Long-term effect of typhoon disturbance on carbon storage capability in an old-growth forest dominated by *Chamaecyparis obtusa* in central Japan

Songqiu Deng[1,*], Masato Katoh[1], Shin-ichi Yamamoto[2], Naoyuki Nishimura[3] and Daisuke Hoshino[4]

[1]Forest Measurement and Planning Laboratory, Faculty of Agriculture, Shinshu University, 8304, Minamiminowa-Vill., Kamiina-Dtrct., Nagano 399-4598, Japan.
[2]Okayama University, 2-1-1 Tsushima-naka, Kita-ku, Okayama 700-8530, Japan.
[3]Faculty of Social and Information Studies, Gunma University, Gunma 377-8510, Japan.
[4]International Research Center for Agricultural Sciences, Tsukuba 305-8686, Japan.

ABSTRACT

This study analyzed the carbon density dynamics of trees in two stands over the period 1989 to 2008. One stand was damaged by the Isewan Typhoon in 1959, while the other had grown in natural succession without disturbance. The total carbon densities of the trees in the damaged and control forests in 1989, 2000, and 2008 were 252.8±24.4, 262.7±26.9, and 272.7±24.1 and 369.9±41.9, 377.6±40.8, and 384.6±40.5 ton/ha, respectively. A T-test indicated that the total carbon density of the typhoon forest was significantly lower than that of the control forest. However, the opposite trend was observed for the regeneration of carbon density in the stands. On an annual basis, no significant difference in the carbon density of the total stand was recorded between the two forests, but in the regeneration layer, carbon density was lower in the control forest than in the damaged forest. Although the carbon density of the total stand for the control forest increased significantly over the study period, the densities of *Thujopsis dolabrata* (Asunaro) and broad-leaved tree species, which are dominant in the regeneration layer, exhibited negative trends of approximately 0.11 and -0.05 ton/ha/yr, respectively. In the damaged forest, the carbon densities of the total stand and the regeneration layer both increased over time. This study indicates that typhoon disturbance not only significantly improved the carbon sink capability of *Thujopsis dolabrata* and broad-leaved trees but also promoted the recruitment of *Chamaecyparis obtusa* (Hinoki) 30 years after the typhoon event.

Keywords: Old-growth *Chamaecyparis obtusa* forest; Carbon density; Wind damage; Long-term impact

INTRODUCTION

Forest carbon storage is easily altered in the short term by human disturbance, including over-harvesting, degradation, fire control, and conversion to non-forest uses, particularly agricultural land and pastures (Brown, 2002; Lindroth et al., 2009; McNulty, 2002). These disturbances are generally thought to alter forests into sources of CO_2 because they cause the net primary productivity (NPP) of the land to be exceeded by the total respiration or oxidation of plants, soil, and dead organic matter (Chen and Li, 2003; Grünzweig et al., 2004; Nave et al., 2010). However, suitable thinning may significantly improve the carbon storage capabilities of forests over other harvest techniques (e.g., Finkral and Evans, 2008; Gonzalez-Benecke et al., 2010; Scheller et al., 2011; Taylor et al., 2008).

Forest carbon storage is also impacted by a number

of natural causes, including large-scale wildfires, strong winds, pest and disease outbreaks, and especially long-term climate change (Brown, 2002; Ni, 2002). A great deal of research has studied the effects of climate change on forest biomass and carbon storage ability (e.g., Falloon et al., 2007; Karjalainen, 1996; Pendall et al., 2011), but relatively few studies have examined the influence of wind damage on the carbon storage capabilities of forests, especially the long-term dynamic changes due to such impacts (Lindroth et al., 2009).

Chamaecyparis obtusa is a tree species with a very high economic value in Japan, and its wood has traditionally been used in the construction of palaces. The species occurs regionally in the temperate montane zone of the Pacific side of central Japan (Yamamoto, 1998). *Chamaecyparis obtusa* is a comparatively shade-intolerant species that reproduces only by seeds, and it is difficult for the species to regenerate itself naturally under a highly closed canopy (Hoshino et al., 2003; Yamamoto, 1998).

Conversely, *Thujopsis dolabrata*, the most dominant tree species in the understories of most old-growth *Chamaecyparis obtusa* stands in the region, has a high degree of shade-tolerance (Yamamoto and Suto, 1994). Therefore, if the current conditions continue, stands of *Chamaecyparis obtusa* are likely to be gradually replaced by *Thujopsis dolabrata* (Yamamoto, 1993). As the timber of *Chamaecyparis obtusa* is valued more highly than that of *Thujopsis dolabrata*, the decline in *Chamaecyparis obtusa* regeneration will greatly decrease the economic value of this type of forest (Asai et al., 2003).

The Akazawa Forest Reserve, located in the Kiso district of central Japan, is a representative *Chamaecyparis obtusa* forest and is considered one of the three most beautiful forests in the nation (Hoshino et al., 2003). The old-growth *Chamaecyparis obtusa* stands in this reserve, like the other *Chamaecyparis obtusa* forests in the Kiso district, were probably established following a period of severe logging between 1688 and 1703 (Asai et al., 2003). From that point onward, most of the stands of the region have been protected from clear-cutting, although controlled selection cutting has been practiced locally for forest management (Nagano Regional Forest Office, 1985).

In this reserve, a small stand has been completely protected from human disturbance since its establishment, and it represents a suitable reference site for comparison with other stands managed by different measures. The stand also offers a way to assess the effects of disturbance history on forest structure and dynamics (Asai et al., 2003). In 1959, a number of old-growth *Chamaecyparis obtusa* trees distributed in the upslope of this area were damaged by the strong winds of the Isewan Typhoon, which resulted in many gaps in the stand and provided an opportunity for the invasion and growth of other tree species. Several studies have examined the effects of the typhoon on the stand structure and community dynamics of this unexploited natural forest, and research has also compared the impacts of different disturbance histories, such as natural causes and selection cutting, on old-growth *Chamaecyparis obtusa* forests (e.g., Asai et al., 2003; Hoshino et al., 2002, 2003; Yamamoto, 1993).

To evaluate the long-term influence of typhoon damage on the carbon storage capability of an old-growth forest dominated by *Chamaecyparis obtusa*, we analyzed the carbon density dynamics of trees with a DBH (Diameter at Breast Height) of larger than 5 cm in two stands over the period 1989 to 2008. One of these stands was damaged by the Isewan Typhoon in 1959, while the other had undergone natural succession with no disturbance and had been strictly protected from human interference until the present study.

The changes of the carbon storage capabilities of these two forests over the past 20 years are discussed, and the results may provide insight into the protection and regeneration of *Chamaecyparis obtusa* and the carbon sink management of forests disturbed by similar strong wind events or other natural damage.

