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Distribution and regeneration strategies of major canopy dominants in species-rich subtropical/warm temperate rainforests in south-western Japan

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The distribution and regeneration strategy of the major canopy dominants in species-rich subtropical/warm temperate rainforests in south-western Japan was studied in a hilly zone below 1100 m a.s.l. Using the patch sampling method, four dominance-community types were numerically identified and they corresponded to four habitats which represented a combination of topography and altitude (i.e. ridges *vs* slopes, and below *vs* above 500 m a.s.l.) Seven major canopy dominants had their respective distributional core in one of these topo-altitudinal habitats. The seven canopy dominants could be classified into three species groups according to their size structure and growth habits. Group A (*Tsuga sieboldii* and *Quercus gilva*) and group B (*Quercus acuta*, *Quercus salicina*, *Machilus thunbergii*) were restricted to the emergent and canopy layer, respectively. These two groups had only a few subcanopy trees and saplings. Saplings of group B showed a rapid growth rate in canopy gaps. Group C (*Distylium racemosum*) was characterized by many subcanopy trees and saplings that grew steadily under the closed canopy. *Castanopsis sieboldii* showed intermediate characteristics between group B and C in the size structure and growth habit of its saplings. The density of *D. racemosum* canopy trees was markedly reduced on ridges and slopes above 500 m and on slopes below 500 m. In these marginal habitats, the three species groups coexisted by sharing different strata within a community. This situation was possible due to the differences in regeneration strategies among the canopy species.

Key words: habitat partitioning; regeneration strategy; species coexistence; stratification; subtropical/warm temperate rainforest.

INTRODUCTION

Subtropical/warm temperate rainforest (SWRF), which represents a transitional forest between tropical rainforest and temperate deciduous/coniferous forest in east Asia, is characterized by a high diversity of leaf type in canopy dominants (i.e. evergreen, deciduous and coniferous species; Wang 1961; Ohsawa 1983, 1993). The mechanism for the coexistence of a number of species that belong to the same guild (e.g. canopy dominant) in a small area is one of the interesting issues that remains to be clarified for this forest formation.

Previous works suggested the following as a mechanism of species coexistence among canopy dominants in a small area in this forest type: the presence of canopy gaps that create heterogeneous environments; and differential species adaptation to the heterogeneous environments (Tanouchi & Yamamoto 1995). Tanouchi and Yamamoto (1995) reported differences in the size structure and the spatial distribution related to canopy gaps among canopy dominants. Tanouchi *et al.* (1994) and Sato *et al.* (1994) reported a difference in the survival rate of seedlings under a closed canopy, and Yamamoto (1992) reported a difference in the abundance of gap successors among canopy dominants.

However, only a few studies have been conducted on the mechanisms of species coexistence in a mesoscale area (e.g. single mountain massif). In a mesoscale area, species may have their distributional

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cores in different habitats along complex gradients of altitude and topography or habitat mosaics (Whittaker 1956, 1960; Peet 1981). Species may change their regeneration strategy depending on habitat and/or abundance and vigor of co-occurring species. This shift in regeneration niche is thought to contribute to species coexistence in a mesoscale area (Veblen *et al.* 1981; Veblen & Stewart 1982; Read & Hill 1988; Read *et al.* 1990; Rebertus & Veblen 1993). However, the hypothesis of habitat partitioning and shift in regeneration niche has not been widely examined for SWRF in mesoscale areas.

We carried out this study to investigate: (i) the partitioning of habitats and regeneration strategies; and (ii) the shift in regeneration niche among major canopy dominants on a mountain covered with SWRF. We analyzed size structure and growth habits of the species to demonstrate habitat partitioning and niche shift.

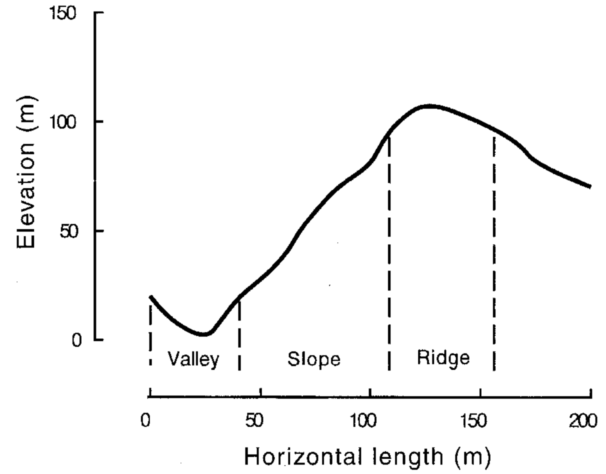

Fig. 1. Schematic diagram of a topography transect on Mt Ohmori drawn based on a 1:25 000 topographical map.

STUDY SITE AND METHODS

Study site

This study was conducted on Mt Ohmori (32°N, 131°E, the summit 1109 m a.s.l.) in Aya, Kyushu, south-western Japan. This mountain is located near the northern limit of SWRF. The mountain is covered with sandstone and shale of the Paleogene, and comprised of steep slopes exceeding 30°. Annual mean temperature, coldest-month mean temperature and mean annual precipitation at the nearest meteorological station (7 m a.s.l., Miyazaki) were 16.9°C, 6.8°C and 2489.5 mm, respectively (Japan Meteorological Agency 1982).

Field research was carried out on the south-east flank of the mountain with an altitudinal range from 100 to 1100 m. The study area was covered with primary SWRF. Almost all major canopy dominants which are commonly found in the SWRF of south-western Japan occur on this mountain. These include *Quercus gilva* Blume, *Quercus acuta* Thunb. ex Murray, *Quercus sessilifolia* Blume, *Quercus salicina* Blume, *Castanopsis sieboldii* (Makino) Hatusima ex Yamazaki et Mashiba, *Castinopsis cuspidata* (Thunb. ex Murray) Schottky of Fagaceae, *Machilus thunbergii* Sieb. et Zucc. of Lauraceae, *Distylium racemosum* Sieb. et Zucc. of Hamamelidaceae, and the evergreen conifers *Abies firma* Sieb. et Zucc. and *Tsuga sieboldii* Carr. The temperate conifers (*A. firma* and *T. sieboldii*) are at their lowest altitudinal limit in south-western Japan. On the mountain, three microtopographical units were classified (Fig. 1): ridge, slope and valley. The former two were included in the present study, and the valleys were excluded. Because the inclination is too steep and the mother rocks are exposed, there are no developed forest communities but only shrubs and herbs in the valleys.

