Title	An alternative management regime of selection cutting for sustaining stand structure of mixed forests of northern Japan: a simulation study
Author(s)	Yasuda, Akira; Yoshida, Toshiya; Miya, Hisashi; Harvey, Brian D.
Citation	Journal of Forest Research, 18(5), 398-406 https://doi.org/10.1007/s10310-012-0362-1
Issue Date	2013-10
Doc URL	http://hdl.handle.net/2115/53442
Type	article (author version)
File Information	Yasuda et al_2013_HUSCAP-1.pdf

[Instructions for use](#)

**An alternative management regime of selection cutting for sustaining
stand structure of mixed forests of northern Japan - a simulation study**

Akira YASUDA, Toshiya YOSHIDA, Hisashi MIYA and Brian D HARVEY

Yasuda A

Graduate School of Environmental Science, Hokkaido University

Yoshida T (corresponding author)

Uryu Experimental Forest, Field Science Center for Northern Biosphere,
Hokkaido University,

Moshiri, Horokanai, 074-0741, Japan

yoto@fsc.hokudai.ac.jp Tel: +81-165-38-2125 Fax: +81-165-38-2410

Miya H

Graduate School of Agriculture, Hokkaido University

Harvey BD

Centre for Forest Research, Université du Québec en Abitibi-Témiscamingue

Article type: original article

Subject area: biology and ecology Field: vegetation dynamics

21 pages for the text (including this page), 4 tables and 3 figures

Abstract

In uneven-aged conifer-broadleaved mixed forests in Hokkaido, northern Japan, single-tree selection cutting has been a common management practice since the early 20th century. This practice is expected to produce timber without major changes in stand structure or tree species composition. The demographic response of forests to this practice has often been unexpected, and degradation of stand properties has been widely observed. We propose here a sustainable management regime of selection cutting, based on an individual-based forest dynamics simulation model, SORTIE-ND. Our simulations, based on demographic data from fifteen long-term monitoring stands, suggest that selection cutting using a lower cutting intensity, together with a longer rotation period and reduced removal of small trees and conifer species is more appropriate than traditional system in terms of maintaining stand structure and tree species composition, as well as being profitable financially. Supplemental regeneration practices, which can counter accidental mortality incurred during harvesting operations, would also be necessary to ensure tree recruitment.

Key Words cutting intensity; cutting rotation period; forest modeling using SORTIE-ND; natural uneven-aged mixed forest; single-tree selection system

Introduction

Forest management regimes are shifting to include greater focus, not only on sustaining wood production, but also on maintaining various functions of ecosystems (Kohm and Franklin 1997; Hunter Jr 1999; Puetmann et al. 2008). Ecological based management of forests generally emphasize maintenance or restoration of stand structure, including tree volume, size distribution and tree species composition, of natural forests based on an improved understanding of emulations of patterns and processes observed in the natural disturbance regime (Coates and Burton 1997; Harvey et al. 2002; Kuuluvainen 2002; Seymour 2002). In this sense, relative to clear cutting, the merits of partial cutting have been recognized, notably for retaining biological legacies that can be important for biodiversity and ecosystem functions (Franklin et al., 2002; Matsuda et al. 2002).

Fine-scale gap disturbance influences stand structure of cool-temperate conifer-broadleaved mixed forests in Hokkaido, northern Japan (Hiura and Fujiwara 1999; Kubota 2000). Single-tree selection cutting, which introduces small gaps in a stand, has been a common management practice since the early 20th century (Matsui 1976). This practice is generally expected to promote growth of residual trees, regardless of tree species and size classes, and to produce timber without major changes in stand structure or tree species composition. However, the response of forests to single-tree selection cutting in Hokkaido has often been unexpected and, to some extent, the positive effects of cutting on growth and survival of residual trees, and on regeneration, have been limited (Noguchi and Yoshida 2007, 2009; Miya et al. 2009). In effect, degradation of stand structure has been widely observed (Noguchi and Yoshida 2004; Yoshida et al. 2006). Improvement of the traditional forest management

regime, to make harmony with resilience and preservation of the ecosystem, is therefore highly desirable. In particular, cutting intensity (amount to be harvested) in relation to a corresponding rotation period, which essentially determines the extent of disturbance, should be reconsidered. They have traditionally been based entirely on net volume growth of the sample stands (Matsui 1976), but their long-term effects on stand structural and compositional attributes have rarely been evaluated.

