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Initial vegetation recovery following a blowdown of a conifer plantation in monsoonal East Asia: impacts of legacy retention, salvaging, site preparation, and weeding

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Initial vegetation recovery following a blowdown of a conifer plantation in monsoonal East Asia: impacts of legacy retention, salvaging, site preparation, and weeding

Abstract:

All or a part of a sequence of forest practices (i.e., salvage logging, site preparation, planting crop trees, and weeding) has been implemented after natural disturbances for the rapid re-establishment of tree cover. Forest policies in Japan have recently changed from monocultural planting of coniferous crop trees to planting native broadleaved trees to restore forests and nurture local biodiversity following large windthrows. However, the effects of this new practice on preserving biodiversity, as well as the effects of legacy retention, have never been verified in Asia. Thus, the objective of our research was to compare the effects of legacy retention with plantation after salvaging on the initial stage of vegetation recovery in a blowdown area, specifically focusing on plant species diversity, the occurrence of alien species, and the composition of plant species. Following the analysis of our results, we finally describe appropriate practices to alter disturbed coniferous plantations to bring the species composition closer to that of the original natural mixed forests.

A control (A, legacy retention) and three experimental treatment sites (B, salvage logged, site prepared, and *Quercus crispula* seedlings planted; C, same as B, but weeded once during the summer; and D, residual rows that emerged after establishing sites for planting) were prepared, and quadrats were set. Eleven indicators of the ground condition and the number of vascular plant species, including ferns, were quantified, and the number and abundance of residual and newly colonized plants of the main woody species were estimated.

Our main findings were as follows: (1) in unsalvaged sites and residual rows, the diversity of plant species was poor, but a variety of plant species compositions were observed due to the heterogeneous conditions of the ground and ample residual plants; (2) in the planting site, many species appeared, but little variety of the species composition was observed due to the homogeneous condition of the ground and the destruction of residual plants; (3) a large number of alien species emerged in broad, unvegetated areas; (4) the impact of site preparation overwhelmed the impact of salvage logging on the initial recovery of plant species; and (5) to restore a natural mixed forest, a combination of legacy retention and plantation after salvaging would be the most appropriate.

Keywords:

wind disturbance; microenvironment; woody debris; plant residues; diversity index; alien species.

1. Introduction

Salvage logging after large-scale natural disturbances, such as windthrows and wildfires, is a common practice worldwide (Elliott et al., 2002; Mountford et al. 2006, Weishampela et al. 2007). Its main purposes are to recoup economic losses before the trees decay (Lindenmayer and Noss, 2006; Prestemon et al. 2006), to reduce fire risk by removing dead trees (Sessions et al., 2004), and to prevent outbreaks of beetles (Sessions et al., 2004). Site preparation before planting crop trees (traditionally by burning and, recently, by using heavy machinery) (Titus and Householder, 2007) and weeding for several years after planting (MacDonald, 2007; Nyland, 1996; Nagai and Yoshida, 2006) are also common practices after salvage logging to reduce the plants that compete with crop trees. A sequence of practices, including salvage logging, site preparation, planting crop trees, and weeding, has traditionally been performed to rapidly establish and increase the growth of crop trees that will later be harvested for timber production.

Over the past century, public demands for forest resources have shifted from wood production and recreation to wilderness protection and biodiversity conservation (Aber et al., 2000). However, an empirical study is required to determine appropriate practices to satisfy the new demand for biodiversity conservation because limited knowledge exists in this field. While few studies on this topic concerning Asian countries have been published (Nagai and Yoshida, 2006; Hino and Hiura, 2009), many empirical studies focusing on the relationships between forest practices after natural disturbances and the recovery of the diversity of flora have been conducted in North America and Europe. It has been suggested that there are advantages of leaving all biological legacies in such disturbed areas (including residual plants and microtopography) (Lindenmayer et al., 2004; Stokstad, 2006; Peterson and Leach, 2008), and salvage logging does not always produce the expected outcomes (Anderson et al., 2007; Donato et al., 2006; Lindenmayer and Noss, 2006).

The effects of forest practices on spermatophytes (herbaceous and woody plants) have been investigated in many cases, but the effects on pteridophytes (ferns) and lycopodiophytes have been ignored. Because the responses of vascular plants to forest practices differ depending on their life-form (Nagai and Yoshida, 2006), all vascular plants should be given equal attention when assessing the recovery of floral diversity.

Additionally, the residual plants and newly colonized plants that are present after disturbances are expected to play different roles in the earliest stage of succession (Roberts, 2004; Haeussler et al., 1999), which has seldom been analyzed separately in previous studies. Furthermore, the collective effects of the sequential practices from salvage logging to site preparation, planting, and weeding on the recovery of natural forests have never been examined in comparison with the effects of legacy retention.

Because tree species diversity and the structural complexity of a forest also enhance the diversity of animal species (Tews et al., 2004; Donald et al., 1998; Palik and Engstrom, 1999), multi-species planting (rather than monocultures), lower-density planting, and longer rotation of tree harvesting to facilitate the establishment of various plant species on the forest floor are recommended to encourage higher biodiversity in forests (Carnus et al., 2006; Hartley, 2002). In Japan, forest policies have recently changed from monocultural planting of coniferous crop trees to planting native broadleaved tree species to restore forests and nurse local biodiversity following large windthrows (Ministry of Agriculture, Forestry and Fisheries of Japan, 2009). This procedure is similar to traditional planting practices, i.e., salvage logging, site preparation, planting native broadleaved trees (instead of coniferous crop trees), and weeding. However, the effects of this practice on the initial recovery of plant communities have never been verified.

