Stand Structure and Regeneration Characteristics of Major Woody Species in a Secondary Evergreen Broad-leaved Forest, in the Suburban Kyushu, Japan

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Abstract Species composition, diameter at breast height (dbh) distribution of major woody species and canopy gap characteristics were investigated in a secondary evergreen broad-leaved forest located at late developmental stages, which was isolated from surrounding matrix. Maximum dbh of each species in this forest was smaller than that in the old-growth forests. Gaps created in the forest had positive correlations to dbh of gap-makers. Those gaps were smaller in area and lower in density than those in old-growth ones owing to the smallness of the stems of gap-makers. Thus, the differences in natural disturbance regimes among forests might partly be explained by the differences in stand structure. Patterns of dbh distributions and seedling emergence suggested that some species showed different regeneration behavior between the forest and the old-growth ones: *Distylium racemosum, Persea thunbergii, Camellia japonica* and *Eurya japonica* maintained their population by the same regeneration behavior both in the forest and the old-growth forests, although *Castanopsis cuspidata, Quercus salicina* and *Zanthoxylum schinifolium* regenerated by different ways to the old-growth ones.

Key Word Canopy gaps, Dbh distribution, Late developmental stages, Seedling bank

Introduction

In the old-growth forests, natural disturbance, especially creation of canopy gaps, plays an important role in dynamics and in maintaining species diversity of forest communities (WHITMORE, 1978; PICKETT and WHITE, 1985). Population responses to natural disturbance have also clarified through direct estimation of demographic parameters at large permanent plots with long-term studies in various ecosystems (ALVAREZ-BUYLLA and MARTINEZ-RAMOS, 1992; MASAKI *et al.*, 1994; SHIBATA and NAKASHIZUKA, 1995; CONDIT *et al.*, 1996; MANABE and YAMAMOTO, 1997; KOMINAMI *et al.*, 1998).

In secondary forests, studies on patterns and processes of recovery of disturbed

forests following human disturbance have been conducted (e.g. MOONEY and GODRON, 1983; NAKAGOSHI et al., 1987; NAKAGOSHI and WADA 1990; FINEGAN, 1996). Those studies have mainly dealt with the communities located at the early and the middle developmental stages. In secondary forests, natural disturbance might also be important for community dynamics especially communities at the late developmental stages that have relatively similar structures to those at the climax stages. Only a few studies have focused on a role of natural disturbance on community dynamics in secondary forests (CLEBSCH and BUSING, 1989; HIGO et al., 1994; LERTZMAN et al., 1996; YAMAMOTO and MANABE, 1997).

In this paper, we analyzed stand structure such as species composition, diameter at breast height (dbh) distribution of major woody species and canopy gap characteristics in a secondary evergreen broad-leaved forest, which is located at the late developmental stages. We also discussed regeneration characteristics of major woody species.

Study sites

The study was conducted at a secondary evergreen broad-leaved forest at the Hakusan-taga Shrine (33°45′N, 130°55′E, a.s.l. 280 m) which located in suburban area of Yukuhashi City, Kanda Town and Kitakyushu City, northern Fukuoka, south-western Japan. The forest, which is ca. 2 ha in area, is surrounded by young secondary evergreen broad-leaved forests dominated by Castanopsis cuspidata (THUNB.) SCHOTTKY and Neolitsea sericea (BLUME) KOIDZ., conifer plantations such as Cryptomeria japonica (LINN. fil.) D. DON and Chamaecyparis obtusa (SIEB. et ZUCC.) SIEB. et ZUCC. apud ENDL., Phyllostachys forests (bamboo forests) and paddy fields, indicating that the forest is isolated from surrounding matrix (MANABE unpublished data). On the other hand, the smallness of maximum dbh of dominant species in this forest suggested the forest was still secondary one (MANABE et al., 1996). This finding was supported by several past documents concerning in the shrine, which tell us that the shrine met devastations of war and was burnt sometime in the middle to the late 16 century (NAGAMINE and UEDA, 1996). That is, the forest had often been disturbed by anthropogenic factors in the past, and it located at the late stages of secondary succession.