The aim of this study is to explore an ecologically sound forest management regime of selection cutting for maintaining original stand structure and species composition of a northern Japanese natural mixed forest. A field experiment involving various cutting regimes (e.g. Jalonen and Vanha-Majamaa 2001; Haeussler et al. 2007) would, in principle, be effective for this purpose; however, time horizons necessary for determining medium- to long-term outcomes, and high establishment and operational costs temper interest for this option. We therefore used a simulation approach for predicting the long term responses of a stand to various silvicultural cutting scenarios (Gratzer et al. 2004; Uriarte et al. 2009). We first estimated the parameters specifying the forest dynamics (i.e. individual growth, mortality and recruitment) which are required by a simulator (SORTIE-ND), based on a large set of field data. Following validation of the model, we determined the effects of several selection cutting scenarios. Allowable cutting intensity, with regard to the net growth rate of sample stands in Hokkaido, is generally estimated to be approximately 1-2 %/ year on average (in terms of volume; Hokkaido Pref. 2000). Consequently, we used a 10 % cutting intensity (to living stock) with a 10 year rotation period as the standard for our study, and compared it with scenarios having different combinations of cutting intensity and rotation period. Finally, in the discussion, we propose a sustainable silvicultural regime

based on the simulation results examining the effects of cutting on changes in the basal area sum, size structure and tree species composition, as well as the financial profit.

Method

1. Study sites

Our simulation was of natural conifer-broadleaved mixed forests in northern Hokkaido. The parameters required for the simulation were estimated from the data for stand structure, dynamics and individual tree properties in fifteen long-term monitoring stands in the Nakagawa (the forest office is at 44°43' N, 142°16'E) and Uryu Experimental Forest (44°22' N, 142°16'E) of Hokkaido University. The mean annual temperatures is around 5°C, and mean annual precipitation is about 1400mm, with 1.5-3m of maximum snow cover in winter. These monitored stands, 0.5-3ha in area, have been studied for 5-25 years at intervals of 1-10 years. For about ten thousands individual trees (consisting of seventeen tree species), we measured the diameter at breast height (DBH) or diameter at the base, tree height, crown depth, crown radius, and location (X-Y coordinate) of individual trees.

The model validation and simulations were performed using the data obtained from a selection-cut stand (3.2 ha in area) in the Nakagawa Experimental Forest. The stand consists of evergreen conifers, mainly *Abies sachalinensis* (Fr. Schm.) Masters, and deciduous broadleaved species including *Quercus crispula* Bl., *Acer mono* Maxim., *Betula ermanii* Cham. and *Tilia japonica* (Miq.) Simonkai commonly in a multi-aged and uneven-sized stand structure (Yoshida et al. 2006). The forest floor in these stands is generally densely covered with dwarf bamboos, *Sasa senanensis* (Franch. et Savat.) Rehd.) and *Sasa kurilensis* (Rupr.) Makino et Shibata (Noguchi and Yoshida, 2005). In

this stand single-tree selection cutting has been conducted at 9–10 year intervals, with harvesting intensities of around 10% in volume (Ohgane et al., 1988; Yoshida et al., 2006). These intensities were determined in consideration of the repeated census data to maintain harvested volume equivalent to the growth increment. The harvested trees were selected from a broad range of size classes and no preference was shown for any particular tree species.

2. Simulator

We employed SORTIE-ND, a spatially explicit, individual-based forest dynamics model (ver 6.09; Murphy 2008; <http://www.sortie-nd.org/>) as the platform for the simulations. The model considers species-specific demographic parameters such as growth, death and establishment of trees. The original SORTIE program was developed for hardwood forests in the northeastern United States (Pacala et al. 1993; 1996), and has since been improved to apply for tropical, temperate, and boreal forests (Coates et al. 2003; Uriarte et al. 2009; Thorpe et al. 2010). The latest version SORTIE-ND, with modular structure and open source code, enables us to look at spatially explicit effects of competition and disturbances including forestry activities. Details of the simulator are available in a SORTIE-ND's manual document (Murphy 2008).

3. Parameter estimations

Forest properties were updated every 5 years (basic timestep) in the simulations. 'Trees' in the model were assigned to one of five conditions: seed, seedling, sapling, adult and coarse woody debris. 'Seedling' represents the first growing stage (defined as trees with height < 2 m in this study) after germination of 'seeds', followed by 'sapling' (height $\geq$ 2 m and DBH < 12.5 cm) and adult (DBH $\geq$ 12.5 cm). Adult trees

were further grouped into four size-classes (DBH 12.5-22.5cm, 22.5-32.5cm, 32.5-42.5cm, ≥ 42.5 cm). Dead trees were regarded as ‘coarse woody debris’. Trees in the SORTIE-ND were assumed to have cylindrical crowns. We estimated the tree height, crown depth and crown radius with their species-specific allometric relations with DBH (cm), based on monitoring data.

If the sample size of a particular tree species for a particular parameter was insufficient, the parameterizations were based on species groups, according to taxonomy (conifer or broadleaved species) and shade-tolerance (tolerant and intolerant), involving shade-tolerant conifers (CF), shade-tolerant broadleaved (BT) and shade-intolerant broadleaved species (BI) (Yoshida et al., 2006).

3.1. Tree growth

The diameter growth parameters, with the assumption of light-dependency, were estimated from the long-term monitoring data. Diameter growth of individual trees was calculated at every timestep, and added to the original tree DBH. Tree height, crown depth, and crown radius were accordingly modified with the updated DBH based on allometric relations.

