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Effects of canopy conditions on the regeneration of major tree species in an old-growth *Chamaecyparis obtusa* forest in central Japan

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Abstract

The regeneration mode of major tree species (*Chamaecyparis obtusa* (Sieb. et Zucc.) Endl., *Thujopsis dolabrata* Sieb. et Zucc., *Chamaecyparis pisifera* (Sieb. et Zucc.) Endl., *Quercus mongolica* Fischer ex Turcz., *Magnolia obovata* Thunb. and *Betula grossa* Sieb. et Zucc.) in relation to four canopy conditions (closed evergreen conifer canopy, closed evergreen conifer canopy adjacent to canopy gap (gap-adjacent), canopy gap, and closed deciduous broad-leaved tree (DBL) species canopy) was studied from 1988 to 1998 in a 4-ha permanent plot in the Akasawa Forest Reserve, central Japan. The vertical distribution of stems and the major species composition in four height (canopy; ≥25 m tall overtopping neighboring trees, subcanopy; ≥25 m tall, middle; ≥10 m tall, and understory; <10 m tall) classes varied with canopy condition. The understory and middle layers were generally dominated by *T. dolabrata*, but this species in the subcanopy layer existed only under gap-adjacent. Canopy gaps were usually filled by DBL tree species, especially *M. obovata* and less often by *T. dolabrata*, while the probability that they were filled by *Chamaecyparis* sp. increased in larger gaps. *C. obtusa* and *C. pisifera* occurred more often under closed DBL canopy, *T. dolabrata* under gap-adjacent canopy, and *Q. mongolica*, *M. obovata* and *B. grossa* under canopy gaps. The mortality and recruitment rates of understory stems of major tree species also varied with canopy condition. Most mortality resulted from suppression with standing-dead and natural disturbances with broken trunks, although the relative importance varied with canopy condition and species. Generally, evergreen conifers died as a result of natural disturbances, especially in the 1998 frost disturbance under canopy conditions other than closed evergreen conifer canopy. In conclusion, canopy conditions affect the vertical population structure, demographic parameters, and causes of tree mortality of major tree species. Of the favored regeneration sites in this old-growth *C. obtusa* forest, *C. obtusa* and *C. pisifera* generally may regenerate under closed DBL canopy, *T. dolabrata* under gap-adjacent canopy, and *Q. mongolica*, *M. obovata*, and *B. grossa* under canopy gaps. Consequently, this semi-natural old-growth *C. obtusa* forest will gradually change into a more diverse forest.

Keywords: *Chamaecyparis pisifera*; *Thujopsis dolabrata*; Gap; Disturbance; Species composition; *Magnolia obovata*

1. Introduction

Extensive areas of *Chamaecyparis* (tall evergreen conifers) forest occur in the temperate montane zone of the Pacific coast of central Japan (Maeda, 1951;

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Maeda and Yoshioka, 1952). Kiso district is in the center of the area where many old-growth (>300 years) and highly stocked stands are found. Although the dominant tree species in this forest is *Chamaecyparis obtusa* (Sieb. et Zucc.) Endl. (Hinoki cypress), *C. pisifera* (Sieb. et Zucc.) Endl. (Sawara cypress), *Sciadopitys verticillata* (Thunb.) Sieb. et Zucc. (umbrella pine), *Thuja standishii* (Gold.) Carriere (Japanese arbor-vitae), and *Thujopsis dolabrata* Sieb. et Zucc. (Hiba arbor-vitae) often occur, and these species are usually called the "five Kiso trees".

In the Kiso district, Akasawa Forest Reserve is an excellent example of a *C. obtusa* forest. Presently, the understory of many old-growth *C. obtusa* stands in this reserve is strongly dominated by *T. dolabrata* saplings; there is very little regeneration of *C. obtusa* (NRFO, 1985; Yamamoto, 1993a; Yamamoto and Suto, 1994). It is expected that if the present situation continues, *C. obtusa* will disappear and the stands will become dominated by *T. dolabrata* (NRFO, 1985; Yamamoto, 1993a). *C. obtusa* timber is much more valuable than that of *T. dolabrata*, so the economic value of this forest reserve will decrease seriously.

Therefore, we began a study of the dynamics of an old-growth *C. obtusa* forest with a *T. dolabrata* understory within the reserve, using a 4-ha permanent plot established in 1988. In these study (Hoshino et al., 2001, 2002), we determined that the dominance of *C. obtusa* in the canopy layer persists for much longer; the increase in *T. dolabrata* is inhibited by frost disturbances, while that of deciduous broad-leaved tree species is promoted by minor disturbances, if a major disturbance does not occur. This old-growth forest has still not reached equilibrium (Hoshino et al., 2001, 2002), as many old-growth forests do so. Thus, this forest will change according to the regeneration mode of each constituent species. However, we have not yet clarified and evaluated the regeneration mode of all of the major tree species that strongly affect the dynamics of this forest. Forest gap studies have revealed that not a few shade-intolerant species occur in old-growth forests that are dominated by shade-tolerant species, due to canopy gap formation (see review of Yamamoto, 2000).

