

Gap Characteristics and Gap Regeneration in Primary Evergreen Broad-leaved Forests of Western Japan

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Gap characteristics and regeneration in gaps were studied in some primary evergreen broad-leaved forests of the warm temperate zone in western Japan. Total observed 161 gaps covered 15.7% of the total land area of 8.23 ha. Gap density was 19.6 gaps ha⁻¹ and mean gap size was 80.3 m². Smaller gaps (< 80 m²) were much more frequent than larger ones, and gaps larger than 400 m² were rare. Gaps created by the death or the injury of single trees were 79.5%. Canopy trees died most often with broken trunks and not so often by uprooting or leaving standing-dead. Different types of gap regeneration behaviour were recognized among the major canopy tree species, though gap regeneration of the common evergreen broad-leaved tree species did not clearly depend on a species-specific gap size. *Distylium racemosum*, which occurred in equal importance (about 25%) in the canopy layer of each study stand, regenerates in gaps from saplings recruited before gap creation and can replace not only its own gaps but also gaps of other species. Therefore, it can be considered a typical climax species in this forest type of western Japan. *Persea thunbergii*, which can reproduce vegetatively, showed a similar type of gap regeneration behaviour. *Castanopsis cuspidata* can replace itself with relatively higher frequency by means of vegetative reproduction (stump sprouting) after gap creation. *Quercus acuta* and *Quercus salicina* did not regenerate under the current gap-disturbance regime. Though the frequency of uprooting is low, soil disturbance by uprooting seems to be important for the perpetuation of the pioneer tree species, *Fagaria aplanthoides*, which recruits from buried seeds in the soil.

Key words: Evergreen broad-leaved forests — Gap regeneration — Soil disturbance — Typhoon — Vegetative reproduction — Warm temperate zone

“Canopy gaps” are small openings created in the forest canopy. Creation of canopy gaps causes a series of dynamic events related with forest regeneration, which is generally termed “gap dynamics” (van der Maarel, 1988). Gap dynamics of climax or mature forests have been intensively studied, since it is assumed to be an important mechanism maintaining the organization or pattern of the forest communities; for recent reviews see Brokaw (1985), Runkle (1985) or Denslow (1987). In Japanese temperate forests, important features such as gap characteristics, regeneration process in gaps and gap regeneration behaviour of tree species in the gap dynamics of climax

Fagus crenata forests in the cool temperate zone have been demonstrated in recent thesis and papers, e.g. Asano (1983) and Yamamoto (1989). Works focused on the gap dynamics of warm temperate evergreen broad-leaved forests, which are very widespread in eastern Asia, also have been intensively conducted. Morita and Tagawa (1981) investigated successional processes in gaps of a *Machilus thunbergii* forest. Naka and co-workers (Naka, 1982; Naka and Yoda, 1984; Naka and Yoneda, 1984) studied revegetation processes in gaps in relation to the gap formation rate in an evergreen oak forest. Kohyama (1986, 1987, 1988) analyzed tree size structures in closed stands and in gaps of a primary warm temperate rain forest. However, main foci of these works have been confined to vegetation dynamics in gaps in one or few stands of a particular district, so that the apparent features of gap characteristics and gap regeneration behaviour of tree species in the gap dynamics of this forest type have not been fully clarified. Clarification of these subjects in the gap dynamics of warm temperate forests, which exist between the cool-temperate and tropical zones, might keep in understanding the latitudinal differences in tree species diversity (Orians, 1982; Runkle, 1989).

The main objectives of the present study in relation to the gap dynamics of climax forests were: (1) to describe and evaluate gap characteristics in some primary evergreen broad-leaved forests of western Japan, based on a larger number of samples and a broader surveyed area than ever studied; and (2) to characterize the regeneration behaviour of the tree species in relation to the gap characteristics of these forests. Particular attention was paid to vegetative reproduction by stump sprouting of tree species, the importance of which in gap regeneration has not been fully recognized (Putz and Brokaw, 1989).