The amount of light available in a growing season (May - Sep) for an individual tree was calculated as the gap light index (GLI; Canham 1988; Beaudet et al. 2011), at the mid-crown of trees, taking into account the sun-track, assumption of open sky distribution, and light transmission in the crown. We referred to Pacala et al. (1996) for the light transmission of various tree species. The light model in SORTIE-ND has been evaluated and used independently by Beaudet et al. (2002, 2011) and Lefrancic et al. (2008). Because of model constraints, we did not explicitly consider topographic factors in this study.

The logistic and linear growth model (sensu SORTIE-ND; Murphy 2008), which assume light-dependent individual growth, were respectively applied for adults and saplings. Growth of seedlings was assumed to be constant in this model; most seedlings in the monitored stands were grown under a dense carpet of understory plants (dwarf bamboos), so that growth dependency on light conditions created by overstory trees is presumably not important (Noguchi and Yoshida 2007). We applied the averages of the diameter increment at the base (height 0.1 m) observed in the monitored stands for each tree species.

3.2. Tree mortality

We considered several factors for tree mortality in our model. First, adult and sapling mortality were assumed to be dependent according to species on the estimated diameter growth; the slower the growth, the higher the probability of mortality (BC mortality in SORTIE-ND; Murphy 2008). Second, a higher mortality rate due to senescence was assumed for adult trees by considering the species-specific maximum DBH observed in the monitored stands (Senescence mortality in SORTIE-ND).

Third, an accidental mortality, caused by harvesting and logging operations, was set for adults and saplings at the timestep when cutting was conducted (Episodic mortality in SORTIE-ND); its regression with cutting intensity was estimated. Previous studies have reported the significance of this type of mortality in managed forests of this type (Noguchi and Yoshida 2009; Miya et al. in preparation). Fourth, for seedlings, a random mortality (Background mortality in SORTIE-ND) was applied based on the observations in the monitored stands.

We also allowed for mortality caused by episodic natural disturbances (Storm behavior in SORTIE-ND). The historical record of wind-induced damage caused by a

powerful typhoon in 1954 (Yoshida and Noguchi 2009) was taken as the most severe windthrow. Severe typhoon damage again occurred throughout the region in 2004 (Yoshida et al. 2011), so that the rotation period of the disturbance was assumed to be 50 years.

3.3. Tree establishment

Tree recruitment in the model is a function of seed dispersal and seed germination. The annual supply of seeds in the forest simulation was taken to be proportional to the basal area sum of parent trees, defined as conspecific trees larger than the minimum seed-production size (given by Koike et al. (1992)), based on the data from one of the monitored stands (Uryu Experimental Forest, unpublished). Because we lacked reliable data on seed germination rate, parameters were set according to the density of current-year seedlings observed for each species for each substrate type (to be explained shortly) at several monitored sites (Yoshida et al. 2005; unpublished); the rates were calculated assuming linear correlation with the estimated seed supply.

Several substrate types (i.e. conditions of forest floor) were specified for the square grid of side 8m, which divide the simulated stand. The standard condition is 'Forest floor'. 'Fresh logs' are supplied by tree death (the proportion in the grid was determined from the DBH of the dead trees); these gradually changed into 'Decayed logs' over 25 years, in which most cut stumps moved into the third decay class (of five classes; Inoue et al., in preparation). 'Tip-up mounds' can be created when a live tree dies, with species- and size-specific probabilities, as presented by Yoshida and Noguchi (2009). 'Scarified soil' represents disturbed areas caused by tree cutting, and are assumed to appear with a certain proportion (estimated as 20 % from personal observation) in the grid after a cutting event. The durations required for the transition

to 'Forest floor' from 'Decayed log', 'Tip-up mound' and 'Scarified soil' were taken as 50, 10, and 10 years, respectively (approximations based on personal observations).

4. Model evaluation

We evaluated the model by comparing the simulated results with actual stand dynamics from a monitored site; the changes in basal area and DBH-class distributions were assessed respectively with 95 percent confidential intervals and chi-square test derived from ten simulation runs. The data observed over 20 years were obtained from the 3.2 ha of selection-cut stand (see study sites), which was not used in the parameter estimations. In the simulations the initial stand condition was set as actually recorded. Because of the absence of data on seedlings, saplings and forest floor substrate in the past data, we set their initial conditions according to values measured in a neighboring unmanaged stand (Miya et al., unpublished). The attributes of cuttings (e.g. cutting intensity for each tree species and for each size class) were chosen to be close to the actual cutting records.

