



Title	Individual growing conditions that affect diameter increment of tree saplings after selection harvesting in a mixed forest in northern Japan
Author(s)	Miya, Hisashi; Yoshida, Toshiya; Noguchi, Mahoko; Nakamura, Futoshi
Citation	Journal of Forest Research, 14(5), 302-310 https://doi.org/10.1007/s10310-009-0136-6
Issue Date	2009-10
Doc URL	http://hdl.handle.net/2115/39414
Rights	The original publication is available at www.springerlink.com
Type	article (author version)
File Information	JFR14-5_p302-310.pdf



[Instructions for use](#)

Title: Individual growing conditions that affect diameter increment of tree saplings after selection harvesting in a mixed forest in northern Japan

Authors: Hisashi Miya^a, Toshiya Yoshida^b, Mahoko Noguchi^c, Futoshi Nakamura^a

Addresses:

^a Department of Forest Science, Graduate school of Agriculture, Hokkaido University; Kita 9-jo, Nishi 9, Kita-ku, Sapporo, Hokkaido, JAPAN, 060-8589

^b Uryu Experimental Forest, Field Science Center for Northern Biosphere, Hokkaido University; Moshiri, Horokanai, Hokkaido, JAPAN, 074-0741

^c Shikoku Research Center, Forestry and Forest Products Research Institute; 2-915 Asakuranishimachi, Kochi, JAPAN, 780-8077

Corresponding author: Hisashi Miya

Address: Department of Forest Science, Graduate school of Agriculture, Hokkaido University; Kita 9-jo, Nishi 9, Kita-ku, Sapporo, Hokkaido, JAPAN, 060-8589

Phone: +81-11-706-3343 **Fax:** +81-11-706-3842

E-mail: miya@for.agr.hokudai.ac.jp

Article type: original article **Subject area:** Biology and Ecology **Field:** Silviculture

Page count: 20

Number of table and figures: table 1, figure 4

Abstract

We analysed temporal patterns in diameter growth of saplings following selection harvesting in an uneven-aged mixed stand dominated by *Abies sachalinensis*, *Acer mono*, *Quercus crispula*, and *Betula ermanii* in Hokkaido, northern Japan. We examined interspecific differences in growth responses to local growing conditions including harvesting intensity, crowding, stem size, and past duration of the small growth period. Consistent with expectations based on shade tolerance of the species, the age at which the individual reached a diameter at breast height of 12.5 cm was highest for *A. sachalinensis* and lowest for *B. ermanii*. The interspecific growth differences between saplings that had or had not experienced local harvesting increased gradually for *A. sachalinensis* and *B. ermanii*, but peaked at around 4–6 years after harvesting for *Q. crispula*. Generalized linear mixed model analysis clearly suggested that individual growth conditions required to enhance diameter growth of saplings differed considerably among species. For *Q. crispula* and *B. ermanii*, local harvesting intensity was most strongly and positively associated with diameter growth rate, whereas for *A. sachalinensis* and *A. mono*, stem size had the strongest negative effect. *Abies sachalinensis* saplings responded more to surrounding harvesting when they were relatively small, whereas *A. mono* showed a weak opposite response. The duration of the small growth period before harvesting had negative effect for *A. sachalinensis*, but not for the other species. Our study indicated that the influence of selection harvesting on growth of shade-tolerant species depends upon pre- and post-harvest growing conditions.

Keywords

Annual ring analysis; Canopy disturbance; Diameter growth; Single-tree selection; Suppression

Introduction

Stand growth and tree density are key factors in the implementation of sustainable selection harvesting. In addition, the original stand structure and species composition should be maintained to preserve resilience and various functions of a forest ecosystem (Franklin 1993; Attiwill 1994; Matsuda *et al.* 2002). Thus, the selection harvesting in an uneven-aged mixed forest is required to conduct to promote the growth of residual individuals of multiple species in all size classes (Lundqvist 1993). In particular, the responses of saplings should be carefully monitored and examined in stands with low regeneration potential. In general, the diameter growth of saplings increases with shelterwood cutting or crown release (e.g., Abrams *et al.* 1999; Latham and Tappeiner 2002; Bebber *et al.* 2004). However, this positive response to canopy opening becomes unclear or temporarily delayed for several years in some cases, because of the time lag in physiological effects (Lovelock 1994; Kneeshaw *et al.* 2002) or physical damages (Jones and Thomas 2004). It is important to understand the individual growing conditions that allow saplings to respond readily to canopy opening induced by selection harvesting.

In Hokkaido, a northern island of Japan, many natural uneven-aged mixed forests have suffered degradation of their stand properties, including tree density and size structure, with selection harvesting (Nagaike *et al.* 1999; Yoshida *et al.* 2006). This degradation has been exacerbated by the dense dwarf bamboo understory, which hinders establishment of tree species (Nagaike *et al.* 1999; Umeki and Kikuzawa 1999). In a stand managed with a single-tree selection system, Yoshida *et al.* (2006) found that the recruitment rates of many component species to sub-canopy layer were very low, suggesting that more careful management is required to ensure regeneration. A subsequent study (Noguchi and Yoshida 2007) also suggested that many saplings (DBH < 12.5 cm) were distributed in small harvest gaps that could be readily closed. The creation

of canopy openings can increase biomass and height of dwarf bamboos very quickly (Noguchi and Yoshida 2005), and the light conditions on the forest floor in large gaps can thus be unsuitable for tree regeneration (Abe *et al.* 2002). These direct or indirect effects of canopy gaps on regeneration have been examined in many studies (Nagaike *et al.* 1999; Takahashi *et al.* 2003a; Umeki and Kikuzawa 1999). However, the response to selection harvesting of saplings, growing above the dwarf bamboos, has rarely been investigated.

