Regeneration responses influenced by single-tree selection harvesting in a mixed-species tree community in northern Japan

Mahoko Noguchi and Toshiya Yoshida

Abstract: The objective of this study was to assess the effects of fine-scale canopy disturbances induced by selection harvesting and its associated practices (artificial planting and machinery skidding) on the successful regeneration of tree species in a northern Japanese mixed forest. We set up 163 plots in a 6.7 ha permanent study stand where trees have been partially harvested at approximately 10-year intervals since 1974. The regeneration of trees (4324 stems-ha⁻¹) occurred more frequently under closed canopies than under canopy gaps, except for a typical shade-intolerant species, *Betula ermanii* Cham. In particular, small canopy openings that tend to close quickly displayed higher understory tree regeneration densities likely due to the suppression of competition from dwarf bamboos. The surface soil disturbances that occurred during planting and harvesting even further enhanced understory regeneration. The results shown here should be generalized carefully because we have investigated only one stand. Nevertheless, our findings clearly indicated that the creation of small canopy gaps associated with site preparation that contains soil disturbances should be examined in management practices to maintain the community structure in this type of mixed forest.

Résumé : L’objectif de cette étude consistait à estimer les effets de perturbations fines de la canopée induites par la coupe de jardinage et par les traitements qui y sont associés (plantation et débardage mécanisé) sur le succès de la régénération en espèces arborescentes dans une forêt mixte du nord du Japon. Nous avons établi 163 parcelles échantillons dans un peuplement sous étude permanente de 6,7 ha ayant fait l’objet, depuis 1974, de coupes partielles environ à tous les 10 ans. La régénération d’arbres (4324 tiges-ha⁻¹) s’est installée plus fréquemment sous les canopées fermées que dans les trouées, sauf dans le cas d’une espèce typiquement intolérante à l’ombre, *Betula ermanii* Cham. De façon plus particulière, les petites ouvertures de la canopée, qui tendent à se fermer rapidement, sont associées à une plus forte densité de la régénération arborescente, probablement attributable à l’élimination de la compétition du bambou nain. Les perturbations de la surface du sol causées par la plantation et la récolte des arbres ont favorisé encore plus la régénération sous couvert. Les résultats de cette étude devraient être généralisés avec précaution puisque nous avons étudié un seul peuplement. Néanmoins, nos résultats indiquent clairement que la création de petites trouées dans la canopée, jumelée à une préparation de terrain incluant une perturbation du sol, devrait être considérée parmi les pratiques d’aménagement pour maintenir la structure de la communauté de ce type de forêt mixte.

[Traduit par la Rédaction]

Introduction

Recently, there has been increased interest in revising silvicultural systems for forest stands to incorporate conservation objectives into management plans (Kohm and Franklin 1997; Angelstam 1998; Hunter 1999). This revision has engendered a widespread shift from clearcut harvesting to partial cut harvesting because the residual trees contribute to the maintenance of the original structure and composition of the forest (Deal 2001; Yoshida et al. 2005a). Consequently, special emphasis has been put on partial cut harvesting systems that are applicable to the regeneration of mixed tree species communities with an uneven-aged structure. (Greene et al. 1999).

Fine-scale canopy openings (canopy gaps) induced by windthrow or other wind-caused tree damage have been recognized as a major force in natural stand dynamics (Borman and Likens 1979; Pickett and White 1985). Selection harvesting can emulate the disturbance (Deal and Tappeiner 2002; Lundquist and Beatty 2002; Perera et al. 2004). Openings generally improve resource availability in the understory, thereby enhancing tree regeneration (Runkle 1981; Poulsom and Platt 1989; Kneeshaw and Bergeron 1998). However, in forests with rich understory cover, tree regeneration under a canopy gap is often hindered through enhanced development of the understory vegetation (Lautenschlager 1999; Beckage et al. 2000; Royo and Carson 2006). To conserve the structure and composition of such a forest under a management regime, it is crucial to clarify whether harvesting (creation of canopy gaps) contrib-


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utes to the regeneration of indigenous tree species over the long term and to understand what kind of functional traits of tree species are important for establishment and growth in these stands.

In addition to canopy openings, practices associated with harvesting also play an important role in developing tree regeneration. Soil disturbances, which appear naturally as landslides or treefall mounds (Nakashizuka 1989; Peterson et al. 1990; Clinton and Baker 2000), can be induced by machinery skidding or site preparation practices (Heninger et al. 2002; Buckley et al. 2003; Yoshida et al. 2005a).