MATERIALS AND METHODS

Study Area

The study site was located in the Akazawa Forest Reserve, an area of approximately 1046 ha at Agematsu-cho in Kiso District, Nagano Prefecture of central Japan (137°37'50"E, 35°43'57"N; for a map of the location, see Figure 1). The altitude of the reserve ranged from 1080 to 1558 m above sea level. Annual average precipitation was approximately 2500 mm, and the snow accumulation was 50-100 cm per year. The annual mean temperature was 7.8°C at an elevation of 1113 m, with the highest monthly mean 14.3°C occurring in August and the lowest -14.8°C in February (Hoshino et al., 2003). The reserve was situated on an elevated peneplain with a gentle slope on bedrock of granite, granite porphyry, and rhyolite.

The soils of the area were mainly dry and wet podzol, while brown forest soils were found on hillsides and along mountain streams (Nagano Regional Forest Office, 1985). *Chamaecyparis obtusa* approximately 300 years in age was the dominant tree species in the canopy of the reserve, with occasional associates of *Thujopsis dolabrata*, *Thuja standishii* (Kurobe or Nezuko), *Pinus parviflora* (Goyoumatsu), or several deciduous broad-leaved tree species. On the lower slopes or along mountain streams, *Chamaecyparis pisifera* (Sawara) was frequently present and dominated in some stands.

The understory of most *Chamaecyparis obtusa* stands was characterized by a dense coverage of *Thujopsis dolabrata* saplings and, in some stands, by deciduous broad-leaved shrubs. A small amount of

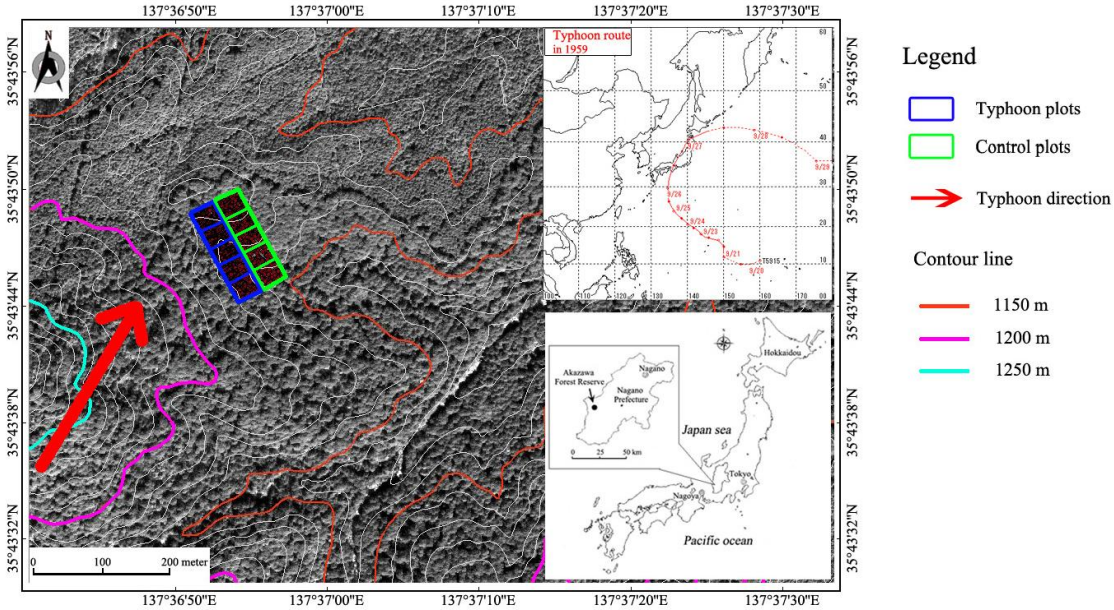

Figure 1. Location of the Akazawa Forest Reserve and the environment of the two stands during the Isewan Typhoon.

regenerating *Chamaecyparis obtusa* was observed randomly distributed in bright areas (Hoshino et al., 2002).

Although the study area had been protected from human disturbances for over 200 years, occasional strong typhoons have been a major source of natural disturbance. In 1959, the Isewan Typhoon severely disturbed the forests in the reserve. At the Gifu Weather Station, 90 km southwest of the reserve, the average wind velocity of and the lowest air pressure recorded for the Isewan Typhoon were 32.5 $m \cdot s^{-1}$ and 956 h Pa, respectively (Hoshino et al., 2002). The Isewan Typhoon was internationally named as Vera, and the storm made landfall at Shionomisaki in southern Japan on September 26, 1959 with a central pressure of 920 h Pa and wind speeds of 60 m/s (For the route of the typhoon, see Figure 1).

Field Measurements

In the reserve, one small natural stand dominated by *Chamaecyparis obtusa* had been strictly preserved from human disturbance since its establishment. In 1959, however, a number of old-growth *Chamaecyparis obtusa* trees distributed in the upslope of this area were damaged by the strong winds of the Isewan Typhoon. Most of the dead and downed tree boles produced by the hurricane were removed from the reserve (Hoshino et al., 2002).

To evaluate the long-term influence of the typhoon on the carbon storage of the old-growth natural stand, ten permanent 40×30 m plots were established in the area in 1989. Five of these plots showed no evidence of either human or natural disturbance and were designated as the control plots (CP) CP-A, CP-B, CP-C, CP-D and CP-E. The others plots, designated TP-A, TP-B, TP-C, TP-D and TP-E, were established in the area damaged by the typhoon. These plots were paired (e.g., CP-A and TP-A, CP-E and TP-E) by slope characteristics and environmental condition. The borders of the plots were adjacent (Figure 1). The results of the forest inventory at the three sampling points are discussed in results section.

All of the trees with a DBH of larger than 5.0 cm were surveyed, and DBH and coordinate measurements were taken in 1989, 2000 and 2008. Each surveyed stem was tagged with a label for the following census. In the case of multi-stemmed shrubs, each individual stem with a DBH of over 5.0 cm was measured. Each stem was identified by species and classified as either live or dead. The stems were mapped to the nearest 0.1 m and measured to the nearest 0.1 cm DBH. A random sample of 105 trees from the ten plots was measured for height and DBH in 2011, and the height of all of the trees at the different sampling points was estimated by regression models between height and DBH. Finally, all of data were saved in a database created by ArcGIS v9.2 for the spatial distribution analyses of carbon storage.