Study Area and Methods

Study area and study stands

Most of present forests in the warm temperate zone of Japan are secondary ones by past human disturbance, but there remain relatively undisturbed primary forests in mountainous regions or islands of the Kyushu district in western Japan. Thus, four primary forest stands in three study areas in the Kyushu district were used for the objectives of this study. The study stands were chosen which fulfilled the following criteria: (1) each stand area > 10 ha; (2) mature stands in the normal conditions of this forest type, i.e. trees > 1 m dbh and height of canopy layer > 20 m; (3) well preserved stands without evidence of major human disturbance in the past. The annual average temperature is 13–21 C, and annual precipitation > 2,000 mm yr⁻¹ in these study areas. Typhoons are a major natural form of disturbance. General descriptions of study stands are summarized in Table 1. Soils of the stands are mostly brown forest soils with a well developed humus layer. Mt Tatera (alt. 559 m) is in the southern part of Tsushima island, about 100 km north-west of Kyushu island. The study stand is in Tatera Forest Reserve at the foot of Mt Tatera. The Reserve is ca. 100 ha in area and has been well preserved as a National Natural Monument. Several

Table 1. Summary of study stands

Study area and stand abbreviation	Elevation (m)	Topographic position	Slope		Height of canopy layer (m)
			Aspect	Degree	
Mt Tatera (34°08'N, 129°13'E)					
T	140	lower slope	N	0-7	20-30
Mt Omori (32°04'N, 131°09'E)					
0-1	700	high plateau	—	flat	20-30
0-2	450	middle slope	N	5-30	24-32
Mt Kurino (31°55'N, 130°41'E)					
K	600	lower slope	N	0-10	22-30

gaps were newly created in the Reserve by Typhoon 12 of 1987. Mt Omori (alt. 1,109 m) is located in 30 km west of Miyazaki city, southern Kyushu. The study stands are on the high plateau and the north-facing slope, respectively, of a broad ridge deriving from Mt Omori. Several gaps were newly created in each study stand by Typhoon 13 of 1985 and Typhoon 11 of 1989. Mt Kurino (alt. 1,094 m) is in the northern part of Kagoshima Prefecture, southern Kyushu. The study stand is on the north-facing gentle slope of Mt Kurino. In this study stand, several gaps were newly created by typhoons of 1989. Detailed environmental or vegetational features of Mt Tatera were described by Itow (1972), Itow and Nakanishi (1987) and Itow (1991), and those of Mt Kurino by Tagawa (1977).

Field methods and data analysis

Next four regeneration categories were defined and used in this study: (1) "canopy trees" were defined as trees which reach the canopy layer (usually with more than 30 cm of dbh); (2) "gap makers" were defined as trees more than 30 cm dbh creating a gap; (3) "suppressed saplings" and (4) "gap successors" were defined as the tallest sapling (taller than 1.3 m height, including non-canopy tree species) beneath the crown of each canopy tree and in a gap, respectively. In the case of canopy and sub-canopy trees, therefore, suppressed saplings mean their advance regenerations (Bormann and Likens, 1979) beneath a closed canopy. Gap successors mean the most probable next occupant in the canopy or the sub-canopy layers of the gap, and include both the advance regenerations and the new individuals (Bormann and Likens, 1979).

In each study stand, along transect lines, species name and diameter at breast height (dbh) of canopy trees were recorded by the point-centered quarter method (Cottam and Curtis, 1956), which has been considered the most efficient of the available distance methods (Mueller-Dombois and Ellenberg, 1974). Dbh of all trunks was measured when canopy trees were individuals with multi-trunks at breast height. According to the rules of the point-centered quarter method, not less than 20 points were selected at random along transect lines in each study stand. The starting point of the initial transect line was located randomly in each study stand. The direction

of transect lines was altered when the top of lines met any microtopographic changes (e.g., creek, small cliff). Beneath the crown of each canopy tree recorded, the species name, dbh, and whether they are sprouts or not for suppressed saplings were also recorded. Based on the point-centered quarter data for canopy trees, the percentage of Wisconsin importance value was used in describing the canopy vegetation of each study stand. The Wisconsin importance value is defined as the sum of relative density, relative dominance, and relative frequency (Curtis, 1959). Absolute individual densities of canopy trees and the relative density and relative dominance of suppressed saplings in each study stand were also calculated from the point-centered quarter data. Individual density was used for the calculation of relative density and basal area was used for the calculation of relative dominance.

The ground area under a canopy opening was defined as a "gap". Therefore, my definition is different from expanded gaps by and is equivalent to canopy gaps by the definitions of Runkle (1981); gaps are taken to become indistinguishable from the background overstory when regeneration within the gap has reached a height of more than about 10 m. All gaps whose rough center was contained within either side of a 10 m distance perpendicular to the transect lines were described. For each gap, the largest distance from gap edge to gap edge (length) and the largest distance perpendicular to length (width) were recorded and the gap area was calculated by the formula for a circle using the mean value of the length and the width. Species name, dbh and the state (live or dead) of gap makers were recorded. The type of injury sustained by the gap makers was also recorded; i.e. standing dead, trunk-broken, uprooted, branch-broken, leaning (trees leaning against other trees) and others. The identities and injury types of very old gap makers could not be identified. Estimated values were used for the dbh of partly decomposed or broken-trunk (at breast height) gap makers, although these were few such cases. The species name, dbh, and whether they are sprouts or not for gap successors were also noted. Densities of gaps and gap makers in each study stand were calculated from their numbers in the total surveyed area of each study stand. Though gap age was not estimated in this study, whether gaps were created by recent (within the last five years) typhoons mentioned before or not was determined by observing the freshness of gap makers and the degree of vegetation development in gaps.