Uneven-aged conifer–broadleaved mixed forests (including Abies, Picea, Acer, Quercus, Tilia, Betula, etc.) are a typical forest type in Hokkaido, the northernmost island of Japan. A selection system (single-tree selection) has been widely employed since the early 20th century to yield sustainable timber of both conifer and broadleaved species. The forests generally have dense understory cover dominated by dwarf bamboos (Sasa spp.), and therefore, there is concern about regeneration failure following the selection harvesting. However, few studies have explicitly clarified the long-term consequences of the practices on the natural regeneration of component tree species.

The objective of this study was to assess the effects of canopy disturbance induced by selection harvesting and its associated practices (artificial planting and machinery skidding) on the successful regeneration of common tree species in northern Japanese mixed forests. Long-term effects of canopy disturbance history (i.e., continuation of open or closed conditions of the canopy in the most recent 30 years) were examined using large permanent study stand data (6.7 ha area) along with spatial information of canopy trees (M. Noguchi and T. Yoshida, unpublished). The following two questions were addressed. (i) Are regeneration densities under canopy gaps larger than those under closed canopies? We predicted that canopy gaps would have a limited contribution to regeneration even in shade-tolerant species because of the exclusive dominance of dwarf bamboos in the understory. (ii) Are regeneration densities in sites affected by surface soil disturbances created during practices such as artificial planting and skidding? We predicted that these practices would considerably enhance regeneration.

**Materials and methods**

**Study site**

The present study was conducted in a conifer–broadleaved mixed forest in the Nakagawa Experimental Forest of Hokkaido University located in Otoineppu Village, Hokkaido Prefecture (44°48’N, 142°15’E). The mean annual temperature is 5.4 °C, the mean annual precipitation is 1449 mm, and the mean maximum snow depth is 190 cm at the nearest meteorological station (8 km from the study site). Small ridges and valleys running southwest from a main ridge on the northwest edge of the stand characterize the topography. The soils are classified as Inceptisol (acidic brown forest soil), and the predominant bedrock is Cretaceous sedimentary rock (Tatewaki and Igarashi 1971).

We selected a 6.7 ha stand for this study because its management history was completely recorded over a 30-year period at an individual tree scale (see below). The original stand (at the first census in 1974) had an uneven-aged structure with a basal area of 27.9 m²·ha⁻¹ that was typical of the region (Takahashi et al. 2003; Yoshida et al. 2006). Before the plot establishment, the stand had been partially harvested for domestic fuel materials at a very low intensity. No large-scale natural disturbances such as windthrows or pest outbreaks were recorded during the study period, which enabled us to clearly evaluate the effects of selection harvesting.

The stand contained 21 tall tree species in all (three evergreen conifers and 18 deciduous broadleaved species) of which Abies sachalinensis (Fr. Schm.) Masters comprised nearly one third of the density followed by Acer mono Maxim., Tilia japonica (Miq.) Simonkai, Quercus crispula Bl., Betula ermanii Cham., and others (Table 1). The understory was densely covered with dwarf bamboo species (Sasa kurilensis (Rupr.) Makino et Shibata and Sasa senanensis (Franch. et Savat.) Rehd.).

**Silvicultural practices**

Single-tree selection harvesting has been conducted at 9- to 10-year intervals (1975, 1984, and 1994) with respective harvesting intensities of approximately 12%, 17%, and 8% in basal area. These intensities were determined carefully in consideration of the census data to maintain harvested volume equivalent to the growth increment. Although little change has been recorded in basal areas over the stand because harvest and growth were at similar levels during the interval (Ohgane et al. 1988; Yoshida et al. 2006), considerable local variation exists within the stand (M. Noguchi and T. Yoshida, unpublished). In these harvestings, the priority in cutting was given to trees with a lower timber value (i.e., with injuries, cracks, etc.) to improve the future economic quality of the stand. Nevertheless, the harvested trees were selected from a broad range of size classes and no preference was shown for any particular tree species, e.g., the total number of harvested conifers and that of harvested broad-leaved trees were roughly equal.

