

Effects of disturbance history on the structure and dynamics of an old-growth *Chamaecyparis* – *Thujopsis* forest in central Japan

Takahiro ASAI¹, Daisuke HOSHINO^{1,3}, Naoyuki NISHIMURA² and Shin-Ichi YAMAMOTO¹

To evaluate the effects of different disturbance histories (typhoon vs. human disturbances) on the structure and dynamics of an old-growth forest, we investigated the structure and ten-year dynamics of a stand with no evidence of disturbance (Stand N), a stand with severe typhoon disturbance (Stand T), and a stand disturbed by humans (*e.g.*, by selection cutting; Stand H). The study site was located in an old-growth *Chamaecyparis obtusa* (canopy dominant) – *Thujopsis dolabrata* (understory dominant) forest in the Akasawa Forest Reserve of central Japan. Stands T and N had the highest and lowest percentage of canopy gaps, respectively. The total density and basal area of canopy stems were highest and largest, respectively, in Stand N, and lowest and smallest in Stand H, but the reverse trend was observed for understory stems. Generally, mortality and recruitment were very low among canopy stems, but high among understory stems. The recruitment rate of understory stems was clearly higher than the mortality rate in Stand T, while the reverse was typical in Stands N and H. Various states of mortality were observed among understory stems. In Stands N and T, understory stems tended to be physically damaged, whereas in Stand H, we recorded more standing dead trees than physical damaged trees. Different disturbance histories clearly affected the structure and dynamics of this forest, although disturbance itself induced understory regeneration. Human disturbance such as selection cutting enhanced understory regeneration of *T. dolabrata* more than *C. obtusa*, due to ensuing light conditions that favored the growth of *T. dolabrata* in the understory.

Keywords: human disturbance, typhoon disturbance, *Chamaecyparis obtusa*, *Thujopsis dolabrata*, gap

Introduction

Disturbance is one of the major factors affecting the structure and dynamics of forests (*e.g.*, White 1979; Pickett and White 1985; Franklin *et al.* 2002). Therefore, many studies have been conducted to elucidate the role of disturbance on structure and dynamics in many forest types, in various parts of the world (*e.g.*, Bormann and Likens 1979; White 1979; Pickett and White 1985; Foster 1988; Lawton and Putz 1988; Franklin *et al.* 2002). From these studies we understand that frequency, scale, severity, and magnitude are

among the more important components of disturbance (Pickett and White 1985). In addition, disturbance history or types of disturbance are factors that have been emphasized recently, typically in studies investigating the differential effects of natural and human disturbances (Orwig and Abrams 1994; Ruffner and Abrams 1998; Motta *et al.* 2002). Generally, strong winds and fire are typical natural disturbances, whereas logging is a common human disturbance that affects forest structure and dynamics (Barnes *et al.* 1998). It is likely that human disturbances and natural disturbances affect forest structure and dynamics in

¹Laboratory of Forest Ecology and Physiology, Graduate School of Bioagricultural Sciences, Nagoya University, Nagoya 464-8601, Japan
名古屋大学大学院生命農学研究科 森林生態生理学研究室

²Bukkyo University Correspondence Division, 96 Kita-hananobo, Murasakino, Kita-ku, Kyoto 603-8301, Japan
佛教大学通信教育部

³Corresponding author. Tel : 052 (789) 4047, Fax : 052 (789) 5014. e-mail : dhoshi2003@yahoo.co.jp

(Accepted : Nov. 30, 2003)

different ways. For examples, a stand which developed after recent human disturbances is not likely to be affected by the effects of natural disturbances; more stable and tolerant to blow down than a natural old-growth stand (Oliver and Larson 1996). Human disturbances or control also bring a variation in cycle of natural disturbances which affect some species depending on disturbances. However, few comparative studies, have investigated these different impacts.

Chamaecyparis forests occur regionally in the temperate montane zone of the Pacific sea side in central Japan (Maeda 1951; Maeda and Yoshioka 1952; Yamamoto 1998); the Kiso district is at the center of this area, and many old-growth *Chamaecyparis* forests grow in this region. Akasawa Forest Reserve is a representative *C. obtusa* forest in the Kiso district. The old-growth *C. obtusa* stands in this reserve, like other *C. obtusa* forests in the Kiso district, were probably established following severe logging between 1688 and 1703. Since then, most stands have been protected from clear-cutting, although a little selection cutting has been made locally for purposes of forest management (NRFO 1985). Although *T. dolabrata* saplings dominate the understories of most old-growth *C. obtusa* stands in this reserve, there has been very little regeneration of *C. obtusa*. Since *T. dolabrata* is a highly shade-tolerant tree species that can reproduce by layering under closed canopy conditions (Yamamoto and Suto 1994), it is likely that if the present situation continues, *C. obtusa* will disappear, and these stands will gradually change to a forest dominated by *T. dolabrata* (NRFO 1985; Yamamoto 1993). *C. obtusa* is a less shade-tolerant species that reproduces only by seeds and cannot establish itself under an intact closed canopy (Yamamoto 1998). *C. obtusa* timber is valued more highly than that of *T. dolabrata*; therefore, a decline in *C. obtusa* regeneration will greatly decrease the economic value of this forest.

