

Comparison of Tree Regeneration between Soil-disturbed and Soil-intact Sites in Canopy Gaps of an Evergreen Broad-leaved (*Castanopsis sieboldii* ssp. *lutchuensis*) Forest on Amami Ohshima Island, South-west Japan

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Abstract The forest floor vegetation and the occurrence of tree seedlings were compared among three micro-sites in a *Castanopsis sieboldii* ssp. *lutchuensis* forest, on Amami Ohshima Island, South-west Japan: soil-disturbed sites in canopy gaps (D-site); soil-intact sites in canopy gaps (I-site); soil-intact sites under closed canopy (C-site). The occurrence of seedlings was concentrated to soil-intact sites in gaps. Seedlings of various size were found in the soil-intact sites in gaps, suggesting the inclusion of both advanced-growth seedlings before gap formation and newly established seedlings after gap formation. On the other hand, on soil-disturbed sites in gaps, the size structure of seedlings was skewed to the smallest class, suggesting that only the newly established seedlings were included. Based on the occurrence pattern of seedlings among micro-sites, species were grouped into four species groups: Group A with seedlings in all micro-sites; Group CI with seedlings in C- and I-sites, but scarce in D-sites; Group I with seedlings mainly in I-sites; Group DI with seedlings in both type of micro-site in gaps (D- and I-sites). The regeneration strategy of each species group is discussed.

Key words: *Castanopsis sieboldii* ssp. *lutchuensis* forest, canopy gap, soil-disturbed sites, soil-intact sites, closed stand, seedlings.

Canopy gaps play an important role in the regeneration process of climax forests. The enhanced light conditions in the canopy gaps enable seed germination and rapid growth of many seedlings and saplings on the forest floor (Naka, 1982; Yamamoto, 1992). Gaps of different size and shape are utilized for regeneration by different species (Runkle, 1982, 1984). Gaps are one of key factors for understanding the co-existence of component species within a climax forest (Denslow, 1980; Runkle, 1984; Brokaw, 1985; Veblen, 1992).

The micro-environment also considerably varies from site to site within a gap (Bazzaz and Pickett, 1980; Veblen, 1992). The light intensity is stronger, supply of rainfall on the soil surface and fluctuation of soil temperature is larger, and soil moisture is smaller in the center of a gap than its edge (Longman and Jenik, 1974; Nakashizuka, 1985; Canham *et al.*, 1990). Decaying foliage of crowns and

logs of fallen trees may create micro-sites of different nutrients levels, which affect plant growth on the forest floor (Uhl *et al.*, 1988). In particular, the uprooted stumps of gap-maker trees disturb the soil surface severely and also make a pit and a mound of the soil surface, which further increases the heterogeneity of micro-environment on the forest floor (Nakashizuka, 1989; Peterson *et al.*, 1990).

Thus, such differences in micro-sites in canopy gaps may cause regeneration of various species and may be important for the co-existence of component species of forests. However, the relationships between differences in micro-sites and regeneration strategies of component species have received only a few studies in the case of Japanese evergreen broad-leaved forest (e.g. Yamamoto, 1992; Yamashita, 1994; Tanouchi *et al.*, 1994). The aim of this study was to examine the

regeneration strategy of component species of evergreen broad-leaved forest, by comparing the density and the size structure of seedlings among three different micro-sites on the forest floor: soil-disturbed sites in gaps; soil-intact sites in gaps; soil-intact sites under the closed canopy.

Study Area and Methods

The field survey was conducted on February 1993, at Kinsaku-baru National Forest, Amami Ohshima Island, South-west Japan (Fig. 1). Based on data from a meteorological station (3m a.s.l.) at Naze from 1977 to 1992, the mean annual temperature is 21.5°C, with 28.7°C the mean for the warmest month, August, and with 14.6°C the mean for the coldest month, January. The mean annual precipitation is 2835 mm/year. There is usually a high rainfall in June, August and September, and low rainfall in December, though with considerable variation among years.