Thus, the aim of our research was to examine the effects of legacy retention and plantation after salvaging on the initial recovery of all vascular plants in a region of monsoonal Asia, where typhoon disturbances dominate. In this study, the terms "unsalvaged sites" and "legacy retention" refer to areas in which human interventions (e.g., salvage logging, site preparation, planting, and weeding) are never conducted and which are, therefore, left to natural recovery. We targeted plant communities in the early stage of succession after a large windthrow because relatively small differences in species responses in the initial years after a disturbance can have a great influence on the future development of the communities therein (Halpern and Spies, 1995; Bråkenhielm and Liu, 1998). The plants at the study sites were distinguished as either residual or newly colonized plants to quantitatively evaluate each of their contributions to the recovery of the forest. Moreover, alien species were distinguished from native species because alien species may alter the trajectory of forest succession (Titus and Tsuyuzaki, 2003). Based on our results, we discuss an appropriate treatment to direct disturbed coniferous plantings to more closely resemble the natural mixed forests that previously grew in the studied area The research area was located in plantation forests of *Abies sachalinensis* Fr. Schm. Masters that were largely blown down by a typhoon in 2004. In one part of the area, fallen trees were left as they had fallen, while in another part of the area, *Quercus crispula* Blume seedlings (i.e., one of the main species in local mixed natural forests) were planted after salvage logging. Precise environmental conditions, plant species diversity, the emergence of alien species, and plant species composition were investigated.

2. Methods

2.1 Study area

Typhoon No. 18 hit northern Japan in September, 2004 and destroyed 369. 6 km^2 of forest. Of the total windthrow area, 30% was concentrated in two adjacent cities, Chitose City and Tomakomai City (Tsushima and Saitoh, 2003). A study area was chosen in a management unit (0.47 km^2) of the national forest in Chitose City (42°45' N 141°30' E; altitude 150 m; average annual temperature 7.1°C; average annual precipitation 1,384 mm). The topography in the area is mostly flat, and the surface soil is volcanic ash and pumice, which were mainly delivered by the eruption of Mt. Tarumai (42°41' N 141°22' E; 1,041 m) during the 17th century. The dominant tree species of the natural forests were *Abies sachalinensis* Fr. Schm, *Picea jezoensis* (Siebold et Zucc.) Carrière, and *Quercus crispula* Blume based on forest inventory archives. Plantations of *A. sachalinensis* and *Picea glehnii* Fr. Schm. Masters were conducted in 1957 and in 1979, respectively, and the typhoon destroyed most stands of *A. sachalinensis* (stand density 900 trees/ha, stand volume 104 m^3/ha, average height 16 m) in 2004. The 15,000-m^2 study area was established in an area where a stand of *A. sachalinensi*s was completely destroyed. No canopy cover was left, and only boles without crowns remained sporadically, though seedlings on the forest floor that did not receive any direct damage from fallen trees survived.

No manipulations were conducted, and woody debris was left as it lay in the northern part of the study area (east-west (EW) 70 m × north-south (NS) 50 m). In the southern part of the study area (EW 50 m × NS 150 m), salvage logging was conducted using bulldozers and harvesters with grapples in September, 2007. Thereafter, site preparation and flattening and clearing of a 4-m wide row for tree planting were performed using backhoes. Woody debris scattered on the forest floor was piled along the sides of each planting row, which are referred to as residual rows. Approximately 10 cm of topsoil was removed, and pumice stones that had been produced by Mt. Tarumai emerged during site preparation.

Seedlings of *Q. crispula* (~60 cm in height) grown in a forestry nursery were transplanted after site preparation to restore the mixed forest of *Q. crispula* and *A. sachalinensis* that originally grew at the site.

The northern border of the study area was salvage logged. The artificial *P. glehni* forests at the western and eastern sides of the study area were not blown down. The southern border of the study area was salvage logged, followed by site preparation and planting of *Q. crispula* seedlings.

2.2 Setting of quadrats for surveys

In April, 2008, the year after salvage logging, site preparation, and planting were conducted, a control and three experimental treatment sites were established to examine the effects of legacy retention and plantation after salvaging on plant communities. The control site (A) was established in the northern part of study area, and treatments B, C, and D were conducted in the southern part of the study area (Fig. 1). The conditions of the control and the three treatments were as follows: A, the area was unsalvaged, and woody debris remained after the blowdown; B, the area was salvaged; the site was prepared; and *Q. crispula* seedlings were planted; C, the area was salvage logged; the site was prepared; *Q. crispula* seedlings were planted; and the area was weeded by rotary grass cutters once in the summer; and D, the area was comprised of residual rows.

A distance of 10 m was set between A (EW 70 m × NS 50 m) and the area including B, D (EW 50 m × NS 70 m), and C (EW 50 m × NS 70 m). Each area was gridded by 10 m, and quadrats of 1 m × 1 m were set up with at the intersecting points of the grid system (Fig. 1). To avoid edge effects, most external points were excluded. Thus, 16 quadrats were placed in the control, and 24 quadrats each were located in each of treatments B, C, and D.

According to the policy of the Japanese government, salvage logging should be implemented soon after a windthrow occurs. Thus, we were able to leave only a small portion of the blowdown area unsalvaged for this study. Additionally, we were only able to set up 16 quadrats in the control area to avoid edge effects from surrounding forest roads and to avoid the occurrence of autocorrelation between quadrats. The limitations resulting from the lack of replication will be discussed below (Bennett and Adams 2004).

2.3 Survey of the physical condition of the ground

Smaller quadrats (0.5 m × 0.5 m) were established on the western sides of the regular quadrats (1 m × 1 m) to measure soil water content and soil hardness because these measurements affect the surface soil and plants. Other physical conditions of the ground, including the light environment on the ground, materials on the ground, and the percent cover and height of coarse woody debris (CWD), were measured in each quadrat.

