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Structure and dynamics of Japanese beech (*Fagus japonica* Maxim.) stools and sprouts in the regeneration of the natural forests

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Abstract

Structure and spatial distribution of stools and root-collar sprouts of Japanese beech (*Fagus japonica*) were studied to clarify the regeneration processes of the stool and the population, and the ecological importance of this stool formation in five quadrats of the natural forests with different forest floor vegetation on the Pacific side of Japan. *F. japonica* dominates in the canopy of each quadrat. Most of sprouts formed a circle around the root-collar and lowest parts of the parent stems of the stool with the youngest sprouts at the periphery. The regeneration by seedlings was slight especially on the forest floor vegetation of the dwarf bamboo *Sasa*. The variety of size structure of stems and the existence of dead traces and/or dead center in each stool, the apparent difference in stool size, and the aggregations of stools in the forests suggest that stool expansion and long persistence of the stool at a given location may contribute to compensate for the scarcity of regeneration by seedlings inhibited by dwarf bamboo, and by the other shrubs and herbs.

Nomenclature: Ohwi (1965).

Introduction

The Japanese beech (*Fagus japonica*) is one of the two beech species in the cool temperate zone of the Japanese archipelago, which is found in the zone with little snow on the Pacific side. The other *F. crenata* is found both in the heavy snowfall zone adjacent to the Japan Sea and on the Pacific side (Sasaki 1970; Nozaki & Okutomi 1990). *F. japonica*, like several other tree species, reproduces both by seed and by production of sprouts from the root-collar. As to the reproductive mode, *F. japonica* is characterized by forming stools, caused by vigorous sprouting from the root-collar (Tohyama 1965; Ohkubo *et al.* 1988; Ohkubo 1989; Peters & Ohkubo 1990). Vegetative reproduction by root sprouts, root-collar sprouts, rhizome production and layering occur in many woody species (Jones & Raynal 1986; Koop 1987; Oldeman 1990; Oliver & Larson 1990). Vegetative reproduction seems to be particularly important under circumstances where natural growth is handicapped e.g., near the limit of tree growth, on dynamic sites, under heavy shade and under ageing (Koop 1987). Peters and Ohkubo (1990) pointed that this *F. japonica* type of sprouting from the stools should not be confused with sprouting of *F. sylvatica* under stressed growth conditions (Koop 1987), e.g. near the timberline in middle European mountains (Fanta 1981). In America, exposure and injury seem to cause sprouting of *F. grandifolia* (Jones & Raynal 1988), and sprouting is extensive in the northern areas where the climate is more severe (Held 1983). The only other species of beech which show this similar stool type are *F. multinervis* in Korea (Kim *et al.* 1986) and *F. engleriana* in China (Peters in press). The conditions that invoke adventitious rooting and vegetative reproduction of trees are largely eliminated by modern forest management, and the ability for vegetative reproduction of forest trees, as for example of beech, may therefore often be underestimated (Koop 1987). Patterns of clone development in woody shade tolerant species like *Fagus* species are less well known (Jones & Raynal 1986).

In a previous paper, the structure of primary *F. japonica* forests from the viewpoint of forest dynamics, concentrating on the distributional pattern of stems, the structure of gaps and canopy strata were studied (Ohkubo *et al.* 1988). Although stool formation of *F. japonica* stems in the primary forests has been observed (Tohyama 1965; Ohkubo *et al.* 1988; Peters & Ohkubo,

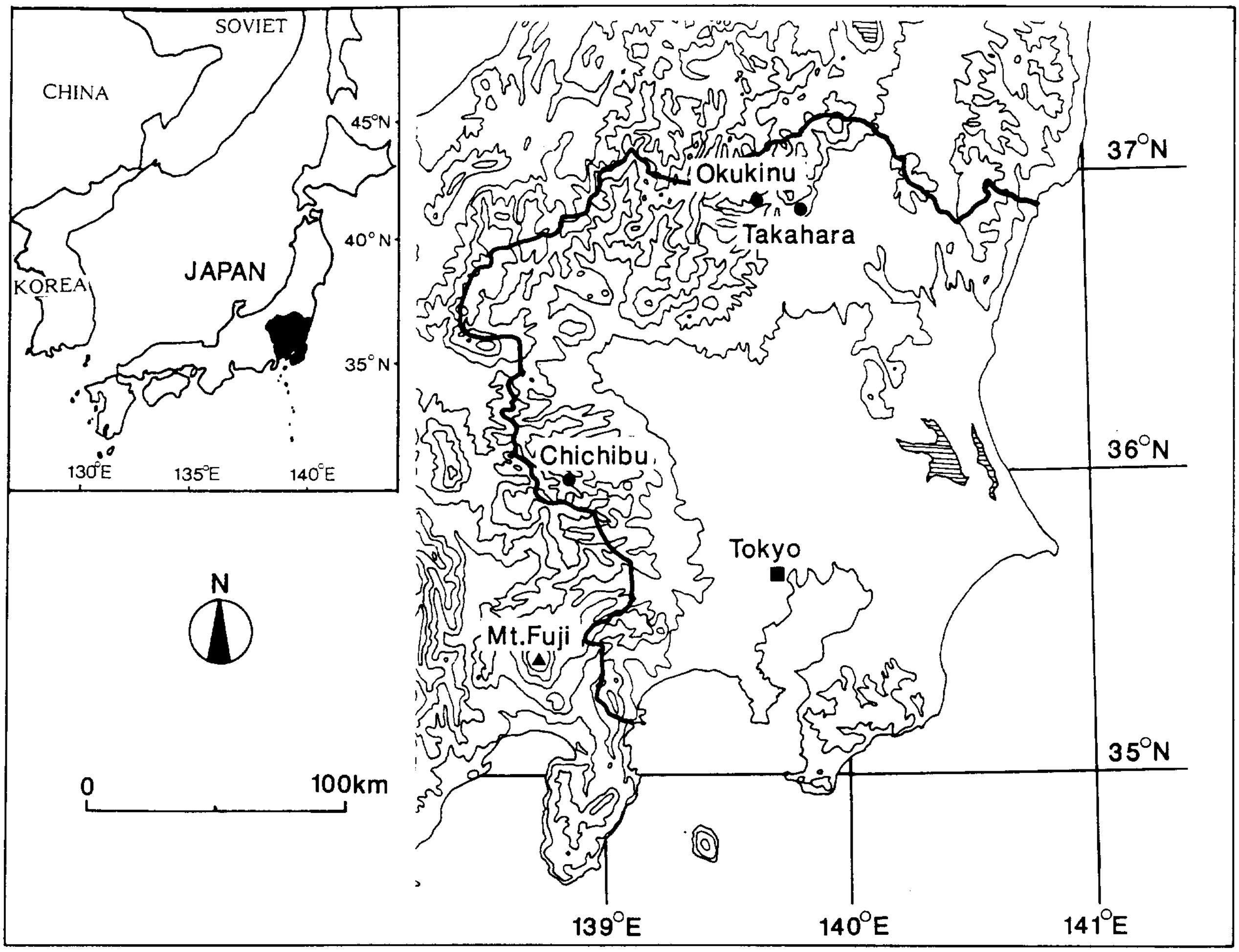


Fig. 1. Map of Kanto district, central Japan indicating the study sites. Contour interval is 500 m.

1990), published information is restricted to a few reports on the beech stools.

This study clarifies the structure, the spatial distributions of *F. japonica* stools in the primary beech forests and discusses the developmental processes of the stools and the ecological significance of the sprouts in the regeneration of the beech forests.

Study sites and methods

Study sites

Three study areas were selected in a portion of the surrounding mountains of the Kanto plain, including Chichibu, Saitama Prefecture (35° 55′ N, 138° 50′ E), Mt.Takahara, Tochigi Prefecture

Table 1. Comparison of species composition, mean stem density per stool and basal area among the three study areas of Chichibu (CQ1–CQ3), Mt. Takahara (TQ) and Okukinu (OQ).

