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Factors responsible for co-dominance of two beech species in a cool temperate forest in central Japan: interspecific comparison of spatial distribution and growth traits

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Abstract. To understand the co-existence mechanisms of related species, the recruitment processes of *Fagus crenata* and *F. japonica* were censused during 3 and 4 years from emergence, respectively, in a cool-temperate forest in Japan. The distributional properties and the growth traits were compared between two *Fagus* species. To evaluate the distributional properties, the spatial abundance of seedlings was estimated by a generalized linear model (GLM), with explanatory variables such as topographic variables, light conditions, the presence of dwarf bamboo, and the abundance of the overstory. To evaluate the growth traits under herbivory pressure, both the elongated shoot length and the proportion of recovery from predation (re-growth) were also compared. No spatial segregation and no species-specific differences were detected by GLM, which was consistent throughout the census period. Only *F. japonica* exhibited a slope-related distribution, while *F. crenata* exhibited no topographical dependence, indicates the distributional overlaps. For the growth traits, contrasting trends were detected, *F. crenata* was superior in shoot growth, whereas the proportion of re-growth was higher in *F. japonica* than *F. crenata*. We concluded that co-dominance of these species was not attributed to the spatial segregation but to the trade-off between growth and resistance to herbivory.
Keywords *Fagus crenata, Fagus japonica*, interspecific comparison, topographic differentiation, trade-off.

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Introduction

Understanding the mechanisms of the co-existence of woody plants can provide insights for maintaining forest ecosystems and the functions thereof. In temperate forests, differences in topographical preferences or demographic strategies may contribute to the co-existence of different woody species (Nakashizuka 2001). However, the mechanisms of co-existence of related species are likely complex, because their resource requirements and/or niche are similar. In this case, differences in the regeneration process from seeds/seedlings can be important for the co-existence (Masaki et al. 2007).

Two beech (Fagaceae) species, *Fagus crenata* and *F. japonica*, are both dominant species (co-dominant species) of a natural, cool-temperate forest in central Japan; this offers a good model system to examine the factors responsible for the co-existence of the related species. Previous studies of the adult stages of these two species indicated the species-specific characters in both their spatial distribution and life history (Ishizuka & Kaji 2010, Ohkubo 1992, Suzuki 2011, Yoshida & Ohsawa, 1996). In a natural forest, *F. japonica* exhibited a topography-related distribution and vigorous sprouting ability (Ishizuka & Kaji 2010, Ohkubo 1992, Yoshida & Ohsawa 1996). In contrast, *F. crenata* exhibited the distribution pattern independent of topographical features and bore a single stem without sprouting in the same natural forest (Ishizuka & Kaji 2010), suggesting the “generalist” in the distributional preference (Suzuki et al. 2002). However, it was also shown along the small scale topography (topographic configuration in 25 m resolution) that there was little topographic difference of these two species in the conditions where was the higher recruitment rate (Suzuki 2011). Therefore, the responsible factors for the co-dominance of these two species cannot be thoroughly explained only from the comparison of the adult stage. In temperate forests, early seedling recruitment is often the most critical stage for regeneration (Harcome 1987, Kitajima & Fenner 2000), thus, interspecific comparisons at early stages are critical for understanding the mechanisms of co-dominance of these two beech species.

For *F. crenata*, several studies have focused on seedling recruitment. In general, seedlings of this species are light-demanding and suffer from low-growth rate under dark conditions, such as when it is shaded by a dwarf bamboo understory (Nakashizuka 1987, Nakashizuka 1988). *F. crenata* seedlings are susceptible to pathogenic fungi, especially during the initial year (Maeda 1988, Sahashi et al. 1994, Shibata & Nakashizula 1995). Thus, successful recruitment is rarely occurred under a closed canopy (Niiyama & Abe 2002). Previous studies have indicated that spatial distribution at the seedling stage is determined by several limiting factors, such as dispersal limitation and density-dependent limitation caused by rodents predation, fungal attack, and/or the effects of abiotic condition (Masaki et al. 2005, Tomita et al. 2002). On the other hand, for *F. japonica*, only seedling demography has been surveyed, and high mortality by predation and dampingoff and/or insect damage occurs at the early demographic stage (Kaji & Ohkubo 1995, Kaji et al. 1992, Ohkubo et al. 1989, Ishizuka et al. in preparation). However, no reports have been available for the interspecific comparison of *F. crenata* and *F. japonica* at the seedling recruitment stage within the same forest.

