

Influence of canopy tree phenology on understorey populations of *Fagus crenata*

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Abstract.

Question: Is light available for subcanopy individuals of *Fagus crenata* spatiotemporally heterogeneous across patches with closed canopies of different foliage phenologies and gaps? Is local abundance of *Sasa* influenced by the composition of the canopy layer? If so, does the *Sasa* layer also affect the amount of light available to small *F. crenata* saplings? Is variation in *F. crenata* population structure consistent with the hypothesis that light is important?

Location: Mt. Kurikoma, Japan 780 m a.s.l.

Methods: Population structure of subcanopy individuals of *Fagus crenata* and importance of *Sasa* were examined in five patch types. The patch-types were Fc (*F. crenata* only in the crown), Qm (*Quercus mongolica* var. *grosseserrata* only in the crown), Mo (*Magnolia obovata* only in the crown), Fc' (periphery of *F. crenata*) and Gap. Seasonal changes in light availability above and below the *Sasa* layer was examined by using hemispherical photographs and quantum sensors.

Results: Subcanopy individuals of *F. crenata* began unfolding their leaves approximately one month earlier than canopy trees of *Q. mongolica* var. *grosseserrata* and *M. obovata*, but a few days later than those of adult *F. crenata*. Accumulated photosynthetic photon flux density above the *Sasa* layer was greatest in Qm and Mo, and lowest in Fc. Importance of *Sasa* was highest in Gap. Maximum height and the number of subcanopy individuals of *F. crenata* were greatest in Qm, followed by Mo, and lowest in Fc.

Conclusions: Differences in canopy layer composition probably influence the regeneration of *F. crenata* both directly through their foliage phenologies, and also indirectly by determining the importance of *Sasa*.

Keywords: Dwarf bamboo; Leaf emergence; Light availability; *Magnolia obovata*; *Quercus mongolica* var. *grosseserrata*; *Sasa*; Size structure; Temperate forest.

Nomenclature: Ohwi & Kitagawa (1983).

Abbreviations: PPFD = Photosynthetic Photon Flux Density; RPPFD = Relative PPFD.

Introduction

Because in many forests light is a major environmental factor limiting the growth and survival of plant species (Grime 1979; Chazdon 1988; Chazdon et al. 1996; Whitmore 1996), spatial patterns of light availability are likely to influence the spatial arrangement of plant species (e.g. Clark & Clark 1992; Clark et al. 1996). It is well known that heterogeneity of light availability across the gap-understorey continuum can strongly determine the local distribution of woody species within a forest (e.g. Canham et al. 1990; Bazzaz 1991; Davies et al. 1998; Denslow et al. 1998). Such heterogeneity has a significant effect on forest regeneration and future composition by influencing the composition and abundance of advance regeneration (e.g. Brokaw 1985; Morin 1994; George & Bazzaz 1999b).

In broad-leaved temperate deciduous forests, variation in understorey light conditions is produced not only by spatial variation of overstorey structure, but also by temporal variation among species in the timing of leaf emergence (Kikuzawa 1983; Lechowicz 1984; Seiwa 1998). A large amount of light is usually available for the understorey plants prior to leaf emergence of canopy trees in early spring. This is particularly evident under canopies that exhibit late leaf emergence, with light conditions deteriorating soon after canopy closure (e.g. Uemura 1994; Seiwa 1998; Maeno & Hiura 2000; Komiyama et al. 2001; Routhier & Lapointe 2002). There is increasing evidence that earlier leaf emergence in tree seedlings, compared with canopy trees, is a crucial factor for their survival and growth (Jones et al. 1997; Seiwa 1997, 1998). By extension, differences in the phenological traits between overstorey and understorey plants could lead to a spatially patchy population structure of woody subcanopy individuals. However, the possible importance of phenological differences for advance regeneration has largely been ignored (e.g. Horn 1975; Canham et al. 1990, 1994).

Fagus crenata (Fagaceae) is the most dominant broad-leaved deciduous tree species of old growth forests in the cool-temperate region of Japan. The canopy trees usually unfold their leaves in early spring when a substantial amount of snow remains on the forest floor (Maruyama 1979). This would suggest that the advantages of early spring leaf development would be minimal for subcanopy individuals of *F. crenata* under conspecific adults. However, several tree species with differing leaf phenologies usually co-exist in the old-growth forests. If some of these species begin to leaf out later, the advantage of early spring leaf development of subcanopy individuals of *F. crenata* could be substantial. If this is the case, the distribution pattern of subcanopy individuals of *F. crenata* should be affected by the variation in light conditions resulting from the different foliage phenologies of canopy species.

