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論　文（Original article）

Effects of typhoons on leaf fall in hinoki cypress (*Chamaecyparis obtusa* Endlicher) plantations in Shikoku Island

Yoshiyuki INAGAKI[1)*], Shigeo KURAMOTO[2)], and Hidehisa FUKATA[3)]

Abstract

Leaf fall was measured for 5 years (2002-2006) in adjacent thinned and unthinned plantations of hinoki cypress (*Chamaecyparis obtusa* Endlicher) at two different elevations in Kochi Prefecture, Shikoku Island, Japan. The region was hit by severe typhoons in 2004 and annual leaf fall in that year was 1.17- 2.25 times greater than that in the pre-typhoon period (2002-2003). The effect of the typhoons on annual leaf-fall was greater at the higher elevation. At each elevation, the effect was greater in the thinned plots than in the unthinned plot. Post-typhoon annual leaf-fall (2005-2006) was 1.05- 1.41 times greater than that in the pre-typhoon period (2002-2003). Although the impact of typhoons was greater in the thinned plots, the recovery of leaf litter was not different between the thinned and unthinned plots. The time of leaf fall in the typhoon year became earlier in forests at the higher elevation. At the lower elevation, leaf-fall duration increased in 2004 but the time of leaf fall did not change. The results indicate that susceptibility to strong winds is different between higher and lower elevations: greater leaf fall occurs immediately after strong winds at higher elevations, whereas leaves do not fall immediately after strong winds and damaged leaves fall gradually at lower elevations. These results suggest that the annual leaf fall can be recovered rapidly and that new leaf production may increase substantially after typhoon disturbance.

Key words : hinoki cypress; leaf litter; phenology; recovery; thinning; typhoon

1.Introduction

Typhoons are a major cause of climatic damage to Japanese forests (Kuboyama et al., 2003; Kamimura and Shiraishi, 2007). Many studies have been conducted on uprooting and stem breakage by strong winds and their relation to topography, soil and forest conditions (Kuboyama et al., 2003; Saito and Sato, 2007; Kamimura and Shiraishi, 2007; Kato and Zushi, 2008). In 2004, Japan was struck by many severe typhoons (Typhoon Research Department, 2006) and some forests were critically damaged (Kamimura and Shiraishi, 2007; Kato and Zushi, 2008). Strong winds can cause defoliation of crowns (Takeuchi et al., 2007; Inagaki et al., 2008a).

Defoliation by strong winds can be evaluated by litterfall measurement. Previous studies have investigated the effect of storms on leaf and branch fall in tropical ecosystems (Vogt et al., 1996; Harrington et al., 1997; Herbert et al., 1999) and evergreen hardwood forests (Xu et al., 2004; Sato, 2004), and conifer plantations in Japan (Saito, 1981; Takeuchi et al., 2007, Inagaki et al., 2008a, 2008b). In hinoki cypress plantations, the effects of typhoons have been evaluated by long-term observations of a single stand (Saito, 1981; Inagaki et al., 2008b) and by comparison of several forests in relation to slope direction (Takeuchi et al., 2007) or thinning practices (Inagaki et al., 2008a). Inagaki et al. (2008a) have revealed that the impact of severe typhoons in 2004 was greater in thinned plots than in adjacent unthinned plots in a hinoki cypress plantation in Kochi Prefecture. However, there is no information on leaf litter production after the disturbance and its relation to thinning practices.

The time of leaf fall becomes earlier when forests suffer strong winds (Inagaki et al., 2008a, 2008b). If trees are damaged by strong winds, there would be a significant change in leaf-fall phenology. Several studies have reported that the time of leaf-fall is related with slope position (Tateno et al., 2005) whereas leaf-fall duration is related precipitation (del Alco et al., 1991) or solar radiation (Inagaki et al., 2008b). These studies indicate that leaf-fall phenology is related with water stress of plants as well as temperature. If trees are damaged, trees suffer severe water stress (Muramoto et al., 1998; Ueda and Shibata, 2004) and the time of leaf fall may occur earlier or the leaf fall duration may become longer.

