

Consequences of various landscape-scale ecosystem management strategies and fire cycles on age-class structure and harvest in boreal forests¹

Andrew Fall, Marie-Josée Fortin, Daniel D. Kneeshaw, Stephen H. Yamasaki, Christian Messier, Luc Bouthillier, and Cheryl Smyth

Abstract: At the landscape scale, one of the key indicators of sustainable forest management is the age-class distribution of stands, since it provides a coarse synopsis of habitat potential, structural complexity, and stand volume, and it is directly modified by timber extraction and wildfire. To explore the consequences of several landscape-scale boreal forest management strategies on age-class structure in the Mauricie region of Quebec, we used spatially explicit simulation modelling. Our study investigated three different harvesting strategies (the one currently practiced and two different strategies to maintain late seral stands) and interactions between fire and harvesting on stand age-class distribution. We found that the legacy of initial forested age structure and its spatial configuration can pose short- (<50 years) to medium-term (150–300 years) challenges to balancing wood supply and ecological objectives. Also, ongoing disturbance by fire, even at relatively long cycles in relation to historic levels, can further constrain the achievement of both timber and biodiversity goals. For example, when fire was combined with management, harvest shortfalls occurred in all scenarios with a fire cycle of 100 years and most scenarios with a fire cycle of 150 years. Even a fire cycle of 500 years led to a reduction in older forest when its maintenance was not a primary constraint. Our results highlight the need to consider the broad-scale effects of natural disturbance when developing ecosystem management policies and the importance of prioritizing objectives when planning for multiple resource use.

Résumé : À l'échelle du paysage, un des indicateurs clés d'un aménagement forestier durable est la distribution des classes d'âges des peuplements étant donné qu'elle fournit un aperçu grossier des habitats potentiels, de la complexité structurale et du volume du peuplement et qu'elle est directement modifiée par le prélèvement de matière ligneuse et les feux de forêt. Nous avons utilisé un modèle de simulation spatialement explicite pour étudier les conséquences de plusieurs stratégies d'aménagement forestier à l'échelle du paysage en forêt boréale sur la structure des classes d'âges dans la région de la Mauricie, au Québec. Nous avons étudié trois stratégies de récolte (celle présentement utilisée dans la pratique et deux autres stratégies visant à maintenir les peuplements de fin de succession) et les interactions entre le feu et la récolte sur la distribution des classes d'âges des peuplements. Nous avons constaté que l'héritage laissé par la structure d'âge initiale de la forêt et sa configuration spatiale peuvent constituer des défis à court (<50 ans) et moyen (150–300 ans) termes pour arriver à concilier l'approvisionnement en bois et les objectifs écologiques. De plus, les perturbations dues aux feux, même avec des cycles relativement longs comparativement aux cycles passés peuvent compliquer encore davantage l'atteinte des objectifs de production de bois et de conservation de la biodiversité. Par exemple, lorsque le feu est combiné à l'aménagement, il y a des problèmes de récolte dans tous les scénarios avec un cycle de feu de 100 ans et dans la plupart des scénarios avec un cycle de feu de 150 ans. Même un cycle de feu de 500 ans entraîne une diminution de la vieille forêt lorsque son maintien n'est pas une contrainte principale. Nos résultats mettent en évidence la nécessité de considérer les effets à grande échelle des perturbations naturelles dans l'élaboration de politiques d'aménagement des écosystèmes et l'importance de prioriser les objectifs lorsqu'on

Received 21 February 2003. Accepted 2 June 2003. Published on the NRC Research Press Web site at <http://cjfr.nrc.ca> on 16 February 2004.

A. Fall,^{2,3} M.-J. Fortin,⁴ and C. Smyth. School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.

D.D. Kneeshaw, S.H. Yamasaki, and C. Messier. Groupe de recherche en écologie forestière interuniversitaire, Université de Québec à Montréal, Montréal, QC H3B 3H5, Canada.

L. Bouthillier. Département des sciences du bois et de la forêt, Université Laval, Québec, QC G1K 7P4, Canada.

¹This paper was presented at the 4th International Workshop on Disturbance Dynamics in Boreal Forests: Disturbance Processes and their Ecological Effects, held 9–14 August 2002, Prince George, B.C., and has undergone the Journal's usual peer review process.

²Corresponding author (e-mail: fall@cs.sfu.ca).

³Present address: 220 Old Mossy Road, Victoria, BC V9E 2A3, Canada.

⁴Present address: Department of Zoology, University of Toronto, Toronto, ON M5S 3G5, Canada.

planifie en vue d'un usage multiple des ressources.

[Traduit par la Rédaction]

Introduction

There is increasing pressure to manage forests for a variety of values, including economic production, ecological services, and social benefits (Côté and Bouthillier 2000; Hegan and Luckert 2000). Given that there may be a conflict in managing for some forest values, and since forests are inherently heterogeneous systems, meeting the breadth of values is likely only possible over large areas (Oliver 1992; Messier and Kneeshaw 1999). In addition, developing fully integrated and sustainable management plans requires information on long-term changes in landscape structure and function (Spies and Turner 1999). The space and time scales involved in assessing sustainable forest management strategies make landscape modelling an important tool for exploring alternative management options (Cissel et al. 1994).