The objective of this study was to identify the effects of selection harvesting on diameter growth of saplings in a natural uneven-aged conifer–broad-leaved mixed stand in Hokkaido. We used an annual ring analysis to understand a diameter growth rate of individual saplings following selection harvesting, while considering their individual size and local growing conditions. The extent of the effect of harvesting, even when single-tree selection is applied, can differ greatly according to the size and spatial arrangement of the harvested tree. The amount of residual trees, which represents the local crowding condition, may also vary in space in uneven-aged forests. In addition, previous studies have shown that it is indispensable to evaluate the effect of past growing history (e.g. duration of suppression and release; Wright *et al.* 2000) of the saplings. In this study, we therefore examined the effects of local harvesting intensity, together with effects of individual stem size, local crowding and the duration of small growth period, with the following hypotheses. First, shade-tolerant species are likely to respond slowly to the canopy opening, and may display only small changes in their diameter growth rates (Hix and Lorimer 1990; Yoshida and Kamitani 1998). Second, relatively smaller saplings grow more quickly after harvesting than do larger ones (DiGregorio *et al.* 1999; Kneeshaw *et al.* 2002; Jones and Thomas 2004). Third, saplings that experience longer suppression show lower diameter growth rates, even after harvesting (Wright *et al.* 2000). Based on our results, we will propose management strategies for selection harvesting to

promote recruitment of saplings to sub-canopy layer in mixed forests with a dense cover of dwarf bamboos.

Methods

Study site

This study was conducted in a conifer–broad-leaved mixed forest in the Nakagawa Experimental Forest of Hokkaido University, located in Ottoineppu Village, Hokkaido Prefecture, northern Japan (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, recorded from 1995 to 2004 at the nearest meteorological station (8 km from the study site). As described by Tatewaki (1958) and Yajima (1982), the typical vegetation in the Nakagawa Forest is mixed forest with an uneven-aged structure. The dominant canopy tree species are *Abies sachalinensis* (Fr. Schm.) Masters, *Acer mono* Maxim., *Tilia japonica* (Miq.) Simonkai, *Quercus crispula* Blume, and *Betula ermanii* Cham. The understory in the study stand is widely and densely covered with dwarf bamboo species (*Sasa senanensis* [Franchet et Savatier] and *S. kurilensis* [Ruprecht] Makino) (Noguchi and Yoshida 2005).

We selected a 6.7 ha stand for our study in a 110 ha experimental site. This 110 ha forest consists of 10 harvesting compartments and one control compartment, and our study stand was one of these harvesting compartments. Each compartment has been managed with a selection-harvesting system since 1967 at approximately 10-year intervals (one compartment per year) (Ohgane *et al.* 1988; Yoshida *et al.* 2006). Harvesting before 1967 was negligible, reflected in the very limited number of corresponding cut stumps (Yoshida *et al.* 2006). Single-tree selection was used, resulting in the maintenance of the uneven-aged structure during the study period. Trees

with a lower timber value were mainly selected for cutting, without bias in terms of species (Yoshida *et al.* 2006). Harvesting rates were determined based on the stand growth rates, which had been monitored for the harvest years in the previous decade (for details, see the following section). The 6.7 ha study stand was harvested in 1976, 1985, 1995, and 2005, with harvesting rates of approximately 12%, 17%, 8%, and 11% of basal area, respectively.

Field data collection

All living trees with a DBH equal to or greater than 12.5 cm (referred to as ‘sub-canopy’ or ‘canopy trees’ in this study) have been monitored at approximately 10-year intervals (1974, 1983, 1993, and 2003). Although the threshold DBH (12.5 cm) was determined from the minimum marketable size of the timber, we consider this size to be a good indicator of recruitment to the sub-canopy layer, because the height of saplings of this DBH (about 7 m) corresponds roughly to the average lowest branch height of the canopy trees (unpublished data). All living trees were identified and their DBH was measured at each monitoring period. The positional data (X–Y coordinates) were also measured for all trees, including snags, fallen trees, and harvested trees.

We focused on ‘recruited trees’ (saplings), which are defined in this study as trees that have passed the threshold DBH (12.5 cm) during the last monitoring period (1993–2003). In total, 363 trees were recruited during monitoring in 2003. To examine the diameter growth of these saplings, we sampled tree cores for the four species (*A. sachalinensis*, *A. mono*, *Q. crispula*, and *B. ermanii*) that dominate the stand. *Abies sachalinensis* and *A. mono* are shade-tolerant, *Q. crispula* is an intermediate shade-tolerant, and *B. ermanii* is a shade-intolerant species (Koike 1988; Masaki 2002). The numbers of samples were *A. sachalinensis* 50, *A. mono* 41, *Q. crispula* 37, and *B. ermanii* 15. The tree cores were taken at the lowest possible height (0.3 m) to estimate the tree ages.

The cores were mounted on plywood and sanded with sandpaper of progressively finer grit until the rings were clearly visible. The annual ring widths were measured to the nearest 0.005 mm with a table-mounted tree-ring increment measurement system (Nikon 20334 Measurescope).

