

# Gap characteristics and gap regeneration in secondary deciduous broad-leaved forests on Mt. Jiri, South Korea

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**ABSTRACT** — The gap disturbance regimes and gap regeneration behaviour were investigated in secondary deciduous broad-leaved forests in a lower-altitude stand and a higher-altitude stand, on a forest floor covered with dense dwarf bamboo on Mt. Jiri, South Korea. The species compositions of the canopy trees, suppressed saplings, and gap successors differed between stands. Gap disturbance regimes, such as the total gap area in the total survey area, and the density of the gaps also differed across stands. The densities of the canopy gaps in both stands were basically similar to those reported in other old-growth forests, although the percentage gap area and the size of each gap were smaller in these stands than those in old-growth forests. Different types of gap regeneration behaviour were identified among the major canopy and sub-canopy tree species. *Quercus mongolica* occurred in all regeneration categories (canopy trees, gap makers, suppressed saplings, and gap successors), indicating that this species can regenerate in gaps from saplings recruited before gap formation. *Lindera erythrocarpa* and *Acer pseudo-sieboldianum* lacked canopy trees and gap makers, suggesting that these species might not yet be large enough to reach the canopy layer, but could have sapling banks beneath the closed canopy. The gap regeneration behaviour observed on Mt. Jiri differed markedly from that in various old-growth forests in Japan. These differences might be attributable to differences in the natural disturbance regimes as well as to differences in the successional stages among the forests. There were also very few canopy and/or sub-canopy species with gap successors, suggesting that the canopy gaps in both stands do not play important roles in the gap regeneration of the component species of the stands. The dense cover of dwarf bamboo on the forest floor may explain why the gaps have little effect on the regeneration of many tree species.

**KEY WORDS:** canopy gap, gap regeneration behaviour, secondary forests, secondary succession

## INTRODUCTION

The formation of canopy gaps induces tree-by-tree replacement processes in climax and mature forests (WOODS, 1979, 1984; BARDEN, 1980; RUNKLE, 1981; VELEN, 1988), and thus affects the structure, dynamics, and functions of various forest ecosystems on different spatio-temporal scales (PICKETT and WHITE, 1985; YAMAMOTO, 2000). Therefore, gap dynamics, defined as the series of dynamic events related to forest regeneration (VAN DER MAAREL, 1988), have been intensively studied in various climax and mature forests throughout the world (McCARTHY, 2001). Gap disturbance regimes and the patterns of gap-phase replacement are therefore crucial factors in clarifying the maintenance mechanisms of climax and

mature forests (YAMAMOTO, 1992a).

The formation of canopy gaps also affects the structure and dynamics of secondary forests (CLEBSCH and BUSING, 1989; YAMAMOTO and MANABE, 1997; KNEESHAW and BERGERON, 1998; YAMAMOTO and NISHIMURA, 1999; HARCOMBE *et al.*, 2002) and modifies the successional pathways in these forests (VANDVIK, 2004; LUTZ and HALPERN, 2006). For example, a powerful typhoon produced more and much larger gaps than those produced before the typhoon, and it accelerated the secondary succession in a ca. 80-year-old evergreen broad-leaved coppice in Japan (YAMAMOTO and MANABE, 1997). Conversely, canopy gaps had only a small effect on the recruitment of less-shade-tolerant trees, because the differences in the light regimes under closed canopies and within gaps was small in 15–63-year-old

secondary deciduous broad-leaved forests in North America (CLEBSCH and BUSING, 1989). Therefore, the role of canopy gaps in the structures and/or dynamics of secondary forests might vary with the stage of their secondary succession (i.e., years after anthropogenic disturbance), the disturbance regime, etc. However, there have been very few studies of the effects of canopy gaps on the structures and dynamics of secondary forests, especially those in the temperate regions of Asia.

The major forest vegetation in the cool-temperate regions of Asia is a deciduous broad-leaved forest. Both old-growth and secondary deciduous forests on the Korean Peninsula and elsewhere in northern Asia are dominated by *Quercus mongolica* FISCH. (QIAN *et al.*, 2003; KRESTOV *et al.*, 2006).

In this paper, we describe the gap disturbance regimes and gap regeneration modes in secondary deciduous broad-leaved forests of *Quercus mongolica* distributed widely in the cool-temperate regions of South Korea. We also discuss the role of canopy gaps on the secondary succession in these forests.