Modeling approaches are often efficiently used to detect interspecific differences in seedling recruitment (Ito et al. 2006, Masaki et al. 2007). Masaki et al. (2007) surveyed emerged seedlings of several co-existing woody plant species in a temperate forest and accounted for a portion of co-existence mechanisms by modeling the relationship between the abundances of seedlings and micro-environmental heterogeneity. A modeling approach using monitoring data of seedling abundance and growth of both *F. crenata* and *F. japonica* at the same time points will provide a promising tool for revealing the interspecific differences responsible for the co-dominance of the two species. Furthermore, the relative importance of factors responsible for co-dominance at the seedling stage could be evaluated by comparison with factors at the adult stage. In the present study, we monitored seedling spatial abundance and growth traits of *F. crenata* and *F. japonica* during the early demographic stage in the forest where the spatial distribution of adult trees has already been surveyed. After applying statistical models, we addressed the following two questions: (i) Do the two species exhibit any differences in seedling spatial distribution or preferable condition? (ii) Do they exhibit differences in seedling traits of shoot growth and recovery from predation?

Materials and Methods

Study site

Our study was conducted in a natural, cool-temperate forest located on the southwest slope of the University of Tokyo Chichibu Forest in Saitama Prefecture, central Japan (35°56'N, 138°48'E, 1,215–1,280 m above sea level, Fig. 1). The mean temperature, annual precipitation, and snow depth were 8.9°C, 1,416 mm (recorded at the nearest meteorological station from 1993 to 2001), and 20–30 cm on average, respectively. In climax forests of this region, the major dominant species are *F. japonica*, *F. crenata*, and *Tsuga sieboldii* (Nozaki & Okutomi 1990). According to census data obtained from the 6.875-ha Long-Term Ecological Research (LTER) site established in this forest (Sawada et al. 2005), total basal area at breast height (BA) in this study site is 46.1 m^2/ha, suggesting old-growth forest, and is dominated by *F. japonica* (relative dominance [RD], 27.9%), followed by *T. sieboldii* (RD = 25.1%) and *F. crenata* (RD = 17.1%). This LTER site was divided into 25 m grid to form 25 × 25 m plots. Ten 25 × 25 m plots across topographical features within similar altitudes were selected in this study, and they were divided into nine 8.3 × 8.3 m subplots arranged 3 by 3 (Figure 1). Additionally, supplemental subplots were established adjacent to the 25 ×

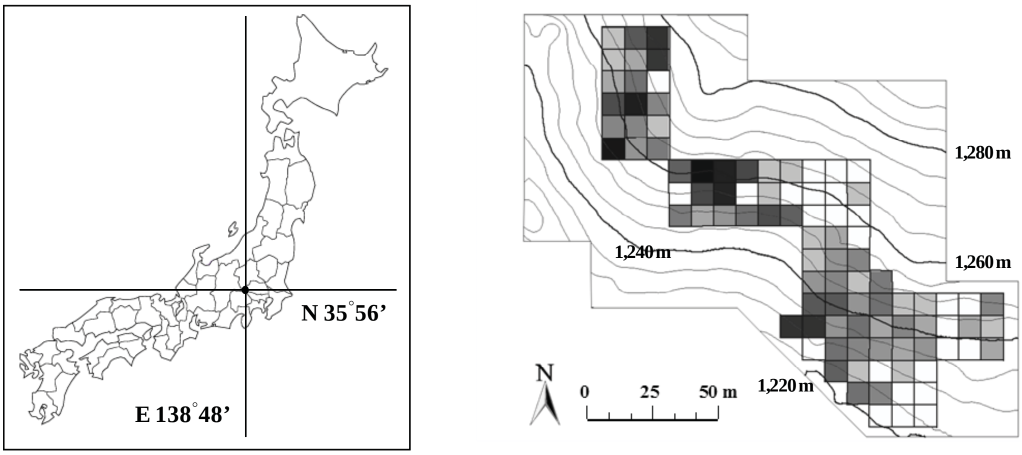

Figure 1 Locations of the study area in the University of Tokyo Chichibu Forest (left) and the study plots divided into 95 subplots (right). As an example, gradations of shading in the subplots indicate the number of seedlings of *Fagus japonica* during the initial growth period in 2007. White cells indicate that no seedlings were distributed within the subplot. Contour lines are projected at intervals of 5 m, and bold lines are drawn every 20 m.