Total surveyed area was calculated by the product of width of belt transects (i.e. 20 m) and total length of the transect lines. Based on the total number and the total basal area of gap makers or gap successors in the total surveyed area of each study stand, relative densities and relative dominances of gap makers or gap successors in each tree species were calculated. The field survey was done in October-November 1989 and in October-December 1990.

Results

Structure of canopy vegetation

Twenty-four canopy tree species, including five deciduous broad-leaved species

and two gymnosperms, occurred in the study stands (Table 2). The canopy layers of the various study stands were dominated by different canopy tree species: one at a lower altitude by *Castanopsis cuspidata* with *Distylium racemosum*, and the other three at higher altitudes by *Distylium racemosum* with *Persea thunbergii*, and/or *Quercus acuta*. *Quercus salicina* was the other major canopy species in all study stands. None of these species showed a strong dominance (>50% in percentage of Wisconsin importance value), although the degrees of dominance varied. *D. racemosum* showed nearly equal percentage of Wisconsin importance value in every stands.

Each stand possessed 110–160 trees ha⁻¹ in the canopy layers, with a mean dbh of 65–76 cm (Table 3). Stand O-1 had a higher density and a smaller mean dbh of canopy trees than other stands. Basal area of canopy trees in each study stand ranged 48.4–70.0 m²ha⁻¹; stand T had the largest basal area. The largest canopy tree obser-

Table 2. Percentage (%) of Wisconsin importance value of each species of canopy tree in each study stand

Species	Stand abbreviation			
	T	O-1	O-2	K
<i>Abies firma</i> ²⁾	—	—	—	1.4
<i>Betula grossa</i> ¹⁾	—	—	—	1.7
<i>Carpinus tschonoskii</i> ¹⁾	1.8	—	1.9	1.5
<i>Castanopsis cuspidata</i>	47.8	2.2	5.2	12.2
<i>Cinnamomum insularimontanum</i>	—	1.5	—	—
<i>Cleyera japonica</i>	0.9	—	—	—
<i>Daphniphyllum macropodum</i>	—	3.4	0.8	—
<i>Dendropanax trifidus</i>	3.7	—	—	—
<i>Distylium racemosum</i>	25.6	23.2	23.2	28.9
<i>Fagaria aphanoides</i> ¹⁾	0.9	—	—	—
<i>Idesia polycarpa</i> ¹⁾	0.9	—	—	—
<i>Ilex integra</i>	0.9	—	—	—
<i>Illicium anisatum</i>	—	1.5	—	—
<i>Litsea lancifolia</i>	—	—	—	1.4
<i>Neolitsea aciculata</i>	0.9	—	—	1.3
<i>Pasania edulis</i>	—	—	1.7	—
<i>Persea japonica</i>	—	—	1.6	—
<i>Persea thunbergii</i>	2.2	11.0	22.3	34.1
<i>Podocarpus macrophyllus</i> ²⁾	1.0	—	1.8	—
<i>Quercus acuta</i>	1.9	43.1	21.5	4.6
<i>Quercus gilva</i>	—	—	6.7	—
<i>Quercus salicina</i>	10.7	7.9	13.2	11.4
<i>Stewartia monadelphica</i> ¹⁾	—	6.4	—	1.6
<i>Ternstroemia gymnanthera</i>	0.9	—	—	—

¹⁾ deciduous broad-leaved.

²⁾ gymnosperm.

Table 3. Density (ha^{-1}), dbh (cm, mean \pm S.D.) and basal area (BA, $\text{m}^2 \text{ha}^{-1}$) of canopy trees and gap makers in each study stand

Stand abbreviation	Canopy trees			Gap makers		
	Density	dbh	BA	Density	dbh	BA
T	130	76.0 \pm 30.2 (30.6-184.0)	70.0	33	79.0 \pm 38.7 (30.0-203.4)	19.7
O-1	160	65.2 \pm 23.7 (30.0-158.7)	60.4	19	70.2 \pm 24.1 (31.6-132.0)	8.2
O-2	110	71.2 \pm 26.4 (31.4-213.7)	50.4	24	72.9 \pm 34.2 (30.0-213.7)	12.2
K	112	71.3 \pm 20.8 (33.8-120.2)	48.4	24	72.9 \pm 27.6 (30.0-166.3)	11.4

Range of dbh is given in parentheses.

ved was a *Quercus salicina* with dbh of 213.7 cm in stand O-2.

