

Structure of Primary Japanese Beech (*Fagus japonica* Maxim.) Forests in the Chichibu Mountains, Central Japan, with Special Reference to Regeneration Processes

Tatsuhiro OHKUBO*, *Department of Forestry, Faculty of Agriculture, University of Tokyo,
Tokyo, 113 Japan*

Mikio KAJI,** *Department of Forestry, Faculty of Agriculture, University of Tokyo, Tokyo,
113 Japan*

and

Toshio HAMAYA, *Department of Forestry, Faculty of Agriculture, University of Tokyo,
Tokyo, 113 Japan*

Abstract

The floristic composition, structure and dynamics of three primary *Fagus japonica* stands were investigated in the Chichibu Mountains. *F. japonica* was dominant [RD(%): 64.9–87.0] and showed a slightly inverse J-shaped DBH class distribution in the quadrats [No. of canopy stems (H>20 m): 87–138/ha]. The stems of *F. japonica* for each size were distributed in the form of colonies, being scattered almost uniformly, and arranged in positive association with each other. Detailed examination of the bases of the stem groups forming colonies revealed that most of them originated from the bases of dead mother stems and that they were from common stools [No. of large stems (H>10 m) per stool: 6–11]. Among six major canopy gaps observed, only one included stems sprouting from the outer part of *F. japonica* stools, while all the others were occupied by individuals of species other than *F. japonica*. After tree-fall, several undercanopy *F. japonica* stems remained. Thus canopy gaps in these forest stands recovered through the sprouting of remaining *F. japonica* stools or by new sprouting of *F. japonica* individuals adjacent to the gaps. However, it was considered difficult to fill canopy gaps only with sprouts when the distance between the center of a gap and that of a stool surpasses the crown vector. Such places that are not fully occupied by sprouts will be filled by individuals of other canopy and/or under-canopy species.

Key words: Canopy gap; *Fagus japonica*; Forest structure; Regeneration process; Sprouting.

Introduction

Beech forests, distributed throughout the cool-temperate zone of Japan, can be divided into either the Japan Sea-side group of associations or the Pacific-side group of associations

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Present addresses: *Department of Forestry, Faculty of Agriculture, Utsunomiya University, 350 Mine-machi, Utsunomiya, 321 Japan.

**The University Forest in Chichibu, the University of Tokyo, 1-1-49 Hinoda, Chichibu, 368 Japan.

(Suzuki, 1952; Sasaki, 1970). *Abieti firmatis-Fagetum japonicae* Yoshioka 1952, *Fagetum crenato-japonicae* Yoshiyuki Sasaki 1970, *Styraco shiraiana-Fagetum japonicae* Yasushi Sasaki 1981 and *Enkiantho subsessilis-Fagetum japonicae* S. Suzuki in Miyawaki 1986 are associations of the Pacific side, and *Torreya-Fagetum japonicae* Nakanishi, Homma et Tasumi 1970 is an association of the transitional area between the Pacific and the Japan Sea side of the Chugoku district.

Fagus crenata individuals regenerate by seedlings (sexual reproduction), and the presence of canopy gaps plays an important role in forest regeneration (Jones, 1945; Watt, 1947; Whitmore, 1978). On the other hand, *F. japonica* shows characteristic sprouting of many adventitious shoots from the lower parts of dead stems (which form gap) and taking a bush-like form, which suggests that these sprouts play a major role in the natural regeneration of forests of this beech (Tohyama, 1965; Tanaka, 1985). Several types of vegetative reproduction have been reported in tree species, for example epicormic branching, as in the case of root suckers, root collar suckers, stem suckers etc., from dormant buds or adventitious buds (Zimmermann and Brown, 1971; Halle et al., 1978). Tree species showing vegetative reproduction may be the principal components in some types of forest community, and such vegetative reproduction plays an important role in forest regeneration, being a problematic factor in plant demography (Harper, 1977).

The main aim of the present study was to investigate the structure of primary *F. japonica* forests from the viewpoint of forest dynamics. This paper, the first of a series of reports, concentrates on the distributional pattern of stems, the structure of gaps and canopy strata, and processes of regeneration and maintenance of canopy strata in primary beech forests located in the Chichibu Mountains, on the Pacific side of central Japan.

Study Area and Methods

The study area was in a primary beech forest located on a slope in the University Forest, the University of Tokyo, in Chichibu, Saitama Prefecture [35°55'N, 138°50'E, 870–1160 m above sea level (a.s.l.)].

The climate of the study area is classified into the Pacific type, which is characterized by low precipitation in winter, and consequently is represented by a correspondingly low value of the Japan Sea Index (this index is calculated in terms of the clockwise angle between the Jan.–Aug. line and the axis of abscissa in a hythergraph; Suzuki, T. and Suzuki, K., 1971) of 52.5°, among the various climatic zones of Japan. At the meteorological station at Tochimoto (750 m a.s.l.) nearest to the study area, the mean annual precipitation is 1503 mm, whereas the warmth and coldness indices (WI, CI) (Kira, 1948) at different altitudes (lapse rate: 0.55°C/100 m) in the study area, reckoned from data obtained in Chichibu (218 m a.s.l.) (Chichibu Meteorological Station, 1976), range from 59.3 WI (–32.4 CI) to 70.5 WI (–24.4 CI) (degree-month), suggesting that this area is located in the temperate deciduous forest zone (Kira, 1948).

Previous researchers (Maeda and Shimazaki, 1951; Maeda and Yoshioka, 1952; Usui, 1971) regarded the area below 1600 m a.s.l. in the Chichibu Mountains as a temperate montane zone and also distinguished different types of plant communities in accordance with the topographic conditions, namely, the *Tsuga sieboldii-Rhododendron dilatatum* community on ridges, the *Fagus crenata-Sasamorpha purpurascens* community on mountain-sides, and the *Fraxinus commemorialis-Dryopteris polylepsis* community in ravines. *Fagus japonica*, growing at lower altitudes than *F. crenata*, dominates the lower region of the tem-

perate montane zone and is also tolerant to a wide range of edaphic conditions. The *F. japonica*-dominant forest community intervenes between the area of the *F. crenata*-*S. purpuracens* community and that of the *T. sieboldii*-*R. dilatatum* community. Takasugi (1965) also mentioned that *F. japonica* occupied a central position in the mesic-xeric gradient in this area.

