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Title: Forest restoration following a windthrow: How does legacy retention vs. plantation after salvaging alter the trajectory of initial recovery?

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ABSTRACT

Recently, the conversion of plantations into natural forests has attracted increasing attention, but little is known about how to convert a windthrown plantation into a natural forest. We examined the initial three-year effects of salvage logging, site preparation, planting, and weeding in comparison to the effects of legacy retention after a typhoon blowdown on the changes in terrestrial environments and plant compositions and the similarity of the species composition to that of the intact natural forest.

Our major findings are as follows. (1) A homogeneous, sunny, and flat environment continued for three years in the planted and weeded plot, whereas a heterogeneous environment was observed in the legacy retention plot; however, the light environment changed slightly in the planted plot. (2) The species composition in the planted plots changed greatly due to the invasion by annual, biennial and perennial herbs and early successional trees. Alien species also invaded the planted row. Conversely, the species composition changed little in the legacy retention, which was likely due to the presence of residual plants that prevented shade-intolerant species from being established. (3) The legacy retention, followed by the residual row, was the closest to the natural forest with respect to species composition, whereas the planted row was the most dissimilar from the natural forest. Legacy retention appears to be the most appropriate way to restore a natural forest immediately after a windthrow, yet supplemental planting may be necessary to restore the desired broadleaved species.

KEYWORDS: disturbance; succession trajectory; natural forest restoration; biological legacies

INTRODUCTION

Windthrow is a major disturbance that maintains the equilibrium in forest ecosystems, although it has been perceived as damaging due to the reduction of log yields in artificial forests (Prestemon *et al.* 2006; Sessions *et al.* 2004). Therefore, salvage logging, site preparation, the planting of crop seedlings for timber production and weeding have been widely performed to reduce economic losses after a windthrow (Elliott *et al.* 2002; Takafumi and Hiura 2009). However, several problems have been detected lately in plantation forests. First, many plantation forests have been abandoned and have deteriorated due to the decrease of demand for wood products (Forestry Agency 2011). Second, single-species and even-aged plantation forests are more susceptible to disturbance than diverse mixed forests (Ford 1979). Third, the public desires forests with diverse functions, including biomass production and the conservation of biodiversity. Indeed, the conversion of coniferous monocultures into natural mixed and broadleaved forests has attracted increasing attention in consideration of the biodiversity and ecosystem services in Japan and other countries (Kint *et al.* 2006; Stephenson 1999; Zerbe 2002). Therefore, the post-disturbance management of plantations to restore natural forests for sustainable management must be reconsidered (Wyatt and Silman 2010).

It is known that the forest pre-disturbance conditions reflect the succession patterns after disturbances (Halpern 1988; Peterson and Leach 2008). Natural disturbances leave many biological legacies, such as residual plants and coarse woody debris (CWD), which are important in restoring the biodiversity and ecosystem functions (Drever *et al*. 2006; Foster *et al*. 1998; Ulanova 2000), and the types and amount of biological legacies left after a disturbance are dependent on the pre-disturbed conditions. Whereas natural forests generally have diverse plants species and forest structures that contribute, with little input, to the realization of the old, pre-disturbed condition after the disturbance, plantations do not contain a variety of plant species or structural complexity due to the past site preparation, the planting of crop trees and/or weeding. Moreover, if the plantations are located far from a natural forest, it may be difficult to restore all of the native species without the deliberate introduction of species by planting or sowing due to the limitations of seed and propagule dispersal (Banner and LePage 2008; Honnay *et al.* 2002; Mabry and Korsgren 1998; Yamagawa *et al.* 2010). For these reasons, it may be difficult to restore natural forests from plantations without human intervention.

The initial conditions after a disturbance also greatly influence forest recovery (Chapman *et al.* 2008). Such forest practices as clear-cutting or site preparation promote thedomination by herbs and alien species due to the concomitant intensive soil disturbance (Peltzer*et al*. 2000; Stahelin 1943; Zenner and Berger 2008), and this colonization may retard forest recovery (Stahelin 1943) or even alter the trajectory of succession (Halpern 1988; Rydgren *et al.* 1998; Rydgren *et al.* 2004). By studying the effects of salvage logging, site preparation, planting and weeding after a windthrow, Morimoto *et al.* (2011) demonstrated that mechanized site preparation had far more impact than salvage logging alone on the environmental conditions and plants, indicating that the management strategy after a windthrow can affect the course of recovery and, thus, the success or failure of forest restoration.

Thus, the effects of active restoration efforts on forest recovery should be examined (e.g., planting broadleaf seedlings after a windthrow, as opposed to leaving an area untouched). Although there have been several studies examining forest restoration attempts after anthropogenic or natural disturbances in natural forests (del Rio 2006; Fischer *et al.* 2002; Halpern 1988; Halpern and Spies 1995; Jonasova *et al.* 2010;

Rydgren *et al.*1998; Rydgren *et al.* 2004; Soltes *et al.* 2010), limited knowledge and information is available on the methods for restoring natural forest in areas with coniferous plantations after a windthrow.

The objectives of our study were to examine the effects of salvage logging, site preparation, planting, weeding and legacy retention on the initial three-year trajectory of plant recovery after a typhoon blowdown and to compare the similarity of the species compositions in windthrown and intact natural forests. We established four different experimental plots in a windthrown forest, including legacy retention and three treatment plots, to examine the regeneration trajectory over three years. To asses the conversion of a fallen plantation forest to the original natural forest, we established reference plots in an old-growth, undisturbed natural forest that included *Picea jezoensis*, *Abies sachalinensis*, and *Quercus crispula*.

METHODS

Study area

In September 2004, Typhoon No. 18 devastated 39,956 ha of forests in Hokkaido, located in northern Japan. Two adjacent cities, Chitose and Tomakomai, suffered damage over large areas, accounting for 30 % of the total damaged area in Hokkaido (Tsushima *et al.* 2005). Our study sites are located in windthrown and intact forest patches in the national forests in Chitose (42°45′N, 141°30′E); the two patches are approximately 4.5 km apart. The reference forest contained *P. jezoensis*, *A. sachalinensis* and *Q. crispula*, the original species in the area. The elevation of the windthrown patch is 150 m, and that of each intact forest plot ranged from 80-250 m above sea level. The annual average temperature is 7.5 degrees Celsius, and the average annual precipitation is 1,005 mm (Japan Meteorological Agency 2010). Each of the windthrown and intact forest patches are mostly flat and are covered with volcanic ash and pumice, which are a legacy of the eruption of Mt. Tarumai (42°41′N, 141°22′E, altitude 1,041 m) in the 17th century.

