	0.2
<i>Cinnamomum yabunikkei</i>	3.6	7.1 (1.5)	7.4	5.3	7.5 (2.1)	14.7	0.1	8.6	0.3	0.1	6.4	0.3
<i>Castanopsis sieboldii</i>	2.8	28.8 (8.4)	11.5	1.1	27.1 (7.4)	6.0						
<i>Distylium racemosum</i>	1.5	13.9 (2.9)	4.0	2.8	8.8 (2.8)	8.2						
<i>Ilex integra</i>	0.9	12.1 (4.0)	2.2	0.1	27.1	0.7						
<i>Quercus salicina</i>	0.9	7.5 (0.7)	1.8	0.5	14.5 (6.4)	1.9						
<i>Ilex rotunda</i>	0.2	8.0	0.5									
<i>Chamaecyparis obtusa</i>	0.2	8.8	0.5									
<i>Dendropanax trifidus</i>	0.2	9.6	0.5	0.6	8.1 (1.8)	1.8	0.3	9.1	0.6			
<i>Machilus thunbergii</i>	0.2	13.5	0.6	1.3	14.2 (4.8)	4.6						
<i>Eurya japonica</i>				0.9	10.0 (2.7)	2.7	1.0	7.3 (2.1)	2.3			
<i>Illicium anisatum</i>				0.8	6.9 (0.7)	2.1	2.9	8.0 (2.6)	6.8	0.3	6.8	0.5
<i>Cleyera japonica</i>				0.5	9.0 (2.4)	1.5						
<i>Neolitsea sericea</i>				0.3	15.6	1.0	0.4	6.8 (0.8)	0.8	0.1	5.2	0.2
<i>Litsea coreana</i>				0.1	10.3	0.4						
<i>Ilex pedunculosa</i>				0.1	10.8	0.4						
<i>Symplocos myrtacea</i>							0.8	6.2 (0.7)	1.6	0.3	5.7	0.5
<i>Ligustrum japonicum</i>							0.4	5.8 (0.5)	0.8	0.1	9.7	0.3
<i>Neolitsea aciculata</i>							0.1	5.1	0.2			
<i>Ilex crenata</i>										0.8	7.1 (2.0)	1.6
Number and density of stem (N 100 m ⁻²)	154, 33.0			198, 24.8			189, 23.6			20, 2.5		
Number and density of species (N 100 m ⁻²)	12, 2.6			16, 2.0			11, 1.4			8, 1.0		
RD of evergreen tree species (%)	85.8			86.7			64.8			6.0		

Note: TP and SP in the Plot column are same as in Table 1. Values in parentheses in Plot column and DBH row indicate plot area and standard deviation, respectively. N and RD means tree number and relative dominance, respectively.

TABLE 3 Stem density, mean diameter at breast height (DBH), and relative dominance (RD) of each deciduous broad-leaf tree species in the plots of this study.