## STUDY STANDS

The study was conducted at cool-temperate zone on Mt. Jiri. Mount Jiri, one of the highest mountains in South Korea, lies in an east-west direction and has more than 20 peaks, with steep slopes and rolling topography. The vegetation on the mountain is rather distinct along an elevation line. Two vegetation belts mainly in national park area can be recognized (NAKAI, 1915): 1) the temperate zone from 300 m to ca. 1,500 m with deciduous broad-leaved forests dominated by *Carpinus tschonoskii* MAXIM., *C. laxiflora* (SIEB. et ZUCC.) BLUME, *Quercus variabilis* BLUME, *Q. serrata* THUNB. and *Q. mongolica*; 2) the subarctic zone above 1,500 m with evergreen coniferous forests dominated by *Abies nephrolepis* (TRAUT. ex MAXIM.) MAXIM. and *Picea jezoensis* (SIEB. et ZUCC.) CARR. All the soils in the study area belong to the Brown Forest Soil Group pedologically (RIM, 1963). The bedrock is mainly granite, which crops out across the whole mountain (LEE, 1987).

The study stands are at a lower-altitude site (L-S) and a higher-altitude site (H-S) on the mountain. Topography of both stands is gentle sloping. The approximate location of L-S, an upper site at Baekmudong, Macheon-myeon, Hamyang-gun, Gyeongsangnam-do, is 35°22'N, 127°41'E, at an altitude of ca. 550 m. H-S, near the Seongsam Pass at Sandong-myeon, Gurye-gun, Jeollanam-do, which is located at 35°18'N, 127°31'E, at an altitude of ca. 1,100 m. L-S and H-S are located at north-east part and west part of Jirisan National Park, respectively.

At Namwon Weather Observation Station nearby (115 m a.s.l., ca. 27 km from Baekmudong and ca. 16 km from Seongsam Pass), the mean annual temperature (1961–1990) is 12.2

°C, and the mean annual precipitation is 1,341 mm (Korea Meteorological Administration, 1991).

## METHODS

### Field survey

The canopy trees in the two study stands were recorded along a transect line using the point-centered quarter method (COTTAM and CURTIS, 1956), which is considered to be the most efficient of the available distance methods (MUELLER-DOMBOIS and ELLENBERG, 1974). In the point-centered quarter method, the distances to the nearest canopy trees from the sampling point, the species name, and the diameter at breast height (DBH) of the canopy tree are recorded for four quarters at each sampling point. The four quarters are established at the sampling point with a cross formed by two lines: one is the transect direction, and the other is a line running perpendicular to the transect direction. Eleven, six, and three sample points were randomly selected along three transect lines at L-S, and ten sample points were also randomly selected along both of the transect lines at H-S. Although the accuracy increases with the number of sampling points, a minimum of twenty points is recommended (COTTAM and CURTIS, 1956). For both stands, the total length of the transect lines were 330 m. The first sample point, which is the starting sample point of the initial line, was located randomly. The initial transect line runs roughly parallel to the contour line of the stand. The direction of a transect line was also altered to the opposite direction, and the transect was continued for 20 m apart from the line when the top of the line met any microtopographic change, such as a gully, small cliff, etc. Thus, the total surveyed area, which was calculated as the product of the width of the transect lines (i.e. 20 m) and the total length of the transect lines, was 0.66 ha at both stands.

A “suppressed sapling” was defined as the tallest stem, including non-canopy tree species, beneath the crown of each selected canopy tree. The species name and DBH were recorded for the suppressed sapling. Whether the suppressed saplings were sprouts of the canopy tree (coppice-suppressed saplings) or not was also recorded.

The ground area under a canopy opening was defined as a “gap”. Gaps were considered indistinguishable from the surrounding canopy layer when the trees regenerating within the gap had attained a height >10 m, according to a study of a secondary evergreen broad-leaved forest in southern Japan (YAMAMOTO and MANABE, 1997). All gaps with a visual centre within 10 m on either side of the transect lines were described. The largest distance between the gap edges (length) and the largest distance perpendicular to the length (width) were recorded for each gap. The gap edge was defined as the vertical projection onto the ground of the edges of the foliage crowns of the canopy trees surrounding a canopy opening. The species

name (if possible), DBH, and the state of death or injury (i.e., standing dead, trunk broken, uprooted, or unknown) of the gap makers were recorded. In each gap, the species and DBH of the tallest sapling as “successor” were also recorded. The method used in this study has been explained in detail by YAMAMOTO (1989, 1992b).

