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Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests

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Abstract

The discipline of silviculture is evolving rapidly, moving from an agricultural model that emphasized simple stand structures toward a natural disturbance- or ecosystem-based model where stands are managed for multiple species and complex structures. Predicting stand dynamics and future yields in mixed-species complex structured stands cannot be easily accomplished with traditional field experiments. We outline the development and structure of SORTIE/BC, a descendent of the SORTIE model. SORTIE/BC is a light-mediated, spatially explicit, mixed-species forest model that makes population dynamic forecasts for juvenile and adult trees. We use the model to simulate partial cutting prescriptions in temperate deciduous, boreal and temperate coniferous mixed-species forests. The species, amount and spatial pattern of canopy tree removal had a major influence on understory light environments. Low and uniform removal of canopy trees were less successful in favouring the growth and survival of regenerating trees of intermediate to shade intolerant species and the growth of retained canopy trees than patch removal. In the boreal mixedwood, strip-cutting can maintain mixed stands but careful attention must be paid to buffer and strip management to optimize stand growth. We conclude that SORTIE/BC can be very useful to explore and explain the silvicultural implications of complex silvicultural prescriptions for which there are no existing long-term experiments.

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1. Introduction

The discipline of silviculture in Canada has strong roots in 19th century European forestry, characterized

by traditional silvicultural systems that describe a cycle in which a stand is harvested, regenerated and tended over time (Matthews, 1989). Over the past half century, as logging rapidly expanded in the temperate and boreal forests of Canada, foresters followed an agricultural model that strove for simple stand structures with an emphasis on even-aged, single species stands. This management is still common today.

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Forest ecologists have increasingly focused on the role of disturbance, especially the implications of varying frequency, intensity and pattern of disturbance on population or community dynamics and ecosystem processes (e.g., Hunter, 1999; Franklin et al., 2000). This work has provided a clearer understanding of the importance of structure in forest stands and landscapes for many species and ecosystem processes, and resulted in a major reassessment of the relationship between conventional silviculture and the disturbance processes that operate in natural, unmanaged environments.

A variety of new silvicultural systems are being considered to move forestry to management based on disturbance ecology and ecosystem processes (Coates and Burton, 1997; Greene et al., 2002; Harvey et al., 2002; Mitchell and Beese, 2002; Lieffers et al., 2003). Foresters are developing more complex stand management prescriptions that view silvicultural interventions in terms of stand structure rather than simply the regeneration and growth of the next crop. However, determining which silvicultural strategy will produce the desired future species composition and growth rates in complex mixed-species stands is not easily accomplished with field studies. Field experiments generally use only a limited set of simple treatments with considerable delay before tree and stand-level responses are observed.

Silvicultural systems research has been plagued by a lack of good experimental data, because of the long-term nature of such studies and the difficulty of conducting research on what are fundamentally descriptive management systems (Coates and Burton, 1997). We fully support the establishment of long-term field experiments; however, it must be recognized that there are many questions regarding tree and stand responses to differing silvicultural interventions that field experiments have difficulty addressing. Unfortunately, long-term silvicultural experiments in Canadian forests (e.g., Decie, 1957; Glew, 1963; Lees, 1964; Hughes, 1967) have rarely been followed for more than a decade or two due to changing priorities and funding problems. Many new long-term studies established in Canada and elsewhere are currently examining alternatives to conventional silviculture, or comparing and contrasting the effects of natural and human disturbances in forest ecosystems (Coates et al., 1997; Arnott and Beese, 1997; Halpern

and Raphael, 1999; Mitchell and Vyse, 1999; Veeman et al., 1999; McClellan et al., 2000). Results will take time to arrive and these experiments may also fade into history before long-term results are available.

Here, we present an approach that combines short-term empirical studies with development of a forest simulation model (SORTIE/BC) to provide insight into long-term forest response to silvicultural strategies. We believe managed forest stands will become increasingly complex in terms of structure and tree species, and that linking empirical studies to models is the best approach for answering the many questions foresters and ecologists have regarding site, stand and landscape conditions in future forested landscapes. Our reliance on predictive models will increase as we try to understand the implications of new silvicultural strategies that include continuous retention of canopy trees and management of multiple tree species with different life history characteristics.

The objectives of this paper are to describe the history and development of SORTIE/BC and to provide three example simulations that demonstrate the types of silvicultural issues that can be addressed by the model.

2. SORTIE/BC model development

SORTIE/BC has been parameterized for conditions in northern British Columbia (Kobe and Coates, 1997; Wright et al., 1998, 2000; Canham et al., 1999; LePage et al., 2000; Canham et al., in review). It is a descendent of the SORTIE model developed in the early 1990s for transitional oak—northern hardwood forests in the northeastern US (Pacala et al., 1993, 1996). SORTIE/BC retains the basic structure of the original model (Fig. 1), but has been extensively modified to account for ecological conditions in British Columbia, and to allow silvicultural interventions during model simulations.

Field research is also underway to develop and parameterize versions of SORTIE/BC in a number of other forest types, including temperate deciduous forests of southern Quebec (Beaudet et al., 2002), mixed southern boreal forests of the Quebec Clay Belt region, *Picea glauca*–*Populus tremuloides* forests across boreal Canada, temperate forests of New Zealand, and tropical forests of Puerto Rico.