Size and number of gaps

The percentage gap area (percentage of total gap area to total surveyed area) ranged from 10.3 to 23.9% in the various stands (15.7% overall mean; Table 4). The average density of gaps was 19.6 ha^{-1} (range 16.8-23.8). The mean gap size ranged from 61.2 to 100.4 m^2 (mean of 80.3 m^2). Of all the observed gaps only two were larger than 400 m^2 . The values of percentage gap area, gap density and mean gap size were higher in Stand T and lower in stand O-1 than in other stands. The size-class distribution of gaps indicated that smaller gaps, especially ones less than 40 m^2 , were much more abundant than larger ones in every stand (Table 5); the percentage at stand O-1 was higher than that at other stands. Gaps larger than 400 m^2 were few in number (1.2%), but they were 7.5% of the total area of all the observed gaps.

The percentages of the number of gaps created by recent typhoons (within the last five years) to total number of observed gaps in each stand were 28%, 13.8%, 18% and 21.9%, and the gap areas ha^{-1} were 724 m^2 , 247 m^2 , 552 m^2 and 168 m^2 , in stands T, O-1, O-2 and K, respectively. These results show that the impact of recent typhoon disturbance was the strongest in stand T and the weakest in stand O-1.

Table 4. Area, density and size of observed gaps

Stand abbreviation	Total gap area (m^2)	Total surveyed area (m^2)	Percentage gap area ¹⁾ (%)	Number of observed gaps	Density of gaps (ha^{-1})	Size of gaps (m^2 , Mean \pm S.D.)
T	5,022	21,000	23.9	50	23.8	100.4 \pm 107.1 (10.5-568.3)
O-1	1,774	17,300	10.3	29	16.8	61.2 \pm 61.4 (7.1-288.0)
O-2	4,010	27,000	14.9	50	18.5	80.2 \pm 81.4 (5.7-346.4)
K	2,129	17,000	18.8	32	18.8	66.5 \pm 78.2 (9.6-401.2)

¹⁾ (Total gap area/total surveyed area) \times 100.

Range of gap size is given in parentheses.

Table 5. The distribution of the gap sizes as percentages of the total number of gaps and as percentages of the total gap area in each study stand (%)

Size class (m ²)	Stand abbreviation										Number of gaps
	T		0-1		0-2		K		Total		
	No. ¹⁾	Area ²⁾	No.	Area	No.	Area	No.	Area	No.	Area	
0-	32.0	7.7	55.2	20.7	40.0	11.1	43.8	14.7	41.0	11.7	66
40-	26.0	15.0	13.8	11.0	34.0	25.7	34.4	28.1	28.0	19.9	45
80-	16.0	14.4	17.2	27.6	4.0	4.4	9.4	13.4	11.2	13.0	18
120-	8.0	11.4	6.9	15.3	4.0	6.3	6.3	13.7	6.2	10.7	10
160-	4.0	6.8	3.4	9.2	6.0	13.2			3.7	8.0	6
200-	2.0	4.4			6.0	16.2			2.5	6.7	4
240-	4.0	10.2			2.0	6.7	3.1	11.3	2.5	7.9	4
280-	4.0	12.0	3.4	16.2	2.0	7.7			2.5	9.3*	4
320-	2.0	6.9			2.0	8.6			1.2	5.3	2
360-											0
400-	2.0	11.3					3.1	18.8	1.2	7.5	2

¹⁾ percentages of the total number of gaps.

²⁾ percentages of the total gap area.

Conditions of gap and gap maker

Gaps created by the fall of a single tree were much more abundant ($\chi^2 = 56.06$, $P < 0.001$) than those made by two or more trees in every stand (Table 6). Gaps due to multiple gap makers originated from multiple tree-falling down in domino fashion (Bormann and Likens, 1979), the multiple falling of trees in the periphery of gaps already made or the falling of trees with multiple stems.