Analysis

To understand the effects of selection harvesting, the diameter growth rate of saplings was analysed with a generalized linear mixed model (GLMM) of the gaussian family with the identity link function. Because the harvestings were conducted every 10 (or nine years) years, we could not examine the change over 10 years in this study. We divided the tree-ring chronology into three periods, with each ending in a harvest year (1976–1984, 1985–1994, and 1995–2004), and treated the three corresponding measurements for each tree as individual samples (thus, we had a maximum of three data sets for each individual tree). To avoid pseudoreplication, we considered the ‘harvest year’ and ‘individual’ as random effects in the analysis. The response variable was a diameter growth rate, which showed a normal distribution:

$$[1] \text{ diameter growth rate} = (G_{\text{post10}} - G_{\text{pre10}})/G_{\text{pre10}},$$

where G_{pre10} is the mean diameter increment per year for a period of 10 (or nine) years before harvest, and G_{post10} is the mean diameter increment per year for the subsequent 10 years. The four main variables and their quadratic interaction terms were included as explanatory variables. Local harvesting intensity was estimated as the total basal area of the cut trees within a radius of 10 m from each sampled tree. We chose a 10 m radius to represent the influential distance because it roughly corresponds to the maximum canopy diameter in this forest (unpublished data). Local crowding after harvesting was represented by the total basal area of the residual trees within a radius of 10 m from each sampled tree. Individual stem size was expressed as the stem diameter

measured 0.3 m above the ground for each sampled tree at the beginning of each period (time of harvesting). We further considered the duration of the small growth period in the model. It has been reported that many canopy trees in uneven-aged mixed forests experience multiple episodes of growth suppression and release before they reach the canopy layer (Canham 1985, 1990; Cho and Boerner 1995). We defined the 'small growth period' as a period in which the sapling diameter is below the species-specific threshold. Wright *et al.* (2000) used the quantitative threshold rate to represent the 'suppression' that is associated with a sapling mortality rate of 10% when the rate continues over a three-year period. However, such threshold values are not available for the current study. Therefore, we examined the chronology of the diameter increments for each species in the study stand using all the data measured throughout the study period (Fig. 1), and used the first lower quartile for each species as the threshold value. We note that these values are comparable with the threshold values for the closely related genera reported by Wright *et al.* (2000). We estimated the durations of the small growth periods as the total number of years below the threshold.

To select important explanatory variables, we performed a GLMM analysis with stepwise backward elimination based on Akaike's information criterion (AIC). The regression model with the smallest AIC value was considered the best model. When the GLMM selected models containing only interaction terms without the main variables, the main variables were preferentially included in the model. We then calculated Δ AIC (the increase in the AIC score when the explanatory variable was eliminated from the final model) for each explanatory variable, to assess the importance of the explanatory variable in the final model.

The difference in the mean diameter growth rates of a species between individuals with and without surrounding harvesting (within a radius of 10 m) were analyzed using a similar model

(GLMM) of the gaussian family with the identity link function., with considering a time-series factor. Again, we considered the ‘harvest year’ and ‘individual’ as random effects in the analysis. The response variable was a diameter growth rate of each year after the harvesting, which showed a normal distribution:

$$[2] \text{ diameter growth rate of year } (x) = (G_{\text{post}(x)} - G_{\text{pre10}}) / G_{\text{pre10}},$$

where G_{pre10} is the mean diameter increment per year for a period of 10 (or nine) years before harvest, and $G_{\text{post}(x)}$ is the diameter increment of year x (0 - 9) after the harvesting. The explanatory variables were presence of local harvesting within a radius of 10 m (binomial) together with the time-series factor (years after harvesting; 0 - 9). We evaluated whether or not the model with the lowest AIC value select the binomial variable (i.e. presence of local harvesting).

The mean annual diameter increments were compared among species also with generalized linear mixed model (GLMM) of the gaussian family with the identity link function. In order to reduce the bias occurring from individual trees from which the data were collected, we incorporated ‘individual’ as a random effect. The explanatory variables were categorical data, representing the tree species. To investigate how mean annual diameter increments differ among species, we created the explanatory variables by merging species in all possible combinations (= 15 models). They include, for example, the effect of species is null (the category '1' is assigned to all the saplings), the effect of a particular species is apparent ('1' is assigned to the particular species, and '2' to the other three species group), and the effect of species is different among all the four species ('1', '2', '3', and '4' were respectively assigned for the four species. We developed models with each of the created combination as explanatory variables. The best combination of the tree species to explain mean annual diameter increment was determined based on AIC values (Johnson and Omland 2004).

All statistical analyses were performed with the statistical language R, version 2.6.2. (R Development Core Team 2008).

Results

There were significant differences in the mean annual diameter increments among the four study species (Fig.1). *A. sachalinensis* showed the lowest increment, and the mode of age taken to reach 12.5 cm was about 50–70 years, with a range of 33–125 years (Fig.2). The age mode of *A. mono* (55–65 years) was similar to that of *A. sachalinensis*, but its range was narrower (42–83 years). *Quercus crispula* and *B. ermanii* exhibited similar ranges (22–63 years and 21–58 years, respectively), but *Q. crispula* had an older age mode (45–55 years) than that of *B. ermanii* (35–45 years). *Betula ermanii* displayed the greatest mean annual diameter increments.

For all the four species, comparison of the diameter growth rate of each year between individuals with and without surrounding harvesting (within a radius of 10 m) showed no significant difference (Fig. 3). The differences in the diameter growth rate of *A. sachalinensis* and *B. ermanii* appeared to increase as the years since harvesting increased, whereas the difference reached a maximum at 4–6 years after harvesting for *Q. crispula*.

The GLMM analysis explaining the diameter growth rates (Table.1) showed that the most important explanatory variable for *A. sachalinensis* was individual stem size ($\Delta\text{AIC} = 11.0$). Also, its interaction with local harvesting intensity was selected, insofar as surrounding harvesting was more important for larger saplings ($\Delta\text{AIC} = 7.2$; Table 1, Fig. 4b). Similarly, the duration of the small growth period was more important for larger saplings, although the effect was relatively weak ($\Delta\text{AIC} = 0.5$). There was also a significant interaction between local crowding and the surrounding harvesting intensity ($\Delta\text{AIC} = 2.1$, Fig. 4a), suggesting that when many trees remain around the

individual after harvesting, its diameter growth rate is limited (Fig. 4a).