Forest canopy structure is very heterogeneous, and includes closed evergreen and deciduous canopies and canopy gaps. This heterogeneity affects forest regeneration dynamics (Kato and Yamamoto, 2000, 2001). For example, canopy gaps allow the component tree species an important opportunity for regeneration (e.g. Runkle, 1982; Denslow, 1987; Yamamoto, 2000). In addition, the crowns of deciduous canopy trees affect the structure and dynamics of the understory sapling bank (Kato and Yamamoto, 2000, 2001). Therefore, to clarify the favored regeneration sites for tree species, it is important to study the effects of canopy conditions on the vertical population structure, demographic parameters, and census of mortality of them. However, such studies have not been conducted, especially using large-plot and long-term data.

The main objective of this study was to examine the effects of canopy condition on the regeneration mode of major tree species in an old-growth *C. obtusa* forest in the Akasawa Forest Reserve, central Japan. The specific objectives were: (1) to clarify the vertical population structure, demographic parameters, and causes of tree mortality of the major tree species (evergreen conifers such as *C. obtusa*, *C. pisifera* and *T. dolabrata* and deciduous broad-leaved tree (DBL) species such as *Quercus mongolica* Fischer ex Turcz., *Magnolia obovata* Thunb. and *Betula grossa* Sieb. et Zucc.) in relation to canopy condition (closed evergreen conifer canopy, adjacent to a gap, canopy gap, and closed DBL canopy) and (2) to estimate potential successors in canopy gaps, using the data obtained in the 4-ha plot over 10 years. We focused on the regeneration of *C. obtusa*, the current dominant species in the canopy layer of this old-growth forest.

2. Study area

The Akasawa Forest Reserve is located in Agematsu-cho, in the Kiso district of Nagano Prefecture, central Honshu, Japan (1046 ha; 35°43′57″N, 137°37′50″E). The altitude ranges from 1080 to 1558 m a.s.l. Annual precipitation is about 2500 mm and snow accumulation is 50–100 cm per year. The average annual temperature is 7.8 °C at an elevation of 1113 m. The mean monthly maximum temperature is in August (14.3 °C) and the mean monthly minimum is in February (−11.8 °C). The reserve is on an elevated peneplain with a gentle slope. The geology is dominated by acidic igneous rocks, such as granitite, granite porphyry, and rhyolite. The soils are mainly dry and wet podzolic soils, although brown forest soils occur on hillsides and along mountain streams (NRFO, 1985).

Occasional strong typhoons are a major natural disturbance. In 1959, the Isewan Typhoon severely disturbed the forests in the reserve. In early 1998, the sudden freezing of rain on leaf surfaces in the canopy and understory trees in a winter ice storm broke and uprooted trunks (Hoshino et al., 2002), we call it as ''frost disturbance.''

C. obtusa generally dominates the overstory within the reserve, with occasional *T. dolabrata*, *T. standishii*, *Pinus parviflora* Sieb. et Zucc., and DBL species, while *C. pisifera* frequently occurs on lower slopes or along mountain streams, and dominates some stands. The understory in most *C. obtusa* stands is characterized by a dense coverage of *T. dolabrata* saplings and in some stands by deciduous broad-leaved shrubs; there is very little regeneration of *C. obtusa*. The vegetation represents the *Disanthus cercidifolius* Maxim. *C. obtusa* association (Yokouchi, 1970; Miyawaki and Okuda, 1990). The typical canopy height of the old-growth stands is 25–30 m.

3. Methods

A 4-ha (200 m × 200 m) permanent plot was established on a gentle slope covered by the most developed canopy within the reserve. The stand on the site was well preserved. A map of the stems of all trees and shrubs ≥5.0 cm in diameter at breast height (dbh) in the plot was made in 1988, and each was identified by species and whether live or dead. Stems were mapped to the nearest 0.1 m, tagged, and measured to the nearest 0.1 cm dbh.

In 1993, each stem tagged in 1988 was classified into one of the following four classes according to crown position and tree height: canopy (≥25 m tall overtopping neighboring trees), subcanopy (≥25 m tall overtopped by neighboring canopy trees), middle (below subcanopy and ≥10 m tall), and understory (<10 m tall) layers. In 1998, the plot was divided into 1600 contiguous 5-m × 5-m quadrats, and the canopy conditions above each quadrat were estimated visually. Each quadrat was classified into one of four canopy types: closed evergreen conifer canopy (CE: canopy cover ≥30%), closed evergreen conifer canopy adjacent to a canopy gap (gap-adjacent, GA), canopy gap (CG: canopy cover <30%), and closed DBL species canopy (CD). A gap was defined by its constituent set of 5-m × 5-m contiguous gap quadrats. Gap area was calculated by totaling the number of gap quadrats.

To assess the light environment under different canopy conditions, digital hemispherical photographs were taken 1.3 m above ground level under each canopy condition with an 8 mm Nikon fisheye lens during the leaf (early October) and leafless (late October) periods in 2001. The photosynthetic photon flux densities (PPFD) directly above the overstory canopy surface and 1.3 m above the ground under each canopy condition were estimated using ter Steege's (1996) image analysis program, WINPHOT ver. 5. The relative PPFD (%) 1.3 m above the ground under each canopy condition for 1 year was calculated using the PPFD values recorded directly above the overstory (closed) canopy surface and at 1.3 m above ground level under each canopy condition.

The tagged stems were measured again in 1998, together with stems that had been recruited since 1988, and the dead stems were recorded. The causes of mortality of standing-dead understory stems were identified as suppression and broken trunks resulting from natural disturbance. The 1998 frost disturbance was distinguished from other natural disturbances. For each new stem, the layer it had reached was indicated. Potential successors (Rebertus and Veblen, 1993) were estimated in each canopy-gap quadrat; the potential successor was defined as the tallest uninjured stem in the middle layer. Detailed floristic and physical characteristics of the plot were given in Hoshino et al. (2001). The nomenclature follows Kitamura and Murata (1974, 1979).