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1) Department of Forest Site Environment, Forestry and Forest Products Research Institute (FFPRI)
2) Hokkaido Research Center, Forestry and Forest Products Research Institute (FFPRI)
3) Kochi Prefectural Forestry Technology Research Center
* Department of Forest Site Environment, Forestry and Forest Products Research Institute, 1 Matsunosato Tsukuba city 305-8687, Japan E-mail: yinagaki@affrc.go.jp

In the present study, the leaf and branch fall for 5 years including typhoon disturbances in the third year are reported following the results by Inagaki et al. (2008a). We selected hinoki cypress (*Chamaecyparis obtusa* Endlicher) forests at two different elevations. Within each forest we established two adjacent study plots (20m × 20m): a thinned plot and an unthinned plot on the same slope. Annual leaf-fall in heavily defoliated forests was expected to be lower after the typhoon disturbances. The objectives of this study were to determine if 1) annual leaf fall after typhoons is lower in heavily defoliated forests, 2) pattern of leaf-fall phenology changes due to sever damage by strong winds.

2. MATERIALS AND METHODS

2.1 Study Site

The study was conducted in hinoki cypress plantations in two areas, Tengu (33° 28′ N, 133° 0′ E) and Furumiya (33° 26′ N, 133° 1′ E), in the upper part of the Shimanto Basin on Shikoku Island in southern Japan. Hinoki cypress is an evergreen conifer and widely planted for timber production in the region. The general stand characteristics are presented in Table 1. Tengu (TNG) is located at 1,150 m in elevation and is among the highest sites for hinoki cypress plantations on Shikoku Island. The mean annual temperature and annual precipitation are 9.6 °C and 3,140 mm. Hinoki cypress trees were planted on former grassland that was often burned. The plantation was 42 years old in 2002. The soil parent material of the study site is volcanic ash over limestone. The soil is classified as Andisol in soil taxonomy (Soil Survey Staff, 1998) and as a drier subtype of moderately moist black forest soil (BlD(d)) in the Japanese classification of forest soils (Forest Soil Division, 1976).

Furumiya (FMY) is located at an elevation of 710 m. The mean annual temperature and annual precipitation are 13.1 °C and 3,270 mm. Hinoki cypress trees were planted on a former hinoki cypress plantation. The plantation was 23 years old in 2002; some trees remained from a previous rotation (aged 46 years). The soil parent material of the study site is sedimentary rock. The soil is classified as Dystrudept in soil taxonomy and as moderately moist brown forest soil (BD) in the Japanese classification of forest soils.

2.2 Thinning

Two adjacent study plots (20m × 20m) were established at both TNG and FMY. These were of the same contour elevation and had similar stand and soil characteristics (Table 1). A summary of the thinning is provided in Table 2. Thinning was conducted in one plot before the growth period in 2002 (in

Table 1
Summary of the study sites

Study site	TNG	FMY
Elevation (m)	1150	710
Mean annual temperature(°C)	9.6	13.1
Mean annual precipitation (mm)	3140	3270
Slope (degree) *	30(30)	30(30)
Slope aspect*	S25W(S60W)	N70W(N50W)
Stand age in 2002 (yr) **	42	23(46)
Parent material	Volcanic ash	Sedimentary rock

*Control plot (thinned plot), **In FMY, there are some 46-year-old trees.

Table 2
Summary of thinning in the study sites.

Plot	Tree number(/400m^2)			Stem volume (m^3/ha)		
	Before thinning	After thinning	Percent thinning	Before thinning	After thinning	Percent thinning
TNG control plot	41	41	0	353	353	0
TNG thinned plot	35	17	51	341	178	48
FMY control plot	68	68	0	190	190	0
FMY thinned plot	65	34	48	219	83	62

April 2002 at TNG, and in December 2001 at FMY), and no trees were cut in the control plots. Felled trees were randomly selected from size classes. The stem volume was decreased by 48% at TNG and by 62% at FMY after thinning (Table 2). This percentage of tree removal is considered to be high because the percentage of tree removal in forests is generally kept to 30% or less as a general rule in Japan.