The coverage of dwarf bamboo under the crown of the canopy trees studied and within the gaps studied was recorded by visual estimation. The field survey was undertaken in August, 2008. The nomenclature used follows that of LEE (1989).

### Data analysis

The relative densities, relative basal areas, and absolute frequencies of the canopy trees were calculated for each stand from the point-centered quarter data. Absolute frequency (%) is defined here as the ratio of the number of points with a canopy tree to the total number of points. The emergence rate, sprouting rate, and cumulative basal area of the suppressed saplings were also calculated for each stand from the point-centered quarter data. The emergence rate is defined as the ratio of the number of quarters with suppressed saplings to the total number of quarters. The sprouting rate is defined as the ratio of the number of suppressed saplings that regenerated by sprouting to the total number of suppressed saplings.

The gap area was calculated with the formula for an ellipse using the length and width of the gap. The densities of the gaps and gap makers in each stand were calculated in the total surveyed area of each stand.

## RESULTS

Among eighty canopy trees studied at each stand, seventeen and ten species occurred at L-S and H-S, respectively (Table

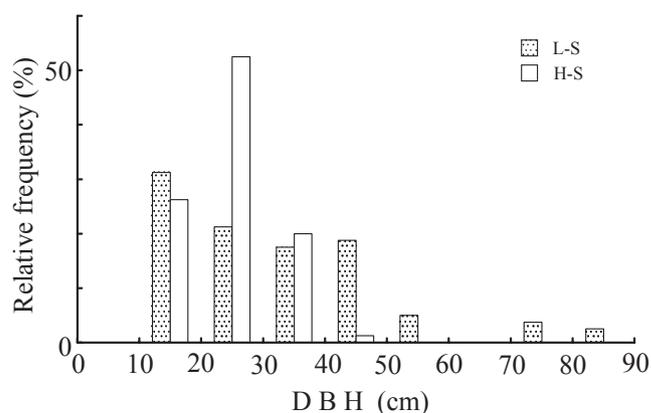


Fig. 1. DBH distributions of canopy trees at L-S and H-S on Mt. Jiri.

Table 1. Densities, basal areas, and absolute frequencies of canopy trees in two study stands on Mt. Jiri.

Species	L-S			H-S		
	Density (ha <sup>-1</sup> )	Basal area (m <sup>2</sup> /ha)	Absolute frequency* (%)	Density (ha <sup>-1</sup> )	Basal area (m <sup>2</sup> /ha)	Absolute frequency* (%)
<i>Quercus mongolica</i>	16.5	12.45	20	465.7	1558.64	100
<i>Styrax obassia</i>	13.2	0.84	15	7.1	0.21	5
<i>Prunus leveilleana</i>	6.6	3.20	10	7.1	0.35	5
<i>Maackia amurensis</i>	3.3	0.08	5	7.1	0.42	5
<i>Quercus serrata</i>	64.9	209.57	65	-	-	-
<i>Fraxinus rhynchophylla</i>	46.3	46.40	30	-	-	-
<i>Carpinus laxiflora</i>	33.1	14.47	30	-	-	-
<i>Quercus variabilis</i>	13.2	6.21	15	-	-	-
<i>Acer mono</i>	16.5	6.02	20	-	-	-
<i>Stewartia koreana</i>	16.5	1.32	20	-	-	-
<i>Alnus hirsuta</i> var. <i>sibirica</i>	6.6	0.77	10	-	-	-
<i>Acer pseudo-sieboldianum</i>	6.6	0.23	10	-	-	-
<i>Quercus acutissima</i>	3.3	1.66	5	-	-	-
<i>Carpinus tschonoskii</i>	3.3	0.60	5	-	-	-
<i>Pinus koraiensis</i>	3.3	0.51	6	-	-	-
<i>Sorbus alnifolia</i>	3.3	0.14	5	-	-	-
<i>Rhus trichocarpa</i>	3.3	0.03	5	-	-	-
<i>Fraxinus sieboldiana</i>	-	-	-	35.3	5.11	20
<i>Carpinus cordata</i>	-	-	-	14.1	0.67	10
<i>Tilia amurensis</i>	-	-	-	7.1	0.43	5
<i>Fraxinus mandshurica</i>	-	-	-	7.1	0.42	5
<i>Sorbus commixta</i>	-	-	-	7.1	0.35	5
<i>Cornus controversa</i>	-	-	-	7.1	0.29	5

\* The number of points with species/total number of points

Table 2. Emergence rates, sprouting rates, and basal areas of the suppressed saplings in two study stands on Mt. Jiri.