A strong negative effect of stem size was detected for *A. mono* ($\Delta\text{AIC} = 9.9$; Table 1, Fig. 4c). The interactions between stem size and local crowding after harvesting and between stem size and local harvesting intensity were also selected (the diameter growth rate of smaller saplings were more strongly affected by local harvesting intensity and local crowding after harvesting), although these effects were relatively small ($\Delta\text{AIC} = 0.6$ and 1.0 , respectively). The duration of the small growth period had a positive effect ($\Delta\text{AIC} = 1.8$), indicating that trees suppressed for a longer period showed higher diameter growth rates.

The most important explanatory variable for *Q. crispula* was local harvesting intensity, which correlated positively with its diameter growth rate ($\Delta\text{AIC} = 13.5$; Table 1, Fig. 4d). Trees that showed longer small growth period exhibited higher diameter growth rates ($\Delta\text{AIC} = 4.5$, Fig. 4e). Stem size correlated negatively with growth rate but the effect was small ($\Delta\text{AIC} = 0.8$).

A positive effect of local harvesting intensity was also detected for *B. ermanii* ($\Delta\text{AIC} = 6.1$; Table 1, Fig. 4f). Local crowding after harvesting and its interaction with the duration of the small growth period had negative and positive effects on its diameter growth rate, respectively ($\Delta\text{AIC} = 4.7$ and 2.0 , respectively). This result means that the diameter growth rates of trees suppressed for shorter periods were more strongly negatively affected by local crowding after harvesting (Fig. 4g). Stem size also correlated positively with diameter growth rate, although the effect was small ($\Delta\text{AIC} = 0.1$).

Discussion

Although we found that harvesting promoted diameter growth rates of all the four species, the conditions under which the effect of harvesting was positive differed considerably among

species (Table 1). The local harvesting intensity itself was the most important explanatory variable for less shade-tolerant species (*Q. crispula* and *B. ermanii*). Whereas it was important only with interaction with variables representing individual stem size or pre- and post-harvest growing conditions for shade-tolerant species (*A. sachalinensis* and *A. mono*).

We found that the effect of stem size was particularly important for shade-tolerant species (Table 1). Irrespective of the general expectation that smaller trees would exhibit higher response in their diameter growth to deal with the opening of the canopy (DiGregorio *et al.* 1999; Jones and Thomas 2004), larger saplings of *A. sachalinensis* clearly responded better to surrounding harvesting, with diameter growth rates, than did smaller saplings (Fig. 4b). Kubota (1994) found that the growth and survival of *A. sachalinensis* declined at a crown height of about 7 m, which is roughly equivalent to the lowest branch height of the canopy trees (also see Ishizuka and Kanazawa 1989). When dwarf bamboos densely cover the forest floor, as in our study stand, *A. sachalinensis* saplings predominantly occur under canopy trees (Kubota 2000; Noguchi and Yoshida 2007). Consequently, the height growth of large saplings should frequently be disturbed by the lower canopy of the overstory trees. Conversely, there are large canopy gap areas in this type of mixed forest (21% in this stand; Miya *et al.* Unpublished). Accordingly, the light conditions may be sufficient for this shade-tolerant species even under canopy cover, before the saplings reach the lowest branch height of the canopy trees, allowing its smaller saplings to maintain good growth. This may be more evident when the saplings are still small because they have lower resource requirements than do larger saplings (cf. Messier *et al.* 1999). In contrast, the effects of harvesting or local crowding were more apparent for the smaller saplings of *A. mono*. However, the model also suggests that these effects are relatively weak, and this is roughly consistent with the results of previous studies, which demonstrated the small response of *A. mono* to changes in light conditions

(Hiura *et al.* 1995; Umeki 2001).

Consistent with our general expectations based on shade-tolerance characteristics, local harvesting intensity had the strongest effect on less shade-tolerant species, *Q. crispula* and *B. ermanii*, showing a positive association with their diameter growth rates (Table 1). Although *Q. crispula* saplings tend to be distributed under canopy trees (Noguchi and Yoshida 2007), interaction with stem size that observed for *A. sachalinensis* (see above) was not selected in the final model (Table 1). We infer that, for broad-leaved species, there is less suppressive interference by the lower canopy of the overstory trees, probably because broad-leaved trees display greater morphological plasticity in their stem structure than do conifers, and can grow into canopy gaps (cf. Umeki 1995; Muth and Bazzaz 2003). Besides these positive effects of local harvesting intensity, only *B. ermanii* experienced a negative effect of local crowding. This may reflect the lowest shade tolerance of this species (Koike 1988).

Regarding the effect of protracted suppression (Wright *et al.* 2000), our results suggested that the duration of small growth period did not seem to be a factor impeding post-harvest sapling growth in the broad-leaved species. It only had a negative effect on diameter growth rate of *A. sachalinensis* (Table 1). In contrast, the models for *A. mono*, *Q. crispula*, and *B. ermanii* indicated that their diameter growth rates increased as the duration of small growth period increased (Table 1). We consider that higher morphological plasticity of stem structures of broad-leaved species (Umeki 1995; Muth and Bazzaz 2003) contributes to this capacity for growth recovery. However, this should be carefully interpreted for *B. ermanii*, because the duration of small growth period for this species was nine years at most, suggesting that individual mortality may be increased under longer suppression.

The positive effect of local harvesting on diameter growth rate after the harvesting

became more evident with time for *A. sachalinensis* and *B. ermanii* (Fig. 3a, d). Many studies have shown that the increase in diameter growth after harvesting can be delayed (Youngblood 1991; DiGregorio *et al.* 1999; Bebber *et al.* 2004). The causes of this delay include time lag in light acclimation, photoinhibition, or photodamage effects (Lovelock 1994), physical damage during harvesting (Jones and Thomas 2004) and a reduced allocation to stem growth resulting from an increasing energy investment in root growth (Kneeshaw *et al.* 2002). We infer that the dense cover of dwarf bamboos in our study stand may have caused the latest phenomenon by increasing below-ground competition (Takahashi *et al.* 2003b), with a significant increase in root biomass of the dwarf bamboos after overstory harvesting (Fukuzawa *et al.* 2006). In contrast, no such delayed diameter growth rate was observed for *Q. crispula*. The reason for this is unclear, and should be evaluated in further studies by investigating the physiological responses of both above- and below-ground tissues.