After thinning, most of the large stems and branches were removed from the study plot, but some woody materials remained in the plot. Most of the small branches and leaves were scattered within the plot. Further information about the thinning practices and forest growth after thinning is given in Fukata (2006) and Inagaki et al. (2008a).

2.3 Litterfall

The leaf litterfall was collected by litter traps. Eight litter traps of 0.5 m^2 each were placed in each plot in two lines at regular intervals (about 4 m). Litterfall was collected every month from July 2002 to June 2007 except during winter snowfall from January to February. We did not collect litterfall in winter because the area had snow cover, especially in TNG at the higher elevation.

The annual litterfall was determined from July to June of the next year since the litterfall rate was lowest in July. The collected litterfall was divided into leaves, small branches, and other organs. The diameter of small branches was less than 5 cm. From July 2002 to June 2005, the sample of each trap was divided into organs. After July 2005, samples from the 8 traps at each collection site were combined into one sample and a part of the combined sample (more than 30 g) was divided into organs. Samples were dried for 48 hours at 75 °C and weighed. The annual leaf-fall biomass and nitrogen input were calculated by summing the monthly leaf fall between July and the following June. Leaves of hinoki cypress are fallen mainly in winter and the leaf-fall during winter was calculated by summing up monthly leaf fall between October and April in the following year. Percentage of winter leaf-fall was calculated as winter leaf-fall divided by annual leaf-fall.

The leaf-fall time for the hinoki cypress in each year was evaluated using the following logistic equation developed by Dixon (1976):

$$W(t) = \frac{W_{year}}{1 + \exp((2.2 / T_{10-50})(T_{50} - t))}$$

where W = cumulative leaf fall (in g·m^{-2}), W_{year} = total annual leaf fall (in g·m-^{2}), T_{50} = time of maximum leaf-fall rate or time of 50% of annual leaf fall (in days), $T_{10\text{-}50}$ = time between 10% and 50% of annual leaf fall (in days), t = time (in days). The date corresponding to t = 0 was set at July 1. In this model, the time of leaf-fall and leaf-fall duration (gradualness of leaf-fall) are determined.

Leaf and branch fall was measured for 5 years (2002-2006). As there were several occurrences of severe typhoons, we divided 5 years into three periods: pre-disturbance period (2002-2003), year of disturbance (2004) and post-disturbance period (2005-2006). Means of annual leaf and branch fall in each period were calculated. The disturbance index is defined as the ratio of annual leaf-fall in 2004 to pre-disturbance annual leaf fall. The recovery index is defined as the ratio of post-disturbance annual leaf fall to pre-disturbance annual leaf-fall.

Pattern of leaf-fall is related with the attacks of typhoons. Because we did not measure the wind speed in the study area, we defined the date of strong winds as being when records of maximum wind velocity at two weather stations (Sukumo and Shimizu, Meteorological Agency Japan) both exceeded 25 m s^{-1}. Although these stations are relatively far from the study area (70-75 km), we considered the data of weather stations along the Pacific Ocean to reflect the impacts of typhoons in the region. There were 7 days in 2004 that had strong winds, which was much greater than in the other 4 years (average of less than 1 day).

2.4 Statistical analysis

Pearson correlation coefficients were determined between disturbance index and recovery index. Properties of leaf-fall phenology (T_{50}, $T_{10\text{-}50}$ and percentage of winter leaf-fall) were compared between the control and thinned plots using liner regression analysis (n=5).