Species	Life form	L-S			H-S		
		Emergence rate <sup>†</sup> (%)	Sprouting rate <sup>‡</sup> (%)	Basal area (m <sup>2</sup> )	Emergence rate <sup>†</sup> (%)	Sprouting rate <sup>‡</sup> (%)	Basal area (m <sup>2</sup> )
<i>Styrax obassia</i>	C	22.5	0.0	3.978	1.3	100.0	0.007
<i>Acer pseudo-sieboldianum</i>	C	10.0	25.0	0.370	20.0	0.0	1.576
<i>Stewartia koreana</i>	C	7.5	16.7	0.257	1.3	0.0	0.002
<i>Magnolia sieboldii</i>	U	3.8	0.0	0.079	3.8	0.0	0.025
<i>Quercus mongolica</i>	C	2.5	0.0	0.062	16.3	7.7	2.484
<i>Cornus controversa</i>	C	1.3	0.0	0.008	1.3	0.0	0.005
<i>Rhododendron schlippenbachii</i>	U	1.3	0.0	0.003	10.0	0.0	0.176
<i>Carpinus laxiflora</i>	C	10.0	0.0	0.843	-	-	-
<i>Fraxinus rhynchophylla</i>	C	7.5	100.0	0.694	-	-	-
<i>Lindera erythrocarpa</i>	C	6.3	0.0	0.290	-	-	-
<i>Acer mono</i>	C	6.3	20.0	0.282	-	-	-
<i>Lindera obtusiloba</i>	U	6.3	0.0	0.025	-	-	-
<i>Quercus serrata</i>	C	5.0	50.0	0.356	-	-	-
<i>Prunus leveilleana</i>	C	2.5	0.0	0.030	-	-	-
<i>Meliosma myriantha</i>	U	2.5	0.0	0.010	-	-	-
<i>Zelkova serrata</i>	C	1.3	0.0	0.068	-	-	-
<i>Fraxinus mandshurica</i>	C	1.3	0.0	0.035	-	-	-
<i>Sorbus alnifolia</i>	C	1.3	0.0	0.011	-	-	-
<i>Maackia amurensis</i>	C	1.3	0.0	0.009	-	-	-
<i>Fraxinus sieboldiana</i>	C	-	-	-	25.0	10.0	2.840
<i>Carpinus cordata</i>	C	-	-	-	8.8	0.0	0.428
<i>Tilia amurensis</i>	C	-	-	-	5.0	0.0	0.153
<i>Euonymus oxyphyllus</i>	U	-	-	-	2.5	0.0	0.021
<i>Symplocos chinensis</i> forma pilosa	U	-	-	-	2.5	0.0	0.007
<i>Corylus sieboldiana</i>	U	-	-	-	1.3	0.0	0.002
<i>Rhamnus yoshinoi</i>	U	-	-	-	1.3	0.0	0.002

\* C, canopy species; U, understory species

† The number of quarters with species / total number of quarters

‡ The number of individuals with the canopy stem(s) / total number of individuals

1). The species compositions and community structures of the canopy layers differed between the two stands, although four canopy trees occurred in both stands: *Quercus mongolica*, *Styrax obassia* SIEB. et ZUCC., *Prunus leveilleana* KOEHNE and *Maackia amurensis* RUPR. et MAX. At L-S, the canopy layer was dominated by *Q. serrata*, followed by *Fraxinus rhynchophylla* HANCE and *Carpinus laxiflora* in terms of density, basal area, and absolute frequency. In contrast, *Q. mongolica* dominated the canopy layer very strongly in terms of its density, basal area, and absolute frequency at H-S. At L-S, the DBH of the canopy trees ranged from 10.3 cm (*Stewartia koreana* NAKAI) to 85.0 cm (*P. leveilleana*), with a peak at 10–20 cm (Fig. 1). Those at H-S ranged from 12.0 cm (*C. cordata* BLUME) to 46.5 cm (*Q. mongolica*) with a peak at 20–30 cm.

Among eighty suppressed saplings studied at each stand, nineteen and fourteen species occurred at L-S and H-S, respectively (Table 2). Seven species, including *Quercus mongolica* and *Acer pseudo-sieboldianum* (PAXTON) KOM., were common in both stands. Among the suppressed saplings, 65% and 36% of the species also occurred in the canopy layer at L-S and H-S, respectively. Understory species comprised

11% and 43% of the suppressed saplings at L-S and H-S, respectively.