Methods

Because the study area was extensive in area, sampling was conducted by stratifying dynamic units (the patch sampling method; Ohsawa 1991a) to understand vegetation patterns and dynamics. Climax forest is the mosaic gathering of patches which are different in size and age. Watt (1947) classified the patches into four phases in the regeneration process of a community after natural disturbance: 'gap', 'building', 'mature' and 'degenerate'. We were able to divide the patches into two phases by the difference in canopy tree size in the SWRF of Mt Ohmori: gap (including the building phase) and mature (including the degenerate phase). Canopy trees of mature-phase patches reached more than 10 m in tree height (H) and 30 cm in diameter at breast height (d.b.h.), and the basal area of the patches was greater than 50 $m^2 ha^{-1}$ in the SWRF of Mt Ohmori. In this study, we mainly sampled mature-phase patches.

We extracted the patches in which canopy trees had a similar tree height and d.b.h., and recorded altitude, topographical unit (ridge or slope), aspect, inclination, and long and short widths of each patch. Patch area was calculated as an ellipse from the two horizontal widths. In each patch, d.b.h., tree height (H) and height to the lowest foliage leaves (HL) was measured for all trees above 2.0 m in height. Also, the number of saplings ($0.3 \text{ m} \le H < 2.0 \text{ m}$) of the major canopy dominants were recorded. In total, 20 mature-phase patches were surveyed from 1990 to 1992.

Growth rate under closed canopy was examined for saplings of the major canopy dominants on ridges at 400 m a.s.l. where we could get an adequate number of sample saplings of almost all major canopy dominants for statistical comparison of growth rate. A similar investigation was applied to gaps of about 50 m^2, which was an average gap size in SWRF of this region (Yamamoto 1992). For the growth rate, paint markings were made at the base of terminal buds of leader shoots before bud-break in May 1992. The increment in length from the marks to the bases of newly formed terminal buds (annual shoot growth) was measured after shoot elongation in November 1992.

In Mt Ohmori, four fundamental temperature indices at 500 m a.s.l. were calculated on the basis of monthly normals using a temperature lapse rate of 0.6°C per 100 m. Annual mean temperature, coldest-month mean temperature, the warmth index and the coldness index (Kira 1948, 1977) were 13.9°C, 3.8°C, 107.6°C · month, and –1.2°C · month, respectively. The warmth index and the coldest-month mean temperature at 500 m a.s.l. on Mt Ohmori coincided with those at the upper limit of *C. sieboldii* forests in Shikoku (Yamanaka 1975) and Izu peninsula (Suzuki & Hatiya 1951): 100–110°C · month and 2–3°C, respectively.

At 110 m a.s.l. on Mt Ohmori, annual mean temperature, coldest-month mean temperature, the warmth index, and the coldness index were 10.3°C, 0.2°C, 74.9°C · month, and –11.7°C · month, respectively. Thus, the warmth index and the coldness index at 1100 m a.s.l. on Mt Ohmori were found to be less than those of the SWRF upper limit in Japan (Kira 1948, 1977): 85°C · month and –10°C · month, respectively. Nevertheless, on Mt Ohmori, SWRF is distributed right up to the mountain tops (i.e. 1109 m).

Topography influences vegetation through soil moisture and nutrients (Hack & Goodlett 1960; Furley 1976; Butler *et al.* 1986; Baillie *et al.* 1987; Johnston 1992). In general, soils on ridges are drier and poorer in nutrients than those on slopes.

In the present study, two altitude classes (> 500 m and < 500 m) and two topography classes (ridge and slope) were considered for the analysis, the combination of which resulted in four habitat types (2 altitude classes × 2 topography classes).

Data analysis

Dominant species of each patch were defined by the dominance analysis (Ohsawa 1984) using the relative basal area (RBA) of each species. To distinguish dominance types and to examine species association of SWRF on Mt Ohmori, the 20 patches were subjected to a cluster analysis (the group average method) using the percentage similarity index (Whittaker 1952).

Because canopy layer was formed above 10 m in height at all sampled patches, we arbitrarily divided sampled trees into two size classes by tree height: canopy trees ($H \ge 10$ m) and subcanopy trees ($2 \text{ m} \le H < 10 \text{ m}$). We could not make a further sharp distinction within subcanopy layer because there was no discontinuity below 10 m in tree height class frequency distributions at all sampled patches. The density of the two size classes and saplings ($0.3 \text{ m} \le H < 2 \text{ m}$) was calculated for major canopy dominants of each dominance type identified by the above procedures. For each dominance type, the total number of individuals in each size class was divided by the summed patch area. These composite data were also used to express quantitative floristics in each dominance type.

RESULTS

Distribution pattern

The cluster analysis of the 20 mature-phase patches revealed four dominance types: (i) *D. racemosum* type; (ii) *T. sieboldii* type; (iii) *Q. gilva* type; and (iv) *Q. acuta* type (Fig. 2a). The four dominance types were clearly separated into four topo-altitudinal habitat types (Fig. 2b).

The RBAs of dominant species that dominate at least one patch are shown in Table 1. Seven major