Methods

A 50 m × 50 m plot (P1) and two 30 m × 30 m plots (P2 and P3) were established at the forest in November, 1994 and May, 1995. We classified each individual into three classes based on the size: mature individuals which were larger than 5 cm in dbh, saplings which were larger than 1.3 m in height and smaller than 5 cm in dbh, and seedlings (0.1 to <1.3 m in height). All mature individuals were

identified their species names and measured dbh for all stems larger than 5 cm in dbh.   Those individuals were also recorded their vertical position: upper individuals that attained the forest canopy, and lower individuals that did not attain the forest canopy.   For all canopy gaps formed in the forest, the largest distance between gap edge (length), the largest distance perpendicular to length (width), species identity, dbh and the type of injury or cause of death of gap-makers were recorded in July, 1995.

Ten 10 m × 10 m quadrats were set in P1 and each of five 10 m × 10 m quadrats were set in P2 and P3 for saplings and seedling investigations.   All saplings in the quadrats were recorded their species names and dbh for all stems taller than 1.3 m in height.   A 5 m × 5 m sub-quadrat was set in all 20 quadrats, and six 1 m × 1 m sub-quadrats were also set in the canopy gaps.   All seedlings in the sub-quadrats were also recorded by their species names and heights except for some shrub species and lianas, which could not be identified their individuality owing to their creeping form.   Data sets obtained in each plot were integrated for analysis.

Results

Species composition and dbh distribution

Mature individuals were composed of 39 species, and the density of them and the total basal area of their stems were 937 ha^{-1} (1,002 stems ha^{-1}) and 51.96 m^2 ha^{-1}, respectively (Table 1).   The individuals of *Symplocos lucida* SIEB. et ZUCC., was the most in number followed by *Castanopsis cuspidata*, *Persea thunbergii* (SIEB. et ZUCC.) KOSTERM.   *Camellia japonica* LINN. and *Distylium racemosum* SIEB. et ZUCC. Basal area of each species was also large in evergreen broad-leaved trees such as *C. cuspidata*, *D. racemosum*, *P. thunbergii*, and deciduous tree *Cornus brachypoda* C. A. MEY was the fourth.

The forest canopy was dominated by *Castanopsis cuspidata*, *Distylium racemosum* and *Persea thunbergii* (Fig. 1).   The dbh distributions for *P. thunbergii*, *C. japonica* and *S. lucida* were reverse-J shape, indicating that those trees regenerate successively.   The dbh distributions for *C. cuspidata* and *P. thunbergii* indicated indistinct mode, although the shape might be formed by some reverse-J cohorts.

The density of saplings and the basal area of their stems were 1,715 ha^{-1} (2,315 stems ha^{-1}) and 6.51 m^2 ha^{-1}, respectively.   Saplings were composed of 32 species including shrubs such as *Callicarpa mollis* SIEB. et ZUCC., *Aucuba japonica* THUNB. and *Maesa japonica* (THUNB.) MORITZI (Table 2).   The number of individuals was the most in *A. japonica*, and sub-canopy trees such as *Symplocos lucida*, *Ilex rotunda* THUNB., *Camellia japonica* and *Eurya japonica* THUNB. were also abundant. *Cornus brachypoda* and *Rhus succedanea* LINN., which were abundant for mature individuals, had no saplings.   Some canopy and sub-canopy trees such as *Clerodendron trichotomum* THUNB and *Prunus spinulosa* SIEB. et ZUCC. had many saplings, even

Table 1. The number (ha^{-1}) and cumulative basal area (m$^2 \cdot$ha^{-1}) of mature
individuals.