The studied windthrown patch is located in the *A. sachalinensis* plantation. The *A. sachalinensis* 900 seedlings/ha were planted in rows in the windthrown patch in 1957, and the first thining was conducted in 2000. However, the plantation was nearly 100 % felled by the typhoon in 2004. Two years after the typhoon, in September and October of 2007, salvage logging was conducted in the windthrown patch (160 m × 50 m). Site preparation using backhoes was then conducted in 4m-wide planting rows, and the woody debris was piled up along the planting rows in an area approximately 4 m wide, with average of height of 0.4 m. The woody debris consisted mostly of the fine branches and stubs that were not salvaged for wood products.We called this row the residual row. The surface soil was removed to a depth of 10 cm when the preparation was conducted, exposing the volcanic ash and pumice. Although they were located along the planting rows, the residual rows were not subjected to the site preparation; therefore, the residual rows received less damage by the heavy machinery than the planting rows. Traditionally, crop conifers have been planted in the national forests after typhoons, but *Q. crispula*, which formerly dominated the area, was planted in 2007 to restore a natural mixed forest in this study. A legacy retention plot (50 m × 70 m) was retained in the windthrown patch adjacent to the planted rows.

The western and eastern sides of the windthrown patch were surrounded by undamaged *Picea glehnii* plantations that were planted in 1978 and 1979, respectively. The southern and northern borders of the patch had also been *A. sachalinensis* plantations and were blown down by the typhoon.

Study design

To examine the effects of legacy retention and planting after salvaging on plant regeneration, the experimental plots were established in the windthrown patch in April 2008 (Fig. 1). The experimental plots included a legacy retention plot and three different treatment plots (T1, T2 and T3). The conditions of the legacy retention and the three treatments were as follows: the legacy retention was unsalvaged, and the woody debris remained after the blowdown; the T1 plot was residual rows in which the woody debris was amassed during the salvage logging; the T2 plot was salvaged, prepared and planted with *Q. crispula* seedlings; and the T3 plot was salvaged, prepared, planted with *Q. crispula* seedlings and weeded using rotary grass cutters in July 2008, June and August 2009 and July 2010.

We established three 50 m × 70 m rectangular plots in the legacy retention and treated areas; quadrats of 1 m × 1 m in size were then installed at the intersecting points of the 10 m × 10m grid system (see Fig. 1). To avoid edge effects, we excluded the external points, resulting in the placement of 16 quadrats in the legacy retention plot and 24 quadrats each in T1, T2 and T3. The quadrats for T1 were established every 10 m on the four residual rows (70 m × 1 m). The residual rows were located in the area of the T2 plot (Fig. 1). A total of 24 1 m × 1 m quadrats were placed in T1, with six in each residual row. All of the quadrats were initially established in 2008. However, as the plants grew rapidly, the quadrats were expanded in 2009 to 2 m × 2 m in the legacy retention, T2 and T3 plots, and to 1 m × 4 m in the T1 plot. A distance of 10 m was maintained between the legacy retention, T2 and T3 plots.

According to Japanese governmental policy, salvage logging should be implemented soon after a windthrow occurs. Thus, we were able to leave only a small portion of unsalvaged area for this study. Additionally, we were only able to arrange 16 quadrats in the legacy retention plot to avoid the edge effects from the surrounding forest roads and to avoid the occurrence of autocorrelation among the quadrats.

The reference was set in an area of intact forest, and five 20 m × 20 m blocks were established; buffer zones greater than 200 m wide were maintained for each block. Five 2 m × 2 m quadrats were established at the center of each block and at the centers of four 10 m × 10 m divided squares in each 20 m × 20 m block, for a total of 25 quadrats.

Environmental conditions

The surface relative photon flux density (PFD), soil water content, soil hardiness and materials covering the surface were evaluated annually from 2008 to 2010 to examine the environmental changes over the three years of the study in the legacy retention and treatment plots. Because the CWD composition, including small and large branches (< 2 cm and 2-5 cm in diameter, respectively) and boles (> 5 cm), was assumed to remain unchanged during the study period, the numbers of CWD pieces were measured only in 2009. The total carbon and nitrogen contents in the soil were measured in 2009 to represent the initial soil nutrient conditions after the disturbances.

The global solar radiation did not differ among the treatments because the trees in the study area had all been blown down simultaneously by the typhoon (Morimoto et al. 2011). The ratio of the PFD under the CWD to that over the CWD was calculated, and the average ratio for each quadrat was used to determine the relative PFD values of the quadrats. The PFD was simultaneously measured over (2 m high) and under (0.2 m high) the CWD using two light sensors (LI-250A light sensor, LI-COR, Lincoln, Nebraska, USA) in all of the plots to examine the effects of shading by the CWD on the ground. The measurements were conducted on sunny days in mid-August from 2008 to

2010. However, in 2008, the relative PFD values in the T2 and T3 plots were assumed to be 100 % and were not measured because there were very few pieces of woody debris and plants shading the ground. The PFD values were measured at the centers of the quadrats in 2008 and at the centers and the four corners of the quadrats in 2009 and 2010 because the sizes of the quadrats had been increased.

The soil water content was measured using time domain reflectometry (TDR; HydroSense, Campbell Scientific, Inc. Logan, Utah, USA) on selected sunny days that followed three continuous sunny days in mid-August from 2008 to 2010. The soil water content was measured at a depth of 5 cm at five randomized points in each quadrat, and the average was calculated. The soil hardiness was also measured using a Yamanaka-style hardiness gauge (Fujiwara Scientific Company, Co., Ltd., Tokyo, Japan) at the same points as the measurements of the soil water content.

Soil samples to a depth of 5 cm, excluding litter, were collected at three points around each quadrat in mid-August 2009, and the C and N contents per 10 mg of soil were analyzed using an NC-900 device (Sumika Chemical Analysis Service, Ltd. Osaka, Japan). Regarding the CWD component, the numbers of the small and large branches and boles were measured at five equally spaced points in October 2009.

The coverage percentages were determined for the litter and soil, gravel, branches, boles, mounds and stumps in August from 2008 to 2010. “Litter and soil” included leaves, small branches and soils with a grain size of < 1 cm. Gravel was classified as being > 1 cm in grain size. The classification of small and large branch and bole is same as that of CWD.

Vegetation sampling

Vegetation sampling was conducted twice annually from late July to early August and in late September from 2008 to 2010. The presence or absence of species was recorded in each quadrat. Because the small seedlings of the *Betula* and *Salix* genera were difficult to identify, they were grouped as *Betula* spp. and *Salix* spp.; all of the other species were identified at the species level. The reference text *Naturalized Plants of Japan* (Shimizu 2003) was used to identify alien species. In the reference, the understory species (< 2 m high) were recorded in each 2 m × 2 m quadrat, and the overstory species (> 2 m) were recorded in each 20 m × 20 m block.

Analysis

A two-way ANOVA was used to examine the differences among the plots, times and plot × time interactions for the soil water content, soil hardiness, relative PFD and surface coverages of the various materials (R ver. 2. 4. 1). When significant differences were found among the plots, Tukey's honestly significant difference test was used for the post hoc multiple comparisons. The soil C and N contents showed non-normal distributions and were analyzed using a Kruskal-Wallis test, followed by Mann-Whitney U tests with Bonferroni adjustments. The numbers of the CWD pieces exhibited non-normal distributions and were analyzed only among the legacy retention and T1 plots using a Kruskal-Wallis test because the CWD was not detected in the T2 and T3 plots; SPSS (14.0J) was used for these analyses.