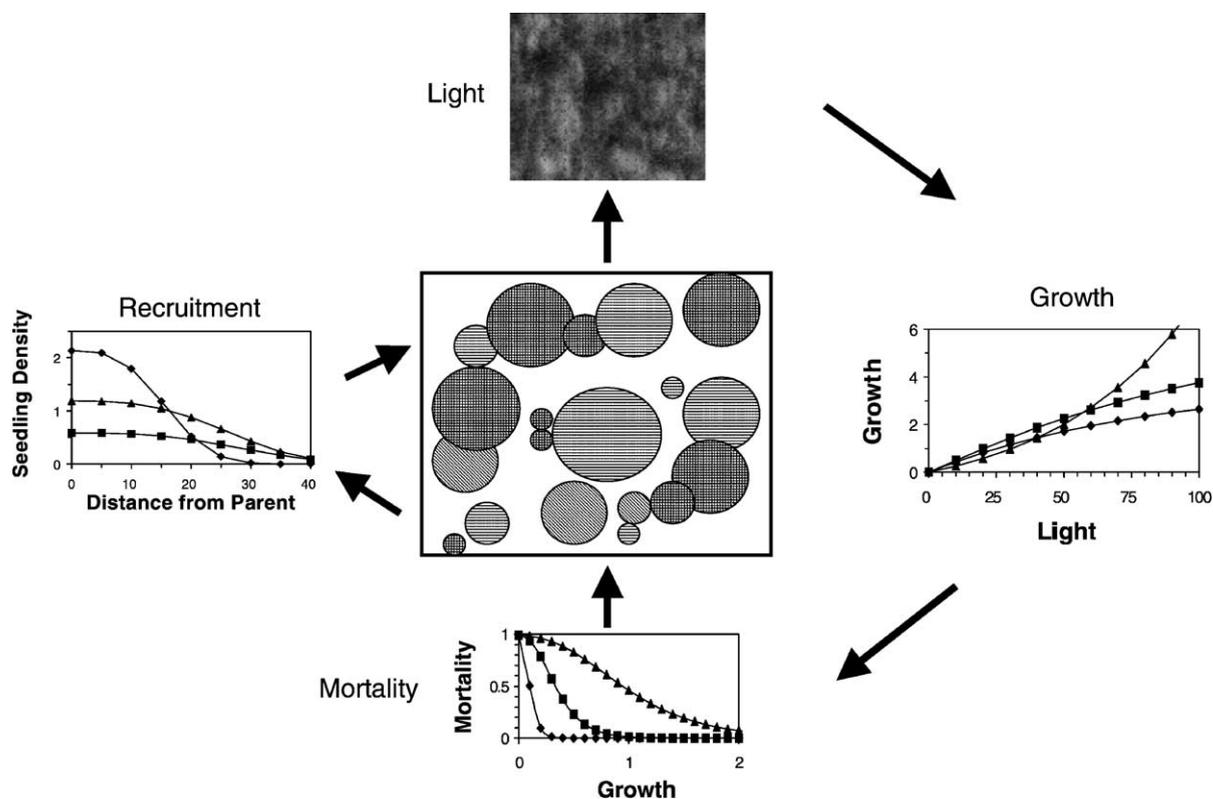


Fig. 1. Schematic diagram of the SORTIE-BC model for a hypothetical forest with three species. The spatial distribution of trees in the forests (central panel) determines both the spatial distribution of light (Light Submodel) and the spatial distribution of new seedlings (Recruitment Submodel). Spatial variation in light levels determines growth (Growth Submodel), and growth rates are used to predict mortality rates (Mortality Submodel), which in turn determine the distribution of trees at the beginning of the next time step.

A flexible user-interface is included in SORTIE/BC that allows a user to incorporate a wide range of silvicultural strategies (e.g., clearcutting, understory protection, understory planting, diameter limit harvesting, shelterwood, single or group selection and variable retention). The model can simulate any type of silvicultural strategy that removes or retains trees by species, size and location. Gaps of any size or orientation can be simulated. Seedlings can be planted by species and starting size. Logging or planting can occur at any time step during a model simulation. Within a simulated plot, up to five subplots can be identified for separate model output summaries. Any plot size can be simulated—the only constraint is the increased computer processing time required as plot size increases.

Model output at any time step (5-year) can include: (1) spatial coordinates, diameter and height of each individual; (2) diameter and height distributions by

plot or individual species; (3) changes in population density of seedlings (<1.3 m tall), saplings (1.3 m tall to <10 cm DBH) and adult trees (10 cm DBH and larger), by species; (4) basal area (m^2/ha), by species, of sapling and adult trees; (5) distribution of sub-canopy light levels on a $2\text{ m} \times 2\text{ m}$ grid. SORTIE/BC does not simulate volume, biomass, wood products or wood quality, or any economic state variables.

2.1. Recruitment submodel

The number and spatial distribution of seedlings is predicted using species-specific equations based on parent tree proximity, size and abundance, and on the abundance and favourability of seedbed substrates under four levels of canopy openness: full canopy, partial canopy, large gaps and clearcuts (LePage et al., 2000).

2.2. Light submodel

Growing season light availability is predicted as a function of (1) species-specific light transmission coefficients, (2) variation in crown geometry as a function of tree size, (3) the identity, size, and spacing of trees in the immediate neighbourhood, and (4) the local sky brightness distribution (Canham et al., 1999).