The main trunks of standing dead and trunk-broken gap makers were all dead; gap makers with broken branches and leaning injuries were all alive. Uprooted gap makers were mostly dead, but a few of these were still alive. Standing dead, trunk-broken, and uprooted injury states were common. Trunk broken injury was the most frequent injury type in all study stands. The type of injury was not clearly related

Table 6. Number of gap makers creating a gap and state of injuries in gap makers

Stand abbreviation	Number of gap makers creating a gap(%)		State of injuries in gap makers (%)					
	Single	Multiple	Standing dead	Trunk-broken	Uprooted	Branch-broken	Leaning	Unknown
T	78.0	22.0	25.7	48.6	17.1	2.9	4.3	1.4
0-1	89.7	10.3	12.1	66.7	21.2			
0-2	74.0	26.0	16.7	51.5	24.2	4.6	1.5	1.5
K	81.3	18.7	14.6	39.0	26.8	19.5		

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<i>Litsea lancifolia</i>	—	—	—	2.0	—	—	1.3	—	1.5	1.5	—	1.2	—	1.2	—	6.3
<i>Morus australis</i>	—	—	—	2.0	—	—	—	—	—	—	—	—	—	—	—	—
<i>Neolitsea aciculata</i>	0.7	—	0.7	4.0	—	—	5.0	10.3	—	0.8	—	1.2	—	—	—	—
<i>Neolitsea sericea</i>	—	—	0.7	—	—	—	—	—	—	1.5	—	—	—	—	—	—
<i>Pasania edulis</i>	—	—	—	—	—	3.0	—	—	1.5	4.6	—	—	—	—	—	—
<i>Persea japonica</i>	—	—	1.5	2.0	—	3.0	2.5	3.5	1.5	—	2.3	2.0	—	2.4	1.2	6.3
<i>Persea thunbergii</i>	1.5	—	—	2.0	11.3	9.1	8.8	6.9	24.2	33.3	6.1	12.0	35.7	24.4	3.6	12.5
<i>Podocarpus macrophyllus</i>	0.7	2.9	3.7	4.0	—	—	—	—	1.5	—	0.8	2.0	—	—	—	—
<i>Prunus grayana</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	2.4	—	—
<i>Quercus acuta</i>	1.5	—	—	—	46.3	30.3	3.8	6.9	22.0	10.6	1.5	—	3.6	—	—	—
<i>Quercus gilva</i>	—	—	—	—	—	—	—	6.1	—	—	—	—	—	—	—	—
<i>Quercus salicina</i>	10.3	18.6	—	—	6.3	3.0	2.5	—	11.4	10.6	0.8	4.0	14.3	14.6	—	6.3
<i>Stewartia monadelpha</i>	—	—	—	—	5.0	—	—	6.9	—	1.5	—	—	1.2	—	—	—
<i>Symplocos lucida</i>	—	—	2.2	2.0	—	—	—	—	—	—	—	—	—	—	—	—
<i>Symplocos prunifolia</i>	—	—	0.7	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Ternstroemia gymnanthera</i>	0.7	—	1.5	—	—	—	2.5	—	—	—	—	8.0	—	—	—	—
Unidentified	—	7.1	—	—	—	45.5	—	—	—	27.3	—	—	—	39.0	—	—
Number of observed trees	136	70	136	50	80	33	80	29	132	66	132	50	84	41	84	32

CT, canopy tree; GM, gap maker; SS, suppressed sapling; GS, gap successor.

to species, although *Quercus acuta* (86.7%, N=15) and *Q. salicina* (63.0%, N=27) died more often with broken trunks.

The average density of gap makers was 25 trees ha⁻¹ with a range of 19-33 (Table 3). In all study stands the mean dbh of gap makers was nearly equal to, or larger than, that of canopy trees. The largest gap maker was a *Q. salicina* with a dbh of 213.7 cm, which possessed a broken-branch injury.

Gap regeneration

Relative density and relative dominance produced similar results and only the results based on relative density are presented here (Table 7).

Only *Distylium racemosum* occurred in all regeneration categories (i.e. canopy trees, gap makers, suppressed saplings, and gap successors) in every stand. *Camellia japonica* and *Cleyera japonica* frequently occurred in suppressed saplings and gap successors. These species, however, did not occur as canopy trees and gap makers, or occurred rarely. *Castanopsis cuspidata* which predominated in the canopy layer of stand T did not occur as suppressed saplings, or did so uncommonly, in every study stand. *Persea thunbergii* occurred in all regeneration categories in every stand except stand T. In stand K, although *P. thunbergii* predominated in the canopy layer, it did not occur frequently among the suppressed saplings. *Quercus acuta* which occurred in the canopy layer of all the study stands and predominated in the canopy layer of stand O-1 did not occur, or did so uncommonly, among the suppressed saplings and gap successors. A similar position was found for *Quercus salicina*. Deciduous broad-leaved tree species did not occur in suppressed saplings in any stand. Though few in number (two individuals), all gap successor plants of *Fagara ailanthoides*, a typical pioneer species (Naka and Yoda, 1984), occurred only in gaps (<60 m² in size, but these were close to the neighboring gaps) created by uprooted gap makers.