Several studies have been conducted in this reserve to assess the dynamics of stands disturbed

by selection cutting and to estimate the future state of these stands (Yamamoto 1993; Hoshino *et al.* 2001, 2002, 2003). In these studies, Hoshino *et al.* (2003) indicated that the occurrence of abundant advanced growth of *T. dolabrata* does not necessarily entail the monopolization of every gap that occurs in these stands; some deciduous broad-leaved trees and a few *Chamaecyparis* trees occupy these gaps. They also suggested that these stands will develop into more diverse stands, with a shifting mosaic of developmental stages, as a result of gap formation. While numbers of *T. dolabrata* tend to decrease by suppression or natural disturbances such as frost, the regeneration potential of this species can be observed in small openings or in the vicinity of gaps. However, these indications and suggestions were based on a stand that was affected by human interference, which does not necessarily represent the natural succession processes in this old-growth forest.

In this reserve, there is one small stand that has not been logged and has been strictly preserved from human disturbance since its establishment. This stand constitutes a good reference site against which to compare other stands where there has been selection cutting; it also offers a way to assess the effects of disturbance history on forest structure and dynamics.

In this study, we investigated the structure and ten-year dynamics of a stand that showed no evidence of disturbance, a stand that had experienced typhoon disturbances, and a stand that had been disturbed by humans, to evaluate the effects of different disturbance histories (typhoon *vs.* human) on the structure and dynamics of an old-growth forest.

Methods

Study site

The study stands were located in the Akasawa Forest Reserve at Agematsu-cho in the Kiso Valley (Nagano Prefecture, central Japan; 35°43' 57"N, 137°37'50"E; for a map of the area, see

Hoshino *et al.* (2002)). The altitude of the reserve ranges from 1080–1558 m a.s.l., annual precipitation is approximately 2500 mm, and snow accumulation ranges from 50–100 cm. The average annual temperature is 7.8°C at an elevation of 1113 m (NRFO 1985). The reserve is situated on an elevated peneplain with a gentle slope, on a bedrock of granite, granite porphyry, and rhyolite. Soils are mainly dry and wet podzol, while brown forest soils are found on hillsides and along mountain streams (NRFO 1985). The vegetation is primarily *Disantho - Chamaecyparidetum obtusae* Yokouchi 1970 (Miyawaki and Okuda 1990). *C. obtusa* dominates the main canopy, with occasional associates such as *T. dolabrata*, *C. pisifera* (Sieb. et Zucc.) Endlicher, *Thuja standishii* Carriere, and *Pinus parviflora* Sieb. et Zucc., or hardwoods such as *Quercus mongolica* Fischer ex Turcz. var. *grosseserrata* (Bl.) Rehder et Wilson, *Magnolia obovata* Thunb., and *Betula grossa* Sieb. et Zucc.

Dominant canopy trees in the reserve are about 300 years old (Hoshino *et al.* 2001). Although the reserve has been protected for 200 years, human disturbances such as selection cutting occurred locally for purposes of forest management between 1914 and 1945 (NRFO 1985). Generally, these selection cuttings were carried out at three times for canopy trees of *T. dolabrata*, *C. pisifera* and hardwoods, with the result that one-third of canopy trees were lost during 31 years (NRFO 1985). Natural disturbances, such as the strong Isewan Typhoon of 1959, have severely disturbed the forests in the reserve. At the Gifu Weather Station, 90 km west-southwest of the reserve, the average recorded wind velocity and lowest air pressure of the Isewan Typhoon were 32.5 m s⁻¹ and 956 hPa, respectively (Japan Meteorological Agency 1960). In early 1998, the weight of freezing rain that coated leaf surfaces of canopy and understory trees during a winter ice storm broke and uprooted trunks (Hoshino *et al.* 2002); we termed this a “frost disturbance”. Most dead tree boles produced by these disturbances have been

removed from the reserve.

Field methods

Two 0.6-ha (150×40 m) plots were established in 1989 in the strictly preserved stand; in this stand the forest floor is covered mainly by small *T. dolabrata* saplings (height <0.7 m) that originated from layering. One of these permanent plots (Stand N) was in a part that showed no evidence of disturbance (*e.g.*, canopy gaps or root mounds), and the other plot (Stand T) was established in a part that was included a large gap formed by severe typhoon disturbance in 1959 (Table 1). A 4-ha plot was established in 1988 on a gentle slope located *ca.* 2 km southeast of Stands N and T (Hoshino *et al.* 2001); most of the understory of this stand is also dominated by *T. dolabrata* saplings that originated from layering. Within this large plot, a 0.6-ha permanent plot (Stand H) was established. This site contained many *T. dolabrata* saplings and some canopy gaps formed by human disturbances, *e.g.*, selection cutting, around 1940.

Stem maps of these plots were made during the

Table 1. Characteristics of three stands in an old-growth *Chamaecyparis obtusa* forest in the Akasawa Forest Reserve.

Stand	Stand N	Stand T	Stand H
Topographic position	Middle slope	Middle slope	Middle slope
Slope direction	SE	SE	NW
Elevation	1170	1170	1190
Census year	1989 2000	1989 2000	1988 1998
Geology	granitite	granitite	granitite
Soil	BFS	BFS	BFS and DPS

Stand N : without any disturbance evidence

Stand T : with severe typhoon disturbance

Stand H : with selection cuttings

BFS : Brown forest soils

DPS : Dry podzolic soils

first census (Stands N and T in 1989, Stand H in 1988). All stems of trees and shrubs over 5.0 cm diameter at breast height (DBH) were included, and each was identified to species and characterized as either live or dead. Stems were mapped to the nearest 0.1 m, tagged for the next census, and measured to the nearest 0.1 cm DBH.

