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Recovery and allocation of carbon stocks in boreal forests 64 years after catastrophic windthrow and salvage logging in northern Japan.

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Abstract

To mitigate the negative effects of climate change, it is necessary to conserve carbon stocks in forests. Typhoons fell many standing trees and generate a substantial amount of coarse woody debris (CWD). In boreal forests, CWD contributes to maintaining carbon stocks for a long time after a disturbance because the decomposition rate of CWD is relatively low. We know that salvage logging after a disturbance tremendously decreases the forest carbon stock over the short term after logging but know little about its long-term effects. We targeted a catastrophic windthrow caused by a super typhoon in 1954 in boreal forests in northern Japan and estimated the long-term effects of salvage logging after the windthrow on the above- and belowground carbon stocks by comparing old-growth forests with low damage from the super typhoon in 1954 or any subsequent typhoons (OG), forests damaged by the typhoon with remaining CWD (i.e., windthrow, WT), and forests damaged by the typhoon followed by salvage logging (WT+SL). The CWD carbon stock of decay class 5 (i.e., the most decayed CWD) in WT was significantly larger than that in OG and WT+SL, suggesting that the CWD in decay class 5 in WT had been generated by the typhoon 64 years ago, and the negative effect of salvage logging on the carbon stock still remains apparent in the CWD carbon stock of decay class 5. The carbon stock of the organic (O) layer in WT was larger than that in WT+SL, probably because of three factors: (1) the slower decomposition rate of fallen leaves and twigs of conifers than broadleaves, as conifer litter is abundant in WT; (2) greater carbon transition from the CWD to the O layer in WT; and (3) the occurrence of a lower decomposition rate in the O layer in WT. However, the total carbon stock in WT+SL has almost recovered to the level of that in WT within the last 64 years. The carbon stocks of broadleaves that grew rapidly after the disturbance and the newly accumulated dead trees generated throughout the stand developmental process might contribute to the recovery of carbon stock in WT+SL. These results indicate that salvage logging affects the allocation of carbon in the forest

even after 64 years after a catastrophic windthrow, although there was no large difference in total carbon stock.

Keywords:

Wind disturbance; Salvage logging; Coarse woody debris; Decay class; Climate change

1. Introduction

To mitigate the negative effects of climate change, it is necessary to conserve and increase forest carbon stocks, which is one of the forest ecosystem services that is currently emphasized (Myers Madeira, 2008). Much carbon accumulates in the various components of forests, such as live trees, coarse woody debris (CWD), organic (O) layers and mineral soils. Forests have much greater carbon stocks than other terrestrial ecosystems, accounting for 80% of the aboveground carbon stock (Intergovernmental Panel on Climate Change, 2013). In particular, boreal forests, which represent the largest biome in the world and are distributed at high latitudes in the Northern Hemisphere, representing approximately 32% of the global forest area (Angelstam and Kuuluvainen, 2004), store 395 to 703 Pg of carbon, which accounts for one-third to half of the global forest carbon stock (Griffiths and Jarvis, 2005; Kasischke and Stocks, 2000). Such forests thus contribute substantially to the terrestrial carbon stock of the Northern Hemisphere (Intergovernmental Panel on Climate Change, 2013). However, East Asia's massive carbon stock has been exposed to the risk of windthrows by typhoons on an unprecedented scale over the past century (Intergovernmental Panel on Climate Change, 2013). In fact, Murakami et al. (2012) predicted that although typhoon occurrence will decrease, intense typhoons will occur more frequently in the northwestern Pacific at the end of this century.

Salvage logging is a conventional forest management strategy used after natural disturbances, including windthrows, and removes CWD to compensate for economic loss (Lindenmayer et al., 2008). To evaluate the carbon stock lost by salvage logging, we have to consider long-lived forest products made from salvaged woods as well as forest carbon stock. Focusing on forest ecosystems, salvage logging decreases the aboveground forest woody carbon stock both temporarily and over the long term in boreal and subalpine forests. Many previous studies (Bradford et al., 2012; Fraver et al., 2017) have proven the existence of lower aboveground woody carbon stocks (live trees and CWD) in forests 10 to 20 years after windthrows and

salvaging in comparison to those in unsalvaged forests. Recent pioneering long-term assessments of carbon stocks after windthrows and salvaging have also proven that the effects after such forest management practices remained for over 50 years (Sass et al., 2018; Suzuki et al., 2019). Reductions in large amounts of CWD carbon stock from the forest floor (D'Amato et al., 2011; Suzuki et al., 2019) and the destruction of advanced seedlings and saplings, delaying their regeneration (Donato et al., 2006; Greene et al., 2006; Lindenmayer et al., 2008; Morimoto et al., 2011), likely explain the decrease in aboveground carbon stocks resulting from salvage logging over a long period of time.

We still do not have sufficient empirical knowledge regarding how the full above- and belowground carbon stocks in forests recover after windthrows and salvaging. It is especially important to examine the carbon in all carbon pools of forests to discuss the long-term effects of salvaging on carbon stocks because salvaging changes many ecosystem processes related to carbon stocks. For example, a substantial amount of carbon in CWD should be transferred to the O layer and mineral soils due to fragmentation after a long period of time following a windthrow, and well-decayed downed logs from conifers slow the decomposition rate of the O layer (Krueger et al., 2017; Strukelj et al., 2013). Although there are long-term modeling studies that estimated the effects of windthrow and salvaging on carbon stocks (Dobor et al., 2020), to the best of our knowledge, total above- and belowground carbon stocks have never been assessed to reveal the long-term effects of windthrows and salvaging empirically. Even pioneering long-term studies of carbon stocks after windthrows and salvaging (Sass et al., 2018; Suzuki et al., 2019) did not estimate the belowground carbon stock.