Harvesting was carried out in winter with snow cover normally 100–200 cm deep on the forest floor. Therefore, the harvesting processes seldom damaged understory vegetation or the soil directly. However, skid trails with 2–3 m widths exist where considerable surface soil (O and A layers) was removed by a tractor during skidding processes. At the current census (conducted in 2003), 9 years had passed from the most recent trail use. On the other hand, tree seedlings were planted artificially to fill some large nonwooded openings (approximately >0.2 ha in area) in the stand. In 1976 and 1986, seedlings of A. sachalinensis were planted with initial densities of 1800–4000 stems·ha⁻¹. The preplanting site preparations involved exposing mineral soil by hand for each planting microsite. Subsequently, a weeding treatment, in which aboveground parts of plants competing with seedlings were cut by hand, was applied once per year during the initial 10 years. Canopies of these plantations had already been closed. Because the variation in environmental conditions among the plantations seemed to be small, we used them as a treatment in this study.

**Field data collection**

The uneven structure of the stand, together with a spatially dispersed distribution of harvested trees with a broad
Table 1. Tree species composition in the 6.7 ha study stand; stem densities of overstory trees (DBH ≥ 12.5 cm), saplings (DBH < 12.5 cm and height ≥ 2 m), and seedlings (height < 2 m).

<table>
<thead>
<tr>
<th>Species</th>
<th>Abbreviation</th>
<th>Group</th>
<th>Seed dispersal agent</th>
<th>Overstory stems ha⁻¹</th>
<th>Sapling stems ha⁻¹</th>
<th>Seedling stems ha⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abies sachalinensis</td>
<td>AS</td>
<td>CF</td>
<td>Wind</td>
<td>134</td>
<td>110 (392)</td>
<td>1014 (2993)</td>
</tr>
<tr>
<td>Acer mono</td>
<td>AM</td>
<td>BT</td>
<td>Wind</td>
<td>59</td>
<td>344 (809)</td>
<td>326 (1210)</td>
</tr>
<tr>
<td>Tilia japonica</td>
<td>TJ</td>
<td>BT</td>
<td>Wind</td>
<td>43</td>
<td>206 (793)</td>
<td>319 (1880)</td>
</tr>
<tr>
<td>Quercus crispula</td>
<td>QC</td>
<td>BI</td>
<td>Animal</td>
<td>41</td>
<td>74 (231)</td>
<td>149 (520)</td>
</tr>
<tr>
<td>Betula ermannii</td>
<td>BE</td>
<td>BI</td>
<td>Wind</td>
<td>41</td>
<td>89 (389)</td>
<td>14 (168)</td>
</tr>
<tr>
<td>Ainus hirsuta</td>
<td>AH</td>
<td>BI</td>
<td>Wind</td>
<td>18</td>
<td>43 (250)</td>
<td>85 (554)</td>
</tr>
<tr>
<td>Kalopanax pictus</td>
<td>KP</td>
<td>BI</td>
<td>Bird</td>
<td>13</td>
<td>60 (257)</td>
<td>14 (168)</td>
</tr>
<tr>
<td>Magnolia obovata</td>
<td>MO</td>
<td>BI</td>
<td>Bird</td>
<td>12</td>
<td>92 (371)</td>
<td>362 (2146)</td>
</tr>
<tr>
<td>Sorbus commixta</td>
<td>SO</td>
<td>BT</td>
<td>Bird</td>
<td>10</td>
<td>89 (375)</td>
<td>241 (1121)</td>
</tr>
<tr>
<td>Phellodendron amurense</td>
<td>PA</td>
<td>BI</td>
<td>Bird</td>
<td>10</td>
<td>39 (135)</td>
<td>35 (251)</td>
</tr>
<tr>
<td>Pirus sargentii</td>
<td>PS</td>
<td>BT</td>
<td>Bird</td>
<td>5</td>
<td>0 (–)</td>
<td>7 (84)</td>
</tr>
<tr>
<td>Salix spp.</td>
<td>SL</td>
<td>BI</td>
<td>Wind</td>
<td>5</td>
<td>4 (42)</td>
<td>0 (–)</td>
</tr>
<tr>
<td>Ulmus laciniata</td>
<td>UL</td>
<td>BT</td>
<td>Wind</td>
<td>4</td>
<td>25 (138)</td>
<td>213 (1428)</td>
</tr>
<tr>
<td>Ulmus davidiana var. japonica</td>
<td>UD</td>
<td>BT</td>
<td>Wind</td>
<td>4</td>
<td>7 (84)</td>
<td>64 (418)</td>
</tr>
<tr>
<td>Sorbus alnifolia</td>
<td>SA</td>
<td>BT</td>
<td>Bird</td>
<td>4</td>
<td>39 (208)</td>
<td>7 (84)</td>
</tr>
<tr>
<td>Fraxinus mandshurica</td>
<td>FM</td>
<td>BT</td>
<td>Wind</td>
<td>2</td>
<td>4 (42)</td>
<td>99 (768)</td>
</tr>
<tr>
<td>Taxus cuspidata</td>
<td>TC</td>
<td>CF</td>
<td>Bird</td>
<td>2</td>
<td>18 (110)</td>
<td>78 (479)</td>
</tr>
<tr>
<td>Swida controversa</td>
<td>SW</td>
<td>BI</td>
<td>Bird</td>
<td>2</td>
<td>14 (103)</td>
<td>0 (–)</td>
</tr>
<tr>
<td>Prinus ssiroi</td>
<td>PR</td>
<td>BT</td>
<td>Bird</td>
<td>1</td>
<td>11 (94)</td>
<td>21 (253)</td>
</tr>
<tr>
<td>Acanthopanax sciadophyloides</td>
<td>AC</td>
<td>BT</td>
<td>Bird</td>
<td>1</td>
<td>4 (42)</td>
<td>0 (–)</td>
</tr>
<tr>
<td>Picea jezoensis</td>
<td>PJ</td>
<td>CF</td>
<td>Wind</td>
<td>0</td>
<td>4 (42)</td>
<td>0 (–)</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td>411</td>
<td>1273 (1768)</td>
<td>3048 (5559)</td>
</tr>
</tbody>
</table>