25 m plot (Figure 1), thus, the total study area was 0.66 ha. The forest canopy at the plot was evenly closed without gaps during the summer. The floor of this forest is widely covered by dwarf bamboo, *Sasamorpha borealis* (Furubayashi & Yamane, 1997), whereas in the study site, dwarf bamboo is sparsely distributed due to retrogression associated with deer browsing (M. Kaji, personal observation).

Seedling census and field survey

F. crenata and *F. japonica* exhibit a habit of mast seeding at an interval of several years, and their mature seeds are usually dispersed by gravity. Mast years for *F. japonica* and *F. crenata* occurred in 2005 and 2006, respectively, and a number of seedlings of *F. japonica* and *F. crenata* emerged in the springs of 2006 and 2007, respectively. Subsequently, all newly emerged seedlings in the plots were identified, and their fates were followed from emergence until November, the end of the growing season in 2009, except for 2006. Many seedlings of *F. japonica* (> 150 seedlings per m^2 where high-density plots), were newly emerged in 2006, therefore, the fate of the emerged year was monitored using 50 × 50 cm quadrats for sampling census (Ishizuka et al., in preparation). Thus, the data in 2006 (living seedlings were only *F. japonica*) was omitted following analysis. Seedling censuses were conducted frequently at least once per week from May to August, and at least twice per month from September to December throughout the growing season in every year in order to obtain the reliable data. Because seedling density decreased markedly over time; in general, nearly 80% of emerged seedlings died within emerged year, and seedling death were continued even after age 2 in this forest (Kaji & Ohkubo 1995, Kaji et al. 1992, Ohkubo et al. 1989), dead seedlings were likely to miss to identify without frequent census. To evaluate the spatial heterogeneity of seedling abundance and its fluctuation during census period, we set six time points: the onset and end of the growth period in 2007, 2008, and 2009. At each time point, the number of living seedlings was calculated within each subplot for each species. At each age, the length of newly-elongated, current-year shoots was measured for randomly selected seedlings after shoot elongation had completed. In this forest, although one of the major mortality factors of *Fagus* species was herbivory (Ishizuka et al., in preparation), under high browsing pressure from *Cervus ni-ppon* (Kaji 1997), the seedlings often recovered from herbivory predation via sprouting secondary shoots at the tip of the remaining branches or adventitious shoots (buds). This recovery from predation was defined as “re-growth” in the present study, and seedling predation and the subsequent re-growth response were carefully surveyed in 2008.

To obtain fine-scale topographic variables, a digital elevation model (DEM) with a resolution of 8.33 m was created using ground measurements within and around the study plot, and slope inclination and convexity were profiled (Table 1). Convexity would be positive value (+) if topographic configuration was convex and negative value (-) if it was concave. Further descriptions of the extraction of topographical features are provided in Ishizuka and Kaji (2010). At the same time, the abundances of the two *Fagus* species were also determined using the following procedure. The diameters at breast height (DBH) and the locations of individuals of the two species over 5 cm in DBH were measured. The basal area (m^2) of each individual was calculated using DBH. The total basal area (BA) in each of the subplots was estimated for each species using the locations of individuals with the Arc GIS 9.3 software (ESRI, Inc.)(Table 1; see also Ishizuka & Kaji 2010).

To evaluate light conditions at the forest floor, we took hemispherical photographs 1 m above the ground at the center of each subplot (n = 95) in summer 2007. Average photosynthetic photon flux density (PPFD) during the

Table 1 Basic statistics for two topographic variables, rPPFD (relative values of Photosynthetic Photon Flux Density), and BA (Basal Area) of two *Fagus* species (*F. crenata* and *F. japonica*) per subplot.

Variables	N	Mean	S.D.	Max.	Min.
Topography					
Inclination	95	34.100	4.950	43.000	20.000
Convexity	95	-0.040	1.250	3.780	-2.310
rPPFD	95	12.510	3.590	24.460	5.660
BA (m^2)					
Fagus crenata	38	0.161	0.180	0.691	0.002
Fagus japonica	50	0.193	0.132	0.517	0.002

Note: S.D., Max., and Min. refer to the standard deviation, the maximum value, and the minimum value of the subplots, respectively. rPPFD refers to the light conditions at the forest floor relative to that without canopy cover. For BA, subplots for which the subject species was absent were omitted.

growth period (May to November) was estimated using the photographs and the software Winphoto 5 (Hans ter Steege 1996). Light conditions were then calculated as relative values of *PPFD* (*rPPFD*) compared with light conditions without canopy cover (Table 1), the resulting values were used in subsequent data analysis. The effects of dwarf bamboo, *Sasamorpha borealis* (hereafter, sasa), which is sparsely distributed throughout the understory, were also evaluated as follows: 0 - absence, 1 - presence in the subplot.