In this study, we analyzed the long-term effects of salvage logging following a windthrow on all carbon pools in boreal forests because it is urgent to mitigate climate change. We targeted a catastrophic windthrow caused by super typhoon Marie in 1954 in boreal forests in northern Japan and compared above-

and belowground carbon stocks among old-growth forests with low damage from typhoon Marie or any subsequent typhoons, forests damaged by typhoon Marie with remaining CWD, and forests damaged by typhoon Marie followed by salvage logging. Although Morimoto et al. (2019) assessed the forest structure in almost the same area, we also assessed the stand structure of the studied forests to evaluate the effects of salvage logging on the recovery of the aboveground carbon stock. In addition, we suggest better forest management strategies following windthrows to maintain as much carbon as possible for a longer period of time in boreal forest ecosystems by revealing whether the whole carbon stock in a forest, including that in the wood and soils, can recover more than half a century after salvaging.

2. Methods and Materials

2.1 Study sites

The study sites are located in the boreal forests in central Hokkaido, northern Japan (Fig. 1). The annual mean temperature and precipitation are 3.7 °C and 1,315 mm, respectively, at the nearest meteorological observatory of Nukabira-Gensenkyo (43° 22' 0"N, 143° 11' 30"E), which is located 16.2 km to 32.1 km away from each plot (Japanese Meteorological Agency, 2012, average of 1981–2010). The forest canopy is dominated by *Abies sachalinensis* (F. Schmidt) Mast., *Picea jezoensis* (Siebold et Zucc.) Carrière var. *jezoensis*, and *Picea glehnii* (F. Schmidt) Mast. Most of the study sites were intact old-growth forests before typhoon Marie severely damaged them. The dominant soil types at the study sites are Andosols (parent material: glass-rich volcanic ash and pumice) and Cambisols (parent material: rhyolite, sandstone or mudstone) (IUSS Working Group WRB, 2015).

The typhoon passed across central Hokkaido on September 26-27, 1954, and broad areas of forest in central Hokkaido were damaged by severe wind. The damage accounted for 21.1×10^6 m³ in timber volume

and 651,844 ha in area and was thus called a “stand-replacement disturbance” (Scientific Investigation Group of the Wind-Damaged Forests in Hokkaido, 1959). In this area, a very large number of trees blown down by the catastrophic wind were salvaged as logs through the use of chain saws, horses, skidders, and tracks over a couple of years (Editorial Board for the 50-year Anniversary of Forest Restoration from the Toyamaru Typhoon 2005, 2005).

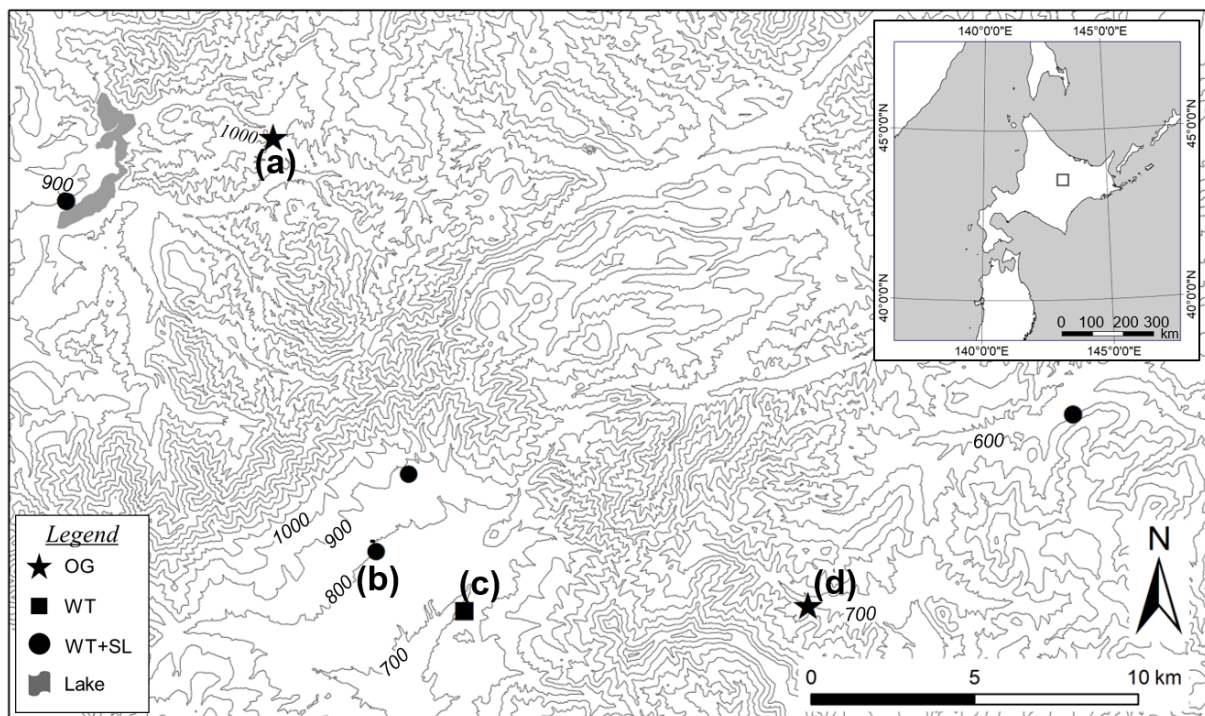


Fig. 1. Locations in the study area. (a) Two *old-growth* (OG) plots; plots are 50 m apart; (b) three *windthrow* + *salvaged* (WT+SL) plots; plots are at least 100 m apart; (c) five *windthrow* (WT) plots; plots are at least 50 m apart; and (d) two OG plots; plots are 100 m apart.