Management implications

We recommend individual growing conditions should particularly be considered for enhancing growth of saplings of shade-tolerant species by overstory harvesting. The efficient timing of the harvesting for *A. sachalinensis* saplings seemed when the saplings have reached the lowest branch height of the canopy trees. However, because *A. sachalinensis* exhibits low morphological plasticity in its stem architecture (Umeki 1995), physical damage (e.g. stem broken or crown loss) should be carefully avoided during harvesting practice. Attention should also be paid to the past individual growth history. An individual that has experienced longer suppression may not respond quickly to harvesting around it. Although we did not examine the effects of harvesting over 10 years in this study, we suppose that the rotation period of overstory harvesting can be

longer for *A. sachalinensis* saplings, because their growth improvement apparently occurred only in the later period (Fig. 3a). For *A. mono*, the improvement in sapling diameter growth rate after harvesting was not practically expected. The effect of harvesting was positive but weak, and occurred only when the saplings were small.

In contrast, harvesting more clearly enhanced the diameter growth rate of less shade-tolerant species. To maintain growth of *B. ermanii* saplings, short interval harvesting in surrounding area is required, because the diameter growth rate of its saplings was significantly reduced with crowding (Fig. 4g). For *Q. crispula*, our results indicate that harvesting has little effect on diameter growth rate after 4–6 years (Fig. 3c), suggesting that the ideal rotation of overstory harvesting is at intervals of less than 10 years.

We did not examine combined effects of repeated harvestings, and effects on sapling mortality in this study. Individual responses to selection harvesting should be further investigated from various standpoints, including physiological and morphological responses of trees to canopy opening. We believe that sustainable selection harvesting that maintains complex stand structures and species compositions can be achieved with greater attention to species-specific and condition-dependent responses, as suggestion in this study.

Acknowledgements

We would like to thank anonymous reviewers for their helpful comments and suggestions. We also thank the staff of the Nakagawa Experimental Forest and the members of the Laboratory of Forest Management, Hokkaido University, for their combined efforts in maintaining the long-term monitoring. We thank Keiichi Aoyama and Akane Harada for their assistance with the fieldwork. We also extend our thanks to the members of the Laboratory of Forest Ecosystem Management,

Hokkaido University. This research was partially funded by Grants in Aid for Scientific Research (nos 18201008 and 19208013) from the Ministry of Education, Science and Culture, Japan.

References

Abe M, Izaki J, Miguchi H, Masaki T, Makita A, Nakashizuka T (2002) The effects of sasa and canopy gap formation on tree regeneration in an old beech forest. *J Veg Sci* 13:565-574

Abrams MD, Copenheaver CA, Terazawa K, Umeki K, Takiya M, Akashi N (1999) A 370-year dendroecological history of an old-growth *Abies–Acer–Quercus* forest in Hokkaido, northern Japan. *Can J Forest Res* 29:1891–1899

Attiwill PM (1994) The disturbance of forest ecosystems—the ecological basis for conservative management. *Forest Ecol Manage* 63:247–300

Bebber DP, Thomas SC, Cole WG, Balsillie D (2004) Diameter increment in mature eastern white pine *Pinus strobus* L. following partial harvest of old-growth stands in Ontario, Canada. *Trees Struct Funct* 18:29–34

Canham CD (1985) Suppression and release during canopy recruitment in *Acer saccharum*. *Bull Torrey Bot Club* 112:134–145

Canham CD (1990) Suppression and release during canopy recruitment in *Fagus grandifolia*. *Bull Torrey Bot Club* 117:1–7

Cho DS, Boerner REJ (1995) Dendrochronological analysis of the canopy history of two Ohio old-growth forests. *Vegetatio* 120:173–183

DiGregorio LM, Krasny ME, Fahey TJ (1999) Radial growth trends of sugar maple (*Acer saccharum*) in an Allegheny northern hardwood forest affected by beech bark disease. *J Torrey Bot Soc* 126:245–254

- Franklin JF (1993) Preserving biodiversity—species, ecosystems, or landscapes. *Ecol Appl* 3:202–205
- Fukuzawa K, Shibata H, Takagi K, Nomura M, Kurima N, Fukazawa T, Satoh F, Sasa K (2006) Effects of clear-cutting on nitrogen leaching and fine root dynamics in a cool-temperate forested watershed in northern Japan. *Forest Ecol Manage* 225:257–261
- Hiura T, Fujiwara K, Hojyo H, Okada J, Udo H, Okuyama S, Morita H, Fukuda H, Fujito E, Fukui T, Takahata M, Udo K, Sugiyama H, Takeda T (1995) Stand structure and long-term dynamics of primeval forest in Nakagawa experimental forest, Hokkaido university. *Res Bull Coll Exp Hokkaido Univ.* 52:85-94 (in Japanese with an English summary)
- Hix DM, Lorimer CG (1990) Growth-competition relationships in young hardwood stands on 2 contrasting sites in southwestern Wisconsin. *Forest Science* 36:1032-1049
- Ishizuka M, Kanazawa Y (1989) Growth process of *Abies sachalinensis* under *Picea jezoensis*, *Tilia japonica*, and *Acer mono* in mixed coniferous–broadleaved forests of Hokkaido. *J Jap Forestry Soc* 71:281–287 (in Japanese with an English summary)
- Johnson JB, Omland KS (2004) Model selection in ecology and evolution. *Trends in Ecology & Evolution* 19:101-108
- Jones TA, Thomas SC (2004) The time course of diameter increment responses to selection harvests in *Acer saccharum*. *Can J Forest Res* 34:1525–1533
- Kneeshaw D, Williams H, Nikinmaa E, Messier C (2002) Patterns of above- and below-ground responses of understory conifer release 6 years after partial cutting. *Can J Forest Res* 32:255–265
- Koike T (1988) Leaf structure and photosynthetic performance as related to the forest succession of deciduous broad-leaved trees. *Plant Species Biol* 3:77–87
- Kubota Y (1995) Effects of disturbance and size structure on the regeneration process in a