Vertical structural layers were classified into the following two classes of crown position or tree height: canopy layer: over 25 m tall, understory layer: less than 25 m tall, in 1989 (Stand N and T) and 1993 (Stand H). In this paper, the canopy layer consists of trees in the canopy layer only, and canopy gaps include trees in the understory. Each plot was divided into 240 quadrats (5 × 5 m) above which canopy condition was recorded by visual estimation: closed canopy (canopy cover over 30 %) by evergreen conifers and deciduous broad-leaved trees, and canopy gaps (canopy cover less than 30 %). Nomenclature followed Kitamura and Murata (1971, 1979).

In the second census (Stands N and T in 2000, Stand H in 1998), the tagged stems were measured again, together with newly recruited stems over 5 cm DBH that had grown since the first census, and the mortality state of dead stems was recorded.

In 2001, to assess the light environment above *T. dolabrata* saplings, photosynthetic photon flux density (PPFD) was measured using a photon flux density meter (LI-190, LI-COR, Inc). When the sky was overcast, PPFD was measured under the sky and above the understory canopy in each plot (Stands N and T: $n=16$, Stand H: $n=8$). Readings above the understory canopy were paired to calculate relative values, using data that were recorded at similar times.

Data analysis

The stem age of two major conifer tree species (*C. obtusa* and *T. dolabrata*) in each plot was estimated by the following regression formula and constants (Hoshino *et al.* 2001):

$$\text{Age} = \{a \times \text{DBH} / (b + \text{DBH})\} + c, \quad (1)$$

where a , b , and c are constants for the two species,

determined from the best fit between DBH and age, based on ring counts from this forest. For *C. obtusa*, $a=450.4$, $b=13.5$, and $c=-66.5$; for *T. dolabrata*, $a=1390.3$, $b=167.8$, and $c=-1.5$.

Demographic and growth parameters were calculated using a logarithmic model (Sheil *et al.* 1995; Condit *et al.* 1999; Miura *et al.* 2001; Hoshino *et al.* 2002). The annual mortality (m) and recruitment (r) rates were calculated from the following equations:

$$m = (\ln N_1 - \ln N_s) / T \quad (2)$$

$$r = (\ln N_2 - \ln N_s) / T \quad (3)$$

where N_1 is the number of living stems in the first census, N_s is the number of surviving stems in the second census ($= N_1 - \text{number of dead stems}$), N_2 is $N_s + \text{the number of recruited stems}$, and T is the time interval. The annual loss (l), gain (g), and ingrowth (i) rates of the basal area (BA) were calculated from the following equations:

$$l = (\ln BA_1 - \ln BAS_1) / T \quad (4)$$

$$g = (\ln BA_2 - \ln BAS_1) / T \quad (5)$$

$$i = (\ln BAS_2 - \ln BAS_1) / T \quad (6)$$

where BA_1 is the BA of living stems in the first census, BAS_1 is the BA in the first census of stems that survived to the second census, BAS_2 is the BA of stems that survived to the second census, and $BA_2 = BAS_2 + \text{BA of recruited stems in the second census}$.

Results

Stand structure

Canopy conditions varied among the three stands, such that Stand T had the highest percentage of canopy gaps, and Stand N had the lowest (Table 2). One large gap was observed in Stand T; there were relatively numerous small gaps in Stand H (Fig. 1). The surface of the understory canopy was significantly lighter in Stand T than in the other stands, as shown by relative PPFD values (t -test, $P < 0.001$).

The total density and basal area of canopy stems were highest and largest in Stand N and lowest and smallest in Stand H, but the reverse

Table 2. Canopy characteristics, light conditions and stand parameters in three stands of an old-growth *Chamaecyparis obtusa* forest in the Akasawa Forest Reserve at first census.

	Stand N	Stand T	Stand H
Canopy characteristics			
Coverage of canopy			
Closed canopy (%)	98.7	62.9	91.2 ¹
Canopy gap (%)	1.3	37.1	8.8 ¹
Canopy gap			
Number (0.6 ha ⁻¹)	3	8	13 ¹
Maximum size (m ²)	25	1525	150 ¹
Average size (m ²)	25	278	44 ¹
Light condition			
Relative PPFD (%)	5.4 ²	28.5 ²	9.4 ²
± S.D.	± 3.6	± 12.7	± 4.1
Stand parameter			
Canopy layer			
Stem density (ha ⁻¹)	373	247	168
Basal area (m ² ha ⁻¹)	81.2	52.0	51.3
Understory layer			
Stem density (ha ⁻¹)	723	1838	2375
Basal area (m ² ha ⁻¹)	6.1	13.3	14.6
Total of plot			
Stem density (ha ⁻¹)	1097	2085	2543
Basal area (m ² ha ⁻¹)	87.2	65.4	65.9
Number of woody plant species (0.6 ha ⁻¹)	15	22	13

¹Values at second census.²Values in 2001.

trend was observed in the understory; this contrast between canopy and understory stems was typical (Table 2). Total stem density and basal area were lowest and largest, respectively, in Stand N. In Stand H, total stem density was highest and total basal area was small.

The number of woody plant species was highest in Stand T (Table 2). Common species with $\geq 0.6\%$ relative stem density throughout the three stands were two conifers, *C. obtusa* and *T. dolabrata*, and two deciduous broad-leaved (DBL) tree species, *Quercus mongolica* var. *grosseserrata* and *Magnolia obovata*; hereafter, the latter two

will be lumped together as DBL species. We considered these to be major tree species. The stem density and basal area of *C. obtusa* and *T. dolabrata* in the canopy layer was highest in Stand N, both in 1989 (Table 3). On the other hand, the stem density and basal area of *T. dolabrata* and DBL species in the understory was highest and largest in Stand H, both in 1988. Understory stems of DBL species were very abundant in this stand, as compared to the others.