TDR (time domain reflectometry; HydroSense, Campbell Scientific, Inc.) was used to measure the water content of the soil by volume. The water content was measured on a day following three continuous sunny days in mid-August, 2008, when water stress for plants was relatively high. At 5 cm beneath the surface, the soil water content was measured at five randomly selected points for each smaller treatment. Additionally, the soil hardness was measured with a Nakayama-style hardness gauge at five randomly selected points for each smaller treatment.

The amount of global solar radiation at the control (A), treatment B, C, and D sites was homogeneous (confirmed in May, 2008) because the *A. sachalinensis* forest in the study area had been blown down completely. However, the light conditions on the ground of the control (A) and treatment D were expected to be different from the global light conditions because CWD and fine woody debris (FWD) covered the ground of these two sites. The photon flux density (PFD) was measured using two light sensors (LI-250A, LI-COR co.) just above the woody debris and just above the ground on a cloudy day in mid-August, 2008 in each quadrat in the control (A) and treatment D. From these results, the percent relative PFD was calculated at ground level to evaluate the cover impact of CWD and FWD on the ground. The relative PFD values at the ground in treatments B and C were assumed to be 100% because no woody debris was left, and no vascular plants except for cultivated *Q. crispula* seedlings and natural fledglings grew.

The percent cover of materials on the ground surface (including gravel, litter and soil, branches, boles, stumps, and mounds) was measured. In this study, gravel is defined as a stone with a grain size ≥ 1.0 cm and < 6.5 cm. The category of litter and soil includes fallen leaves, small branches (diameter < 2 cm), and soils with a grain size < 1.0 cm. Mounds are clods containing the root system of a fallen tree. Branches are defined as pieces of trees with a diameter ≥ 2 cm and < 5 cm. Boles are defined as pieces of trees with a diameter ≥ 5 cm.

The percent cover of CWD on and off the ground, including branches, boles, stumps, and crowns, was measured. The height of the CWD was also measured at the highest point.

2.4 Survey of the plant community

The species of ferns, herbaceous plants, and woody plants present at the study sites were surveyed in all quadrats from late September to early October in 2008. The botanical picture book Naturalized Plants of Japan (Shimizu, 2003) was used to identify alien species.

Specimens of the five main woody plants with the highest frequency of occurrence were identified as either residual plants or newly colonized plants, and their percent cover was measured. These species were *A. sachalinensis*, *Fraxinus lanuginose*, *Salix bakko, Acanthopanax sciadophylloides,* and *Prunus maximowiczii* Rupr. The annual growth of *A. sachalinensis* was determined, and plants older than four years were regarded as residual. For the other four species, the heights of all of the samples present in the quadrats were measured. Next, 10 juveniles of each species growing around the study area were cut at the ground, and their annual rings and heights were measured. An approximate equation to estimate age from height was then derived for each species from these data. Regression equations were derived for *F. lanuginose* ($Y = 2.05 \text{ Log } X + 6.47$; $R^2 = 0.80$; X = height in meter, Y = age), *S. bakko* ($Y = 1.45 \text{ Log } X + 5.55$; $R^2 = 0.89$), *A. sciadophylloides* ($Y = 1.53 \text{ Log } X + 5.86$; $R^2 = 0.81$) and *P. maximowiczii* ($Y = 1.61 \text{ Log } X + 6.27$; $R^2 = 0.68$), and specimens of these species with heights > 0.30, 0.24, 0.30 and 0.24 m, respectively, were estimated to be > 4 years old and therefore were regarded as residual plants.

2.5 Analyses

The median, minimum and maximum values of the physical condition of the ground in each treatment were calculated. The percent water content of the soil, percent relative PFD on the ground, percent cover of materials on the ground, percent cover of CWD, and percent cover of residual woody species were transformed by the arcsine square root and analyzed by the Kruskal-Wallis test to determine differences among the control and the treatments. The soil hardness and the maximum height of CWD were analyzed by the Kruskal-Wallis test without transformation. When significant differences were detected, the Mann-Whitney U-test with Bonferroni correction was employed.

The number and percent cover of residual plants of the five major woody species were calculated. Because residual plants appeared only in the control (A) and treatment D areas, the differences in the number and percent cover of residual plants between A and D were assessed by the Mann-Whitney U-test.

Species richness, two diversity indices, the Shannon's and Simpson's diversity indices (DI) excluding alien species, and the number of alien species was calculated for each quadrat. The differences among the control and treatment sites were analyzed by the Kruskal-Wallis test, followed by Sheffé's post-hoc test.

The compositions of plant species in the control and treatment sites were compared using presence-absence data in each quadrat by detrended correspondence analysis (DCA). Species that occurred in fewer than three quadrats were excluded from the analysis. Subsequently, Pearson's correlation between the axis values derived from the DCA and the variables of the physical condition of the ground were examined. The variables of the physical condition that exhibited a high correlation ($r < -0.6$ or, $r > 0.6$) with the DCA axes were selected for canonical correspondence analysis (CCA), together with the presence-absence data for the plant species in each quadrat.

In the analyses of species diversity and species composition, planted seedlings of *Q. crispula* were excluded because our focus was to understand the natural recovery of the plant community. SPSS software (ver.16.0J, SPSS Inc.) was used for statistical tests and correlation analyses, and PC-ORD software (ver.4.25, MjM Software Design) was used for the DCA and CCA.