Additionally, the regenerated trees in every plot at the three sampling points were defined by the following method: First, all of the trees with DBH≤5.0 cm in 1959 were considered as the regeneration layer. The average growth rate of old-growth *Chamaecyparis obtusa* was then approximated using the largest tree in the stand, which had a size of 101.3 cm and an age of approximately 300 years, yielding a rate of 0.3377 cm/yr. We assumed

Table 1. The average growth rates (T_{avg}) of different species (cm/yr)

Forest	Species	Min	Max	Avg.	σ	T_{avg}
Control forest	*Chamaecyparis obtusa*	0.0050	0.0352	0.0156	0.0127	0.0409
	Thujopsis dolabrata	0.0050	0.1491	0.0299	0.0214	0.0727
	Broad-leaved trees	0.0017	0.0821	0.0459	0.0267	0.0994
	Others	0.0017	0.1491	0.0304	0.0203	0.0710
Typhoon forest	*Chamaecyparis obtusa*	0.0017	0.3870	0.1276	0.1181	0.3638
	Thujopsis dolabrata	0.0017	0.4540	0.0827	0.0747	0.2322
	Broad-leaved trees	0.0050	0.4088	0.0998	0.0981	0.2960
	Others	0.0168	0.4674	0.1719	0.1300	0.4319

Table 2. Calculation method for the volume (V) of individual trees

Species	DBH class (cm)	Volume formula (v: m^3; d: cm; h: m)
Chamaecyparis obtusa; *Chamaecyparis pisifera*	4-10	$logv$=-5+0.7736171+1.9709522$logd$+0.8801095$logh$
	12-20	$logv$=-5+0.6285839+1.9688490$logd$+1.0166030$logh$
	22-30	$logv$=-5+0.5657307+1.9418846$logd$+1.0942478$logh$
	32-40	$logv$=-5+0.6175452+1.9125607$logd$+1.0814890$logh$
	42-50	$logv$=-4+0.0134394+1.7022045$logd$+1.0390683$logh$
	over 52	$logv$=-5+0.8936810+1.7516722$logd$+1.0694202$logh$
Thujopsis dolabrata	6-10	$logv$=-5+0.7908348+1.9183687$logd$+0.8966176$logh$
	12-20	$logv$=-5+0.8124379+1.7120116$logd$+1.1141249$logh$
	22-30	$logv$=-5+0.2613485+2.1613151$logd$+1.0727478$logh$
	over 32	$logv$=-5+0.7938255+1.7750576$logd$+1.0946404$logh$
Pinus parviflora	4-10	$logv$=-5+0.7639+1.7700$logd$+1.0987$logh$
	12-20	$logv$=-5+0.71335+1.78364$logd$+1.13056$logh$
	22-40	$logv$=-5+0.65368+1.88856$logd$+1.067932$logh$
	over 42	$logv$=-4+0.063020+1.683851$logd$+0.985842$logh$
Broad-leaved trees	4-20	$logv$=-5+0.7372896+1.8447874$logd$+1.0088782$logh$
	22-30	$logv$=-5+0.5794780+1.8292605$logd$+1.1567557$logh$
	32-40	$logv$=-5+0.3896770+1.8435209$logd$+1.2867129$logh$
	over 42	$logv$=-5+0.7740694+1.7769320$logd$+1.0830437$logh$

Table 3. Coefficients for the calculation of biomass

Species	D	E		R	φ
		Under 20 yr	Over 20 yr		
Chamaecyparis obtusa	0.407	1.55	1.24	0.26	0.5
Chamaecyparis pisifera	0.407	1.55	1.24	0.26	0.5
Thujopsis dolabrata	0.314	1.57	1.23	0.25	0.5
Pinus parviflora	0.451	1.63	1.23	0.26	0.5
Broad-leaved trees	0.622	1.45	1.30	0.26	0.5

that the stand had a maximum growth rate of 0.5 cm/yr over the past 50 years (1959-2008) because the DBH of *Chamaecyparis obtusa* was 30.0 cm (0.5×50+5.0) in 2008.

We then used 30.0 cm as a threshold value to calculate the growth rate of the other species in the stand. All of the trees alive in 1989, 2000, and 2008 with DBH≤30.0 cm in

2008 were selected, and their growth rates (*T*) were calculated using the following formula (1):

$$T = (DBH_{2008} - DBH_{1989})/19 \quad (1)$$

Second, because differences in environmental conditions result in different growth rates for individual trees (especially for regenerated trees), the growth rates of individual trees in the two forests were calculated separately. The average growth (T_{avg}) of different species, including *Chamaecyparis obtusa*, *Thujopsis dolabrata*, broad-leaved trees, and others, were estimated using the following formula (2):

$$T_{avg} = \sum T / N + 2\sigma \quad (2)$$

where σ is the standard error of the growth rate (*T*) of individual trees by species, and *N* is the number of individuals. The results are listed in Table 1. Therefore, in the control forest, *Chamaecyparis obtusa* with DBH≤6.2 cm (0.0409×30+5.0) in 1989, DBH≤6.7 cm (0.0409×41+5.0) in 2000, and DBH≤7.0 cm (0.0409×49+5.0) in 2008 were considered as regenerated trees from the 1959 event. In the typhoon forest, *Chamaecyparis obtusa* with DBH≤15.9 cm (0.3638×30+5.0) in 1989, DBH≤19.9 cm (0.3638×41+5.0) in 2000 and DBH≤22.8 cm (0.0409×49+5.0) in 2008 were classified as regenerated trees.

Individual trees of the other species in the two forests were classified as regenerated using the same method (*Thujopsis dolabrata*: 7.2, 8.0, 8.6, and 12.0, 14.5, 16.4 cm; broad-leaved trees: 8.0, 9.1, 9.9, and 13.9, 15.1, 19.5 cm; others: 7.2, 7.9, 8.5, and 18.0, 22.7, 26.2 cm in the control forest and typhoon forest in 1989, 2000, 2008, respectively).

Data Analysis

The carbon contents of individual trees were calculated by the following formula (Katoh, 2010):

$$C = V \times D \times E \times (1+R) \times \phi \quad (3)$$

where *C* is the carbon storage of an individual tree (ton), including aboveground and underground biomass, *V* is the volume (m^3), *D* is the bulk density ($g \cdot cm^{-3}$), *E* is the expansion coefficient reflecting the ratio of the branches and leaves for the individual tree, *R* is the ratio of the underground and aboveground parts of the individual tree, and ϕ is the carbon content fraction of the biomass. In this study, the calculation of the volume (*V*) of individual trees was based on the work of the Japan Forestry Agency (2007) (Table 2), and the values of the other coefficients for the different tree species were derived from Katoh (2010) (Table 3).

The carbon densities for *Chamaecyparis obtusa*, *Thujopsis dolabrata*, broad-leaved trees and other trees in every plot were calculated for the total stand and the regenerated trees in 1989, 2000 and 2008. The equation for carbon density in a plot is as follows:

$$M = \frac{10000}{S} \sum C_i \quad (4)$$

where *M* is the carbon density in the plot (ton/ha), $\sum C_i$ is the sum of the carbon storage of the individual trees in the plot (ton) (calculated by equation 1), and *S* is the area of the plot (m^2).