2.2 Placement of plots by reviewing wind disturbance and management history

To estimate the differences in aboveground woody carbon stock according to the presence or absence of windthrow and salvage logging, we established 15 plots of 25 m × 25 m in 2018 as follows: 4 stands of

old-growth (OG: hardly affected by typhoon Marie or any other subsequent natural or human disturbances), 5 stands of *windthrow* (WT: windthrow caused by typhoon Marie with fallen trees left intact), and 6 stands of *windthrow* + *salvaged* (WT+SL: salvage logged after the windthrow caused by typhoon Marie). We also established 4 quadrats of 0.25 m × 0.25 m in random locations in each plot for the estimation of carbon stock in the soil.

We selected suitable stands and established plots according to the following procedure. First, we reviewed aerial photographs taken before typhoon Marie (1944–1948) and confirmed that the study area had been entirely covered with the major coniferous tree species, *A. sachalinensis*, *P. jezoensis*, and *P. glehnii*. All WT plots were established at least 50 m apart within a permanent reserved area (Ishibashi et al., 2018; Hokkaido Regional Forest Office, 2015) because most of the windthrown area was salvaged after the typhoon. Old-growth forests also remain only in certain areas in another permanent reserved area (Nishimura et al., 2009) because even intact forests experienced large-scale logging simultaneously with the surrounding windthrown forests. Therefore, 2 OG plots were established at least 50 m apart within a permanent reserved area. We additionally established the other 2 OG plots and the WT + SL plots in the suitable area by checking a map of forest gaps created by typhoon Marie (Tamate et al., 1977) and the record of management history up to 2017 from the Forestry Agency of the Japanese Government. We tried our best to select the appropriate stands to satisfy the disturbance history criteria. Additionally, we confirmed the initial conditions before the disturbance. We roughly estimated the initial tree density before the windthrow, although the initial conditions before the windthrow could not be confirmed exactly. Regarding WT+SL, we used our data of stumps with decay class 4 or 5 and upper diameters larger than 30 cm because the CWD generated by the windthrow was assumed to be in decay class 4 or 5 (from our results) and most small stumps generated by the windthrow and salvaging 64 years ago have already been decomposed and can no longer be observed.

Regarding WT, the data of living trees and CWD (whose diameter at breast height (DBH) was over 30 cm) just after the windthrow in 1954 was used for estimation (Ishibashi et al., 2018). Tree densities (over 30 cm in diameter) in WT and WT+SL were 128 trees/ha and 131 trees/ha, respectively; therefore, we assumed that the initial conditions of WT and WT+SL were almost the same. All plots occurred at 607-989 m above sea level (Fig. 1).

2.3 Field measurements

We identified living trees to species and measured the DBH with a tree caliper for the trees with a DBH larger than 5 cm (when the diameter was larger than 46 cm, it was measured with a measuring tape). Additionally, the heights of some trees were measured with a TruPulse 360 rangefinder (Laser Technology Inc., USA) (approximately 10 individuals per species and disturbance category (OG, WT, or WT+SL)). We generated allometric equations for each species and disturbance category with the DBH and height data: $Height = a (DBH)^b$, where a and b are parameters to be estimated. We applied each equation to all trees for which the height was not measured (supplementary materials S2).

We classified the CWD into three types, i.e., (1) snags: standing dead trees taller than 1.5 m; (2) downed logs: CWD that lay on the ground and did not have roots and CWD that lay on the ground with roots and stems longer than or equal to 1.5 m; and (3) stumps: standing dead trees shorter than 1.5 m and CWD laying on the ground with roots and stems shorter than 1.5 m. We identified the species (conifers or broadleaves) of snags, measured their DBH (for those with a DBH larger than 5 cm) and heights, and determined their decay class (Forestry and Forest Products Research Institute, 2016). Downed logs larger than 10 cm in diameter at the larger end were targeted for the evaluation of the decay class and the measurement of the length and diameter at both ends (D'Amato et al., 2017; Suzuki et al., 2019). In the case

that downed logs protruded from a plot, we targeted only the parts of the downed logs within a plot. For stumps, we determined the decay class and measured the heights and diameters at both ends of stumps larger than 5 cm in diameter at the upper end (Forestry and Forest Products Research Institute, 2016). In this study, we used the six-level decay classification system (0, 1, 2, 3, 4 and 5, where 0 is the newest and 5 is the most decayed) described in the Forest Soils Inventory Manual version 3 (Forestry and Forest Products Research Institute, 2016). We determined the decay class of each CWD item based on the morphological characteristics and the depths of the knife sticks (Fukasawa, 2012; Heilmann-Clausen, 2001). Since judgment with a knife was originally applied for the five-level decay classification (1-5), CWD with fresh leaves on branches was classified into decay class 0.