Quadrat No.	CQ1			CQ2			CQ3			TQ			OQ			Freq.
Altitude (m)	1160			1040			870			885			1220			
Slope (°)	28.6			16.5			37.5			16.8			41			
Direction	N84° E			N70° E			N87° E			S19° E			W30° N			
Horizontal projected area (ha)	0.31			0.33			0.16			0.24			0.06			
Species	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	
Fagus japonica	2355	15.9	26.82	606	11.8	21.72	2839	13	25.98	933	16	24.11	2500	12.5	40.64	5
Fagus crenata	38	1	7.61	24	1	3.29	44	1	0.1	38	1	4.57	67	1	8.98	5
Acer shirasawanum	296	1.5	0.61	39	1	0.53	6	1	+	13	1	+	200	6	0.45	5
Styrax obassia	3	1	+[1)]	60	1	0.39	13	1	0.14	8	1	0.35	17	1	+	5
Acer sieboldianum	196	1.1	0.18	130	1	0.72	232	1.1	0.21	17	1	+	.	.	.	4
Acer palmatum var. *amoenum*	13	1	+	61	1	0.1	31	1	0.64	8	1	0.11	.	.	.	4
Abies firma	10	1	+	21	1	0.67	69	1.1	0.61	8	1	+	.	.	.	4
Stewartia pseudo-camellia	6	1	+	103	1.1	1.38	19	1.5	+	25	1	1.07	.	.	.	4
Carpinus cordata	.	.	.	12	1	0.18	25	1	+	200	1	1.67	433	1.5	0.56	4
Fraxinus lanuginosa	.	.	.	15	1.3	+	157	1.1	0.6	154	1.5	0.62	233	2	0.52	4
Acer tenuifolium	171	1.4	0.52	642	1	0.99	150	1.1	0.34	.	.	.	.	.	.	3
Acer micranthum	48	1	0.1	124	1	0.38	69	1	+	.	.	.	.	.	.	3
Tilia janponica	3	1	+	6	1	0.61	13	2	+	.	.	.	.	.	.	3
Acanthopanax sciadophylloides	13	1.3	+	18	1	0.24	19	1	+	.	.	.	.	.	.	3
Tsuga sieboldii	10	1	+	6	1	+	26	1.3	0.34	.	.	.	.	.	.	3
Hydrangea petiolaris	3	1	+	6	1	+	.	.	.	.	.	.	183	2.2	0.23	3
Acer distylum	22	7	+	81	1	0.76	.	.	.	.	.	.	167	1.3	0.17	3
Meliosma myriantha	.	.	.	73	3.4	0.26	425	1.7	0.34	79	2.4	0.16	.	.	.	3
Prunus grayana	.	.	.	6	1	+	25	1	+	4	1	0.31	.	.	.	3
Acer nikoense	.	.	.	3	1	+	6	1	+	29	1	0.88	.	.	.	3
Magnolia obovata	.	.	.	6	1	0.15	6	1	+	.	.	.	33	1	+	3
Acer rufinerve	.	.	.	24	1	0.19	12	1	+	.	.	.	17	1	+	3
Carpinus laxiflora	.	.	.	3	1	+	6	1	0.11	.	.	.	.	.	.	2
Aesculus turbinata	12	1	0.15	.	.	.	.	.	.	.	.	.	.	.	.	1
Acer japonicum	.	.	.	76	2.1	0.47	.	.	.	.	.	.	.	.	.	1
Cornus controversa	.	.	.	6	1	0.1	.	.	.	.	.	.	.	.	.	1
Torrea nucifera	.	.	.	.	.	.	88	3.5	0.13	.	.	.	.	.	.	1
Hovenia dulcis	.	.	.	.	.	.	.	.	.	4	1	0.42	.	.	.	1
Acer diabolicum	.	.	.	.	.	.	.	.	.	33	2	0.93	.	.	.	1
Sapium japonicum	.	.	.	.	.	.	.	.	.	63	1	0.17	.	.	.	1
Acer palmatum var. *matsumurae*	.	.	.	.	.	.	.	.	.	.	.	.	50	1	0.34	1
Carpinus japonica	.	.	.	.	.	.	.	.	.	.	.	.	100	3	0.28	1
Others (33 spp.)[2)]	212	2.25	0.21	90	1.07	0.22	965	1.75	0.28	157	2.08	0.14	233	1.29	0.16	
Total	3411	2.34	36.37	2241	1.43	33.47	5245	1.77	29.91	1773	2.1	35.6	4233	2.24	52.33	

N.B. I: no. of stems per ha, II: Mean Stem Density Per Stool (MSDPS), III: Basal Area (m^2/ha) (BA).
Nomencalture after Ohwi (1965). 1) and 2): species with BA less than 0.1 m^2/ha.
Underlines show the species higher than 20 m.

(36° 53′ N, 139° 48′ E), and Okukinu, Tochigi Prefecture (36° 55′ N, 139° 38′ E) in central Japan (Fig. 1). The climate of the study areas is classified in the Pacific type, which is characterized by lower precipitation (snowfall) in winter than the Japan Sea side, and is illustrated by a low value on the Japan Sea Index (this index is calculated by 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° (Chichibu), 43° (Mt.Takahara) and 38° (Okukinu). Annual mean precipitation in the areas is

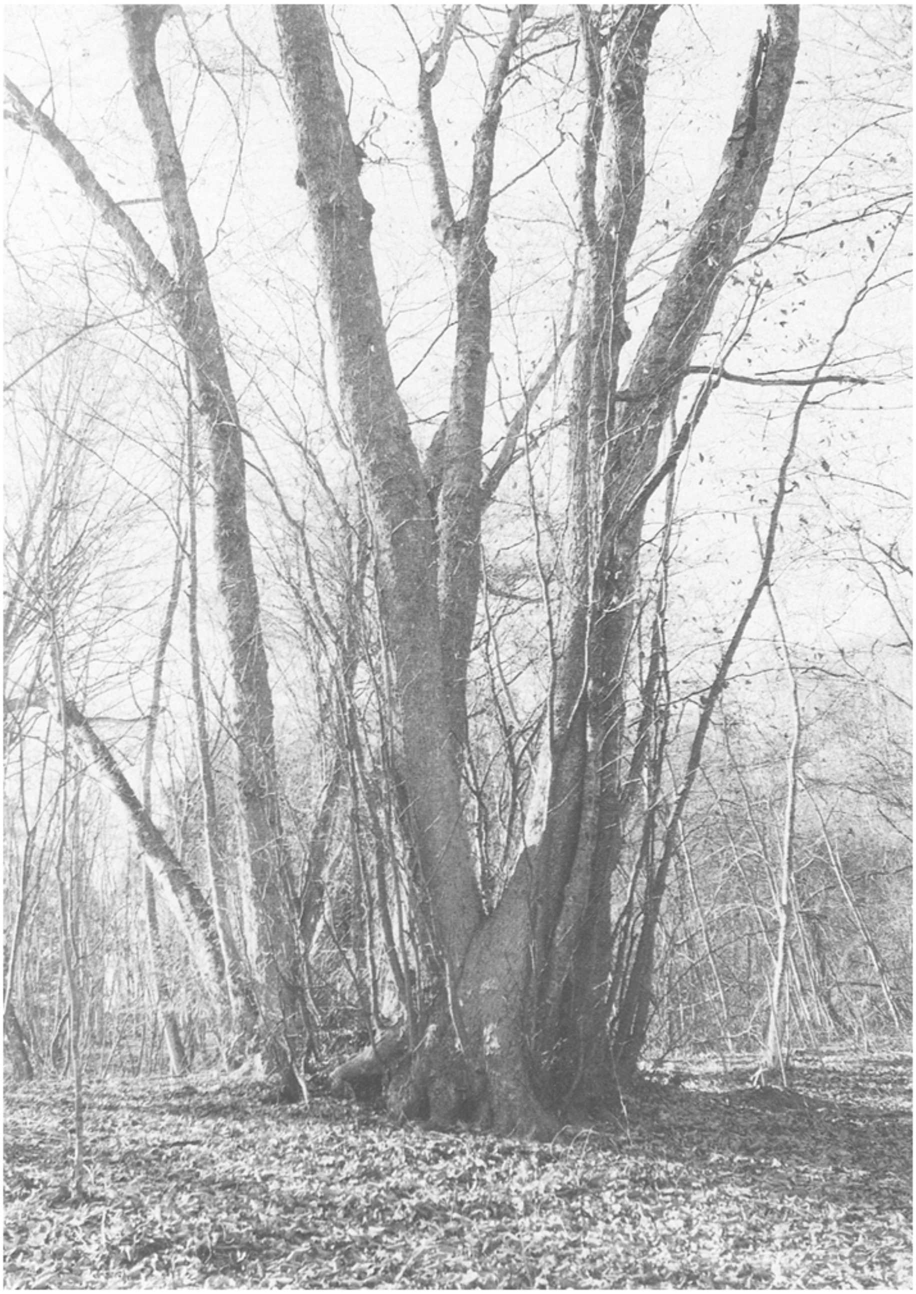


Fig. 2. A *Fagus japonica* stool in a quadrat (CQ1) in Chichibu.