Among the suppressed saplings, the most dominant species in terms of its emergence rate and basal area was *Styrax obassia* SIEB., followed by *Carpinus laxiflora* and *Fraxinus rhynchophylla* at L-S. *Quercus mongolica* had the largest

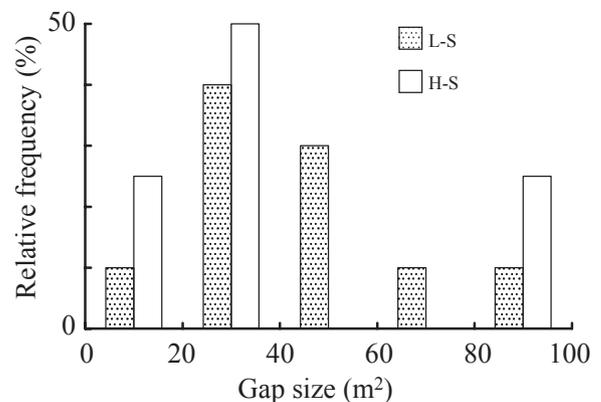


Fig. 2. Gap size distributions of canopy trees at L-S and H-S on Mt. Jiri.

Table 3. The numbers of study points and gaps for each dwarf bamboo coverage class in two study stands on Mt. Jiri.

Coverage (%) classes of dwarf bamboo	L-S		H-S	
	Point	Gap	Point	Gap
<10	24	0	0	0
<20	3	0	1	0
<30	2	0	0	1
<40	0	0	2	0
<50	1	1	5	0
<60	1	0	3	0
<70	3	0	15	0
<80	3	2	11	1
<90	18	1	23	0
≤100	25	6	20	2

Table 4. Characteristics of the canopy gaps in two study stands on Mt. Jiri.

	L-S	H-S
Gap area (%)*	6.8	2.5
Density (ha <sup>-1</sup> )	15.2	6.1
Size (m <sup>2</sup> )		
Mean	45.1	41.5
S.D.	23.6	36.1
Range (Min. –Max.)	19.2–92.3	18.1–95.1

\* Total gap area/total surveyed area

cumulative basal area at H-S, although the emergence rate was highest for *F. sieboldiana* BLUME, followed by *Acer pseudo-sieboldianum*, and *Q. mongolica*. Some suppressed saplings, such as *F. rhynchophylla* and *Q. serrata* at L-S and *S. obassia* at H-S, were sprouts of canopy trees. Dwarf bamboo covered the forest floor widely and densely, although some sites had no or little dwarf bamboo (Table 3).

Ten and four canopy gaps existed at L-S and H-S, respectively. The percentage gap area (percentage of the total gap area relative to the total survey area) and the density of the gaps differed between the two stands, although the mean gap sizes and their ranges were similar for both stands (Table 4). The canopy at H-S had relatively fewer gaps than that at L-S, although the ranges of gap size were similar for both stands. The size class distribution of the gaps indicated that gaps of 20–40 m<sup>2</sup> in area were most abundant in both stands (Fig. 2). All the gaps recorded were created by the fall of a single tree. Standing dead gap makers were most common (Table 5). Gaps

Table 5. State of death or injury of the gap makers in two study stands on Mt. Jiri.

Species	L-S				H-S			
	Standing-dead	Trunk broken	Uprooted	Unknown	Standing-dead	Trunk broken	Uprooted	Unknown
<i>Quercus mongolica</i>	4	-	-	-	-	1	1	-
<i>Quercus serrata</i>	2	-	-	-	-	-	-	-
<i>Fraxinus sieboldiana</i>	-	-	-	-	-	1	1	-
Unknown	1	2	-	1	-	-	-	-

Table 6. The numbers of successors in the gaps in two study stands on Mt. Jiri.

Species	Life form*	L-S	H-S
<i>Stewartia koreana</i>	C	3	-
<i>Styrax obassia</i>	C	2	-
<i>Carpinus laxiflora</i>	C	1	-
<i>Magnolia sieboldii</i>	C	1	-
<i>Ilex macropoda</i>	U	1	-
<i>Quercus mongolica</i>	C	1	1
<i>Acer pseudo-sieboldianum</i>	C	-	1
<i>Fraxinus sieboldiana</i>	C	-	1
<i>Rhododendron schlippenbachii</i>	U	-	1

\* C, canopy species; U, understory species

were created by only three and two species at L-S and H-S, respectively. More gaps were created by *Quercus mongolica* than by *Q. serrata*, although *Q. serrata* was more dominant in the canopy layer at L-S. Gaps created by uprooted gap makers were found at H-S.