Demographic parameters were calculated using a logarithmic model (Sheil et al., 1995; Condit et al., 1999; Masaki et al., 1999). The annual mortality (m) and recruitment (r) rates were calculated from the following equations:

$$m = \frac{(\ln N_{88} - \ln N_{\mathrm{S}})}{T}$$

$$r = \left(\frac{N_{98}}{N_S}\right)^{1/T} - 1$$

where N_{88} is the number of living stems in 1988, N_{S} is the number of surviving stems in 1998

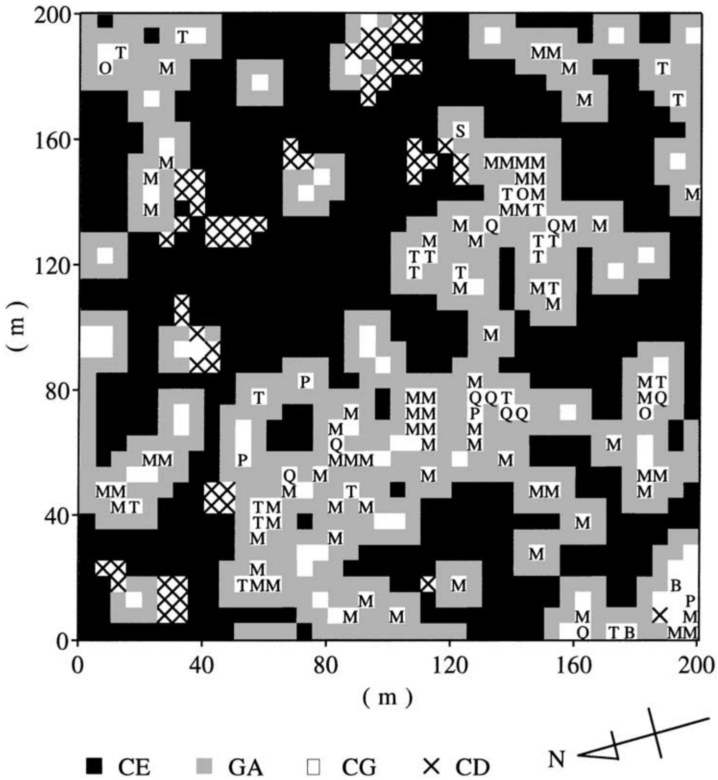

Fig. 1. Map of the 4-ha permanent plot for canopy conditions and potential successors in an old-growth *Chamaecyparis obtusa* forest of the Akasawa Forest Reserve, central Japan. Species names of the potential successors are as follows: O, *C. obtusa*; T, *T. dolabrata*; P, *C. pisifera*; Q, *Q. mongolica*; M, *M. obovata*; B, *B. grossa* and S, other species. Canopy conditions are: CE, closed canopy by evergreen conifers; GA, gap-adjacent; CG, canopy gap; CD, closed canopy by DBL species.

(= N_{88} − number of dead stems), $N_{98} = N_S$ + number of recruited stems, and T is the time interval.

All percentage and ratio data were arcsine transformed before statistical analysis.

4. Results

4.1. Canopy condition and vertical population structure

In the 4-ha plot, 46.5% of the canopy was CE, 38.5% was GA, 11.3% was CG, and 3.7% was CD (Fig. 1). The different canopy conditions were distributed throughout the plot. There were 77 gaps, most of which were single-tree gaps smaller than 200 m^2 (Fig. 2).

The light environment 1.3 m above ground level differed significantly with canopy condition and period (ANOVA, $P < 0.05$, Table 1). The relative PPFD was significantly higher under GA than under other canopy conditions during the leaf period (ANOVA, $P < 0.05$). During the leafless period, the relative

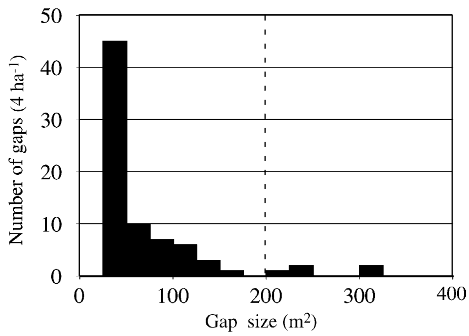

Fig. 2. Size distribution of gaps in the 4-ha plot of the Akasawa Forest Reserve, central Japan.

Table 1
Relative photosynthetic flux density (% per year) at 1.3 m above ground level under different canopy conditions in the 4-ha plot of Akasawa Forest Reserve, central Japan

Period	Canopy conditions			
	CE	GA	CG	CD
Leaf	11.0 ± 2.7 a (20)	12.7 ± 2.6 b (20)	10.7 ± 1.9 a (20)	11.1 ± 2.0 a (20)
Leafless	9.4 ± 1.9 a (20)	13.9 ± 5.7 b (20)	15.5 ± 5.9 b (20)	13.3 ± 6.2 ab (8)

Values with different letters differ significantly in each canopy condition (one-way ANOVA, $P < 0.05$). Sample numbers are given in parentheses.

PPFD was highest under CGs, second highest under GA, and lowest under CE.