Until recently, the boreal forest was mostly subjected to stand-replacing fire as the principal process of forest renewal (Johnson 1992; Payette 1992). As the boreal forest is increasingly subjected to pressure for timber production as well as conservation, foresters are exploring the possibility of managing forests within the "range of natural variability" (Cissel et al. 1994). This is the basis of the "natural disturbance paradigm", which attempts to reduce the impacts of human interventions on organisms and ecosystem processes by mimicking natural disturbances (Attiwill 1994; Lertzman et al. 1997; Kneeshaw et al. 2000b). This is based on the hypothesis that species present in a landscape evolved with natural disturbances and that maintaining the system within the bounds imposed by the natural regime may reduce the risk of ecosystem degradation (Galindo-Leal and Bunnell 1995; Gauthier et al. 1996; Landres et al. 1999).

The range of natural variability may be defined at the landscape scale for a variety of ecological indicators that capture patterns, such as patch size distribution and amount of edge, and proportions, such as species composition (Eng 1998; Kneeshaw et al. 2000a). Forest stand age-class structure, defined as the distribution of stand ages in the study area (as opposed to the distribution of tree ages within a stand), is one of the most critical and sensitive indicators, since it is correlated with many other biodiversity indicators (Franklin and Forman 1987; Gauthier et al. 1996), and it is strongly influenced by harvest rates (Daust 1994). Furthermore, together with disturbance intensity, species, and site characteristics (e.g., elevation, soil type), stand age forms a basis from which other indicators, such as volume, composition, and structural attributes (e.g., snags, coarse woody debris), are often estimated (Schoonmaker and McKee 1988; Daust 1994; Bergeron 2000). Thus, stand age-class structure is an important and relatively simple indicator allowing the incorporation of biological conservation in forest policy.

The range of forest stand age distributions resulting from natural regimes typically differs significantly from the range that is optimal for sustained-yield forestry, indicating a potential conflict in management objectives. Owing to the periodicity of fires and other agents of natural disturbance, and

variation in fuels across time and space, a landscape often has an uneven age-class distribution (Baker 1989; Parminter 1998). The age-class distribution of boreal landscapes of sufficient size may be approximated using an exponential distribution where the fire cycle is equal to the mean stand age (Van Wagner 1978). On the other hand, the maximum long-term sustained yield occurs when the age-class distribution is closer to a uniform distribution, so there is a discrepancy between the goals of timber extraction and biodiversity maintenance.

When forest management plans are developed, most planners and researchers ignore the possible synergistic effects between disturbance types on forest structure. As a result, forest managers have to readapt to postfire situations. Although information on the effect of fires is only possible over long time scales and across large spatial horizons, empirical studies are conducted on scales that do not permit an evaluation of these effects. There is therefore a need to explore interactions between natural disturbance and management regimes in the boreal forest to assist sustainable forest management and to integrate ecological and biodiversity management with timber management (Kneeshaw et al. 2000a, 2000c, 2000d). This requires projecting forest regeneration over large areas and long time frames, exploring interactions and feedbacks between fire and harvesting, and evaluating the impact of various management scenarios.

Our goal here was to explore the evolution of the forest age-class structure over time under various management options and their synergistic interactions with fire in the boreal forest of Quebec (Canada), expanding certain concepts explored by Van Wagner (1983) to the spatial domain. We contrasted a forest management strategy aiming to maintain timber supply with alternatives based on the ecosystem management proposals of Bergeron et al. (1999) and Burton et al. (1999), both of which specify target age-class structures that attempt to balance forestry and biodiversity objectives. This was achieved using models of timber harvesting that captured the essential landscape-scale aspects of these proposals and a spatial wildfire model based on fire history information. Hence, our models were not created to predict the state of the ecosystem but to test the feasibility of harvest regimes regarding impacts to timber and habitat supply with and without consideration of fire. Thus, the models were designed to show the possible compromises between timber yield and ecological objectives according to different harvest scenarios.

Materials and methods

Study area

The upper Mauricie study area is a boreal forest landscape of approximately 3.5×10^6 ha in south-central Quebec between 47.57°N and 49.08°N and 74.52°W and 73.45°W (Fig. 1). It is dominated by black spruce (*Picea mariana* (Mill.) BSP), which is the leading species on over 60% of

Fig. 1. Location of the study area in Quebec and harvest cost layer, where brightness increases with cost. The lowest cost area is towards the southeast, while higher cost is in the northwest, on islands in the Gouin reservoir (center), and on tree islands in bogs in the northwest. The white area on the lower right is outside the study area.