**Note:** For saplings and seedlings, the averages and the standard deviations (in parentheses) of the 141 plots that have not experienced marked soil disturbances are shown.

*CF, conifer; BT, shade-tolerant broadleaved; BI, shade-intolerant broadleaved species. The classification is based on Koike (1988) and Masaki (2002).*

range of size classes, led to the introduction of considerable variation in environmental conditions within the stand (M. Noguchi and T. Yoshida, unpublished). Although we could not make a stand replication in this study, the following intensive sampling, along with historical records, enabled us to evaluate the effects of the local variation.

Long-term monitoring of trees has been conducted since 1974 in the study stand. All living overstory trees (≥12.5 cm diameter at breast height (DBH)) were identified and classed by DBH at intervals of 5 cm. The survey was repeated at approximately 10-year intervals (1974, 1983, 1993, and 2003). During 2000–2002, we mapped all of the living overstory trees and the identifiable dead trees (including cut stumps) in the whole stand.

We sampled the saplings (height ≥ 2 m and DBH < 12.5 cm) and seedlings (height < 2 m, except for current-year seedlings) at 163 plots set up at 20 m intervals in the 6.7 ha stand. In the summer of 2003, saplings were identified and densities recorded in the 20 m² circular subplot for each plot. Similarly, seedlings with heights ≥ 50 cm and those with heights < 50 cm were recorded, respectively, in the nested 10 and 5 m² circular subplots.

We recorded the forest floor condition of each sampling plot: (i) intact, (ii) disturbed to create a plantation, or (iii) disturbed by a skid trail. The regular setup (at 20 m intervals) of the plots obtained small samplings for the latter two. Therefore, we made 10 additional plots for plantations and eight for skid trails. Plots that had undergone a marked natural disturbance (such as treefall mounds) were excluded; such plots were very few, probably because of the repetitive partial harvestings (Noguchi and Yoshida 2004).

For the plots with intact forest floors (141 plots), we also recorded the current canopy condition (gap or closed). In this study, the canopy gap was defined as an area without tree crowns larger than 5 m in height and 10 m² in area. The plot was designated as a “canopy gap” when such an opening was found within the surrounding 20 m² area. We then characterized the canopy condition with the past disturbance history, which was derived from the long-term tree census and their location (coordinate) data. Within the circular area with a radius of 7.5 m (roughly corresponding to the largest crown radius of the trees) from the plot center, we checked the occurrence of harvesting and the natural death of large trees (trees with DBH ≥ 32.5 cm, which are assumed to attain the canopy layer) during the total census period (30 years). The plots were then categorized into four classes: (i) canopy gaps with a recorded disturbance, where harvesting or natural death in the 30-year period was assumed to contribute to the current canopy condition, (ii) canopy gaps without a recorded disturbance, where gaps predated the first census 30 years before, (iii) closed canopies with a recorded disturbance, where the canopy briefly opened but closed again in the period, and (iv) closed canopies without a recorded opening, where canopy closure was maintained in the period.