3. RESULTS

3.1 Amount of leaf and branch fall

The seasonal pattern of leaf fall rate showed clear seasonality, being higher in winter (Fig. 1). The time of strong winds recorded at the weather station is indicated by plus signs. In the control plots, pre-typhoon annual leaf fall (2002-2003) was greater at TNG than at FMY (Table 3). At each forest, pre-typhoon annual leaf fall was smaller in the thinned plots than in the unthinned plots. The ratio of annual leaf fall in 2004 to pre-typhoon leaf fall (Disturbance index) ranged from 1.17 to 2.25. The disturbance index of leaf fall was greater at the higher elevation and greater in the thinned plots than in the control plots (Table 4). The ratio of post-typhoon leaf fall (2005-2006) to pre-typhoon leaf fall (Recovery index) ranged from 1.05 to 1.41. We did not find a negative correlation between disturbance index and recovery index ($p > 0.05$, Fig. 2). The disturbance index of branch fall ranged from 1.25 to 4.41. The recovery index of branch fall ranged from 0.56 to 2.4. The recovery index of branch fall was smaller where the disturbance index was greater ($r = -0.96$, $p = 0.04$, n =4, Fig. 2).

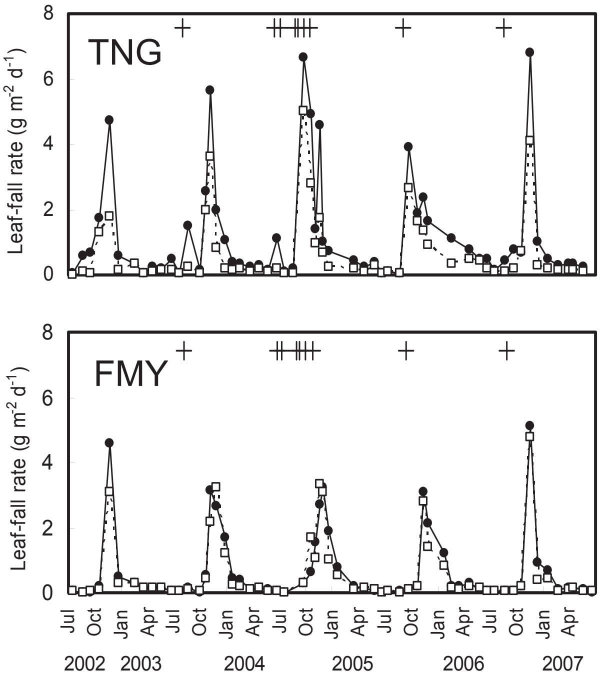

Fig. 1 Temporal changes in leaf-fall rate in the thinned (open squares) and unthinned plots (closed circles). The date of strong winds is indicated by the plus symbols at the upper part of the graphs.

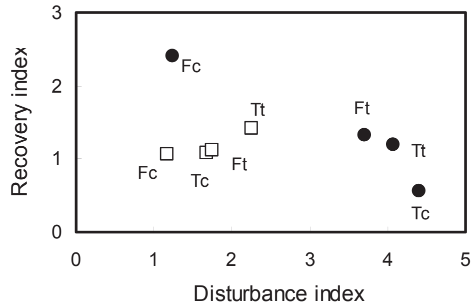

Fig. 2 The relationships between disturbance index and recovery index of leaf fall (open square) and branch fall (closed circle). Abbreviations of the study plots are as follows: TNG control (Tc); TNG thinning (Tt); FMY control (Fc); FMY thinning (Ft). The recovery index of branch fall is negatively correlated with the disturbance index (r=-0.96, p=0.04), whereas no significant relationship was found for leaf fall (p>0.05).

Table 3 Annual leaf-fall and branch-fall in the thinning experiment

year	TNG control	TNG thinning	Thinning /control	FMY control	FMY thinning	Thinning /control
Leaf-fall (g m^{-2} yr^{-1})						
2002	317.4	140.1	0.44	208.1	147.7	0.71
2003	312.1	146.6	0.47	190.3	158.0	0.83
2004	530.4	323.0	0.61	233.6	266.3	1.14
2005	332.4	219.7	0.66	194.9	151.9	0.78
2006	346.9	184.1	0.53	224.9	189.1	0.84
Mean	367.9	202.7	0.55	210.4	182.6	0.87
Branch-fall (g m^{-2} yr^{-1})						
2002	36.6	11.1	0.30	4.9	15.8	3.22
2003	45.7	17.6	0.38	15.9	17.0	1.07
2004	181.5	58.5	0.32	13.0	60.8	4.68
2005	29.2	17.1	0.58	17.9	15.7	0.88
2006	16.8	17.0	1.01	32.0	28.0	0.87
Mean	62.0	24.2	0.39	16.8	27.4	1.64