Seven species occurred as successors in the gaps at L-S, and four species occurred as successors in the gaps at H-S (Table 6). The species compositions of the successors differed greatly among gaps and between stands. *Quercus mongolica* was the only species that occurred in both stands. *Stewartia koreana* and *Styrax obassia* grew in three and two gaps at L-S, respectively. One of the four successors at H-S was an understory tree species.

Most of the gaps studied were largely covered by dwarf bamboo (Table 3). The coverage of dwarf bamboo exceeded 70% of the gap area for nine of 10 gaps at L-S, and for three of four gaps at H-S.

## DISCUSSION

### Gap disturbance regimes

The canopy layer at L-S was dominated by *Quercus serrata*, indicating that the stand might be located in a transition zone between the warm-temperate zone and the cool-temperate zone. L-S may be slightly older than H-S, because the maximum DBH of the canopy trees is larger at L-S than at H-S. Conversely, H-S is located in the cool-temperate zone because of the extreme predominance of *Q. mongolica* in the

Table 7. Previously reported gap disturbance regimes in old-growth deciduous broad-leaved forests.

Gap area (%)*	Density of gaps (ha <sup>-1</sup> )	Size of gaps (m <sup>2</sup> )		Locality	Reference
		Mean ± S.D.	Range		
9.9	9.3	105.9 ± 82.9	33.2–323.7	Japan	YAMAMOTO (1989)
14.0	16.2	86.1 ± 61.2	13.2–264.5	Japan	YAMAMOTO (1989)
20.6	12.5	164.9 ± 153.3	27.3–728.2	Japan	YAMAMOTO (1989)
15.2	15.3	99.6 ± 55.4	22.1–228.3	Japan	YAMAMOTO (1989)
11.2	20.5	53.1 ± 33.6	10.2–166.3	Japan	YAMAMOTO (1989)
13.2	35.8	36.8 ± 24.5	5.3–130.7	Japan	YAMAMOTO (1989)
18.3	16.3	112.5 ± 77.1	20.4–339.8	Japan	YAMAMOTO (1989)
4.1	6.7	60.8 ± 52.5	7.1–276.1	Japan	YAMAMOTO (1989)
10.3	17.4	58.9 ± 39.0	13.2–162.8	Japan	YAMAMOTO (1989)
21.1	13.7	141.5 ± 94.5	39.6–380.1	Japan	YAMAMOTO (1989)
31.0	-	-	≤450	Japan	NAKASHIZUKA and NUMATA (1982)
20.5	-	137	≤470	Japan	NAKASHIZUKA (1984)
-	-	82	16–474	Japan	HARA (1985)
17.6	-	-	-	USA	VANKAT <i>et al.</i> (1975)
9.0	-	101	22–252	USA	WILLIAMSON (1975)
-	-	51	2–215	USA	BARDEN (1980)
9.5	-	31	≤1490	USA	RUNKLE (1982)

\* Percentage of total gap area to total surveyed area.

canopy layer. The stand age of H-S might be ca. 50–60 years, because the maximum DBH of the canopy trees in the stand is similar to that of a secondary *Q. mongolica* forest at a similar altitude in South Korea, which was estimated to be ca. 50 years old (DOLEZAL *et al.*, 2009).

The densities of the canopy gaps in both stands were similar to those in other old-growth deciduous broad-leaved forests in Japan (Table 7). However, the percentage gap area and the size of each gap were smaller in both stands than those in old-growth deciduous broad-leaved forests in Japan and the USA. These differences are partly attributed to the differences in the successional stages of the forests studied. In general, canopy trees growing in secondary broad-leaved forests have small crowns, indicating that the gaps created by those canopy trees are small, as reported by CLEBSCH and BUSING (1989). Indeed, the DBH of the canopy trees was relatively small, indicating that the crowns of those trees were also small in both stands.