**Data analysis**

To elucidate the effects of the canopy opening, we exam-
ined only the sampling plots without soil disturbances (141 plots). The $\chi^2$ test was used to test the preference in frequency occurrence of saplings or seedlings of major component species for sites under canopy gaps (72 plots) compared with those under closed canopies (69 plots). In the case when the frequency occurrence was small, Fisher’s exact test was applied. Regarding sites under canopy gaps and closed canopies, respectively, similar comparisons were made for sites with and without recorded disturbances during the most recent 30 years.

Although gap size is often used to characterize canopy gaps, it is difficult to measure their size exactly in forests of this region because of their continuous spatial distribution, which is attributable to a high gap rate (frequently >20%) (Kubota 2000; Takahashi et al. 2003). Therefore, to examine the comparisons of regeneration densities among classes, we used regression analysis, which incorporates the basal area of surrounding overstory trees (roughly corresponding to the gap area) as explanatory variables. Because of the total low densities and frequent absence of regenerated trees in the particular plots, a logistic regression model was employed. The occurrence probability of saplings or seedlings in a plot ($p_{oc}$) was modeled as

$$\log(p_{oc}/(1-p_{oc})) = \beta_1 + \beta_2 \times CFBA + \beta_3 \times BLBA + \beta_4 \times CBGA$$

where CFBA and BLBA, respectively, denote the sums of basal area in the surrounding area (7.5 m radius from the plot center) in 1974 of coniferous and broadleaved canopy trees (DBH ≥ 32.5 cm). In addition, CBGA is the change in the sum of basal area of the surrounding canopy trees during 1974–1993 that represents the intensity of disturbances (harvesting and natural death) in its balance of basal area. Explanatory variables were selected using a stepwise procedure.

In addition, we compared the frequency occurrence in plots that were disturbed by associated practices (21 plantations and 19 skid trail sites) with intact plots. We used the R 2.2.1 statistical package (R Development Core Team 2005) for these analyses.

**Results**

In terms of stem density, the most dominant species in the overstory (DBH ≥ 12.5 cm) was A. sachalinensis followed by A. mono, T. japonica, Q. crispula, and B. ermanii (Table 1). Among the saplings (height ≥ 2 m and DBH < 12.5 cm, 1276 stems-ha$^{-1}$), A. sachalinensis occurred in a considerably lower proportion compared with the overstory, and A. mono and T. japonica were dominant. The proportion of seedlings (height < 2 m, 3048 stems-ha$^{-1}$) of A. sachalinensis was similar to that in the overstory but was considerably lower for B. ermanii and Kalopanax pictus (Thunb.) Nakai. In contrast, Sorbus commixta Hedl. and Ulmus laciniata (Trautv.) Mayr occurred in high proportions despite their only slight dominance in the overstory.

Among the saplings, B. ermanii showed a significant preference for sites under canopy gaps, but A. sachalinensis, A. mono, and Magnolia obovata Thunb. occurred significantly more frequently in sites under closed canopies (Fig. 1a). In seedlings, A. sachalinensis again showed a significant preference for closed canopies, similarly to T. japonica, S. commixta, and Q. crispula (Fig. 1b). In contrast, seedlings of Ulmus davidiana Planch. var. japonica (Rehd.) Nakai and Fraxinus mandshurica Rupr. var. japonica Maxim. occurred primarily in canopy gap sites.

Regarding the canopy disturbance history of the most recent 30 years, a significant preference for canopy gaps with a recorded disturbance was found only in saplings of B. ermanii (Fig. 2a) and seedlings of M. obovata (Fig. 2b). In contrast, seedlings of A. mono in gaps were more frequent at sites without a recorded disturbance. Those of U. davidiana and F. mandshurica occurred only in canopy gaps without a recorded disturbance.

Under the current closed canopy, saplings of A. sachalinensis and Q. crispula were more frequent at sites with a recorded disturbance (Fig. 2c), the opposite preference was not found. Among seedlings, many species (A. sachalinensis, T. japonica, S. commixta, and M. obovata) showed a preference for closed canopies with a recorded disturbance (Fig. 2d), but few species showed the opposite preference.