The study area (ca. 300 m a.s.l.) is covered with a natural evergreen broad-leaved forest

dominated by *Castanopsis sieboldii* (Makino) Hatsusima ex Yamazaki et Mashiba ssp. *lutchuensis* (Koidz.) H. Ohba. Also, *Schima wallichii* (DC.) Korthals and *Distylium racemosum* Sieb. et Zucc. are common in the canopy, and *Myrsine seguinii* Lév., *Syzygium buxifolium* Hook. et Arn., *Ternstroemia gymnanthera* (Wright et Arn.) Beddome and *Podocarpus macrophyllus* (Thunb.) D. Don are abundant in the understorey (Hara *et al.*, 1996).

Many newly formed gaps were found in the forest, when the study was made in February 1993. The enumeration of bud scars of sprouting stems of leaning, but live, trees in the canopy gaps, indicated that many of these gaps had been created about two growing years before the survey. In September 1990, a very large and strong typhoon (Typhoon No. 19) passed through near the island and seriously disturbed forests in this region. Thus, it is very probable that these newly formed gaps were created by this typhoon. Most gap-maker trees were *Castanopsis sieboldii* ssp. *lutchuensis*, whose diameter at breast height ranged from 30 to 50 cm. There were many gaps over 200 m². Most gaps were accompanied by uprootings of gap-maker trees.

In order to compare the floristic composition of seedlings (defined in this study as individuals shorter than 2.0 m) between gaps and closed stand, or between soil-disturbed sites and soil-intact sites in gaps, thirteen plots were settled on the forest floor; four plots on soil-intact sites in gaps (I-site), five on soil-disturbed sites in gaps (D-site), and four on soil-intact sites under closed canopy (C-site). All plots on D-sites were settled on shallow pits in canopy gaps, where the pre-existing surface soil had been almost completely removed by the uprootings of gap-maker trees. Plot size was 4 m² except for one (4.5 m²) of the D-sites. In each plot, seedlings were counted according to the six height classes; seedlings shorter than 5 cm, 5–10 cm, 10–30 cm, 30–50 cm, 50–100 cm, 100–200 cm. The shoots of surrounding, larger trees were not included. The coverage of all species including herbs was also recorded for each plot according to Braun-Branquet's scale (1964).

The significance of the concentration of

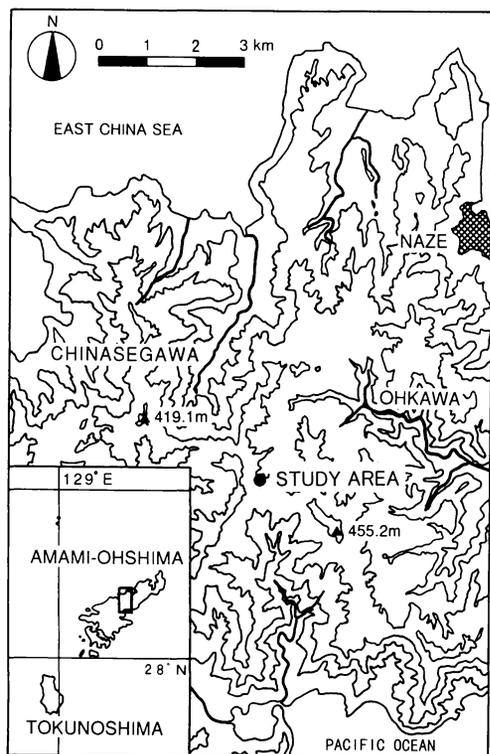


Fig. 1. Location of study area. Contours are drawn at 100-m intervals.

seedlings to a particular micro-site (C-, I-, and D-site) was tested by binomial test. The expected number of seedlings in each of the particular micro-sites and the other remaining micro-sites was calculated as the total number of seedlings multiplied by the proportional area of the micro-site and the other micro-sites, respectively. The expected numbers were compared with the actual number of seedlings occurring in a particular micro-site. The test was done with an original basic program made with reference to Sokal and Rohlf (1981).

Results

1. Floristic composition

The total coverage of the herb layer (< 2 m in height) in all I-sites reached 60%, which was considerably higher than values in the other micro-sites (Table 1); these values were 20% or less in C-sites, and rang from 15% to 50% in D-sites.