The vertical distribution of stems in the four height classes differed with species (Fig. 3) and canopy condition (Fig. 4a). The stem height distributions under CE and GA were both bimodal, while that under CD was inverse J-shaped. There were slightly fewer middle stems than understory stems under CGs, and

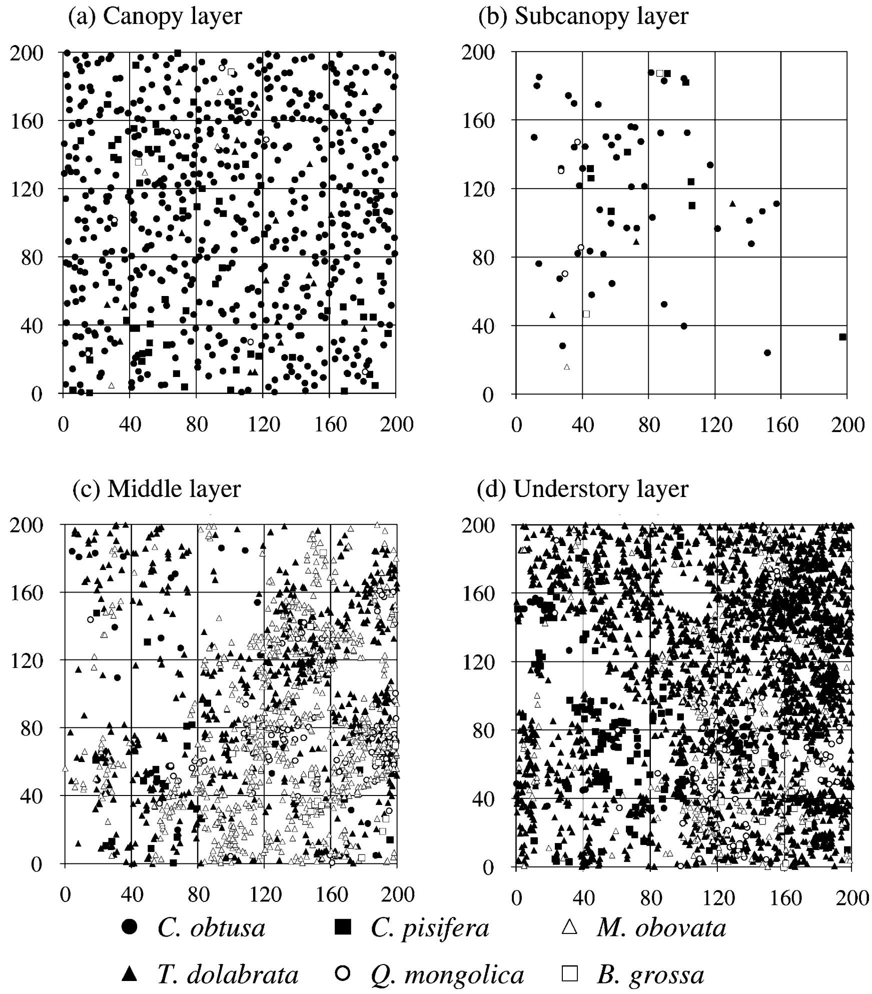

Fig. 3. Dispersion maps of individual living stems in four height classes of major tree species in the 4-ha permanent plot. Scale in meters.