Plot	L630 (466 m ²)			L650 (800 m ²)			TP (800 m ²)			SP (800 m ²)		
	Stem density (N 100 m ⁻²)	DBH (cm)	RD (%)	Stem density (N 100 m ⁻²)	DBH (cm)	RD (%)	Stem density (N 100 m ⁻²)	DBH (cm)	RD (%)	Stem density (N 100 m ⁻²)	DBH (cm)	RD (%)
<i>Lyonia ovalifolia</i>	0.2	16.4	0.6	0.1	20.4	0.6	3.1	8.1 (2.9)	7.4	9.0	7.4 (1.9)	19.4
<i>Acer sieboldianum</i>	0.4	10.0	1.0	0.1	10.2	0.4	0.4	6.8 (1.4)	0.8	7.0	9.5 (3.6)	17.0
<i>Rhododendron reticulatum</i>				0.1	6.3	0.3	0.3	5.7	0.5	3.8	6.3 (1.0)	7.5
<i>Clethra barbinervis</i>	0.2	7.8	0.5				3.8	10.1 (3.6)	9.8	2.6	10.5 (4.1)	6.7
<i>Carpinus tschonoskii</i>	0.2	11.5	0.5	0.1	25.6	0.6	0.3	14.6	0.8	2.5	9.0 (3.4)	5.9
<i>Fagus crenata</i>	2.1	37.1 (9.2)	10.5	1.5	41.3 (8.3)	10.7	1.1	38.8 (25.4)	6.9	2.3	19.2 (8.7)	8.3
<i>Styrax japonica</i>							3.1	8.7 (3.3)	7.6	2.3	12.0 (2.3)	6.2
<i>Carpinus japonica</i>										2.3	8.2 (2.6)	5.1
<i>Neoshirakia japonica</i>										2.1	7.3 (1.7)	4.6
<i>Symplocos coreana</i>										1.8	6.6 (1.4)	3.6
<i>Cornus kousa</i>							0.5	8.4 (2.2)	1.2	1.4	8.6 (3.0)	3.2
<i>Ilex macropoda</i>	0.2	12.6	0.6							0.8	10.2 (3.1)	1.9
<i>Lindera triloba</i>										0.5	5.6 (0.7)	1.1
<i>Cerasus jamasakura</i>										0.3	11.9	0.7
<i>Acer crataegifolium</i>										0.1	29.2	0.6
<i>Rhododendron kaempferi</i>										0.1	7.2	0.3
<i>Acer rufinerve</i>							0.1	5.8	0.3			
<i>Chengiopanax sciadophylloides</i>				0.3	7.6	0.7						
<i>Acer palmatum</i>	0.2	13.2	0.6									
Uncertained										0.9	9.1 (4.4)	2.1
Number and density of stem (N 100 m ⁻²)	17, 3.6			18, 2.3			101, 12.6			316, 39.5		
Number and density of species (N 100 m ⁻²)	7, 1.5			6, 0.8			9, 1.1			16+, 2.0+		
RD of deciduous broad-leaf tree species (%)	14.2			13.3			35.2			94.0		

Note: TP and SP in the Plot column are same as in Table 1. Values in parentheses in Plot column and DBH row are same as in Table 2. N and RD means tree number and relative dominance, respectively. Character “+” in the SP row means seven trees with uncertain.

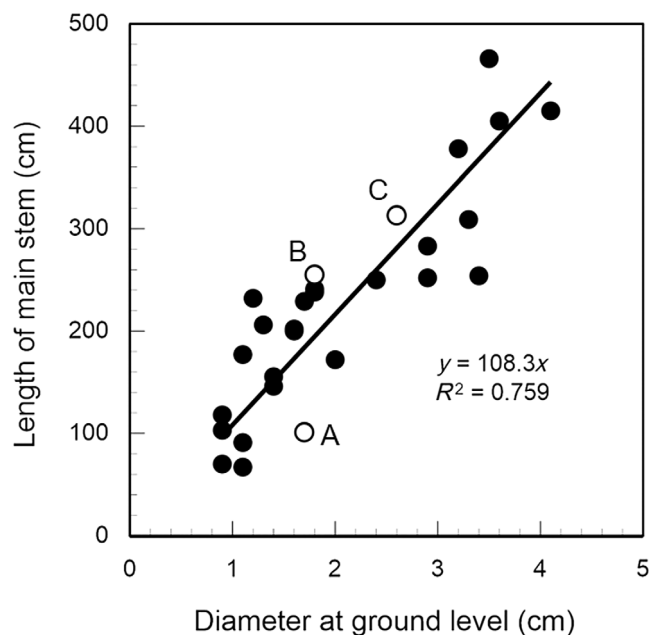


FIGURE 3 Relationship between diameter at ground level and length of main stem for beech seedlings at the natural regeneration site in the Mt. Toishi lower-elevation area. Hollow circles (A, B, and C) represent the age-investigated trees. [Correction added on 3 November 2023, after first online publication: Figure 3 has been replaced to show the correct position of the three hollow circles.]

to '102' and '314', respectively.]. The age of these juvenile trees was estimated to be 11 years for A, 17 years for B, and 20 years for C, based on observation of growth rings at the cut surface at ground level.