The seral pattern of species composition in each plot was analyzed with Canonical Correspondence Analysis (CCA) using the presence-absence data for 2008 to 2010. The species that appeared in the summer and/or fall were combined to represent each year. Any species present in less than four quadrats was excluded from the analysis. To remove the non-significant environmental variables, a permutation test was conducted for each explanatory variable. One non-significant variable was removed at each time, and the CCA was repeated until all of the variables became significant at a 0.1 significant level. This analysis was computed using R 2.15.0.

A DCA was used to examine the similarity of the species compositions in the reference and the windthrown plots with the presence-absence data for 2010; the DCA was conducted using PC-ORD (4.0).

RESULTS

Surface environmental conditions

The relative PFD, soil water content, soil hardiness and material surface coverage all differed significantly among the plots (Table 1). The relative PFD values were higher in the T2 and T3 plots than in the legacy retention and T1 plots. Over the three years of this study, the PFD did not change in the legacy retention and changed only slightly in the T1 plot; in contrast, the PFD changed dramatically in the T2 plot ($p < 0.01$) and moderately in the T3 plot ($p < 0.01$). The soil water content in the legacy retention plot was higher than that in the treatment plots in 2008 ($p < 0.01$) but decreased in 2009, and no significant differences were observed among the plots after 2009. The soil hardiness was higher in the T2 and T3 plots than in the legacy retention and T1 plots ($p < 0.01$) and remained unchanged during the three years of the study. The surface coverage by litter and soil was greater in the legacy retention plot than in the T2 and T3 plots ($p < 0.01$) throughout the study period. In the legacy retention and T1 plots, the gravel cover was lower than in the T2 and T3 plots ($p < 0.01$).The branch cover in the T1, T2 and T3 plots was higher than in the legacy retention plot ($p < 0.01$), the bole cover in the legacy retention and T1 plots was higher than in the T2 and T3 plots ($p < 0.01$), and the mound and stump cover in the T1 plot was higher than in the T2 and T3 plots ($p < 0.01$). The soil C and N contents in the legacy retention and T1 plots were higher than the T2 and

T3 plots (Table 2). The number of CWD pieces did not differ significantly for the legacy retention and T1 plots (Table 2).

Species composition

Based on the permutation test for each explanatory variable, the plot ID, relative PFD, soil water content, soil hardiness, and ground cover by the litter, gravel, branch, mound, and stub were selected. A total of 65.9 % of the variance of the species composition in the CCA was explained by these environmental variables ($p < 0.05$, eigenvalues of 27.3 % [axis 1] and 9.1 % [axis 2]).

The species composition of the legacy retention and T1 plots became less diverse over the study period (Fig. 2abc). The T2 and T3 plots were in almost the same region on the ordination graph in 2008, and they subsequently moved to an upper region over the course of the three years with the decreasing soil water content, particularly for the T2 plot (Fig. 2def). When the species were laid out (Fig. 3), the legacy retention plot was characterized by tree species and fern and herb species that tend to grow on the forest floor, whereas the T2 and T3 plots were characterized by light-demanding herb species, alien herbaceous species and early successional species, including *Betula* spp. and *Salix* spp. In the first year, annual and biennial plants, such as *Persicaria nepalensis* (*PN*), *Persicaria longiseta* (*PL*), *Oenothera biennis* (ob) and *Rubus idaeus* (RI), invaded. In the second and the third years, perennial herbs, including *Hypericum ascyron* (*HA*), *Artemisia montana* (AMa), *Poa trivialis* (pt) and such early successional tree species as *Betula* spp. and *Salix* spp., were established in succession (Fig. 3b, the species abbreviations are defined in the Appendix).

Three axes were derived from the DCA ordination with the presence-absence data for the windthrown and reference plots in 2010 (with a total inertia of 4.57 and eigenvalues of 67.8% [axis 1], 30.9% [axis 2] and 15.0% [axis 3]). Both the understory and overstory species compositions of the reference were located on the right side of the ordination diagram, and the legacy retention was the closest to the reference, followed by T1, whereas T2 and T3 were found on the other side of the diagram (Fig. 4a). The reference was characterized by such tree species as *P. jezoensis*, (**PJ**), *Kalopanax pictus* (**KP**), *Fraxinus lanuginose* (**FL**), *F. mandshurica* (**FM**) and *Acer mono* (**AM**) (Fig. 4b). Both the reference and legacy retention plots were characterized by tree species that included *Prunus maximowiczii* (**PM**) and *Cornus controversa* (**CC**), such ferns as *Dryopteris crassirhizoma* (*dc*) and such shrubs as *Pachysandra terminalis* (PT). The legacy retention was characterized by tree species, such as *Acanthopanax sciadophylloides* (**ASf**) and *A. sachalinensis* (**AS**), and ferns, such as *Dryopteris austriaca* (*da*), *Osmunda cinnamomea* (*oc*) and *Lycopodium obscurum* (*lo*). The T1 plot consisted of such tree species as *Sorbus commixta* (**SC**), such ferns as *Thelypteris nipponica* (*tn*) and *Athyrium yokoscense* (*ay*) and such shrub species as *Hydrangea paniculata* (HP). In contrast, the T2 and T3 plots were distinguished from the other plots by the early successional species of *Betula* (**B**), *Salix* (**S**) and *R. idaeus* (RI), which are light-demanding herbaceous species and alien herbaceous species.

DISCUSSION

Environmental conditions during the initial three years

In the initial three years after the windthrow, the treatments of salvage logging and site preparation created completely different homogenous environmental conditions, including the light, soil, and ground cover, than in the legacy retention plot. Although several conditions, including the relative PFD on the forest floor and soil water content of the surface soil, changed slightly throughout the study period, according to Lang *et al*.

(2009), the differences in a variety of environments can persist for hundred of years.

The salvage logging and site preparation removal of the vegetation and woody debris on the ground resulted in a uniform light environment during the first year. However, as the newly colonized plants and planted trees grew, the light flux slightly decreased and varied in the planted rows, a situation that will increase the competition among plants for light resources (Banta *et al.* 2008). Weeding prevented the newly colonized plants from growing thickly and resulted in less change in the light conditions, meaning that the light competition was reduced, which would promote the growth of the planted *Q. crispula* seedlings (Hannah 1987). In contrast, the light flux density changed little in the legacy retention plot because the ground was prevented from the exposure to sunlight from the beginning, as the biological legacies, including the CWD and residual plants, remained. The soil water content did not decrease in any of the plots, with the exception of the legacy retention plot. Soil water content is affected by both transpiration and evaporation, as the plants grew, the transpiration increased in all of the plots which reduced soil water content. Although the removal of biological legacies increased evaporation from the ground surface, it was gradually suppressed by the growing plants. These evaporation and transpiration changes counteracted the change of soil water content. However, since legacy retention already had vegetation and CWD cover, only transpiration increased, which reduced soil water content over the study period. In the residual row, the accumulation of volcanic ash and other woody debris may have destroyed any porous soil structures (Morimoto *et al.* 2011), which would have reduced the water-holding capacity for the three-year study period. Few studies have monitored the changes in the soil moisture after a windthrow, making the evaluation of our results difficult. However, the structural types of legacies created by treefalls can be key factors in maintaining the long-term soil patterns and variety in forest communities; thus, the uniform or various soil moisture patterns created by windthrows and subsequent treatments are expected to persist for a long time (Beatty and Stone 1986; Peterson and Campbell 1993; Peterson and Leach 2008).