ca. 1500 mm–1700 mm and the warmth index (WI) (Kira 1948) is 66.3 WI (Chichibu), 62.4WI (Mt.Takahara) and 54.9 WI (Okukinu), suggesting that the areas are located in the temperate deciduous forest zone. Mean annual maximum depth of snow of the areas is 20 cm–50 cm.

In Chichibu, three quadrats (CQ1: 50 m × 70 m, the upper part of a gentle slope (28.6°), N84°E, 1160 m a.s.l.; CQ2: 50 m x 70 m, the middle part of a gentle slope (16.5°), S70°E, 1040 m a.s.l.; CQ3: 50 m x 40 m, the lower part of a steep slope (37.5°), S87°E, 870 m a.s.l.) were set in

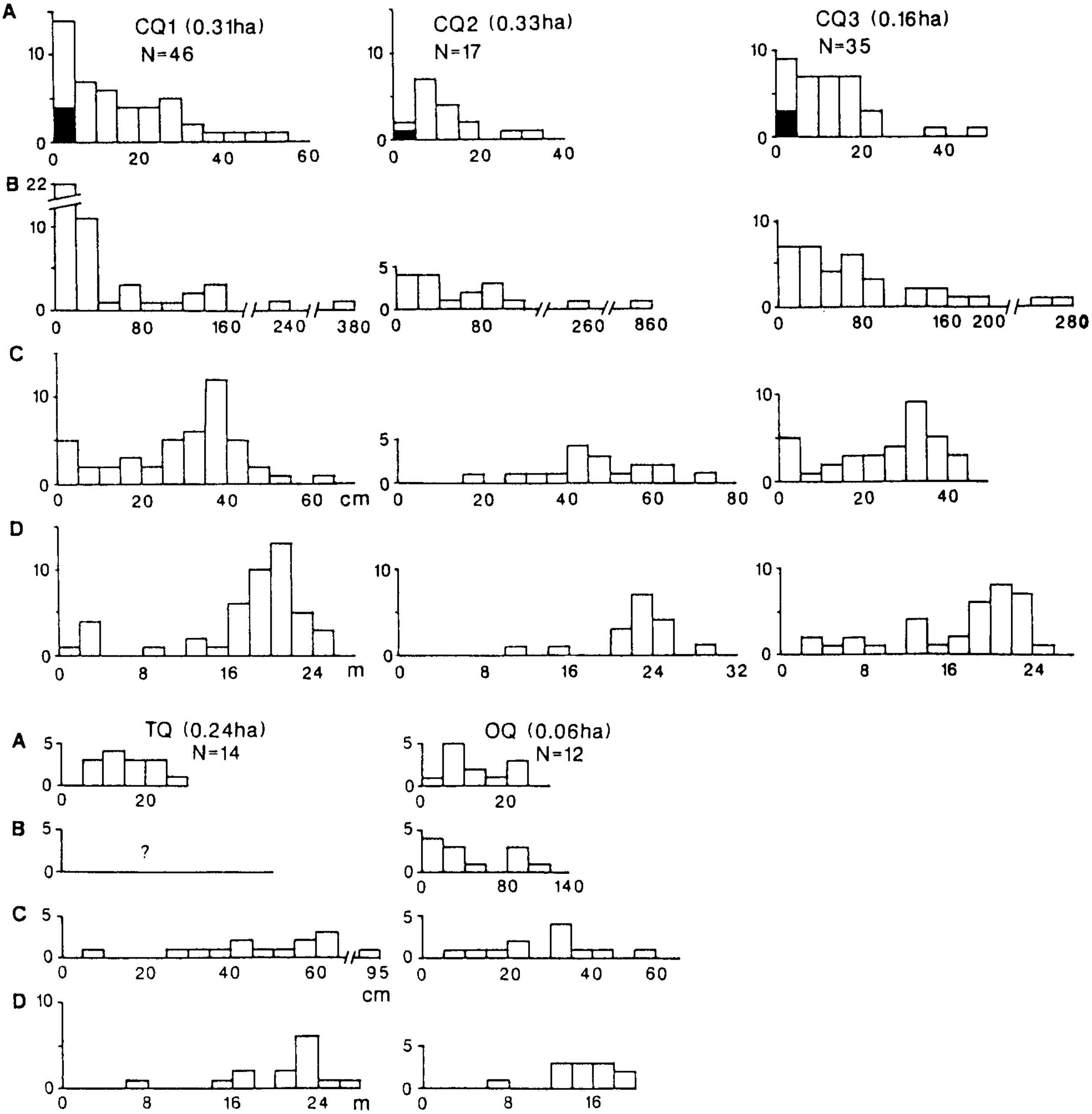


Fig. 3. Structure of *Fagus japonica* stools in each quadrat (CQ1–3, TQ, OQ). N.B. A: no. of stems (H ≥ 1.3 m) in a stool (solid bars represent the numbers of stools of single stems), B: no. of sprouts (H < 1.3 m) in a stool, C: max. DBH of living stems in a stool (cm), D: max. height of living stems in a stool (m).

1983 and 1984; CQ1, CQ2 and CQ3 are the same as C1, C2 and C3 in Ohkubo *et al.* 1988, respectively. On Mt.Takahara one quadrat (TQ: 50 m x 50 m) was set on the lower part of a gentle slope (16.8°), S19°E, 885 m a.s.l. in 1986 and in Okukinu one quadrat (OQ: 20 m x 40 m) was set in the upper part of a steep valley (41°), W30°N, 1220 m a.s.l. in 1984.

Measurement of variables

In each quadrat, small grids (10 m x 10 m) were laid out and used to map the location of stools (permanent base with more than two stems (Height ≥ 1.3 m)) and single stems of the component species. In the quadrats slope aspects were determined by a handy compass and plot slopes were measured using a clinometer. And for all stems (woody stems more than 1.3 m in height) in each quadrat, DBH(cm) (diameter at 1.3 m in height), height(m) and map coordinates were measured. Especially in the case of the stool of *F. japonica*, the length of the sprouts (length < 1.3 m) and the Mean Stool Diameter (MSD) (the arithmetical mean of the longest diameter, the shortest diameter perpendicular to the longest one) were measured. And the projection diagrams of the living and dead stems, and the dead traces in each *F. japonica* stool were drawn in the quadrats of Chichibu and Mt.Takahara. In each quadrat the coverage of the forest floor vegetation (height < 1.3 m) was checked by Braun-Blanquet's method, and the height of the seedlings below 1.3 m originating from seeds was measured.