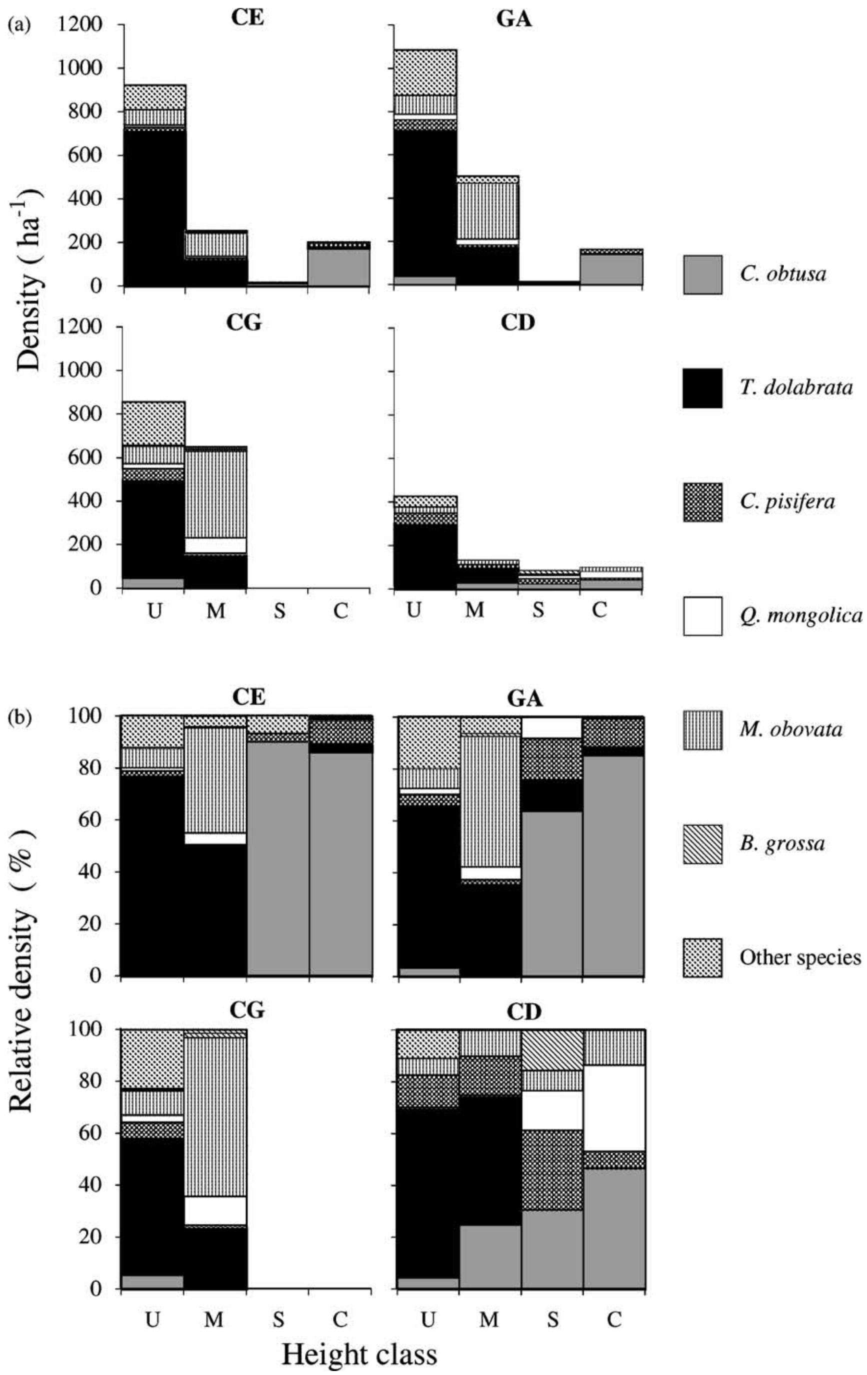

Fig. 4. Density (a) and relative density (b) of six major tree species in four hight classes under four canopy conditions: CE, closed canopy by evergreen conifers; GA, gap-adjacent; CG, canopy gap; CD, closed canopy by DBL species; in 1998. Four hight classes are: C, canopy layer; S, subcanopy layer; M, middle layer and U, understory layer.

much fewer under other canopy conditions, especially under CE. In addition, there were fewer understory and middle stems under CD than under other canopy conditions. Under CD, there were many subcanopy stems.

The species composition of the major tree species in the four height classes varied with canopy condition (Fig. 4b). The proportion of *C. obtusa* gradually increased with layer height under CD, and middle stems were relatively abundant compared to other canopy conditions. *T. dolabrata* dominated understory stems under every canopy condition, but its importance decreased with layer height; a substantial fraction of this species in the canopy and subcanopy layers was found under GA. *C. pisifera* occurred in every layer under GA and CD. Many *Q. mongolica* occurred in the middle layer under CGs and in the canopy and subcanopy layers under CD. *M. obovata* dominated the middle layer under GA and CGs, and was important in the middle layer under CE, while its importance was low in the middle layer under CD, although canopy and subcanopy stems of this species occurred only under CD. *B. grossa* occurred only in the middle layer under CGs.

4.2. Regeneration under canopy gaps

In the middle layer, the stem density of each evergreen conifer species under CGs was similar to that under all canopy conditions, while in the understory layer, the stem density of *T. dolabrata* was lower and that of *Chamaecyparis* sp. was higher under CGs (Table 2). The stem density of each DBL species in the middle and understory layers, especially in the middle layer, was higher under CGs.

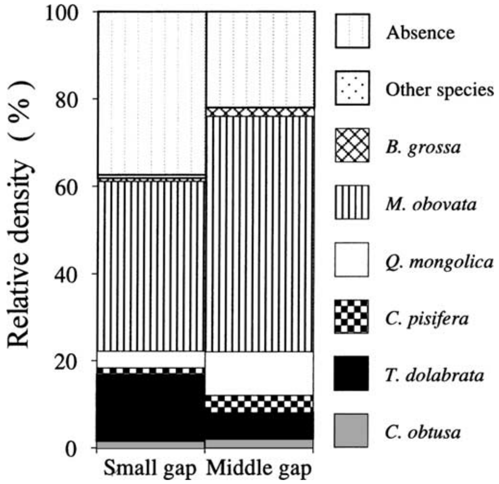

Fig. 5. Relative density of potential successors based on tree height in small gap (25–175 m^2) and middle gap (200–300 m^2) in the 4-ha plot of the Akasawa Forest Reserve, central Japan.

Approximately, half of the CGs would be filled by *M. obovata* according to the investigation of potential successors for each gap (Fig. 1 and Table 2). The next most dominant species in gaps was *T. dolabrata*, which occupied 13% of the total number of canopy gaps, while 33% of canopy gaps did not have potential successors. The species of the potential major successor tree species varied with gap size; the proportion of potential *T. dolabrata* successors decreased with increasing gap size, and that of DBL species and *Chamaecyparis* sp. increased under middle-sized gaps (Figs. 1 and 5).

Table 2
Number (ha^{-1}) of stems of major tree species in each layer under all canopy conditions and under canopy gaps, and percentage of potential successors, in the 4-ha plot of the Akasawa Forest Reserve, central Japan

Species	All canopy conditions			Canopy gap		
	Canopy and subcanopy layer	Middle layer	Understory layer	Middle layer	Understory layer	Potential successors (%)
Chamaecyparis obtusa	149	7	28	7	49	2
Thujopsis dolabrata	6	142	646	146	449	13
Chamaecyparis pisifera	18	6	36	9	53	2
Quercus mongolica	3	24	18	73	24	6
Magnolia obovata	1	190	73	396	80	43
Betula grossa	1	4	4	11	7	1

The potential successor means the tallest uninjured stem in the middle layer in each canopy-gap quadrat.