3. Results

3.1 Physical condition of the ground

All of the environmental factors investigated, except the percent cover of stumps on the ground, were different among the control and treatment areas (Table 1). The soil water content in treatments B, C, and D was lower than in the control. The soil hardness and relative PFD on the ground in treatments B and C were higher than those in the control (A), but those in treatment D were the same as those in A. Among the materials on the ground, the gravel cover and branches in treatments B, C, and D were higher than in A. The litter cover and soil in treatments B, C, and D were lower than in the control. The cover by boles was lower in treatments B and C than in A but was the same in treatment D as in A. The mound cover in B and C was the same as in A but was higher in treatment D than in A. The CWD cover and height in treatments B and C were lower than in A, but those in treatment D were the same as in A.

3.2 Amount of residual woody species

The five major woody species rarely appeared in treatments B and C (Table 2). Most of the major woody species that appeared in the control (A) and treatment D were residual plants. The density and cover of residual plants in treatment D were lower than in A.

3.3 Diversity of plant species

The species richness and Shannon's DI in treatments B, C and D were higher than in the control (A) (Table 3). Simpson's DI also tended to be higher in treatments B, C and D than in A. The woody species in treatments B, C and D constituted < 30 % of all of the plant species established, whereas those in A constituted 47%. The number of alien plant species was highest in treatment B, followed by treatments C and D; the number of alien plant species was lowest in A.

3.4 Plant species composition

Three axes were derived by DCA, which accounted for 52.4% of the variance of species composition (Table 4). Three clusters (the control (A), treatments B and C, and treatment D) were found along axis I, suggesting that these three clusters were different in their species assemblages (Fig. 2). All environmental factors were significantly correlated with axis I (Table 4), indicating that the separation of the three clusters could be explained by the environmental variables.

The environmental variables that were highly correlated with axis I ($r > 0.6$ or $r < -0.6$) were selected for CCA. However, *litter and soil cover* was omitted because *gravel cover* and *litter and soil cover* were highly negatively correlated ($r = - 0.746$) and *gravel cover* had a higher correlation with axis I compared to *litter and soil cover*. As a result, four variables were used for CCA: the water content of the soil, relative PFD, gravel cover, and CWD height.

Two axes were derived by CCA, which accounted for 41.4% of the variance of the species composition and environmental variables (Table 5). The quadrats of treatments B and C exhibited a clumped distribution in the ordination diagram (Fig. 3 (a)), indicating that the species compositions and environments at these sites were homogeneous and resembled each other. Conversely, the quadrats in the control and treatment D were distributed broadly in the ordination diagram, indicating that the species composition and environment were heterogeneous.

The quadrats in treatments B and C were distributed in the direction of a higher relative PFD and higher gravel cover, being characterized by nearly bare land with limited woody debris (Fig. 3 (a)). In contrast, the quadrats in A and D were distributed in the direction of a higher CWD and higher soil water content, where the land was covered with a large amount of woody debris and was relatively wet. The control and treatment D slightly overlapped. The quadrats of A were distributed on the left side of axis I, and the quadrats of treatment D were distributed in the middle position of axis I, indicating that the amount of CWD and water content were lower in treatment D than in A.

The plant species that were more highly correlated with either axis I or II ($r>0.3$ or $r<-0.3$) are displayed on a CCA diagram in Fig. 3. Because *Q. crispula* (the species planted in treatments B and C) did not naturally occur in any quadrat, it does not appear in the diagram. The species that characterized both A and treatment D and were distributed in the overlapping zone between these sites are as follows: fern species, such as *Dryopteris austriaca* (D) and *Lycopodium obscurum* (L), woody vine species (including *Actinidia polygama* (A), *Rhus ambigua* (R), *Schizophragma hydrangeoides* Sieb. et Zucc. (S)), and *A. sachalinensis* (a), which had been growing before the windthrow. The species that characterized treatment D include fern species, such as *Osmunda cinnamomea* var. *fokiensis* (O) and *Thelypteris nipponica* (T), and woody vine species, such as *Celastrus orbiculatus* (C) and *Schisandra chinensis* (s). The species distributed on the right side of the CCA biplot that characterized treatments B and C (Fig. 3 (b)) are perennial forbs and grasses, including *Eupatorium chinense* ssp. *sachalinense* (E), *Artemisia montana* (M), *Solidago gigantea* var. *leiophylla* (G), *Carex puberula* (p), *Hypericum erectum* (E), *Stenactis annuus* (t) and the annual grass species *Persicaria nepalensis* (P).

4. Discussion

Legacy retention versus plantation after salvaging created different types and levels of legacies, which resulted in pronounced differences in the diversity of plant species, the occurrence of alien species, and the plant species composition.

4.1 Effects of legacy retention and plantation after salvaging on the physical condition of the ground and residual plants

Salvage logging and site preparation after the large windthrow (treatments B and C) greatly altered the physical conditions of the ground and residual plants. Because these practices removed all of the FWD and CWD (structural types of biological legacies, after Lindenmayer and Noss (2006)) on the ground, the level of sunlight exposure on the ground was high, and the ground was covered by pumice stones, without any residual plants (propagule types of biological legacies, after Lindenmayer and Noss (2006)) (Tables 1 and 2). Propagules are recognized as directly affecting the composition of early successional communities, while structural legacies can have effects on vegetation recovery by mitigating the environmental extremes within disturbed areas through shading and preventing excessive heat loss at night (Kohm & Franklin, 1997). In addition to these impacts, the use of heavy machines resulted in compact, hard soil. The soil water content was decreased as a consequence of a reduced water infiltration rate and greater surface runoff because soil compaction increases mineral soil bulk density and reduces aeration porosity (Tan et al., 2005). These characteristics of the surface physical conditions were commonly observed in the study areas after salvage logging and site preparation (treatments B and C) (Fig. 3).