Additionally, although the carbon contents of trees that died over the period 1989 to 2008 were released into the atmosphere by decomposition, the release of carbon occurs over a number of years. Therefore, the changed in carbon density for every plot in the year 2000 were calculated by the following formula:

$$\Delta D_{2000} = M_{2000} - M_{1989} \quad (5)$$

where ΔD is the change in carbon density (ton/ha), and *M* is carbon density (ton/ha). The annual change of carbon density in the year 2000 was obtained using the annual increment divided by 11 years:

$$\Delta A_{2000} = \Delta D_{2000}/11 \quad (6)$$

where ΔA is the annual increment (ton/ha/yr).

The ΔD and ΔA of the carbon density in 2008 were calculated using the same methods. Finally, the differences in carbon density between the control stand and the typhoon stand were tested by the paired samples T-test in SPSS 13.0 software.

RESULTS

Basic Characteristics of the Two Forests

As can be seen in the DBH class structure, the two forests were dominated by trees with DBH≤20 cm throughout the study period, and the ratio of this class in the typhoon stand was higher than that of the non-disturbed stand (Figure 2). Conversely, the number of trees with a DBH of greater than 50 cm exhibited the opposite pattern. The total stem density of the damaged stand was greater than 2000 stems/ha throughout the study period, a value two times that of the control stand (Figure 3). *Thujopsis dolabrata* was clearly a dominant species in terms of density for both stands from 1989 to 2008, but *Chamaecyparis obtusa* was also dominant in the non-disturbed forest (Figure 3).

Additionally, the number of broad-leaved trees in the typhoon plots was greater than that in the control plots, while the number of *Chamaecyparis obtusa* was less, presumably because a number of these trees were damaged by the strong wind. The average stem density of the typhoon plots was approximately four times that of the control plots in 1989, 2000 and 2008 (Figure 4). The regeneration layer of the typhoon plots was mainly composed by *Thujopsis dolabrata* and broad-leaved trees, whereas *Thujopsis dolabrata* was the only dominant

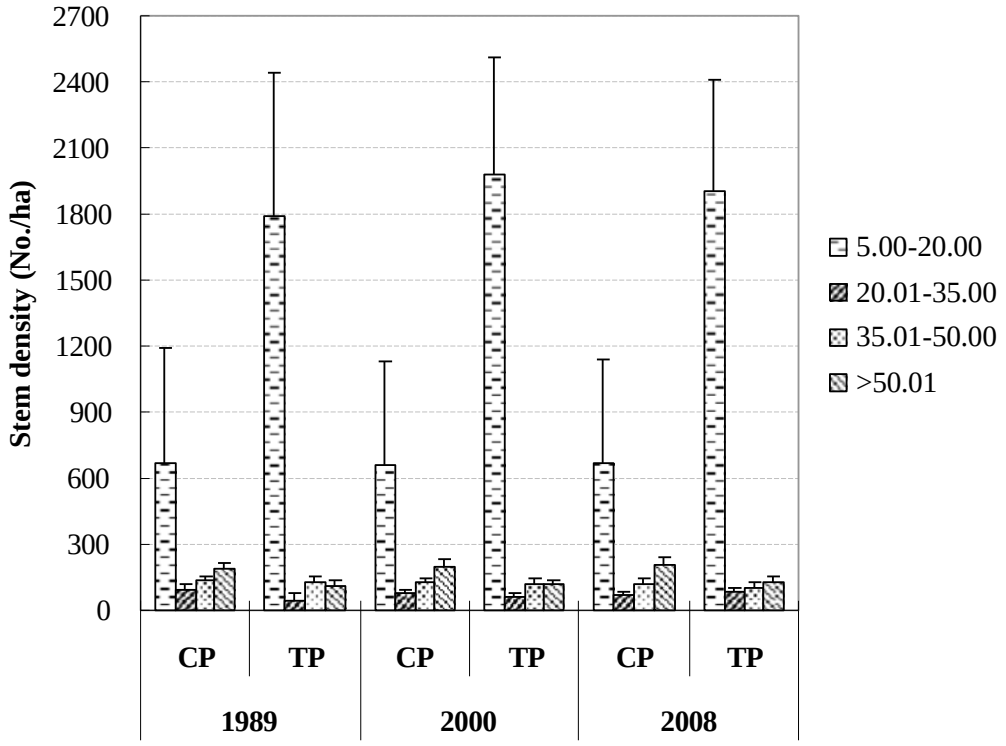

Figure 2. DBH class (cm) structure of the two forests at three sampling points. CP: control plots; TP: typhoon plots.

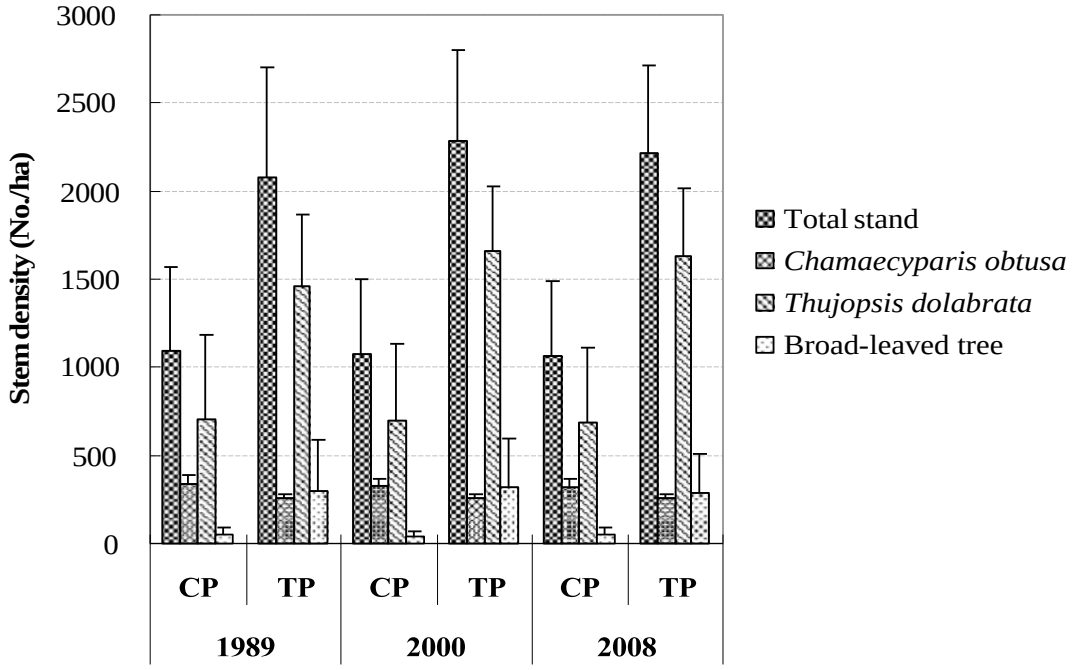

Figure 3. Stem density of all live trees in the two forests at three sampling points.