Three quadrats (Q1 and Q2: 50 m × 70 m, Q3: 50 m × 40 m) were set in 1983 and 1984. Q1 was located on the upper part of a gentle slope (28.6°), facing N84°E, at an altitude of 1160 m a.s.l., Q2 was on the middle part of a gentle slope (16.5°), facing S70°E, at an altitude of 1040 m a.s.l. and Q3 was on the lower part of a steep slope (37.5°), facing S87°E, at an altitude of 870 m a.s.l.

Diameter at breast height (DBH) and height (H) for all living stems taller than 1.3 m were measured, and their locations, together with those of fallen dead stems and the bases of standing dead stems, were also recorded. Furthermore, the crown projections of all stems taller than 5 m within the quadrats were drawn on charts.

Results

Component species and their size structure

A total of 53 woody species ($H \geq 1.3$ m) were found in all three quadrats, among which 22 species had basal areas (BA) larger than 0.1 m²/ha. The height class distribution, the relative dominance (RD: % of BA) of component species and the total BA are shown in Table 1. *F. japonica* was dominant in each quadrat, and the RD of any tree species other than the two beeches (*F. japonica* and *F. crenata*) did not exceed 5%. Three strata could be distinguished on the basis of the height class distribution of all living stems. *F. crenata*, *Acer sieboldianum*, *Acer shirasawanum*, *Abies firma* and *Acer palmatum* var. *amoenum* were occasionally found in the canopy stratum ($H > 20$ m). The middle stratum ($8 < H \leq 20$ m) was composed of *Acer tenuifolium*, *Styrax obassia*, *Stewartia pseudo-camellia*, *Acer distylum*, *Fraxinus lanuginosa*, *Acer rufinerve*, *Meliosma myriantha* and others. *Callicarpa japonica*, *Euonymus oxyphyllus* and other species were observed in the shrub stratum ($1.3 \leq H \leq 8$ m). Large differences in total BA were found between Q1 and Q3. Since the specific total BA of *F. japonica* was less variable (Q1: 26.82, Q3: 25.98) (m²/ha), such large differences in total BA must have been attributable to that of *F. crenata*. The total stem density of *F. japonica* per hectare in Q2 was the lowest. Upon comparing the height class distribution of *F. japonica* (Table 1), the density of stems taller than 20 m was nearly equal among the quadrats, and the difference in total density among the quadrats resulted from that of the small-sized stems. The DBH class distribution of *F. japonica* was slightly inverse J-shaped (Fig. 1). The patterns of size class distribution for *F. japonica* were similar to those of the size structure of shrubs noted by Yamanaka and Tamai (1986).

Distribution of standing live stems

The distribution pattern of live stems standing in the quadrats was analyzed by means of Iwao's method (Iwao, 1968, 1972, 1977), in which \hat{m} -m regression is used as a measure expressing the randomness or clustering of stems. The analysis was applied to each of three categories of stems in the quadrats distinguished by their DBH-height relation curves as follows; A: DBH < 10 cm, B: $10 \leq \text{DBH} < 30$ cm, C: DBH ≥ 30 cm. Most of the standing live stems found in A, B and C belonged to the shrub, middle and canopy strata, respectively. Since it was proved that the regression of \hat{m} (mean crowding) or m (mean density) was approximately linear in most cases ($\hat{m} = \alpha + \beta m$), the above-mentioned analysis was per-

Table 1. Species composition and height class distributions of stems in the three quadrats.

Species	Quadrat No.												Freq.		
	1 (0.31 ha) ¹⁾				2 (0.33 ha)				3 (0.16 ha)						
	I	II	III	Total	RD	I	II	III	Total	RD	I	II		III	Total
<i>Fagus japonica</i>	1913	355	87	2355	73.7	342	170	94	606	64.8	2288	413	138	2839	87.0
<i>Fagus crenata</i>	3	16	19	38	20.9	9	6	9	24	9.8	31	13	.	44	0.3
<i>Acer sieboldianum</i>	190	6	.	196	0.5	115	12	3	130	2.1	219	13	.	232	0.7
<i>Acer shirasavanum</i>	277	19	.	296	1.7	30	6	3	39	1.6	6	.	.	6	+
<i>Abies firma</i>	10	.	.	10	+ ³⁾	15	3	3	21	2.0	50	19	.	69	2.1
<i>Acer palmatum</i> var. <i>amoenum</i>	13	.	.	13	+	58	3	.	61	0.3	25	.	6	31	2.1
<i>Acer tenuifolium</i>	158	13	.	171	1.4	624	18	.	642	3.0	144	6	.	150	1.1
<i>Styrax obassia</i>	.	3	.	3	0.1	42	18	.	60	1.2	19	.	.	13	0.5
<i>Stewartia pseudo-camellia</i>	3	3	.	6	0.1	39	64	.	103	4.1	19	.	.	19	+
<i>Acanthopanax sciadophyloides</i>	13	.	.	13	0.1	9	9	.	18	0.7	19	.	.	19	+
<i>Acer micranthum</i>	48	.	.	48	0.3	118	6	.	124	1.1	69	.	.	69	+
<i>Tilia japonica</i>	3	.	.	3	+	.	6	.	6	1.8	13	.	.	13	+
<i>Tsuga sieboldii</i>	10	.	.	10	+	6	.	.	6	+	13	13	.	26	1.1
<i>Acer distylum</i>	19	3	.	22	0.2	45	36	.	81	2.3
<i>Fraxinus lanuginosa</i>	12	3	.	15	0.1	144	13	.	157	2.0
<i>Acer rufinerve</i>	15	9	.	24	0.6	6	6	.	12	0.2
<i>Meliosma myriantha</i>	67	6	.	73	0.8	419	6	.	425	1.1
<i>Carpinus cordata</i>	6	6	.	12	0.5	25	.	.	25	+
<i>Magnolia obovata</i>	3	3	.	6	0.5	6	.	.	6	+
<i>Aesculus turbinata</i>	.	.	.	12	0.4
<i>Acer japonicum</i>	6	6	.	.	.	55	21	.	76	1.4
<i>Torreya nucifera</i>	87	27	.	114	1.2	996	6	.	1002	1.1
Others ²⁾	206	9	.	215	0.6	87	27	.	114	1.2	996	6	.	1002	1.1
Total	2872	433	106	3411	100.0	1697	432	112	2241	100.0	4580	521	144	5245	100.0
Total BA	(36.37)														
(33.47)															
(29.91)															

Height class; I: 1.3 < H ≤ 8 m, II: 8 < H ≤ 20 m, III: H > 20 m (No./ha). RD: Relative dominance. Nomenclature after Ohwi (1978).