The amount of light available for tree seedlings and small saplings in forest understories is also reduced by the abundance of understorey herbs and shrubs (Messier et al. 1989; Lorimer et al. 1994; George & Bazzaz 1999a, b), resulting in lower growth and survival of tree seedlings (Nakashizuka 1987; Taylor & Qin 1988, 1992; Wada 1993; Humphrey & Swaine 1997; Takahashi 1997). In Japanese beech forests, *F. crenata* regeneration is particularly inhibited by the evergreen dwarf bamboo *Sasa* (Nakashizuka 1988; Abe et al. 2001, 2002), which forms dense stands in gaps (Saitoh et al. 2000). Decrease in the abundance by simultaneous death of *Sasa* enhances regeneration of trees (Abe et al. 2002). Thus, advance regeneration of late-successional species such as *F. crenata* may be influenced, not only by attributes of the canopy layer, but also by the abundance of *Sasa*.

This study aims to evaluate the relationships between abundance of advance regeneration of *F. crenata*, composition of the canopy layer and the abundance of *Sasa*. The differences in leaf phenology between subcanopy individuals of *F. crenata* and canopy trees, together with seasonal light conditions above and below the *Sasa* layer, were investigated in five dominant patch types in a deciduous broad-leaved forest dominated by *F. crenata*. In each patch, the size and age structure of subcanopy individuals of *F. crenata* populations was also investigated. We use the term 'subcanopy individuals' to include both the large and small saplings above and below the *Sasa* layer. In this study, the following questions were posed.

1. Is light available for subcanopy individuals of *F. crenata* spatio-temporally heterogeneous across patches with closed canopies of different foliage phenologies and gaps?

2. Is local abundance of *Sasa* influenced by the composition of the canopy layer? If so, does the *Sasa* layer also affect the amount of light available to small *F. crenata* saplings?

3. Is variation in *F. crenata* population structure consistent with the hypothesis that light is important?

Material and Methods

Study site

The study was conducted on Mt. Kurikoma (38°58' N, 140°47' E, 1628 m a.s.l.), northern Japan. The mean annual temperature and precipitation were 8.1 °C and 2072 mm, respectively, at the Komanoyu automated meteorological data acquisition system (AMeDAS) station (520 m a.s.l.), located 3 km southeast of the study site (Anon. 1993). The study site was established on a southeast gentle slope (780 m a.s.l.). Therefore microtopography and soil conditions were relatively homogeneous.

The study site (ca. 20 ha) consisted of primary forest dominated by *F. crenata*. Density of all trees with DBH (diameter at breast height) > 2 cm was 3138 ind.ha⁻¹ (Hara et al. 1991). The canopy layer (ca. 24 m in height) was dominated by *F. crenata*, which accounts for 77.8% of the total basal area (36.7 m².ha⁻¹), as measured in a 1-ha plot (Hara et al. 1991; Kanno et al. 2001). Other tall tree species present were *Quercus mongolica* var. *grosseserrata* (relative basal area: 5.6%), *Magnolia obovata* (2.6%), and the shrub species *Viburnum furcatum* (0.9%), *Lindera umbellata* var. *membranacea* (0.2%), *Ilex leucoclada* and *Skimmia japonica* var. *intermedia* fo. *repens*. Dwarf bamboos, *Sasa palmata* and *S. kurilensis* were observed in the understorey. All of these species are common in Japanese beech forests (Hukushima et al. 1995).

Population structure of subcanopy individuals

Five patch types were designated on the basis of different overstorey phenology. Three of these patch types consisted of only *F. crenata* (Fc), only *Q. mongolica* var. *grosseserrata* (Qm) and only *M. obovata* (Mo) in the crown (height of each patch was over 16 m), respectively. A fourth patch type, 'Gap', was defined as an area of maximum canopy height less than 8 m, in accordance with the vegetation height profile technique (Tanaka & Nakashizuka 1997). The gaps were created naturally by single or multiple treefalls. The gaps ranged in area from 120 m² to 880 m² in 1999. A fifth type of patch, the periphery of Fc (Fc'), was assigned separately due to the substantial differences in environmental