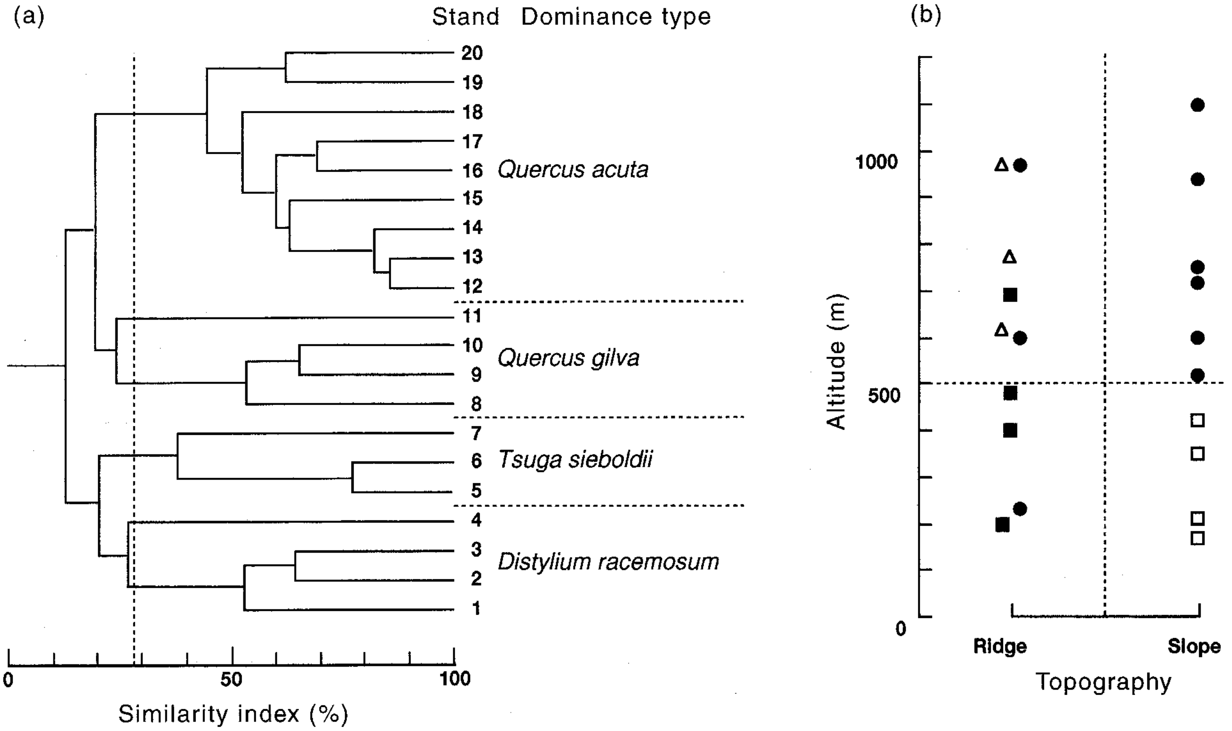

Fig. 2. (a) A dendrogram showing similarities of species composition among 20 patchs. Four dominance types were distinguished. (b) Distribution of the four dominance types along altitudinal and topographical gradients: *Distylium racemosum* (■); *Tsuga sieboldii* (△); *Quercus gilva* (□); *Quercus acuta* (●).

canopy dominants occurred in more than 10% of the patches: *D. racemosum*, *C. sieboldii*, *Q. salicina*, *T. sieboldii*, *Q. gilva*, *Q. acuta* and *M. thunbergii*.

Figure 3 shows distribution patterns of species abundance for the seven species in the topo-altitudinal habitat matrix. Each species had its distributional core (the most abundant habitat type) in one of the four topo-altitudinal habitat types. *Distylium racemosum* and *C. sieboldii* was most abundant on the ridges below 500 m a.s.l., while *T. sieboldii* was most abundant on the ridges above 500 m. *Quercus salicina* tended to be more abundant on the ridges, but this did not differ with altitude. *Quercus gilva* and *Q. acuta* was most abundant on the slopes below and above 500 m, respectively. *Machilus thunbergii* was more abundant on the slopes, but its altitudinal pattern was not apparent. *Distylium racemosum*, *C. sieboldii*, *Q. gilva* and *M. thunbergii* were. not found above 900 m a.s.l.

Tsuga sieboldii and *Q. gilva* were each restricted to one of the four topo-altitudinal habitat types and to one dominance type. On the other hand, *D. racemosum*, *C. sieboldii*, *Q. salicina*, *Q. acuta*, and *M. thunbergii* occurred across more than two types of topo-altitudinal habitats and two dominance types (Fig. 3, Table 1). Thus, the distribution ranges of the seven species broadly overlapped with each other, and more than two dominant species occurred together in each patch.

Size structure and stratification

Height class frequency distributions of the seven dominant species at one representative patch in each dominance type are shown in Fig. 4. Densities of canopy trees and subcanopy trees of the seven dominant species in each dominance type are shown in Table 2.

The seven species had a characteristic size distribution and could be classified into three species groups (group A, B and C). Group A included *T. sieboldii* and *Q. gilva*, which showed a unimodal size distribution in the *T. sieboldii*-type and the *Q. gilva*-type patches, respectively (Fig. 4). In these two dominance types, the maximum height of *T. sieboldii* and *Q. gilva* was about 5 m higher than the other species (Table 3), and their crowns projected above the evergreen closed canopy as emer-

Table 1 Species composition of 20 mature phase patches showing the relative basal area (RBA) of dominant species that dominated at least one patch

Dominance type	*Distylium racemosum*				*Tsuga sieboldii*			*Quercus gilva*				*Quercus acuta*								
Patch number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Area (m^2)	360	420	100	112	225	270	189	240	207	264	352	799	342	90	62	198	117	483	203	528
Altitude (m)	400	480	200	690	770	615	970	350	420	210	170	520	750	600	230	1100	970	715	600	940
Aspect	N	N10E	S20W	N60E	S60E	N15E	S70E	N20W	N50W	S45W	N75W	N	N40W	N80W	S85W	S60E	S70E	N30W	N10E	N40E
Inclination	20°	27°	30°	0°	0°	40°	0°	25°	35°	35°	10°	30°	25°	45°	35°	25°	0°	40°	15°	30°
Topography	R	R	R	R	R	R	R	S	S	S	S	S	S	S	R	S	R	S	R	S
Distylium racemosum	**42.2**	**89.6**	**62.3**	**13.9**	**16.4**	**19.4**		3.5	2.4	0.1	0.2	2.6	0.1	6.7	7.4			**43.0**	3.9	
Castanopsis sieboldii	**17.3**	1.0			**11.4**	4.7						<0.1			**26.6**				0.8	
Quercus salicina	**15.8**	<0.1	**15.1**	**23.2**	4.2	0.2	**9.0**	0.1	1.7	8.7		1.6	<0.1	<0.1			<0.1	<0.1	4.6	**14.9**
Castanopsis cuspidata	0.2		**17.1**			<0.1					1.9									
Michelia compressa				**10.3**							0.6									
Cinnamomum japonicum	0.4	1.2	<0.1	**21.4**	<0.1	0.1	<0.1	<0.1	3.1	0.8	<0.1	0.2	2.0	1.8	<0.1		2.1	1.2	0.1	0.9
Tsuga sieboldii					**50.7**	**66.8**	**29.1**										0.1			
Acer sieboldianum					1.6		**25.9**									<0.1	**16.0**			
Quercus gilva								**39.3**	**46.8**	**42.2**	**14.1**									
Quercus myrsinaefolia											**21.2**									
Quercus glauca									<0.1	2.4	**5.4**									
Machilus japonica		0.5		0.1				**12.8**	2.9	0.9	**6.5**	6.0	4.1	0.6				3.8		0.6
Litsea acuminata		<0.1						**8.4**		0.1	0.3	0.4								
Meliosma rigida			0.01							0.7	**6.6**									
Sapindus mukorossi								7.7			**16.4**									
Aphananthe aspera											**8.6**									
Idesia polycarpa											**8.6**									
Quercus acuta	6.0	<0.1		<0.1	**9.7**	3.4	2.6	**17.7**	**20.3**			**52.6**	**62.3**	**59.3**	**56.8**	**71.5**	**55.1**	**43.2**	**40.4**	**28.6**
Machilus thunbergii	0.7	<0.1		6.2		2.0			**18.2**	**40.1**	1.9	**29.2**	**24.0**	**18.1**					6.3	
Stuartia monadelpha							6.2						0.2			4.1	1.7		**23.0**	**29.5**
Camellia japonica		1.4	1.2	**9.7**	1.2	0.1	**10.9**	0.1	0.7	0.3	4.4	2.0	1.0	3.6	3.3	0.1	6.0	1.6	1.6	**10.1**
Illicium anisatum	0.2	<0.1		**9.1**	<0.1	0.1	2.1	0.7	0.6			0.1	2.3	<0.1		9.8	10.0	0.1	2.2	4.9

Dominant species at each patch are indicated by bold figures. R, ridge; S, slope.