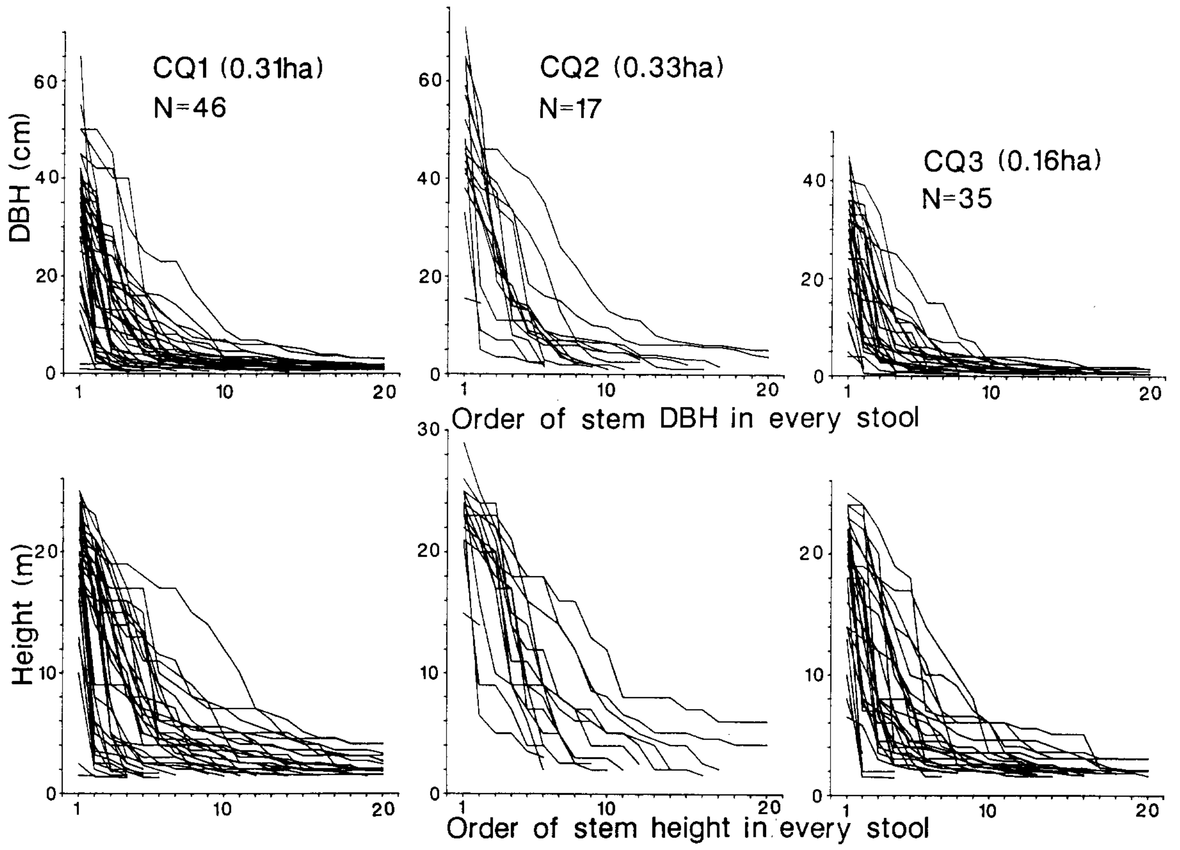


Fig. 4. Arrangements in the order (below twentieth) of DBH and height of the stems in each stool of *Fagus japonica* in the quadrats in Chichibu (CQ1–CQ3). N.B. N: total number of stool in each quadrat.

Results

Stool structure of the component species

For the component species in each quadrat, stem density per hectare, Mean Stem Density Per Stool (MSDPS) and Basal Area (BA) per ha are shown in Table 1. *F. japonica* dominated the area whereas *F. crenata*, *Acer* spp. and *Abies firma* were also found in the forest canopy. *F. japonica* showed the highest MSDPS (11.8–16.0) among the component species in each quadrat. The other species of high MSDPS were *Acer distylum*, *Ilex macropoda* (CQ1), *Zanthoxylum piperitum* (TQ), and *Acer shirasawanum* (OQ) and are subcanopy and shrub species. The MSDPS of the component species other than *F. japonica* mostly varied in each quadrat.

Stem and sprout structure in each F. japonica stool

In every forest *F. japonica* stools were composed of some big canopy stems and a large number of small stems and sprouts. Most *F. japonica* sprouts formed a circle around the root-collar and lowest parts of the parent stems of the stools with the youngest sprouts at the periphery (Fig. 2). The transition of root sprouts to trunk sprouts is a gradual one (Koop 1987). According to Koop's definition, as these sprouts do not produce their own more or less independent root system, the type of sprout may be interpreted like the one of trunk sprouts.

The number of stems and sprouts per stool, max. DBH and height of stems per stool were scaled in Figure 3. The number of *F. japonica* stools per hectare was different among the quadrats (131.4(CQ1), 48.6(CQ2), 175(CQ3) 150(OQ) and 56(TQ)). In each stool there were fewer than 15 stems and fewer than 20–40 sprouts, the number of stools with more stems and sprouts started to decrease. Stools with only one stem were found in Chichibu (CQ1–CQ3). The max. number of stems and sprouts per stool was 54(CQ1), 35(CQ2), 49(CQ3), 25(OQ) and 27(TQ) stems and 366(CQ1), 855(CQ2), 282(CQ3) and 114(OQ) sprouts. There were modes of distribution of max. DBH per stool at 35–45 cm in DBH and 18–24 m in height. The max. values of DBH and height were 65 cm(CQ1), 71 cm(CQ2) and 45 cm(CQ3) in DBH and 25 m(CQ1), 29 m(CQ2), 25 m(CQ3), 27 m(TQ) and 20 m (OQ) in height.

The arrangements in the order (below twentieth) of DBH and height of the living stems in each stool of *F. japonica* are shown in Figure 4. Most of the traits of size-sequence in each quadrat showed L-shaped distributions except some of stools in CQ2, namely there were a few middle size of stems in each stool.

Dead stems in the F. japonica stools

Dead stems were found in 60.9%(CQ1), 82.4%(CQ2), 31.4%(CQ3), 41.7%(OQ) and

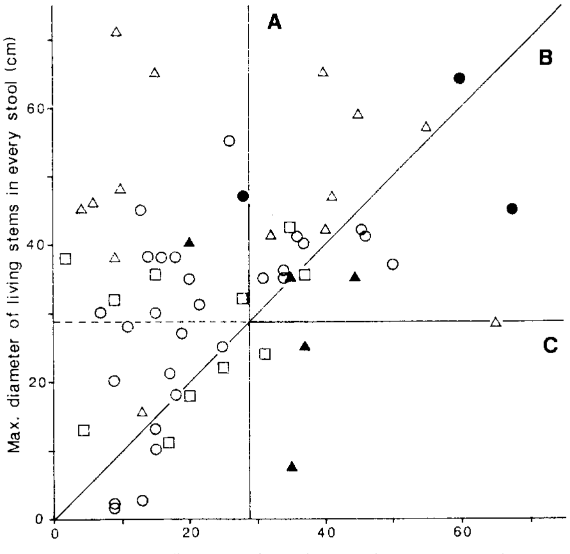
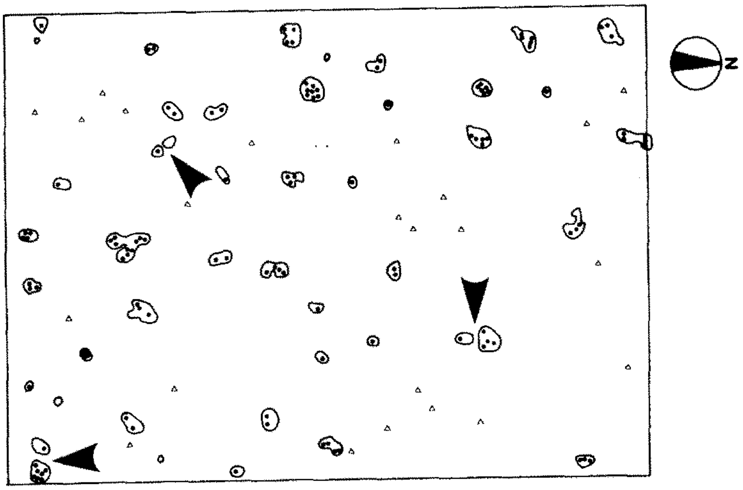
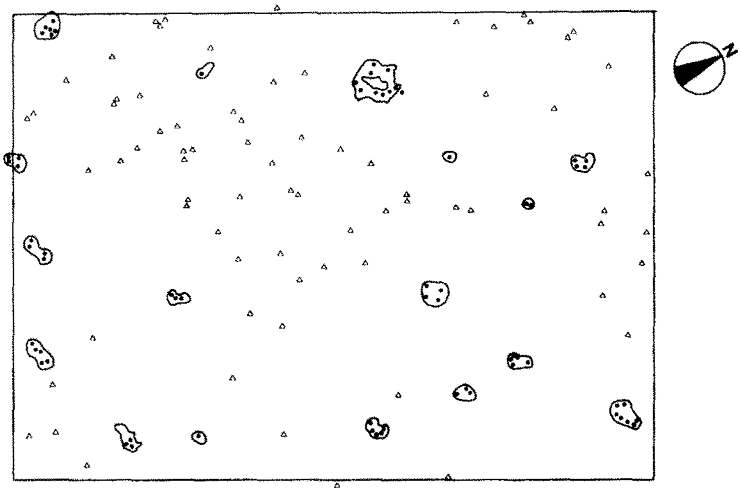