Table 4 Indices of disturbance and recovery in leaf litter and small branches

		TNG control	TNG thinning	FMY control	FMY thinning	Mean
Leaf litter (g m^{-2} yr^{-1})						
2002-2003	a	314.8	143.3	199.2	152.9	202.5
2004	b	530.4	323.0	233.6	266.3	338.3
2005-2006	c	339.7	201.9	209.9	170.5	230.5
Disturbance index	b/a	1.69	2.25	1.17	1.74	1.67
Recovery index	c/a	1.08	1.41	1.05	1.12	1.14
Branch (g m^{-2} yr^{-1})						
2002-2003	a	41.1	14.4	10.4	16.4	20.6
2004	b	181.5	58.5	13.0	60.8	78.4
2005-2006	c	23.0	17.0	25.0	21.8	21.7
Disturbance index	b/a	4.41	4.08	1.25	3.71	3.81
Recovery index	c/a	0.56	1.19	2.4	1.33	1.05

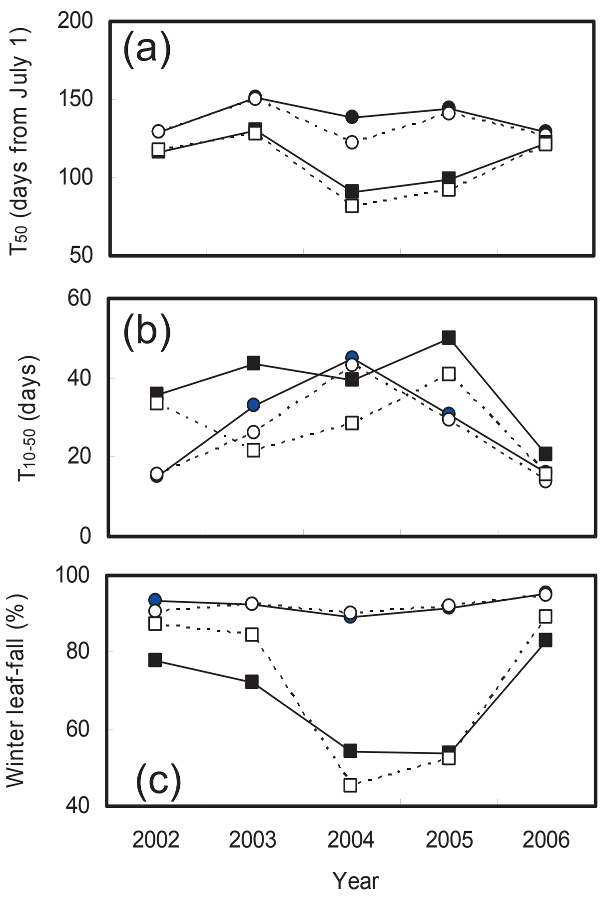

Fig. 3 Yearly variation in time of leaf-fall(T_{50})(a), leaf-fall duration ($T_{10\text{-}50}$)(b) and the percentage of winter leaf-fall (c) in the TNG control plot (closed square), TNG thinned plot (open square), FMY control plot (closed circle) and FMY thinned plot (open circle).