conditions (i.e. light, abundance of *Sasa*) experienced between the periphery and interior of the Fc patch (Saitoh et al. 2000, 2002). A plot (5 m × 5 m) was set in the centre of each of the five patch types, with one side of the plot facing true north. A quadrat (2.5 m × 2.5 m) was established on the southwest edge of each plot. Five sub-quadrats (each 0.5 m × 0.5 m) were set in each quadrat. One was positioned in the centre and the other four on each corner. For each patch, except for Fc', the centre was defined as the intersection of the longest dimension with the widest perpendicular measurement. Approximate patch size was determined as the mean distance from the centre of the plot to the periphery (i.e. extension of two diagonals and four cardinal points of the plot, mean ± SD: Fc = 16.0 ± 7.9 m, Mo = 5.0 ± 1.6, Qm = 9.5 ± 4.7, Gap = 9.3 ± 6.1). There were 15 randomly assigned replicates of Fc, Fc', Qm and Gap, and only 10 replicates of Mo due to the lack of *Magnolia* adults within the study site. In total 70 patches were surveyed.

To distinguish between the effect of *Sasa* importance and canopy phenologies on the population structure of subcanopy individuals of *F. crenata*, we sampled the subcanopy individuals of *F. crenata* in two different height strata, above and below the foliage layer of *Sasa*. The height of the *Sasa* foliage layer varied little among patch types, reaching a maximum of 134 cm (mean ± SD: 75 cm ± 59). Therefore, we defined those subcanopy individuals taller than 1.3 m as large saplings and those shorter than 1.3 m as small saplings. The height of all the saplings was measured. Age of the subcanopy individuals was determined by counting bud scale scars (Nakashizuka & Numata 1982; Nakashizuka 1983). If the bud scale scars were unclear, increment cores were used to determine the sapling age. Cores were extracted from the stems near the ground surface. Some trees were rejected from the age analysis because of extensive heartrot. Importance of *Sasa* (*Sasa* quantity index) was estimated by multiplying the number of culms by the mean height of the foliage layer (total length of *Sasa* culms). The number of culms and the mean height of the foliage layer were measured in each sub-quadrat.

Leaf phenology

Leaf emergence of short subcanopy individuals (0.1 m to 5 m tall), was defined as the time when more than half of the terminal buds of all the first-year shoots unfolded their first leaf. The time of leaf emergence in tall subcanopy individuals (5 m to 10 m tall) and canopy trees was when more than half of the terminal buds of 150 shoots (50 randomly chosen current-year shoots each from the upper, middle and

lower crown) unfolded their first leaves, in accordance with Seiwa (1999a, b). Percent leaf emergence (Fig. 1) was defined as the fraction of the total number of leaves that had emerged by a particular date. Binoculars were used to investigate leaf emergence. To determine the growth of individual leaves of the canopy trees, the length of the major axis and minor axis of individual leaves of three and five randomly selected canopy trees was chosen for each study species in 1999 and 2000, respectively. Samples were obtained within our reach. Sample sizes are shown in Fig. 1. Leaf area was calculated as the major axis multiplied by the minor axis of the leaf. Relative increment of leaf area was calculated as $x_i/x_{max} \times 100$, where x_i represents the leaf area at the measurement date i , and x_{max} represents the maximum leaf area. These measurements were conducted at 1- to 4-day intervals in 1999 and 2- to 7-day intervals in 2000.

Light conditions

We measured light availability both above the *Sasa* foliage layer (2 m in height) and below the *Sasa* foliage layer (0.5 m in height). This was initially carried out by directly measuring the photosynthetic photon flux density at the two heights (PPFD_{2.0} and PPFD_{0.5}) with quantum sensors (MDS-L, ALEC ELECTRONICS CO., Ltd. Kobe, Japan) calibrated with a LI-COR quantum sensor (LI-189, LI-COR Inc., Nebraska, USA). Eight sensors were set and the PPFD measurement was instantaneously read at 1-min intervals from 11 May 2000 to 31 July 2000. Secondly, as an indirect measurement, hemispherical photographs were taken using a levelled fish-eye lens (LC-ER1, Nikon CO., LTD. Tokyo, Japan) attached to a digital camera body (COOLPIX 950, Nikon CO. Ltd. Tokyo, Japan) mounted on a tripod. This investigation was replicated five times for each of four patch types (a total of 20 patches), at two heights in each patch, four times in spring and once in summer (a total of 200 photographs). Canopy openness was calculated from these photographs as the percentage of unobstructed sky, weighted for the angle of incidence, according to ter Steege (1993). The photographs were transformed into computer data, and the PPFD was computed with HEMIPHOTO software (ter Steege 1993). Relative PPFD (RPPFD) was obtained by dividing PPFD in each height class (RPPFD_{2.0} and RPPFD_{0.5}) in each patch by that in an unobstructed sky.