The size and age distribution of *C. obtusa* was rather unimodally bell-shaped in Stand N and had a bimodal bell-shaped distribution in Stands T

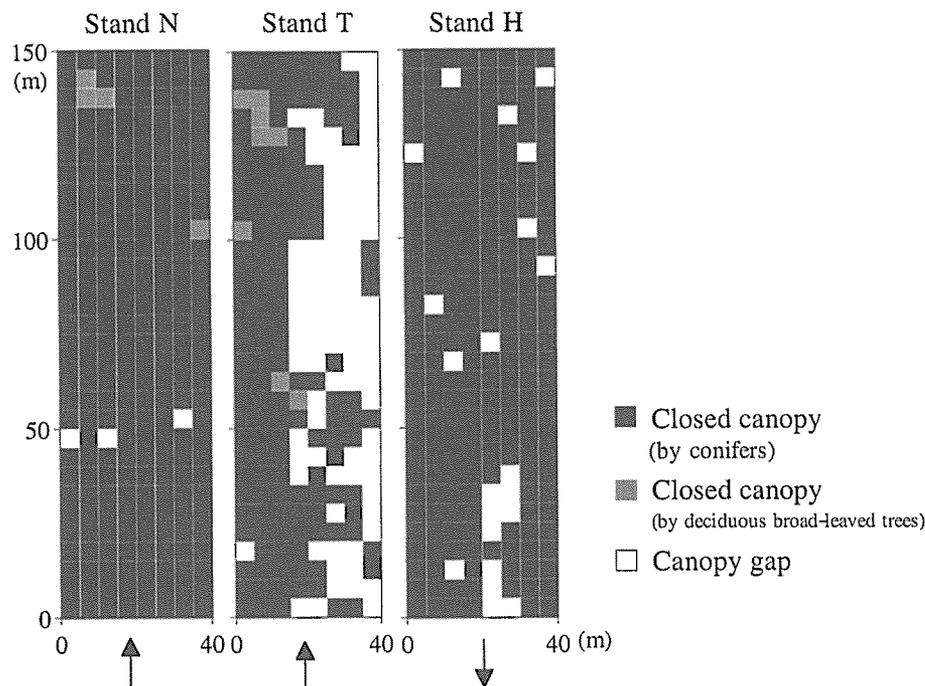


Figure 1. Canopy conditions of plot in Stands N and T in 1991 and Stand H in 1998. Slope direction was indicated by arrows. Stand N; without any disturbance evidence, Stand T; with severe typhoon disturbance, Stand H; with selection cuttings.

Table 3. Population parameters of major tree species in each layer in three stands in an old-growth *Chamaecyparis obtusa* forest in the Akasawa Forest Reserve.

Species	Stand N				Stand T				Stand H			
	Stem density		Basal area		Stem density		Basal area		Stem density		Basal area	
	(ha ⁻¹)	(m ² ha ⁻¹)	(ha ⁻¹)	(m ² ha ⁻¹)	(ha ⁻¹)	(m ² ha ⁻¹)	(ha ⁻¹)	(m ² ha ⁻¹)	(ha ⁻¹)	(m ² ha ⁻¹)	(ha ⁻¹)	(m ² ha ⁻¹)
	1989	2000	1989	2000	1989	2000	1989	2000	1988	1998	1988	1998
Canopy layer												
<i>C. obtusa</i>	313	310	71.1	72.7	220	223	47.4	49.2	157	157	48.5	49.3
<i>T. dolabrata</i>	47	43	6.0	5.7	10	12	1.3	1.5	5	5	1.1	1.1
DBL species	5	3	1.5	1.4	12	12	2.0	2.1	-	-	-	-
All species	373	363	81.2	82.3	247	248	52.0	53.1	168	168	51.3	52.2
Understory layer												
<i>C. obtusa</i>	20	15	0.7	0.4	40	38	1.1	0.7	23	15	0.2	0.2
<i>T. dolabrata</i>	662	653	5.2	5.0	1450	1647	9.5	12.8	1832	1542	12.0	11.7
DBL species	13	8	0.1	0.1	53	57	0.5	0.8	438	435	2.1	2.7
All species	723	705	6.1	5.5	1838	2028	13.3	16.1	2375	2093	14.6	15.0
Total of the plot												
<i>C. obtusa</i>	333	325	71.8	73.2	260	262	48.5	49.8	180	172	48.6	49.5
<i>T. dolabrata</i>	708	697	11.3	10.7	1460	1658	10.9	14.3	1837	1547	13.1	12.8
DBL species	18	12	1.6	1.5	65	68	2.5	2.8	438	435	2.1	2.7
All species	1097	1068	87.2	87.9	2085	2277	65.4	69.2	2543	2262	65.9	67.3

and H (Fig. 2). The median of the size distribution was larger in Stand H than in the other stands, which indicates that the canopy of Stand H consisted of larger *C. obtusa* canopy trees than the canopy of the other stands. On the other hand, the size and age distribution of *T. dolabrata* was inverse-J shaped and continuous in Stands N and T, and L-shaped and discontinuous in Stand H. The peak of size and age distribution was clearly very small and young in all stands, as compared to *C. obtusa*. The oldest individuals were estimated to 327 (*C. obtusa*) and 356 years (*T. dolabrata*), which was essentially almost the same.