Table 3
Conditions of subcanopy stems of major tree species for 10 years in the 4-ha plot of the Akasawa Forest Reserve, central Japan

Species	Under closed canopy by evergreen conifers	Gap filler	Under closed canopy by DBL species	Top broken	Unknown
C. obtusa	1 (9)	5 (40)	4 (32)	–	2 (19)
T. dolabrata	–	<1 (100)	–	–	–
C. pisifera	–	<1 (33)	1 (56)	–	<1 (11)
Q. mongolica	–	–	–	<1 (75)	<1 (25)
M. obovata	–	–	–	–	<1 (100)
B. grossa	–	–	–	<1 (50)	<1 (50)

Figures show stem number (ha^{-1}). Percentages are given in parentheses.

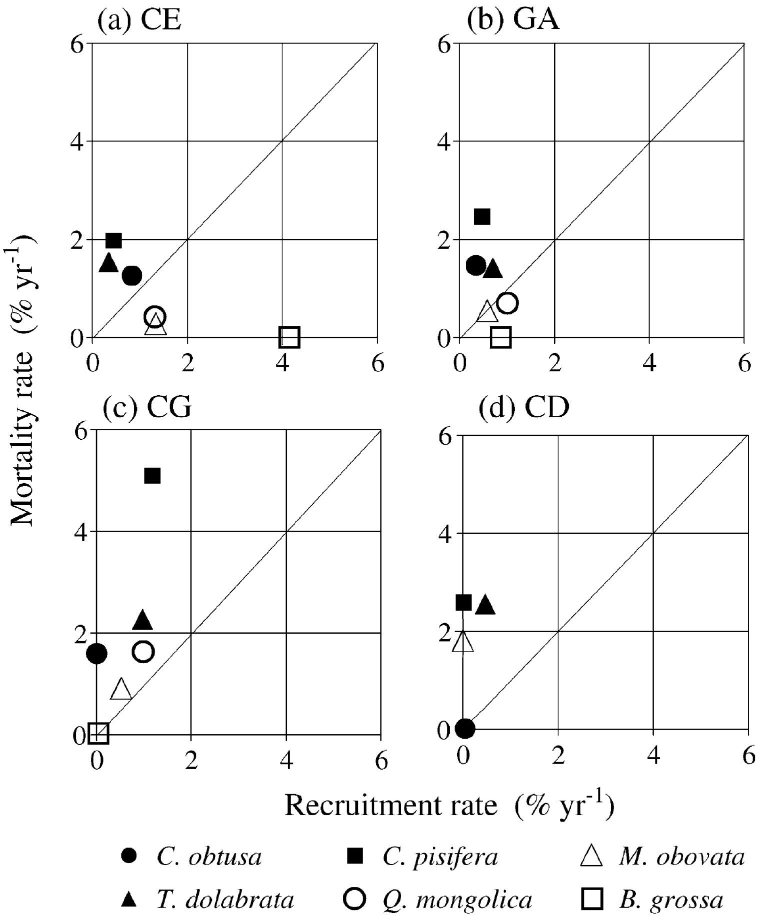

Fig. 6. Relationships between mortality and recruitment rate of understory stems of six major tree species under different canopy condition for 10 years in the 4-ha plot of the Akasawa Forest Reserve, central Japan. Canopy conditions are: CE, closed canopy by evergreen conifers; GA, gap-adjacent; CG, canopy gap; CD, closed canopy by DBL species.

Table 4
Number (ha^{-1}) of dead understory stems of major tree species by each mortality cause under different canopy conditions for 5 years (1993–1998) in the 4-ha plot of the Akasawa Forest Reserve, central Japan

Species	Closed canopy by evergreen conifers			Gap-adjacent			Canopy gap			Closed canopy by DBL species		
	Suppression	Natural disturbance	Unknown	Suppression	Natural disturbance	Unknown	Suppression	Natural disturbance	Unknown	Suppression	Natural disturbance	Unknown
C. obtusa	1	1 (0)	0	2	5 (1)	0	2	7 (0)	0	0	0 (0)	0
T. dolabrata	62	60 (28)	3	42	64 (30)	1	40	91 (29)	2	0	93 (47)	0
C. pisifera	3	1 (0)	0	8	5 (5)	2	9	27 (15)	0	7	13 (7)	0
Q. mongolica	1	0 (0)	0	3	0 (0)	0	15	0 (0)	0	–	–	–
M. obovata	4	1 (0)	1	13	1 (1)	0	33	4 (0)	0	0	7 (7)	0

Number of dead stems by frost disturbance in 1998 are given in parentheses. *B. grossa* had no mortality.

Subcanopy stems of *Chamaecyparis* sp. were fillers in CGs and suppressed trees under CD (Table 3). Those of *T. dolabrata* were fillers in CGs, although the number was only one.

4.3. Population dynamics and mortality

In the canopy layer, only one *C. obtusa* died in 10 years, after its stem was broken in a frost disturbance; there was no mortality in the subcanopy layer and very little mortality in the middle layer (four stems per 4 ha). In the understory layer, 612 stems of major tree species died in the 4-ha plot over 10 years, and the mortality and recruitment rates varied with canopy condition (Fig. 6). The mortality exceeded the recruitment rate for conifers and the reverse trend was true for DBL species under CE and GA. On the other hand, the mortality rate exceeded the recruitment rate for both conifers and DBL species under CGs and CD.