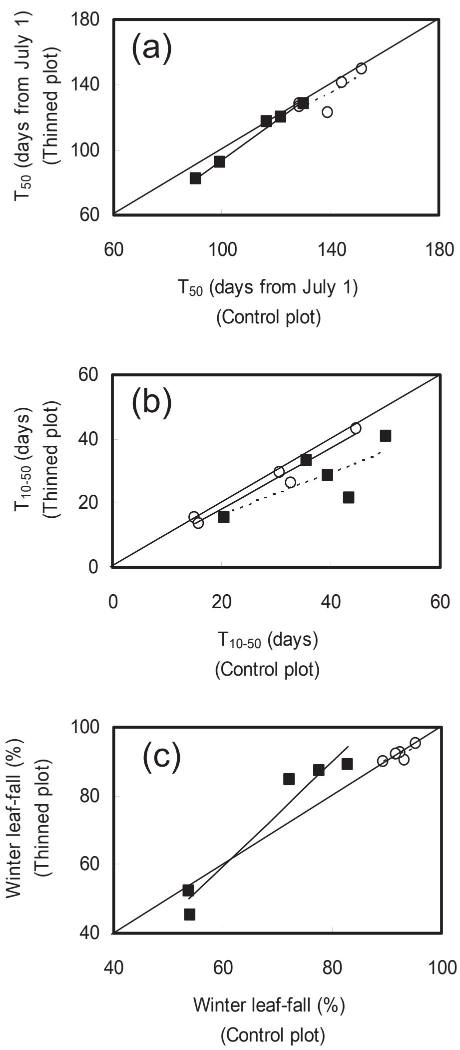

Fig. 4 The relationships of time of leaf-fall (a), leaf-fall duration (b) and the percentage of winter leaf-fall (c) between control and thinned plots at TNG (closed square) and FMY (open circle). Significant relations are indicated by solid lines.

3.2 Leaf fall phenology

In 2004, the time of leaf fall (T_{50}) in TNG was more than 30 days earlier than in the pre-disturbance period whereas the time of leaf fall in FMY did not change appreciably (Fig. 3a). In contrast, the leaf-fall duration ($T_{10\text{-}50}$) in 2004 at FMY became longer (43-45 days, Fig. 3b). For five years the time of leaf-fall was similar between control and thinned plots (Fig. 3a). Leaf-fall duration in the thinned plot at TNG was 5-22 days shorter than that in the control plot except in 2002 but no clear difference was found at FMY (Fig. 3b). The percentage of winter leaf-fall was lower at TNG than FMY (Fig. 3c). The percentage in the control plot at TNG was lower than that in the thinned plot in the pre-disturbance period (2002-2003) but no clear difference was found after typhoon disturbance. At FMY, the percentage was not different between the control and thinned plot.

The time of leaf-fall in the control and thinned plots at TNG was linearly correlated (Fig 4a, Table 5) but was not correlated at FMY. The leaf-fall duration in the control and thinned plots at FMY was linearly correlated (Fig. 4b, Table 5). Percentage of winter leaf-fall in the control and thinned plot was linearly correlated at TNG but not at FMY (Fig. 4c, Table 5)

Table 5 The results of leaner regression analysis. The regression line is indicated in Fig. 4.

Properties	site	slope	intercept	r^2	p
T_{50}	TNG	1.2	-25.8	0.99	0.001
T_{50}	FMY	0.92	5.7	0.66	0.09
$T_{10\text{-}50}$	TNG	0.67	2.8	0.55	0.15
$T_{10\text{-}50}$	FMY	0.94	-0.5	0.96	0.004
Winter leaf-fall (%)	TNG	1.52	-31.6	0.94	0.006
Winter leaf-fall (%)	FMY	0.7	27.4	0.6	0.12

4. DISCUSSION

4.1 Amount of leaf and branch fall

When affected by the severe typhoons, annual leaf-fall in 2004 increased by 1.17-2.25 fold, corresponding to an increase of 34-215 g m^{-2}. Takeuchi et al. (2007) reported that the amount of leaf fall of four hinoki cypress forests by the storm events in 2004 was 20-100 g m^{-2} in the Kyushu District. Saito (1981) measured litter fall for 10 years at hinoki cypress forests in Shiga Prefecture, central Japan. The annual leaf fall in 1972, when a severe typhoon affected the area, was 1.17 times higher than the average of leaf fall for 10 years. Typhoons did not increase annual leaf fall clearly although the time of leaf fall became earlier when the area had strong winds. Because other climatic factors can also affect annual leaf fall (Saito, 1981), it is sometimes difficult to isolate the typhoon effect only. Nonetheless, it was concluded that the effects of the typhoons at TNG of this study were greater than those in previous studies.