Species	Life form[1]	Number of individuals		Cumulative basal area	
		Living	Dead	Living	Dead
Symplocos lucida	EB	174	19	2.07	0.33
Castanopsis cuspidata	EB	167	33	29.95	5.67
Persea thunbergii	EB	98	7	3.37	0.26
Camellia japonica	EB	84	2	1.37	0.04
Distylium racemosum	EB	81	—	6.18	—
Cornus brachypoda	DB	40	2	1.91	0.01
Eurya japonica	EB	40	—	0.24	—
Rhus succedanea	DB	28	—	0.67	—
Actinodaphne lancifolia	EB	23	—	1.66	—
Ligustrum japonicum	EB	21	—	0.12	—
Daphniphyllum macropodum	EB	16	—	0.70	—
Quercus salicina	EB	14	—	1.00	—
Styrax japonica	DB	14	—	0.18	—
Cleyera japonica	EB	14	—	0.07	—
Trachelospermum asiaticum var. *intermedium*	EB, L	14	—	0.04	—
Premna japonica	DB	12	—	0.07	—
Ilex chinensis	EB	9	—	0.08	—
Ilex integra	EB	9	—	0.03	—
Acer palmatum	DB	7	—	0.12	—
Dendropanax trifidus	EB	7	—	0.05	—
Persea japonica	EB	7	—	0.03	—
Ficus erecta	DB	7	—	0.03	—
Actinidia polygama	DB, L	7	—	0.02	—
Neolitsea sericea	EB	5	—	0.17	—
Symplocos glauca	EB	5	—	0.03	—
Ilex rotunda	EB	5	—	0.02	—
Actinidia arguta	DB, L	5	—	0.01	—
Neolitsea aciculata	EB	2	—	0.27	—
Platycarya strobilacea	DB	2	—	0.24	—
Zanthoxylum ailanthoides	DB	2	—	0.21	—
Aphananthe aspera	DB	2	—	0.07	—
Euscaphis japonica	DB	2	—	0.03	—
Symplocos myrtacea	EB	2	—	0.01	—
Wisteria floribunda	DB, L	2	—	0.01	—
Viburnum awabuki	EB	2	—	0.01	—
Ternstroemia gymnanthera	EB	2	—	0.01	—
Cinnamomum japonicum	EB	2	2	0.01	0.04
Acuba japonica	EB	2	—	0.01	—
Hedera rhombea	EB, L	2	—	0.00	—
Cryptomeria japonica	EN	—	2	—	0.07
Unidentified	—	—	9	—	0.17

1) EB: evergreen broad-leaved tree, DB: Decidupus broad-leaved tree, EN: evergreen
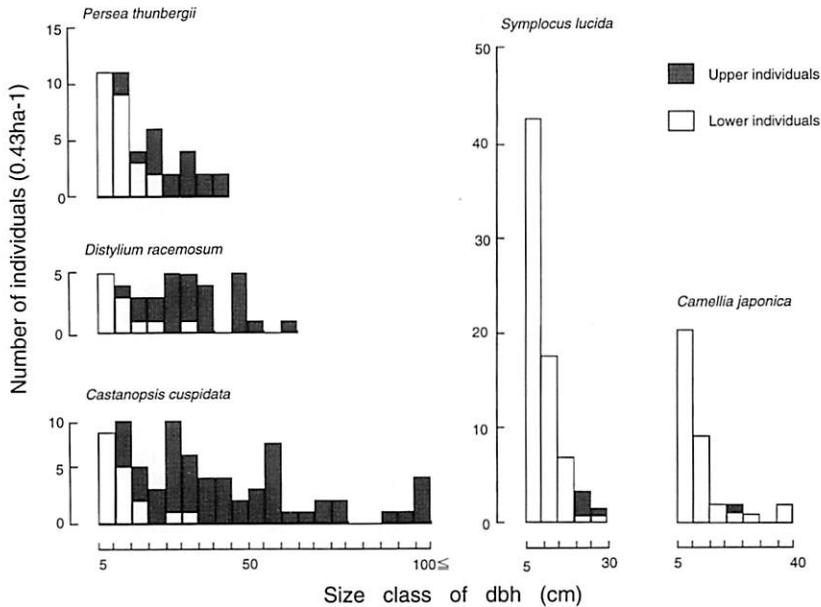needle-leaved tree, L: liane

Fig. 1.   Dbh distribution for mature individuals (≥ 5 cm in dbh) of major tree species.   Upper
and lower individuals are those attained forest canopy and those did not attained forest
canopy, respectively.

though they had no mature individuals.

Seedlings were composed of 46 species, and the density of them was 19,568 ha^{-1}.   All species which had mature individuals also had seedlings except for *Acer palmatum* THUNB. and *Symplocos myrtacea* SIEB. et ZUCC (Table 2).   Some canopy and sub-canopy trees such as *Celtis sinensis* PERS. var. *japonica* (PLANCH.) NAKAI, *Carpinus tschonoskii* MAXIM. and *S. prunifolia* SIEB. et ZUCC. as well as some shrubs such as *Viburnum erosum* THUNB., *Zanthoxylum schinifolium* SIEB. et ZUCC. and *Euonymus sieboldianus* BLUME had seedlings, although they had no mature individuals and saplings.   *Neolitsea sericea*, which had a few mature individuals and saplings, had the most abundant seedlings.   Some evergreen canopy trees such as *Castanopsis cuspidata* and *Distylium racemosum*, which had many mature individuals and saplings, also had many seedlings, and the height distributions for them were reverse-J shape (Fig. 2).