3.5 | Environment at natural regeneration site

Relative light intensity estimated from the whole-sky image was 0.26 ± 0.09 along the forest road and 0.1 ± 0.03 in the forest interior, with values 2.6 times higher ($p < 0.05$) along the forest road than in the forest interior. The depth of the litter layer on the soil surface at the natural regeneration site and on the neighboring forest floor is shown in Figure 4. The angle of the slope where the juvenile beech trees grew was steep ($>60^\circ$) and the ground was almost bare, with only limited accumulation of fallen leaves and other debris at the base of the invading trees. The slopes within the mixed beech forest near the natural regeneration site ranged from approximately 0 to 50° , and the litter layer (A_0 layer) was generally 2–4 cm on the small ridges with slopes of 0 – 10° , 5–7 cm on gentle slopes of 10 – 30° , and 3–4 cm on steeper slopes of 30 – 50° . The thickest litter layer in the interior of the forest was 7 cm on a gentle slope.

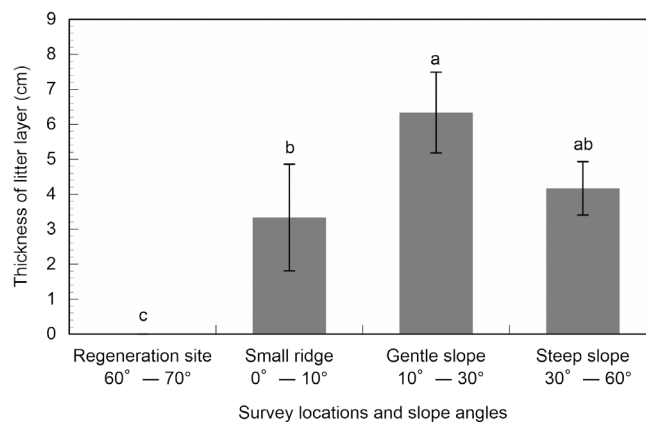


FIGURE 4 Mean litter layer thickness at the natural regeneration site and on the beech mixed forest floor (ridge and slopes). Means with a different letter within the figure are significantly different, based on ANOVA, and Scheffe's- F test ($p < 0.05$). Vertical lines indicate the standard deviation.

4 | DISCUSSION

4.1 | Current status of beech trees in the Sangun mountain range

From the preliminary research for this study, almost half of the mature beech trees in the Sangun mountain range were distributed below 800 m, and the lowest elevation at which a tree was observed was 450 m, which is notably low for beech (Itabashi et al., 2020). Although the distribution of beech trees at an elevation of 650 m has been reported at Mt. Kosho (859 m) and Mt. Iwara (982 m) in Fukuoka Prefecture (Environment Agency, 1980; Tsutsui, 1993), this study showed that beech is distributed at lower elevations. While beech formed mixed forests with mainly deciduous broad-leaf trees near the peaks, beech formed mixed forests with evergreen broad-leaf trees at lower elevations. Thus, beech trees in the Sangun mountain range were found to cohabit with a wide variety of tree species at a wide range of elevations. One possible cause of this is the effect of snow cover. Fukuoka Prefecture faces the Sea of Japan and, during winter, is often affected by cold air from a continental anticyclone, and monsoon winds are experienced on many days (Natural Environment Division, Environment Department, Fukuoka Prefecture, 2001). Areas above 200 m in Fukuoka Prefecture belong to a mountainous climate zone, where snow falls from December to April and snow cover occurs, although it is not very deep (Natural Environment Division, Environment Department, Fukuoka Prefecture, 2001). Snow cover is one factor that gives beech a competitive advantage for survival because beech trees are resistant to the physical pressure of snow cover,

and snow cover has the effect of retaining moisture and providing insulation during winter (Homma et al., 1999). Therefore, it can be inferred that the seasonal climatic characteristics owing to slope orientation are one factor that allows beech to survive at lower elevations.