1) Horizontally projected area. 2) Species with BA less than 0.1 m²/ha (31 spp.). 3) RD less than 0.1%.

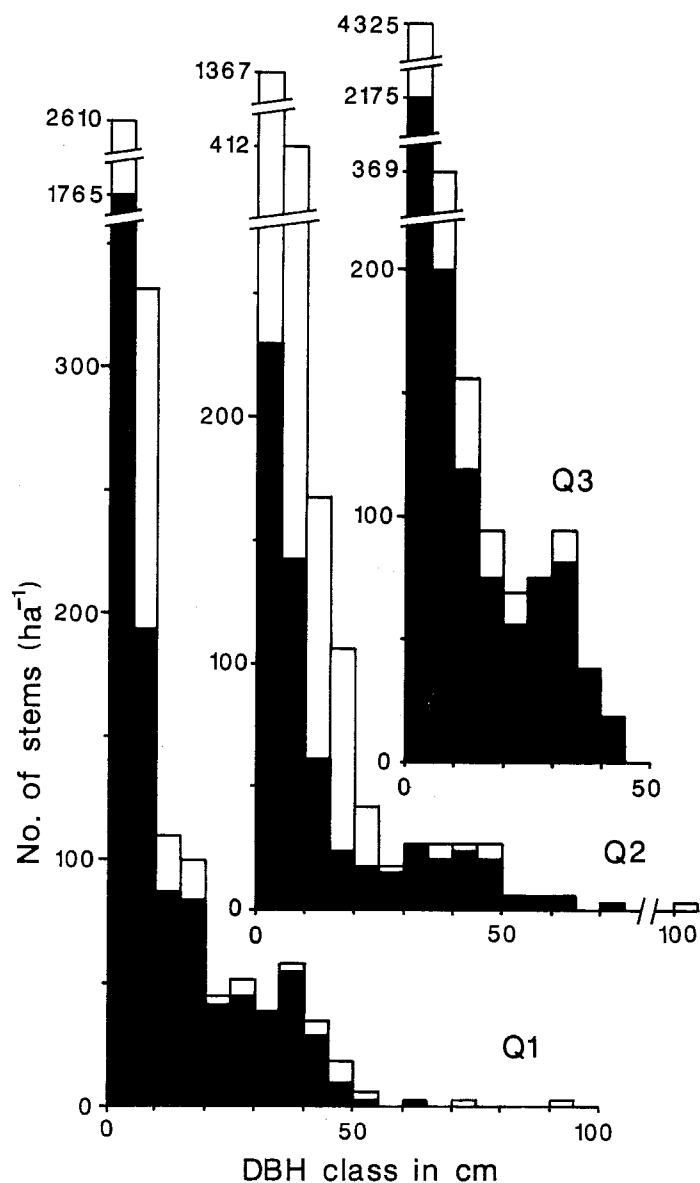


Fig. 1. DBH class distributions of all trees and shrub species in the quadrats. Solid areas indicate *Fagus japonica*.

formed using by means of the values of the intercept (α) and the regression coefficient (β) (Fig. 2). Here, α indicates the basic components of the distribution [single individuals ($-1 \leq \alpha < 0$) or colonies ($\alpha > 0$) (index of basic contagion)], while β denotes the pattern of distribution of the basic components [uniform ($\beta < 1$) or clustered ($\beta > 1$) (density-contagiousness coefficient)]. Stems of all species, including *F. japonica*, were distributed in the form of colonies either in every category or in every quadrat. Especially small-sized stems (A) clearly showed compact colonies. The distribution of these colonies was uniform for most of the

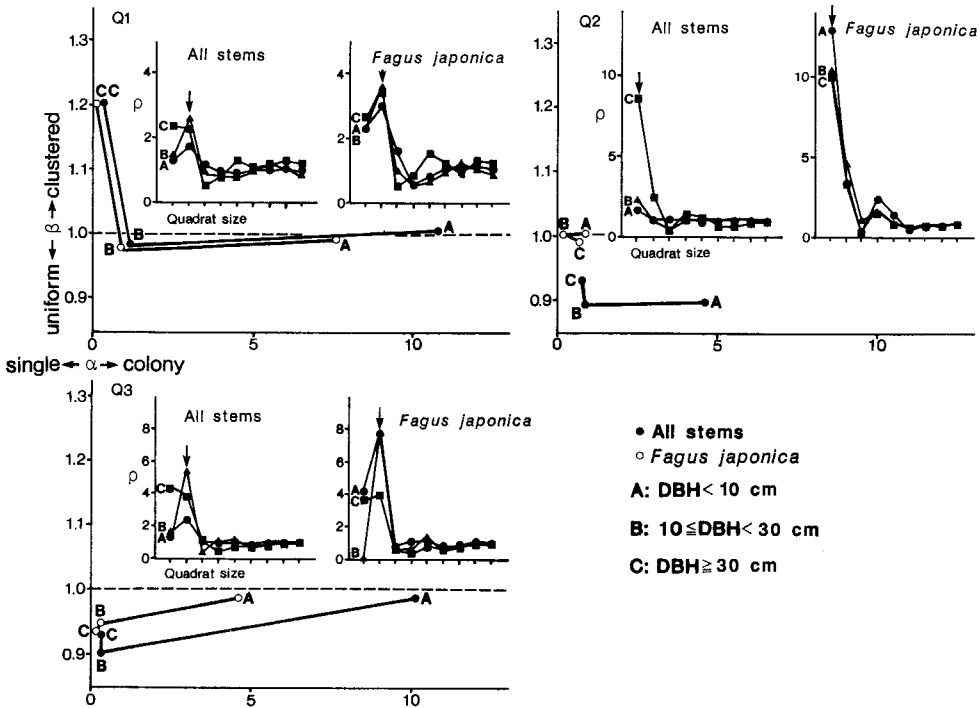


Fig. 2. The distributional pattern upon combination of the values of α and β for stems belonging to each of the three categories (A, B and C defined in the text) in every quadrat, α and β representing the basic components of distribution (single individuals or colonies) and the pattern of distribution of the basic components (uniform or clustered), and the fluctuations of ρ -index sets, applied to determine the sizes of colonies. Arrows show the sizes of stools (for details see text). Quadrat sizes of ρ -index sets are the same as in Figure 3.