There are few case studies that have reported the combined impact of salvage logging and site preparation after a windthrow on surface physical conditions. The effects of only salvage logging, after a catastrophic windthrow have been reported, e.g., the complexity of the microtopography, including fallen tree crowns, boles, slash, stumps, treefall pits and mounds, increase (Peterson and Leach, 2008; Elliot et al., 2002; Nelson et al., 2008), and consequently, the heterogeneity of the light environment (Peterson and Pickett, 2000; Nelson et al., 2009), water content, and ground temperature (Peterson and Leach, 2008) also increases. It has also been reported that weaker salvage logging leaves more residual plants (Roberts, 2004; del Rio, 2006). Conversely, it has previously been found that the impacts of mechanical site preparation, alone, include destroying the microtopography and creating a homogeneous environment (Hino and Hiura, 2009), as well as damaging residual plants (Roberts, 2004; Haeussler et al., 1999). Considering the combined impacts of salvage logging and site preparation, our results suggest that the effects of site preparation overwhelm those of salvage logging (i.e., resulting in homogeneous ground conditions and damaged residual plants).

In contrast, in the residual rows (treatment D), the physical conditions of the ground were heterogeneous because the ground was covered with various types of biological legacies that were piled up during the site preparation. Although soil compaction by heavy machinery was not observed in the residual rows, the soil water content in D was as low as in the sites subjected to salvage logging and site preparation (treatments B and C) (Table 1). Piling up volcanic ash and other woody debris may destroy porous soil structures and thereby reduce water-holding capacity. This finding suggests that manipulated legacies are different in their ecological functioning from those left unmanipulated after natural disturbances. In the residual rows, physical conditions, such as the water content of the soil, relative PFD, height of CWD, and gravel cover, exhibited a wide range of values (Fig. 3). The combination of the amount and location of woody debris and soil perturbation should create heterogeneous physical conditions. More residual woody plants were left in the residual rows (treatment D) than at the planting sites (treatments B and C) (Table 2) because no mechanical site preparation was conducted in treatment D, and the damage to residual plants was limited only to what occurred during salvage logging. There are no other studies that have separately evaluated the environmental features of residual rows. However, Peterson and Leach (2008) and Elliot et al. (2002) reported a high complexity of microhabitat conditions after salvage logging, which was ostensibly caused by the presence of piles of woody debris left at their study site after salvage logging.

Legacy retention (A) resulted in the most heterogeneous ground conditions among the four research sites (Fig. 3). Previous studies have reported that the various types of structural legacies (e.g., branches, boles and stumps) left after a windthrow create complex conditions of light and water on the ground (Ulanova, 2000; Okland et al., 2008). Tan et al. (2005) reported that ground cover materials protect the soil layer from being disturbed by raindrops and contribute to a greater infiltration rate and reduced surface runoff of water. This is likely the reason that the water content in the unsalvaged site was higher than in any other treatment (Table 1). Additionally, more propagule legacies, such as residual plants, were left undamaged at the unsalvaged site because no heavy machinery was used there (Table 2). This is a unique phenomenon associated with wind disturbance because other natural disturbances, such as fires and floods, destroy a majority of residual plants (Roberts, 2004).

4.2 Effects of physical conditions of the ground and residual plants on the recovery of plant communities

The diversity of plant species (alpha diversity) was poor, but the plant species composition (beta diversity) was rich where plentiful biological legacies were left (unsalvaged site). In contrast, where biological legacies were disturbed (planting site), numerous species became established (high alpha diversity), but the species compositions among the sampling plots were similar (low beta diversity). Without biological legacies, the invasion of alien species was promoted.

4.2.1 Diversity of plant species and alien species

The salvage logging sites with site preparation (treatments B and C) and residual rows (treatment D) exhibited higher levels of species richness and diversity than the unsalvaged site (A), although woody species occupied a small portion of these sites. Hino and Hiura (2009) reported that strong anthropogenic and natural disturbances affect species richness for an extended period by altering propagule and structure types of legacies. In particular, when the ground conditions are homogenized and residual plants are severely damaged, the diversity of plant species decreases in the long-term (Haeussler et al., 1999 ; Hino and Hiura, 2009 ; Newmaster and Bell, 2002). Conversely, in the short-term, species diversity increases after disturbances, with increased species richness of forbs and grasses, while the species richness of woody plants decreases (Peltzer et al., 2000 ; Swindel et al., 1984), which is similar to what was observed in our investigation conducted one year after the treatments.

The highest number of alien species was found in the planting site with no weeding after planting (treatment B) (Table 3). The planting site with weeding (treatment C) had slightly fewer alien species than treatment B. Alien species, which have superior dispersal abilities and tolerance to habitat disturbance compared to native species (Didham et al. 2005), invade the sunny, unvegetated microsites generated after strong disturbances (Corbin and D'Antonio, 2004; Alston and Richardson, 2006; Roberts, 2004; del Rio, 2006;

Collins et al., 2007). However, weeding removes alien species before they reach a reproductively mature stage (Kennedy et al., 2002). Accordingly, in the present study, salvage logging and site preparation facilitated the establishment of alien species, and subsequent weeding slightly reduced the number of alien species. In contrast, the unsalvaged and residual row sites exhibited few alien species, likely because the considerable amount of residual plants present impeded the invasion of alien species.