Logistic regression analyses suggested that the change in the surrounding basal area had a positive influence on regeneration densities: the coefficient was significant for saplings and seedlings of A. sachalinensis (marginally significant for saplings of A. mono and seedlings of A. mono, Q. crispula, and S. commixta). In addition, the basal area of surrounding conifers appeared to be influential for many species; a significant positive coefficient was found for saplings of Q. crispula, A. sachalinensis, and K. pictus and for seedlings of A. sachalinensis (marginally significant for saplings of S. commixta and seedlings of A. mono). The basal area of the surrounding broadleaved trees had a significant negative coefficient for saplings of S. commixta.

Saplings of B. ermanii, Phellodendron amurense Rupr., and K. pictus appeared more frequently in plantations, whereas those of A. mono and T. japonica were more frequent in intact sites (Fig. 3a). Alnus hirsuta Turcz was the only species whose saplings showed a significant preference for skid trails (Fig. 3c); it did not occur at all in plantations. In seedlings, a significant preference for disturbed sites was common, particularly in A. sachalinensis but also in A. mono, S. commixta, P. amurense, and Q. crispula (Figs. 3b and 3d). Similarly to its saplings, seedlings of A. hirsuta did not occur at all in plantations.

**Discussion**

**Effects of canopy opening**

The total regeneration density (sum of saplings and seedlings) of this stand was 4324 stems-ha$^{-1}$ (Table 1), which was low in comparison with similar mixed stands with less dwarf bamboo dominance (Ishida et al. 1991; Nagaike et al. 1999). In all, the regeneration of tall tree species occurred more frequently under closed canopies than under canopy gaps in this mixed forest. This trend was found not only for shade-tolerant species but also for shade-intolerant species in this study; only a few species showed an occurrence preference for sites under canopy gaps (Fig. 1). Regression analyses also indicated positive effects of the change in surrounding basal area (indicating the negative effect of canopy opening) in many cases (Table 2). Particularly under closed
Fig. 1. Densities of (a) saplings and (b) seedlings with respect to the current condition; mean densities under the canopy gap were plotted against those under the closed canopy. The equivalent line is shown. Asterisks indicate the significant preference for the particular site ($\chi^2$ test or Fisher’s exact test at $p < 0.05$). Abbreviations of species name are listed in Table 1.

Fig. 2. Densities of (a and c) saplings and (b and d) seedlings with respect to the current condition (gap or closed) together with the past disturbance history; mean densities in sites with recorded disturbance were plotted against those in sites without disturbance (see text for details). The equivalent line is shown. Asterisks indicate the significant preference for the particular site ($\chi^2$ test or Fisher’s exact test at $p < 0.05$). Abbreviations of species name are listed in Table 1.
canopies, the sites that had once experienced canopy disturbance (i.e., opened briefly but again closed within the last 30 years) had higher regeneration densities, especially in seedlings (Figs. 2c and 2d). On the other hand, under current canopy gaps, canopy disturbance in the last 30 years did not seem to contribute to the regeneration of many of these tree species (Figs. 2a and 2b). These results strongly suggested that canopy gaps in the forest can enhance the establishment and growth of tall tree species only when the gap size is sufficiently small to allow its rapid closure. The potential positive effects of canopy openings on regeneration seemed to be neutralized, and negative effects were rather apparently attributable to the enhanced growth of understory dwarf bamboos (*Sasa* spp.). The mean density and height of dwarf bamboos, respectively, reached 14.7 culms/m² (SD = 11.3) and 176.7 cm (SD = 43.5) and the latter showed a significant increase with canopy openings in this stand (Noguchi and Yoshida 2005). Several researchers have reported the negative effects of the abundance of dwarf bamboos on tree regeneration as well as on plant species diversity (Hiura et al. 1996; Nagaike et al. 1999; Noguchi and Yoshida 2004).