Canopy gaps

Fifteen canopy gaps were formed in the forest, and the causes of gap formation were identified in eleven gaps (Table 3).   Gaps formed by a single treefall were found in 53.3% of all gaps, and those formed by multiple treefalls were 20.0%. Four gaps that the cause of gap formation was not identified, were regarded as very

Table 2.   The number of saplings and seedlings (ha^{-1}).

Species	Life form[1]	Saplings	Seedlings[2]
Aucuba japonica	EB	315	*
Symplocos lucida	EB	280	1317
Eurya japonica	EB	160	432
Ilex rotunda	EB	150	267
Camellia japonica	EB	130	2572
Distylium racemosum	EB	95	638
Ligustrum japonicum	EB	70	1276
Ficus erecta	DB	65	267
Cleyera japonica	EB	65	103
Castanopsis cuspidata	EB	50	885
Persea thunbergii	EB	40	370
Neolitsea sericea	EB	35	5391
Maesa japonica	EB	30	*
Dendropanax trifidus	EB	30	165
Ilex integra	EB	25	62
Neolitsea aciculata	EB	20	494
Quercus salicina	EB	15	453
Daphniphyllum macropodum	EB	15	1564
Premna japonica	DB	15	62
Callicarpa mollis	DB	15	412
Euscaphis japonica	DB	15	185
Acanthopanax sciadophylloides	DB	10	—
Viburnum awabuki	EB	10	21
Symplocos glauca	EB	10	62
Cinnamomum japonicum	EB	10	185
Prunus spinulosa	EB	10	823
Persea japonica	EB	10	82
Aralia elata	DB	5	—
Clerodendron trichotomum	DB	5	800
Styrax japonica	DB	5	800
Rhododendron kaempferi	DB	5	*
Ternstroemia gymnanthera	EB	5	21
Aphananthe aspera	DB	—	226
Cornus brachypoda	DB	—	800
Zanthoxylum ailanthoides	DB	—	103
Actinodaphne lancifolia	EB	—	82
Ilex chinensis	EB	—	82
Rhus succedanea	DB	—	82
Carpinus tschonoskii	DB	—	41
Elaeagnus pungens	EB	—	41
Symplocos prunifolia	EB	—	21
Celtis sinensis var. *japonica*	DB	—	21
Diospyros kaki	DB	—	21
Mallotus japonicus	DB	—	21
Rhus javanica	DB	—	21
Aralia elata	DB	—	21
Viburnum erosum	DB	—	21
Zanthoxylum piperitum	DB	—	21
Zanthoxylum schinifolium	DB	—	21
Euonymus sieboldianus	DB	—	21

1)   EB: evergreen broad-leaved tree, DB: Decidupus broad-leaved tree, EN: evergreen needle-leaved tree
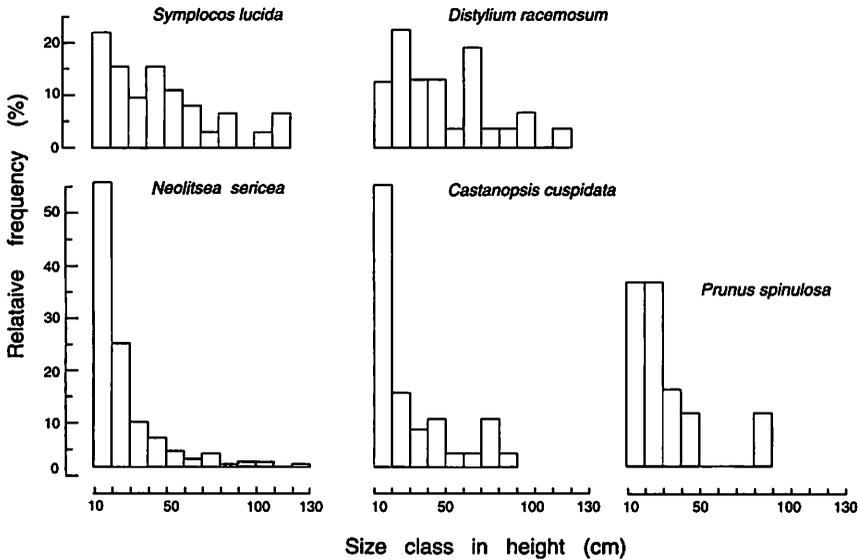2)   *: species which were not investegated

Fig. 2. Frequency distribution of height measurement for seedlings (< 1.3 m in height) of the woody species having abundant seedlings.