4.2.2 Composition of plant species

The species composition in the sites without weeding (treatment B) and with weeding (treatment C) mainly consisted of shade-intolerant, herbaceous, perennial species. In particular, large shade-intolerant, herbaceous perennial plant species (e.g., *E. chinense*, *A. Montana*, and *S. gigantean*) that usually dominate in large gaps after natural disturbances (Toyooka and Sugawara 1980) appeared. Few tree and shrub species were found, and no fern species emerged. According to previous reports, after salvage logging, an increase in the light intensity promotes the establishment of shade-intolerant shrub and herb species (del Rio 2006 ; Lain et al. 2008). In contrast, mechanical site preparation increases the number of herbaceous species (Haeussler et al. 1999; Newmaster and Bell 2002) but reduces ferns (Haeussler et al. 1999; Newmaster and Bell 2002). Our results indicate that the impact of site preparation overwhelmed the impact of salvage logging on the initial recovery of plant species.

Although weeding decreased the number of alien species (Table 3), this effect was not reflected in the CCA biplot (Fig. 3). Roscher et al. (2009) found that immigration of plant species was more frequent at sites that were regularly weeded for three years than at sites that were never weeded. Thus, continuous weeding may retard the succession of plant communities. It has also been reported that weeding reduces species richness and the abundance of cryptogams because this treatment reduces the cover of other vegetation (Bell et al., 1997), thereby exposing sensitive cryptogams to desiccation by wind and sun. Accordingly, we expect that the differences of species composition observed between treatments B (without weeding) and C (with weeding) would become larger after continuous weeding.

In the unsalvaged (A) and residual row (treatment D) sites, a wide range of species were observed, including the crop tree species *A. sachalinensis* (which was growing before the windthrow), woody vine species that generally grow in coniferous forests, and various fern species (Fig. 3). *Q. crispula* did not naturally occur, which was likely because no potential mother trees were present nearby. The common fern species in the unsalvaged (A) and residual row sites (treatment D) were *L. obscurum* and *D. austriaca*. These ferns were thought to be residual species because they generally grow on forest floors characterized by a slightly cool and dark environment. In contrast, two other fern species (*O. cinnamomea* and *T. nipponica*) were frequently found in the residual rows (treatment D). Because these species generally grow in open spaces with wet conditions, it is likely that they newly colonized the area after the treatment. These four fern species were distributed along the CWD height in the CCA ordination (Fig. 3). Fern species tend to respond more sensitively to microhabitat conditions than do woody species (Murakami et al., 2005). In our case, the microtopography created by fallen tree crowns, boles, slashes, stumps, treefall pits and mounds and a pile of surface ash soil may provide suitable habitats for various fern species.

4.3 Appropriate treatment for the restoration of natural mixed forests

The only tree species that uniquely appeared in the unsalvaged areas was *A. sachalinensis*; *Q. crispula* did not occur. The acorns of *Q. crispula* are carried by jaybirds (*Garrulus* spp.), and 290 m is the longest record of their dispersal in Japan (Nakamura and Kobayashi, 1984). Because *A. sachalinensis* and *P. glehnii* have been widely planted in the national forests of Northern Japan for the past 50 years, few reproductively mature trees of *Q. crispula* are found in the vicinity of the study site. Without potential *Q. crispula* mother trees, it is unlikely that unsalvaged blowdown sites will develop a mixed forest of *A. sachalinensis* and *Q. crispula*, although this site retained many *A. sachalinensis* seedlings.

In contrast, plantation of *Q. crispula* after salvaging destroyed most residual plants, including *A. sachalinensis.* Natural regeneration of *A. sachalinensis* cannot be expected for an extended period because the majority of the *A. sachalinensis* seeds fall within the height of the mother tree (Sato and Hiura, 1998), and no reproductively mature trees of *A. sachalinensis* have survived around the study area. Over a longer time frame, the *A. sachalinensis* individuals growing in the unsalvaged and residual sites may provide seeds for the areas subjected to planting practices using *Q. crispula*, and thus, these areas might develop into mixed forests of *A. sachalinensis* and *Q. crispula.*

Considering other species, the unsalvaged areas may provide refuges for shade-tolerant species after a catastrophic disturbance, while the areas subjected to plantation after salvaging provide safe sites for the establishment of pioneer species. Because these silvicultural practices disturb indigenous plant species and the structure of the surface soil and, thereby, promote the invasion of alien species (Haeussler et al 1999, Roberts 2004), they may alter the trajectory of succession (Titus and Tsuyuzaki 2003) and may delay forest recovery.

Consequently, a spatial mosaic pattern of legacy retention and plantation of *Q.*

crispula, with sufficient attention given to alien species, should facilitate an ideal initial stage for succession toward a mixed forest of *A. sachalinensis* and *Q. crispula*. At the landscape level, studies on the appropriate arrangement, shape, and area ratios of legacy retention, planting and residual sites are necessary, while at the stand level, methods for site preparation and weeding for nursing broadleaved trees and controlling alien species should be examined under a long-term monitoring scheme.

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Figure Captions

Fig. 1. Arrangement of the control and treatment plots.

Fig. 2. DCA ordination diagram of 88 plots in the control (■), treatment B (o), treatment C (+), and treatment D (◊) area.

Fig. 3. CCA ordination diagram of (a) all 88 plots and (b) a portion of the plots shown at a larger scale.

Plant species are indicated alphabetically: A (*Actinidia polygama*), L (*Lycopodium obscurum*), S (*Schizophragma hydrangeoides*), T (*Thelypteris nipponica*), R (*Rhus ambigua*), C (*Celastrus orbiculatus*), O (*Osmunda cinnamomea var. fokiensis*), s (*Schisandra chinensis*), t (*Stenactis annuus*), D (*Dryopteris austriaca*), a (*Abies sachalinensis*), H (*Hypericum erectum*), M (*Artemisia montana*), G (*Solidago gigantea var. leiophylla*), P (*Persicaria nepalensis*), E (*Eupatorium chinense* ssp. sachalinense), and p (*Carex puberula*). M, G, P, E, and p are drawn concentrated in one spot.