2.3. Growth submodel

Species-specific equations predict radial growth of juvenile trees based on growing season light availability (Wright et al., 1998). We can also incorporate growth functions that account for past periods of suppression and release (Wright et al., 2000). Adult tree growth rates can be estimated by species from re-measurement of permanent sample plots or from more mechanistically derived functions based on neighbourhood competition (Canham et al., *in review*). The neighbourhood function is an extension of traditional distance-dependent, spatial competition models. It allows independent estimates of (1) the potential maximum tree growth for a given set of climatic and edaphic conditions, as a function of tree species and size, and (2) the magnitude of the competitive effects of neighbouring trees on target tree growth as a function of the species, size, and distance to neighbouring trees. Empirical allometric equations are used to convert tree diameter to tree height.

2.4. Mortality submodel

Juvenile mortality is based on the well-documented empirical relationship between growth rates and survival of understory seedlings and saplings. The probability of survival for each juvenile tree is predicted by species as a function of recent radial growth rates (Kobe and Coates, 1997). The user can also specify species-specific random background mortality rates for juvenile or adult trees, and there is a separate senescence mortality function for old-age mortality. For dense even-aged and single-species stands, self-thinning functions can be implemented for specific model simulations. Parameter values for random, senescence and self-thinning mortality should be estimated from locally available data.

2.5. Model limitations

SORTIE/BC is a resource-mediated model, in which only light is directly taken into account for predicting growth of seedlings and saplings. Light is the resource most directly manipulated by partial cutting silvicultural treatments in mixed-species stands, however, caution should be exercised in using the model in situations where fertility or water availability will be significantly modified over time by silvicultural interventions. Ongoing research is developing methods to incorporate variability in soil nutrient availability into the general SORTIE model structure (e.g., Finzi and Canham, 2000; Kobe et al., 2002). Finally, the degree of confidence in model predictions is largely a function of the quality of the data used to parameterize the model. This is a limitation or strength, depending on ones' perspective.

3. SORTIE/BC model simulations

We provide three simulations that manipulate the spatial pattern or species of retained canopy trees and demonstrate how the model can be used to understand the consequences of different silvicultural strategies: (1) predict spatial variation in understory light levels after selection cutting in temperate deciduous forests of Quebec; (2) predict stand composition and growth after strip-cutting in boreal mixedwood forests; (3) predict how varying the spatial pattern of retained canopy trees in northern temperate conifer forests affects survival and growth of planted seedlings, and growth of the retained canopy trees. Each simulation was designed to answer a specific research question that typically might have been addressed by establishing a field experiment. The simulations are not intended as an exhaustive analysis of each question.

3.1. Light levels in temperate forests of southern Quebec

The selection system is the most widely used silvicultural system in uneven-aged hardwood forests of southern Quebec, with more than 600,000 ha cut between 1990 and 2000. The selection system is generally applied with a relatively narrow range of

removal rates (25–35% of basal area) and uniform canopy retention (Majcen, 1994). It has been shown to favour the recruitment of pre-established regeneration of shade-tolerant species, but there is some concern that the micro-environmental conditions that it creates might not allow an adequate regeneration of mid-tolerant species (Crow and Metzger, 1987).

In response to those concerns, recent changes in forest policy (MRNQ, 1998) have made new silvicultural options available to forest managers. These silvicultural options rely on more aggregated patterns of tree harvest leading to the creation of gaps and patches of various sizes (e.g., group selection with 500–1500 m² gaps in a matrix of single-tree selection cutting, and patch selection with 1–2 ha patches in a matrix of single-tree selection cutting). Here, we use the SORTIE/BC light submodel to examine how understory light conditions are affected by variation in stand species composition and basal area, and by variation in the spatial pattern of harvest.

3.1.1. Methods

The SORTIE/BC light submodel was parameterized and tested for sugar maple (*Acer saccharum*)–yellow birch (*Betula alleghaniensis*)–beech (*Fagus grandifolia*) forests in Duchesnay, Quebec (46°55'N, 71°40'W) (Beaudet et al., 2002). Starting conditions for our simulations were a 9 ha stand with 29 m²/ha basal area, 400 stems/ha (>10 cm DBH), 500 stems/ha (<10 cm DBH), an inverse-J-shaped DBH distribution with a *q*-value of 1.09 and a maximum DBH of 60 cm. SORTIE/BC predicted percent full sunlight 1 m above-ground on a 5 m × 5 m grid in each plot.

In our first set of simulations, we compared three species compositions to examine how increasing the proportion of the very shade-tolerant and deep-shade casting beech would affect the stand-level understory light conditions: (1) 80% sugar maple, 20% yellow birch and 0% beech (based on % of basal area); (2) 60% sugar maple, 20% yellow birch and 20% beech; (3) 40% sugar maple, 20% yellow birch and 40% beech. For each species composition, we examined how decreasing the basal area from 29 to 17 m²/ha would affect the light conditions.

Our second set of simulations used a stand of 60% sugar maple, 20% yellow birch, 20% beech (type 2 composition above) and a basal area of 29 m²/ha. We predicted light environments in the unlogged stand

and following three harvest treatments: (1) 30% removal (% of basal area) with uniform single-tree selection; (2) 30% removal with small-group selection (12 evenly distributed 675 m² gaps and uniform single-tree selection in the forest matrix between gaps); (3) 30% removal with large-group selection (six evenly distributed 1350 m² gaps with uniform single-tree selection between gaps). The three harvest treatments were planned to result in the same post-harvest stand basal area (20 m²/ha) but differed in the spatial aggregation of the residual trees.