Gap successor plants of all the commoner tree species occurred in a wide range of gap size (Table 8). However, species-specific occurrence pattern in relation to gap size was not clear, though the percentage occurrences of *Cleyera japonica* and *Distylium racemosum* were higher than those of other species in gaps <80 m². This result indi-

Table 8. Percentage (%) of gap successors of each tree species occurring in each gap size-class

Species	Gap size class (m ²)					Number of gap successors
	0-	80-	160-	240-	320-	
<i>Camellia japonica</i>	7.2	10.7	10.0	37.5		15
<i>Castanopsis cuspidata</i>	4.5	14.3		12.5		10
<i>Cinnamomum insularimontanum</i>	7.2	10.7		12.5		12
<i>Cleyera japonica</i>	25.2	7.1	20.0	12.5		33
<i>Distylium racemosum</i>	26.1	17.9	30.0	25.0		39
<i>Persea thunbergii</i>	7.2	14.3			25.0	13

Species with more than ten gap successors are listed.

Table 9. Percentage (%) of each gap successor in gaps created by each single gap maker of major canopy tree species

Gap successor	Gap maker				
	<i>Castanopsis cuspidata</i>	<i>Distylium racemosum</i>	<i>Persea thunbergii</i>	<i>Quercus acuta</i>	<i>Quercus salicina</i>
<i>Castanopsis cuspidata</i>	23.3				6.3
<i>Distylium racemosum</i>	36.7	22.2	17.4	33.3	37.5
<i>Persea thunbergii</i>		22.2	8.7	16.7	
<i>Quercus acuta</i>				8.3	
<i>Quercus salicina</i>			8.7		
Others	40.0	55.6	65.2	41.7	56.3
Number of gap makers	30	9	23	12	16

cates that there is not a clear niche differentiation along gap-size gradient in the gap regeneration of these tree species.

Gap successors of major canopy tree species other than *Quercus salicina* occurred in gaps created by their own single gap makers (Table 9). *Castanopsis cuspidata* and *Distylium racemosum* occurred in their own gaps with higher percentages than *Persea thunbergii* and *Quercus acuta*. Only gap successors of *Distylium racemosum* occurred in gaps created by all major canopy tree species.

Suppressed saplings reproduced vegetatively from canopy trees could be found in only *Castanopsis cuspidata* (though only one suppressed sapling was found for this species) and *Persea thunbergii* (Table 10). Canopy trees of *C. cuspidata* had many sprouts from their bases, but they were smaller than 1.3 m in height or could not be the tallest suppressed sapling beneath the crowns of canopy trees except only one sprout. Gap successors reproduced vegetatively from gap makers could be found in *Castanopsis cuspidata*, *Cinnamomum insularimontanum*, *Persea japonica* and *Persea*

Table 10. Sprouts in suppressed saplings and gap successors of each tree species

Species	Suppressed sapling			Gap successor		
	Number of sprouts	Number of suppressed sapling	% ¹⁾	Number of sprouts	Number of gap successor	% ²⁾
<i>Camellia japonica</i>	0	69	0	0	15	0
<i>Castanopsis cuspidata</i>	1	1	100.0	6	10	60.0
<i>Cinnamomum insularimontanum</i>	0	18	0	1	12	8.3
<i>Cleyera japonica</i>	0	125	0	0	33	0
<i>Distylium racemosum</i>	0	122	0	0	39	0
<i>Persea thunbergii</i>	5	18	27.8	3	13	23.1

¹⁾ (Number of sprouts/number of suppressed saplings) × 100.

²⁾ (Number of sprouts/number of gap successor) × 100.

Species with more than ten gap successors are listed.

thubergeri. Among the gap successors of *Castanopsis cuspidata*, most were sprouts from stumps. Suppressed saplings and gap successors in *Camellia japonica*, *Cleyera japonica* and *Distylium racemosum* were not of sprout origin.