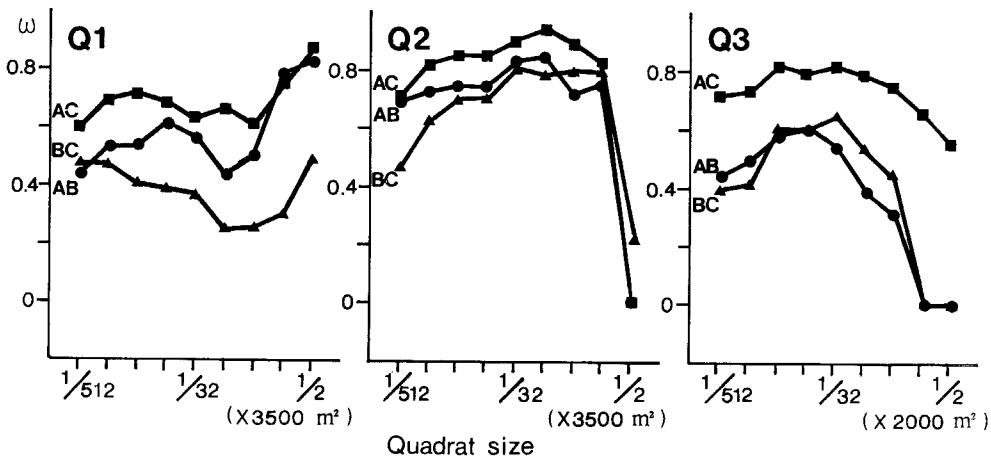


Fig. 3. Relationships between the ω -indices of *Fagus japonica* stems and quadrat sizes, showing the distributional associations between the three categories (A, B and C defined in the text) in each quadrat (for details see text).

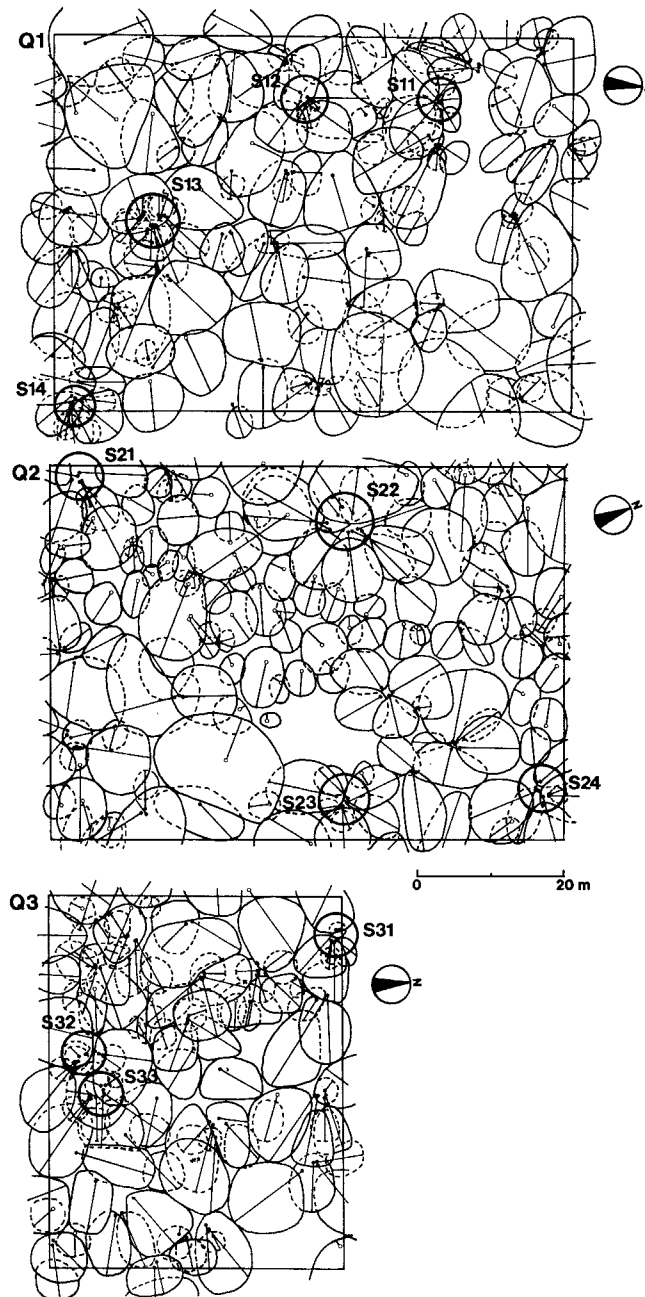


Fig. 4. Crown projection diagrams of stems higher than 10 m in the three quadrats (solid and dashed lines show respectively the margin of canopy crowns and that of crowns under the canopy). The large circles marked S11–S33 represent large-sized stools composed of more than six stems. Small clear and solid circles show the positions of stem bases of *Fagus japonica* and other species, respectively.

categories except the large-sized stems (C) in Q1. The ρ -index, proposed by Iwao (1972), was applied to determine the size of these colonies. As shown in Fig. 2, the approximate size of colonies was found to lie within the range from 6.8 to 13.7 m², and the peak for *F. japonica* was higher than that of all other stems in every quadrat. The fact that the ω -index, proposed by Iwao (1977), yielded a positive value in any size of quadrat, as shown in Figure 3, suggests that *F. japonica* stems of different diameter categories are arranged in positive association with each other. In all the quadrats, combinations of two among the three categories, especially between A and C, yielded positive ω -indices for every size of quadrat.