4.2 | Stand structure

At the study sites at lower elevations, beech was intermixed with *Quercus acuta*, *Camellia japonica*, and other tree species, which was characteristic of the beech—*Neoshirakia japonica* community at lower elevations (Hukushima et al., 1995), but also by a high dominance of *Castanopsis sieboldii* and *Distylium racemosum* (Table 2). Deciduous broad-leaf trees were scarce, with only beech trees exceeding 1.0 ($N\ 100\ m^{-2}$) in density (Table 3). However, typical evergreen broad-leaf tree species, such as *Castanopsis sieboldii* and *Distylium racemosum*, were not observed in the TP and SP plots (Table 2). The dominance of deciduous broad-leaf trees increased in these peak plots, with RD of 35.2% in TP and 94.0% in SP (Table 3). The difference in elevation between the low-elevation study sites (L630 and L650) and TP was about 140 m, and that between the low-elevation study sites and SP was about 255 m. The temperature lapse rate with elevation is $0.60^{\circ}C/100\ m$ (Fukuoka, 1966). Considering the difference in elevation as analogous for the average difference in temperature, the difference in temperature between the study sites at the lower elevations on Mt. Toishi and those near the peak is approximately $0.84^{\circ}C$, and the difference in temperature between the lower-elevation study sites and the peak of Mt. Sangun is approximately $1.53^{\circ}C$. According to the past 30 years anomalous mesh data (Ministry of Land, Infrastructure, Transport and Tourism, 2010), these values were 0.6 and $1.4^{\circ}C$, respectively, and the warmth index (WI) and coldness index (CI) (Kira, 1991) for each study site were 95.1 and 6.5 for L630 and L650, 89.9 and 8.3 for TP, and 83.5 and 11.4 for SP, respectively (in $^{\circ}C$ months). Vegetation distribution under a macroclimate is basically determined by temperature and precipitation, but in Japan, where there is ample precipitation, vegetation distribution is largely controlled by temperature (Hukushima & Iwase, 2005). Kira (1991) suggested that $WI = 85$ is the boundary between cool temperate zone and warm temperate zone, and that the forests of warm temperate zone are divided into deciduous and evergreen broad-leaf forest at $CI = 10$, which is generally consistent with the results of this study. On the other hand, the conditions that Matsui et al. (2004b) showed from model simulations using temperature and precipitation to predict the probability of potential beech forest distribution in

southwestern Japan, including Kyushu, were not in good agreement with the climatic conditions at each site in this study. These considerations suggest that it may be worthwhile to take measurements of the actual meteorological conditions at each of the study sites. It is unclear whether the environmental conditions are favorable for beech, as evidenced by the observation that more evergreen broad-leaf species were present at lower elevations of Mt. Toishi than near the peak. Detailed observations of climatic variables at each study site are considered essential to determine the health and vigor of beech in such environments and the potential for future regeneration.

At the lower elevations in the current study, the peak of Mt. Toishi, and the peak of Mt. Sangun, the mean stem DBH declined with an increase in elevation of the study site. All the study sites had a large number of stems with a DBH between 5 and 10 cm, but the percentage increased with elevation of the study site (Figure 2). These results suggested that, although the forest regenerated at all of the study sites, the regeneration status varied among the study sites, with those sites at higher elevations experiencing more progressive regeneration. In the two decades since the study by Inoue and Yamano (2000), it can be inferred that the population of larger-sized beech trees on the peaks of Mt. Toishi and Mt. Sangun has declined (from 93 to 7 at Mt. Toishi and from 55 to 15 at Mt. Sangun), with a corresponding increase in the number and variety of other species and populations of beech trees in the forest area. The size ranges for beech trees were 21.4–56.1 cm at L630 and L650, 5.2–69.7 cm at TP, and 5.4–34.1 cm for SP (Figure 2). At TP, beech trees ranged from small to large, and at SP, beech trees with a small DBH were more abundant than at the other study sites, suggesting that beech regeneration was occurring around the peaks. In contrast, no beech trees less than 20 cm in DBH were observed at the lower-elevation study sites. Thus, the regeneration status of beech at the study sites at lower elevations differed from that near the mountain peaks. The presence or absence of beech seedlings in the forest will help to determine whether the mixed beech forests at low elevations in the Sangun mountain range will be maintained in the future.