Data analysis

The distributional properties of seedlings, such as spatial abundance or topographic preferences, were estimated for each species by generalized linear model (GLM). In this model, the dependent variable was the number of seedlings per subplot, and the independent variables were: 1) three topographic variables (inclination, convexity, and the square of convexity), 2) a measure of relative light conditions (*rPPFD*), 3) the presence of dwarf bamboo (sasa), and 4) the basal area (*BA*) of two *Fagus* overstory. The square value of convexity was included because convexity has both negative and positive values. The full model for the seedling abundance of species *i* of subplot *j* (N_{ij}) can be described as:

$$N_{ij} \sim \mathrm{Poisson}(\mu_{ij})$$

$$\log(\mu_{ij}) = \beta_0 + \beta_1 INC_j + \beta_2 CON_j + \beta_3 CON_j^2 + \beta_4 \mathrm{rPPFD}_j + \beta_5 P_{(sasa)j} + \beta_6 \mathrm{BA}_{Z\cdot ij}$$

where INC_j is the inclination of subplot *j*, CON_j is the convexity of subplot *j*, and $P_{(sasa)j}$ is the presence of sasa (0/1) of subplot *j*. In the parameter *BA*, *z* has two values, which represents species *i* or two *Fagus*. Former refers to conspecific basal area of subplot *j*, and latter refers to summed basal area of the two *Fagus* species of subplot *j*. These two types of variables were separately tested in the constructed model, because we assumed the effects of both seed source (positive effect) and the limitation of seedling recruitment under the beech canopy (negative effect). The GLM was set with Poisson error structure and a log link function. To exclude variables that did not affect goodness-of-fits of models, then, model selection was carried out by a backward stepwise procedure from the constructed full model. We used Akaike Information Criterion (AIC) to judge the goodness-of-fits in model selection (Akaike 1973, Johnson & Omland, 2004). Finally, the model with the lowest AIC value was selected as the best-fit model. This model analysis was performed separately at six independent time points (onset/end of the growth period for 3 years), and each species. For each of the best-fit model, the confidence of the selected model was validated by likelihood-ratio tests using differences in deviance from the null model which did not include the independent parameter used in full model described above, based on the χ^2 statistics. Interspecific comparisons were performed using the best-fit models.

Subsequently, interspecific comparisons were carried out by the evaluation of the growth traits under herbivory pressure. First, elongated current-shoot length of seedlings of two *Fagus* species in each year (2007–2009) was estimated by a linear model (LM). In this model, the independent variables were species (*F. crenata* or *F. japonica*), seedling age, and a measure of relative light levels (rPPFD). The full model for the shoot length of seedlings *k* of species *i* in subplot *j* (L_{ijk}) can be described as:

$$L_{ijk} = \beta_0 + \beta_1 SP_i + \beta_2 AGE_k + \beta_3 \mathrm{rPPFD}_j$$

where SP_i is species as *F. crenata* being the reference type, AGE_k is the age of seedling *k*. LM included the effects of seedling age and light conditions in addition to the effect of species, because these would not be negligible. To determine the best-fit model, model selection was performed also in LM, using AIC to judge the goodness-of-fits (Akaike 1973, Johnson & Omland 2004). The model with the lowest AIC value was selected as the best-fit model.

Second, the seedling potential of recovery from predation was compared between species. From monitoring data, the number of seedlings predated, exhibited re-growth response, survived after re-growth were summed separately at two species, and the proportions of recovery from predation were calculated and compared.

All statistical analyses were performed using R 2.10.1 (R Development Core Team, 2009).