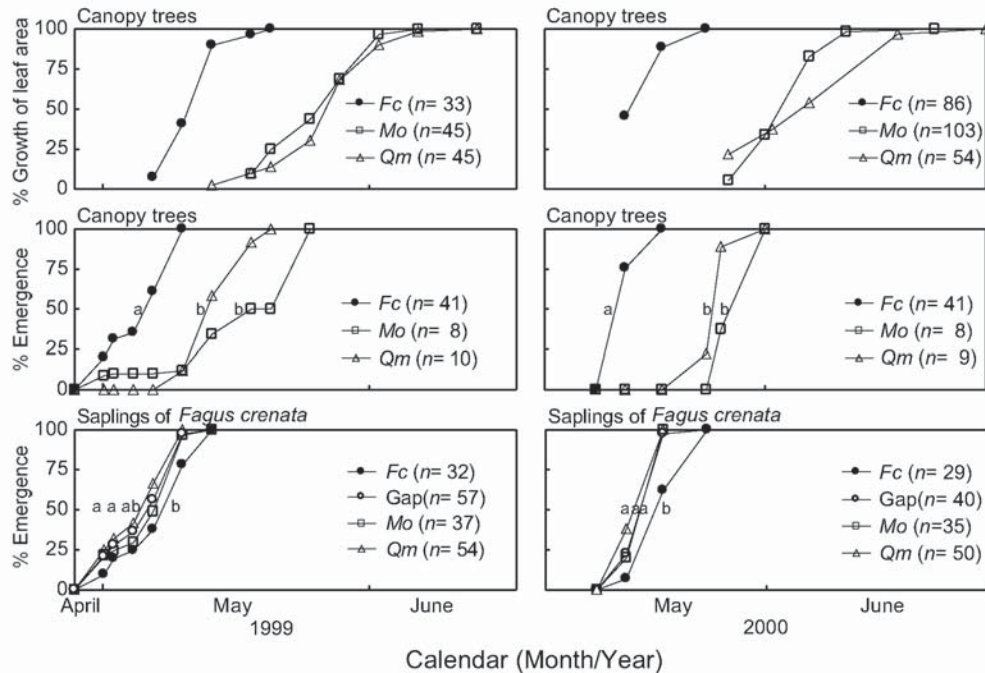


Fig. 1. Relative frequency of leaf emergence of individual saplings of *F. crenata* and canopy trees (% Emergence), and percent leaf-area growth of individual leaves of canopy trees (% Growth of leaf area) during the growing season in 1999 and 2000. Timing of leaf emergence followed by the same letter is not significantly different at $P < 0.05$ by Dunn's test after Kruskal-Wallis test for the juveniles. Fe, Mo and Qm indicate *Fagus crenata*, *Magnolia obovata* and *Quercus mongolica* var. *grosseserrata*, respectively.

Statistical analyses

To evaluate the difference in timing of leaf emergence, the Kruskal-Wallis test was chosen to compare the period (days) from the date of first observation to the date of leaf emergence (29 April in 1999; 10 May in 2000). This test was chosen because the data did not meet assumptions of normality. When an overall significant difference was found by the Kruskal-Wallis test, comparisons for all pairs were performed using Dunn's test (Zar 1999).

Seasonal changes in RPPFD were analysed using multivariate analysis of variance (MANOVA) with the five investigation dates as repeated measures, patch type and height class (nested in patch type) as factors (Anon. 2000). Statistical significance was assessed using exact F -contrast tests for between-subject effect; we used an unadjusted univariate F -test for within-subject effect because the sphericity test was not significant (Anon. 2000). A significant interaction was observed in the within-subject effect. Therefore, a nested analysis of variance (nested ANOVA) was used to compare the differences in the RPPFD among the four patch types in each investigation. Comparisons for all pairs were performed using the Tukey-Kramer HSD test ($P < 0.05$) when an overall significant difference was found by nested ANOVA.

To compare the *Sasa* quantity index between patch types, we used a nested ANOVA for completely randomized partial hierarchical designs. The experimental model is composed of patch types as the main treatment and plots (nested in patch types). Comparisons for all pairs were performed using the Tukey-Kramer HSD test ($P < 0.05$) when an overall significant difference was found using the nested ANOVA.