5. Cutting scenarios

We then simulated (ten repetitions) a series of silvicultural scenarios, with particular focus on effects of cutting intensity and rotation period. The number of repetitions was ten. As the net growth rate of natural forests in Hokkaido is estimated to be approximately 1-2 %/ year on average (in terms of volume; Hokkaido Pref. 2000), we used a 10 % cutting intensity (defined in this study as percentage of basal area sum of cut trees to the living stock) with a 10 year rotation period as the standard for our study, and compared it with scenarios having different combinations of cutting intensity and rotation period (Table 1). Since the traditional regime has often caused stand degradation (Yoshida et al. 2006), we allowed a halved cutting intensity (relative to the

standard) in the latter two scenarios. Initial stand properties were set as the recent condition of the 3.2 ha area (160m×200m) of the selection-cut stand (Table 2). Cutting intensity was assigned proportional to the pre-harvest basal area sum of each tree species-group and each DBH-class.

6. Analyses

Results of the simulations, the averages of ten repetitions, were evaluated using three indices. Basal area recovery is expressed as a percentage of the term-end basal area sum relative to the initial value. Similarities in tree species composition and size structure are represented by the Bray-Curtis index. The statistical differences in these variables among scenarios were tested with one-way ANOVA and Tukey's HSD *post-hoc* test.

To assess the economic feasibility of the scenarios, we estimated potential financial profit based on income from timber sales and costs of harvesting operations. The former was calculated by multiplying the amount of merchantable trees (empirically assumed to be 65 % of cut volume, with 90 % of lower grade timber for pulp and wood chips; personal communication with Nakagawa Exp. For.) by the current timber price of each tree species (Hokkaido prefecture, 2010). Harvesting expenses included labor and machinery costs for cutting and skidding, and were estimated based on their relation to the amount of harvested trees (Nakagawa Exp. For. personal communication). Because economic conditions are volatile in a long-term, the resulting financial income and expenses is shown separately as a proportion relative to the standard scenario.

Results

The simulation reproduced the 20 years of change in the basal area sum and size structure (Fig.1); the observed basal area from the monitored stand were within the 95 percent confidential interval derived from the ten runs for validation exercise. Moreover, the term-end DBH-class distributions were not significantly different between the model and the field data, both when considering all species ($p=0.75$) and each species group (conifer, $P=0.58$; shade-tolerant broadleaved, $P=0.53$, shade-intolerant broadleaved, $P=0.73$).

The basal area sum fell to 53.2% of the initial value under the scenario #10-10 in one hundred years (Table 3). The greatest decrease was for conifers (38.8% of initial basal area sum), followed by shade-intolerant broadleaved (63.3%) and shade-tolerant broadleaved species (70.7%). The similarity of tree species composition and size structure were respectively 0.62 and 0.53 (Table 3 and Fig 2).

Scenario #20-20, with doubled cutting intensity (20%) and doubled rotation period (20 years), resulted in a 62.7% recovery. Conifers again showed a drastic decrease (43.9% of initial basal area sum), whereas shade-tolerant broadleaved species showed greater recovery (91.3%) than in scenario #10-10. The similarities of tree species composition and size structure were respectively 0.67 and 0.62. Financial income was similar (101%), but expenses were less than two-thirds of the scenario #10-10 (64%).

Scenario #5-10, with halved cutting intensity (5%) together while maintaining a 10 year rotation period, gave significantly higher recovery in basal area sum (75.3%). Shade-intolerant broadleaved species recovered fully (96.2%) to the initial condition, but conifers and shade-tolerant broadleaved species recovered less, at 61.0% and 78.9%, respectively. The similarity of tree species composition was 0.75, and that of size structure was 0.60. Financial income and expenses decreased respectively to 67

and 90% of scenario #10-10.

Scenario #10-20, with the doubled rotation period (20 years), resulted in an 83.5% recovery, which was the highest of the scenarios considered (difference with scenario #10-10 was significant). This higher recovery was derived mainly from shade-intolerant and shade-tolerant broadleaved species (97.9% and 87.7%, respectively), while that for conifers was still lower (71.5%). Similarity of tree species composition was 0.78, and of size structure was 0.63 (Table 3). Financial income fell to 70%, but expenses also fell to 54% relative to scenario #10-10.

Discussion

This work constitutes one of the first long-term simulation studies of managed mixed-species stands in Hokkaido and, as such, further studies are clearly needed to validate assumptions and refine simulations. SORTIE-ND is a flexible open source program, and it would be possible to include artificial regeneration options in further studies. Topographic considerations could also be integrated to reflect real site conditions of sloped sites. As well, we could increase confidence in assumptions regarding mortality and recruitment by more detailed demographic studies. In particular, seedling dynamics beneath understory dwarf bamboos should be included in the subsequent models.

None of the four scenarios, especially #10-10 and #20-20, produced adequate recovery in terms of the basal area sum, tree species composition and size structure (Table 3, Fig 2), suggesting that these management regimes are not sustainable over the long-term. The simulated stand degradation ostensibly reflects negative factors associated with cutting. Traditional thinking concerning allowable cutting intensity,

based on estimated net volume growth rate (Matsui 1976), clearly appears to fall short in terms of maintaining forest structural attributes. It is highly required to account for natural variability, notably episodic disturbances and unexpected demographic responses due to cutting, to estimate the cutting strategy.