4.3 | Factors influencing natural regeneration of beech

The vegetation on the stand floor around Mt. Hiko, which is located near the Sangun mountain range, has been severely damaged by deer. The renewal of beech seedlings has been inhibited (Kaneko et al., 2021; Kondoh et al., 2007). In contrast, no significant feeding

damage by deer has been observed in the Sangun mountain range. In this study, no juvenile beech trees were present near the peaks or within the lower elevation plots. However, natural regeneration sites with relatively high densities of juvenile trees were present along the forest roads near L630 and L650. The juvenile beech trees here were located on a cut slope created by the opening of a forest road around 1990, and the variation in individual size and age of the trees suggested that continuous recruitment of seedlings was occurring (Figure 3).

One characteristic of this natural regeneration site was that no beech seedlings grew in the adjacent mixed beech forest, only on the slope along the forest road. Comparing the light environment along the forest road where juvenile beech trees were present and in the mixed beech forest floor, a marked difference in relative light intensity was observed. In Hokkaido, beech is shade-tolerant and light is said to be a potent factor in inhibiting regeneration when the relative light irradiance falls below 5% (Saito et al., 2011). For the forest in this study area, the light environment is considered to be suitable for regeneration. However, the regional characteristics of beech differ, with the Japan Sea-type beech distributed in Hokkaido and the Pacific-type beech in Kyushu (Terazawa & Koyama, 2008). Furthermore, the light environment in forests in Hokkaido changes more significantly with the seasons than in Kyushu because of the almost complete absence of evergreen broad-leaf trees in Hokkaido. All of this suggests that careful investigation is needed to determine how the light environment of the forests in the Sangun mountain range affects the natural regeneration of beech trees.

The other important feature, was that juvenile beech trees grew only on steep cut slopes. It has been pointed out previously that slopes are a safe site for beech seedlings in Hokkaido and other areas because they are outside the habitat of rodents, which are seed predators (Kobayashi & Watanabe, 2003). However, the slope in such cases is approximately 30°, whereas a different cause can be assumed for the distribution only on a cut slope of approximately 60° in this study (Figure 4). The depth of the litter layer measured in December in the current study was more than 2 cm in the forest interior, compared with almost no litter layer in the regeneration site. In a case study in Hokkaido, it was reported that the litter layer has little influence on beech seedling development and establishment (Kitabatake, 2001). However, the litter layer in that study was due to beech, *Quercus crispula*, and *Betula maximowicziana* litter. The area around the natural regeneration site in this study was a mixture of evergreen broad-leaf tree species with a well-developed cuticular layer together with adult beech trees that serve as mother trees, and the litter characteristics were very different from those of deciduous broad-leaf

forests. The defoliation in deciduous broad-leaf tree species, including beech, is most common in November, whereas the defoliation in evergreen broad-leaf tree species is most common in early summer, from April to May (Nakane, 1980). In the case of mixed beech and evergreen broad-leaf trees, beech seeds will be spread over a thick litter layer because of the accumulation of evergreen broad-leaf litter prior to the beech seed dispersal period (July–October). It cannot be ruled out that seeds dispersed on top of the litter layer may be affected by a lack of moisture, as the presence of leaves with a thick cuticular layer on the soil surface will impede root penetration of the soil, thus affecting seedling establishment. These differences in defoliation characteristics may affect the establishment of beech and other juvenile trees. In a study of tree age estimation using annual ring cores, which is different from this study, most of the warm-temperate evergreen broad-leaf tree species mixed with adult beech trees in the low-elevation study site at Mt. Toishi are younger than beech trees (unpublished data) and are thought to have invaded at a time when beech trees were more dominant.

No juvenile beech trees were observed on the floor of the mixed beech forest at L630 and L650 in this study, which may be related to the thickness of the litter layer due to species composition and slope angle. By applying the environmental characteristics of such microsites to management practices (e.g., increase of canopy openness and removal of evergreen-leaf litter), regeneration of the beech population could be facilitated at the lower elevation sites and the whole of the Sangun mountain range.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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