We sampled the O layer and mineral soils in each quadrat in all plots. We initially classified the O layer into the Oi layer, the Oa/Oe layer (the Oi layer contains fresh leaf litter, but the Oa/Oe layer contains well-decomposed litter), and twigs and then sampled the entire O layer in each quadrat. Additionally, we sampled mineral soils (0-5 cm depth) with cylindrical cores (100 mL) to measure the bulk density. Approximately 200 g of mineral soil from 0-5 cm depth was also collected with shovels to measure the carbon concentrations. We conducted all surveys including living trees, CWD and soil in August and September 2018.

2.3 Soil analysis

All samples of the O layer and mineral soils were analyzed as follows.

(1) O layer

The samples were dried in an oven (70 °C, 48 hours), and their dry weights were measured. We then roughly ground them by using a Wiley mill (W-100S, IRIE SHOKAI Co. Ltd., Japan) and then further ground

small amounts using a bead cell disrupter (Micro Smash, TOMY, Japan). Finally, the carbon concentration of each sample was measured using a CHNS/O analyzer (PE 2400, Perkin Elmer Co., Ltd., Japan).

(2) Bulk density of mineral soils

After air drying, we classified each sample collected in the 100-mL core into fine soil particles, gravel, and roots by passing them through a 2 mm sieve. Each fine soil sample was dried in an oven (105 °C, 24 hours), and its dry weight was measured. The bulk density was calculated according to the dry weight of soil particles (excluding gravel and roots) divided by the volume (i.e., 100 mL).

(3) Carbon concentration in mineral soils

The mineral soil collected for measuring the carbon concentration was air dried and then passed through a 2 mm sieve followed by a 500 µm sieve. The carbon concentration of each sample was measured using a CHNS/O analyzer (PE 2400).

2.4 Estimation of carbon stock

(1) Live trees

The carbon stock of live trees (CS_{live}) was calculated as $CS_{live} = V \times BEF \times (R+1) \times M \times CC$, where V is the volume of the stem, BEF is the biomass expansion factor, R is the ratio of the root, M is the volume density, and CC is the carbon concentration.

The volumes of the stems of *A. sachalinensis* and *P. jezoensis* were calculated using regionally derived allometric equations for each species (Japanese Forestry Agency planning division, 1970). Those of *P. glehnii* were calculated using the equations for *P. jezoensis*. The broadleaved species were classified into 3 groups, and we applied the respective allometric equations to each species. For BEF , R , M , and CC , we used specific values for the species described in the National Greenhouse Gas Inventory Report of Japan

2016 (GIO, 2016).

(2) Snags

The carbon stock of snags (CS_{snag}) was calculated using equations 2.4.1, 2.4.2, 2.4.3, and 2.4.4.

$$1 / L_1 = 1 / (a \times D^{0.946}) + 1 / b \quad \dots\dots \text{eq. 2.4.1}$$

$$d_u = b_0 D^{b_1} b_2^{D \times \{(1 - \sqrt{q}) / (1 - \sqrt{p})\} \{b_3 q^2 + b_4 \ln(q + 0.001) + b_5 \sqrt{q} + b_6 \exp(q) + b_7 D / L_1\}} \quad \dots\dots \text{eq. 2.4.2}$$

$$d_b = (D + 2.1977) / 0.9720 \quad \dots\dots \text{eq. 2.4.3}$$

$$CS_{snag} = [L_1 / 12 \times \{5A_b + 5A_u + 2\sqrt{(A_b A_u)}\} + V_1 \times R] \times M \times CC$$

$$= V_{snag} \times M \times CC \quad \dots\dots \text{eq. 2.4.4}$$

* L_1 : Height of the snag when the full body remained; D : DBH; L : height of the snag; d_u : diameter of the upper end of the snag; $q = L / L_1$, $p = 0.3 / L_1$; d_b : diameter of the lower end of the snag; A_b : cross-sectional area of the upper end of the snag; A_u : cross-sectional area of the lower end of the snag; V_1 : volume of the snag when the full body remained; R : ratio of the root; M : volume density; CC : carbon concentration; V_{snag} : volume of the snag.

In the case of intact snags, we applied allometric equations for live trees to estimate the volume of the snags and multiplied the volume by $(1 + R)$ to estimate the carbon stock of snags. In the case of defective snags, we first used equation 2.4.1 (Goto et al., 2003) to estimate the heights of snags when the full body remained ($a=1.21$ and $b=19.5$ (Goto et al., 2003)) and then estimated the diameters of the upper and lower ends of the snags using eq. 2.4.2 (Kozak, 1988; $b_0 = 1.3912$, $b_1 = 0.8714$, $b_2 = 1.0012$, $b_3 = 1.6149$, $b_4 = 0.3067$, $b_5 = 1.8491$, $b_6 = 1.1547$, and $b_7 = 0.2196$) and eq. 2.4.3 (ÖZçelik et al., 2010), respectively. Finally, we estimated the carbon stock of the snags using equation 2.4.4 (Fraver et al., 2007; Russell et al., 2015). Regarding “ M ”, we used specific values of volume density for each decay class and tree species, as described by Ugawa et al. (2012). We assumed “ CC ” to be “0.5” for all CWD (Suzuki et

al., 2019; Ugawa et al., 2012).