Lang *et al*. (2009) reported that the soil C and N contents were higher in salvaged plots than in unsalvaged plots after a windthrow. Whereas salvage logging alone can leave many residues, such as fine woody debris, that provide nutrients for the soil (Johnson and Curtis 2001), the subsequent site preparation in our case removed these residues and the nutrient-containing surface soil, reducing the soil's C and N contents.

Changes in the species composition among the plots during the initial three years

Temporal changes in species compositions

Several types of biological legacies, including propagule legacies (residual plants and propagules) and structural legacies (microsites and CWD), contributed to the differences in the succession trajectories among the plots after the disturbances. The salvage logging and site preparation removed all of the biological legacies, resulting in considerable changes in the species composition. On the open, legacy-scarce ground, light-demanding species appeared in succession over the three years: the pattern of succession began with annual herbaceous species and then progressed from biennials and perennials to woody perennials, and weeding slightly altered the course of the ensuing succession. Weeding provided light and room for growth, allowing for the continuous establishment of extreme pioneer species, such as annual herbs and *R. idaeus*. The same pattern was reported in a prior study of early succession following clear-cutting and slash burning (Halpern 1988). When the ground is severely disturbed by salvage logging, early successional herb species dominate, and these species then prevent shade-tolerant species from becoming established (Peltzer *et al.* 2000;

Stahelin1943; Zenner and Berger 2008); however, weeding has the same effect.

Conversely, although the species composition in the legacy retention plot became less diverse, the species composition changed little over the course of the three years. This is because the residual plants already dominated in the legacy retention plot, a situation that inhibited the colonization of newly established species. In contrast, as the residual plants remained to a lesser extent in the residual rows than in the legacy retention area (Morimoto *et al*. 2011), the diversity in the residual rows remained relatively high over the study period. The treatment of biological legacies had significant effect on the initial species composition, which may affect the subsequent succession trajectory.

The ferns were exemplary for the importance of biological legacies in species succession during the early stage: the ferns relied on both propagule and structural types of biological legacies and scarcely regenerated on the severely disturbed, legacy-scarce site. There are three possible reasons for this observation. First, the biological legacies with propagule types that mainly fall within several meters from the source, including both ferns themselves and their spores, were completely removed by the site preparation (Peck *et al.* 1990; Penrod and McCormick 1996). Second, the ground conditions became unfavorable for the ferns because the variable microsites favored by ferns (Beatty 1984; McGee 2001; Peterson and Campbell 1993) were eliminated by the site preparation. Flinn (2007) reported that ferns were little established on the flattened ground caused by a man-made disturbance. Third, with the legacy removed, the newly created environment was not favorable for the germination of fern spores. The ground was exposed to strong sunlight and wind due to the removal of the fallen logs and branches, thereby limiting the soil moisture (Newmaster and Bell 2002). Intensive weeding removes shading and may, therefore, also prevent ferns from becoming established over the long term.

In their study of 15 years of plant succession after a windthrow in a mixed natural forest, Fischer *et al*. (2002) reported that *R. idaeus* and light-demanding herbs dominated initially, and then *Betula* spp. and *Salix* spp. dominated, followed by coniferous species in salvaged plots; in contrast, the species composition changed little in unsalvaged plots because the residual plants already dominated. These results may predict the future of our legacy retention plot and the salvaged and site preparation plots; however, the salvaged and site preparation plots may require longer periods of time to recover than the plot studied by Fischer *et al*. (2002) because site preparation alters the initial environment and plant population to a greater extent than salvage logging alone.

Invasion of alien species

Both the propagule and structural legacy types acted as barriers to the invasion by alien species for the three years of the study. In contrast, the salvage logging and site preparation, which expose the mineral soil and reduce the plant cover, provided a perfect opportunity for alien species, such as *Solidago gigantean* and *Taraxacum officinale*, to invade the plots in the first year (Morimoto *et al.* 2011), and these alien species persisted for two more years. The weeding further promoted the invasion of alien species for three years. These results are consistent with those of Bell and Newmaster (2002) who reported that clear-cutting, site preparation and weeding resulted in increased numbers of alien species. New invasions by alien species should decrease for several years after a disturbance, but the dominance by alien species may persist for a long time (Rydgren *et al.* 2004).

Species composition between the intact natural forest and windthrown forest

The legacy retention was the closest to the reference natural forest in the species composition, and the salvage logging, site preparation and planting created totally different species compositions in comparison to the natural forest (Fig. 4a). The propagule legacy type greatly contributed to the recovery of the plant species in the legacy retention plot. However, a different species composition was observed with respect to the reference because the windthrow created the small gaps that are favored by shade-intolerant tree species, such as *C. controversa*, and light-demanding herbs, such as *Senecio cannabifolius* and *Solidago virgaurea* (del Rio 2006; Peterson and Pickett 1995).

In contrast, the salvage logging and site preparation resulted in a different species composition from the natural forest: these treatments created suitable habitats for shade-intolerant species, including *Betula* spp., *Salix* spp. and native and alien herbs that were not present in the old-growth natural forest. These results are consistent with those of Del Rio (2006) and Soltes*et al*. (2010) who reported that, when comparing intensively salvaged plots with unsalvaged plots, the unsalvaged plots were more similar in species composition to intact natural forests.

The residual rows that had not been considered to be regeneration sites in the plantation forests showed relatively similar species compositions to those of the legacy retention areas. This is most likely because the residual plants remained in part and both shade-tolerant and -intolerant species appeared in the residual rows. Bell and Newmaster (2002) also reported that missed strips (untreated areas) that were not considered to be regeneration sites provided refuges for variable species and played important roles in maintaining biodiversity.

Management implications

Biological legacies are equally important for natural forests and for the conversion of coniferous monoculture plantations into natural forest. During the initial three years after the disturbances, the legacy retention plot had the most similar species composition to that of the natural forest due to the presence of the residual plants. Takafumi and Hiura (2009) reported that the disturbance history determines the propagule availability and habitat structure, strongly affecting the species richness, even more than 50 years after the disturbance. Therefore, the recovery of plant species would be delayed or would ultimately fail due to salvage logging and site preparation.

However, legacy retention alone after a windthrow may be insufficient to restore a natural mixed forest state. The remaining propagule and/or seed dispersal from the surroundings may be limited, particularly in large blowdown areas, as plantations have been broadly implemented for many decades. Our study area was originally dominated by *A. sachalinensis*, *P. jezoensis* and *Q. crispula*, but there were insufficient numbers of adult *Q. crispula* trees to provide acorns near the windthrown patch. Supplemental planting may, therefore, be necessary to restore the *Q. crispula* populations. In this situation, leaving broad residual rows may be an effective management for converting monoculture plantation forests into natural mixed forests. Due to the limitations in the number of replicates and the plot sizes in this study, further studies in different settings and long-term monitoring will be required to implement the appropriate management.