Detailed examination of the bases of the stem group in which colonies were formed revealed that most had sprouted from around the dead mother stems or category C stems and become connected with each other at their epigeal parts. Thus these stems were from common stools.

Structure of *F. japonica* stools

Three or four large stools of *F. japonica* consisting of six or more stems with a height of more than 10 m were selected in each of the quadrats in order to study stool structure (Fig. 4). The DBH frequency of living stems in these stools is shown in Figure 5. The DBH frequency

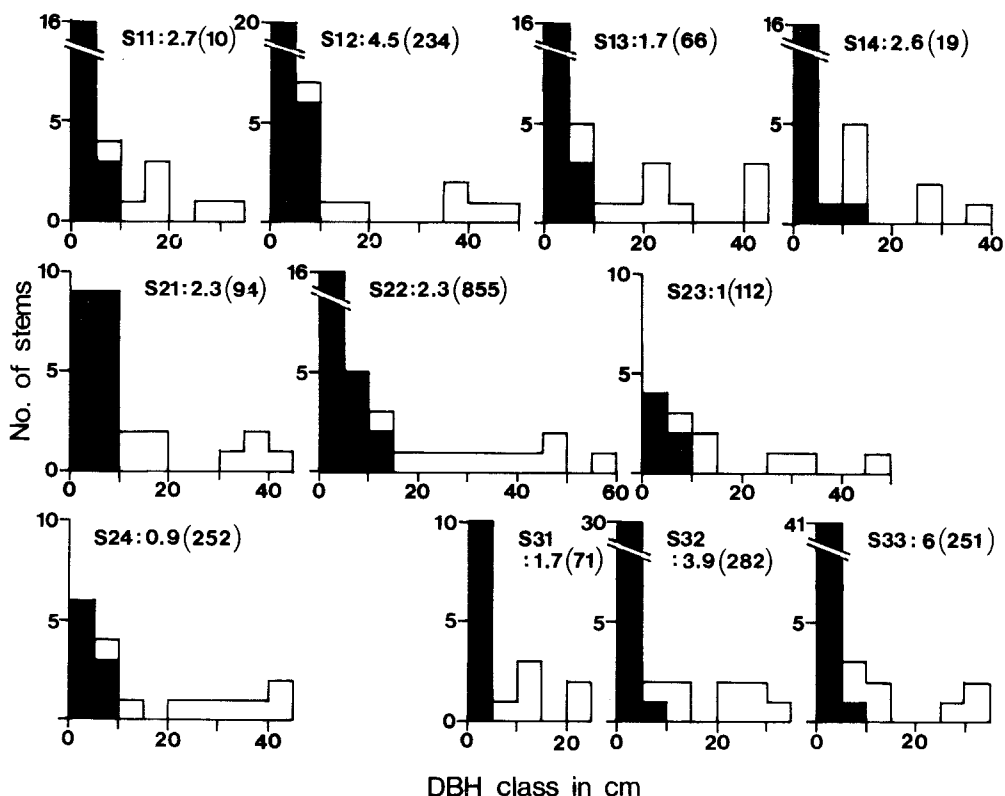


Fig. 5. DBH class distributions of stems in each stool of *Fagus japonica*. Solid and clear bars indicate the numbers of stems below and above 10 m in height, respectively. The figures combined with the stool numbers (S11–S33) by colons represent the ratios of the two stem-height classes (above 10 m/below 10 m). Those in parentheses represent the numbers of sprouts ($H < 1.3$ m) in each stool.