Most mortality of understory stems resulted from suppression or natural disturbances (Table 4). Many dead understory stems of *C. obtusa* resulted from natural disturbances under GA and CGs. On the other hand, many dead understory stems of *T. dolabrata* resulted from suppression and natural disturbances under all canopy conditions except for CD; all dead stems of this species resulted from natural disturbance under CD. The mortality of *Q. mongolica* and *M. obovata* understory stems was generally due to suppression. The natural disturbances included not only the 1998 frost disturbance, but also other unknown disturbances.

5. Discussion

T. dolabrata generally dominated the understory and middle layer in the plot, probably due to its high shade tolerance and vegetative reproduction by layering (Yamamoto and Suto, 1994; Hoshino et al., 2001). However, since the density and importance of understory and middle stems of *T. dolabrata* were low under CGs and there were no canopy or subcanopy stems under CD, these sites may not be favorable for the regeneration of *T. dolabrata*. Being sited under CD may also be unfavorable for understory and middle stems of DBL species, such as *M. obovata*, while CD favors the occurrence of *C. obtusa* and *C. pisifera*. *C. obtusa* and *C. pisifera* are less shade-tolerant than *T. dolabrata* (Yamamoto and Suto, 1994), and require bare soils without a thick litter layer for seedling establishment (Yamamoto, 1993b, 1994). DBL species are generally shade-intolerant; *B. grossa* and *Q. mongolica* are typical pioneers (Yamamoto, 1989; Masaki et al., 1992). *M. obovata* is more shade-tolerant than other DBL species (Hara, 1983; Yamamoto, 1989; Masaki et al., 1992) and forms a buried seed bank (Mizunaga, 1998). *C. pisifera* also reproduces vegetatively by layering (Yamamoto et al., 1994). In the study site, the probability of *C. obtusa* regeneration seems to be highest under CD, among the four canopy conditions.

Differences in canopy conditions alter understory light conditions. Sites under CE are much darker than those under other canopy conditions. During the leaf period, sites under GA were the brightest. During the leafless period, sites under CGs were the brightest and sites under CGs, GA, and CD were brighter than those under CE. These differences in light conditions may affect the regeneration of major tree species in this stand.

Under CGs, the stems of DBL species in the middle and understory layers, which colonize gaps from seed after gap formation, were abundant, while understory stems of *T. dolabrata* were only two-thirds of the numbers found elsewhere in the plot. This clearly indicates that the number of *T. dolabrata* stems decreased after gap formation, because there was abundant *T. dolabrata* undergrowth originating from layering under the closed canopy, as mentioned above. Canopy gap formation may favor the understory regeneration of *C. obtusa*, because the stem number in the understory exceeded that in the middle layer under CGs.

Stems in the subcanopy layer are thought to be stems suppressed by competitors in the canopy layer, and may be considered stems awaiting the opportunity to reach the canopy layer. From the investigation of potential successors in a gap, a large CG would be filled by DBL species. Larger gaps may not be favorable regeneration sites for *T. dolabrata*, although there are many saplings before gap formation; moreover, the area under the crowns of DBL species may not be a favorable regeneration site for *T. dolabrata*. By contrast, *C. obtusa* and *C. pisifera* can establish on the forest floor under CD, although the diameter growth of

Chamaecyparis sp. is slower than that of DBL species (Hoshino et al., 2002). *Chamaecyparis* sp. in the subcanopy layer might occur with DBL species in the canopy layer, and they may await the opportunity to reach the canopy layer after the death of a tree or breakage of a large branch of a DBL species canopy tree. By contrast, *T. dolabrata* may have a chance to reach the canopy layer under GA or smaller gaps where there are subcanopy *T. dolabrata* trees; these sites are brighter than CE and are not affected by unknown mortality factors seen under CD.

The causes of mortality varied with species and canopy condition. Generally, evergreen conifers died as a result of natural disturbances, especially in the 1998 frost disturbance under canopy conditions other than closed evergreen conifer canopy. When DBL species in the upper layer were leafless, the lower stems of evergreen conifers might have been affected by the frost disturbance directly. On the other hand, the lower stems of DBL species might not have been affected by the disturbance, because they were leafless. Sites with more living understory stems of *C. pisifera*, *T. dolabrata*, and *M. obovata* also tend to have more dead understory stems (Hoshino et al., 2002); a local density effect may operate on mortality. A higher stem density weakens each understory stem, and stem weakness may induce mortality of understory stems due to normal snow loads.

In conclusion, canopy conditions affect vertical population structure, demographic parameters, and tree mortality for major tree species, thereby affecting the regeneration mode. In this old-growth *C. obtusa* forest, favorable *C. obtusa* and *C. pisifera* regeneration sites are generally under CD, that of *T. dolabrata* is under GA, and *Q. mongolica*, *M. obovata* and *B. grossa* are under CGs. Therefore, this old-growth *C. obtusa* forest will gradually change into a more diverse forest with a shifting mosaic of developmental stages due to gap formation (Bormann and Likens, 1979).

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References

Bormann, F.H., Likens, G.E., 1979. Pattern and Process in a Forested Ecosystem. Springer, New York.

Condit, R., Ashton, P.S., Manokaran, N., LaFrankie, J.V., Hubbell, S.P., Foster, R.B., 1999. Dynamics of the forest communities at Pasoh and Barro Colorado: comparing two 50-ha plots. Philosophical trans. Royal Soc. Lond. 354, 1739–1748.