- sub-boreal coniferous forest, northern Japan. *Ecol Res* 10:135–142
- Kubota Y (2000) Spatial dynamics of regeneration in a conifer/broad-leaved forest in northern Japan. *J Veg Sci* 11:633–640
- Kubota Y, Konno Y, Hiura T (1994) Stand structure and growth patterns of understory trees in a coniferous forest, Taisetsuzan National Park, northern Japan. *Ecol Res* 9:333–341
- Latham P, Tappeiner J (2002) Response of old-growth conifers to reduction in stand density in western Oregon forests. *Tree Physiol* 22:137–146
- Lovelock CE, Jebb M, Osmond CB (1994) Photoinhibition and recovery in tropical plant species—response to disturbance. *Oecologia* 97:297–307
- Lundqvist L (1993) Changes in the stand structure on permanent *Picea–Abies* plots managed with single-tree selection. *Scand J Forest Res* 8:510–517
- Masaki T (2002) Structure and dynamics. In: Nakashizuka T, Matsumoto Y (eds) *Diversity and interaction in a temperate forest community: Ogawa Forest Reserve of Japan*. Springer-Verlag, Tokyo, pp 53–65
- Matsuda K, Shibuya M, Koike T (2002) Maintenance and rehabilitation of the mixed conifer–broadleaf forests in Hokkaido, northern Japan. *Eurasian J Forest Res* 5:119–130
- Messier C, Doucet R, Ruel JC, Claveau Y, Kelly C, Lechowicz MJ (1999) Functional ecology of advanced regeneration in relation to light in boreal forests. *Can J Forest Res* 29:812–823
- Muth CC, Bazzaz FA (2003) Tree canopy displacement and neighborhood interactions. *Can J Forest Res* 33:1323–1330
- Nagaike T, Kubota Y, Watanabe N (1999) The effects of selective logging on stand structure and the regeneration of subboreal forests in Hokkaido, northern Japan. *J Forest Res* 4:41–45
- Noguchi M, Yoshida T (2005) Factors influencing the distribution of two co-occurring dwarf

bamboo species (*Sasa kurilensis* and *S. senanensis*) in a conifer–broad-leaved mixed stand in northern Hokkaido. *Ecol Res* 20:25–30

Noguchi M, Yoshida T (2007) Regeneration responses influenced by single-tree selection harvesting in a mixed-species tree community in northern Japan. *Can J Forest Res* 37:1554–1562

Ohgane E, Nigi T, Hishinuma Y, Koshika K, Fukui T (1988) Managerial progress and result of an experimental forest practiced by the control method. *Res Bull Coll Exp Hokkaido Univ* 45:61–113 (in Japanese with an English summary)

R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>

Takahashi K, Mitsuishi D, Uemura S, Suzuki JI, Hara T (2003a) Stand structure and dynamics during a 16-year period in a sub-boreal conifer–hardwood mixed forest, northern Japan. *Forest Ecol Manage* 174:39–50

Takahashi K, Uemura S, Suzuki JI, Hara T (2003b) Effects of understory dwarf bamboos on soil water and the growth of overstory trees in a dense secondary *Betula ermanii* forest, northern Japan. *Ecol Res* 18:767–774

Tatewaki M (1958) Forest ecology of the islands of the North Pacific Ocean. *J Fac Agr Hokkaido Univ* 50:371–486

Umeki K (1995) A comparison of crown asymmetry between *Picea–Abies* and *Betula maximowicziana*. *Can J Forest Res* 25:1876–1880

Umeki K, Kikuzawa K (1999) Long-term growth dynamics of natural forests in Hokkaido, northern Japan. *J Veg Sci* 10:815–824

Umeki K (2001) Growth characteristics of six tree species on Hokkaido island, northern Japan.

Ecol Res 16:435–450

Wright EF, Canham CD, Coates KD (2000) Effects of suppression and release on sapling growth for 11 tree species of northern, interior British Columbia. *Can J Forest Res* 30:1571–1580

Yajima T (1982) Study on the growth of main tree species in the mixed forest of needle-leaved and broad-leaved trees. *Res Bull Coll Exp Hokkaido Univ* 39:1–54 (in Japanese with an English summary)

Yoshida T, Kamitani T (1998) Effects of crown release on basal area growth rates of some broad-leaved tree species with different shade-tolerance. *J Forest Res* 3:181–184

Yoshida T, Noguchi M, Akibayashi Y, Noda M, Kadomatsu M, Sasa K (2006) Twenty years of community dynamics in a mixed conifer–broad-leaved forest under a selection system in northern Japan. *Can J Forest Res* 36:1363–1375

Youngblood AP (1991) Radial growth after a shelterwood seed cut in a mature stand of white spruce in interior Alaska. *Can J Forest Res* 21:410–413

Figure captions

Fig. 1. Box plots of the annual diameter increment in the saplings of the four species. All annual increments of the measured trees were considered. Different letters associated with the species name indicate the statistical differences among species, which are based on the AIC values of the GLMM (see detail in the text). In this case, the model considering the categorical variable with the categories 1 – 4 (i.e. assigning to each species) had the lowest AIC value, suggesting that differences are found for all the combinations of the four species.

Fig. 2. Frequency distributions of the estimated ages of the trees of the four species at the time their DBH was 12.5 cm. The estimation was based on increment cores taken at 0.3 m height. See details in the text.