Species richness was highest in I-sites (Table 1). Among many species found in

I-sites, the largest coverage were shown by trees such as *Castanopsis sieboldii* ssp. *lutchuensis*, *Myrsine seguinii* and *Syzygium buxifolium*, and a vine, *Psychotria serpens*. These species also occurred in C-sites, but their coverage was lower there, except for *Castanopsis sieboldii* ssp. *lutchuensis*, the coverage of which was almost equal in C-sites to that in I-sites.

Species richness was lowest in D-sites. Two trees, *Syzygium buxifolium* and *Schima wallichii*, and two ferns, *Dicranopteris linearis* (Burm. fil.) Underw and *Plagiogyria adnata* (Bl.) Bedd. showed the highest coverage. *Schima wallichii* and these two ferns were also found in the other micro-sites, but their coverage was lower.

2. Seedling occurrence and density of woody species

Trees and shrub species, the total number of seedlings of which was more than six, were grouped into four species-groups based on the occurrence patterns among micro-

Table 1. Vegetation coverage of herb layer (below 2 m in height) in each plot. The coverage for each species is presented as the coverage class of Brown-Branquet (1964). Species which reached a coverage class of 1 or more in at least one plot are shown.

MICRO-SITE PLOT NO	C				I				D				
	1	8	9	10	4	13	6	11	2	5	12	7	3
PLOT AREA (m ²)	4	4	4	4	4	4	4	4	4	4	5	4	4
INCLINATION (°)	20	20	5	0	15	15	10	10	20	10	5	0	20
SLOPE DIRECTION	S75° E	S20° E	S20° E	—	W	N35° W	N25° W	N25° W	S5° W	N25° W	N40° W	—	S5° W
TOTAL COVERAGE (%)	3	20	20	5	60	60	60	60	50	30	15	40	20
SPECIES RICHNESS	15	13	16	13	15	37	32	29	8	11	14	21	9
Tree and Shrub													
<i>Castanopsis sieboldii</i>													
ssp. <i>lutchuensis</i>	1	1	2	1	2		1	2	+				+
<i>Distylium racemosum</i>	+		+	+	2	1	2					+	
<i>Podocarpus macrophyllus</i>	+							1					
<i>Symplocos prunifolia</i>	+	+		+		1	1	2				+	
<i>Neolitsea aciculata</i>	+				1	1		+					
<i>Schima wallichii</i>	+				1	1	+	1	2	2	2	2	2
<i>Symplocos confusa</i>			+		+	+	1	1		+	+	1	
<i>Syzygium buxifolium</i>	1	2	1	1	2	2	2	2	1	1	1	3	+
<i>Cinnamomum doederleinii</i>	+		+			+		1					
<i>Symplocos microcalyx</i>				+		+	1						
<i>Diospyros morrisiana</i>	+			1		+	1	1			+		
<i>Myrsine seguinii</i>	+	1	1	1	3	2	2	2					1
<i>Antidesma japonicum</i>		+	+		+	+	+	1		+			+
<i>Rhaphiolepis indica</i>													
var. <i>umbellata</i>		+	+					1	+				
<i>Illicium anisatum</i>		+			+		2	2					+
<i>Cleyera japonica</i>						1							
<i>Randia canthioides</i>					+	+	+	1					+
<i>Psychotria rubra</i>						+	1	+					
<i>Ilex maximowicziana</i>													
var. <i>kanehirae</i>						1		+					+
Vine													
<i>Psychotria serpens</i>	+	+	+	1	2	2	3	1					1
Herb													
<i>Sarcandra glabra</i>							1	+					
Fern													
<i>Lindsaea chieni</i>	+	+	+	+	+	+	+	2					
<i>Dicranopteris linearis</i>						+	+		2	1	1		1
<i>Plagiogyria adnata</i>						+			3	+	2		+

sites (Table 2): (1) Group A, whose seedlings were found in all micro-sites (*Syzygium buxifolium* etc.); (2) Group CI, whose seedlings were found in C- and I-sites, but scarce in D-sites (*Castanopsis sieboldii* ssp. *lutchuensis* etc.); (3) Group I, whose seedlings occurred mainly in I-sites (*Symplocos prunifolia* etc.); (4) Group DI, whose seedlings were found in both micro-sites in gaps (I- and D-sites), but were almost absent in C-sites (*Symplocos confusa*, *Schima wallichii*, etc.).