A Kolmogorov-Smirnov test was used to compare height and age structure of the subcanopy individuals of *F. crenata* between all pairs of the five patch types. Comparisons for all pairs of the patches were performed using a Bonferroni adjustment (Sokal & Rohlf 1995), in which the overall $\alpha = 0.05$ was divided by the total number of comparisons ($\alpha' = 0.05/10 = 0.005$). A one-way ANOVA was used to compare the difference in the number of subcanopy individuals of *F. crenata* among the five patch types. A comparison of all pairs was carried out using the Tukey-Kramer HSD test ($P < 0.05$) when the overall significant difference was found by ANOVA.

To estimate the influence of *Sasa* importance on the subcanopy individuals, an ANCOVA was also performed using the *Sasa* quantity index as a co-variable, patch type as a factor, and the total number of the subcanopy individuals as a dependent variable. Spearman rank correlations were used to investigate

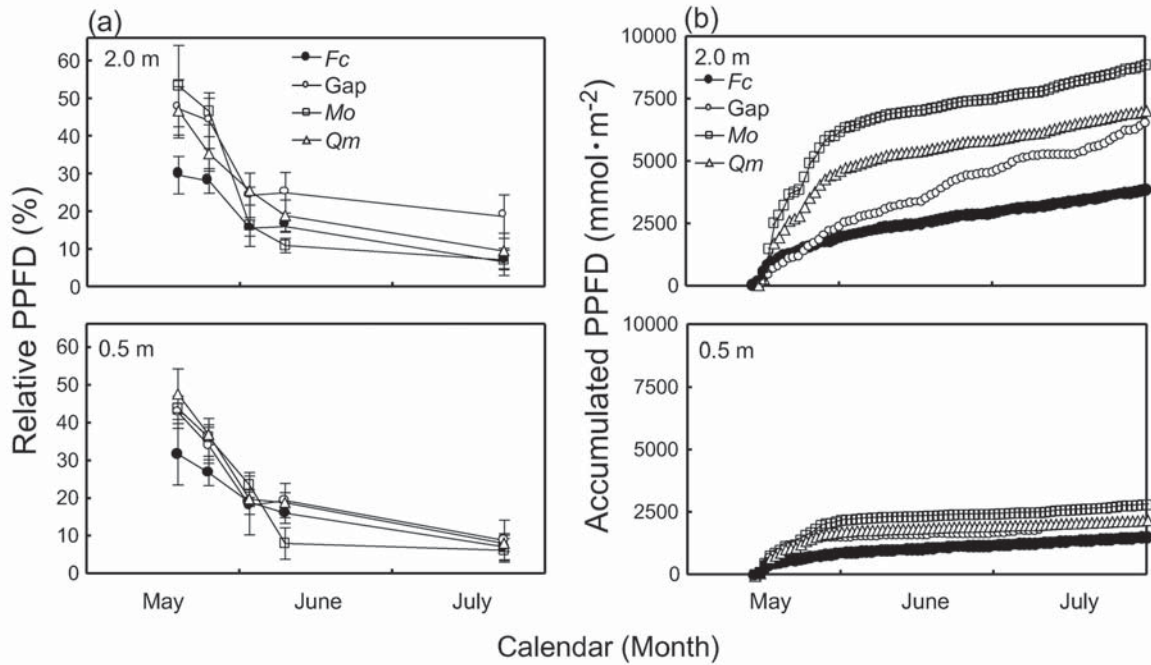


Fig. 2. Seasonal changes in (a) relative photosynthetic photon flux density (Relative PPF) and (b) accumulated photosynthetic photon flux density (accumulated PPF) above the *Sasa* spp. layer (at 2 m) and below the *Sasa* spp. layer (0.5 m) above the ground in the four patch types observed.

correlation between height and age of subcanopy individuals in each of the five patch types. Data were transformed to square root-, $\ln(x + 1)$ - or arcsine- (used for % values) when necessary to meet the assumptions of normality. Calculations of Kolmogorov-Smirnov tests were carried out with the Statview software program (Anon. 1998). All other statistical analyses were performed using JMP (Anon. 2000).

Table 1. Multivariate nested analysis of variance with repeated measures in time of RPPFD (%; arcsine transformed) under the four patch types.

	df	F	P
Within-subjects effects			
Time	4	63.3600	< 0.0001
Time × Patch type	12	2.1230	0.0273
Time × Height (Patch type)	16	0.6869	0.7961
Between-subjects effects			
Patchtype	3	4.1589	0.0234
Height (Patch type)	4	3.6352	0.0273

Results

Seasonal changes of understorey light conditions in different canopy types

In canopy trees, timing of leaf emergence of *F. crenata* was approximately two weeks earlier than that of *Quercus mongolica* var. *grosseserrata* and *Magnolia obovata* in both 1999 and 2000 (Fig. 1: Dunn's test, $P < 0.001$ after Kruskal-Wallis test $H > 42.77$, $P < 0.05$). Leaf area growth also occurred earlier in the season for *F. crenata* than *Q. mongolica* var. *grosseserrata* and *M. obovata*, both of which completed their leaf expansions approximately three weeks later than *F. crenata* (Fig. 1).