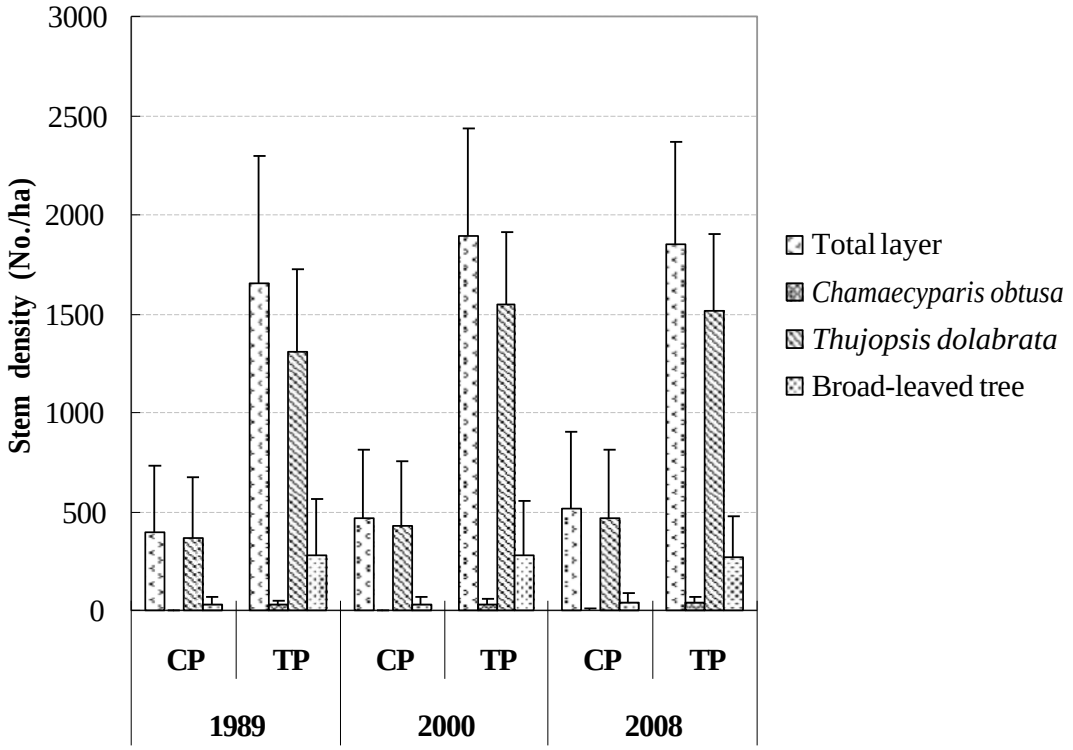

Figure 4. Stem density of regenerated trees in the two forests at three sampling points.

species in the regeneration layer of the control forest.The average DBH of the total stand for the non-disturbed forest approached 27.0 cm, while it was only 14.0 cm in the typhoon forest (Figure 5). *Chamaecyparis obtusa*, the dominant species in terms of DBH or basal area, had average DBH values of greater than 50 cm and 45 cm in the control stand and damaged stand, respectively, with little growth observed from 1989 to 2008.

However, average DBH was approximately 10 cm for *Thujopsis dolabrata*, and the DBH for this species was greater in the control plots than in the typhoon plots. Regarding the vertical structure of the two stands, the average tree height of the control plots was approximately 15 m, while it was only 10 m in the typhoon plots (Figure 6). *Chamaecyparis obtusa* was the only canopy tree species in the studied plots, whereas *Thujopsis dolabrata* and broad-leaved trees were distributed mainly in the understory with heights of less than 10 m. Differences of Carbon Density between Two Forests in 1989, 2000 and 2008.The average carbon densities of the live trees in the control plots were approximately 369.9±41.9, 377.6±40.8 and 384.6±40.5 ton/ha in 1989, 2000 and 2008 respectively; these values greatly exceeded those of the typhoon plots for the same sampling points (252.8±24.4, 262.7±26.9 and 272.7±24.1 ton/ha) (Figure 7).

Although the study area was located in central Japan, which was generally impacted by the typhoon to a lesser degree than the coastal regions, and only partial stems in the top layer of the forests were destroyed by the typhoon, the biomass loss of live trees due to the typhoon was much higher than that measured in coastal forests by other studies (Chambers et al., 2007; Chapman et al., 2008). This result is due to the domination of the forest in the present study by large old-growth trees with high amounts of biomass. In terms of the different species, the carbon density of the two forests was dominated by *Chamaecyparis obtusa* throughout the study, and the ratio of this species in the control plots was higher than that in the typhoon plots.

Although *Thujopsis dolabrata* was clearly the dominant species in terms of stem density, its carbon densities in the two stands at each of the sampling points were less than 40 ton/ha. The carbon densities of the broad-leaved trees in the total stand exhibited no significant differences between the two forests and were less than the densities of *Chamaecyparis obtusa* and *Thujopsis dolabrata*.

The average annual change of carbon density for the total stand in the typhoon plots was 1.07 ton/ha/yr, a value higher than that of the non-typhoon plots (0.79 ton/ha/yr) (Figure 8). However, the carbon accumulation in the damaged forest was much lower in comparison to

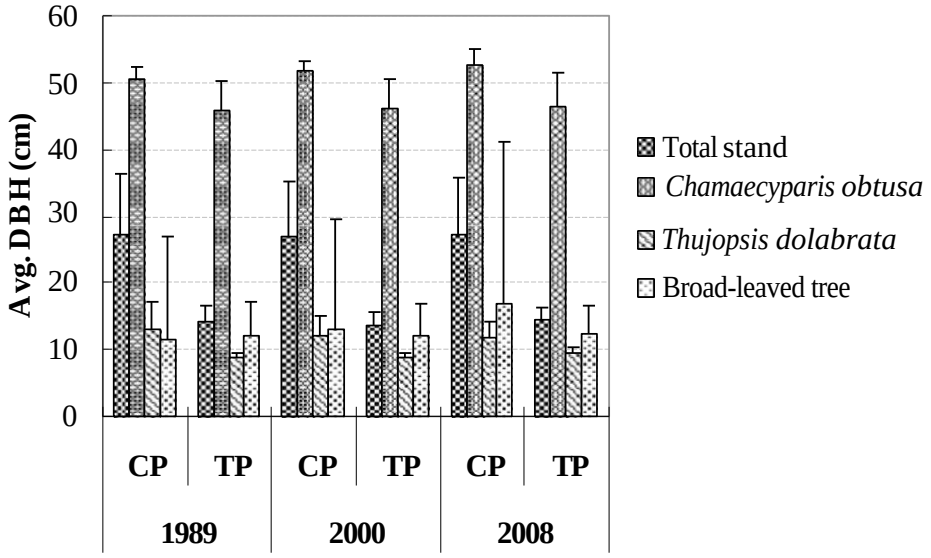

Figure 5. Average DBH of the total stand and the main tree species at three sampling points (cm).

previous results for a tropical wet forest after hurricane damage (2.68±0.39 ton/ha/yr) (Mascaro et al., 2005). The carbon accumulation in the damaged forest was also slow relative to previous studies on forest regeneration conducted in southern Hokkaido in northern Japan, where a typhoon event catastrophically destroyed a 45-year-old Japanese larch plantation, knocking down approximately 90% of the trees in the area (Sano et al., 2010). However, the rate of carbon accumulation in the typhoon plots was higher than that observed in another temperate forest over 300 years in age (Uriarte and Papaik, 2007).