(3) Downed logs

The carbon stock of downed logs (CS_{dl}) was calculated using equations 2.4.5, 2.4.6, and 2.4.7.

$$CS_{dl} = L / 12 \times \{5A_b + 5A_u + 2\sqrt{(A_b A_u)}\} \times M \times CC$$

$$= V_{dl} \times M \times CC \quad \dots\dots \text{eq. 2.4.5}$$

$$DBH_E = -2.1977 + 0.9720 \times d_b \quad \dots\dots \text{eq. 2.4.6}$$

$$CS_R = (1.5 \times DBH_E)^2 \times \pi \times M \times CC \quad \dots\dots \text{eq. 2.4.7}$$

* L : Length of the downed log; A_b : cross-sectional area of the large end of the log; A_u : cross-sectional area of the small end of the log; M : volume density; CC : carbon concentration; V_{dl} : volume of the downed log; DBH_E : estimated DBH; d_b : diameter of the large end of the log; CS_R : carbon stock of the root,

We used the formula described by Fraver et al. (2007) to estimate the volume of downed logs (eq. 2.4.5) because this is the best formula according to Russell et al. (2015). For downed logs with roots, the DBH of the downed log was first estimated using equation 2.4.6 (ÖZçelik et al., 2010); then, the carbon stock of the root was calculated using equation 2.4.7 (Suzuki et al., 2019). Finally, we summed the carbon stocks of the downed log and root.

(4) Stumps

The carbon stock of stumps (CS_{stump}) was calculated according to equation 2.4.8.

$$CS_{stump} = \pi H / 12 \times (d_b^2 + d_b d_u + d_u^2) \times M \times CC$$

$$= V_{stump} \times M \times CC \quad \dots\dots \text{eq. 2.4.8}$$

* d_b : Diameter of the lower end of the stump; d_u : diameter of the upper end of the stump; M : volume density; CC : carbon concentration; V_{stump} : volume of the stump.

The shape of the stump was approximated by a truncated cone (Russell et al., 2015). Estimating the carbon stock of the buried part of the stumps was very difficult because its decay class is unknown.

Therefore, we assumed that the decay class of the buried part of the stumps was the same as the decay class of the stumps above ground, and the carbon stock of their roots was estimated using eq. 2.4.6 and 2.4.7.

(5) Oi layer, Oa/Oe layer, and twigs

The carbon stocks of the Oi layer, Oa/Oe layer, and twigs were calculated as $(W \times CC) / (S \times \cos\theta)$, where W , S , θ , and CC are the dry weight, area sampled (0.0625 m²), slope angle, and carbon concentration, respectively (Ugawa et al., 2012).

(6) Mineral soils

The carbon stocks of mineral soils were calculated as $BD \times T \times CC$, where BD , T , and CC are the bulk density, thickness of the soil layer (= 0.05 m), and carbon concentration, respectively (Ugawa et al., 2012). In this study, we only estimated the area 5 cm above the mineral soil because the top of the mineral soil is the most sensitive to salvage logging.

2.5 Statistical analysis

All statistical analyses were conducted in R x64 3.5.0 (R core team, 2018). Differences in total carbon stocks, live tree carbon stocks, CWD carbon stocks, and CWD carbon stocks by decay class among disturbance categories were tested with ANOVA and multiple comparisons (Tukey-Kramer). Differences in the dry weight, carbon concentration, and carbon stock of the Oi layer, Oa/Oe layer, twigs, and mineral soils among disturbance categories were tested with a generalized linear mixed model (GLMM; *lmerTest* package). The explanatory variable was the disturbance category, the random effect was the plot identity, and the error structure was a normal distribution. Subsequently, we conducted ANOVA and multiple comparisons (Tukey-Kramer by using the *multcompView* and *lsmeans* packages).

3. Results

3.1 Carbon stocks

The CWD carbon stock of decay class 5 was significantly higher in WT than in OG ($p < 0.05$) and WT+SL ($p < 0.01$), and the carbon stock of the O layer in WT was marginally significantly higher than that in WT+SL ($p = 0.06$) (Table 1). Furthermore, although the result was not significant, the live tree carbon stock was largest in OG, followed by WT and WT+SL, and the live tree carbon stock of broadleaves in WT+SL was larger than that in OG and WT. The total CWD carbon stock did not significantly differ among the disturbance categories, but that in WT was slightly larger than that in OG and WT+SL (Table 1). The total carbon stocks, including those of live trees, CWD, the O layer, and mineral soils, were the same among the disturbance categories, as were the above- and belowground carbon stocks (Table 1).

Table 1. Carbon stocks (Mg C ha⁻¹) of live trees, CWD and soil in each disturbance category. OG, WT, and

WT+SL represent the following: OG: hardly affected by typhoon Marie or any other kind of natural or

artificial disturbance; WT: windthrow caused by typhoon Marie with fallen trees left intact; WT+SL:

salvage logged after the windthrow caused by typhoon Marie. Different letters next to the mean values

indicate significant ($p < 0.05$; *) or marginally significant ($p < 0.10$; †) differences between disturbance

categories according to ANOVA.