Discussion

Gap characteristics

Compared with other studies on gaps in primary evergreen broad-leaved forests of Japan, the percentage gap area (15.7%) was within the range of the maximum (20% ; Naka, 1982) and the minimum (4.7% ; Kohyama, 1986) figures, and the mean gap size (80.3 m²) was remarkably similar to the figures in the other studies ; 87 m² by Morita and Tagawa (1981), 92 m² by Naka (1982) and 83 m² by Kohyama (1986). Also, these two figures (15.7% and 80 m²) obtained in this study were similar to the figures (12% and 92 m²) obtained in the study on 278 gaps in *Fagus crenata* forests (Yamamoto, 1989). Stand-to-stand variations could be found in the percentage gap area and the mean gap size ; stand T had higher and stand O-1 had lower values in these figures than other stands. One of the causes is apparently due to the differential impact of recent typhoon disturbance on the gap creation.

The gap size-class distributions showed a negative skewness with a few large and many small gaps in every stand. In the case of lumping all observed gaps, gaps smaller than 80 m² were 68.9% and those larger than 200 m² were 9.9% of 161 gaps, although larger gaps contributed to available gap area important for gap regeneration ; similar to the results obtained by Lawton and Putz (1988). Similar distributions were also reported by Acevedo and Marquis (1978) and Brokaw (1982) for tropical evergreen forests, and by Morita and Tagawa (1981) and Naka (1982) for warm temperate evergreen forests and by Runkle (1982) and Nakashizuka (1984) for cool-temperate deciduous forests. The distribution truncated at a gap size of about 400 m² ; there were two gaps larger than 400 m². Naka (1982) and Brokaw (1982), in intensive surveys, also found very few gaps over 400-500 m² in area. Thus, it can be concluded that almost all gaps are smaller than 400 m² and larger gaps are very few or rare in evergreen broad-leaved forests, as found for *Fagus crenata* forests (Yamamoto, 1989).

Most gaps in every stand were created by the death of single trees and gaps by death of multiple trees were few ; about 80% of 161 gaps were created by the death of single trees. Though few in number, gaps by death of multiple trees are important because they can account for most of the larger gaps in which the possibility for the regeneration of shade-intolerant species is enhanced. The importance of the death of single trees as a dominant mode of gap creation has been recognized in *Fagus crenata* forests (Nakashizuka, 1984 ; Yamamoto, 1989) and in tropical rain forest on BCI, Panama (Putz and Milton, 1982).

Trunk-break was the most common type of death of canopy trees, with stand-to-stand variations, in every stand ; standing dead = 18.6%, trunk-broken = 50.5% and uprooted = 21.9% of 210 trees. The value of standing dead is obviously lower than the value obtained in *Fagus crenata* forests (45.2% ; Yamamoto, 1989). One probable

cause may be that this study was done after recent typhoon disturbances to each study stand, because trunks of dead-standing trees are easily broken by strong wind by typhoons. Uprooting is also an uncommon type of death of canopy trees as in *Fagus crenata* forests (Nakashizuka, 1984; Yamamoto, 1989), an evergreen broad-leaved forest (Naka, 1982) and *Fagus grandifolia* forests (Runkle, 1982), although uprooting of canopy trees is less uncommon in some tropical rain forests (Acevedo and Marquis, 1978; Brokaw, 1982).

Gap regeneration behaviour

Based on the results of Table 7, gap regeneration behaviour of the major component tree species in primary evergreen broad-leaved forests of western Japan can be summarized as Table 11, though the variations in occurrence and relative density among areas and stands.

Type I is for species occurring in all regeneration categories. Two canopy tree species belong to this type. *Distylium racemosum* is typical in this type of gap regeneration behaviour. *D. racemosum* can replace not only its own gaps, but also gaps of other species, created by death of single trees, though other species can regenerate in gaps of *D. racemosum*. *Persea thunbergii* also belongs to this type; in contrast to *D. racemosum*, some of suppressed saplings and gap successors were of sprout origin. *P. thunbergii* has a strong capacity for coppicing (Nakamura *et al.*, 1986). Type I implies that canopy trees regenerate in gaps from saplings recruited before gap creation. Such types of gap regeneration behaviour have been termed "extremely shade-tolerant species" (Spurr and Barnes, 1980), "gap phase replacement species" (Hibbs, 1979; Hibbs *et al.*, 1980) "primary tree species" (Brokaw, 1985) or "climax (non-pioneer) species" (Whitmore, 1989).