3.1.2. Results and discussion

Our first simulations showed that the stand basal area and species composition (more specifically the relative proportion of beech vs. sugar maple) had a marked impact on understory light conditions (Fig. 2). We observed non-linear relationships between stand-level mean GLI and stand basal area, indicating that a given reduction in basal area would have a more pronounced effect for stands with lower initial basal area. Similar trends have been observed in other forest ecosystems (e.g., Drever and Lertzman, 2003; Prévost and Pothier, 2003). An ANCOVA showed that the slopes of those relationships did not vary with species composition ($P = 0.095$). When the non-significant

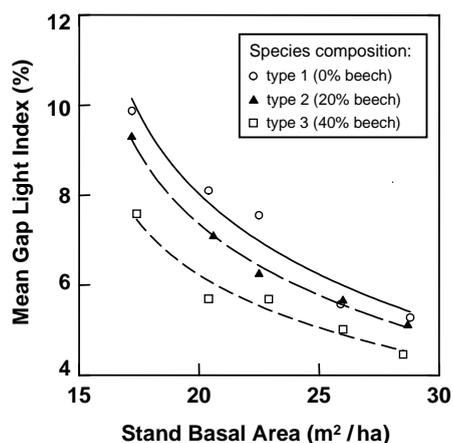


Fig. 2. Mean light availability (GLI, %) at 1 m above-ground in 9 ha uneven-aged northern hardwood stands with various basal area and species composition (see text for a more detailed description of each type of species composition). Fitted regression lines are: $y = 36.3 - 9.3 \ln x$, $P = 0.001$, $R^2 = 0.969$ for type 1 composition; $y = 31.5 - 7.9 \ln x$, $P = 0.006$, $R^2 = 0.923$ (type 2); $y = 23.6 - 5.7 \ln x$, $P = 0.013$, $R^2 = 0.874$ (type 3).

interaction term (composition \times ln basal area) was removed from the ANCOVA model, a significant composition effect was detected ($P = 0.001$), showing that the stand-level mean GLI decreased with an increase in the proportion of beech in the stands. This is as expected given the previously reported deep-shade casting effect of beech, an effect which was related to both its lower canopy openness and deeper crown (Canham et al., 1994; Beaudet et al., 2002). The results from these simulations not only allowed us to quantitatively estimate the effect of reduction in basal area on understory light conditions, but also underscored the importance of taking into account stand species composition when planning harvests.

In our second set of simulations, the three harvest treatments all led to increased stand-level mean GLI, but the magnitude of the increase varied among treatments (Fig. 3). The single-tree selection led to a 39% increase in mean GLI compared to pre-harvest conditions, the small-group selection to a 108% increase, and the large-group selection to a 123% increase. These results clearly show that the increase in light availability is not only affected by the reduction in stand basal area, but also by the spatial arrangement of residual trees, in agreement with field results in Battaglia et al. (2002). The harvest treatments also differed in the frequency distribution of GLI (Fig. 3). The maximum GLI increased from 23% in the pre-harvest conditions, to 56% in the single-tree selection cut, and to 75 and 82% in the small- and large-group selection cuts, respectively (Fig. 3). Light conditions were also increasingly variable (see coefficient of variation (CV) values in Fig. 3).

These differences in post-harvest light conditions may have important implications for regeneration dynamics. Yellow birch is the most commercially valuable species in these forests, but is less shade-tolerant than its companion species. Light conditions lower than 10% produce strong reductions in yellow birch survival (Kobe et al., 1995). Our simulations show that under the pre-harvest conditions, 95% of the stand area had light conditions $<10\%$ GLI. Reducing the basal area by 30% decreased the proportion of the stand area with dark conditions ($<10\%$ GLI) to 81, 71 and 74% for the single-tree, small- and large-group selection, respectively. Surprisingly, the small-group selection had a lower proportion of dark microsites (GLI $<10\%$) than the large-group selection treatment.

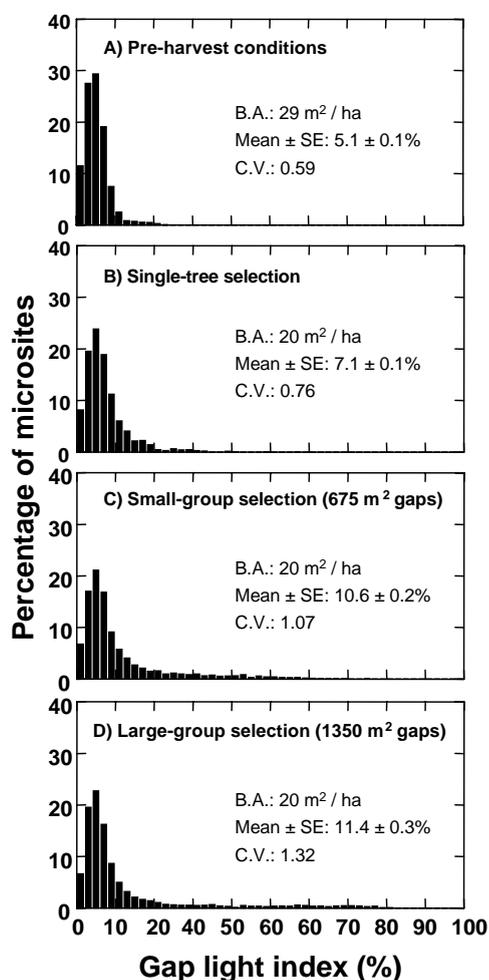


Fig. 3. Frequency distribution of light availability (GLI, %) at 1 m above-ground in 9 ha uneven-aged sugar maple–yellow birch–beech stands with 60% sugar maple, 20% yellow birch, and 20% beech (% basal area), submitted to various types of harvest (see text for more details).