			Disturbance category						<i>F</i>	<i>p</i>
			OG		WT		WT+SL			
			n	Mean (SD) (Mg C ha ⁻¹)	n	Mean (SD) (Mg C ha ⁻¹)	n	Mean (SD) (Mg C ha ⁻¹)		
Aboveground	Live trees	Conifers	4	168.24 ^a (41.72)	5	143.64 ^a (27.09)	6	96.26 ^a (12.99)	2.007	0.18
		Broadleaves	4	19.34 ^a (11.4)	5	10.92 ^a (4.68)	6	31.06 ^a (5.57)	2.299	0.14
		Total	4	187.58 ^a (32.30)	5	154.57 ^a (23.16)	6	127.32 ^a (9.38)	2.028	0.17
	CWD	Decay class 1	4	1.03 ^a (0.98)	5	1.83 ^a (0.89)	6	1.61 ^a (0.31)	0.296	0.75
		Decay class 2	4	1.25 ^a (0.63)	5	3.39 ^a (1.36)	6	3.97 ^a (1.11)	1.416	0.28
		Decay class 3	4	5.69 ^a (1.13)	5	5.25 ^a (1.22)	6	4.38 ^a (0.73)	0.448	0.65
		Decay class 4	4	4.68 ^a (1.81)	5	3.44 ^a (1.01)	6	1.86 ^a (0.46)	1.796	0.21
		Decay class 5	4	1.94 ^b (0.73)	5	5.06 ^a (0.82)	6	0.69 ^b (0.19)	15.430	<0.01*
		Total	4	14.60 ^a (4.26)	5	18.96 ^a (2.50)	6	12.50 ^a (1.73)	1.606	0.24
	Total	4	202.18 ^a (32.30)	5	173.53 ^a (21.88)	6	139.82 ^a (9.53)	2.318	0.14	
Belowground	Organic layer	Oi layer	16	4.38 ^a (0.73)	20	5.59 ^a (0.60)	24	4.14 ^a (0.30)	2.301	0.14
		Oa/Oe layer	16	5.21 ^a (1.39)	20	4.86 ^a (0.57)	24	3.24 ^a (0.31)	2.262	0.16
		Twigs	16	2.45 ^a (0.35)	20	3.10 ^a (0.53)	24	2.62 ^a (0.61)	0.758	0.49
		Total	16	12.04 ^{ab} (2.34)	20	13.56 ^a (0.92)	24	10.00 ^b (0.63)	3.458	0.07 [†]
	Mineral soil	0-5 cm	16	13.00 ^a (2.87)	20	14.54 ^a (1.96)	24	17.45 ^a (1.48)	1.069	0.38
	Total	16	25.04 ^a (4.27)	20	28.10 ^a (2.79)	24	27.46 ^a (1.18)	0.372	0.70	
Total			4	227.22 ^a (33.12)	5	201.63 ^a (22.98)	6	167.28 ^a (8.74)	1.999	0.18

3.2 Stand structure and composition

The stem density was lowest in OG, but there were more trees with large diameters than in WT and WT+SL. At $10 \text{ cm} \leq \text{DBH} < 30 \text{ cm}$, conifers were dominant in WT, but in WT+SL, there were half as many conifers as in WT. On the other hand, at $5 \text{ cm} \leq \text{DBH} < 30 \text{ cm}$, there were more broadleaves in WT+SL than in WT. Regardless of the disturbance category, the major conifer species in all stands were *A. sachalinensis*, *P. jezoensis*, and *P. glehnii*. In terms of broadleaves, shade-tolerant species such as *Tilia japonica* (Miq.) Simonk dominated in the stands of OG3. There were no dominant broadleaves in the other stands of OG. On the other hand, shade-intolerant species such as *Betula platyphylla* Sukaczew var. *japonica* (Miq.) H. Hara, *Betula ermanii* Cham (pioneer species), and *Alnus hirsuta* (Spach) Turcz. ex Rupr. var. *hirsute* dominated in the stands of WT and WT+SL.

4. Discussion

4.1 Live tree carbon stock and stand structures

Considerable recovery of the total carbon stock of forests was observed 64 years after the stand-replacing windthrow and salvage logging. Up to approximately 90% of OG was reached in WT and 70% of OG in WT+SL (Table 1). This recovery could be attributed to the fast growth of broadleaves, pioneer species such as birch in WT+SL, and advanced conifer regeneration, such as that observed for *A. sachalinensis* and *P. glehnii* in WT. Forests before the windthrow had been dominated by three major coniferous species. Most dominant trees were blown down, but advanced conifer seedlings on the forest floor of WT were left intact. Therefore, new seedlings, including broadleaves, would have had little space to invade in WT. This is why the percentage of broadleaves in relation to the total live tree carbon stock was higher in WT+SL (24%) than in WT (7%). A decrease in conifers (Donato et al., 2006) and an increase in tree species diversity (Royo et al., 2016; Taerwe et al., 2019) due to salvage logging have been noted in previous studies assessing its effect over less than 10 years. It has also been observed that the ratio of broadleaves is high in salvaged areas even 20 years after salvage logging (Bottero et al., 2013; Fischer and Fischer, 2012). These studies support our discussions that the temporary decrease in the carbon stock of live trees due to salvage logging was compensated for by the fast growth of pioneer broadleaf species during the first several decades after the event.

4.2 CWD carbon stock

The CWD carbon stock of decay class 5 in WT was significantly higher than that in OG and WT+SL (Table 1), suggesting that the CWD of decay class 5 in WT was decomposing CWD that had been generated by typhoon Marie 64 years ago. The reduced carbon stock of CWD due to salvage logging was

still observed in WT+SL.