Fig. 5. Relationships between the maximum diameter of living stems and that of dead stems in every *Fagus japonica* stool in the quadrats CQ1 (○), CQ2(△), CQ3(□), TQ(●) and OQ(▲). N.B. Part A: The maximum diameter of living canopy stems in a stool is larger than that of dead stems which had attained the canopy when alive in the stool (DBH = 28.5 cm, Ohkubo et al. 1988). Part B: The maximum diameter of living canopy stems in a stool is smaller than that of dead stems which had attained the canopy when alive in the stool. Part C: The maximum diameter of living under-canopy stems in a stool is smaller than that of dead stems which had attained the canopy when alive in the stool.

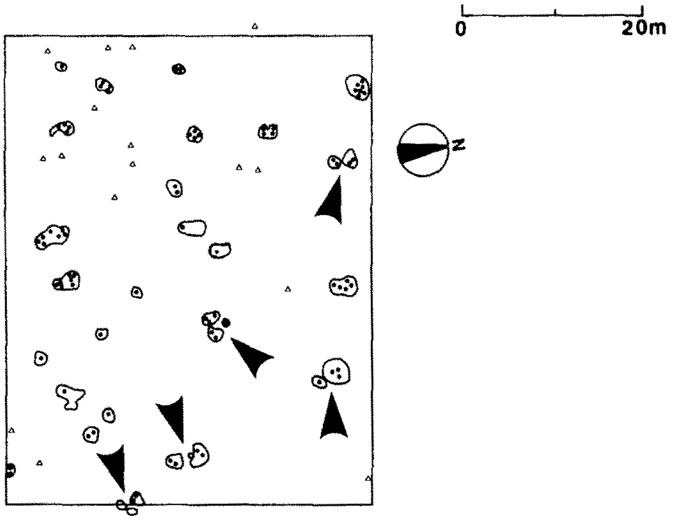
CQ1



CQ2



CQ3



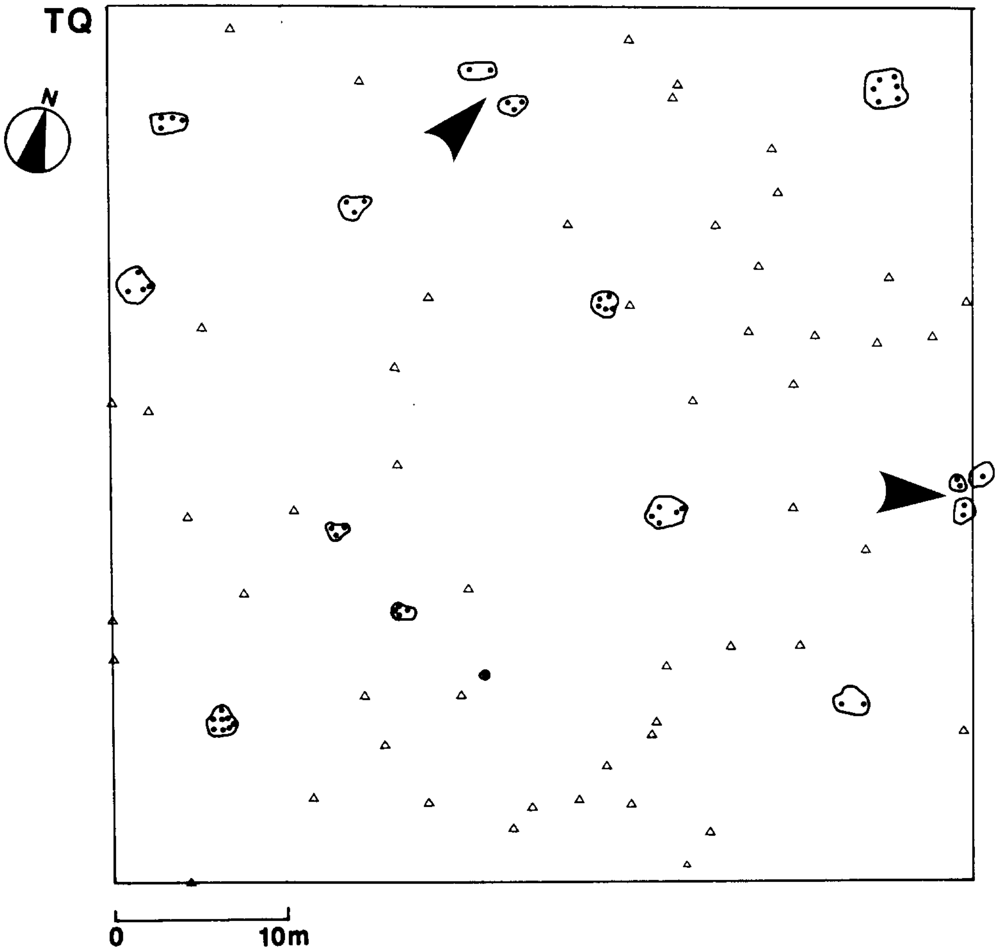
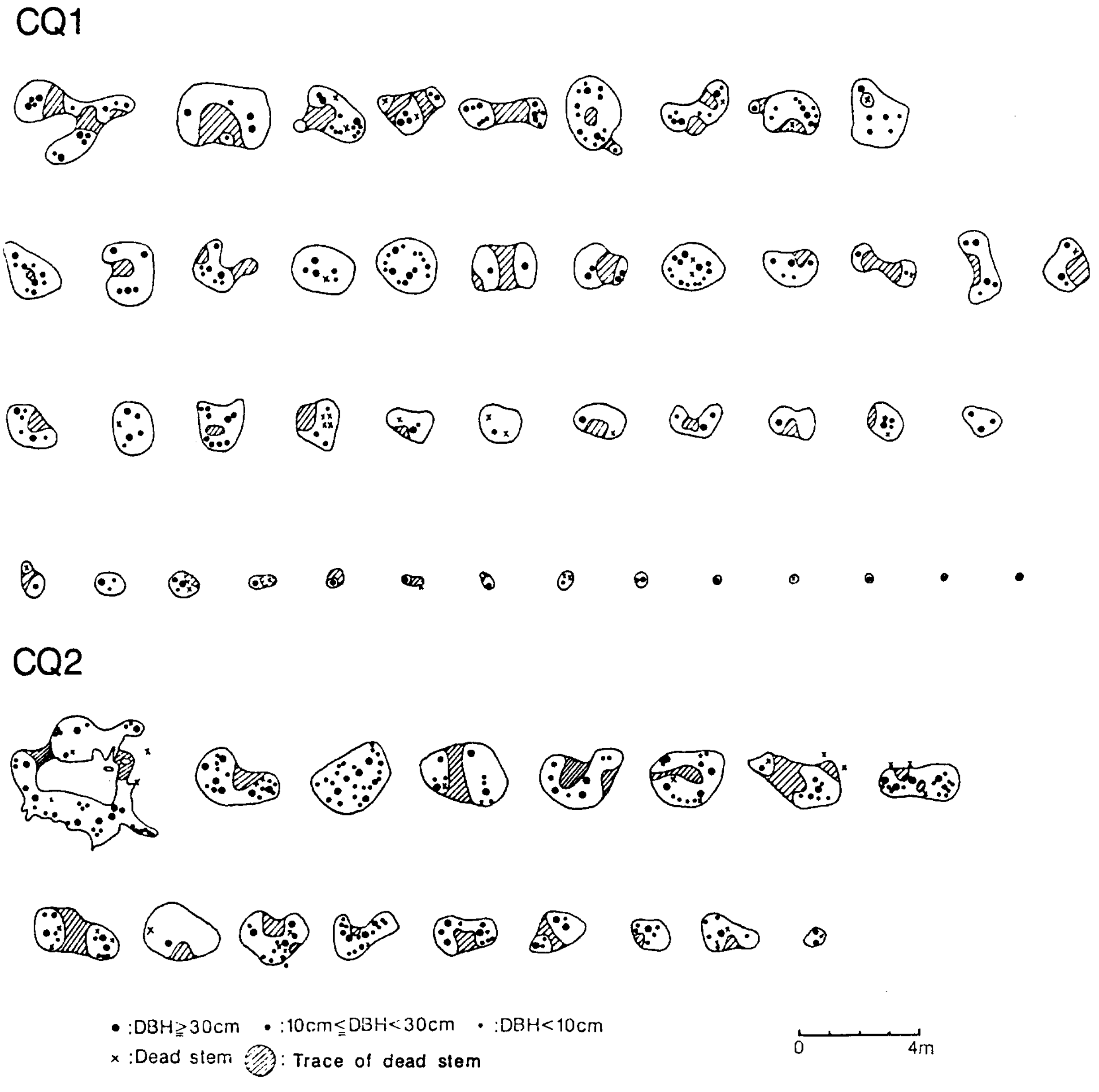