In mid-May, RPPFD was significantly greater in Qm, Mo and Gap (46.6-53.2%) than in Fc both above and below the *Sasa* layer (29.6%; Table 1, Fig. 2, Tukey Kramer HSD tests, $P < 0.05$ after nested ANOVA: $F = 6.52$; $P < 0.01$), due to the earlier leaf flushing of the canopy trees of *F. crenata*. By early June, there was little difference in RPPFD among the patches (Fig. 2). In late July, the RPPFD reached minima in all patch types. RPPFD_{2.0} was greatest in Gap (18.6%); in the other three types of patch (Qm, Mo, Fc) it was lower and showed no significant difference (Tukey Kramer HSD tests: $P < 0.05$ after nested-ANOVAs; $F = 6.85$; $P < 0.01$).

During the short period in May, accumulated PPF_D_{2.0} increased rapidly in both Qm and Mo, but more slowly in Fc, resulting in accumulated PPF_D_{2.0} in Fc being less than half of that in Qm and one-third of that in Mo by the end of May (Fig. 2). After canopy closure, accumulated PPF_D_{2.0} increased faster in gaps than in the other three patch types. Temporal patterns in accumulated PPF_D_{0.5} were similar to accumulated PPF_D_{2.0} for most patches, although the increases slowed in May in Gap, resulting in little differences in the accumulated PPF_D_{0.5} and RPPFD_{0.5} between all patches in late July (Fig. 2, Table 2).

Leaf emergence in subcanopy individuals of *F. crenata* under Fc was later than under Qm and Gap in both 1999 and 2000 (Fig. 1: Dunn's test, $P < 0.01$ after Kruskal-Wallis test $H > 18.49$, $P < 0.0003$). As a result, approximately two to three weeks were available to the subcanopy individuals of *F. crenata* for carbon gain prior to the leaf emergence of canopy trees in Qm in both years and Mo in 2000, but fewer days were available in Fc.

Population structure of subcanopy individuals of *F. crenata* under different patch types

Frequency distributions by both height and age of subcanopy individuals of *F. crenata* differed significantly between some of the five patch types (Fig. 3; Kolmogorov-Smirnov test, Bonferroni-adjusted $P < 0.05$). Maximum height of the subcanopy individuals was greatest in Qm and Mo, but lowest in Fc' and Fc, and intermediate in Gap (Table 2). The density of large saplings (height ≥ 1.3 m) per plot followed a similar pattern. The density of small saplings (height < 1.3 m) was also greatest in Qm and decreased in the order Fc', Gap, Mo, Fc (Table 2: Tukey Kramer HSD test, $P < 0.05$ after one-way ANOVA: $F = 6.83$; $P < 0.001$). As a result, the total number of subcanopy individuals (mean \pm SE) per plot (25 m²) was greatest in Qm and decreased in the order Fc', Mo, Gap, Fc

(Fig. 3, Table 2: Tukey Kramer HSD test: $P < 0.05$; after one-way ANOVA: $F = 12.56$; $P < 0.001$).

The number of subcanopy individuals of more than 40 yr old observed per total plot area (375 m²) was also greatest in Qm (185) and Mo (93), lowest in Fc' (12) and Fc (3), and intermediate in Gap (30; Fig. 3). Maximum age of the subcanopy individuals was greatest in Qm (210 yr old) and decreased in the order, Gap (84 yr old), Fc' (83 yr old), Mo (81 yr old), Fc (49 yr old) (Fig. 3). In each patch type, height of the subcanopy individuals was positively correlated with age (Fc: $r_s = 0.5912$, $P < 0.0001$; Fc': $r_s = 0.6928$, $P < 0.0001$; Gap: $r_s = 0.8434$, $P < 0.0001$; Mo: $r_s = 0.5062$, $P < 0.0001$; Qm: $r_s = 0.7416$, $P < 0.0001$).