Obviously reduction of the cutting intensity (amount to be harvested) is necessary for a sustainable silvicultural scenario in this type of mixed forest. Even in the scenarios with halved cutting intensity (#5-10 and #10-20), the recovery in terms of basal area sum was only around 80 % (Table 3). This was due to the effects of disturbance (i.e. periodic typhoon), and the shortage of regeneration; the densities of small trees were less than 50 % in any of the scenarios (Fig 2). The understory of forests in northern Hokkaido are generally covered with dense dwarf bamboo carpet, and it is therefore difficult to expect significant increase in regeneration density after a cutting (Nagaike et al. 1999; Noguchi and Yoshida 2004, 2007). Consequently, we propose that the reduction of the cutting intensity should be associated with targeting less on small trees to a maximum extent.

In addition, to reduce the chance of accidental mortality induced by harvesting and skidding operations (i.e. to reduce cutting frequency) would be effective. This type of mortality is particularly significant in small trees (Noguchi and Yoshida 2007), so careful attention to conservation of those during the operations should also contribute to maintain regeneration. In this case, we suppose extending rotation period is more effective than reducing each cutting intensity for enhancing recovery, because the mortality does not increase proportionally to the cutting intensity (it rather appeared to be affected by the total distance of skidding; Miya et al. in preparation). In actual, the scenario with shorter rotation (e.g. scenario #10-10) gave significantly greater

size-class similarity than that with correspondent longer rotation (#20-20; Table 3).

Our model simulations would also suggest that reducing the cutting intensity of conifer species is likely to have a positive effect on maintaining initial stand properties. The basal area sum of conifers recovered only 68.5% of maximum in these simulations (Table 3), indicating that these scenarios would be unable to maintain tree species composition. Conifer regeneration has been shown to be limited under selection cut management (Yoshida et al. 2006; Noguchi and Yoshida 2007), due apparently to increased mortality of small trees in canopy gaps created by cutting (Yoshida and Noguchi 2010). Higher mortality of adult conifers was also observed where cutting was conducted in the surrounding area, probably as a result of sudden changes in growth conditions (Noguchi and Yoshida 2009).

In summary, the necessary conditions for a selection cutting that is more likely to sustain stand structure and dynamics of mixed forests are (1) to set a lower cutting intensity with a longer rotation period, (2) reducing the accidental mortality, and (3) targeted less on small trees and conifer components. Based on these, we present an alternative selection cutting regime, with the simulation set at a 10% cutting intensity and 20 year rotation period, with more trees cut in the larger DBH-classes and broadleaved species. Specifically, the cutting avoided targeting trees with DBH 12.5-22.5cm (irrespective of species), and the cutting intensity for conifers was set at 8%; the reduction in cutting intensity was compensated by proportionally targeting trees in the larger DBH classes and broadleaved species. At the same time, we assumed accidental mortality would be reduced by 50%.

The simulation outcome at 100 years (Table 4; Fig 3) showed considerable improvements; basal area sum had recovered to 93.6% and that of conifers,

shade-tolerant broadleaved and shade-intolerant broadleaved species attained values of 83.9%, 101.1%, and 103.8% respectively relative to the initial values.

As well, while financial income was three-quarters (77%), expenses fell to about half (54%). The improved basal area recovery enabled the increase in cutting, producing better income in the period. It seemed to be contributed also by targeting broadleaved species, which generally have higher timber prices in the current market. On the other hand, the effect of extended rotation on the expenses was also significant; as shown in the comparison between the scenario #10-20 and #10-10 (the former brought two-thirds of the income, but involved only half of the expenses), the proportion of fixed costs per cutting was considerable. The profit is particularly pronounced in the current market conditions of low timber prices and high costs of cutting.

Nevertheless, the similarity of tree species composition and size structure of the alternative scenario remained at a relatively low level (0.71 and 0.82, respectively), as a result of the reduced tree density in smaller size-classes. This effect should be countered by practicing artificial regeneration (fill planting) in zones that are poorly stocked, besides reducing accidental mortality and targeting less on small trees. Conifer plantations and soil scarification for natural regeneration are practiced in this region and it is generally recognized that plantations can improve conifer recovery whereas scarification tends to result in dominance by pioneer species (particularly *Betula* sp.; Yoshida et al. 2005). The former is more preferable with considering the decrease in conifer component, but it clearly requires more costs. To apply natural regeneration practice, in combination with targeting more on broadleaved species (especially shade-intolerant ones) could be a more potent substitute for the traditional

selection management system.

Acknowledgements

We would like to thank anonymous reviewers for their helpful comments and suggestions. We are most grateful to the developers of SORTIE-ND. M. Beaudet and C. Messier kindly provided useful information about the program. We also thank the staff of the Nakagawa and Uryu Experimental Forests of Hokkaido University, for providing the data of the long-term field censuses. Thanks are also extended to M. Noguchi, S. Uemura, H. Shibata, T. Hiura and members of the Nayoro laboratory for their helpful comments and encouragements on this study.