Fig. 6. Distributions of *Fagus japonica* stools in the quadrats in Chichibu (CQ1–CQ3) and in Mt.Takahara (TQ). N.B. Solid lines represent the margin of stools. ●: *Fagus japonica*, △: other species. Arrows in the quadrats (CQ1, CQ3, TQ) show the clumps of *Fagus japonica* stools.

21.4%(TQ) of stools in each quadrat. The number of dead stems per stool was mostly one, with a maximum of four. Relationships between the maximum diameter of living stems and that of dead stems in every *F. japonica* stool in the quadrats are shown in Figure 5. The maximum diameter of the dead stem in a quadrat was 67.5 cm in TQ. The mean diameter (28.5 cm) of living *F. japonica* stems which attain to 'canopy layer' (more than 20 m in height) in Chichibu quadrats (CQ1, CQ2 and CQ3) (Ohkubo *et al.* 1988) was applied to this relationship on the basis of the assumption that dead stems of *F. japonica* with the above diameter had attained the canopy when alive. About 40% of stools with dead stems had dead stems which had attained the canopy when alive (parts of A + B + C in Fig. 5). And about 60% of the above stools had living stems which attained the canopy later (20 m in height). There were some differences of distribution among quadrats. Most of the stools which belonged to part A and B were in CQ1 and CQ2.

Spatial distributions of the F. japonica stools

Spatial distributions of *F. japonica* stools in the quadrats (CQ1–CQ3, TQ) are shown in Figure 6.



In the quadrats the stools are distributed at random, and some of which were close to each other and formed clumps in CQ1, CQ3 and TQ. Projection diagrams of *F. japonica* stools are shown in CQ1, CQ2 and TQ (Fig. 7). The shape of the stools was round, elliptical and irregular, respectively. One of the stool shapes in CQ2 was a circle type. The large stems stood in the center of each stool. Small stems and sprouts stood around the large (or old) stems. The smallest sprouts were formed at the periphery of each stool. Around the center or the margin of the stools, dead traces of large or small stems were found (some of them formed a dead center). Some of the stools seemed to be divided by the dead traces and separated into some small stools.

The MSD of the stools in each quadrat were compared (Fig. 8). The distributions of MSD were mono-modal except OQ and most of the MSD were smaller than about 260 cm (maximum

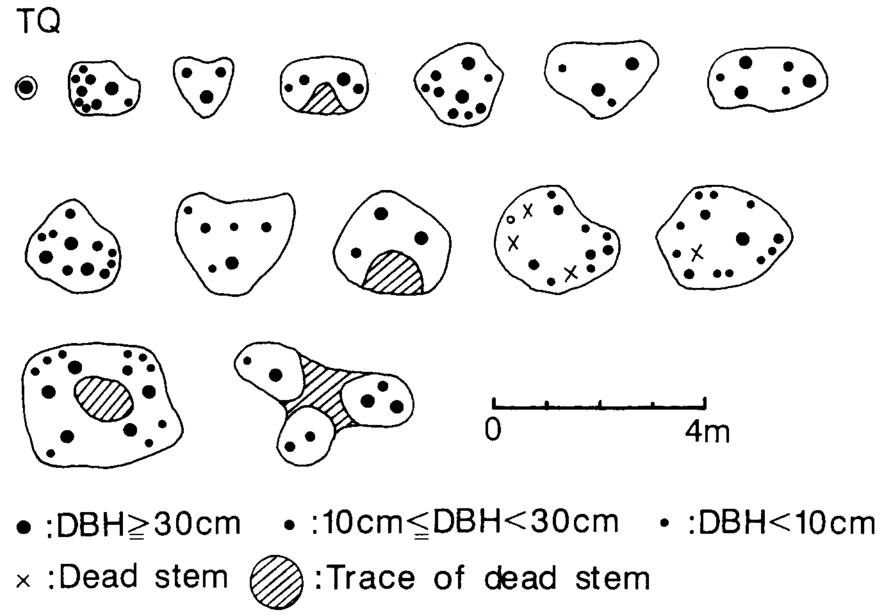


Fig. 7. Projection diagrams of *Fagus japonica* stools in the quadrats in Chichibu (CQ1–CQ3) and in Mt. Takahara (TQ). N.B. Solid lines represent the margin of stools.

430 cm in OQ). There were stools of small-sized classes in CQ1 and CQ3. As shown in Figure 9, the Stool Areas (SA) calculated from the Mean Stool Diameter (MSD) were positively correlated to the total Basal Area (BA) in every stool in all the quadrats. Most of the total basal areas were about one-tenth of the Stool Area (SA) in each stool.

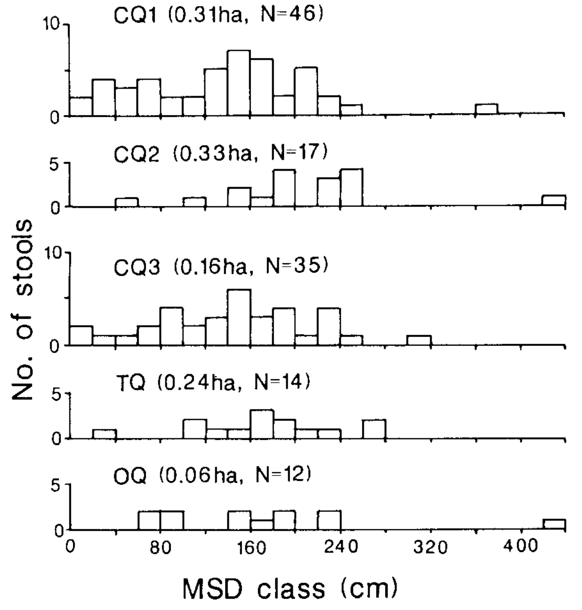


Fig. 8. Frequency distributions of the Mean Stool Diameter (MSD: referred to text) of *Fagus japonica* in each of the quadrats CQ1–3, TQ and OQ. N.B. N: no. of stools in each quadrat.

Forest floor vegetation and beech seedlings (Table 2)

The amounts of beech seedlings are significantly correlated to the types of forest floor vegetation in the beech (*F. crenata*) forests in Japan (Kataoka 1982; Maeda 1988). In CQ1 shrubs and herbs such as *Hydrangea petiolaris*, *Hydrangea hirta*, *Lindera umbellata* and *Ainsliaea acerifolia* grow sparsely (Shrub type). In CQ2 dwarf bamboo (*Sasa borealis*) grow densely, but there are few species other than *Sasa* (*Sasa* type). In CQ3 *Carex reinii* dominates and the species composition is similar to CQ1, but the coverage of the species is low (*Carex* type). And on Mt-.Takahara (TQ) and Okukinu (OQ) *Sasa nipponica* grows densely, the same as CQ2 in Chichibu (*Sasa* type). *Sasa borealis* and *Sasa nipponica* are characterized in the Pacific type of

Table 2. Forest floor vegetation and the number of beech seedlings in the five quadrats Chihibu (CQ1, CQ2, CQ3), Mt. Takahara (TQ) and Okukinu (OQ).