Results

Distributional properties

Model estimations and model selections were performed at each time point along the age for each species (Table 2). Based on the likelihood-ratio tests, all six models for *F. japonica* were highly significant (all models; $p < 0.01$), indicating that these models adequately explained variation in seedling abundance (Table 2). For *F. crenata*, three early models (until the onset time point in 2008) were highly significant (all models; $p < 0.001$), whereas the later two models were not significant ($p = 0.077$ and 0.115, respectively); the last model for the end time point in 2009 could not be tested, because the best-fit model was the same as the null model (Table 2). Across all ages, the distributional patterns of *F. crenata* seedlings appeared to be independent of these variables. Based on the comparison between the two species, different distributional properties were represented in the topographic variables and light conditions (rPPFD), while the effects of the presence of sasa and the abundance of the beech overstory exhibited similar trends (Table 2). However, no opposite effects were detected for any variable (Table 2). For the topographic variables, the distributional patterns of *F. japonica* were affected by inclination and the square of convexity throughout the monitoring period, whereas the distribution of *F. crenata* did not exhibit a clear trend. Namely, seedlings of *F. japonica* tended to be distributed along steeper slopes but in areas of more moderate relief. For light conditions (rPPFD), *F. crenata* tended to be distributed under better light conditions at the early stage, whereas no effects of light condition were apparent for *F. japonica.* For the presence of sasa, negative effects were consistently detected in most of censuses for both species. For the basal area of the beech overstory, consistent negative trend was estimated, however, the time-series trend was not completely consistent between the two species; the negative effects disappeared in the latter models for *F. crenata*, and conspecific effects were only selected in the best-fit model at the end of 2007 and at the onset of 2008 for *F. japonica*.

Table 2 Results of GLMs and subsequent model selections to estimate the distributional properties of seedling of two *Fagus* species (*F. crenata* and *F. japonica*) at six time points from 2007 to 2009.

	Inclination	Convexity	(Convexity)^2	rPPFD	Sasa	Overstory	Model deviance
Fagus crenata							
’07 onset				*0.038*		**-1.713** (*Fc, Fj*)	**-16.798**
’07 end	**0.073**	*0.164*	-0.082	**0.066**	-1.000	**-1.382** (*Fc, Fj*)	**-26.681**
’08 onset	**0.074**	0.222	**-0.247**	0.052	-32.555	**-1.885** (*Fc, Fj*)	**-28.957**
’08 end					-29.907		*-3.132*
’09 onset					-29.517		-2.479
’09 end							0.000
Fagus japonica							
’07 onset	**0.052**				**-2.297**	**-1.276** (*Fc,Fj*)	**-62.052**
’07 end	**0.049**		-0.042		**-2.298**	**-2.310** (*Fj*)	**-69.282**
’08 onset	**0.044**		*-0.057*		**-2.290**	**-2.132** (*Fj*)	**-56.760**
’08 end	**0.046**		*-0.067*		**-1.976**	**-1.805** (*Fc,Fj*)	**-35.850**
’09 onset	**0.051**		-0.094		**-1.807**	**-1.731** (*Fc,Fj*)	**-32.011**
’09 end	*0.038*				*-1.799*	**-1.625** (*Fc,Fj*)	**-13.187**

Note: The variables with values refer to those selected in best-fit models, of which bold, italic, and plane font refers to the significant level, $p < 0.05$, $0.05 < p < 0.1$, and $0.1 < p$, respectively. Variable of “rPPFD” and “Sasa” refers to the effect of light conditions at the forest floor and that of the presence of dwarf bamboo (Sasamorpha borealis), respectively. For “Overstory” variables, total basal area of conspecific and two *Fagus* species (*Fc, F. crenata: Fj, F. japonica*) were both tested separately in the process of model selection. “Model deviance” was used in likelihood-ratio test.

Shoot growth

The average (± SD) values of shoot growth for *F. crenata* at ages 2 and 3 were 2.52 ± 1.64 and 1.16 ± 0.26 cm, respectively. The average shoot growths for *F. japonica* at ages 2, 3, and 4 were 1.48 ± 1.59, 1.46 ± 1.43, and 0.68 ± 0.45 cm, respectively. Based on the result of best-fit model, seedlings of *F. crenata* exhibited significantly superior growth compared to *F. japonica* ($p < 0.05$, Table 3). In addition to the difference between species, age-dependent shoot growth was also significant ($p < 0.0001$), whereas the light effect was not selected in the best-fit model (Table 3). Thus, light condition would not be important for the difference in shoot growth between species.

Recovery from predation

For *F. crenata,* 40.0% of the predated seedlings exhibited recovery via shoot re-growth response, and 15.0% survived until the end of the growth period (i.e. 25.0% of sampled seedlings exhibited re-growth response but died within the subsequent growing period;

Table 3 Results of GLMs and subsequent model selections to estimate the distributional properties of seedling of two Fagus species (*F. crenata* and *F. japonica*) at six time points from 2007 to 2009.