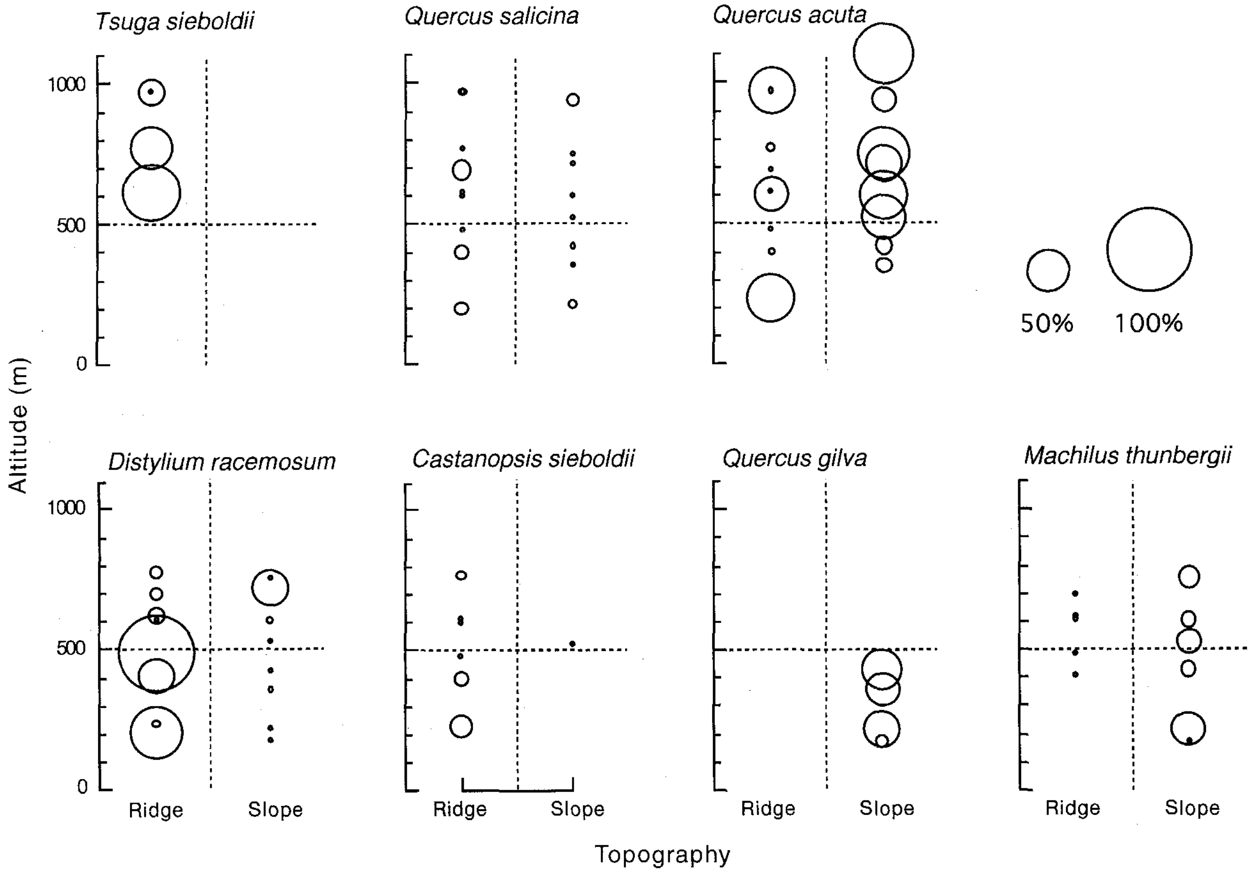

Fig. 3. Distribution of species abundance for the major canopy dominants along altitudinal and topographical gradients. Species abundance is expressed in relative basal area indicated by circle size superimposed on the distribution of the 20 patches as shown in Fig. 2(b).

gent trees. These species had few subcanopy trees (Table 2). This type of size distribution is comparable to the 'emergent type' of Ohsawa (1991a,b) that was based on stem-diameter frequency distribution.

Group B included *Q. acuta*, *Q. salicina* and *M. thunbergii*. These species corresponded with the unimodal or the 'sporadic type' of Ohsawa (1991a,b), and formed a canopy layer above 10 m in height in every dominance type. They had a few subcanopy trees in almost all patches.

Group C included *D. racemosum,* which showed a continuous size distribution with more trees in smaller size classes than in larger classes. This type was comparable to the 'inverse-J type' of size distribution of Ohsawa (1991a,b). Although *D. racemosum* occupied the subcanopy layer in every dominance type, the species could not reach the canopy layer in most cases except for *D. racemosum* type. The canopy tree density of *D. racemosum* in the *T. sieboldii* type, the *Q. gilva* type and the *Q. acuta* type was 2/5, 1/18 and 1/12 of that in *D. racemosum* type, respectively. These values were significantly lower ($P < 0.01$, Chi-squared test), compared to that in the *D. racemosum* type. This pattern corresponded with the tendency for the canopy tree density of *D. racemosum* to show a peak on the ridges below 500 m a.s.l. and to decrease with altitude (Fig. 5). Also, the density of *D. racemosum* was always low on the slopes irrespective of altitude.

The size distribution of *C. sieboldii* varied with patches. *Castanopsis sieboldii* showed both the unimodal and inverse-J type size distribution in the *D. racemosum* type. It showed a sporadic type of size distribution with more trees in the smaller size classes in the *T. sieboldii* type and the *Q. acuta* type. Thus, *C. sieboldii* was an intermediate species between group B and group C with respect to population structure.

Consequently, the three groups of major canopy dominants (group A, B and C, except *C. sieboldii*)