Brown et al. (1998) and Fraver et al. (2013) discussed the decay classes of logs downed by windthrows. The annual mean temperatures at the study sites used by Brown et al. (1998) and Fraver et al. (2013) are lower than 3.6°C, which are almost the same as those at our study sites. Brown et al. (1998) found that most of the downed logs of two coniferous species in subalpine forests decomposed into decay classes 4 and 5 over 60 years since windthrow. Fraver et al. (2013) assessed the changes in volume density, biomass, volume, and carbon stock of each downed log up to approximately 70 years since windthrow or felling and found that 30% of the original carbon stock of the conifer (*Pinus resinosa*) CWD just after windthrow or felling remained 70 years after the windthrow, suggesting that downed logs maintain part of their original carbon for 70 years. These previous studies support our expectation that CWD generated by a windthrow that occurred 64 years ago is still a detectable carbon pool. Additionally, we roughly estimated the retention rate and the decomposition rate-constant “ k ” of CWD (for details of calculations, see supplementary material S3). The carbon stock of CWD generated by the windthrow in 1954 was 41.0 Mg C ha⁻¹ when calculated from the data of Ishibashi et al. (2018). If we assumed that the CWD of decay class 5 in WT+SL was the CWD generated before the windthrow in 1954 and that the CWD generated by 1954 windthrow is now classified as decay class 4 or 5, we could estimate 4.37 - 7.81 Mg C ha⁻¹ as the current carbon stock of CWD still remaining since the 1954 windthrow. Therefore, the retention rate of CWD generated by the windthrow in 1954 is 11 - 19%; thus, the decomposition rate-constant of CWD “ k ” [retention rate = $\exp(-tk)$, $t = 64$ (years since the windthrow)] was estimated as 0.026 - 0.035. According to Mackensen et al. (2003), “ k ” is approximately equal to 0.023, where the mean annual temperature is 3.7 °C. Our estimation proves to be reasonable. Suzuki et al. (2019) is the only other study that we know of that has assessed the long-term effects of windthrow and subsequent salvage logging on carbon stocks in boreal

forests (in 2 areas with annual mean temperatures of 2.1 and 3.5 °C). In that study, the CWD carbon stocks of decay classes 3 and 4 that had been generated by a typhoon approximately 55 years ago in unsalvaged forests were three times higher than those in undisturbed and four times higher than those in salvaged forests, respectively. This result is also analogous to our result that the CWD carbon stock of decay class 5 in WT was higher than that in WT+SL.

On the other hand, the total CWD carbon stock was not significantly different among the different disturbance categories (Table 1). This is likely because much of the new CWD had been generated in WT and WT+SL after the windthrow in the stage of self-thinning, thereby reducing the proportion of CWD carbon stock in the high decay class. The successional process of boreal forests after disturbances includes the stages of *stand initiation*, *young*, *middle-aged*, *mature*, *aging*, and *old-growth* forest (Angelstam and Kuuluvainen, 2004), and the forests of WT and WT+SL currently fall into the “*mature*” stage, while those of OG fall into the “*old-growth*” stage according to their definitions (for a detailed discussion, see supplementary material S4). Because self-thinning generally occurs at the “*middle-aged*” stage, all stands of WT and WT +SL should have experienced self-thinning. These trends in the total CWD carbon stock are also shown in Suzuki et al. (2019).

4.3 Carbon stocks of organic and mineral soils

Three factors have been suggested to have caused the carbon stock in the O layer in WT to be greater than that in the WT+SL and OG plots: (1) the slower decomposition rate of fine litter (fallen leaves and twigs) of conifers than broadleaves, as those of conifers are abundant in WT; (2) the greater transition of carbon from the CWD to the O layer in WT; and (3) the occurrence of a lower decomposition rate in the O layer in WT. Specifically, (1) the fine litter of conifers is substantially more difficult to decompose than

that of broadleaves because the former has more lignin and polyphenol concentrations and lower nutrient concentrations (Perry et al., 1987). As conifers are more abundant in WT than in WT+SL (Table 1), it was expected that input of fine litter of conifers was greater in WT than in WT+SL, which might contribute to the larger carbon stock in the O layer in WT. In addition, (2) the transition of carbon from the CWD to the O layer in WT would be greater than that in WT+SL because most of the CWD was removed by salvage logging just after the windthrow. As the decay of CWD progresses, some portions of CWD are fragmented and incorporated into the O layer (Krueger et al., 2017; Magnússon et al., 2016). (3) Furthermore, in addition to fine litter, well-decayed fragmented CWD from conifers is also difficult to decompose because it contains secondary decomposition products, such as preserved lignin, carbohydrates and alkyl-C compounds, with the potential to slow microbial decomposition (Kawada, 1989; Krueger et al., 2017; Lorenz and Lal, 2005; Magnússon et al., 2016), and could function as a carbon stock for a long time. These secondary decomposition products also decrease the decomposition rate of the O layer for the same reason (Kawada, 1989; Krueger et al., 2017; Strukelj et al., 2013). Most of the CWD in decay class 5 in WT was from conifers. Therefore, the transition of carbon from fallen leaves and FWD of conifers and the CWD to the O layer in WT would have been greater than that in WT+SL, and well-decayed coniferous CWD would decrease the decomposition rate of the O layer in WT.