In the regeneration layer of the two forests, the majority of the carbon in live trees was present in *Thujopsis dolabrata* and the broad-leaved trees, and the carbon densities in typhoon stand were significantly higher than those of the control stand throughout the study (Figure 9). Furthermore, the growth of carbon density in the regeneration layer of the control plots was less than 1.0 ton/ha over the two sampling periods, while it was more than 4.0 ton/ha in most of the typhoon plots and reached 6.2 ton/ha in TP-C. The annual rate of change in the carbon density of the regenerated trees in the control stand was less than 0.04 ton/ha/yr, lower than the 0.46 ton/ha/yr observed for the damaged stand (P<0.01) over the course of the study (Figure 8).

The paired samples T-test indicated that for the total stand, carbon density in the typhoon forest was significantly less than that of the control forest (P<0.05) throughout the study (Table 4), a result primarily due to the collapse of several large *Chamaecyparis obtusa* individuals damaged by the typhoon.

However, the carbon density of the regenerated trees in the typhoon stand was higher than that of the control stand (P<0.01) over the study period (Table 4). The annual change in carbon density did not significantly differ (P>0.05) between the total stands of the two forests, while for the regeneration layers, the rate was significantly lower in the non-disturbed forest than in the damaged stand (P<0.05) (Table 5).

Changes in the Pattern of Carbon Density in Each Stand over Time

For the total stands of the two forests, the average annual changes of total carbon density in the typhoon plots were 0.90 and 1.25 ton/ha/yr in 1989-2000 and 2000-2008, respectively; these values are greater than those of the control plots, 0.70 and 0.88 ton/ha/yr, respectively, for the two sampling periods (Figure 8). Additionally, in terms of species, the carbon sink capacity of *Chamaecyparis obtusa* in the typhoon stand was slightly higher from 1989 to 2000 than from 2000 to 2008, with values of 0.68 and 0.65 ton/ha/yr, respectively, while the results for *Thujopsis dolabrata* exhibited the opposite pattern, with values of 0.35 and 0.41 ton/ha/yr, respectively.

In the control stand, however, the average annual change of carbon sink capacity for *Chamaecyparis obtusa* was lower in 1989-2000, with a value of 0.81 ton/ha/yr, than in 2000-2008, with a value of 0.97 ton/ha/yr. The carbon densities of *Thujopsis dolabrata* and broad-leave trees decreased at rates of approximately -0.11 and -0.05

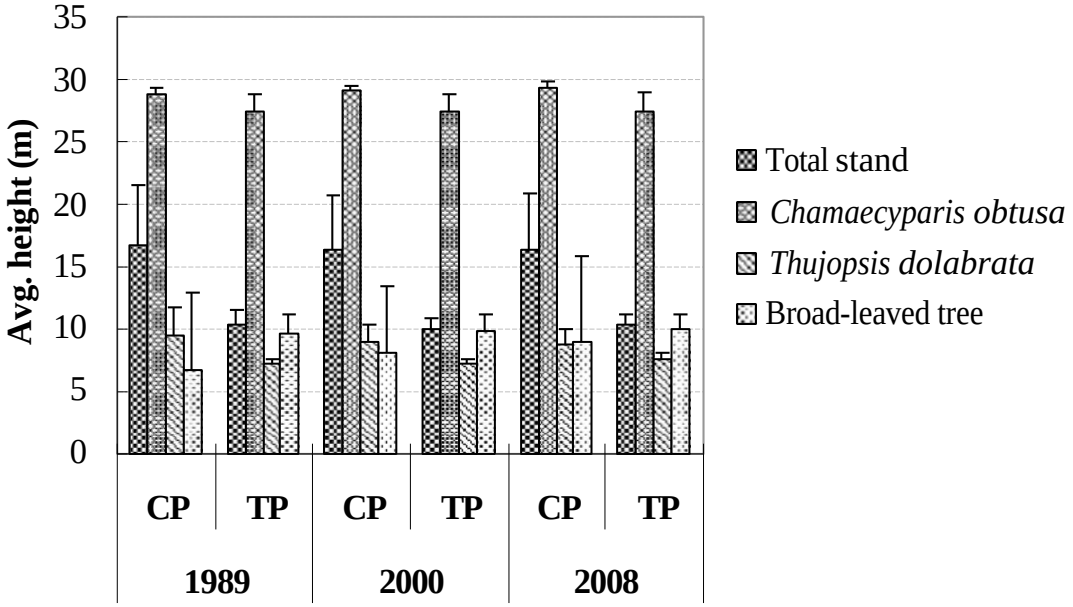

Figure 6. Average tree height of the total stand and the main tree species at three sampling points (m).

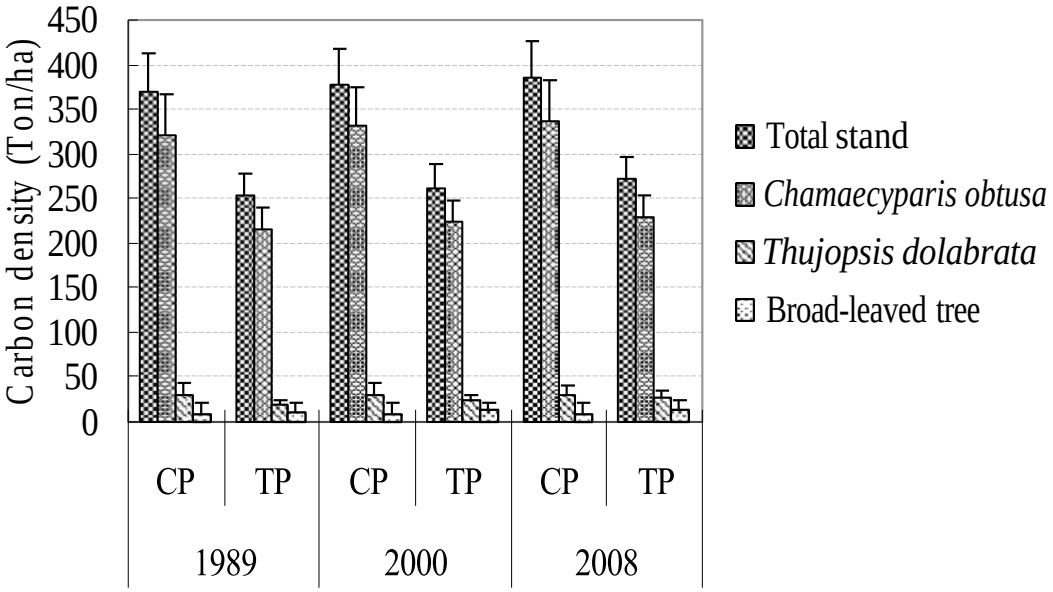

Figure 7. Carbon density of all trees in the total stand of the two forests at three sampling points.