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Figure captions

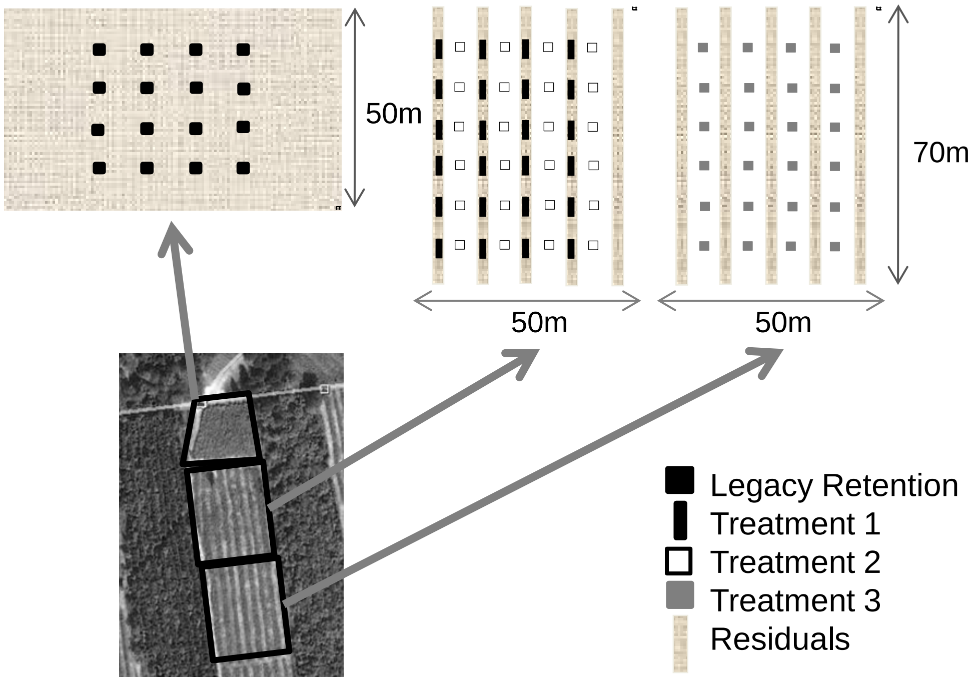
Fig. 1 Study setting

Fig. 2 Canonical correspondence analysis diagram of the quadrats from 2008 to 2010. (a)(d) 2008, (b)(e) 2009 and (c)(f) 2010. (d)-(f) show the right-side area in detail. ●, legacy retention; ▲, T1; ×, T2; ◇, T3.

Fig. 3 Canonical correspondence analysis diagram of the species.The species abbreviations are defined in the Appendix. Bold capital letters, tree species; underlined capital letters, shrubs; italicized capital letters, herbs; lowercase letters, alien herbs; italicized lowercase letters, ferns.

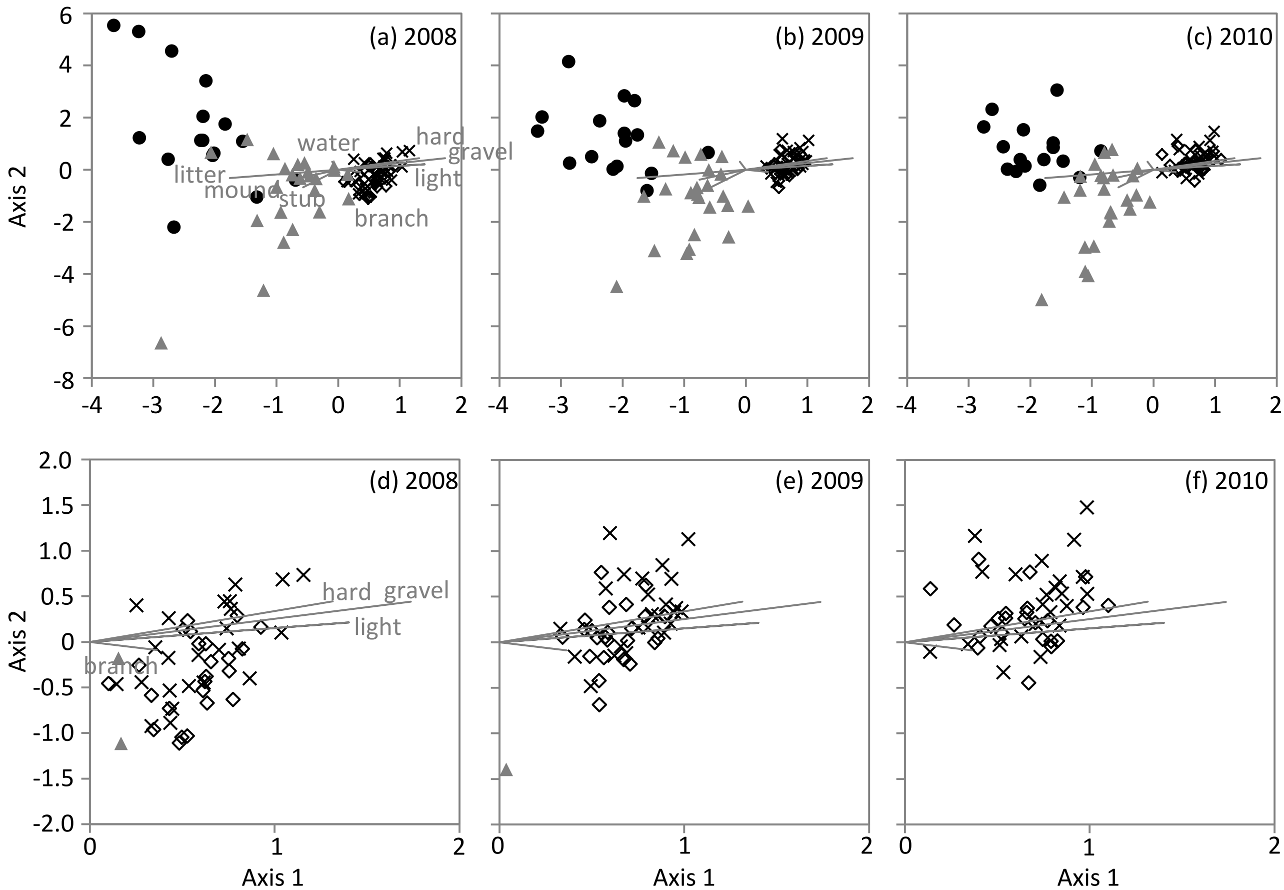
Fig. 4 Detrended correspondence analysis diagram of (a) plots and (b) species and plots in 2010. ●, legacy retention; ▲, T1; ×, T2; ◇, T3; *, R (understory); ■, R (overstory).The species abbreviations are defined in the Appendix. Bold capital letters, tree species; underlined capital letters, shrubs; italicized capital letters, herbs; lowercase letters, alien herbs; italicized lowercase letters, ferns.