This could be due to the higher number of gaps in the small-compared to the large-group selection (twelve 675 m² gaps vs. six 1350 m² gaps), a situation which might have increased the importance of edge effect in the small-group selection treatment. While the small-group selection treatment reduced the greatest proportion of microsites with dark light conditions ($<10\%$ GLI), the large-group selection led to the highest proportion of microsites with brighter light conditions. Data from southeastern Quebec show that yellow birch saplings reach 90% of their maximum radial

growth (i.e., growth at 100% GLI) at 35% GLI (Beaudet, unpublished results). In the large-group selection, 8.5% of the understory microsites measured at 1 m received >35% GLI, compared to 6% for the small-group selection.

The relatively low removal rates (~30% basal area) commonly used in the northern hardwood forests of Quebec are unlikely to favour the growth and survival of mid-tolerant species unless careful attention is paid to the spatial distribution of the retained canopy trees. Variable retention silvicultural systems, where harvesting is spatially aggregated (i.e., in discrete gaps), has the potential to create better light conditions for the survival and growth of less tolerant species than the traditional single-tree selection system.

3.2. Strip-cutting in boreal mixedwood forests

The aspen–spruce mixedwood is a common stand type across boreal Canada. Historically, management has been designed to promote the dominance of either aspen or spruce after logging—the so called un-mixing of the mixedwood. Silvicultural practices that retain an intimate spatial mixture of both tree species are being advocated in mixedwood stands (Man and Lieffers, 1999). Various prescriptions designed to protect residual understory white spruce while removing overstory trembling aspen are being considered or implemented across Canada. Here, we simulate one of the most common prescriptions—strip-cutting. Our objective is to see if strip-cutting can maintain mixed stands of aspen and spruce, and see how basal area of the two species develops over time.

3.2.1. Methods

We used parameter values from Kobe and Coates (1997), Wright et al. (2000), Canham et al. (1999), LePage et al. (2000) and ongoing field studies in boreal forests (unpublished data). Adult tree radial growth was derived from 33 permanent sample plots near Fort Nelson, British Columbia (58°50'N, 122°40'W). Allometric relationships between tree diameter, tree height and crown radius, and between tree height and crown length were derived from the permanent sample plot data and from ongoing studies near Fort Nelson. Self-thinning functions for trembling aspen were developed from a compilation of data from yield tables or studies

Table 1

Stand description of the three sites used as starting conditions for the strip-cutting in boreal mixedwood forests simulation

Stand statistics	Capot blanc	Mile 308	Simpson trail
Density (stems/ha)			
Spruce residuals <17.5 cm DBH	693	897	1041
Mature spruce >17.5 cm DBH	30	31	102
All spruce	723	928	1143
All aspen	656	877	512
Stand density	1379	1805	1655
Basal area (m ² /ha)			
Spruce residuals <17.5 cm DBH	0.9	1.9	4.9
Mature spruce >17.5 cm DBH	4.8	6.8	5.5
All spruce	5.7	8.7	10.4
All aspen	45.7	42.2	39.9
Stand basal area	51.4	50.9	50.3

that followed aspen self-thinning through time (Bella, 1975; Bella and De Franceschi, 1980; Peterson and Peterson, 1992; Lux, 1998).

Simulations ran for 120 years following strip-cutting and protection of understory white spruce. Starting conditions were three approximately 80-year-old mixedwood stands located near Fort Nelson (Table 1). Cut strips were 78 m wide. Each had four 6 m wide machine access corridors where all trees were removed. Elsewhere, individual spruce with diameters >17.5 cm and all aspen were removed, thus releasing the smaller residual spruce. Buffer areas, each 18 m wide, where no cutting occurred flanked each cut strip. Across the top of the plot area was an 18 m wide roadside processing area (road) where all trees were removed. Five years after cutting we randomly removed a further 10% of the remaining residual spruce in the cut strips to simulate losses due to mechanical injury during the initial logging entry and/or subsequent wind damage. Aspen sucker density was specified to be 20,000 stems/ha in logged areas. We performed additional simulations with fixed aspen sucker densities of 10,000 and 50,000 stems/ha to examine the influence of initial aspen sucker density on final stand development.