The total number of subcanopy individuals of *F. crenata* significantly decreased with an increase in *Sasa* quantity index (Table 2; ANCOVA: Patch type; $F = 5.621$; $P = 0.0006$; *Sasa* quantity index; $F = 16.146$; $P = 0.0002$). There was a negative correlation between the number of small saplings of *F. crenata* and *Sasa* quantity index not only among the all patch types ($n = 70$; $\log Y = -4.83 \log X + 10.47$; $P < 0.01$) but also in Gap ($n = 15$; $\log Y = -8.87 \log X + 13.20$; $P < 0.05$), indicating that the dense *Sasa* layer strongly inhibited the regeneration of small saplings of *F. crenata*.

Table 2. Maximum height and mean number (\pm SE) of individuals of *F. crenata*, *Sasa* quantity index and accumulated PPF_D in each patch type.

Patch-type	Max. height (m)	Number of individuals (25 m ²)			<i>Sasa</i> quantity index (cm.cm ⁻²)	Accumulated PPF _D (mmol.m ⁻²)*	
		SS	LS	Subcanopy ind.		0.5 m in height	2.0 m in height
Fc ($n = 15$)	1.9	8.8 \pm 2.6 ^a	0.3 \pm 0.2 ^a	9.1 \pm 2.6 ^a	942.6 \pm 313.3 ^a	1514.4	3866.8
Fc' ($n = 15$)	3.3	21.9 \pm 6.5 ^a	1.3 \pm 1.1 ^a	23.1 \pm 6.7 ^a	1250.1 \pm 278.2 ^b	-	-
Gap ($n = 15$)	8.0	14.1 \pm 5.1 ^a	3.3 \pm 2.6 ^a	17.5 \pm 5.7 ^a	2585.9 \pm 754.6 ^b	1804.6	6601.1
Mo ($n = 10$)	9.7	10.0 \pm 4.0 ^a	7.8 \pm 2.1 ^b	17.8 \pm 4.3 ^a	1156.9 \pm 357.9 ^{ab}	2820.1	8931.0
Qm ($n = 15$)	16.0	51.7 \pm 9.6 ^b	13.9 \pm 1.6 ^c	65.7 \pm 9.2 ^b	311.6 \pm 103.4 ^c	2218.3	7103.6

Values with same superscripts are not significantly different between patches at $P < 0.05$ (Tukey-Kramer HSD test).

SS = small saplings < 1.3 m tall; LS = large saplings 1.3 - 10 m tall. * Values are obtained without repetition.

Discussion

Our survey in a Japanese beech forest revealed that light conditions available for subcanopy individuals of *F. crenata* were spatially heterogeneous. The amount of light available to subcanopy individuals during the study period was largely determined by the phenological events in spring, clearly evident from the differences in accumulated PPFD between patch types in spring compared with summer. For example, during the season, *F. crenata* patches received only 30% and 50% as much light as *M. obovata* and *Q. mongolica* var. *grosseserrata* patches, respectively. Such lower light availability in spring is likely to reduce the growth of subcanopy individuals of *F. crenata* (see Seiwa 1998), beneath *F. crenata* compared to *Q. mongolica* var. *grosseserrata* and *M. obovata*. In autumn, timing of leaf fall of *F. crenata* canopies is similar to those of *Q. mongolica* var. *grosseserrata* and later than those of *M. obovata* (see also Maruyama 1979). Such differences in the leaf fall phenology may also enhance dry mass gain of the subcanopy individuals of *F. crenata* (see Seiwa 1998), although reductions in photosynthetic capacity in autumn should also be considered (Koike 1990).

As a consequence, subcanopy individuals of *F. crenata* growing beneath the canopies of older *F. crenata* endure shaded conditions throughout their growing season. Such continuously shaded conditions would inhibit growth of subcanopy individuals and cause higher mortality, resulting in low population density and more L-shaped age distribution. In contrast, in the understories of *Q. mongolica* var. *grosseserrata* and *M. obovata*, greater light availability enhances survival of subcanopy individuals of *F. crenata* particularly in large ones, possibly explaining the greater number of old subcanopy individuals (i.e. age classes 40- to 60 yr old). It must be noted, however, that, there is a limit to which response of the through several decades is explained by the phenological events measured at a single point in time. We can only infer that differences in light conditions between patches, if these have persisted long enough, could cause the differences in population structure.

In temperate deciduous broad-leaved forests, several authors have previously noted that early leaf deployment of tree seedlings promotes biomass gain and enhances survival rates (Jones et al. 1997; Seiwa 1997, 1998). In *F. crenata*, such phenological advantage was also seen in current-year seedlings where greater survival was observed under heterospecific adults compared with conspecific ones (M. Tomita unpubl.).