Stand dynamics

Canopy stem density in Stand N was 373 ha⁻¹ in 1989 and slightly less in 2000, but the total basal area increased; the density and basal area of understory stems in this stand decreased slightly (Table 3). In Stand T, canopy stem density was 247 ha⁻¹ in 1989, and was nearly unchanged in 2000, while the total basal area increased. The understory stems in this stand, most of which were *T. dolabrata*, typically increased in density and basal area. Canopy stem density in Stand H did not change, but the total basal area increased. Understory stems in this stand largely decreased in density, which was typical for *T. dolabrata*, but slightly increased in basal area.

The annual mortality rate of all stems in these plots ranged from 0.78 to 1.50 % year⁻¹, and the annual recruitment rate ranged from 0.43 to 1.59 % year⁻¹ (Table 4). Only mortality occurred for canopy stems, and the gain rate was larger than the loss rate in Stand N. In Stand T, the recruitment rate was higher than the mortality rate for canopy stems, and the gain rate was larger than the loss rate; ingrowth was highest in this stand, as compared to the others. We recorded no recruitment or mortality for canopy stems in Stand H; only ingrowth was observed.

For understory stems, the mortality rate was slightly higher than the recruitment rate, and the loss rate was substantially higher in Stand N. The

recruitment rate was highest in Stand T, and was much higher than the mortality rate. The gain rate of this stand, which consisted mostly of *T. dolabrata* and DBL species, was the highest. Mortality was much higher than recruitment in Stand H, and gain was slightly higher than loss. The highest ingrowth rate of understory stems was observed in Stand T, and ingrowth in Stand H much higher than that in Stand N. In all stands, ingrowth rate of DBL species was higher than that of conifers.

Mortality state

Five canopy stems died in Stand N; two were *C. obtusa*, two were *T. dolabrata*, and one was a DBL species. These dead stems were all standing dead, except for one broken *C. obtusa* stem. One canopy *C. obtusa* stem broke in Stand T, and no canopy stems died in Stand H.

In the understory layer, various mortality states were observed (Table 5). In Stand N, all dead *C. obtusa* stems and 27 % of all dead *T. dolabrata* stems were standing dead, and 50 % of all dead *T. dolabrata* stems were the result of physical damage (stem broken, uprooted, or leaning). In Stand T, about 70 % of all stem death in *T. dolabrata* was the result of physical damage. In Stand H, however, 44 % of all dead *T. dolabrata* stems and 79 % of all dead DBL stems were standing dead. Only *T. dolabrata* had the effect of the 1998 frost disturbance. In the mortality state of physical damage, the ratio of frost disturbance in Stands T and H was much larger than that in Stand N.

Discussion

Stand structure

The stand that had experienced no disturbances (Stand N) clearly had a very dense stock of canopy trees and was considered overcrowded, based on its mortality rate and the causes (standing-dead) of mortality among canopy trees. This, in addition to fewer and smaller gaps, resulted in darker light conditions on the surface of the understory crown, which may have led to poorer