Quadrat number	CQ1		CQ2		CQ3		TQ		OQ		Freq.
Species	Cv.	Cn.	Cv.	Cn.	Cv.	Cn.	Cv.	Cn.	Cv.	Cn.	
Tree (canopy and subcanopy)											
Acer rufinerve	1.8	IV	0.1	I	0.1	I	.	.	0.1	I	4
Acer tenuifolium	1.3	IV	0.1	I	0.1	III	.	.	0.1	I	4
Styrax obassia	0.1	I	.	.	0.1	I	0.1	III	0.1	IV	4
Stewartia pseudocamellia	0.7	II	.	.	0.1	I	0.1	IV	0.1	II	4
Fraxinus lunuginosa	0.9	IV	.	.	1.3	V	0.1	V	0.1	IV	4
Acer micranthum	1.0	IV	0.1	I	0.1	III	.	.	.	.	3
Acer nikoense	0.1	I	.	.	0.1	I	0.1	III	.	.	3
Acer sieboldianum	1.2	IV	.	.	0.1	II	.	.	0.1	I	3
Acanthopanax sciadophylloides	0.8	III	.	.	0.1	I	.	.	0.1	I	3
Acer distylum	1.0	II	.	.	0.1	I	.	.	0.1	IV	3
Cornus controversa	0.1	I	.	.	.	.	0.1	III	0.1	I	3
Pterocarya rhoifolia	0.1	I	.	.	.	.	.	.	0.1	III	2
Carpinus cordata	0.1	I	.	.	.	.	.	.	0.1	V	2
Acer mono var. *marmoratum*	.	.	.	.	.	.	0.1	III	0.1	II	2
Acer diabolicum	.	.	.	.	.	.	0.1	III	.	.	1
Shrub											
Lindera umbellata	2.9	V	0.1	II	1.3	IV	.	.	1.73	IV	4
Callicarpa japonica	2.1	II	0.1	I	0.1	II	.	.	0.1	III	4
Viburnum wrightii	1.3	I	.	.	0.1	I	0.1	I	0.1	IV	4
Rubus palmatus var. *coptophyllus*	1.2	II	.	.	0.1	I	0.1	I	0.1	IV	4
Euonymus oxyphyllus	0.8	III	0.1	I	.	.	.	.	0.1	V	3
Hydrangea involucrata	5	I	.	.	2.6	I	.	.	0.92	IV	3
Hydrangea hirta	10.6	II	.	.	2.7	IV	.	.	.	.	2
Stephanandra incisa	.	.	.	.	.	.	0.1	III	0.1	V	2
Euonymus alatus var. *apterus*	.	.	.	.	.	.	0.1	III	.	.	1
Berberis thunbergii	.	.	.	.	.	.	0.1	III	.	.	1
Herb											
Ainsliaea acerifolia	4.7	III	.	.	0.1	I	.	.	2.6	II	3
Tricytris affinis	0.6	III	.	.	0.1	IV	.	.	0.1	V	3
Dryopteris sabaei	0.1	I	.	.	0.1	IV	.	.	0.1	I	3
Dryopteris polypesis	0.6	I	.	.	0.6	III	.	.	.	.	2
Disporum smilacinum	1.2	II	.	.	.	.	0.1	III	.	.	2
Astilbe thunbergii	0.1	I	.	.	.	.	.	.	0.1	V	2
Carex reinii	.	.	.	.	65	V	.	.	0.1	V	2
Smilacina japonica	.	.	.	.	.	.	0.1	III	0.1	I	2
Cacalia delphinifolia	.	.	.	.	.	.	0.1	I	0.1	III	2
Lonicera gracilipes	.	.	.	.	.	.	0.1	IV	.	.	1
Cacalia hastata var. *farfaraefolia*	.	.	.	.	.	.	.	.	0.1	IV	1
Synurus pungens	.	.	.	.	.	.	.	.	0.1	IV	1
Cirsium tanakae	.	.	.	.	.	.	.	.	0.1	IV	1
Struthiopteris nipponica	.	.	.	.	.	.	.	.	0.1	IV	1
Cimicifuga acerina	.	.	.	.	.	.	.	.	1.94	V	1
Dryopteris crassirhizoma	.	.	.	.	.	.	.	.	0.8	V	1
Dwarf bamboo											
Sasa borealis	.	.	76.8	V	.	.	.	.	1.7	II	2
Sasa nipponica	.	.	.	.	.	.	87.5	V	42.2	V	2

Table 2. Continued.

Quadrat number		CQ1		CQ2		CQ3		TQ		OQ		Freq.
Species		Cv.	Cn.	Cv.	Cn.	Cv.	Cn.	Cv.	Cn.	Cv.	Cn.	
Liana												
Schitzophragma hydrangeoides		3.3	V	0.1	I	0.1	III	0.1	III	0.1	II	5
Hydrangea petiolaris		16.4	III	.	.	0.1	I	.	.	0.7	V	3
Rhus ambigua		7.5	II	.	.	0.1	IV	.	.	0.1	II	3
Schisandra repanda		1.5	III	.	.	0.1	I	.	.	0.1	II	3
Actinidia arguta		0.8	I	.	.	.	.	0.1	III	0.1	I	3
Dioscorea nipponica		.	.	.	.	.	.	.	.	0.1	III	1
Height class of *Fagus japonica* seedlings (no./ha)	– 10 (cm)		88		0		0		0		0	
	– 20		128		0		0		0		13	
	– 20		3		0		0		0		0	
	– 40		9		0		0		0		0	
	– 50		6		0		3		0		0	
	– 130		0		0		0		0		13	
	Total		234		0		3		0		26	
Height class of *Fagus crenata* seedlings (no./ha)	– 10 (cm)		23		0		3		4		0	
	– 20		39		0		3		0		0	
	– 20		6		0		0		0		0	
	– 40		0		0		0		0		0	
	– 50		3		0		0		0		0	
	– 130		0		0		0		4		13	
	Total		71		0		6		8		13	

N.B. Cv.: Coverage (%), Cn.: Constancy, Cv. and Cn. are calculated from the data of 35 sub-quadrats (CQ1), 35 sub-quadrats (CQ2), 20 sub-quadrats (CQ3), 4 sub-quadrats (TQ) and 8 sub-quadrats (OQ).

forest floor vegetation under beech forests (Sasaki 1970).

Few *F. japonica* seedlings (H ≧ 1.3 m) were found in the quadrats with a dense undergrowth of dwarf bamboo. There were no beech seedlings in CQ2 and TQ. In OQ there were two *F. japonica* seedlings (55 cm, 13 cm in height) and one *F. crenata* seedling (60 cm in height) only on the mound of the fallen-log in the canopy gap. There was an increase in the numbers in the *Carex* and shrub types, especially in the shrub type (CQ1) where there were 234 seedlings of *F. japonica* per hectare. Most of the seedlings were small-sized ones (less than 20 cm in height). The *F. japonica* seedlings less than 20 cm in height mostly originated from the current ones which fell in the last mast year (1983) (Ohkubo *et al.*, 1989).