3.2.2. Results and discussion

Aspen basal area in cut strips and the road processing area peaked 30–40 years after logging and then declined slightly (Fig. 4). Spruce basal area increased

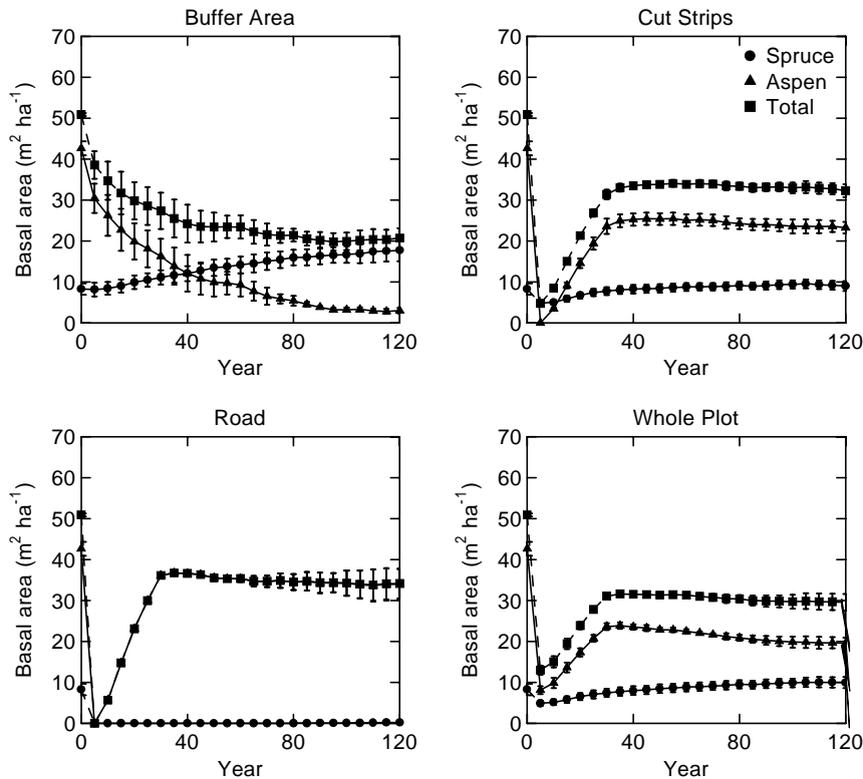


Fig. 4. Predicted average aspen and spruce basal area (m^2/ha) over 120 years for the three sites (see Table 1) in the strip cuts, buffers, road processing area and whole plot. Error bars represent one standard error of the mean.

slowly in the cut strips but was minimal in the road processing area (Fig. 4). Aspen basal area dropped steadily in the buffers because of mortality of the older trees and little new aspen recruitment. At the end of the 120-year simulation few of the original aspen canopy stems remained. Spruce basal area increased in the buffers over time due to the longevity of the species and the improved growth of understory trees as the original aspen slowly died.

Aspen and spruce whole plot average basal area (strips, road and buffers combined) at the end of the simulation was considerably lower than at the start (Fig. 4). Aspen senescence mortality in the buffers combined with a shading effect of buffer trees on aspen regeneration in strip cuts likely explains the overall lower total basal area production. Another factor may be the initial aspen density in the logged areas. We found that initial aspen sucker density strongly influenced aspen basal area at the end of the simulation, but had little impact on spruce basal area (Fig. 5). None of

the three aspen sucker densities tested allowed for complete recovery of aspen basal area to original levels, although the 50,000 stems/ha sucker density was close. Mature aspen stands in the Ft Nelson area were of fire origin and likely had very high aspen densities at establishment (commonly 30,000–150,000 stems/ha, see Peterson and Peterson, 1992).

In conclusion, the strip-cutting treatment resulted in a well-mixed stand of aspen and spruce—a desired outcome for mixedwood management in aspen–spruce stands. To optimize stand yield, careful attention to buffer management, strip width and aspen regeneration within the strips is required.

3.3. Seedling and retained canopy tree response to the spatial pattern of tree removal in conifer dominated temperate forests of northwestern BC

Partial cutting prescriptions are increasingly being used in the forests of British Columbia to meet an

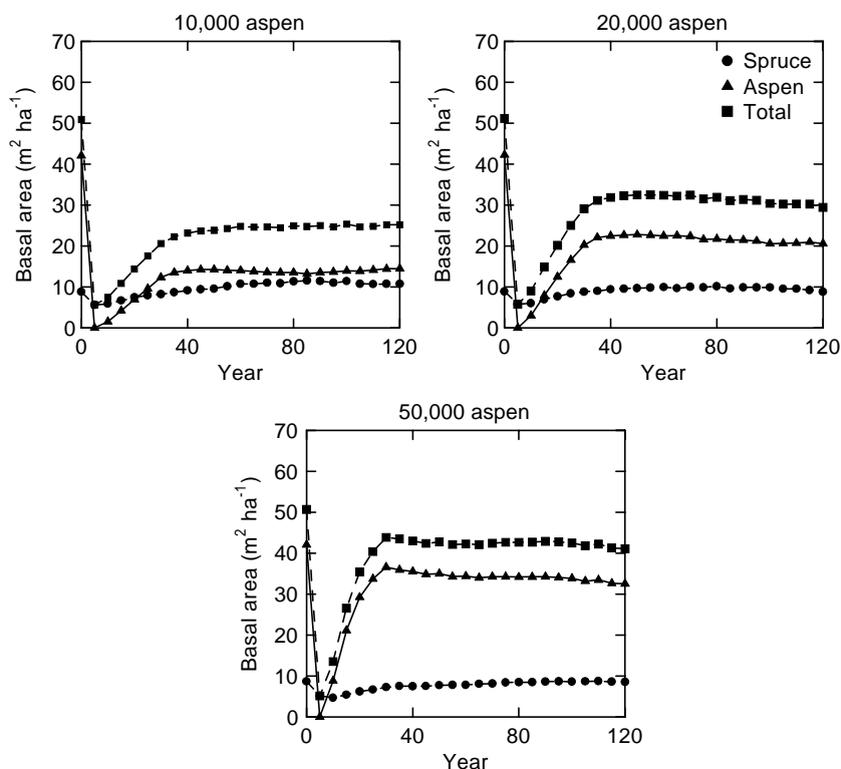


Fig. 5. Predicted basal area (m^2/ha) over 120 years in one stand (Mile 308) after strip-cutting and variable aspen sucker regeneration densities in the cut strips and the road processing area.