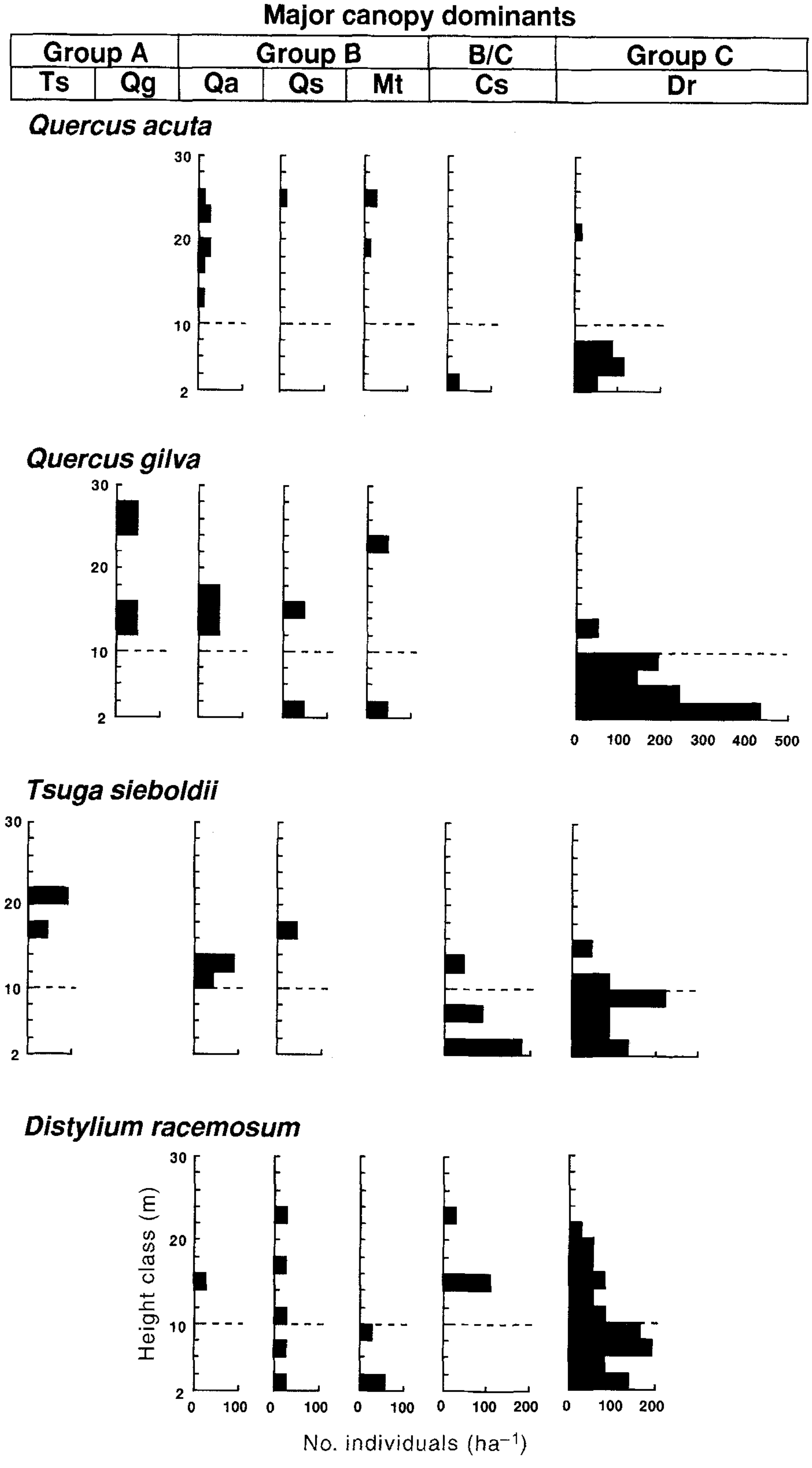

Fig. 4. Height class frequency distributions for the major canopy dominants (seven columns) at a representative patch of each dominance type. The major canopy dominants are classified into three species groups (group A, B and C). Species abbreviations are shown in Table 2. Broken lines indicate an arbitrary limit at 10 m in height that demarcates canopy from subcanopy layers.

Table 2 Density (ha^{-1}) of subcanopy trees (height < 10 m) and canopy trees (10 m ≤ height) in each of the four dominance types

	Dominance type							
	Dr		Ts		Qg		Qa	
Area (m^2)	992		684		1063		2822	
Species	S	C	S	C	S	C	S	C
Tsuga sieboldii (Ts)	0	0	15	161	0	0	7	0
Quercus gilva (Qg)	0	0	0	0	9	103	0	0
Quercus acuta (Qa)	20	10	146	73	0	56	60	120
Quercus salicina (Qs)	40	60	117	58	28	19	35	14
Machilus thunbergii (Mt)	71	10	0	15	9	38	4	21
Castanopsis sieboldii (Cs)	131	50	146	29	0	0	9	4
Distylium racemosum (Dr)	706	343	395	132	339	19	174	28

Dr, *Distylium racemosum* type; Ts, *Tsuga sieboldii* type; Qg, *Quercus gilva* type; Qa, *Quercus acuta* type; S, subcanopy tree; C, canopy tree. Letters in parentheses are species abbreviations.

Table 3 Maximum tree height (m) of the major canopy dominant species at each dominance type

	Dominance type			
	Dr	Ts	Qg	Qa
Tsuga sieboldii		20.0		3.1
Quercus gilva			27.0	
Quercus acuta	15.0	12.0	17.0	24.0
Quercus salicina	22.0	16.0	14.0	24.0
Machilus thunbergii	13.0	11.0	22.0	25.0
Castanopsis sieboldii	22.0	15.0		12.0
Distylium racemosum	21.0	15.5	13.0	20.0

Dr, *Distylium racemosum* type; Ts, *Tsuga sieboldii* type; Qg, *Quercus gilva* type; Qa, *Quercus acuta* type.

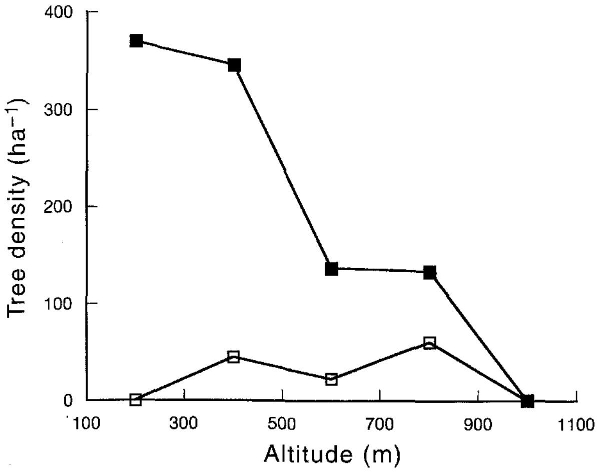

Fig. 5. Change in canopy tree density for *Distylium racemosum* on ridges (■) and on slopes (☐) along altitudinal gradients. Canopy tree density was calculated by adding the number of trees above 10 m in height divided by the summed area from all patches in 200 m intervals in altitude.

could be stratified into two or three layers within forest structure in the *T. sieboldii* type, the *Q. gilva* type, and the *Q. acuta* type. Group A, B and C occupied the emergent layer, canopy layer and subcanopy layer, respectively.

Sapling density under closed canopy

Sapling densities for the seven dominant species are shown in Table 4. The three species groups exhibited a characteristic pattern of sapling density. *Distylium racemosum* of group C showed the highest sapling density among the seven species in two of the four dominance types, and the second or third highest densities in the remaining two dominance types. Group A species, such as *T. sieboldii* and *Q. gilva*, had very low densities in most of the dominance types. Group B species such as *Q. acuta*, *Q. salicina*, *M. thunbergii* and *C. sieboldii* showed inter-

Table 4 Sapling density (ha^{-1}) of the major canopy dominant species at each dominance type

	Dominance type			
	Dr	Ts	Qg	Qa
Tsuga sieboldii	0	0	0	0
Quercus gilva	0	0	160	14
Quercus acuta	222	249	0	10
Quercus salicina	252	599	38	89
Machilus thunbergii	151	88	0	7
Castanopsis sieboldii	343	570	9	99
Distylium racemosum	786	453	122	163

Dr, *Distylium racemosum* type; Ts, *Tsuga sieboldii* type; Qg, *Quercus gilva* type; Qa, *Quercus acuta* type.