Total density of seedlings was lowest in C-sites and highest in I-sites. The variation in density among plots within the micro-site was largest in D-sites (Table 2). In addition to eight species of Group I, three species of Group CI (*Diospyros morrisiana*, *Illicium anisatum* and *Myrsine seguinii*) and three species of Group DI (*Glochidion acuminatum*, *Symplocos prunifolia* and *Ilex lukiensis*) showed significantly higher densities in I-sites (Table 2; binomial test, $P < 0.05$).

On the other hand, only *Schima wallichii*

showed a significantly higher density in D-sites. Although their difference was statistically nonsignificant, seedlings of *Syzygium buxifolium* were also relatively abundant there. These two species comprised about 90% of the total number of seedlings in D-sites.

3. Frequency distribution of seedlings in height class

As shown in Fig. 2, height class distribution clearly differed among micro-sites. In C-sites, seedlings taller than 30 cm were rare and the largest number of seedlings occurred in the class of 5–10 cm. In I-sites, seedlings higher than 30 cm were more abundant than in C-sites, and there was a peak in the 10–30 cm class. On the other hand, in D-sites, the number of seedlings in the smallest class (0–5 cm) was the largest and considerably larger than values in the same class in C- and I-sites. However, it decreased rapidly as the height increased and seedlings taller than 50 cm

Table 2. Numbers of seedlings occurring in each plot. Species having more than six seedlings in total are shown. Abbreviations in bias column represent micro-site where seedlings are biased (binomial test; $P < 0.05$). Species were grouped into four (group C, CI, I and DI) based on the pattern of occurrence.

MICRO-SITE PLOT NO PLOT AREA(m ²) SEEDLING DENSITY (/m ²)	C					I					D					BIAS	
	1	8	9	10	MEAN	4	13	6	11	MEAN	2	5	12	7	3		MEAN
	10.8	17.8	14.3	13.8	-	17	24.0	23.3	36.8	-	12.8	10.8	19.8	45.8	17.8	-	
Group C																	
<i>Syzygium buxifolium</i>	14	30	22	10	19.0	18	19	7	23	16.8	25	11	28	26	2	18.4	
<i>Daphniphyllum teijsmannii</i>	3		1	1	1.3		3	2		1.3			4	2		1.2	
<i>Antidesma japonicum</i>		4	3		1.8	1	1	2	4	2.0		1		2		0.6	
Group CI																	
<i>Castanopsis sieboldii</i> ssp. <i>lutchuensis</i>	11	15	14	24	16.0	4	8	5	4.3	1				1	0.4	C	
<i>Podocarpus nagi</i>		1	4	2	1.8		1	2		0.8						0.0	C
<i>Diospyros morrisiana</i>	4			7	2.8		2	2	10	3.5			1			0.2	I
<i>Illicium anisatum</i>		5			1.3	2		9	15	6.5				4		0.8	I
<i>Myrsine seguinii</i>	1	12	5	7	6.3	24	14	19	13	17.5				9		1.8	I
Group I																	
<i>Distylium racemosum</i>	1		1	1	0.8	4	3	6		3.3			1			0.2	I
<i>Neolitsea aciculata</i>	1				0.3	3	4		1	2.0						0.0	I
<i>Symplocos prunifolia</i>	1	1		1	0.8		3	6	11	5.0			2			0.4	I
<i>Rhaphiolepis indica</i> var. <i>umbellata</i>			1	1	0.5				10	2.5	1					0.2	I
<i>Randia canthioides</i>					0.0	1	5	1	2	2.3				1		0.2	I
<i>Camellia sasanqua</i>					0.0				6	1.5				1		0.2	I
<i>Rhus saccadanea</i>					0.0		2	5	1.8							0.0	I
<i>Ilex maximowicziana</i> var. <i>kanehirae</i>					0.0					0.0						0.0	
					0.0	1	5	1.5					1			0.2	I
Group DI																	
<i>Glochidion acuminatum</i>					0.0	1	5	3		2.3			2	1		0.6	I
<i>Symplocos confusa</i>			1		0.3	2	4	5	6	4.3		1	4	9		2.8	I
<i>Ilex lukiensis</i>					0.0	1	5	1	5	3.0		1	2	2		1.0	I
<i>Tricalysia dubia</i>					0.0		3	1	1	1.3				3		0.6	
<i>Eurya japonica</i>					0.0		4			1.0			2	1		0.6	
<i>Schima wallichii</i>	1				0.3	7	7	4	17	8.8	24	27	47	113	67	55.6	D