Discussion

Regeneration of F. japonica stems and stools

In each quadrat *F. japonica* showed characteristic bush-like forms compared with the other component species in the canopy. Although trunk suckers are often found in component species of forests suffering severe conditions (Oliver & Larson 1990) and in some species of forest shrubs (Yamanaka & Tamai 1986), there are few examples in the case of late-successional or shade tolerant species in natural forests (Jones & Raynal 1986). In Japan similar types of the tree forms are found in the late successional species like *Tilia japonica*, *Tilia maximowicziana*, and *Cercidiphylllum japonicum* (Kikuzawa 1983) in cool-temperate forests and *Castanopsis cuspidata* in

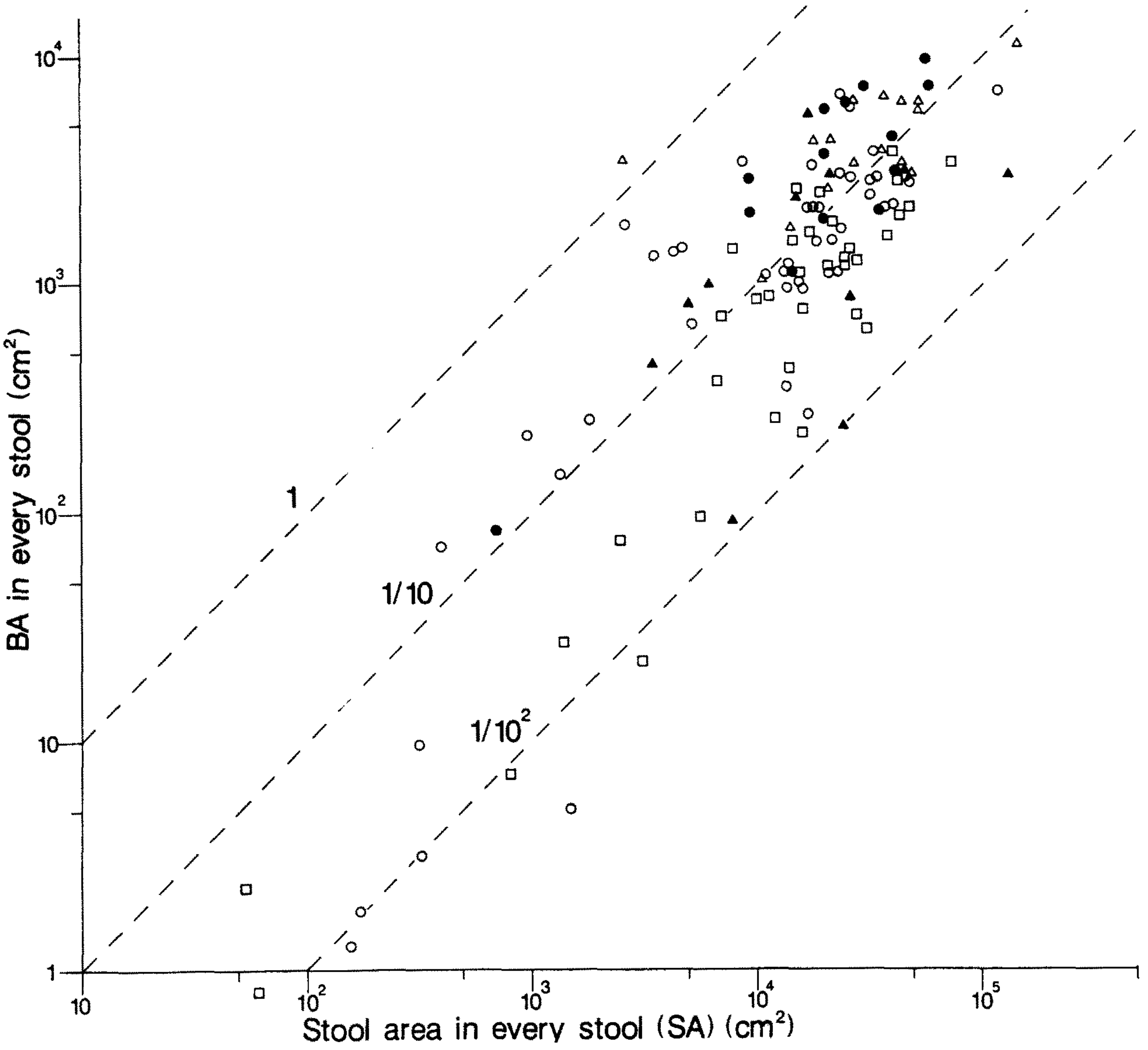


Fig. 9. Relationships between the Stool Area (SA) (cm^2) from Mean Stool Diameter (MSD) and the total Basal Area (BA) (cm^2) in every *Fagus japonica* stools in all the quadrats CQ1(○), CQ2(△), CQ3 (□), TQ(●) and OQ(▲).

warm-temperate forests. As in the case of the above species, the results concerning the size structure of living stems suggest that *F. japonica* has a self replacement process of canopy stems in each stool. The stems of subcanopy layers and the sprouts around the canopy stems can take over the canopy stems in the same stool. Koop (1987) pointed that trunk suckers can replace dying trees (including endogenous damage resulting from senescence, damage caused by disease and mechanical damage that results in partial uprooting or breaking of the stem) and ageing parent trees (e.g. *Alnus gultinosa*, *Betula pubescens*, *Salix alba*, *Tilia cordata*, *Ulmus laevis* and *U. minor*.). Although in the case of *F. japonica* both cases could be found, such conditions are not derived from previous coppicing.

As shown in the results of the frequency distributions of max. DBH and max. height of living *F. japonica* stems in each stool (Fig. 3), some stems in the stools can be maintained as canopy trees for a certain period. After the death or ageing of the canopy stems, the sub-canopy stems and sprouts within the stool can grow up successively. On the other hand, as shown in Fig. 4, size structures of *F. japonica* stems in the stools are not only continuous distributions like catenary curves, but also discontinuous distributions like L-shaped curves, thus in those stools the canopy stems in the stools regenerate discontinuously. These phenomena were found in the cases of the stools of B (29%) and C (17%) area in Figure 5.

The various sizes and shapes of the living stems, the dead stems and the dead traces existed in the same *F. japonica* stool and the shapes of the stool were varied as shown in Figure 7. The stools were distributed randomly and in some parts contiguously in the quadrats as shown in Figure 6. And MSD of *F. japonica* stools showed monomodal distributions in each quadrat as shown in Figure 8. The above phenomena suggest that the size of *F. japonica* stools is gradually expanded by the repetitions of sprout regeneration. Relationships between the stool area and the basal area in every stool as shown in Figure 9 support the potential ability of the expansion growth in the stool. And after reaching considerable dimensions, the stools are separated and/or the dead center is created. A similar pattern of clonal expansion by vegetative organs exists for *Calluna* bushes (Barclay-Estrup & Gimingham 1969) and forest herbs: *Mercurialis prennis*, *Filipendula ulmaria* and *Germanium robertianum* (Falińska 1985).

Maintenance of the forest canopy and the population

As previously mentioned, *F. japonica* is one of the important component canopy trees in the natural cool-temperature forests on the Pacific side of Japan. The large number and various sizes of sprouts strongly affect the regeneration of the canopy layer. But sprouts concentrate close to the parent stem within the same stool, and there is a limited stool expansion. Root-collar sprouting is effective in the case of the gap closure created by small-scale disturbance to the canopy as shown in Chichibu (Ohkubo *et al.* 1988).

Various types of forest floor vegetation were found in each quadrat. The dwarf bamboos, *Sasa borealis* and *Sasa nipponica* which are characteristic to the Pacific side of Japan dominate in a part of Chichibu (CQ2) and in Takahara (TQ) and Okukinu (OQ), respectively. There are a few *F. japonica* seedlings in these sites. The dwarf bamboos are great inhibitors to the regeneration of beech seedlings in Japan (Maeda 1988; Nakashizuka & Numata 1982), and also the scarcity of beech juveniles under the dwarf bamboos, *Sinaarundinaria chungii* in Chinese *Fagus lucida* forests and under *Arundinaria* sp. in Taiwanese *F. hayatae* forests was observed (Peters & Ohkubo 1990).

In the case of *F. japonica* forests there were a few seedlings even in the forests with a sparse undergrowth of dwarf bamboo. Thus *F. japonica* seedlings do not play an important role as successors under the closed natural beech forests (Ohkubo *et al.* 1989). On the other hand the apparent occurrence of stool expansion and many larger stools may contribute to the persistence of beech at a given location and period. Thus strong root-collar sprouting in the beech compensates for the scarcity of regeneration by seedlings.

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