The effect at FMY was similar to that in previous studies. The typhoon effect at TNG was large, probably due to three reasons. First, there were many severe typhoons in 2004 (Typhoon Research Department, 2006). Secondly, winds in TNG areas at higher elevations were higher than in previous studies. We did not measure the wind speed directly but we found indirect evidences of strong winds at TNG; damage of litter traps by winds and soil observation. The soil in TNG has a strong nutty structure in subsurface horizon that indicates soil is dry due to higher transpiration affected by strong winds (Forest Soil Division, 1976). Thirdly, typhoon effects also related with the slope direction. As located at slope of south west direction, plots in TNG might have strong winds. Greater effect of typhoon on defoliation in south facing slope was previously reported in Takeuchi et al. (2007).

Post-disturbance annual leaf fall recovered to the level of the pre-disturbance period (Table 4). Although we expected slower recovery in the highly disturbed forest, the recovery was not related with the disturbance index (Fig 2). These results are different from Sato's (2004) study of an evergreen hardwood forest where annual leaf fall decreased significantly after disturbance. Previous studies on hinoki cypress did not find a clear reduction after typhoon disturbances (Saito, 1981, Inagaki et al., 2008b). There are two main reasons for the small reduction of annual leaf fall after typhoon disturbance. First, leaf biomass in the crown of hinoki cypress is large because leaf longevity of hinoki leaves is 5-7 years (Saito and Tamai, 1989). Takeuchi et al. (2007) reported that less than 8% of the leaves in the crown were defoliated by typhoons in 2004. In this study, higher percentage of leaves in TNG sites would be fallen than previous studies but the percentage would be still low. Secondly, the production of new leaves may increase rapidly after typhoon disturbance. Supporting evidence is presented by Fukata et al. (2009), who reported that the relative light intensity of a forest floor was increased by typhoon disturbance, but it decreased gradually following the disturbance. This result suggests that leaf production accelerates after a typhoon disturbance. However we did not evaluate the leaf production in this study. Further study is needed to evaluate the leaf production by direct measurement of leaf area index using canopy analyzer (Miyamoto et al., 2009).

The disturbance index of branch fall ranged from 1.25 to 4.41. These values are higher than those of leaf fall. The reason of higher branch fall is that the branch fall includes dead branches that have no leaves. The mean of the recovery index for branch fall was 1.05. This indicates that the recovery of branch fall was relatively rapid, although the index varied among forests. The recovery index was negatively correlated with the disturbance index (Fig 2). This pattern is different from that for leaf fall. These results suggest that the recovery of branch fall was slower when large amount of branch was fallen by strong winds.

4.2 Leaf fall phenology

In 2004, the study area was hit by many typhoons (Typhoon Research Department, 2006). The leaf-fall phenology in 2004 was determined by occasional strong winds. This situation is different from previous studies that generally evaluated the impact of strong winds from a single storm (Vogt et al., 1996; Harrington et al., 1997; Herbert et al., 1999; Xu et al., 2004; Sato, 2004).

The response of leaf fall pattern to the typhoons was different between the two elevations (Fig 3). The time of leaf fall became earlier at the higher elevation and the leaf-fall duration became longer at the lower elevation. At the higher elevation, a large amount of leaves could fall immediately in response to strong winds (Fig.1) and the time of leaf-fall in the control and thinned plots was significantly correlated (Fig. 4a). In contrast, leaves at the lower elevation did not fall immediately in response to strong winds; instead, the damaged leaves fell gradually after the typhoon events. Leaf-fall duration in the control and thinned plots at FYM was significantly correlated. The results suggest that changes of leaf-fall duration are more important than the time of leaf-fall in response to typhoon disturbance at the lower elevation (FMY).