Fig. 1



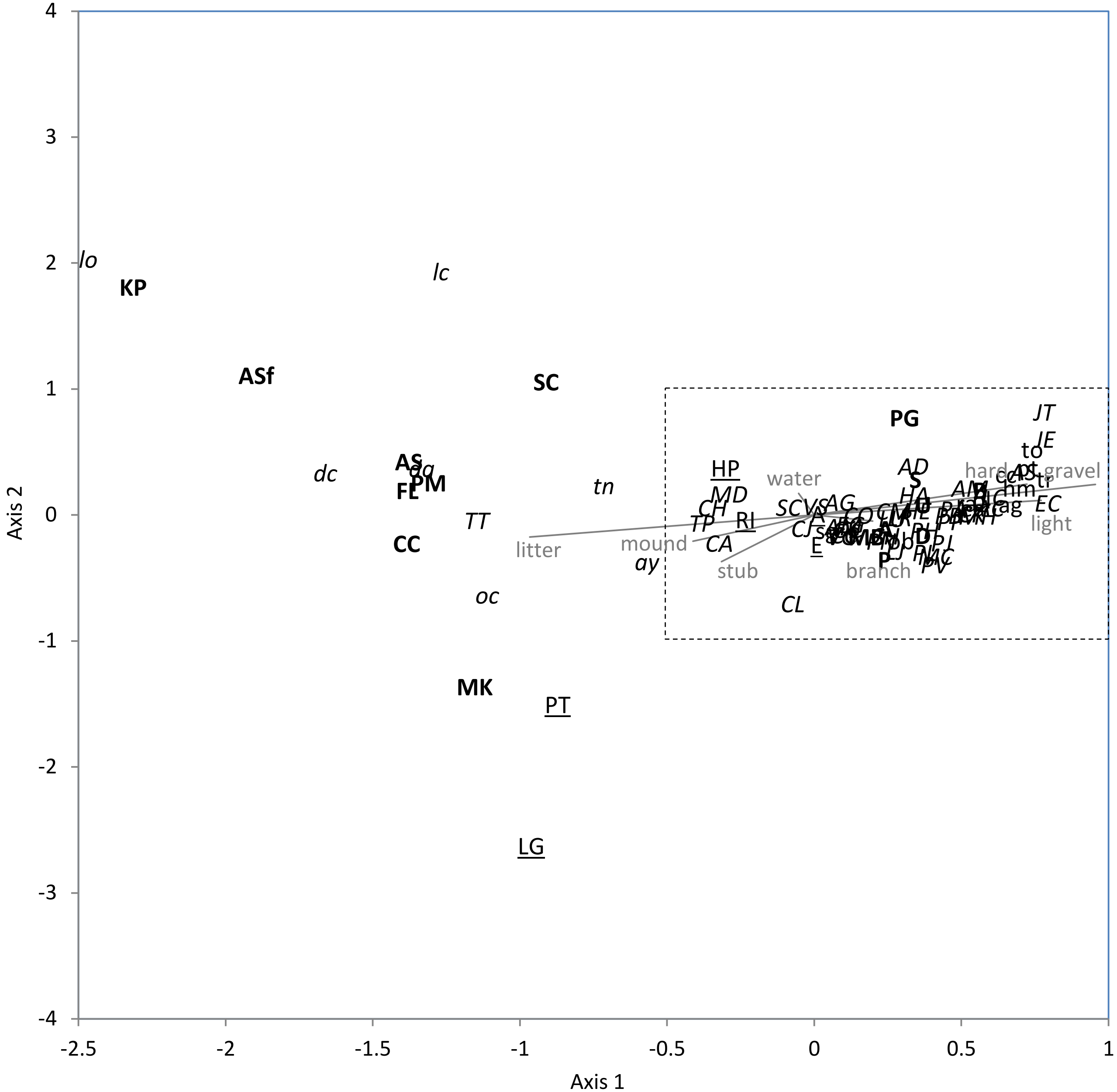
Legacy Retention
T1 and T2
T3
50m
70m
50m
50m
Legacy Retention
Treatment 1
Treatment 2
Treatment 3
Residuals

Fig. 2



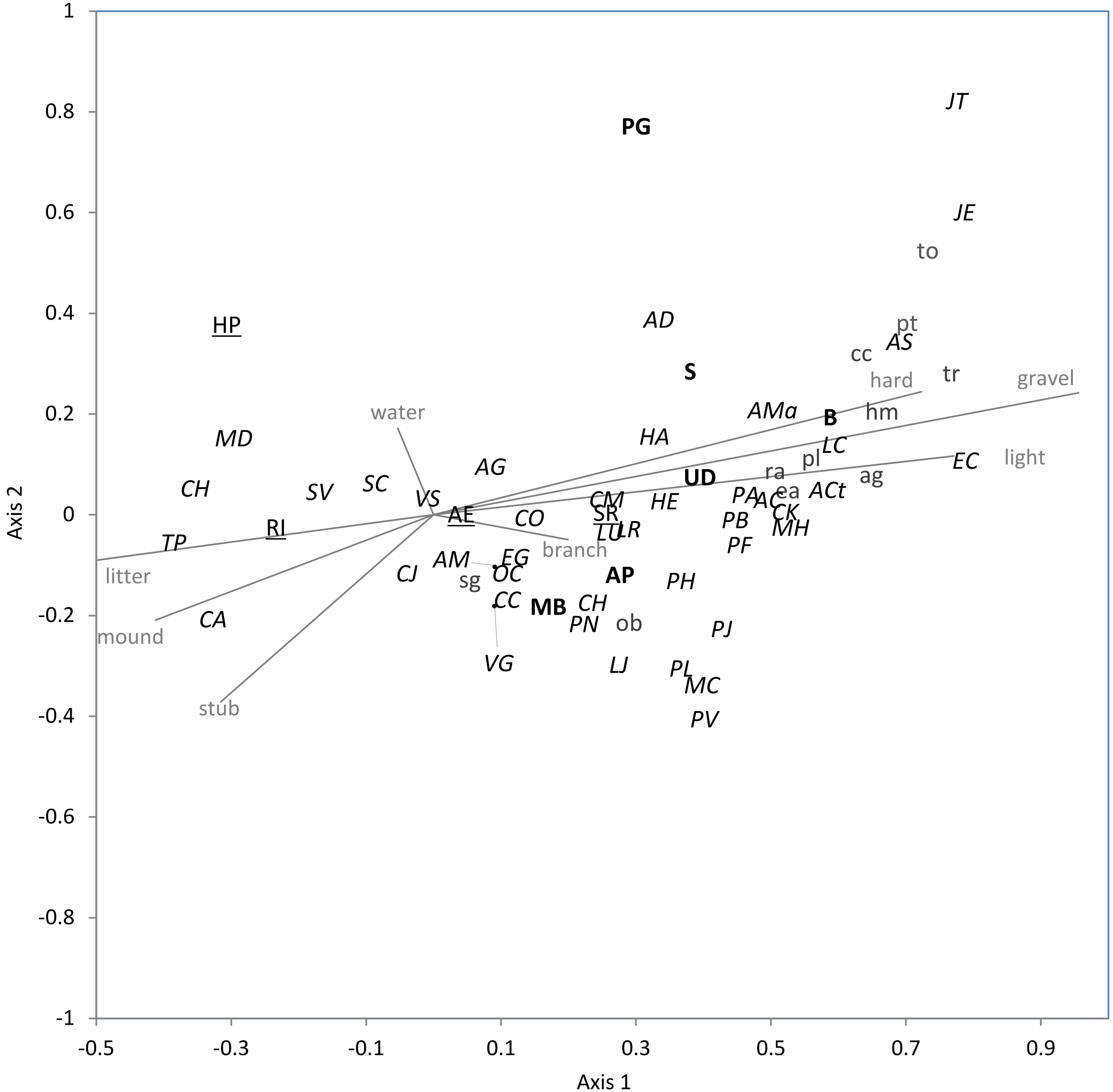
(a) 2008
(b) 2009
(c) 2010
(d) 2008
(e) 2009
(f) 2010
Axis 2
Axis 1
water
hard
gravel
litter
light
mound
stub
branch