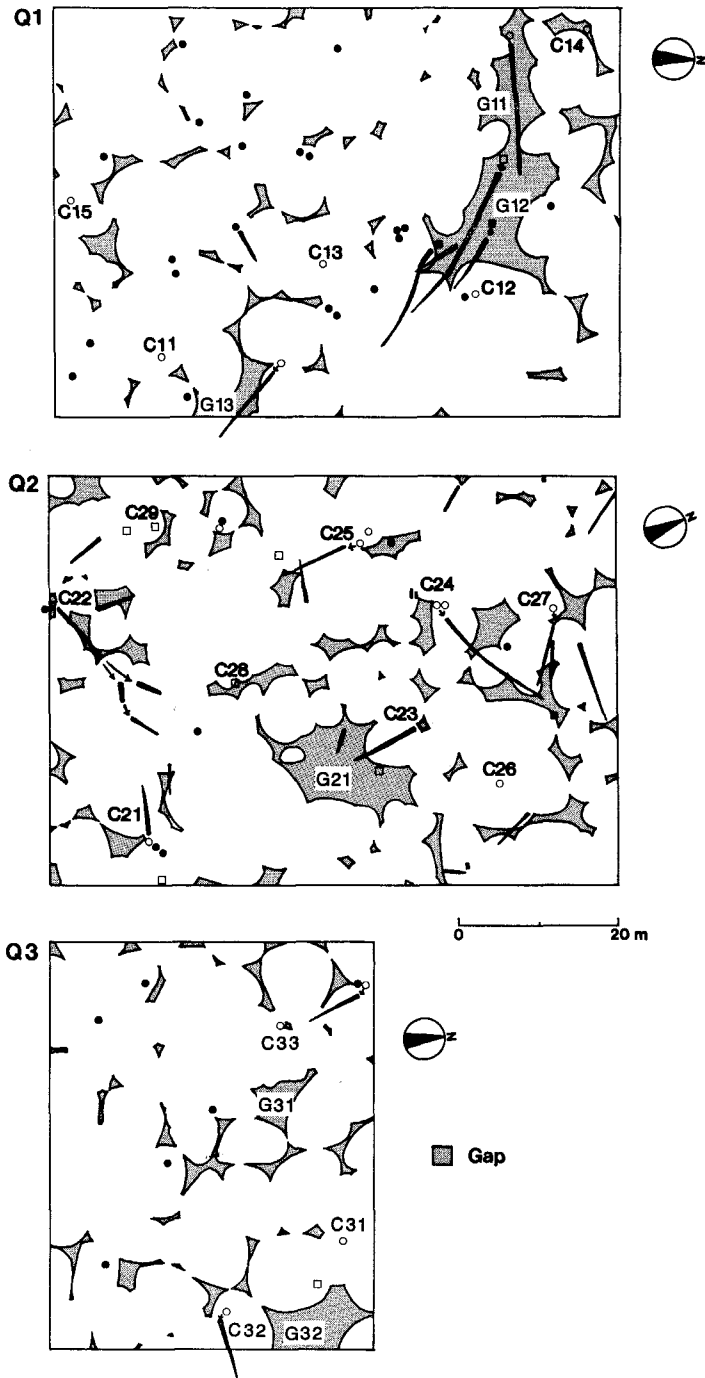


Fig. 6. Superimposed diagrams of the crown projection, the location of the bases of standing dead stems and those of fallen dead stems. The bases of standing and fallen dead stems; ○: *Fagus japonica*, □: Other species. Height class of dead stems (for detail see text): Empty; Height > 20 m, Solid: $10 < \text{Height} \leq 20$ m. →: Fallen trees. The symbols C11–C33 are the same as in Fig. 8.

for each stool showed an L- or slightly inverse J-shaped histogram, with a mode at about 5 cm. Most of the stools lacked stems with a DBH of around 20–30 cm, and showed maximum abundance for the class of stems with a height of less than 10 m, this being about six times greater than that of stems with a height of more than 10 m. This size structure seemed to reflect the age structure in most cases. The lack of middle-sized stems seemed to be due to a high death rate of stems in the size category. Every stool also consisted of a large number of sprouts ($H < 1.3$ m), with a maximum of 855 in S22.

Structural features of gaps in the forest canopy

In the present paper, blanks left in the projection diagrams of crowns taller than 10 m are

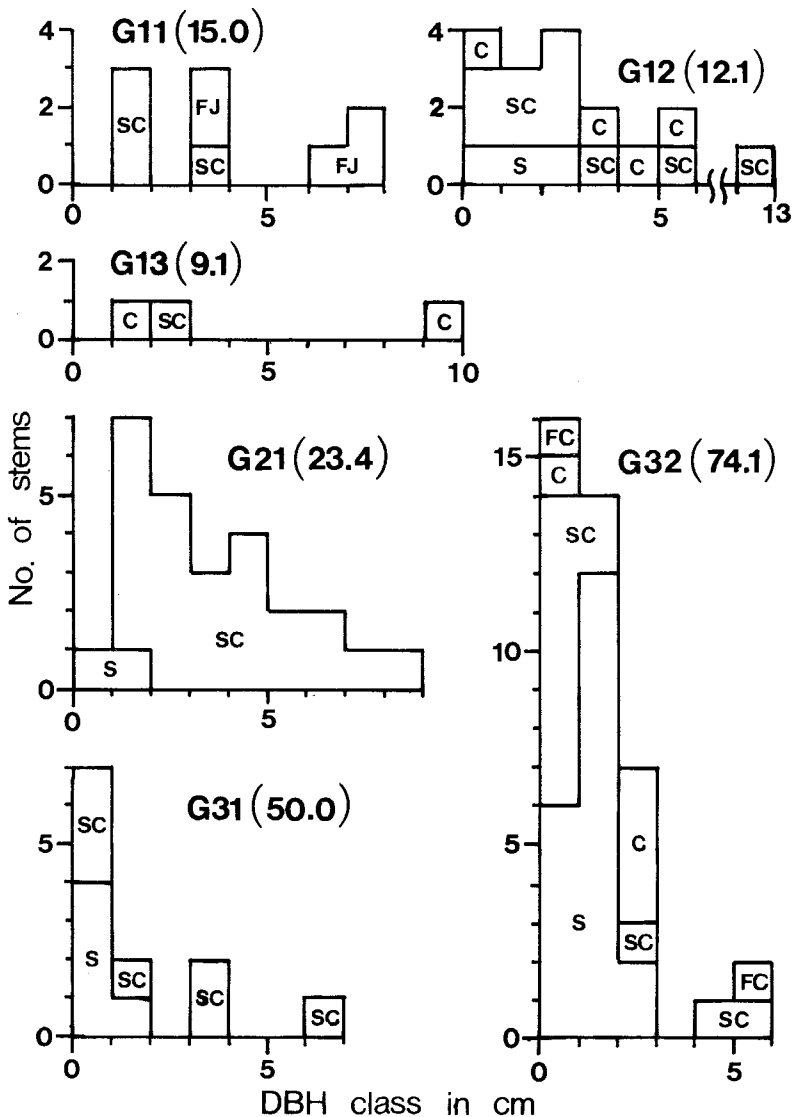


Fig. 7. DBH class distributions in representative gaps (G11–G32). Figures in parentheses represent the stem density: numbers per 100 m². FJ, *Fagus japonica* (sprout); FC, *Fagus crenata*; C, species in canopy stratum; SC, species in subcanopy stratum; S, species in shrub stratum.

referred to as gaps in the forest canopy. Among a number of gaps of various sizes in the three quadrats, six major gaps (Fig. 6) were subjected to analysis of floristic composition and the size (DBH) structure of young stems under these gaps. As seen in Figure 7, only a few successor stems of *F. japonica* were found in most of the gaps, with the exception of G11 where these had doubtlessly originated from the sprouts of marginal stools rather than from seedlings. Also, only a few *F. crenata* saplings were found in G32. Most of the other stems were those of canopy species such as *Acer sieboldianum* and *Acer palmatum* var. *amoenum*, and subcanopy species such as *Acer tenuifolium*, *Acer shirasawanum*, *Fraxinus lanuginosa* and *Acer micranthum*.

Distribution of dead stems and species composing the under-canopy above the bases of gap-makers

The positions of dead stems on the forest floor were superimposed on the crown projection diagrams, as shown in Figure 6, in order to find the causes of gap formation and to clarify which trees had filled the gaps concerned, i.e., the crown area of existing before stem death. Here dead stems represent both standing dead stems and fallen dead stems, the latter of which include broken trunks but not uprooted stems. Most of the dead stems had fallen downward.