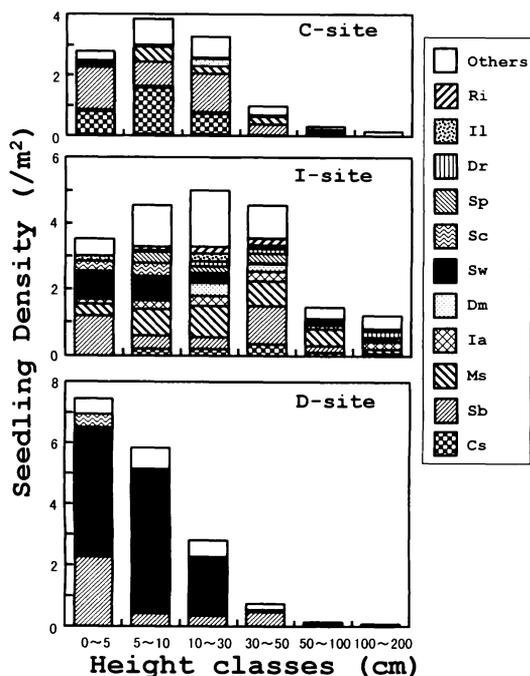


Fig. 2. Frequency distribution of tree and shrub seedlings in height classes for each micro-site. Cs, *Castanopsis sieboldii* ssp. *lutchuensis*; Sb, *Syzygium buxifolium*; Ms, *Myrsine seguinii*; Ia, *Illicium anisatum*; Dm, *Diospyros morrisiana*; Sw, *Schima wallichii*; Sc, *Symplocos confusa*; Sp, *Symplocos prunifolia*; Dr, *Distylium racemosum*; Il, *Ilex liukiensis*; Ri, *Raphiolepis indica* var. *umbellata*. Note: the intervals are different among the classes.

were quite rare.

The species composition of seedlings in each height class also differed among micro-sites. In C-sites, seedlings of *Castanopsis sieboldii* ssp. *lutchuensis*, *Syzygium buxifolium*, and *Myrsine seguinii* were abundant, particularly in the classes lower than 30 cm. In I-sites, seedlings of *Syzygium buxifolium* and *Myrsine seguinii* occurred in almost all classes. In addition, seedlings of *Schima wallichii* and *Symplocos confusa* Brand were abundant in the classes lower than 10 cm, and various species such as *Castanopsis sieboldii* ssp. *lutchuensis*, *Diospyros morrisiana* Hance etc. were included in the classes taller than 10 cm. In D-sites, every height class was dominated by only *Schima wallichii* and *Syzygium buxifolium*.

Discussion

This study reveals that the floristic composition of the under storey vegetation and the density of seedlings of each component species changes markedly when a canopy gap is made in evergreen broad-leaved forest on Amami Ohshima Island. Among the three type of micro-sites recognized in this study, soil-intact sites in gaps (I-site) seems to be the most important for the regeneration of many species, this being suggested by the highest species richness of seedlings and the highest density of seedlings of many species (Table 2). The largest variation in seedling size in I-sites (Fig. 2) also suggests that there are both new individuals which are established after gap formation and advanced-growth of seedlings present before gap formation. However enhanced light conditions there caused not only the rapid growth of seedlings, but also an increase in the coverage of the other plants in the herb layer. Increased coverage of herb layer (Table 1) may sometimes prevent the establishment and growth of seedlings appearing after gap formation, especially in the case of *Schima wallichii* and *Symplocos confusa* (Table 2). These species are recruited well in soil-disturbed sites in gaps (D-site), as suggested by the high density of seedlings. The height class distribution of seedlings in D-sites, which was strongly skewed to the lower height class, suggests that new seedlings were recruited abundantly after gap formation.