References

- Beaudet M, Messier C, Canham CD (2002) Predictions of understorey light conditions in northern hardwood forests following parameterization, sensitivity analysis, and tests of the SORTIE light model. *For Ecol Manag* 165:235-248
- Beaudet M, Harvey BD, Messier C, Coates KD, Poulin J, Kneeshaw DD, Brais S., Bergeron Y (2011) Managing understory light conditions in boreal mixedwoods through variation in the intensity and spatial pattern of harvest: a modeling approach. *For Ecol Manage* 261: 84-94
- Canham CD (1988) An index for understorey light levels in and around canopy gaps. *Ecology* 69:1634-1638
- Coates KD, Canham CD, Beaudet M, Sachs LD, Messier C (2003) Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forest. *For Ecol Manag* 186:297-310

400 Coates KD, Burton PJ (1997) A gap-based approach for development of silvicultural
 401 systems to address ecosystem management objectives. For Ecol Manag
 402 99:337-354

403 Franklin JF, Spies TA, Van Pelt R, Carey AB, Thornburgh DA, Berg DR,
 404 Lindenmayer DB, Harmon ME, Keeton WS, Shaw DC, Bible K, Chen J (2002)
 405 Disturbances and structural development of natural forest ecosystems with
 406 silvicultural implications, using Douglas-fir forests as an example. For Ecol
 407 Manag 155:399-423

408 Gratzner G, Canham CD, Dieckmann U, Fischer A, Iwasa Y, Law R, Lexer MJ,
 409 Sandmann H, Spies TA, Splechtna BE, Szwagrzyk J (2004) Spatio-temporal
 410 development of forests - current trends in field studies and models. Oikos
 411 107:3-15

412 Haeussler S, Bergeron Y, Brais S, Harvey BD (2007) Natural dynamics-based
 413 silviculture for maintaining plant biodiversity in *Populus tremuloides*-dominated
 414 boreal forests of eastern Canada. Can J Bot 85:1158-1170

415 Harvey BD, Leduc A, Gauthier S, Bergeron Y (2002) Stand-landscape integration in
 416 natural disturbance-based management of the southern boreal forest. For Ecol
 417 Manag 155:369-385

418 Hiura T, Fujiwara K (1999) Density-dependence and coexistence of conifer and
 419 broad-leaved trees in a northern mixed forest. J Veget Sci 10:843-850

420 Hokkaido Prefecture (2000) Forest Statistics in Hokkaido: time-series version.
 421 Hokkaido Prefecture, Sapporo, pp187 (in Japanese)

422 Hokkaido Prefecture (2010) Forest Statistics in Hokkaido: 2009. Hokkaido
 423 Prefecture, Sapporo, pp112 (in Japanese)

- 424 Hunter Jr ML (1999) Maintaining Biodiversity in Forest Ecosystems. Cambridge
425 University Press 698pp
- 426 Jalonen J, Vanha-Majamaa I (2001) Immediate effects of four different felling
427 methods on mature boreal spruce forest understorey vegetation in southern
428 Finland. *For Ecol Manag* 146:25-34
- 429 Kohm KA, Franklin JF (1997) Creating a Forestry for the 21st Century: the science
430 of ecosystem management. Island Press. 475pp
- 431 Koike T, Nagasaka K, Kishida A (1992) The age of first reproduction of deciduous
432 broadleaved tree species and their successional traits in northern Japan. *Forest tree*
433 *breeding of Hokkaido* 34:22-28 (in Japanese)
- 434 Kubota Y (2000) Spatial dynamics of regeneration in a conifer/broad-leaved forest in
435 northern Japan. *J Veget Sci* 11:633–640
- 436 Kuuluvainen T (2002) Natural variability of forests as a reference for restoring and
437 managing biological diversity in boreal Fennoscandia. *Silva Fennica* 36:97-125
- 438 Lefrançois MJ, Beaudet M, Messier C (2008) Crown openness as influenced by tree
439 and site characteristics for yellow birch, sugar maple and eastern hemlock. *Can J*
440 *For Res* 38:488-497
- 441 Matsuda K, Shibuya M, Koike T (2002) Maintenance and rehabilitation of the mixed
442 conifer–broadleaf forests in Hokkaido, northern Japan. *Eurasian J For Res.*
443 5:119-130
- 444 Matsui Y (1976) History of Forestry in Hokkaido. In: *History of Forestry Vol.2:*
445 *issue for local forestry.* Japan Forest Technology Association, Tokyo, pp 411-667
446 (in Japanese; the title was tentatively translated by the authors)
- 447 Miya H, Yoshida T, Noguchi M, Nakamura F (2009) Individual growing conditions

448 that affect diameter increment of tree saplings after selection harvesting in a
 449 mixed forest in northern Japan. J For Res 14:302-310