Physical site conditions are indicated by vectors as follows: (water), water content of the soil; (light), relative PFD; (gravel), gravel cover; and (CWD), CWD height. The longer the vector, the stronger the relationship of that variable to the dataset.

Table 1. Median, minimum and maximum values of environmental variables in each treatment.

Treatment	A (Control)				B				C				D				Kruskal Wallis test	
Number of plot	16				25				25				25				χ^2	*p*
	Median		Min	Max	Median		Min	Max	Median		Min	Max	Median		Min	Max		
% water content of soil by volume	7.2	a	3.4	15.8	4	b	2.4	6.4	4.1	b	2.8	6.6	4	b	3	7	19.11	<0.001
soil hardness (mm)	8.7	b	3.9	11.2	11	a	6.5	13.8	11.8	a	6.9	16.4	7	b	4	14	34.67	<0.001
% relative PFD on ground surface	6.8	b	1.2	70.0	100	a	100	100	100	a	100	100	5.6	b	0.5	99.6	77.27	<0.001
% cover of materials on ground surface																		
% gravel cover	0.0	c	0.0	37.5	62.5	a	37.5	87.5	87.5	a	37.5	87.5	5.5	b	0.0	37.5	70.56	<0.001
% litter and soil cover	87.5	a	17.5	87.5	5.5	c	0.5	17.5	5.5	c	0.5	37.5	37.5	b	0.0	87.5	50.69	<0.001
% branch cover	0.0	b	0.0	0.5	3.0	a	0.5	5.5	5.5	a	0.5	5.5	0.5	a	0.0	17.5	42.72	<0.001
% bole cover	0.0	a	0.0	37.5	0.0	b	0.0	0.0	0	b	0.0	0.0	0	a	0.0	5.5	24.89	<0.001
% stump cover	0.0		0.0	5.5	0.0		0.0	0.0	0		0.0	0.0	0		0.0	17.5	15.03	0.002
% mound cover	0.0	b	0.0	5.5	0.0	b	0.0	0.0	0	b	0.0	0.0	5.5	a	0.0	37.5	68.68	<0.001
% CWD cover	37.5	a	0.0	87.5	0.0	b	0.0	0.0	0.0	b	0.0	0.0	17.5	a	0.5	87.5	71.84	<0.001
the highest height of CWD (m)	0.98	a	0.00	2.15	0.0	b	0.0	0.0	0.0	b	0.0	0.0	0.68	a	0.25	1.45	74.65	<0.001

Different letters on the mean values indicate significant differences by Mann-Whitney U tests using a Bonferroni correction ($p<0.01$).

PFD: photon flux density.

Table 2 - The number and % cover of residual and total (residual and newly colonized) woody species

		Number (/m^2)				% cover			
		Residual		Total		Residual		Total	
Treatment	N	median	(range)	median	(range)	median	(range)	median	(range)
A	16	7[a]	(0-47)	7	(0-53)	10.0[a]	(0.0-62.5)	10	(0-75)
B	24	0	(0-0)	0	(0-1)	0	(0-0)	0	(0-2.5)
C	24	0	(0-0)	0	(0-1)	0	(0-0)	0	(0-2.5)
D	24	0[b]	(0-4)	1	(0-5)	0.0[b]	(0-11.3)	0	(0-11.3)

Small letters indicate significant differences by Mann-Whitney U-test ($p<0.01$).

Total means both of residual and newly colonized plants.

Table 3. Species diversity and the number of alien species in each treatment.

Control and Treatment	N	Species richness					Shannon's DI				Simpson's DI				Species number of alien plant species			
		median		min	max	% of woody species	median		min	max	median		min	max	median		min	max
A(control)	16	9	b	3	14	47%	2.14	b	1.10	2.64	0.88	b	0.67	0.93	0	c	0	1
B	24	17	a	9	21	29%	2.83	a	2.20	3.05	0.94	a	0.89	0.95	4	a	0	7
C	24	15	a	6	20	27%	2.71	a	1.79	3.00	0.93	a	0.83	0.95	1	b	0	3
D	24	14	a	2	26	21%	2.64	a	0.69	3.26	0.93	ab	0.50	0.96	1	bc	0	4

Small letters indicate significant differences found by the Kruskal-Wallis test followed by Sheffé's post-hoc test ($p<0.05$).

Table 4. Summary of the DCA ordination.

Axis	1		2		3	
Eigenvalues	0.359		0.173		0.134	
% variance explained in species data	26.7		14.4		11.3	
Correlations for environmental values						
water content of soil	0.609	**	-0.144		-0.200	
soil hardness	-0.442	**	0.111		-0.317	**
relative PFD	-0.742	**	0.179		-0.067	
gravel cover	-0.721	**	0.120		-0.052	
litter and soil cover	0.699	**	-0.240	*	-0.168	
branch cover	-0.466	**	0.055		0.050	
bole cover	0.364	**	0.277	**	0.015	
stump cover	0.261	*	-0.053		-0.003	
mound cover	0.225	*	0.001		0.197	
CWD cover	0.555	**	-0.150		0.174	
CWD height	0.693	**	0.037		-0.036	