Table 3. The number of canopy gaps created in the forest.

Type of injury of gap-makers	Number of gap-makers creating a gap		
	Single	Multiple	Unknown
Snapped	8	2	—
Snapped + incline	0	1	—
Unknown	—	—	4

old ones, since the degree of rotting in the gap-makers was high. Those old gaps were partly closed by lateral expansion of the tree branches surrounding the gaps. Most of the gap-makers were *Castanopsis cuspidata* (Table 4). Among gap-makers, four individuals were resprouted ones with multiple stems, and had one or more living stems. All gap-makers were snapped except for one individual that formed a gap by its inclination. Among snapped gap-makers, three individuals might break their stems after they die. The average gap size was 54.7 m^2 (range: 7.8 – 203.6 m^2). Most of the gaps were smaller than 100 m^2, although two gaps formed by multiple treefalls were larger than 180 m^2 (Fig. 3). There was a following significant relationship between dbh of gap-maker (DG; cm) and gap area (GA; m^2):

$$GA = 0.82DG - 6.22 \ (r = 0.890; \ P < 0.001, \ d.f. = 9, \ t\text{-test})$$

Table 4. Species and the number of gap-makers
creating canopy gaps.

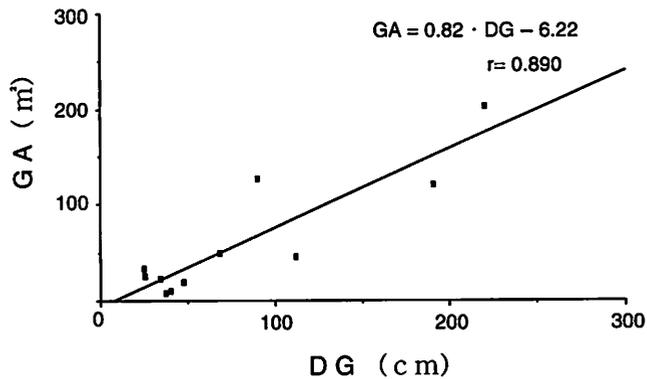| Species and trunk form	Type of injury	
	Snapped	Incline
Castanopsis cuspidata		
Single	8	0
Multiple	3	1
Symplocos lucida		
Single	2	0
Prunus jamasakura		
Multiple	1	0

Fig. 3. Relationship between dbh of gap-makers (DG) and gap area (GA) formed by them.

Discussion

Stand structure

Species composition in this secondary evergreen broad-leaved forest was similar to that in the old-growth forests (MANABE et al., 1996).   But, maximum dbh of major dominant tree species such as *Castanopsis cuspidata*, *Distylium racemosum* and *Persea thunbergii* was only a half of that in the old-growth ones (MANABE et al., 1996).

Natural disturbance regimes in the forest differed from those in the old-growth forests. Mean and maximum gap areas were smaller and the density of canopy gaps was lower in the forest than those in old-growth evergreen broad-leaved forests in Kyushu (YAMAMOTO, 1992). Same trends were observed in other secondary forests at different climatic zone (CLEBSCH and BUSING, 1989). In the forest, the area of canopy gaps had positive correlations to dbh of gap-makers which have relatively small dbh to compare with the old-growth forests. Large gaps are often formed by uprooted trees and/or multiple trees falls (PUTZ, 1983; NAKASHIZUKA,

1989).   Most of the gaps were formed by single canopy trees and no gaps were formed by uprooted trees in the forest.   Gaps created in the forest, therefore, can be small in area.   Those differences are attributed to the differences in forest structure between old-growth forests and secondary ones.

In this forest, about 27% of canopy gaps were not identified the cause of the death of gap-makers, and those gaps were regarded as very old ones.   This suggests that many gaps need a long time to be closed in the forest.