Denslow, J.S., 1987. Tropical rain forest gaps and tree species diversity. Ann. Rev. Ecol. Systemat. 18, 431–451.

Hara, M., 1983. A study of the regeneration process of a Japanese beech forest. Ecol. Rev. 20, 115–129.

Hoshino, D., Nishimura, N., Yamamoto, S., 2001. Age, size structure and spatial pattern of major tree species in an old-growth *Chamaecyparis obtusa* forest, central Japan. For. Ecol. Manage. 152, 31–43.

Hoshino, D., Nishimura, N., Yamamoto, S., 2002. Dynamics of major conifer and deciduous broad-leaved tree species in an old-growth *Chamaecyparis obtusa* forest, central Japan. For. Ecol. Manage. 159, 133–144.

Kato, K., Yamamoto, S., 2000. Effects of canopy on the sapling composition and structure in a subalpine old-growth forest, central Japan. Ecoscience 7, 237–242.

Kato, K., Yamamoto, S., 2001. Effects of canopy heterogeneity on the sapling dynamics of a subalpine old-growth forest, central Japan. Ecoscience 8, 96–104.

Kitamura, S., Murata, G., 1974. Colored Illustration of Woody Plants of Japan, Vol. 1. Hoikusya, Osaka (in Japanese).

Kitamura, S., Murata, G., 1979. Colored Illustration of Woody Plants of Japan, Vol. 2. Hoikusya, Osaka (in Japanese).

Masaki, T., Suzuki, W., Niiyama, K., Iida, S., Tanaka, H., Nakashizuka, T., 1992. Community structure of a species-rich temperate forest, Ogawa Forest Reserve, central Japan. Vegetatio 98, 97–111.

Masaki, T., Tanaka, H., Tanouchi, H., Sakai, T., Nakashizuka, T., 1999. Structure, dynamics and disturbance regime of temperate broad-leaved forests in Japan. J. Veget. Sci. 10, 805–814.

Maeda, T., 1951. Sociological Study of *Chamaecyparis obtusa* Forest and its Japan-Sea Elements, Vol. 8. Ensyurin (Tokyo University Forest), pp. 21–44 (in Japanese with English summary).

Maeda, T., Yoshioka, J., 1952. Studies on the Vegetation of Chichibu Mountain Forest. Part II. The Plant Communities of the Temperate Mountain Zones, Vol. 42. Bulletin of Tokyo University Forest, pp. 129–150 (in Japanese with English summary).

Miyawaki, A., Okuda, S., 1990. Vegetation of Japan. Shibundo, Tokyo (in Japanese).

Mizunaga, H., 1998. Effects of disturbances on large patch formation of *Magnolia obovata*, a deciduous broad-leaved tree: field investigation and simulation. J. Sustain. For. 6, 251–266.

NRFO (Nagano Regional Forest Office), 1985. Report for the Management of Akasawa *Chamaecyparis obtusa* Forest (enlarged). Nagano Regional Forest Office, Nagano, 102 pp. (in Japanese).

Rebertus, A.J., Veblen, T.T., 1993. Structure and tree-fall gap dynamics of old-growth *Nothofagus* forest in Tierra del Fuego, Argentina. J. Veget. Sci. 4, 641–654.

Runkle, J.R., 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology 63, 1533–1546.

Sheil, D., Burslem, D.F.R.P., Alder, D., 1995. The interpretation and misinterpretation of mortality rate measures. J. Ecol. 83, 331–333.

ter, Steege, H., 1996. WINPHOT 5: a programme to analyze vegetation indices, light and light quality from hemispherical photographs. In: Proceedings of the Tropenbos Guyana Reports 95-2, Tropenbos Programme. Georgetown, Guyana.

Yamamoto, S., 1989. Gap dynamics in climax *Fagus crenata* forests. Bot. Magazine Tokyo 102, 93–114.

Yamamoto, S., 1993a. Structure and dynamics of an old-growth *Chamaecyparis* forest in the Akasawa Forest Reserve, Kiso district, central Japan. Jpn. J. For. Environ. 35, 32–41.

Yamamoto, S., 1993b. Seedling establishment of *Chamaecyparis obtusa* in different microenvironments in the Akasawa Forest Reserve, central Japan. J. Jpn. For. Soc. 75, 519–527.

Yamamoto, S., 1994. Seedling establishment of *Chamaecyparis pisifera* on different substrata in an old-growth *C. pisifera* stand, Akasawa Forest Reserve, central Japan. J. Jpn. For. Soc. 76, 178–181.

Yamamoto, S., 2000. Forest gap dynamics and tree regeneration. J. For. Res. 5, 223–229.

Yamamoto, S., Suto, A., 1994. Occurrence pattern of *Thujopsis dolabrata* saplings in the understory of an old-growth *Chamaecyparis* forest, Akasawa Forest Reserve, central Japan. J. Jpn. For. Soc. 76, 553–559.

Yamamoto, S., Moriyama, Y., Kobayashi, M., 1994. Two types of vegetative reproduction of *Chamaecyparis pisifera* Sieb. et Zucc. Endl. Jpn. J. For. Environ. 36, 57–59.

Yokouchi, F., 1970. *Chamaecyparis* forest in the Kiso District, Nagano prefecture. Bull. Bot. Soc. Nagano 3, 12–18, (in Japanese).