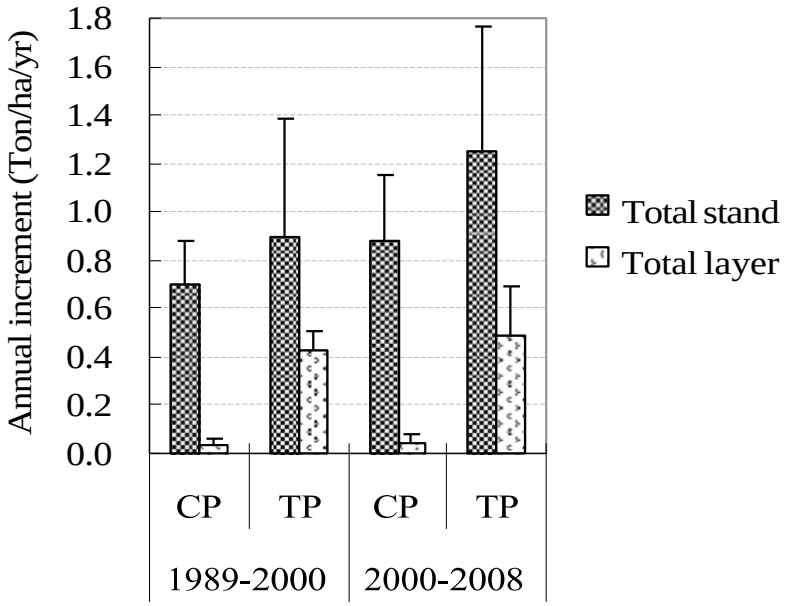

Figure 8. Annual changes in the carbon densities of the total stand and the regeneration layer over two sampling periods.

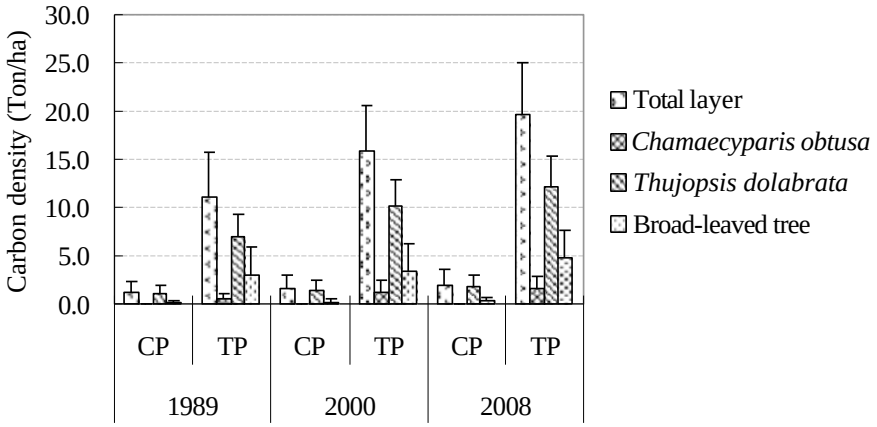

Figure 9. Carbon density of regenerated trees in the two forests at three sampling points.

Table 4. Paired samples T-test for the carbon density of live trees in the two forests at three sampling points (Ton/ha)

Group	Year	Pair	Mean	Std. deviation	Sig. (2-tailed)
Total stand	1989	CP-TP	117.094	66.259	0.017*
	2000	CP-TP	114.942	68.168	0.020*
	2008	CP-TP	111.965	66.765	0.020*
Regenerated trees	1989	CP-TP	-9.853	4.154	0.006**
	2000	CP-TP	-14.154	4.283	0.002**
	2008	CP-TP	-17.668	4.827	0.001**

* Significant at the 0.05 level.
** Significant at the 0.01 level.

Table 5. Paired samples T-test for the annual change in carbon density in the two forests over two sampling periods (Ton/ha/yr)

Group	Period	Pair	Mean	Std. deviation	Sig. (2-tailed)
Total stand	1989-2000	CP-TP	-0.196	0.705	0.568^{ns}
	2000-2008	CP-TP	-0.372	0.350	0.076^{ns}
Regenerated trees	1989-2000	CP-TP	-0.391	0.106	0.001**
	2000-2008	CP-TP	-0.439	0.237	0.014*

Ns: not significant.
* Significant at the 0.05 level.
** Significant at the 0.01 level.

Table 6. Paired samples T-test for differences of carbon density in the two forests between different sampling periods (Ton/ha)

Forest	Group	Pair	Mean	Std. deviation	Sig. (2-tailed)
CP	Total stand	2000-1989	7.712	2.119	0.001**
		2008-2000	7.021	2.425	0.003**
	Regenerated trees	2000-1989	0.386	0.314	0.052^{ns}
		2008-2000	0.369	0.339	0.072^{ns}
TP	Total stand	2000-1989	9.864	8.476	0.045*
		2008-2000	9.998	4.587	0.008**
	Regenerated trees	2000-1989	4.686	0.963	0.000**
		2008-2000	3.884	1.855	0.009**

Ns: not significant.
* Significant at the 0.05 level.
** Significant at the 0.01 level.

control forest, less than 0.05 ton/ha/yr over the study carbon density change for the regenerated trees in the recorded for the second sampling period (Figure 8). However, the most striking result is the very low value of ton/ha/yr respectively, over the study period. In the damaged forest, the annual change of carbon density for the regenerated trees was 0.43 ton/ha/yr from 1989 to 2000, a value slightly lower than the 0.49 ton/ha/yr period. Although the carbon sink capacity of *Chamaecyparis obtusa* in the regeneration layer of the typhoon stand only increased by approximately 0.05 ton/ha/yr from 1989-2008, the carbon densities of *Thujopsis dolabrata* and broad-leave trees both increased significantly, with speeds of approximately 0.3 and 0.1 ton/ha/yr, respectively. Conversely, in the control stand, the carbon densities of *Chamaecyparis obtusa*, *Thujopsis dolabrata* and broad-leaved trees in the regeneration layer exhibited no positive (or even slightly negative) changes over the study.

The paired samples T-test was also used to analyze the differences in carbon density for each stand between different sampling periods of the study. In the non-disturbed forest, the carbon density of the total stand exhibited significant growth at the 0.01 level from 1989 to 2000, as well as from 2000 to 2008 (Table 6). However, the layer of regenerated trees exhibited only a small and non-significant increase in carbon density over the two periods (P>0.05).