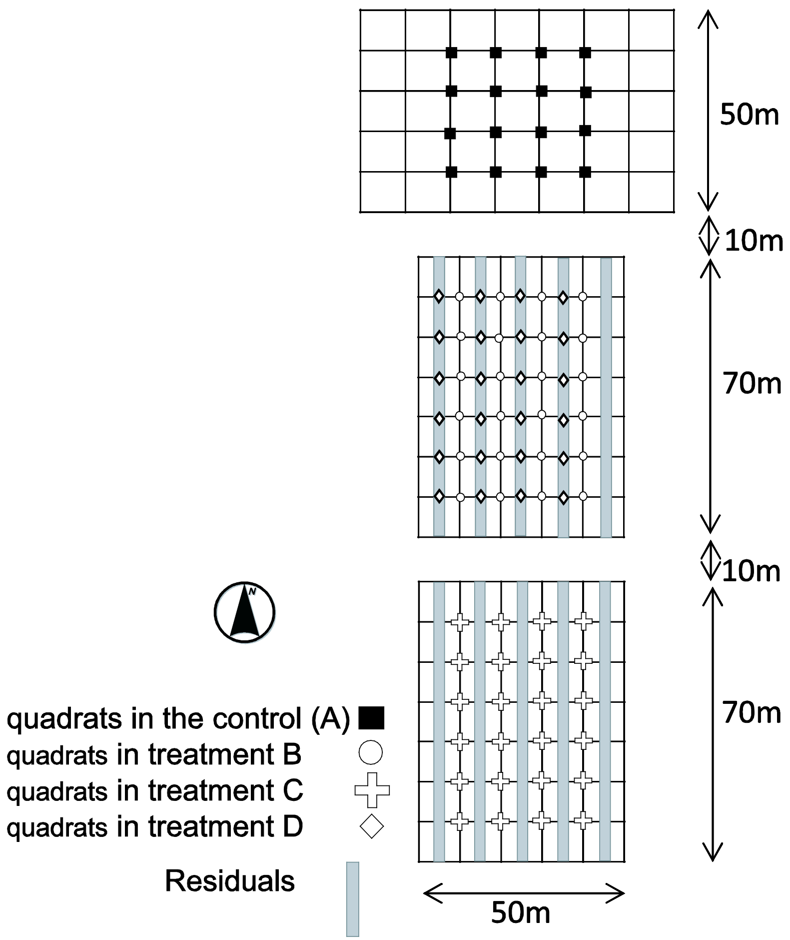
*, ** Significant between axis scores and environmental variables by Pearson's correlation test (* : <0.05, ** : <0.01).

Table 5. Summary of the CCA ordination.

Axis	1	2
Eigenvalues	0.234	0.077
Species-environment correlation*	0.841	0.740
% variance explained in species data	26.7	14.4
Correlations** for environmental values		
water content of soil	-0.558	0.589
relative PFD	0.904	0.262
gravel cover	0.931	0.103
CWD height	-0.908	0.226

* Correlation between sample scores for an axis derived from the species data and the sample scores that are linear combinations of the environmental variables.

** Correlations are "intraset correlations" of ter Braak (1986).



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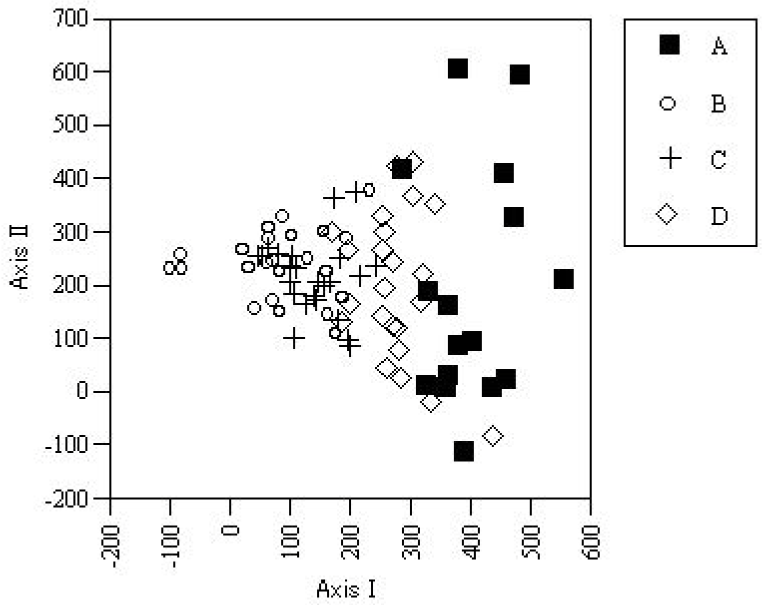

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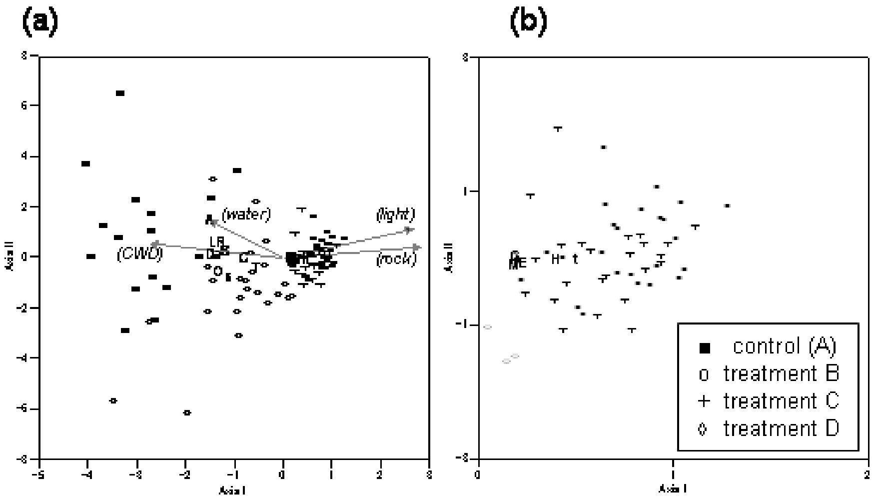

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