Regeneration characteristics

Canopy species such as *Distylium racemosum, Castanopsis cuspidata* and *Quercus salicina* had abundant seedlings in this forest.   *D. racemosum* maintains its population by abundant seedlings with high survival rate based on strong shade tolerance ability in the old-growth forests (YAMAMOTO, 1992; SATO *et al.*, 1994; TANOUCHI *et al.*, 1994).   This species may regenerate successively in the forest the same as in the old-growth forests.   The density of *C. cuspidata* seedlings was low within gaps as well as beneath a closed canopy in the old-growth forests (YAMAMOTO, 1992), suggesting that the species have relatively weak shade tolerant ability (TANOUCHI, 1990). Catastrophic natural disturbances such as occasional and strong typhoons and landslides might be effective for successful regeneration of the species (YAMAMOTO, 1992).   Abundant seedlings of the species, however, grow within gaps in the old-growth forests without *D. racemosum*, indicating that regeneration behavior of the species varies with stand structure, especially the presence or absence of key dominant species (YAMAMOTO, 1994).   The density of *C. cuspidata* was high in the forest, although the density of *D. recemosum* was also high.   Thus, regeneration behavior of the species in the forest differs from that in the old-growth forests with *D. racemosum*.   Seedlings of *Q. salicina* have less shade tolerant ability than that of *D. racemosum* (TANOUCHI, 1990; TANOUCHI and YAMAMOTO, 1995).   *Q. salicina* has relatively small seedling and sapling banks, and needs large canopy gaps for recruiting into upper layer (YAMAMOTO, 1992; TANOUCHI and YAMAMOTO, 1995).   The seedling and sapling density of the species, however, was high in the forest.   Thus, this species regenerates by different way from the forest to the old-growth forests.

Camellia japonica, which is a typical sub-canopy species, has high sapling density, and maintains its population beneath a closed canopy in the old-growth forests (YAMAMOTO, 1992).   This species had high sapling and seedling density in the forest.   The species can form enough seedling and sapling banks, and regenerates successively beneath a closed canopy in the forest as well as in the old-growth ones.

Seedlings were also abundant for *Persea thunbergii, Neolitsea aciculata, N. sericia,* and *Eurya japonica.*   The seeds of those species might disperse widely over the plots, since their seeds are often dispersed by birds (MANABE *et al.*, 1993; KOMINAMI *et al.*, 1995).   In the old-growth forests, seedling and sapling banks contribute largely to successive regeneration for *P. thunbergii* (YAMAMOTO, 1992; SATO *et al.*, 1994;

TANOUCHI *et al.*, 1994) and *E. japonica* (MANABE and YAMAMOTO, 1997). Shade tolerance ability might be lower for *P. thunbergii* than *Distylium racemosum* and *Quercus salicina* (SATO *et al.*, 1994). But, *P. thunbergii* and *E. japonica* maintain their seedling and sapling banks by abundant seed supply (SATO *et al.*, 1994; MANABE and YAMAMOTO, 1997). These species maintain their population by the same regeneration behavior both in the old-growth forests and the forest. Seedling and sapling banks might also contribute to successive regeneration for *N. sericia*, although regeneration characteristics of the species have not been reported in the old-growth forests. *N. sericia* had very high seedling density, although mature individuals which might be able to produce seeds were very few in the forest. This finding suggests that most of *N. sericia* seedlings might come from the seeds produced outside the forest, since the species produce endozoochory seeds and occurs often at young coppice surrounding the forest.

Pioneer trees such as *Zanthoxylum ailanthoides* and *Prunus spinulosa* had high seedling density, although they had few mature individuals. Seedlings of some pioneer canopy trees established vigorously in large gaps and gaps formed by up-rooted trees with exposed mineral soil (PUTZ, 1983; BROKAW, 1985; NAKASHIZUKA, 1989). In an old-growth evergreen broad-leaved forest in Miyazaki Prefecture, the density of *Z. ailanthoides* mature individuals was very low, suggesting that the species require catastrophic disturbances for their population maintenance (YAMAMOTO, 1992). The species, however, regenerate at some gaps formed under ordinal disturbance regimes in other evergreen broad-leaved forest in Nara Prefecture (SHIMODA *et al.*, 1994). In this forest, seedlings of *Z. ailanthoides* were also abundant in gaps with small area (MANABE unpublished data). Current disturbance regimes in this secondary forest may be useful for regeneration of *Z. ailanthoides*.

In the old-growth evergreen broad-leaved forests, four types of gap regeneration behavior were recognized based on the difference in replacement patterns of the canopy layer through canopy gaps (YAMAMOTO, 1992). Thus, relative importance of canopy gaps on population dynamics of trees varies with species (YAMAMOTO, 1992; TANOUCHI and YAMOMOTO, 1995). In this secondary forest, patterns of dbh distribution and seedling emergence differed among species, suggesting that regeneration characteristics also vary with species. Further, some species show different regeneration behavior between this secondary forest and the old-growth ones. Those differences might be partly due to the differences of forest structure and of the characteristics of canopy gap formation among them.

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