In the damaged forest, the carbon storage of the total stand in the year 2000 was significantly greater than in 1989 (P<0.05), and the carbon density in 2008 was significantly greater than in 2000 at the 0.01 level. Additionally, the carbon density of the regenerated trees in the typhoon forest showed significant increases at the 0.01 level from 1989-2000 and also from 2000-2008 (Table 6).

Impact of Typhoon Disturbance on Recruitment of *Chamaecyparis obtusa*

Chamaecyparis obtusa has a very high economic value in Japan, and it has been the target species for protection in the study reserve from its inception. However, the species is comparatively less shade-tolerant and does not easily regenerate itself under highly closed canopy conditions. Therefore, in this study, the impact of typhoon disturbance on the recruitment of young *Chamaecyparis obtusa* is examined separately. From 1989 to 2000, the average stem density of *Chamaecyparis obtusa* distributed in the

regeneration layer of the control forest showed no change, while it increased by 0.7 stem/ha/yr in the typhoon stand.

The annual change of this value in the non-disturbed forest from 2000-2008, 0.4 stem/ha/yr, was also lower than that of the typhoon forest over the entire study, 0.9 stem/ha/yr. The carbon density of *Chamaecyparis obtusa* in the control stand exhibited no change from 1989-2000, while it increased by 0.063 ton/ha/yr in the damaged forest. From 2000 to 2008, the carbon density of the species increased by 0.043 ton/ha/yr in the typhoon stand, a rate significantly higher than the 0.002 ton/ha/yr observed in the control forest. The above data indicate that typhoon disturbance to some extent promoted the growth and regeneration of young *Chamaecyparis obtusa* trees.

DISCUSSION

In this study, the total carbon density of the typhoon forest was found to be significantly lower than that of the control forest (Figure 7), although the total stem density of the damaged forest was greater than that of the non-disturbed forest (Figure 3). The significant number of trees collapsed by the typhoon explained the difference in total carbon storage between the two stands. This damage also resulted in the formation of many large gaps in the typhoon stand, which provided a favorable environment for the regeneration of *Thujopsis dolabrata* and broad-leaved trees; the density of these species in the typhoon forest was four times that of the non-disturbed forest. In terms of species, the carbon density of the two forests was dominated by *Chamaecyparis obtusa*, and the ratio of this species was higher in the control plots than in the typhoon plots; *Chamaecyparis obtusa* was the only dominant species in the canopy layer, and its DBH or volume far exceeded that of the other species (Figure 5).

The differences in canopy conditions altered the light environment of the understory. The sites under the typhoon stand were significantly brighter than those under the control stand. In addition, the decreased density of *Chamaecyparis obtusa* cover in the typhoon stand provided more space for the invasion and growth of other tree species and reduced the competition between populations, allowing *Thujopsis dolabrata* and broad-leaved trees to grow at high speeds and significantly increase their carbon densities. In the non-disturbed forest, however, the closed canopy created a serious shortage of light in the understory, restricting the growth of *Thujopsis dolabrata* despite its high shade-tolerance. When the species reached a certain size in this environment, its photosynthetic rate was unable to match the demands of respiration, preventing growth and even leading to death. Consequently, the number of *Thujopsis dolabrata* and the average DBH of the species decreased over the study period, resulting in the observed negative change in carbon density.

This impact was more obvious for broad-leaved trees, whose density showed little change but whose average DBH was significantly reduced over time. Moreover, the population of *Thujopsis dolabrata* may also have been impacted by the density effect (Hoshino et al., 2003; Yamamoto, 1993), which has been vertified by a number of studies in different forest types (Long and Smith, 1984; Solomon and Zhang, 2002; Zeide, 1987; Zhang et al., 2007).

Although the density of the *Chamaecyparis obtusa* distributed in the understory did not increase as quickly as that of *Thujopsis dolabrata* and broad-leaved trees, its stem number and the sum of its carbon storage in the regeneration layer of the typhoon stand were significantly greater than of the same variables in the control stand, indicating that typhoon disturbance also promoted the growth and regeneration of young *Chamaecyparis obtusa* trees. However, the increases in stem number and carbon density from 2000-2008 were lower than those observed from 1989-2000, most likely due to the canopy closure of fast-growing *Thujopsis dolabrata* and broad-leaved trees in the typhoon forest during the 1990s. This canopy closure was a significant detriment to the growth of small *Chamaecyparis obtusa* trees in the understory and led to the decrease of the average carbon content in individual trees observed from 2000 to 2008.

Therefore, while the typhoon disturbance promoted the regeneration of young *Chamaecyparis obtusa* from 30 to 50 years after the event due to the favorable light environment and wide space created, in the species is currently at a competitive disadvantage with *Thujopsis dolabrata* and broad-leaved trees due to its lower growth speed and higher light requirements. If management is not conducted to promote the recruitment of *Chamaecyparis obtusa*, it will be difficult for this species to reassume dominance in the future. When the old-growth individuals of the species finally disappear from the canopy layer due to natural death or damage by disease or insects, the forest will be gradually dominated by *Thujopsis dolabrata*. In 2011, several thinning experiments on *Thujopsis dolabrata* were conducted in a secondary forest derived from clear cutting and dominated by *Thujopsis dolabrata* and *Chamaecyparis obtusa* with the aim of protecting the latter species. The effects of these measures should be analyzed in further studies.

CONCLUSION

The present study analyzed the carbon density dynamics of the trees in two stands from 1989 to 2008. One of these stands had been damaged by the Isewan Typhoon in 1959, while the other had undergone natural succession. The differences of carbon density between the two forests were analyzed for the three sampling points 1989, 2000,

and 2008.

The results indicated that for the total stands, the carbon density in the typhoon forest was significantly lower than that of the control forest. However, the opposite trend was observed for the carbon density of regenerated trees. Although the growth rate of the damaged forest was slightly higher than that of the non-disturbed forest, the T-test showed no significant difference in the carbon densities of the total stand between the two forests. In the regeneration layer, however, the rate of carbon increase was significantly lower in the control forest than in the damaged forest. Despite the increase in the carbon densities of the total stand observed over the study period in the control forest, *Thujopsis dolabrata* and broad-leaved trees, the dominant species in the regenerated layer, had decreasing carbon densities over time. However, in the typhoon forest, the carbon densities of both the total stand and the regenerated trees exhibited significant growth. Finally, because *Chamaecyparis obtusa* was the target species of conservation and has a very high economic value in the study area, the effect of typhoon disturbance on the recruitment of young *Chamaecyparis obtusa* was discussed briefly in this study. The results suggested that the typhoon disturbance promoted the growth and regeneration of young *Chamaecyparis obtusa* trees to some extent. A further study on the recruitment and management of *Chamaecyparis obtusa* after typhoon disturbance should be conducted.

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