Fig. 3a



Axis 1
Axis 2
-2.5
-2
-1.5
-1
-0.5
0
0.5
1
4
3
2
1
0
-1
-2
-3
-4
lo
KP
lc
ASf
SC
PG
JT
IE
to
HP
water
hard
gravel
light
litter
mound
stub
branch
AD
EC
dc
AS
PM
FL
tn
TT
CC
ay
oc
CL
MK
PT
LG
MD
CH
TP
RI
CA
E

Fig. 3b



Axis 1
Axis 2
-0.5
-0.3
-0.1
0.1
0.3
0.5
0.7
0.9
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
JT
PG
JE
to
HP
AD
pt
AS
cc
S
tr
hard
gravel
water
AMa
B
hm
MD
HA
LC
EC
light
AG
pl
UD
ra
ag
CH
SV
SC
VS
CM
HE
PA
ea
ACt
AC
CK
AE
CO
SR
PB
MH
TP
RI
LU
LR
branch
PF
AM
EG
litter
CJ
sg
OC
AP
PH
CC
MB
CH
CA
PN
ob
PJ
mound
VG
LJ
PL
MC
stub
PV

Fig. 4

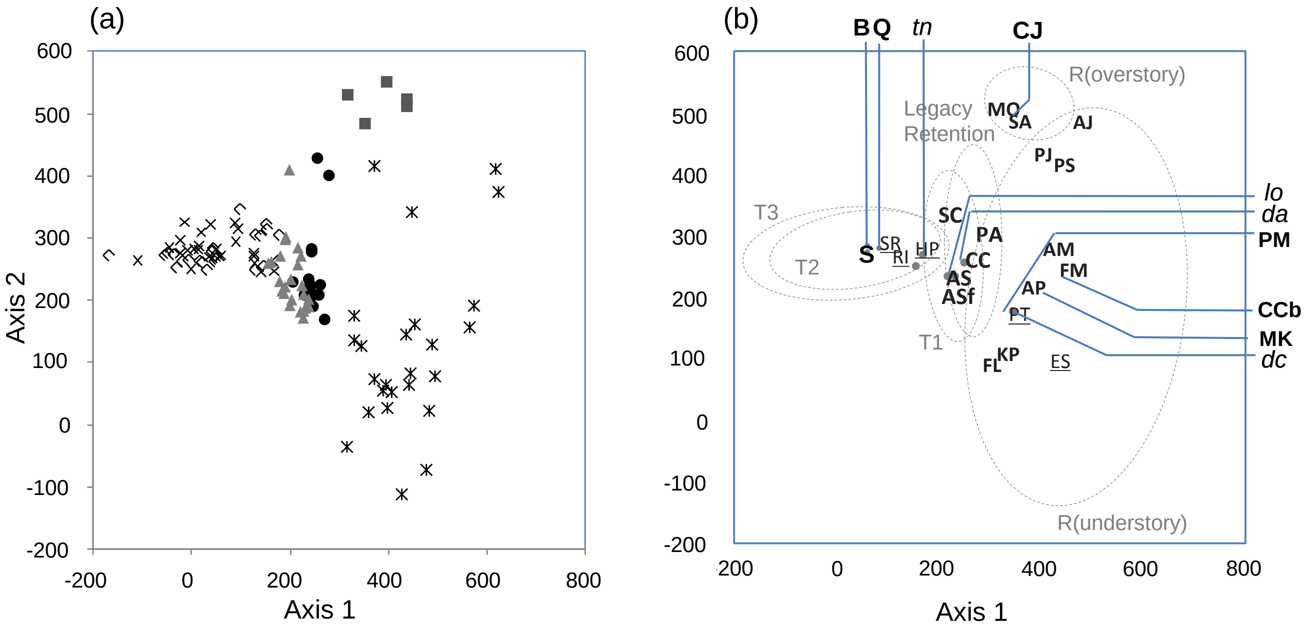

(a)
Axis 1
Axis 2
600
500
400
300
200
100
0
-100
-200
-200
0
200
400
600
800
(b)
BQ
tn
CJ
R(overstory)
Legacy
Retention
MQ
SA
AJ
PJ
PS
T3
SC
PA
S
SR
RI
HP
CC
AS
ASf
T2
AM
FM
AP
PT
T1
FL
KP
ES
R(understory)
lo
da
PM
CCb
MK
dc
Axis 1
600
500
400
300
200
100
0
-100
-200
-200
0
200
400
600
800

Table 1 Environmental variables in each treatment, year, and their interaction.