450 Murphy LE (2008) SORTIE-ND user manual version 6.09. <http://www.sortie-nd.org/>

451 Nagaike T, Kubota Y, Watanabe N (1999) The effects of selective logging on stand
 452 structure and the regeneration of subboreal forests in Hokkaido, northern Japan. J
 453 For Res 4:41-45

454 Noguchi M, Yoshida T (2004) Tree regeneration in partially cut conifer-hardwood
 455 mixed forests in northern Japan: roles of establishment substrate and dwarf
 456 bamboo. For Ecol Manag 190:335-344

457 Noguchi M, Yoshida T (2005) Factors influencing the distribution of two
 458 co-occurring dwarf bamboo species (*Sasa kurilensis* and *S. senanensis*) in a
 459 conifer–broadleaved mixed stand in northern Hokkaido. Ecol Res 20:25-30

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

463 Noguchi M, Yoshida T (2009) Individual-scale responses of five dominant tree
 464 species to single-tree selection harvesting in a mixed forest in Hokkaido, northern
 465 Japan. J For Res 14:311-320

466 Ohgane E, Nigi T, Hishinuma Y, Koshika K, Fukui T (1988) Managerial progress
 467 and results of an experimental forest practiced by the Control Method. Res Bull
 468 Coll Exp For Hokkaido Univ 45:61-113 (in Japanese with English summary)

469 Pacala SW, Canham CD, Saponara J, Silander Jr JA, Kobe RK, Ribbens E (1996)
 470 Forest models defined by field measurement. II. Estimation, error analysis, and
 471 dynamics. Ecol Monogr 66:1-43

- Pacala SW, Canham CD, Silander Jr, JA (1993) Forest models defined by field measurements. I. The design of a northeastern forest simulator. *Can J For Res* 23:1980-1988
- Puettmann KJ, Coates KD, Messier C (2008) *A Critique of Silviculture: Managing for Complexity*. Island Press. pp188
- Seymour RS, White AS, deMaynadier PG (2002) Natural disturbance regimes in northeastern North America - evaluating silvicultural systems using natural scales and frequencies. *For Ecol Manag* 155:357-367
- Thorpe HC, Vanderwel MC, Fuller MM, Thomas SC, Caspersen JP (2010) Modelling stand development after partial harvests: An empirically based, spatially explicit analysis for lowland black spruce. *Ecol Modelling* 221:256-267
- Uriarte M, Canham CD, Thompson J, Zimmerman JK, Murphy L, Sabat AM, Fetcher N, Haines BL (2009) Natural disturbance and human land use as determinants of tropical forest dynamics: results from a forest simulator. *Ecol Monographs* 79: 423-443
- Vanderwel MC, Caspersen JP, Malcolm JR, Papaik MJ, Messier C (2011) Structural changes and potential vertebrate responses following simulated partial harvesting of boreal mixedwood stands. *For Ecol Manag* 261:1362-1371
- Yoshida T, Iga Y, Ozawa M, Noguchi M, Shibata H (2005) Factors influencing early vegetation establishment following soil scarification in a mixed forest in northern Japan. *Can J For Res* 35:175–188
- Yoshida T, Noguchi M (2009) Vulnerability to strong winds for major tree species in a northern Japanese mixed forest: analyses of historical data. *Ecol Res* 24:909-919
- Yoshida T, Noguchi M (2010) Growth and survival of *Abies sachalinensis* seedlings

for three years after selection harvesting in northern Hokkaido, Japan. *Landscape and Ecological Engineering* 6:37-42

Yoshida T, Noguchi M , Uemura S, Yanaba S, Miya H, Hiura T (2011) Tree mortality in a natural mixed forest affected by stand fragmentation and by a strong typhoon in northern Japan. *J For Res* 16:215-222

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

Figure captions

Fig 1. Comparisons of changes in basal area (relative to initial values) (left) and the end-term DBH-class distributions (averages of ten simulations) (right) predicted by the simulator with those observed in the field censuses.

Fig 2. Simulation results showing the end-term DBH-class distributions of the four scenarios (See also Table 3). Averages of ten simulations are shown.

Fig 3. Simulation results showing the end-term DBH-class distributions of the alternative scenario (See also Table 4). Averages of ten simulations are shown.

Table 1. Cutting scenarios examined by the simulation in this study.

Scenario ID#	Cutting intensity (% to living stock)	Rotation period (years)
10-10	10	10
20-20	20	20
5-10	5	10
10-20	10	20

Cutting targets in terms of tree species and size were set proportionally to the initial stand conditions (shown in Table 2 and Fig 1). See text for the details.

Table 2. Species composition of the sample stand, which corresponds to the 'measured' stand in Fig 1. Trees with DBH equal to or larger than 12.5 cm (defined as 'adults' in this study) were considered in this table. The condition was used for the initial state for the simulations.