Table 5 Mean annual growth rate of leader shoot (cm year^{-1}) under closed canopy and in gaps (SD in parentheses)

	Under closed canopy	In gaps	Significance
Quercus acuta	1.4 (2.0) $n = 13$	5.1 (3.4) $n = 4$	$P < 0.2$
Quercus salicina	0.7 (1.1) $n = 18$	4.2 (2.7) $n = 19$	$P < 0.002$
Machilus thunbergii	2.0 (2.3) $n = 7$	8.9 (8.5) $n = 15$	$P < 0.02$
Castanopsis sieboldii	3.1 (3.5) $n = 16$	10.2 (9.5) $n = 18$	$P < 0.02$
Distylium racemosum	3.6 (7.5) $n = 37$	4.3 (3.0) $n = 31$	$P < 0.01$

Differences in growth rate between 'under closed canopy' and 'in gaps' were tested using Mann-Whitney *U*-test. *n*, Number of sample trees.

mediate sapling densities between group A and group C.

Growth rates of saplings under closed canopy and canopy gaps

The mean annual growth rate of leader shoots of *D. racemosum* saplings in gaps was only 1.2 times larger than that under closed canopy (Table 5). In the three species of group B, and *C. sieboldii*, mean annual growth rates were 3–4 times larger in gaps than those under closed canopy. Under closed canopy, the mean annual growth rate of *D. racemosum* was significantly higher than that of *Q. salicina* ($P < 0.05$, Mann–Whitney *U*-test). In gaps, the mean annual growth rate of *D. racemosum* was small compared to the other dominants, and it was significantly lower than that of *C. sieboldii* ($P < 0.05$), which showed the highest growth rate.

DISCUSSION

Regeneration strategies of the major canopy dominants in SWRF

Quercus acuta, *Q. salicina*, and *M. thunbergii* (group B) occupied the canopy layer with an emergent layer of *T. sieboldii* and *Q. gilva* (group A). These two groups had few subcanopy trees and saplings under the closed canopy, and their survival rates (Tanouchi *et al.* 1994; Sato *et al.* 1994) and growth rates (Table 5) were low. The three species of group B (*Quercus acuta*, *Q. salicina*, and *M. thunbergii)* were able to grow rapidly in canopy gaps (Table 5), and they often occupied the top layer of the gap. Figure 6 shows an example of such a gap (area =110 m^2) with the height class frequency distribution of the major dominants. However, saplings of *T. sieboldii* and *Q. gilva* could not be found in the gap as well as under closed canopy.

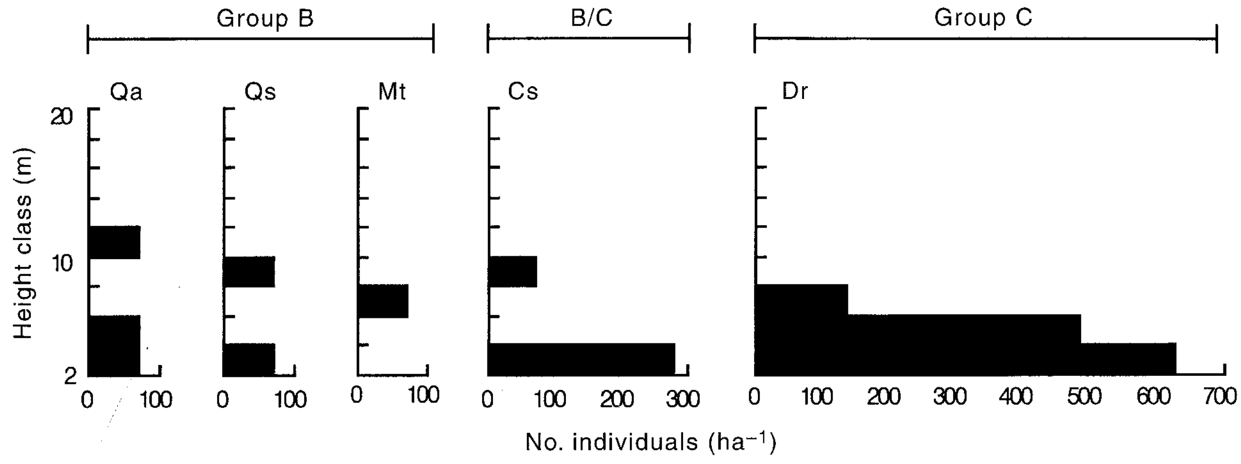

Fig. 6. Height class frequency distributions for the major canopy dominants in a gap sampled on a ridge at 700 m in altitude. Species abbreviations are shown in Table 2.

Distylium racemosum (group C) had many saplings and subcanopy trees under closed canopy, and the saplings had a high survival rate (Sato *et al.* 1994) and growth rate (Table 5) under closed canopy. *Distylium racemosum* is able to continuously grow up into canopy layer.

The size distribution of *C. sieboldii* varied from a unimodal to an inverse-J type. This species showed a high growth rate next to *D. racemosum* under closed canopy. In gaps, it showed the highest growth rate among species and often occupied the canopy layer (Fig. 6). Accordingly, *C. sieboldii* may have an intermediate regeneration requirement between group B and group C species.

Habitat partitioning among canopy dominants along the altitudinal and topographical gradients

In mesoscale studies (e.g. mountain transects), Whittaker (1956, 1960) and Peet (1981) have found that coexisting dominant species have their distributional cores in different habitats along altitudinal and topographical gradients. In the present study, each of the seven major dominants had its distributional core in one of four topo-altitudinal habitat types on Mt Ohmori, although their distribution ranges broadly overlapped with each other. This habitat partitioning among the species may contribute to species coexistence on this mountain.

However, it is difficult to pinpoint the mechanisms for habitat partitioning among the species because altitudinal and topographical gradients include different variables. One of the important environmental factors corresponding to altitude may be a decrease in air temperature. Kusumoto (1961) has revealed that at a low temperature in winter, photosynthetic activity of *Q. acuta* is higher than those of *D. racemosum*, *C. sieboldii* and *M. thunbergii*, and this may be the most cold-tolerant among the four evergreen broad-leaved dominants.