We found no significant differences in the carbon stock in mineral soils among the different disturbance categories ($p > 0.10$), suggesting that the past salvaged logging would have low impacts on the mineral soils 64 years after the salvage logging. Because of the long turnover time of organic matter in the Oe layer, which was reported as 100-140 years in spruce forests (Schulze et al., 2009), it takes longer for carbon stock of well-decayed CWD and the O layer to be transferred to the mineral soil. Further, the distribution of carbon (i.e., organic matter) in mineral soil is highly heterogeneous, and we sampled soils

from only the top 5 cm of the mineral soils. Although the effects of salvage logging would first appear at the top of the mineral soil, to detect the effects of salvage logging on the mineral soil layer, more intensive and longer-term surveys of mineral soils are needed.

4.4 The total carbon stocks

The total carbon stocks were not significantly different among forest types, suggesting that the total carbon stock of salvaged forest has almost recovered to the level of that of forests with fallen trees left intact in 64 years. However, the average of the total carbon stock of WT+SL was much lower than those of the others. The differences in the averages were attributed to the differences in live trees, CWD and organic layer. This suggests that past salvage logging have some impacts on the total carbon stock of the boreal forest. The reason that we could not find significant differences among the forest types may have been the low statistical power of our analysis because of the small sample size. The estimated statistical power of the analysis with the observed inter- and intragroup variance of total carbon stock was only 30%, when $n = 5/\text{group}$, although our study design was unbalanced ($n = 4-6$). In this study, total carbon stocks were not significantly different, but it was possible that the low statistical power led to Type II error. Moreover, the required sample size was estimated to be $n = 19/\text{group}$ for a statistical power of 90%. Unfortunately, our sample size was limited because we could not find any sites suitable for evaluating the long-term effects of salvage logging other than the sites of this study. However, we believe that this study provides valuable implications for evaluating long-term effects of salvage logging even with the small sample size.

4.5. Comparison of “retention rate” of salvaged and unsalvaged woods

Additionally, we roughly estimated the retention rate of salvaged woods, and it was suggested that

there was little difference between the current carbon stock of CWD that remained since the 1954 windthrow and the carbon stock of salvaged trees that is now stored as long-lived forest products. Thus, the effects of salvage logging on carbon stock can be reduced by using salvaged woods for long-lived products. In Section 4.2, we estimated the retention rate of CWD generated by the windthrow in 1954 to be 11 - 19%. Thus, 81 - 89% of the CWD would have been lost due to respiration (2/3) as well as fragmentation and leaching (1/3) over 64 years (Mattson et al., 1987; Bond-Lamberty and Gower, 2008). Furthermore, using the equation in Suzuki et al. (2019), the percentage of total carbon that was included in salvaged wood and remained 64 years later as terrestrial carbon stock, which was estimated to be 12.8% ($= [\{0.70 \times 0.65 \times \exp(-0.0198 \times t)\} + \{0.30 \times 1.00 \times \exp(-0.347 \times t)\}] \times 100$, $t = 64$, where -0.0198 and -0.347 are exponential decay coefficients for long- and short-lived products, respectively). This equation assumed that 70% of salvaged wood is used for building houses and making furniture and that 35% of this wood was lost to the atmosphere during the manufacturing process (the yield rate is 45.5%), while 30% of salvaged wood is used for short-lived products, such as paper. Therefore, there was little difference between the current CWD carbon stock that remaining since the 1954 windthrow and the carbon stock of salvaged trees that is now stored as long-lived forest products.

5. Implications for forest management

The recovery of whole carbon stock in a forest, including that in the wood and soils, requires more than half a century after salvaging. However, there was a lack of information regarding the spatial variation in the initial input of CWD by windthrow and the temporal variation of each component of carbon stocks for the past 64 years; therefore, the findings should be interpreted with caution and the limitations should be

considered.

To mitigate the effects of salvage logging on carbon stocks, it is important to use salvaged wood for long-lived forest products, such as buildings and furniture, as much as possible, and not as short-lived products, such as wood pulp. However, it is clear that salvage logging temporarily decreases forest carbon stock immediately after the practice. Because more intense and frequent typhoon landfalls are expected in the northwestern Pacific at the end of this century (Murakami et al., 2012) due to climate change, there is a probability that salvaged forests will be blown down before the carbon stock recovers if conventional salvage logging is performed following every windthrow.

This study reveals changes in certain components of forest carbon stocks, well-decayed CWD, total organic layer and conifers vs. broadleaves in living trees (not significant). These changes might affect forest functions other than carbon stocking. For example, a decrease in CWD decreases the opportunities for certain CWD-dependent species, such as spruce, to establish on downed logs (Narukawa et al., 2003), which may prevent succession into typical old-growth boreal forests dominated by conifers (Morimoto et al., 2019). To select the appropriate forest management strategy, we must consider the conservation of not only carbon stock but also biodiversity, which is the basis of other ecosystem services. It is necessary to verify the uncertainties of the consequences caused by changing windthrow regimes and the effect of a decrease in CWD as a nursery on species diversity.

6. Conclusions

The total carbon stock of salvaged forest has almost recovered to the level of that of forests with fallen trees left intact within the last 64 years. The results suggested that the carbon stock loss as a result of salvage logging has been offset by the carbon stocks of broadleaves that grew rapidly after the disturbance and by

the many dead trees that were generated during the long process of forest development after the disturbance. However, the effects of salvage logging after the windthrow remained apparent in two components of carbon stock: CWD of decay class 5 and the O layer. Even 64 years after the windthrow, in salvaged forests, the CWD carbon stocks of decay class 5 and the O layer were relatively lower than those in the forests with fallen trees left intact.

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Supplementary material

Supplementary materials.docx

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