	Intercept	Species	Age	Light	Model deviance
Shoot length	3.472***	-0.621*	-0.526***		-69.073***

Note: Significance level: *** $p < 0.001$, * $p < 0.5$.
The variables with values refer to those selected in best-fit models. The “Species” variable contains *Fagus crenata* (set as a reference type) and *F. japonica*. “Age” and “Light” variables refer to seedling ages from 2 to 4 and rPPFD (relative Photosynthetic Photon Flux Density) values of each subjected subplot, respectively.

Figure 2). In contrast, 62.6% of predated seedlings exhibited re-growth response, and 36.2% survived for *F. japonica* (Figure 2). Thus, the proportion of recovered seedlings was significantly higher for *F. japonica* than for *F. crenata* (χ^2 test, $p = 0.015$).

Discussion

Factors responsible for co-dominance

Spatial segregation and differences in growth/survival characteristics were examined as the possible mechanisms of co-dominance of related species in the present study. Opposite patterns were not observed in distributional properties of *F. crenata* and *F. japonica* at the seedling stage (Table 2). The comparison of the spatial distributions relating to the topographical features between these species revealed that the range of the seedling distribution of *F. crenata* included that of *F. japonica*, indicating the distributional overlaps of these species. From the evidence, therefore, the spatial segregation hypothesis is not necessarily required for the co-dominance in the case of these species. It might be due to the species-specific properties of *F. crenata*; generalist species that exhibited the pattern independent of topographical features (Suzuki et al. 2002).

In contrast, shoot growth and the potential for herbivory resistance significantly differed between the two species, *F. crenata* exhibited superior shoot growth, whereas the proportion of seedlings recovered from predation was significantly higher in *F. japonica* than in *F. crenata* (Table 3, Fig. 2). These results indicated that the co-dominance would be caused by growth/survival characteristics rather than spatial segregation. The frequent recovery from predation via re-growth, especially detected in *F. japonica*, may contribute longer seedling resistance under herbivory pressure. Therefore, herbivory resistance would be one of the important traits to increase opportunities for the seedling establishment or subsequent seedling regeneration. Since seedling dynamics were examined focusing on the mortality factors, spatial pattern, and its density in most of previous studies conducted in a natural, cool-temperate forest, the resistance to herbivory has not been sufficiently quantified or compared in details (Maeda 1988, Masaki et al. 2005, Nakashizuka 1988, Ohkubo et al. 1989, Tomita et al. 2002). However, adaptive re-growth traits to small-scale disturbances were known in other *Fagaceae* species, *Fagus sylvatica* and *Quercus robur* (Harmer 1999), and *Quercus crispula* (Kabeya et al. 2003), through the experiment of the shoot clipping of seedlings. They also revealed that the re-growth responses were limited under the low light conditions, due to the lack of stored resources in

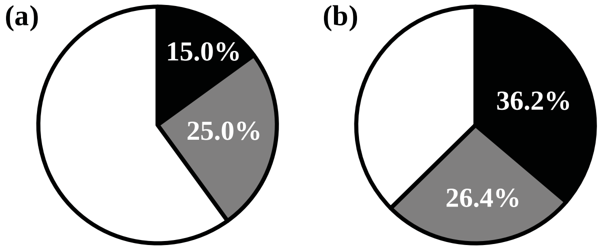

Figure 2 The proportion of re-growth seedlings of all predated seedlings for *Fagus crenata* (a) and *F. japonica* (b) in 2008. Re-growth seedlings were categorized into those that survived throughout the growth period (black) and those that died during growth period, even after exhibiting signs of recovery from predation (gray).