In addition to the effects of different phenologies, subcanopy individuals of *F. crenata* may also experience the effects of other biotic factors in seed and seedling stages (Nakashizuka 1988; Homma et al. 1999;

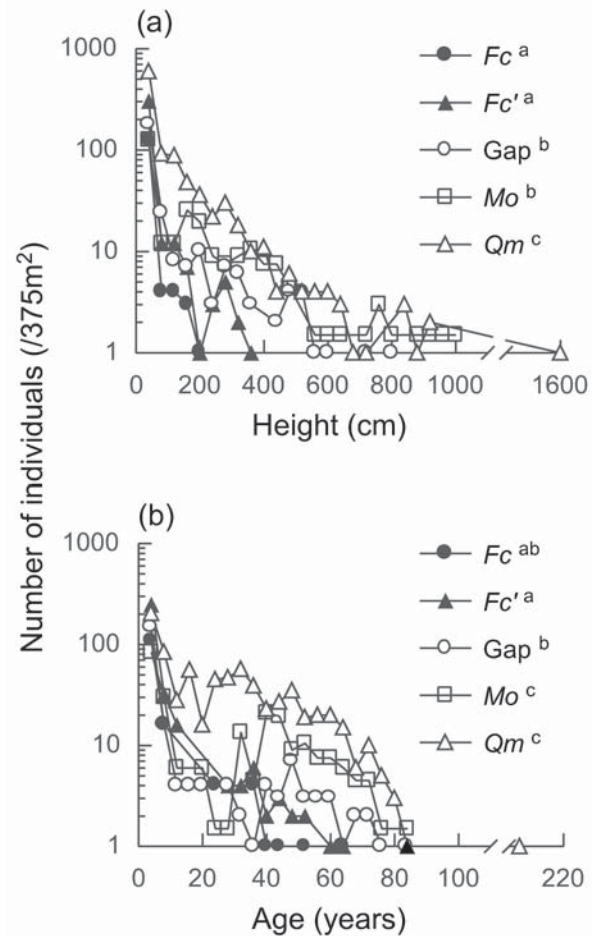


Fig. 3. Height (a) and age (b) structures of subcanopy individuals of *Fagus crenata* in all types of patch. The same letters are not significantly different by the Kolmogorov-Smirnov two-sample goodness-of-fit procedure (Bonferroni adjusted $P < 0.05$).

Abe et al. 2001). Seeds of *F. crenata* are severely attacked by rodents and fungi beneath the conspecific adults, resulting in a drastic decrease in the abundance of viable seeds beneath the adult plants compared to away from the adult plants, which leads to non-significant difference in the abundance of viable seeds between beneath and away from the adults (Tomita et al. 2002). These phenomena, occurring in the seed stages, instead of the phenological events, could also lead to a low population of subcanopy individuals of *F. crenata* under conspecific adults, compared with heterospecific ones.

Regeneration of small saplings of *F. crenata* appeared to be strongly inhibited by the abundance of dwarf bamboo, *Sasa*, particularly in the patches of *M. obovata*, periphery of *F. crenata* and gaps where *Sasa* density is high, probably due to the considerable reduction of available light under the evergreen foliage, a

conclusion that concurs with results of Nakashizuka (1988) and Abe et al. (2002). Dense *Sasa* also promotes the foraging activity of wood mice (Manson & Styles 1998; Seiwa et al. 2002), resulting in greater probability of death of seeds and seedlings of *F. crenata* (Ida & Nakagoshi 1996; Abe et al. 2001). Mean density of small saplings was also low beneath *M. obovata*, probably because of high *Sasa*. In gaps, mean density of small saplings was moderate in spite of greatest *Sasa* density, possibly because of high variability of *Sasa* density among gaps.

These results indicate that variation in both foliage phenology and *Sasa* density must be invoked to explain variation in *F. crenata* sapling density. It is evident that further research will be necessary to evaluate the relative contribution of environmental, biotic and abiotic factors (e.g. overstorey phenology, abundance of *Sasa* and wood mice activity) affecting the regeneration success of small saplings in the mosaic of patches in the Japanese beech forest.

Previous studies have shown that gaps influence spatial distribution of understorey plants (e.g. Runkle 1985; Hughes & Fahey 1991; Sipe & Bazzaz 1995; Bazzaz 1996), and focused on species differences in canopy density, not phenology (e.g. Horn 1975; Canham et al. 1990, 1994). In this study we infer that variation among canopy species in phenology can also influence the spatial distribution of an important tree species. These results suggest that the canopy influences saplings both directly through differences in foliage phenologies and indirectly by affecting the abundance of other understorey plants (i.e. *Sasa* spp.).

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