Habitat partitioning along a topographical gradient may be largely controlled by moisture and nutrients in the soil. In general, soils on ridges are thought to be drier and poorer in nutrients than those on slopes (Hack & Goodlett 1960; Furley 1976; Butler *et al.* 1986; Baillie *et al.* 1987; Johnston 1992). Nakao and Suzaki (1981) have suggested that two evergreen conifers, *T. sieboldii* and *A. firma*, have the advantage of being able to grow in drier habitats than *Q. acuta*, *Q. myrsinaefolia* and *Fagus crenata* (a cool temperate deciduous tree), because the transpiration rate of these conifers is lower than that of fagaceous trees in drier habitats. Further, the disturbance regime may be different among the four topo-altitudinal habitat types. Along with ground moisture concentration on the slopes, slopes in comparison to ridges are thought to be susceptible to erosions and landslides (Hack & Goodlett 1960; Tamura 1987). Slopes steeper than 30° and the surface geology of sandstone and shale, in particular, are reported to be prone to such disturbances (Nakamura 1990). Ridge crests at higher altitudes receive stronger typhoon winds (Takyu *et al.* 1994) or hurricanes (Bellingham 1991; Boose *et al.* 1994) than slopes and ridges at lower altitude. The ridges above 500 m a.s.l., where *T. sieboldii*-type patches occur, are prone to the strong typhoon winds, and the slopes where *Q. gilva*-type patches occur are prone to erosions and landslides.

Shade-intolerant emergent species of group A, which show a unimodal size distribution, may require large-scale disturbances for their regeneration. Many studies have demonstrated that forests dominated by such emergent species are restricted to sites where large-scale disturbances, such as floods (Duncan 1991, 1993), landslides (Veblen & Ashton 1978; Guariguata 1990) and fires (Platt *et al.* 1988) recur. Both *T. sieboldii* and *Q. gilva*, which might need catastrophic disturbances for their regeneration, were restricted to one of the four habitat types which might be prone to catastrophic disturbances: the former to ridges affected by typhoons and the latter to lower slopes that often suffer from landslides.

Effects of *Distylium racemosum* on species coexistence

Veblen and Stewart (1982) have revealed that the size distribution of emergent conifers in New Zealand changed from a unimodal type on mesic gentle slopes to an inverse-J type in a poorly drained valley where the abundance and vigor of co-occurring shade-tolerant species were low. Veblen *et al.* (1981) reported a similar change in size distribution for *Nothofagus* species along an altitudinal gradient in the Andes. It is thus suggested that the regeneration of shade-intolerant species may be affected not only by a disturbance regime but also by the change in abundance and vigor of co-occurring shade-tolerant species (Read & Hill 1988; Read *et al.* 1990; Rebertus & Veblen 1993).

In the present study, the size distribution of group A and B species did not vary with habitat, but their distributions were influenced by *D. racemosum*. The distributional cores of group A and B species were located in the marginal habitats of *D. racemosum* (i.e. on the ridges and slopes above 500 m a.s.l. and on the slopes below 500 m). In these sites, *D. racemosum* was less than half in RBA than at the distributional core (i.e. on the ridges below 500 m). The canopy tree density of *D. racemosum* was less in its marginal habitat than at the core of its distribution (Fig. 5). Thus, in such marginal habitats, the three species groups, that is emergent (group A), canopy (group B) and sub-canopy (group C), coexisted by sharing different strata. The stratification, on the other hand, may be determined by size structure and growth characteristics among the three species groups (Kohyama 1993, 1994). Accordingly, both recurrent disturbances and decrease in canopy abundance of *D. racemosum* may provide group A and B species with chances to regenerate and dominate in the three topo-altitudinal habitat types. The canopy tree density of *D. racemosum* may be determined by environmental factors other than disturbance, such as climate and soil properties as mentioned above. The underlying factors need to be investigated in a further study.

Yamamoto (1994) showed that the densities of saplings and gap successors of *Castanopsis cuspidata* (he did not distinguish *C. sieboldii* from *C. cuspidata*) in forests without *D. racemosum* were higher than those in forests with *D. racemosum*. However, we could not find a negative correlation between densities of saplings and subcanopy trees of *C. sieboldii* and canopy abundance of *D. racemosum* in this study (Tables 2 and 4). Although the distribution pattern of *C. sieboldii* was similar to that of *D. racemosum*, *C. sieboldii* may be able to coexist with *D. racemosum* through the processes of gap regeneration as shown in Fig. 6., as *C. sieboldii* can grow significantly faster than *D. racemosum* in gaps.

Conclusion

In a microscale study, Tanouchi and Yamamoto (1995) concluded that various canopy gaps differing in size and frequency within a habitat type play an important role in the coexistence of canopy species that have different regeneration requirements in SWRF of this region, since such gaps may be able to provide adequate chances for each species to regenerate (Grubb 1977; Denslow 1987). Our finding is partly in agreement with this hypothesis. At a mesoscale level, altitude and topography add to the heterogeneity of habitats, to each of which different species adapt.

We conclude that (i) habitat partitioning among species, and (ii) variability in the abundance of the most widely occurring and shade-tolerant species in the community, are related to the coexistence of several canopy species. This situation is possible due to the difference in regeneration strategy of associated species that is reflected in their size structure and growth characteristics.

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REFERENCES

BAILLIE P. S., ASHTON P. S., COURT M. N., ANDERSON J. A. R., FITZPATRICK E. A. & TINSLEY J. (1987) Site characteristics and the distribution of tree species in mixed dipterocarp forest on tertiary sediments in central Sarawak, Malaysia. *Journal of Tropical Ecology* **3**: 201–220.

BELLINGHAM P. J. (1991) Landforms influence patterns of hurricane damage: evidence from Jamaican montane forests. *Biotropica* **23**: 427–433.

BOOSE E. R., FOSTER D. R. & FLUET M. (1994) Hurricane impacts to tropical and temperate forest landscapes. *Ecological Monographs* **64**: 369–400.

BUTLER J., GOETZ H. & RICHARDSON J. L. (1986) Vegetation and soil–landscape relationships in the North Dakota Badlands. *American Midland Naturalist* **116**: 378–386.

DENSLOW J. S. (1987) Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics* **18**: 431–451.

DUNCAN R. P. (1991) Competition and the coexistence of species in a mixed podocarp stand. *Journal of Ecology* **79**: 1073–1084.

DUNCAN R. P. (1993) Flood disturbance and the coexistence of species in a lowland podocarp forest, south Westland, New Zealand. *Journal of Ecology* **81**: 403–416.

FURLEY P. A. (1976) Soil–slope–plant relationships in the northern Maya mountains, Belize, Central America. *Journal of Biogeography* **3**: 303–319.

GRUBB P. J. (1977) The maintenance of species-richness in plant communities: the importance of regeneration niche. *Biological Review of the Cambridge Philosophical Society* **52**: 107–145.

GUARIGUATA M. R. (1990) Landslide disturbance and forest regeneration in the Upper Luquillo Mountains of Puerto Rico. *Journal of Ecology* **78**: 814–832.

HACK J. T. & GOODLETT J. C. (1960) Geomorphology and forest ecology of a mountain region in the central Appalachians. *Geological Survey Professional Paper* **347**: 1–66.