This difference cannot be explained only by the strength of the wind. The intrinsic resistance of leaves to strong winds may differ between the two elevations. Leaf morphology such as leaf thickness can be related with leaf longevity (Reich et al., 1992; Wright et al., 2005) and possibly resistance to strong winds. Therefore, environmental factors that determine leaf morphology can be involved with the resistance of leaves to strong winds. Longer leaf longevity is often characterized as an adaptation to a nutrient-poor environment (Chapin, 1980, Chabot and Hicks, 1982, Aerts and Chapin, 2000). Nitrogen was less available at the lower elevation (Inagaki et al., 2008a) and trees there may have had leaves of longer longevity and higher resistance to strong winds. Inagaki et al. (2010) compared leaf-fall phenology in 17 hinoki cypress forests and showed that the time of leaf-fall of hinoki cypress forests varied 86 days and could not be explained solely by temperature. The results implied that intrinsic resistance of leaves can vary greatly in hinoki cypress forests. This evidence is indirect and further study is needed to investigate intrinsic resistance for winds and leaf longevity of hinoki cypress across wide range of climatic and soil conditions.

After disturbance, leaf-fall phenology may change due to water stress by strong winds. However in this study the time of leaf fall after a typhoon-disturbance generally returned to their respective values in the pre-typhoon period (Fig.3). These results suggest that the effect of sever typhoons was not critical and hinoki trees can recover to the pre-disturbance condition rapidly. After disturbance, the time of leaf-fall was similar between thinned and unthinned plots (Fig.3). Leaf-fall in the thinned plots returned to values in the pre-typhoon period. From these findings we concluded that the thinned forest in this study was not critically damaged by sever typhoons although the disturbance index was greater in the thinned plots and at higher elevations. In TNG at higher elevation, the effect of typhoons was larger than previous studies (Saito, 1981; Takeuchi et al., 2007) but leaf-fall recovered rapidly. The results suggest that leaf fall by strong winds may not cause critical damages for hinoki cypress plantations generally.

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四国のヒノキ人工林において台風が落葉動態に及ぼす影響

稲垣善之 [1)*]，倉本恵生 [2)]，深田英久 [3)]

要 旨

四国地域の標高の異なる２つのヒノキ林において、間伐区と対照区を設定し、落葉量の動態を 5 年間評価した（2002-2006 年）。この地域には 2004 年に多くの台風が接近したが、この年の年間落葉量は台風前 (2002-2003 年) の 1.17 － 2.25 倍の値を示した。台風の影響は高標高域で低標高域よりも大きく、間伐区で対照区よりも大きかった。一方、台風後（2005-2006 年）の年間落葉量は、台風前 (2002-2003 年) の 1.05―1.41 倍を示した。台風の影響は間伐林分で大きかったものの、台風後の回復は間伐区と対照区の間に差が認められなかった。高標高域では 2004 年の落葉時期（落葉が年間量の 50% に達する時期）が早い傾向が認められた。一方、低標高域では 2004 年の落葉時期は変化せずに落葉期間（落葉が年間量の 10% から 50% に達するまでの期間）が長かった。この結果は、台風に対する落葉の反応が標高によって異なることを示す。すなわち、高標高域では、台風後直ちに落葉するが、低標高域では台風後にすぐには落葉せず、しばらく経過してから徐々に落葉した。これらの結果、ヒノキ人工林において台風後に落葉生産は速やかに回復しており、台風後に新しい葉の生産が急速に増加することが示唆された。

キーワード：ヒノキ；落葉；季節性；回復；間伐；台風

1) 森林総合研究所立地環境研究領域
2) 森林総合研究所北海道支所
3) 高知県立森林技術センター
＊森林総合研究所立地環境研究領域　〒 305-8687　茨城県つくば市松の里 1 e-mail: yinagaki@affrc.go.jp