expanding range of social and ecological management objectives, however, their effects on future stand development are difficult to predict. Stand yield will depend on residual tree growth plus the contribution of newly established regeneration. We also think the spatial patterning of tree removal will affect future yields as canopy trees can be removed (or retained) in many different spatial patterns. We conducted simulations to examine how the spatial arrangement of logging effects the survival and growth of planted seedlings, and growth of the retained canopy trees.

3.3.1. Methods

This simulation used stand conditions found at the Date Creek silvicultural systems study in northwestern British Columbia ($55^{\circ}22'N$, $127^{\circ}50'W$; 370–665 m elevation). The initial conditions were from a mature forest that established after stand destroying fire in 1855, for which we have detailed stand data (Coates et al., 1997). The stand was a mixture of six conifer and

three deciduous tree species. Western hemlock (*Tsuga heterophylla*) dominates stand composition, followed by western redcedar (*Thuja plicata*) and minor amounts of hybrid spruce (*P. glauca* \times *sitchensis*), subalpine fir (*Abies lasiocarpa*), amabilis fir (*Abies amabilis*), lodgepole pine (*Pinus contorta* var *latifolia*), paper birch (*Betula papyrifera*), trembling aspen (*P. tremuloides*) and black cottonwood (*Populus balsamifera* ssp. *trichocarpa*). Total stand basal area (Table 2) and stem densities were high: 1166 stems/ha with diameters >10 cm and 2676 smaller stems/ha.

We simulated development of the mature stand without silvicultural intervention (0% removal) and after four spatially different partial cutting treatments: (1) 40% removal across all species and diameters to create a thinned but still mostly full canopy stand with only single-tree gap openings; (2) 40% removal in sixteen $50\text{ m} \times 20\text{ m}$ (0.1 ha) small openings; (3) 40% removal in eight $50\text{ m} \times 40\text{ m}$ (0.2 ha) medium openings; (4) 40% removal in four $80\text{ m} \times 50\text{ m}$

Table 2

Initial basal area (m²/ha) in a mature northern temperate forest and predicted basal area after 100 years in uncut forest and after four spatial patterns of 40% basal area removal of canopy trees

Tree species	Matrix ^a				Stand ^b Planted spruce	Gaps only ^c Planted spruce	Stand total ^d All species
	Hemlock	Cedar	Other	All			
Starting conditions	36.1	18.6	10.4	65.1			
After 100-year simulation							
Uncut	28.1	15.8	2.9	46.8	0	na	46.8
Uniform	21.3	13.0	1.6	35.9	0.03	na	35.9
0.1 ha gaps	34.3	20.1	3.3	57.7	14.1	35.5	48.8
0.2 ha gaps	32.1	17.6	3.7	53.4	16.8	42.3	48.9
0.4 ha gaps	31.6	18.8	2.6	53.0	19.1	47.6	50.9

^a The forest matrix is all areas with retained canopy trees in each removal treatment, i.e., the entire area in the uncut and uniform removal treatments and the area between the gaps in the gap removal treatments.

^b Spruce basal area for the stand is averaged over the 4 ha simulation plot.

^c Spruce basal area in the logged gaps is given on a per hectare basis.

^d Stand total basal area is the basal area in each 4 ha simulation plot after 100 years.

(0.4 ha) large openings. Each simulation lasted 100 years.

The long axis of each cut opening was north–south to maximize light levels within each opening in these high latitude forests. Cut openings were equally spaced in each simulated stand (4 ha). Each simulated 4 ha plot was planted with 640 seedlings/ha, but in accordance with the spatial pattern of the logging. In the uncut forest (0% removal) and the 40% uniform removal treatments, planted spruce were evenly distributed over the entire four hectares. In the remaining treatments, spruce seedlings were planted only in cut openings at a density representing 1600 stems/ha in the 0.1, 0.2 and 0.4 ha openings—no seedlings were planted under retained canopy trees. A total of 2560 spruce seedlings were planted in each simulation.

The recruitment submodel was turned off for each simulation to ensure plot level results represented only the growth of the planted spruce trees and retained residual trees. We used neighbourhood growth functions to predict growth of residual western hemlock and western redcedar canopy trees (see Section 2.3), and growth rates estimated from re-measurement of permanent sample plots for other species. Hemlock and cedar represented 84% of the initial stand basal area. Use of this neighbourhood function allowed us to examine the effect of the spatial arrangement of tree removal on residual tree growth.

At each time step, the model predicted percent of full sunlight values at 1 m above-ground along a

2 m × 2 m grid covering the entire 4 ha, from which was calculated mean light under either a uniform canopy or within the individual cut openings. Also, we determined the total number of living planted spruce trees after each time step.