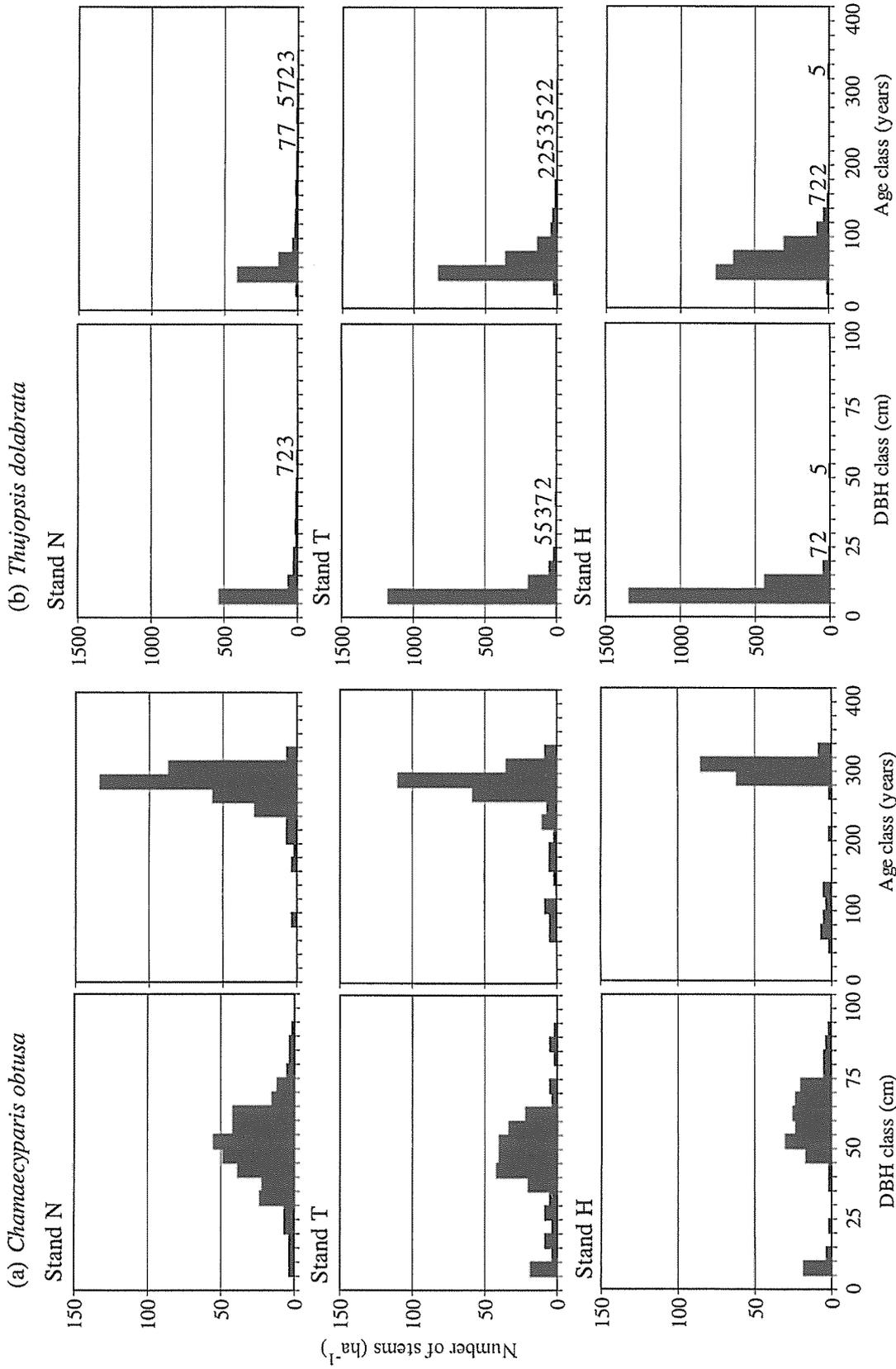


Figure 2. Size (DBH) and age class distribution of *Chamaecyparis obtusa* and *Thujopsis dolabrata* in each plot. Note the different scale of the X-axis. Stand N; without any disturbance evidence, Stand T; with severe typhoon disturbance, Stand H; with selection cuttings.

Table 4. Demographic parameters (% year⁻¹) of major tree species in each layer in three stands in an old-growth *C. obtusa* forest in the Akasawa Forest Reserve.

Species	Stand N				Stand T				Stand H						
	Recruitment	Mortality	Gain	Loss	Ingrowth	Recruitment	Mortality	Gain	Loss	Ingrowth	Recruitment	Mortality	Gain	Loss	Ingrowth
Canopy layer															
<i>C. obtusa</i>	0.00	0.10	0.26	0.05	0.26	0.21	0.07	0.41	0.08	0.31	0.00	0.00	0.16	0.00	0.16
<i>T. dolabrata</i>	0.00	0.67	0.13	0.47	0.13	1.41	0.00	1.14	0.00	0.19	0.00	0.49	0.00	0.49	
DBL-species	0.00	3.69	0.28	0.66	0.28	0.00	0.00	0.33	0.00	0.33	-	-	-	-	
All species	0.00	0.25	0.24	0.11	0.24	0.25	0.19	0.43	0.25	0.31	0.00	0.17	0.00	0.17	
Understory layer															
<i>C. obtusa</i>	0.00	2.62	0.15	3.82	0.15	1.47	0.39	1.31	0.03	0.85	0.00	4.02	1.28	1.85	1.28
<i>T. dolabrata</i>	1.36	1.46	0.74	1.24	0.33	2.27	0.79	4.21	0.63	2.78	0.33	1.90	1.03	1.28	0.93
DBL-species	0.00	4.27	1.11	4.70	1.11	2.80	0.29	8.06	4.93	3.38	0.25	0.50	2.57	0.26	2.35
All species	1.37	1.60	0.72	1.57	0.32	2.19	0.86	4.10	1.04	2.57	0.43	1.62	1.36	1.14	1.19
Total of the plot	0.88	1.12	0.27	0.21	0.25	1.59	0.78	0.92	0.40	0.78	0.43	1.50	0.42	0.24	0.38

Table 5. Number (ha^{-1}) of dead understory stems of major tree species by each mortality state.

State	<i>C. obtusa</i>	<i>T. dolabrata</i>	DBL species	
Stand N				
Standing dead	5	27	2	
Stem broken	0 (0)	32 (5)	0	(0)
Uprooted	0 (0)	15 (0)	0	(0)
Leaning	0 (0)	3 (0)	0	(0)
Unknown	0	22	3	
Stand T				
Standing dead	0	28	2	
Stem broken	0 (0)	33 (55)	0	(0)
Uprooted	1 (0)	18 (36)	0	(0)
Leaning	0 (0)	32 (53)	0	(0)
Unknown	0	8	0	
Stand H				
Standing dead	0	153	18	
Stem broken	5 (0)	132 (52)	2	(0)
Uprooted	2 (0)	15 (44)	2	(0)
Leaning	2 (0)	37 (9)	0	(0)
Unknown	0	8	2	

Ratio (%) of dead stems by frost disturbance in 1998 are given in parentheses.

development of the understory layer in this stand. The stand that had experienced typhoon disturbance (Stand T) was moderately dense, and less well stocked in terms of canopy trees. The formation of large gaps resulted in high light conditions on the surface of the understory canopy. Development of the understory layer was intermediate. In contrast, the stand that had been disturbed by human activity (Stand H) was clearly less dense (46 % of density in Stand N), and poorly stocked (63 % of basal area in Stand N) in terms of canopy trees. This situation may be the result of past selection cutting; one-third loss of basal area conforms them in the around stands with selection cuttings. Numerous medium-sized gaps, distributed fairly evenly throughout the plot, resulted in moderate light conditions on the surface of the understory canopy. The good development of the understory, including *T. dolabrata* as well as DBL species, may have been due to these light conditions.