Fig. 3. Ten-year changes in the diameter growth rate after harvesting of individual saplings with and without surrounding harvesting. The base year (0) indicates the time at which harvesting was conducted. The diameter increment of each year after the harvesting (see equation [2] in the text), is shown. The inter-specific difference between saplings that had or had not experienced local harvesting was not found by GLMM with considering a time-series factor (i.e. the model excluded the effect of harvesting showed lower AIC value).

Fig. 4. Variables explaining the diameter growth rate in the four species. Only the variables for which $\Delta\text{AIC} > 2$ are presented. In cases when the quadratic interaction terms were selected in the

model (a, b, g; see Table 1), one explanatory variable is shown on the x-axis, with the effect of another variable shown by the symbols defined on the figure. LC: local crowding; LH: local harvesting intensity; DS: duration of small growth; SS: stem size in terms.

Table 1. The results of the generalized linear mixed model (GLMM). Response variable is the diameter growth rate for each decade (see equation [1] in the text). The four main variables and their quadric interaction terms are included as explanatory variables.

	<i>A.sachalinensis</i>		<i>A.mono</i>		<i>Q.crispula</i>		<i>B.ermanii</i>	
	estimates	Δ AIC	estimates	Δ AIC	estimates	Δ AIC	estimates	Δ AIC
AIC	232.5	-	206.2	-	115.9	-	39.3	-
(Intercept)	0.5934	-	1.3762	-	0.1198	-	-0.5019	-
local crowding after harvesting (LC)	0.0835	1.7	-0.8356	1.6	ns	-	-0.7737	4.7
local harvest intensity (LH)	0.1275	2.0	1.5038	1.7	0.7681	13.5	1.6510	6.1
duration of small growth period (DS)	-0.0078	1.4	0.0099	1.8	0.0110	4.5	0.0092	2.0
stem size (SS)	-0.0511	11.0	-0.1150	9.9	-0.0187	0.8	0.0349	0.1
LC×LH	-1.6350	1.9	ns	-	ns	-	ns	-
LC×DS	ns	-	ns	-	ns	-	0.1406	2.6
LC×SS	ns	-	0.0644	0.6	ns	-	ns	-
LH×DS	ns	-	ns	-	ns	-	ns	-
LH×SS	0.1557	7.2	-0.1211	1.0	ns	-	ns	-
DS×SS	0.0012	0.5	ns	-	ns	-	ns	-
Standard deviation of the random effect								
year	1.3×10^{-1}	-	1.2×10^{-5}	-	0.9×10^{-5}	-	0.7×10^{-5}	-
individual	1.1×10^{-5}	-	1.1×10^{-5}	-	0.9×10^{-5}	-	0.7×10^{-5}	-

Note: LC: local crowding, represented by the total basal area of residual trees in the surrounding area (with radius of 10 m). LH: local harvesting intensity, represented by the total basal area of harvested trees in the surrounding area. DS : duration of small growth, defined as the period when the annual diameter increment is below the species-specific threshold. SS: stem size in terms of diameter at 0.3 m height at the time of the harvesting. The 'year' and 'individual' were considered as a random effect. The coefficients for the selected variable by a backward stepwise procedure are shown. 'ns' indicate the variable not selected. Δ AIC represents an increase in AIC score when the explanatory variable is eliminated from the final model. See details in the text.

Fig. 1. Box plots of the annual diameter increment in the saplings of the four species. All annual increments of the measured trees were considered. Different letters associated with the species name indicate the statistical differences among species, which are based on the AIC values of the GLMM (see detail in the text). In this case, the model considering the categorical variable with the categories 1 – 4 (i.e. assigning to each species) had the lowest AIC value, suggesting that differences are found for all the combinations of the four species.

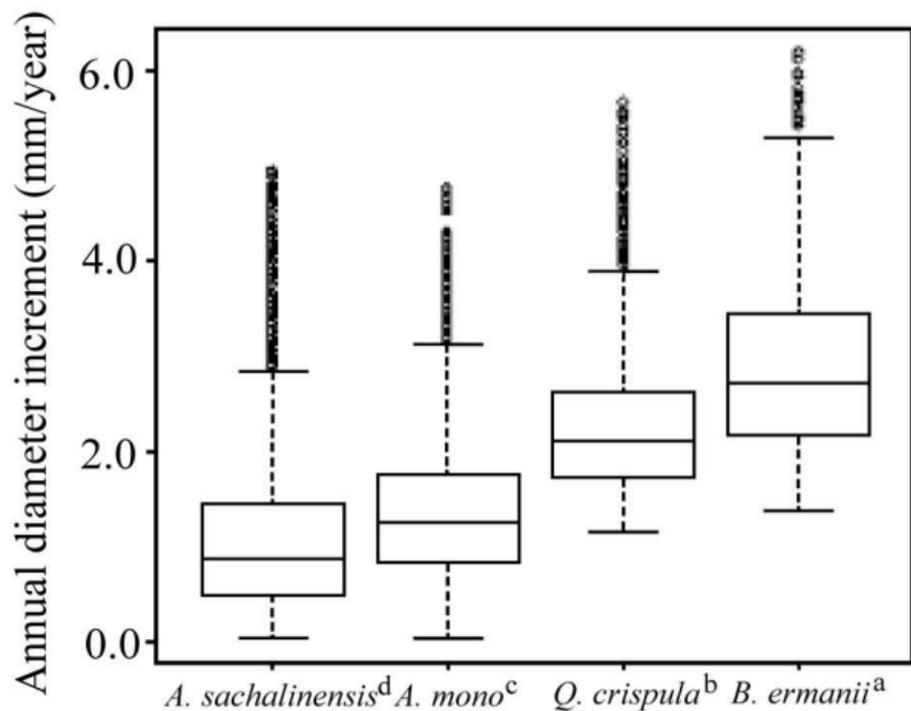


Fig. 2. Frequency distributions of the estimated ages of the trees of the four species at the time their DBH was 12.5 cm. The estimation was based on increment cores taken at 0.3 m height. See details in the text.