Tree species composition differed considerably among overstory trees (DBH ≥ 12.5 cm), saplings (height ≥ 2 m and DBH < 12.5 cm), and seedlings (height < 2 m). Proportions of *A. sachalinensis*, a shade-tolerant conifer, were much lower in saplings at all densities than in the overstory or seedlings: the distinct lower density of saplings suggested limited recruitment from the seedling stage. The trait of this species to survive under shaded conditions by reducing its extension growth (Yajima 1982; a similar trait was reported for other *Abies* species in Hara et al. (1991) and Messier et al. (1999)) might cause limited recruitment because seedlings under a canopy gap must compete with dense dwarf bamboo (the foliage crown of which is actually densest at 50–150 cm in height) during their recruitment process. Saplings and seedlings of *A. sachalinensis* showed a clear preference for sites under closed canopies, especially where the canopy had been opened within the last 30 years. This fact strongly suggests the importance of small-scale disturbances in this type of forest. Results of regression analyses, where the surrounding basal area (especially that of conifers) as well as the change in basal area were selected as positive coefficients (Table 2), also supported this tendency. The lower mortality of overstory trees, which has frequently been observed in natural stands in this region (<1%/year⁻¹: Hiura and Fujiwara 1999; Kubota 2000), might contribute to maintaining the population of this species.
Seedlings of shade-intolerant broadleaved species (*Q. crispula, B. ermanii, A. hirsuta*, and *K. pictus*) occurred less frequently (Table 1) in accordance with the general expectation that they have high mortality in shaded conditions. Nevertheless, the density of their saplings was not low (Table 1). Probably, once such trees exceed the height of the dense dwarf bamboo cover, they grow rapidly (Hiura et al. 1996). *Betula ermanii*, which showed the most distinct early successional traits among these species (Koike 1988), was the only species whose saplings occurred more frequently under a canopy gap (Fig. 1a). The rapid growth response seemed to be a crucial advantage in competing with dwarf bamboos in canopy gaps.

Seedlings of *Q. crispula* frequently occurred under closed canopies (Fig. 1b). Seed limitation might be apparently important for this species because of the limited seed (acorn) supply in large openings and the increased seed predation in canopy gaps from the enhanced activities of rodents (Wada et al. 1993). Actually, our supplemental analysis ($\chi^2$ test at $p < 0.05$) showed that its seedlings were significantly frequent in sites with conspecific overstory trees in the surrounding area (7.5 m radius). This frequency might partly explain the higher density under closed canopies. Similar preferences for the sites with conspecific overstory trees were apparent for other common species (saplings of *A. sachalinensis, T. japonica, and B. ermanii* and seedlings of *A. Sachalinensis, S. commixta, and A. hirsuta*). This needs further consideration for spatial information (e.g., the location and distance from seed trees, and prevailing wind directions) to clarify the detailed effects of seed dispersal on regeneration densities.

Shade-tolerant broadleaved species (such as *A. mono, T. japonica*, and *S. commixta*), which can be expected to survive and maintain growth under shaded understories (e.g., Canham 1988; Kobe and Coates 1997), showed high dominance among both saplings and seedlings (Table 1). The most dominant sapling species, *A. mono*, did not generally respond to a canopy disturbance history. Nevertheless, considering only seedlings in canopy gaps (Fig. 2b), the occurrence was rather frequent in gaps without a recorded canopy disturbance (i.e., sites where gap conditions were maintained for at least 30 years). A similar trend was also found in two other shade-tolerant species, *U. davidiana* and *F. mandschurica*. Although their densities were not necessarily high, these wind-dispersed shade-tolerant species could be major successors in large openings.

Responses through sprouting were frequently found only in *T. japonica* (data not shown), which was most frequent at sites under closed canopies with a recorded disturbance (Figs. 2c and 2d). Many saplings (approximately 60%) and seedlings (approximately 30%) were recognized as having a sprouting origin. The partial removal of stem(s) from a multiple-stem individual seemed to enhance the growth of the residual small stems.

One point we have missed in this study is the impact of time; we did not consider the effect of the individual harvesting 9, 19, and 28 years before the survey. The duration after the latest disturbance should be examined together with the differences in growth rates among species. In this study stand, to attain 12.5 cm DBH, shade-intolerant *B. ermanii* took 38 years ($SD = 8, n = 22$) on average, whereas the shade-tolerant *A. sachalinensis* and *A. mono* took 49 years ($SD = 20, n = 61$) and 50 years ($SD = 12; n = 42$), respectively (H. Miya et al., unpublished). Long-term observations of saplings and seedlings in relation to overstory dynamics are imperatively needed for more accurate evaluations.

Table 2. Results of the stepwise logistic regression analyses for the occurrence of understory trees or saplings of major tree species.