The bimodal bell-shaped size and age distributions of *C. obtusa* show that there has been recent regeneration of this species in stands with typhoon

and human disturbances. On the other hand, the L- or inverse-J-shaped size and age distribution of *T. dolabrata* indicate recent active regeneration of this species in all stands, especially in the stand with human disturbance. Past selection cutting may have induced this active regeneration of *T. dolabrata*.

Stand dynamics and mortality

In the stand that had experienced no disturbances, mortality was observed only among canopy trees, and recruitment to the canopy layer did not occur. Under current light conditions (5.4 % of relative PPFD), understory stems are unable to grow to the canopy layer, so they grow and die within the understory; this is evidenced by the almost balanced recruitment and mortality rates during 11 years. On the contrary, continuously of size and age distribution of *T. dolabrata* in this stand is the evidence that a slightly recruitment into canopy layer was continued for a long time (Fig. 2). Most *T. dolabrata* stems are reproduced by layering (Yamamoto and Suto 1994); *T. dolabrata* juveniles remain prostrate on the ground when light conditions are unfavorable for growth and begin to grow straight up only when light conditions become favorable. For *T. dolabrata*, a small gap formation may be enough to recruit into canopy layer, because one of their favorable regeneration sites is smaller gaps (Hoshino *et al.* 2003).

In the stand with typhoon disturbance, recruitment into the canopy layer was observed; recruitment was higher than mortality for canopy trees as well as for understory trees. This higher recruitment may have been due to improved light conditions (28.5 % of relative PPFD) in the interior of this stand. Clearly, *T. dolabrata* understory stems increased between 1989 and 2000.

On the other hand, numerical changes in canopy stems did not occur in the stand disturbed by human activities. The lack of mortality may have been due to release from density-dependent mortality by selection cutting. Much higher mortality than recruitment was obvious for understory trees

in this stand, which indicated density-dependent mortality (Hoshino *et al.* 2002).

Various mortality states were observed among understory stems. In Stands N and T, dead trees tended to be physically damaged, whereas Stand H contained more standing dead. A large portion of the standing-dead mortality originated from density effects (Kikuzawa 1988; Ogawa and Hagihara 2003). Frost disturbance occurred only in the understory stems of *T. dolabrata* in Stands N and T which has canopy gaps. Understory stems of *T. dolabrata* are thin for density effects but have thick, heavy evergreen leaves at the top; they may be vulnerable to physical damages such as freezing rain or ice loads making through canopy gaps.

Especially in the understory, different effects of typhoon and human disturbances may be included into the time-lag (20 years); the different length after disturbance will produce difference of the initiation time of understory development. In the stand with typhoon disturbance, much higher recruitment and growth rates than mortality and loss rates may indicate the pre-occurrence of density-dependent mortality in the stand disturbed by human activity.

Different disturbance histories have clearly affected the structure and dynamics of this forest, although disturbance itself induced understory regeneration. Human disturbance such as selection cutting enhanced understory regeneration of *T. dolabrata* more than that of *C. obtusa*, due to the favorable light conditions for the growth of understory stems created by the cutting. Light conditions similar to small openings or the vicinity of gaps (Hoshino *et al.* 2003) may be produced by selection cutting, which then promotes the growth of understory *T. dolabrata* and DBL species.

Acknowledgements

Field assistance was provided by T. Miyadokoro, Y. Nakao and T. Hayakawa whose help is greatly acknowledged. We thank the Agematsu

District Forest Office for permitting this survey and N. Tomaru for his advice about this study. This study was partly supported by Grants-in-Aid for Scientific Research (13356003) from the Ministry of Education, Science, Sports and Culture of Japan.

Literature cited

- Barnes B.V., Zak D.R., Denton S.R. and Spurr S.H. (1998) *Forest Ecology* (4th Edition). John Wiley & Sons, New York.
- Bormann F.H. and 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. and Foster R.B. (1999) Dynamics of the forest communities at Pasoh and Barro Colorado: comparing two 50-ha plots. *Philosophical transactions of the Royal Society of London* 354: 1739–1748.
- Foster D.R. (1988) Species and stand response to catastrophic wind in central New England, USA. *Journal of Ecology* 76: 135–151.
- Franklin J.F., Spies T.A., Pelt R.V., Carey A.B., Thornburgh D.A., Berg D.R., Lindenmayer D.B., Harmon M.E., Keeton W.S., Shaw D.C., Bible K. and Chen J. (2002) Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* 155: 399–423.
- Hoshino D., Nishimura N. and Yamamoto S. (2001) Age, size structure and spatial pattern of major tree species in an old-growth *Chamaecyparis obtusa* forest, Central Japan. *Forest Ecology and Management* 152: 31–43.
- Hoshino D., Nishimura N. and Yamamoto S. (2002) Dynamics of major conifer and deciduous broad-leaved tree species in an old-growth *Chamaecyparis obtusa* forest, central Japan. *Forest Ecology and Management* 159: 133–144.
- Hoshino D., Nishimura N. and Yamamoto S. (2003) Effects of canopy conditions on the regeneration of major tree species in an old-growth *Chamaecyparis obtusa* forest in central Japan. *Forest Ecology and Management* 175: 141–152.
- Japan Meteorological Agency (1960) The feature of Isewan typhoon. *Geophysical Review* 721: 33–57 (in Japanese).
- Kikuzawa K. (1988) Intraspecific competition in a natural stand of *Betula ermanii*. *Annals of Botany* 61: 727–734.
- Kitamura S. and Murata G. (1971) *Colored Illustration of Woody Plants of Japan*. Vol. I, Hoikusya, Osaka (in Japanese).
- Kitamura S. and Murata G. (1979) *Colored Illustration of*