The heights of these dead stems when alive were estimated from their DBH data (or diameter at the stem bases) with the aid of the DBH-height curves for living stems. Ogawa (1969) proposed a hyperbolic equation representing the relation between the DBH and the height of component stems in a forest stand, as follows:

$$1/H = 1/[A \cdot (\text{DBH})^h] + 1/\dot{H} \quad (1)$$

where h , A and \dot{H} are coefficients specific to the forest. The maximum value of $H(\dot{H})$ is found when the DBH approaches its maximum. Applying the data for DBH and H of living stems of all the species (Q1: $N = 1059$, Q2: $N = 741$, Q3: $N = 838$) and *F. japonica* (Q1: $N = 730$, Q2: $N = 200$, Q3: $N = 454$) to this equation, the following figures are obtained by means of Demming's method of least squares (those for *F. japonica* in parentheses):

$$\text{Q1: } h = 1.014 (1.025), A = 1.572 (1.606), \dot{H} = 32.237 (31.185)$$

$$\text{Q2: } h = 1.165 (1.276), A = 1.082 (0.88), \dot{H} = 31.307 (29.224)$$

$$\text{Q3: } h = 1.003 (1.112), A = 1.776 (1.73), \dot{H} = 33.273 (29.216)$$

Further, eq. (1) may be modified into the following form:

$$\text{DBH} = \{1/A \cdot [\dot{H} \cdot H / (\dot{H} - H)]\}^{1/h} \quad (2)$$

If it is presupposed that the stems composing the canopy of each quadrat died after they had grown to over 20 m, the following figures can be obtained as the average DBH of these dead stems by application of eq. (2): Q1: 31.9 (31.9), Q2: 29.26 (28.58), Q3: 28.19 (25.47) (cm). Dead stems of such sizes, most of which were *F. japonica*, must have been endowed with considerably large crowns when alive. However, the spaces above their bases did not always remain as gaps, and sometimes were overhanged by the crowns of other trees. For example, the gaps G11 and G13 doubtless resulted from the death of *F. japonica* stems and G12 from that of *F. crenata* stems. In contrast, no base of dead stems was found in the gaps G21, G31 and G32. Most of these gaps probably resulted from the death of stems standing around gaps (Halle et al., 1978).

For the purpose of investigating the species composition of the under-canopy strata above

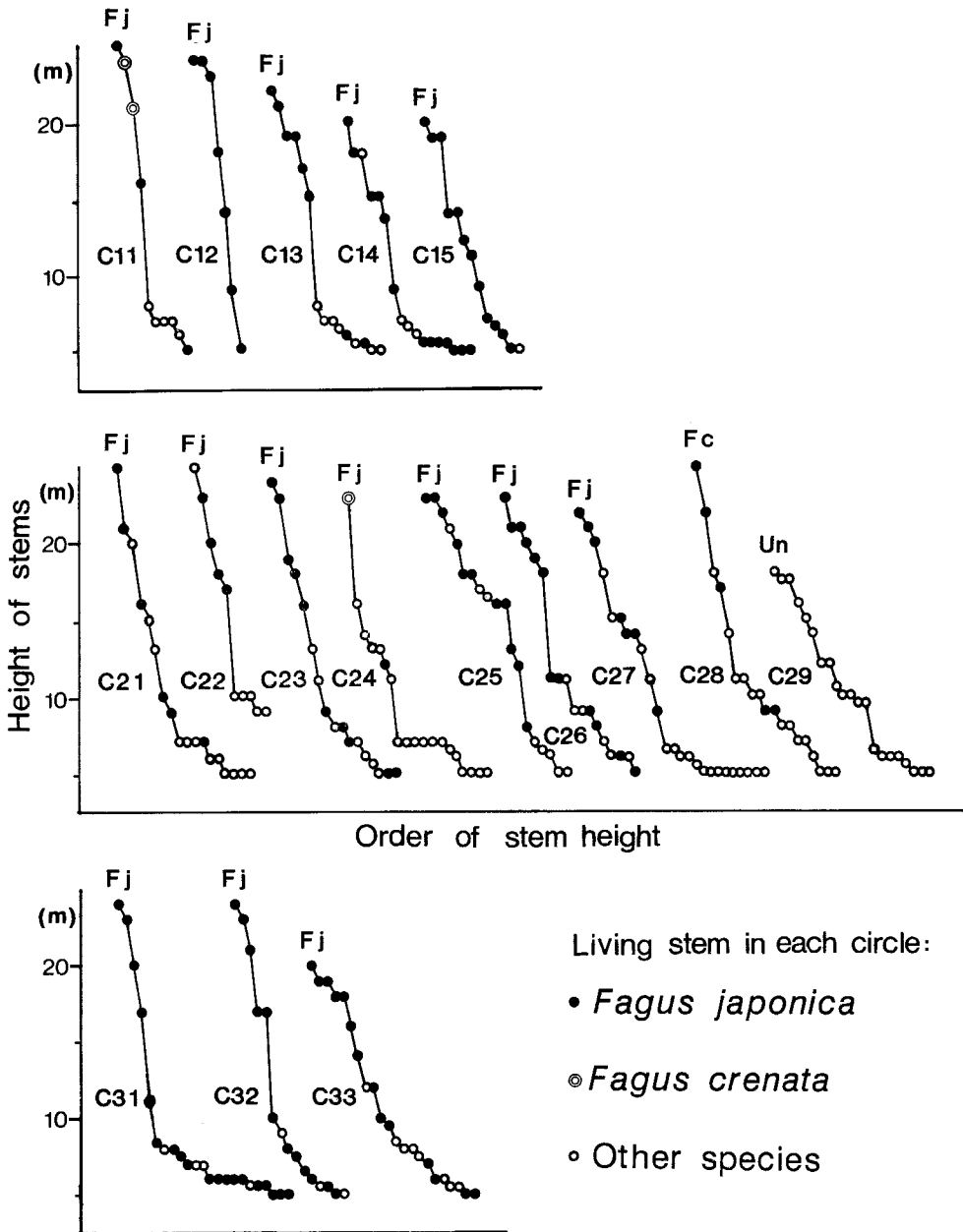


Fig. 8. Order of stem height of trees of various species composing the under-canopy strata within each of 17 representative crown circles of dead stems, C11–C33. Identification of dead stems (gap-makers): Fj, *Fagus japonica*; Fc, *Fagus crenata*; Un, unidentified species.

the bases of dead stems (gap maker), a hypothetical circle was placed in every quadrat, whose radius (Q1: 8.0, Q2: 8.8, Q3: 8.3) (m) was represented by the sum of the mean crown radius (Q1: 4.3, Q2: 4.3, Q3: 3.8) (m) and the mean “crown vector” (the crown vector being the distance from the center of the projection to the base of the stem) (Q1: 3.7, Q2: 4.5, Q3: 4.5) (m) (Takiguchi, 1983; Ishizuka, 1984). This circle was assumed to represent the extent of the

area which the dead stems had occupied with their crowns when alive, and hereafter is referred to as the "crown circle".