Species	Species group ⁺	Basal area m ² /ha (%)	Stem density /ha (%)
<i>Abies sachalinensis</i>	CF	5.6 (48)	42 (36)
<i>Quercus crispula</i>	BI	1.4 (12)	11 (9)
<i>Acer mono</i>	BT	1.2 (10)	18 (15)
<i>Betula ermanii</i>	BI	1.0 (9)	12 (10)
<i>Tilia japonica</i>	BT	0.9 (8)	11 (10)
other species *	-	1.7 (15)	24 (20)
Total	-	11.8 (100)	117 (100)
shade-tolerant conifer	CF	5.7 (48)	43 (37)
shade-tolerant broadleaved	BT	2.7 (23)	38 (32)
shade-intolerant broadleaved	BI	3.4 (29)	37 (31)

⁺ The classification was based on Yoshida et al., (2006); CF, conifer; BI, shade-intolerant broadleaved species; BT, shade-tolerant broadleaved species. * 'Other species' include *Ulmus davidiana* (BT), *Kalopanax pictus* (BI), *Alnus hirsuta* (BI), *Sorbus alnifolia* (BT), *Magnolia obovata* (BI), *Phellodendron amurense* (BI), *Picea glehnii* (CF), *Sorbus commixta* (BT), *Salix hultenii* (BI), *Betula platyphylla* (BI), *Acanthopanax sciadophylloides* (BT) and *Fraxinus mandshurica* (BT) (in order of dominance).

Table 3. Simulation results for the four cutting senarios.

Scenario ID#	Amount of cut in BA (m ² / year /ha)	BA change (% of the term-end to the initial)				Similality (index of the term-end to the intial)		Financial profit (proportion relative to scenario #10-10)	
		CF	BT	BI	Total	Species composition	DBH-class distribution	Expences	Income
10-10	0.095 <i>a</i> (0.008)	38.8 <i>a</i> (10.4)	70.7 <i>a</i> (5.6)	63.3 <i>a</i> (12.7)	53.2 <i>a</i> (8.2)	0.62 <i>a</i> (0.07)	0.53 <i>a</i> (0.03)	1.00 <i>a</i> (0.02)	1.00 <i>a</i> (0.16)
20-20	0.102 <i>b</i> (0.006)	43.9 <i>a</i> (11.6)	91.3 <i>b</i> (8.1)	71.8 <i>a</i> (10.8)	62.7 <i>a</i> (7.3)	0.67 <i>a</i> (0.05)	0.62 <i>bc</i> (0.02)	0.64 <i>b</i> (0.02)	1.01 <i>a</i> (0.12)
5-10	0.058 <i>c</i> (0.003)	61.0 <i>b</i> (11.5)	78.9 <i>a</i> (6.5)	96.2 <i>b</i> (12.1)	75.3 <i>b</i> (7.4)	0.75 <i>b</i> (0.04)	0.60 <i>b</i> (0.02)	0.90 <i>c</i> (0.01)	0.67 <i>b</i> (0.07)
10-20	0.061 <i>c</i> (0.004)	71.5 <i>b</i> (21.4)	87.7 <i>b</i> (6.5)	99.9 <i>b</i> (17.1)	83.5 <i>b</i> (14.4)	0.78 <i>b</i> (0.07)	0.63 <i>c</i> (0.03)	0.54 <i>d</i> (0.01)	0.70 <i>b</i> (0.07)

The averages (standard deviations in parentheses) of the ten simulations are shown. Different letters indicate significant difference ($p < 0.05$ at one-way ANOVA, Tukey's test) between scenarios. BA: basal area at breast height. Explanations of each senario are provided in Table 1. CF, BT and BI indicate conifer, shade-tolerant broadleaved and shade-intolerant broadleaved species, respectively. See text for the details of the indices.

Table 4. Simulation results for the alternative cutting senario.

Scenario ID	Amount of cut in BA (m ² / year /ha)	BA change (% of the term-end to the initial)				Similality (index of the term-end to the intial)		Financial profit (proportion relative to scenario #10-10)	
		CF	BT	BI	Total	Species composition	DBH-class distribution	Expences	Income
alternative	0.062 (0.004)	83.9 (14.9)	101.1 (13.1)	103.8 (7.7)	93.6 (8.3)	0.71 (0.02)	0.82 (0.05)	0.54 (0.01)	0.77 (0.08)

The averages (standard deviations in parentheses) of the ten simulations are shown. BA: basal area at breast height. CF, BT and BI indicate conifer, shade-tolerant broadleaved and shade-intolerant broadleaved species, respectively. See text for the details of the indices.

Fig 1. Comparisons of changes in basal area (relative to initial values) (left) and the end-term DBH-class distributions (averages of ten simulations) (right) predicted by the simulator with those observed in the field censuses.

Fig 2. Simulation results showing the end-term DBH-class distributions of the four scenarios (See also Table 3). Averages of ten simulations are shown.

Fig 3. Simulation results showing the end-term DBH-class distributions of the alternative scenario (See also Table 4). Averages of ten simulations are shown.