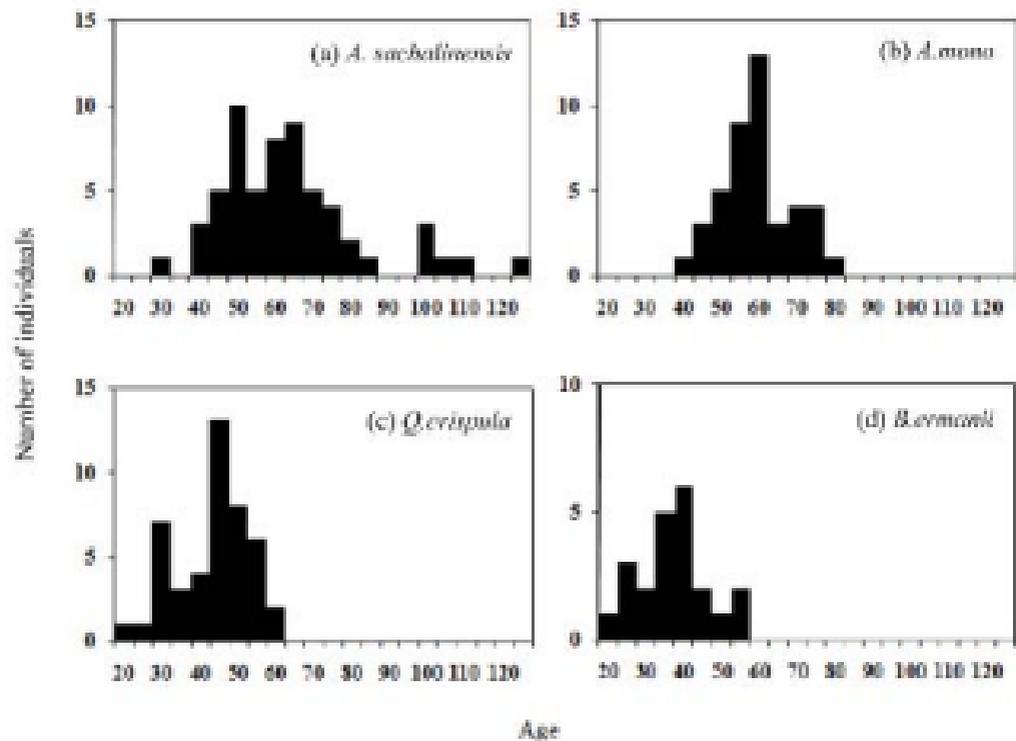


Fig. 3. Ten-year changes in the diameter growth rates after harvesting of individual saplings with and without surrounding harvesting. The base year (0) indicates the time at which harvesting was conducted. The diameter increment of each year after the harvesting (see equation [2] in the text), is shown. The explanatory variables had not been selected by AIC. The inter-specific difference between saplings that had or had not experienced local harvesting was not found by GLMM with considering a time-series factor (i.e. the model excluded the effect of harvesting showed lower AIC value).

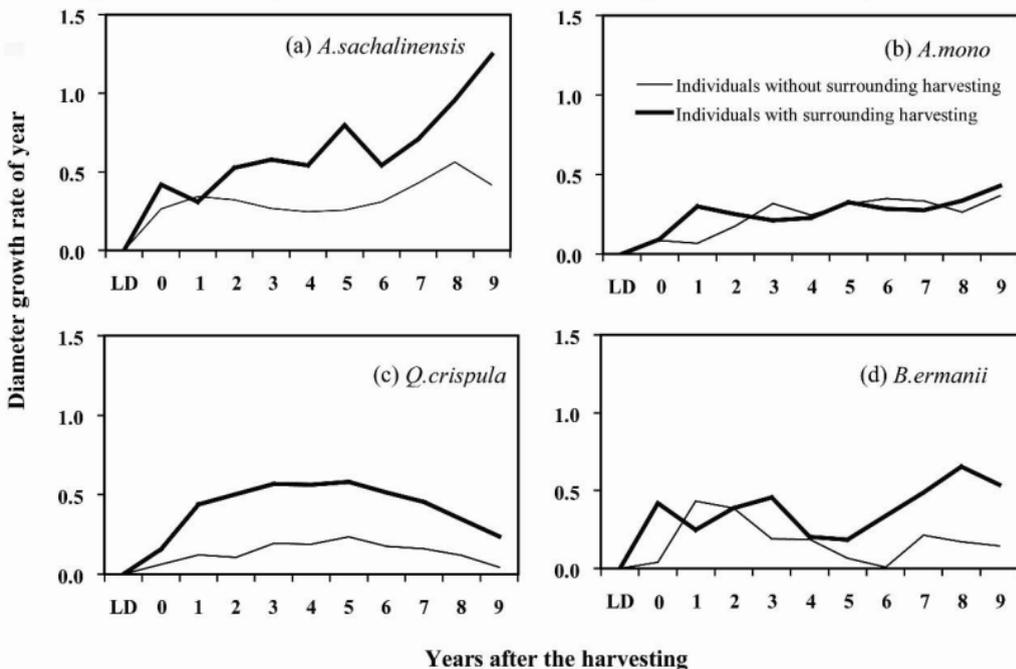


Fig. 4. Variable explaining the diameter growth rate in the four species. Only the variables for which $\Delta\text{AIC} > 2$ are presented. In cases when the quadratic interaction terms were selected in the model (a, b, g; see Table 1), one explanatory variable is shown on the x-axis, with the effect of another variable shown by the symbols defined on the figure. LC: local crowding; LH: local harvesting intensity; DS: duration of small growth; SS: stem size in terms.