In Figure 8, the trees of various species composing the under-canopy strata within 17 representative crown circles are shown with the heights of their living stems in order of height in each crown circle (C11–C33). Most of the dead stems formerly having dominated these crown circles were identified as *F. japonica*, except those of C28 (*F. crenata*) and C29 (unidentified species). Seven to 25 living stems were recorded in each of these crown circles, and most of them were *F. japonica* except those in C22 (*Abies firma*), C24 (*F. crenata*) and C29 (*Styrax obassia*). The largest height of the living stems was over 20 m in every circle with the only exception of C29 (18 m). In most of the crown circles, the height-height order relation of living stems exhibited catenary-like or L-shaped lines, while the top and upper parts of the lines were represented by living stems of *F. japonica* having extended from the surrounding stools. The lower concave parts were represented by a number of living stems of other species, but even in these parts, in the case of some crown circles, a few living stems of *F. japonica* were present, which had doubtless grown from sprouts rather than from seedlings.

Discussion

Since the study by Watt (1947), various kinds of investigations have been carried out on forest regeneration from the viewpoint of forest structure, especially the distribution pattern of components in both space and time (Whitmore, 1982). According to some studies on *F. crenata* forests (Nakashizuka and Numata, 1982a; Honma and Kimura, 1982; Hara, 1983), large stems of this beech are distributed either randomly or uniformly, while middle- or small-sized stems are distributed in clusters consisting of stems of nearly the same age. When these *F. crenata* forests lack dwarf bamboo or sasa, which is a major agent preventing their regeneration, on the floor, probably as a result of grazing, dense colonies of *F. crenata* seedlings and saplings occur in the gaps and occupy them. These facts suggest that *F. crenata* forests have a mosaic structure of cohorts, and that the process of regeneration is repeated in every unit of this mosaic (Nakashizuka and Numata, 1982b).

It was clarified from a comparison of the patterns of distribution of living stems, stool structure of *F. japonica* and species composition in the present canopy gaps with those in the former gaps estimated from the condition of the undercanopy above the stubs of the major dead stems in each quadrat that in primary *F. japonica* forests mosaic regeneration was repeated, as in *F. crenata* forests.

As several authors have pointed out, component species respond to disaster or disturbance (e.g. canopy gap formation) with various forms of vegetative reproduction and play an important role in forest regeneration (Forcier, 1973, 1975; Marks, 1974; Horn, 1975; Harper, 1977; Hälle et al., 1978; Grime, 1979; Bormann and Likens, 1979; Oliver, 1981). Marks (1974) cited examples of forest communities reorganizing their structure after disturbance by means of different types of vegetative reproduction such as production of epicormic branches on undamaged trees adjacent to or within an opening, and stump sprouts and/or root suckers from damaged individuals within an opening. Harper (1977) called this type of regeneration from dormant buds the "specialized bank of reserve buds". This bud type can be compared with the seed bank, seedling bank and sapling bank in its response to disturbance.

Sprouts (root collar suckers) doubtless play an important role in maintenance of the canopy in the processes of regeneration of primary *F. japonica* forests. Canopy gaps in these

Table 2. The longest crown vectors in individual stools and the areas of crown cover of individual stems attaining the canopy in *Fagus japonica* forest, the distances from the centers of gaps to the nearest adjacent stools, and the areas of gaps in each quadrat in a *Fagus japonica* forest.

		Longest crown vectors in individual stools (m)	Distance from the center of gaps to the nearest adjacent stools (m)	Area of crown cover of individual stems attaining the canopy (m ²)	Area of gaps in each quadrat (m ²)
Q1	Mean	4.0	4.5	53.2	—
	Range	1–8	2–8	19–133	–144
Q2	Mean	4.6	10	53.6	—
	Range	1–8	—	25–108	–111
Q3	Mean	4.6	5.8	45.9	—
	Range	1–8	5.5–6	26–89	–54

forests recovered by the sprouting of remaining *F. japonica* stools or by new sprouts of *F. japonica* stools adjacent to the gaps.

However, few stems had grown from sprouts in all of the gaps except for G11. Many sprouts and stems within *F. japonica* stools located around the gaps are important for the processes of gap closure in most cases. In order to clarify the possibility of gap closure by sprouts invading from outside the gaps, the longest crown vectors in individual stools, the distances from the center of gaps to the nearest adjacent stools, the areas of crown cover of individual stems attaining the canopy, and the areas of gaps in each quadrat are shown in Table 2. The areas of the largest gaps ranged from 54 to 144 m². These figures are 1.2 to 2.7 times of the crown areas of stems attaining the canopy (C). When the longest crown vector in each stool is compared with the distance from the center of the canopy gap to the nearest neighboring stool, the latter (the distance) is 1.1 to 2.2 times longer than the former on average. However, the ranges of both are rather wide. This result suggests that, although most of the canopy gaps in *F. japonica* forests may be filled with several stems grown from the sprouts of neighboring stools, some remain incompletely filled.

If gaps are not fully occupied by the stems of *F. japonica* grown from sprouts, these places must be filled with individuals of other canopy and/or subcanopy species. In other words, the canopy stratum of the forests is not always composed purely of *F. japonica*, but a mixture of this and other tree species such as *F. crenata*, *Acer shirasawanum* and *Acer sieboldii*.

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