JAPAN METEOROLOGICAL AGENCY (1982) *Climatic Table of Japan. Part 2. Monthly normals by Stations.* Japan Meteorological Agency, Tokyo (in Japanese).

JOHNSTON M. H. (1992) Soil-vegetation relationships in a tabonuco forest community in the Luquillo Mountains of Puerto Rico. *Journal of Tropical Ecology* **8**: 253–263.

KIRA T. (1948) On the altitudinal arrangement of climatic zones in Japan. *Kanti-Nogaku* **2**: 142–173 (in Japanese).

KIRA T. (1977) A climatological interpretation of Japanese vegetation zones. In: *Vegetation Science and Environmental Protection* (eds A. Miyawaki & R. Tuxen) pp. 21–30. Maruzen, Tokyo.

KOHYAMA T. (1993) Size-structured tree populations in gap-dynamic forest—the forest architecture hypothesis for the stable coexistence of species. *Journal of Ecology* **81**: 131–143.

KOHYAMA T. (1994) Size-structure-based models of forest dynamics to interpret population- and community-level mechanisms. *Journal of Plant Research* **107**: 107–116.

KUSUMOTO T. (1961) An ecological analysis of the distribution of broad-leaved evergreen trees, based on the dry matter production. *Japanese Journal of Botany* **17**: 307–331.

NAKAMURA F. (1990) Perspectives for the effects of geomorphic processes. *Biological Science* **42**: 57–67 (in Japanese).

NAKAO T. & SUZAKI T. (1981) Ecological studies of *Tsugion sieboldii* (IX): the influence of soil moisture on the transpiration, photosynthesis and respiration of some species in the fir and hemlock zone. *Transcript of 92nd Meeting of Japanese Forestry Society*: 299–300 (in Japanese).

OHSAWA M. (1983) Comparative study on zonation of vegetation in East Asia. In: *Contemporary Ecology of Japan* (ed. Editorial Committee of Contemporary Ecology of Japan) pp. 206–213. Kyoritsusyuppan, Tokyo (in Japanese).

OHSAWA M. (1984) Differentiation of vegetation zones and species strategies in the subalpine region of Mt Fuji. *Vegetatio* **57**: 15–52.

OHSAWA M. (1991a) Montane evergreen broad-leaved forests of the Bhutan Himalaya. In: *Life Zone Ecology of the Bhutan Himalaya* (ed. M. Ohsawa) pp. 89–156. Chiba University, Chiba.

OHSAWA M. (1991b) Structural comparison of tropical montane rain forests along latitudinal and altitudinal gradients in south and east Asia. *Vegetatio* **97**: 1–10.

OHSAWA M. (1993) Latitudinal pattern of mountain vegetation zonation in southern and eastern Asia. *Journal of Vegetation Science* **4**: 13–18.

PEET R. K. (1981) Forest vegetation of the Colorado Front Range. *Vegetatio* **45**: 3–75.

PLATT W. J., EVANS G. W. & RATHBUN S. L. (1988) The population dynamics of a long-lived conifer (*Pinus palustris*). *American Naturalist* **131**: 491–525.

READ J. & HILL R. S. (1988) The dynamics of some rainforest associations in Tasmania. *Journal of Ecology* **76**: 558–584.

READ J., HOPE G. & HILL R. S. (1990) The dynamics of some *Nothofagus*-dominated rain forests in Papua New Guinea. *Journal of Biogeography* **17**: 185–204.

REBERTUS A. J. & VEBLEN T. T. (1993) Structure and tree-fall gap dynamics of old-growth *Nothofagus* forests in Tierra del Fuego, Argentina. *Journal of Vegetation Science* **4**: 641–654.

SATO T., TANOUCHI H. & TAKESHITA K. (1994) Initial regenerative processes of *Distylium racemosum* and *Persea thunbergii* in an evergreen broad-leaved forest. *Journal of Plant Research* **107**: 331–337.

SUZUKI T. & HATIYA K. (1951) The forest vegetation of Izu peninsula. *Bulletin of the Tokyo University Forests* **39**: 145–170 (in Japanese with English summary).

TAKYU M., OHSAWA M., OZAKI K. *et al.* (1994) Community dynamics of a *Cryptomeria japonica* forest during 10 years in the Yakushima wilderness area, Yakushima island, southern Japan. In: *Long Term Ecological Studies in the Yakushima Wilderness Area and its Surrounding Areas – 1994 Reports* (ed. Environment Agency, Nature Conservation Bureau) pp. 3–19. Nature Conservation Society of Japan, Tokyo (in Japanese with English summary).

TAMURA T. (1987) Landform-soil features of the humid temperate hills. *Pedologist* **31**: 135–146 (in Japanese).

TANOUCHI H., SATO T. & TAKESHITA K. (1994) Comparative studies on acorn and seedling dynamics of four *Quercus* species in an evergreen broad-leaved forest. *Journal of Plant Research* **107**: 153–159.

Tanouchi H. & Yamamoto S. (1995) Structure and regeneration of canopy species in an old-growth evergreen broad-leaved forest in Aya district, southwestern Japan. *Vegetatio* **117**: 51–60.

Veblen T. T. & Ashton D. H. (1978) Catastrophic influences on the vegetation of the Valdivian Andes, Chile. *Vegetatio* **36**: 149–167.

Veblen T. T., Donoso Z. C., Schlegel F. M. & Escobar R. B. (1981) Forest dynamics in south-central Chile. *Journal of Biogeography* **8**: 211–247.

Veblen T. T. & Stewart G. H. (1982) On the conifer regeneration gap in New Zealand: the dynamics of *Libocedrus bidwillii* stands on South Island. *Journal of Ecology* **70**: 413–436.

Wang C. (1961) The forest of China with a survey of grassland and desert vegetation. Maria Moors Cabot Foundation Publication No. 5, Harvard University, Cambridge, MA.

Watt A. S. (1947) Pattern and process in plant community. *Journal of Ecology* **35**: 1–22.

Whittaker R. H. (1952) A study of summer foliage insect communities in the Great Smoky Mountains. *Ecological Monographs* **22**: 1–44.

Whittaker R. H. (1956) Vegetation of the Great Smoky Mountains. *Ecological Monographs* **26**: 1–80.

Whittaker R. H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* **30**: 279–338.

Yamamoto S. (1992) Gap characteristics and gap regeneration in primary evergreen broad-leaved forests of western Japan. *Botanical Magazine Tokyo* **105**: 29–45.

Yamamoto S. (1994) Gap regeneration in primary evergreen broad-leaved forests with or without a major canopy tree, *Distylium racemosum*, southwestern Japan: A comparative analysis. *Ecological Research* **9**: 295–302.

Yamanaka T. (1975) The *Machilus thunbergii* and the *Castanopsis cuspidata* forest in southern Shikoku. *Bulletin of the Faculty of Education, Kochi University (Series 3)* **27**: 9–15 (in Japanese with English summary).