<table>
<thead>
<tr>
<th>Species</th>
<th>No. of plots with occurrence</th>
<th>AIC</th>
<th>Selected variables in the best-fit model</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Saplings</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acer mono</td>
<td>51 of 141</td>
<td>185.1</td>
<td>+CFBA, +CGBA*</td>
</tr>
<tr>
<td>Tilia japonica</td>
<td>16 of 141</td>
<td>99.7</td>
<td>-BLBA*</td>
</tr>
<tr>
<td>Quercus crispula</td>
<td>16 of 141</td>
<td>96.7</td>
<td>+CFBA*</td>
</tr>
<tr>
<td>Abies sachalinensis</td>
<td>15 of 141</td>
<td>90.1</td>
<td>+CFBA, +CGBA</td>
</tr>
<tr>
<td>Kalopanax pictus</td>
<td>12 of 141</td>
<td>82.3</td>
<td>+CFBA*</td>
</tr>
<tr>
<td>Sorbus commixta</td>
<td>11 of 141</td>
<td>78.4</td>
<td>+CFBA, -BLBA, +CGBA</td>
</tr>
<tr>
<td><strong>Seedlings</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Abies sachalinensis</td>
<td>34 of 141</td>
<td>153.0</td>
<td>+CFBA, -BLBA, +CGBA</td>
</tr>
<tr>
<td>Acer mono</td>
<td>16 of 141</td>
<td>100.8</td>
<td>+CFBA, +CGBA*</td>
</tr>
<tr>
<td>Quercus crispula</td>
<td>11 of 141</td>
<td>77.6</td>
<td>+CGBA*</td>
</tr>
<tr>
<td>Sorbus commixta</td>
<td>11 of 141</td>
<td>77.3</td>
<td>+CGBA*</td>
</tr>
</tbody>
</table>

Note: Number of quadrats with the occurrence, the Akaike information criterion (AIC) for the best-fit model, and selected variables in the model are shown. CGBA and BLBA are the sum of basal area in the surrounding area in 1974 of canopy conifers and broadleaved trees, respectively. CGBA is the change in basal area during 1974–1993. “+” and “−” indicate the positive and negative coefficient, respectively. No variables were selected for saplings of *B. ermanii, M. obovata, P. amurense, and S. alnifolia* and seedlings of *T. japonica*.

$p < 0.10$.
$p < 0.05$.
$p < 0.01$.

Effects of associated practices

The associated practices of harvesting (artificial planting and machinery skidding) significantly increased the regener-
ation densities of various species. In a natural process, canopy gap creation is associated with the supply of mound-pit topography as well as fallen logs, which often enhance opportunities for seedling establishment (Nakashizuka 1989; Peterson et al. 1990; Clinton and Baker 2000). However, as is widely recognized, repeated selection harvesting might degrade these important structures (Noguchi and Yoshida 2004). Therefore, the contribution of mound-pits or fallen logs to regeneration densities in this forest was very small (only 1% of recorded regeneration).

Regarding saplings, the associated practices were more preferable for shade-intolerant species (cf. Frey et al. 2003). Nevertheless, in seedlings, positive effects were particularly apparent in shade-tolerant species (in particular, A. sachalinensis and A. mono) (Figs. 3b and 3d). Such a contrast seemed to result from the different growth rates of the two groups. It has been reported that topsoil removal can contribute to the establishment of many species, especially when the canopy is not completely opened (Resco de Dios et al. 2005; Yoshida et al. 2005b). A. hirsuta was dominant both as saplings and as seedlings on skid trails but was not found at all in plantations. This was presumably because of its sensitivity to weeding treatments, which are generally conducted during the initial 10 years after planting. Its sprouting ability might be reduced after repeated aboveground cuttings (e.g., Hasegawa 1998).

Conclusion

Results of this study demonstrate that the effects of canopy opening on the continuous regeneration of tall tree species community were neutral or negative in this forest. The negative effect was rather common, especially when the canopy does not close for a long period. For the selection harvesting system in this region, more attention is required regarding the spatial arrangement of residual trees to avoid large openings. This would involve considering gap size and species composition surrounding the gap, which would influence the rate of gap closure. On the other hand, we observed higher regeneration densities on skid trails and plantations, both of which were not intended for natural regeneration but had undergone soil disturbance. Regarding the small regeneration density in the whole stand, artificial soil disturbance should be introduced to emulate the role of mound-pit topography. Surface soil displacement using civil engineering machinery (soil scarification), which has been utilized in the region for silvicultural site preparation, could be a convincing option. The application of this treatment on sites under closed canopies or small gaps appeared to enhance the regeneration of not only shade-intolerant species but also shade-tolerant species (Resco de Dios et al. 2005; Yoshida et al. 2005b).

We should note that the results of this study are limited due to lack of replication of stands. Further studies are required to extrapolate our findings to a larger spatial scale, and such trials would engender a sustainable forest management regime with continuous tree regeneration in this type of mixed forest.

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