	Year	Legacy Retention		T1 (Residual row)		T2 (S+M+P)		T3 (S+M+P+W)		Treatment		Year		Interaction	
		Mean	(SD)	Mean	(SD)	Mean	(SD)	Mean	(SD)	*F*	*P*	*F*	*P*	*F*	*P*
Relative PFD (%)	2008	9.55	(16.44)	25.39	(33.60)	100.00	(0.00)	100.00	(0.00)	524.22	<0.01	86.70	<0.01	14.74	<0.01
	2009	5.92	(4.29)	7.51	(8.99)	61.71	(13.91)	74.43	(6.97)						
	2010	8.45	(4.57)	13.89	(8.92)	48.88	(14.63)	78.45	(4.81)						
Soil water content (%)	2008	7.43	(3.14)	4.62	(1.08)	4.13	(1.11)	4.20	(0.96)	10.85	<0.01	2.30	0.10	9.93	<0.01
	2009	4.72	(0.84)	4.48	(0.77)	5.15	(0.84)	4.98	(0.70)						
	2010	5.49	(1.28)	4.80	(1.51)	5.70	(1.23)	4.96	(0.90)						
Soil hardiness (mm)	2008	8.01	(2.38)	6.87	(2.33)	10.53	(2.15)	11.46	(2.66)	125.32	<0.01	13.81	<0.01	5.00	<0.01
	2009	5.71	(1.85)	5.73	(2.32)	11.02	(2.14)	9.99	(1.36)						
	2010	6.48	(1.68)	6.35	(2.29)	13.49	(1.51)	12.43	(1.94)						
Ground surface cover (%)															
Litter and soil	2008	75.31	(21.45)	40.33	(26.60)	9.04	(7.56)	8.71	(8.27)	458.17	<0.01	31.44	<0.01	14.21	<0.01
	2009	88.81	(10.08)	82.08	(16.43)	13.25	(9.24)	11.88	(16.42)						
	2010	88.81	(10.08)	82.08	(16.43)	9.29	(7.73)	7.25	(5.11)						
Gravel	2008	2.34	(9.38)	8.02	(10.91)	68.75	(18.43)	76.04	(14.71)	1307.77	<0.01	15.18	<0.01	7.49	<0.01
	2009	4.00	(8.56)	2.96	(5.37)	82.50	(9.78)	87.71	(5.51)						
	2010	4.06	(8.53)	3.98	(5.35)	87.92	(7.93)	89.38	(5.58)						
Branch	2008	0.03	(0.13)	2.58	(3.96)	3.00	(2.55)	4.04	(2.32)	5.96	<0.01	11.11	<0.01	5.37	<0.01
	2009	1.56	(1.09)	1.25	(0.68)	1.58	(1.38)	1.58	(1.18)						
	2010	1.56	(1.09)	1.25	(0.68)	1.81	(1.33)	1.55	(0.96)						
Bole	2008	4.06	(9.29)	1.69	(2.51)	0.00	(0.00)	0.00	(0.00)	29.42	<0.01	1.77	0.17	1.48	0.19
	2009	4.13	(5.32)	4.58	(3.09)	0.00	(0.00)	0.00	(0.00)						
	2010	4.13	(5.32)	4.58	(3.09)	0.00	(0.00)	0.04	(0.00)						
Mound	2008	1.03	(2.22)	18.85	(13.64)	0.00	(0.00)	0.00	(0.00)	52.71	<0.01	0.10	0.91	1.39	0.22
	2009	7.81	(10.95)	15.38	(15.99)	0.00	(0.00)	0.00	(0.00)						
	2010	7.81	(10.95)	15.38	(15.99)	0.00	(0.00)	0.00	(0.00)						
Stub	2008	1.38	(2.46)	1.90	(4.02)	0.00	(0.00)	0.00	(0.00)	52.79	<0.01	2.38	0.09	4.96	<0.01
	2009	0.19	(0.54)	5.00	(4.08)	0.00	(0.00)	0.00	(0.00)						
	2010	0.19	(0.54)	5.00	(4.08)	0.00	(0.00)	0.00	(0.00)						

Note: PFD = photon flux density, S = salvaging, M = machinery site preparation, P = planting, W = weeding.

Table 2 . Environmental variables in each treatment.

	Legacy Retention			T1 (Residual row)			T2 (S+M+P)			T3 (S+M+P+W)			Kruskal Wallis test	
	Median	Min	Max	Median	Min	Max	Median	Min	Max	Median	Min	Max		
Soil C content (%)	24.63 a	15.56	35.20	21.63 a	13.67	29.94	13.25 b	7.85	19.81	14.56 b	10.28	20.92	52.08	<0.01
Soil N content (%)	1.18 a	0.77	1.85	0.99 a	0.52	1.43	0.61 b	0.26	0.96	0.65 b	0.35	1.04	47.09	<0.01
CWD														
# of small branch	1.11 a	0.00	3.60	0.97 a	0.00	3.60	0	0	0	0	0	0	0.00	0.94
# of branch	0.58 a	0.00	3.00	0.40 a	0.00	1.20	0	0	0	0	0	0	0.03	0.87
# of stem	0.41 a	0.00	1.40	0.37 a	0.00	1.40	0	0	0	0	0	0	0.07	0.79

Note: Values with different letters among treatments are significantly different. (Mann-Whitney U test, $\alpha = 0.05$). S = salvaging, M = machinery site preparation, P = planting, W = weeding.

Appendix

Abbreviation	Species name
Tree	
AJ	*Acer japonicum*
AM	*Acer mono*
AP	*Acer palmatum*
AS	*Abies sacarinensis*
ASf	*Acanthopanax sciadophylloides*
AU	*Acer ukurunduense*
B	*Betula spp.*
CC	*Cornus controversa*
CCb	*Carpinus cordata*
CJ	*Cercidiphyllum japonicum*
FL	*Fraxinus lanuginosa*
FM	*Fraxinus mandshurica*
KP	*Kalopanax pictus*
MB	*Morus bombycis*
MK	*Magnolia kobus*
MO	*Magnolia obovata*
PA	*Phellodendron amurense*
PG	*Picea glehnii*
PJ	*Picea jenoenssis*
PM	*Prunus maximowiczii*
PS	*Prunus ssiori*
Q	*Quercus crispra*
S	*Salix spp.*
SA	*Sorbus alnifolia*
SC	*Sorbus commixta*
UD	*harunire*
Shrub	
AE	*Aralia elata*
HP	*Hydrangea paniculata*
LG	*Leucotoe grayana*
PT	*Pachysandra terminalis*
RI	*Rubus idaeus*
SR	*Sambucus racemosa*
Herb	
AC	*Aralia cordata*
ACt	*Agrostis clavata*
AD	*Aruncus dioicus*
AG	*Aster glehnii*
AM	*Anaphalis margaritacea*
AMm	*Artemisia montana*
AS	*Agrostis scabra*
CA	*Circaea alpina*
CH	*Calamagrostis hakonensis*
CJ	*Carex japonica*
CK	*Cirsium kamtschaticum*
CL	*Calamagrostis langsdorffii*
CM	*Clinopodium micranthum*
CO	*Carex oxyandra*

Abbreviation	Species name
CP	*Carex puberula*
EC	*Elsholtzia ciliata*
EG	*Eupatorium glehnii*
HA	*Hypericum ascyron*
HE	*Hypericum erectum*
JE	*Juncus effusus*
JT	*Juncus tenuis*
LC	*Luaula capitata*
LJ	*Lysimachia japonica*
LR	*Lactuca raddeana*
LU	*Lycopus uniflorus*
MC	*Muhlenbergia curviaristata*
MD	*Maianthemum dilatatum*
MH	*Muhlenbergia hakonensis*
PA	*Plantago asiatica*
PB	*Panicum bisulcatum*
PF	*Potentilla freyniana*
PH	*Picris hieracioides*
PJ	*Petasitis japonicus*
PL	*Persicaria longiseta*
PN	*Persicaria nepalensis*
PV	*Patrinia villosa*
SC	*Senecio cannabifolius*
SV	*Solidago virgaurea*
TP	*Tiarella polyphylla*
TT	*Trillium tschonoskii*
VG	*Viola grypoceras*
VS	*Viola selkirkii*
Alien species	
ag	*Agrostis gigantea*
cc	*Conyza canadensis*
ea	*Erigeron annuus*
hm	*Hypericum majus*
ob	*Oenothera biennis*
pl	*Panicum lanuginosum*
pt	*Poa trivialis*
ra	*Rumex acetosella*
sg	*Solidago gigantea*
to	*Taraxacum officinale*
tr	*Trifolium repens*
Fern	
ay	*Athyrium yokoscense*
da	*Dryopteris austriasa*
dc	*Dryopteris crassirhizoma*
lc	*Lycopodium clavatum*
lo	*Lycopodium obscurum*
oc	*Osmunda cinnamomea*
tn	*Thelypteris nipponica*