seedlings (Harmer 1999, Kabeya et al. 2003). In forests with a closed canopy (without a gap formation), light available for plants was usually limited (Nakashizuka 1987), and the stored resources tended to be insufficient under such relatively low light condition (Collet et al. 2001, Kabeya et al. 2003). Thus, resource limitation would be occurred in the present study site, i.e. climax forest dominating two *Fagus* species and one coniferous species with little gap above the plots providing only 12.5% of light on average (Table 1). These evidences indicated that both of two *Fagus* species possibly had the ability of re-growth, but the degree of response to harbivory was different due to the "trade-off" of resource allocation between seedling growth and herbivory resistance in study site. *F. japonica* would allocate more to increase herbivory resistance rather than the growth rate, compared to *F. crenata*. Although physiological data to support the differentiation of the resource allocation are not available between two *Fagus* species, the trade-off of resource allocation at the seedlings stage is known by interspecies and intraspecific comparison under the low light condition (Seiwa 2007). Due to this trade-off, both species will possess recruitment opportunities in the long-time scale. *F. crenata* would have a recruitment advantage at some cases due to its superior growth potential, whereas *F. japonica* would be more advantageous in other cases under small-scale disturbance, such as under high herbivory pressure, because its seedlings tend to persist longer. Thus, which species will recruit at a given location may be akin to winning a 'lottery' (*sensu* Masaki et al. 2007). Note that other important factors, such as the timing of mast seeding, gap formation, and/or the abundance of predators may also contribute to successful regeneration. Nevertheless, we demonstrated that the trade-off between growth and resistance to herbivory is one of the important factors responsible for the co-dominance of these two species.

Relationship between seedling and adult stages

The distributions of adult trees of *F. crenata* and *F. japonica* were also surveyed at the same study site of the present study (Ishizuka & Kaji 2010). Thus, we can compare the spatial preferences of seedlings with those of adults in the same forest. Based on the present results and those of Ishizuka and Kaji (2010), *F. crenata* exhibited consistent patterns during both stages (i.e., no relationship between distribution and topography). In contrast, the distribution of *F. japonica* seedlings was somewhat consistent with that of adult trees, steeper slopes were favored during both stages. These findings indicate that *F. crenata* consistently performs as a generalist, from the early seedling stage to the adult stage, and the distribution pattern of *F. japonica* is determined to some extent during the early seedling stage. Thus, seedling distribution patterns may be one of the important aspects of regeneration dynamics of these two beech species. Similar distribution patterns have been also detected in other forests: i.e., the general distributional pattern of *F. crenata* and a topography-related pattern for *F. japonica* (Masaki et al. 2005, Suzuki et al. 2002, Yoshida & Ohsawa 1996). Thus, the topographic preferences of the two beech species observed in the present study may be common in a beech forest.

We expected that the basal area of conspecific adult trees would positively affect seedling abundance, because they will serve as a seed-source of their seedlings. In this study, however, negative effects of the basal area of conspecific adults were detected, indicating that the seed-source effects would be negligible (Table 2). One possible reason is host-dependent mortality near the conspecific adult trees, such as predation by rodents or fungal attack at the seed-seedling stage, which has been previously detected for *F. crenata* in the cool-temperate forest (Tomita et al. 2002). As a result of these mortality processes following seed dissemination, such negative effects of adult trees at the early seedling stage would occur in both species. However, the topographic dependence was maintained, indicating the relative importance of topographic preferences during the early recruitment stage of both species.

We also detected significant differences in growth traits during the seedling stage between the two species (i.e., allocation to growth versus increasing resistance to herbivory; Table 3, Figure 2). Differences in life history traits were maintained even at the adult stage. Only *F. japonica* exhibits good sprouting ability by forming multi-stemmed stool in a natural forest (Ohkubo 1992), with an average of 3.3 stems per stool in this forest (Ishizuka & Kaji, 2010). This sprouting trait may allow the long persistence of each individual of *F. japonica* by maintenance of the stool. In contrast, *F. crenata* has a single stem and depends only on seedling regeneration that would be proceeded after gap formation (Nakashizuka 1987). The consistency of these interspecific differences between seedling and adult stages would provide strong evidence to understand the critical mechanism of co-dominance of these two species throughout the demographic stages.

Conclusion

Co-existence can be explained by several factors or mechanisms, but their relative importance would be different among forest systems (Nakashizuka 2001). In the present study, distribution patterns related to topography, current-year shoot growth, and re-growth from herbivory were examined at the seedling establishment stage of the related two beech species, *Fagus crenata* and *F. japonica*, in a cool-temperate forest in central Japan. This study indicated that not the spatial segregation but the trade-off of resource allocation between seedling growth and seedling resistance must be one of the important factors for the co-existence of these related species. The regeneration advantage of these two species would shift depending on the extent of the small-scale disturbance, such as herbivory pressure. Therefore, the temporal or spatial environmental heterogeneity in this study site might allow the forest to maintain the dominance of these two species.

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