### Gap regeneration behaviour

YAMAMOTO (1989, 1992b, 1995, 1996) analyzed the gap-phase regeneration of canopy and sub-canopy tree species by evaluating the replacement patterns of the trees in various mature forests in Japan. Four regeneration categories (i.e., canopy trees, gap makers, suppressed saplings, and gap successors) were assigned, which were also used in this study, and canopy and sub-canopy tree species were classified into following four types of regeneration behaviour. Type I species occur in all regeneration categories, indicating that the canopy trees regenerate in gaps from saplings recruited before gap formation (i.e., advanced regeneration). Type II species

lack suppressed saplings, suggesting that the species cannot establish under a closed canopy and that saplings of the species establish and/or grow within gaps. Type III species lack canopy trees and gap makers. These species are typical sub-canopy trees, which regenerate by advanced regeneration. Type IV species lack suppressed saplings and gap successors. These species cannot regenerate in the gaps formed under the current gap disturbance regimes.

Only a few species were classified as conforming to those regeneration behaviours (Tables 8 and 9): type I, *Quercus mongolica* in both stands; type III, *Lindera erythrocarpa* MAKINO and *Magnolia sieboldii* K. KOCH at L-S, and *Acer pseudo-sieboldianum* and *Rhododendron schlippenbachii* MAX. at H-S, although *M. sieboldii* and *R. schlippenbachii* were understorey species.

The gap regeneration behaviour of the major species in the stands on Mt. Jiri differed greatly from those in various old-growth forests in Japan (YAMAMOTO, 1989, 1992b, 1995, 1996), and other types of regeneration behaviour were observed on Mt. Jiri. These differences might be attributable to differences in the natural disturbance regimes and differences in the successional stages among the forests.

A different type of regeneration behaviour was observed in both stands. *Quercus serrata* had no gap successors but had suppressed saplings at L-S. Half the suppressed saplings of the species were coppice of canopy trees, suggesting that the species does not always have sapling banks beneath the closed canopy within the current gap disturbance regime. The species, therefore, might be similar to species classified as type IV. Many species, such as *Alnus hirsuta* TURCZ. var. *sibirica* (SPACH)

Table 8. Densities ( $\text{ha}^{-1}$ ) of canopy trees (CT), gap makers (GM), suppressed saplings (SS), and gap successors (GS) at L-S on Mt. Jiri.

Species	Life form *	CT	GM	SS	GS
<i>Quercus mongolica</i>	C	16.5	6.7	3.3	1.7
<i>Quercus serrata</i>	C	64.9	3.3	6.7	-
<i>Styrax obassia</i>	C	13.2	-	30.0	3.3
<i>Carpinus laxiflora</i>	C	33.1	-	13.3	1.7
<i>Stewartia koreana</i>	C	16.5	-	10.0	5.0
<i>Prunus leveilleana</i>	C	6.6	-	3.3	-
<i>Maackia amurensis</i>	C	3.3	-	1.7	-
<i>Fraxinus rhynchophylla</i>	C	46.3	-	10.0	-
<i>Quercus variabilis</i>	C	13.2	-	3.3	-
<i>Acer mono</i>	C	16.5	-	8.3	-
<i>Acer pseudo-sieboldianum</i>	C	6.6	-	13.3	-
<i>Sorbus alnifolia</i>	C	3.3	-	1.7	-
<i>Alnus hirsuta</i> var. <i>sibirica</i>	C	6.6	-	-	-
<i>Rhus trichocarpa</i>	C	3.3	-	-	-
<i>Quercus acutissima</i>	C	3.3	-	-	-
<i>Carpinus tschonoskii</i>	C	3.3	-	-	-
<i>Pinus koraiensis</i>	C	3.3	-	-	-
<i>Lindera erythrocarpa</i>	C	-	-	8.3	1.7
<i>Magnolia sieboldii</i>	U	-	-	5.0	3.3
<i>Meliosma myriantha</i>	U	-	-	3.3	-
<i>Fraxinus mandshurica</i>	C	-	-	1.7	-
<i>Zelkova serrata</i>	C	-	-	1.7	-
<i>Cornus controversa</i>	C	-	-	1.7	-
<i>Rhododendron schlippenbachii</i>	U	-	-	1.7	-
<i>Lindera obtusiloba</i>	U	-	-	8.3	-
<i>Ilex macropoda</i>	U	-	-	-	1.7
Unknown	-	-	6.7	-	-

\* C, canopy species; U, understory species

Table 9. Densities ( $\text{ha}^{-1}$ ) of canopy trees (CT), gap makers (GM), suppressed saplings (SS), and gap successors (GS) at H-S on Mt. Jiri.