3.3.2. Results and discussion

The spatial pattern of tree removal (or retention) had a major impact on survival of the planted spruce seedling. All spruce seedlings planted in the undisturbed forest died early in the simulation. The uniform removal also did not create high enough understory light levels for the long-term survival of the planted spruce. Only 5.8% of the microsites received >12% full sunlight 5 years after tree removal. Hybrid spruce is intermediate in shade tolerance (Kobe and Coates, 1997; Klinka et al., 2000) and seedlings and saplings are considered in a state of suppression at about 12% full sunlight, with an expected mortality rate of 10% over a 3-year period (Wright et al., 2000). It is therefore not surprising that after 10 and 20 years only 23 and 3%, respectively, of the planted spruce seedlings had survived in the uniform 40% removal treatment. Spruce survival was much higher in gaps regardless of gap size. After 20 years 78, 87 and 86% of the planted spruce were alive in small, medium and large gaps, respectively. Light levels in small (0.1 ha), medium (0.2 ha) and large gaps (0.4 ha) 5 years after logging averaged 29, 44 and 55% of full sunlight, respectively. The simulation results are consistent with observed

mortality rates of planted spruce in understory and gap environments at the Date Creek experiment (Coates, 2000). Spruce density in gaps declined from 1600 seedlings/ha initially to 490, 545 and 570 trees/ha in small, medium and large gaps at 100 years, respectively.

Spruce basal area increased slowly with increasing gap size (Table 2). Spruce basal area in the 0.1 ha gap treatment was 84 and 75% of that in 0.2 and 0.4 ha gap treatments. Spruce basal area represented 29, 34 and 38% of total stand basal area in small, medium and large gap cuts, respectively at 100 years (Table 2). Total stand basal area was lower after 100 years than the initial starting level in all five treatments (Table 2), but we need to remember that the recruitment function was turned off. The uncut treatment lost 28% of its basal area over the simulation because of senescence mortality in large canopy trees.

The spatial pattern of tree removal affected growth of residual western hemlock and western redcedar adult trees. Hemlock and cedar adult tree growth was highest in the gap cutting treatments, with the best growth occurring in the small gap cuts (0.1 ha) (Table 2), where the highest level of edge environment was created.

The uniform removal treatment did not reduce crowding or shading sufficiently for residual trees to release and increase their growth rates. The combination of greatly improved survival of planted spruce in gaps and the release of adult hemlock and cedar adjacent to cut gaps explains the increased growth observed in the gap cutting treatments compared to the uniform removal or the uncut forest (Table 2).

4. Conclusions

Social, economic, and ecological considerations combined with management objectives determine the applicability of a silvicultural system for any given forest stand or group of stands, and also determine the desirable mix of systems within a landscape unit. One of the most fundamental challenges in developing new silvicultural systems is determining how the distribution of harvested and retained trees affects future stand composition, growth and development.

Predicting stand growth and development is an especially perplexing issue following partial cutting in complex structured mixed-species forests. Partial

cutting should accomplish at least one goal from a silvicultural perspective: (1) create good conditions for the establishment and growth of new trees; or (2) significantly improve the growing conditions of retained trees. Prescriptions that achieve both silvicultural goals, while meeting objectives attached to non-timber resource values, can be considered the ideal prescriptions. Our simulations focused on determining how silvicultural prescriptions in different forest types influence understory light levels, juvenile and adult tree growth, and stand dynamics.

Understory light availability is a good proxy for predicting juvenile tree growth in complex structured northern latitude forests (e.g., Klinka et al., 1992; Chen, 1997; Wright et al., 1998; Coates and Burton, 1999; Drever and Lertzman, 2001; Claveau et al., 2002). SORTIE/BC can predict light levels after any type of partial cutting, and it can be easily parameterized for different forest ecosystems (Canham et al., 1994, 1999; Beaudet et al., 2002). By simply predicting light environments, as in our example from temperate forests of southern Quebec, SORTIE/BC can be used to aid prescription development (e.g., minimum opening size) that will meet the known ecological requirements of different regenerating trees species.

Our three simulations clearly indicated that the species and spatial distribution of retained canopy trees should be a major consideration in harvest planning. Spatial pattern and tree species composition strongly affected understory light environment, regeneration survival, and stand-level growth in the simulated forest ecosystems. Uniform removal across a stand where all retained canopy trees were evenly distributed after logging appears to be most detrimental to newly regenerating trees, especially intermediate- to shade-intolerant species. For regenerating such species, patch applications should be favoured where defined openings are created in the tree canopy in order to optimize growth rates and encourage survival. By the same token, low uniform removal rates do not appear to create an environment where retained adult trees are effectively released.

We agree with various authors (e.g., Korzukhin et al., 1996; Landsberg and Gower, 1997) that traditional growth and yield models will continue to be more precise when addressing phenomena that fall within the range of conditions for which the empirical relationships were developed—generally single

species, even-aged management. These models, however, have considerable difficulty simulating complex silvicultural prescriptions for which there are no existing long-term experiments incorporating those treatments. Traditional forest ecology models were not designed to easily input forestry data or be readily used to address the management questions of foresters (Robinson and Monserud, 2002; Messier et al., 2003). Considerable effort has been put into SORTIE/BC to make the model suitable for addressing ecological and silvicultural questions of interest. The model can explore the consequences of a wide range of silvicultural strategies, at different spatial scales and over different time periods—an impossible undertaking for field-based research. The SORTIE/BC model approach is particularly well suited to addressing issues under the emerging natural disturbance- or ecosystem-based forest management paradigm.

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