Type II is for species without suppressed saplings. *Castanopsis cuspidata* belongs to this type. This type of gap regeneration behaviour may be assumed that seedlings can not be established under a closed canopy; seedlings can be established and/or grow only in gaps. However, *Castanopsis cuspidata* regenerates not only from seeds

Table 11. Gap regeneration behaviour of major component tree species in primary evergreen broad-leaved forests of western Japan

Type	Category				Species
	CT	GM	SS	GS	
I	○	○	○	○	<i>Distylium racemosum</i> , <i>Persea thunbergii</i>
II	○	○		○	<i>Castanopsis cuspidata</i>
III			○	○	<i>Camellia japonica</i> , <i>Cinnamomum insularimontanum</i> <i>Cleyera japonica</i>
IV	○	○			<i>Quercus acuta</i> , <i>Quercus salicina</i>

Species are listed of only species with more than ten percent in relative density and relative dominance in each regeneration category, clumping all study stands.

○, occurrence in its category with more than ten percent.

CT, canopy tree; GM, gap maker; SS, suppressed sapling; GS, gap successor.

but also by sprouting from injured gap makers in gaps. Stump sprouting may be important for the regeneration of *Castanopsis cuspidata* in gaps (Table 10), as in the case of *Fagus japonica* (cf. Ohkubo *et al.*, 1988) or some tropical tree species (Hartshorn, 1989; Putz and Brokaw, 1989). Deciduous broad-leaved trees such as *Fagara ailanthoides* and *Stewartia monadelphica*, though few in numbers, may also belong to Type II, but in contrast to *C. cuspidata* these may be assumed that trees regenerate in gaps only from seeds germinated after gap creation. Such species have been termed "pioneer tree species" (Spurr and Barnes, 1980; Brokaw, 1985; Whitmore, 1989). Occurrence of gap successors of *F. ailanthoides*, a typical pioneer species, is limited to gaps created by uprooted gap makers. Though the frequency of uprooting is low, soil disturbance by uprooting seems to be an important factor for the perpetuation of this species which recruits mainly from buried seeds (Naka and Yoda, 1984). The importance of soil disturbance by uprooted trees for the recruitment of pioneer tree species has been emphasized in an old-growth cool temperate forest of Japan (Nakashizuka, 1989) and, together with the importance of large gaps, in tropical rain forest on BCI, Panama (Putz, 1983). The amount of available sunlight also seems to be another important factor for the perpetuation of this species, because many small saplings of *F. ailanthoides* could be found in large gaps.

Type III is for species without canopy trees and gap makers. This type of gap regeneration behaviour is somewhat unfamiliar, but implies that trees regenerate in gaps from saplings recruited before the gap formation, the same as Type I. Species belonging to this type are considered typical "sub-canopy tree species" that rarely reach a canopy layer or attain a size more than 30 cm dbh. Thus, species with this type of gap regeneration behaviour usually regrow, mature and die in gaps without reaching the canopy layer or attaining the size of about 30 cm dbh.

Type IV is for species without suppressed saplings and gap successors. This type of gap regeneration behaviour implies that trees can not regenerate in gaps created under current gap-disturbance regime. *Quercus acuta* and *Quercus salicina* belong to this type; very few number of *Quercus salicina* saplings was found in a primary warm temperate rain forest on Yakushima island of southern Japan (Kohyama *et al.*, 1984).

These different types of gap regeneration behaviour were recognized, while there was not a clear niche differentiation along gap-size gradient in the gap regeneration of common evergreen broad-leaved tree species (Table 8).

Typhoons are the chief agent of natural disturbance influencing on the gap characteristics in primary evergreen broad-leaved forests of western Japan. Under this gap-disturbance regime, Type I and Type III species gradually reach the canopy and the sub-canopy, respectively, as overstory trees die or windthrow provides openings for them. *Distylium racemosum* could maintain their saplings under the closed canopy and replace not only its own gaps but also gaps created by all major canopy tree species. Therefore, it can be considered a typical climax species in this forest type. Infrequent and/or less severe disturbances may favor Type I and Type III species. For Type II species, vegetative reproduction by stump sprouting enables *Castanopsis cuspidata* to survive and reestablish itself in place after disturbance; the

higher success by stump sprouting in the gap regeneration seems to afford a major fitness to asexual reproduction of *C. cuspidata* under gap-disturbance regime. Frequent and/or more severe disturbances may favor *Castanopsis cuspidata* and a typical pioneer species such as *Fagaria aplanthoides*. Regeneration mechanism of Type IV species, i.e. *Quercus* spp., is unknown. Large or catastrophic disturbances may be needed for the regeneration, or these species may regenerate by any episodic events other than gap-disturbance; e.g. extreme success of the seedling establishment in a certain year.

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