The different patterns of occurrence of seedlings among micro-sites (Table 2) corresponds with the differences in regeneration strategy (Grubb, 1977) of each species. Species of Group I, whose seedlings were found only in the soil-intact sites in gaps (I-site), might have a seed bank on the forest floor. The scarce occurrence of seedlings of these species in the closed stands (C-site), indicates that there was no seedling-bank before gap formation. Moreover, the scarce occurrence of seedlings in soil-disturbed sites in gaps (D-site), where most of the advanced-growth seedlings and the seed bank in the soil had been removed with the surface soil when the canopy gaps were formed, indicates that their seedlings were also rarely recruited

from seeds dispersed after gap formation. It is known that *Symplocos prunifolia*, which belongs to Group I in this study, has a seed-bank (Naka and Yoda, 1984).

Seedlings of Group DI such as *Schima wallichii* and *Symplocos confusa* were probably recruited from dispersed seeds after gap formation. The relatively abundant seedlings of *Schima wallichii* in D-sites suggest that abundant seeds were dispersed into the sites after gap formation and many seedlings then appeared. A high ability for seed dispersal of the species has been suggested (Ohsawa and Ohtsuka, 1989). This species dominates in successional forests in South-west Japan (Shimizu *et al.*, 1988; Ohsawa and Ohtsuka, 1989).

Seedlings of Group CI such as *Castanopsis sieboldii* ssp. *lutchuensis* and *Myrsine seguinii* occurred on soil-intact sites in closed stands and in gaps. Because seedlings were found abundantly in closed stands (C-site), these species have a seedling-bank on the forest floor. Among species of this group, *Castanopsis sieboldii* ssp. *lutchuensis* and *Diospyros morrisiana* had only taller seedlings in gaps (Fig. 2). These were probably advanced-growth seedlings before the formation of gaps. It is known that acorns of *Castanopsis* species are short-lived in soil (Tagawa, 1974; Naka and Yoda, 1984), but that they form a seedling-bank under closed canopy (Yamashita, 1994). On the other hand, *Myrsine seguinii* and *Illicium anisatum* also had many shorter seedlings in gaps (Fig. 2). Thus, it is suggested that these species may be recruited not only from a seedling-bank but also from a seed bank.

Finally, seedlings of Group A such as *Syzygium buxifolium* and *Daphniphyllum teijmannii* were abundant in all micro-sites (Table 2). The fact that seedlings in closed stands (C-site) were shorter (Fig. 3) suggests that seeds of these species were dispersed widely, and that the seedlings were continuously recruited and also established under closed canopy.

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奄美大島オキナワジイ林のギャップにおける 土壌攪乱と木本性実生の更新

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奄美大島のオキナワジイ林における木本性実生の種構成とサイズ構成を、閉鎖林冠の下 (C-site)、ギャップ内で土壌攪乱を受けた部分 (D-site) 及び同じくギャップ内で土壌の攪乱を受けなかった部分 (I-site) の3立地間で比較した。ほとんどの種の実生は、ギャップ内の土壌攪乱のない部分で出現頻度、密度ともに最も高い値を示した。I-site では、高さのばらつきが大きいことから、実生集団はギャップ形成以前に実生バンクとして生育していた個体と、ギャップ形成後に新たに成立した個体から構成されていることが推測された。一方、D-site では、ほとんどの実生の高さが低く、これらの実生は、ギャップ形成後に新たに侵入・定着したと推測された。各立地間の出現パターンの違いによって、各種は、すべての場所に頻繁に出現した種群 (グループ A)、C-site と I-site に出現し D-site にほとんど出現しなかった種群 (グループ CI)、D-site と I-site に出現し C-site にほとんど出現しなかった種群 (グループ DI)、I-site にのみ高頻度で出現する種群 (グループ I) の4グループに区分された。各グループの更新戦略の違いを論じた。