- Woody Plants of Japan. Vol. II, Hoikusa, Osaka (in Japanese).
- Lawton R.O. and Putz F.E. (1988) Natural disturbance and gap-phase regeneration in a wind-exposed tropical forest. *Ecology* 69: 764-777.
- Maeda T. (1951) Sociological study of *Chamaecyparis obtusa* forest and its Japan-sea elements. *Ensyurin* (Tokyo University Forest) 8: 21-44 (in Japanese with English summary).
- Maeda T. and Yoshioka K. (1952) Studies on the vegetation of Chichibu mountain forest II. The plant communities of the temperate mountain zones. *Bulletin of Tokyo University Forest* 42: 129-150 (in Japanese with English summary).
- Miura M., Manabe T., Nishimura N. and Yamamoto S. (2001) Forest canopy and community dynamics in a temperate old-growth evergreen broad-leaved forest, south-western Japan: a 7-year study of a 4-ha plot. *Journal of Ecology* 89: 841-849.
- Miyawaki A. and Okuda S. (1990) Vegetation of Japan Illustrated. Shibundo, Tokyo. (in Japanese)
- Motta R., Nola P. and Piussi P. (2002) Long-term investigations in a strict forest reserve in the eastern Italian Alps: Spatio-temporal origin and development in two multi-layered subalpine stands. *Journal of Ecology* 90: 495-507.
- Nagano Regional Forest Office (1985) Report for the Management of Akasawa *Chamaecyparis obtusa* forest (enlarged). Nagano Regional Forest Office, Nagano, 102pp. (in Japanese).
- Ogawa K. and Hagihara A. (2003) Self-thinning and size variation in a sugi (*Cryptomeria japonica* D. Don) plantation. *Forest Ecology and Management* 174: 413-421.
- Oliver C.D. and Larson B.C. (1996) Forest Stand Dynamics (Update Edition). John Wiley & Sons, New York.
- Orwig D.A. and Abrams M.D. (1994) Land-use history (1720-1992), composition and dynamics of oak-pine forests within the Piedmont and Coastal Plain of northern Virginia. *Canadian Journal of Forest Research* 24: 1216-1225.
- Pickett S.T.A. and White P.S. (eds.) (1985) The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.
- Ruffner C.M. and Abrams M.D. (1998) Relating land-use history and climate to the dendroecology of a 326-year-old *Quercus prinus* talus slope forest. *Canadian Journal of Forest Research* 28: 347-358.
- Sheil D., Burslem D.F.R.P. and Alder D. (1995) The interpretation and misinterpretation of mortality rate measures. *Journal of Ecology* 83: 331-333.
- White P.S. (1979) Pattern, process, and natural disturbance in vegetation. *Botanical Review* 45: 229-299.
- Yamamoto S. (1993) Structure and dynamics of an old-growth *Chamaecyparis obtusa* forest in the Akasawa Forest Reserve, Kiso district, Central Japan. *Japanese Journal of Forest Environment* 35: 32-41.
- Yamamoto S. (1998) Regeneration Ecology of *Chamaecyparis obtusa* and *Chamaecyparis pisifera* (Hinoki and Sawara Cypress), Japan. In *Coastally Restricted Forests* (Laderman A.D. eds.), pp.101-110. Oxford University Press, Oxford.
- Yamamoto S. and Suto A. (1994) Occurrence pattern of *Thujaopsis dolabrata* saplings in the understory of an old-growth *Chamaecyparis* forest, Akasawa Forest Reserve, Central Japan. *Journal of Japanese Forest Society* 76: 553-559.
- Yokouchi F. (1970) *Chamaecyparis* forest in the Kiso District, Nagano Prefecture. *Bulletin Botanical Society Nagano* 3: 12-18. (in Japanese)

攪乱履歴がヒノキ-アスナロ老齢林の構造と動態に与える影響

浅井孝博・星野大介・西村尚之・山本進一

異なる攪乱履歴(自然, 人為)が, 赤沢ヒノキ老齢林の構造と動態に与える影響を評価するために, 無攪乱林分, 台風攪乱林分, 択伐による人為攪乱林分の, 3林分の構造と10年間の動態を調査した。林冠ギャップ率は, 台風攪乱林分で最も高く, 無攪乱林分で最も低かった。林冠木の幹密度, 胸高断面積合計ともに無攪乱林分で最も高く大きく, 人為攪乱林分で最も低く小さかった。反対に下層木は人為攪乱林分で最も高く大きく, 無攪乱林分で最も低く小さかった。林冠木における10年間の枯死・加入は殆どない一方, 下層木でより多く発生した。台風攪乱林分において, 下層木の加入率は枯死率よりも高いが, ほか2林分では逆傾向にあった。無攪乱および台風攪乱林分における下層木の枯死状態は, 主に物理的損傷である一方, 人為攪乱林分では主に立ち枯れであった。これらの結果より人為攪乱がアスナロの更新と競争による枯死を促進させているなど, 攪乱履歴の違いに対するヒノキ老齢林の構造と動態の影響が明らかとなった。

キーワード: 人為攪乱, 自然攪乱, ヒノキ, アスナロ, ギャップ