Species	Life form *	CT	GM	SS	GS
<i>Quercus mongolica</i>	C	465.7	3.3	21.7	1.7
<i>Styrax obassia</i>	C	7.1	-	1.7	-
<i>Prunus leveilleana</i>	C	7.1	-	-	-
<i>Maackia amurensis</i>	C	7.1	-	-	-
<i>Fraxinus sieboldiana</i>	C	-	3.3	33.3	1.7
<i>Acer pseudo-sieboldianum</i>	C	-	-	26.7	1.7
<i>Rhododendron schlippenbachii</i>	U	-	-	13.3	1.7
<i>Carpinus cordata</i>	C	-	-	11.7	-
<i>Tilia amurensis</i>	C	-	-	6.7	-
<i>Cornus controversa</i>	C	-	-	1.7	-
<i>Stewartia koreana</i>	C	-	-	1.7	-
<i>Magnolia sieboldii</i>	U	-	-	5.0	-
<i>Euonymus oxyphyllus</i>	U	-	-	3.3	-
<i>Symplocos chinensis</i> forma <i>pilosa</i>	U	-	-	3.3	-
<i>Corylus sieboldiana</i>	U	-	-	1.7	-
<i>Rhamnus yoshinoi</i>	U	-	-	1.7	-

\* C, canopy species; U, understory species

SCHNEID. and *Rhus trichocarpa* MIQ. at L-S and *Styrax obassia* and *Prunus leveilleana* at H-S, occurred only as canopy trees. These species might not be large enough to reach the canopy layer, and might therefore lack gap makers. Furthermore, these species do not regenerate in the forests under the current gap disturbance regime, although they maintain their populations for a while as canopy and/or sub-canopy trees. Therefore, these species and *Q. serrata* will decline over time in the stands, suggesting that those species are major components of secondary forests.

Another gap regeneration behaviour observed in both stands involved species represented only by suppressed saplings, such as *Fraxinus mandshurica* RUPR. and *Cornus controversa* HEMSLEY at L-S and *Carpinus cordata* and *Tilia amurensis* RUPR. at H-S. These species are major components of old-growth forests in the region and might be more shade tolerant than *Quercus serrata* and *Q. mongolica* (DOLEZAL *et al.*, 2009). These species might not be large enough to reach the canopy layer but might maintain sapling banks beneath the closed canopy, suggesting that the species might become major components of the stands.

DOLEZAL *et al.* (2009) investigated the patterns of regrowth of major trees in a ca. 50-year-old post-logging *Quercus mongolica*-dominated forest in South Korea, which was in a similar successional stage to that at H-S, and predicted that the stand would become increasingly dominated by shade-tolerant species such as *Tilia amurensis*, *Acer pseudo-sieboldianum* and *Fraxinus rhynchophylla*, and that *Q. mongolica* would decline over time. At H-S, *Q. mongolica* had saplings beneath the closed canopy and the gaps, suggesting that this species may not decline for a while. However, some shade-tolerant species, such as *F. rhynchophylla* and *A. pseudo-sieboldianum*, had many suppressed saplings and gap successors. Therefore, these shade-tolerant species should become major canopy components in the stand for a long time, as in the forest studied by DOLEZAL *et al.* (2009).

#### Effects of canopy gaps on secondary succession

For both the stands studied, only a few canopy and/or sub-canopy species had gap successors. Therefore, the canopy gaps in the stands played less important roles in the gap regeneration of the component species of the stands, although a few species (such as *Styrax obassia* at L-S and *Acer pseudo-sieboldianum* at H-S) could regenerate both beneath the closed canopy and in the gaps. The dense cover of dwarf bamboo on the forest floor is thought to be one possible reason that the gaps had little effect on the regeneration of many tree species in the stands, as has been reported for old-growth cool-temperate and sub-alpine forests (FRANKLIN *et al.*, 1979; HIURA *et al.*, 1996; TAKAHASHI, 1997) and a secondary deciduous broad-leaved forest (YAMAMOTO and NISHIMURA, 1995). Therefore, the canopy gaps in both stands might have little effect on the secondary

succession under the current gap disturbance regime. However, the simultaneous death of all the dwarf bamboo might change the role of the gaps in the secondary succession, as seen in old-growth forests (NAKASHIZUKA, 1988).

In a ca. 80-year-old secondary evergreen broad-leaved forest in Japan, infrequent severe typhoons changed the gap disturbance regime and accelerated the secondary succession of the forest (YAMAMOTO and MANABE, 1997). The natural disturbance regimes must be evaluated over long periods to clarify the gap dynamics of these stands, which are at a relatively early secondary successional stage.

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