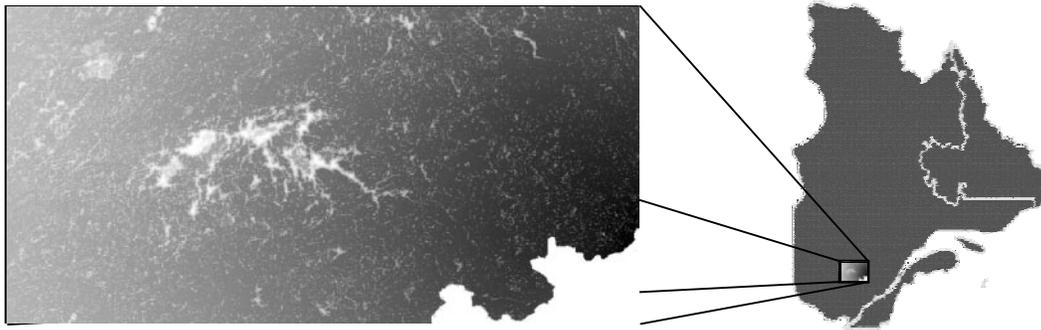
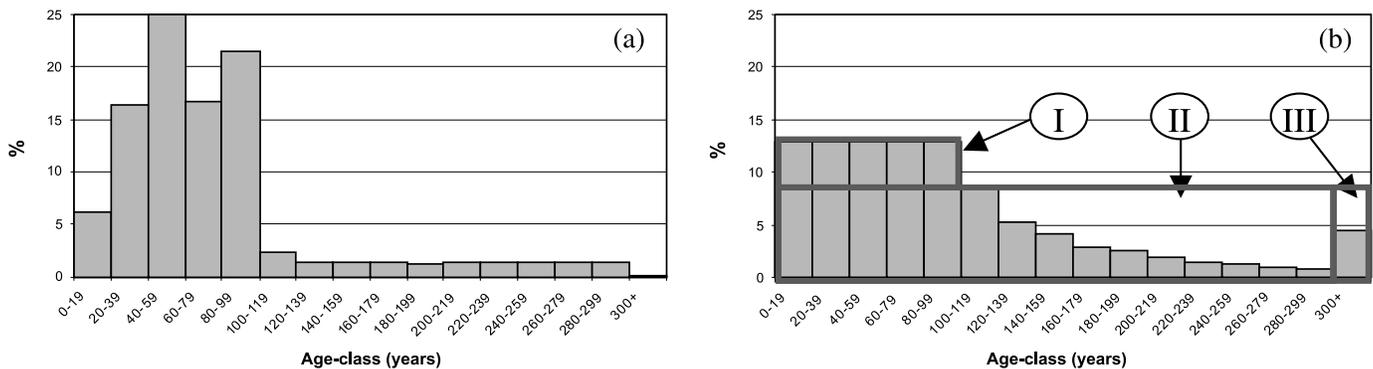


Fig. 2. Percentage of forest in the study area (percentage of 2 332 624 ha total forest area) for (a) initial age-class distribution and (b) emergent distribution under the status quo (SQ) scenario after 500 years of simulation. Three different zones (I, II, and III) emerge in the age-class structure under the SQ scenario as a result of interaction between harvest preference based on stand age and harvest cost as described in the Management-only scenarios section.



the landscape. Other important tree species include jack pine (*Pinus banksiana* Lamb.), balsam fir (*Abies balsamea* (L.) Mill.), trembling aspen (*Populus tremuoides* Michx.), and white birch (*Betula papyrifera* Marsh.). There are many lakes, wetlands, and bogs (approximately 18%, 12%, and 7% of the total area, respectively). Fire is the dominant natural disturbance agent, with most fires resulting in stand-replacing levels of mortality (Bergeron 2000). In the 1920s, large fires affected much of the area. Other disturbance agents include windthrow (Kneeshaw and Bergeron 1998) and spruce budworm, which causes varying levels of mortality primarily to balsam fir and to a lesser extent to black spruce. Commercial forestry has been taking place since the middle of the nineteenth century in the southern portion of the study area and since the second decade of the 20th century in the northern portion. Intensive forest management started in the 1950s and has continued until the present. Given the disturbance history of the upper Mauricie, the study area provides a good opportunity to explore the influence of natural and anthropogenic disturbance processes on forest structure at the landscape scale and to gain insight into the potential impacts of future forest disturbance on the sustainability of forestry in Canada.

Input GIS data

The primary source of spatial information was the SIFORT database (Bissonnette 2000), which provided data

at a resolution of 14 ha/cell (approximately 375 m × 375 m) for about 2 332 624 ha of forest. As the original data from Quebec's ministry of natural resources grouped forests over 100 years of age into a single age-class, we assumed a uniform distribution from 100 to 300 years (Fig. 2a).

We derived a "relative harvest cost" layer based on access to a mill to the southeast of the study area by assigning a cost value to each cell based on the distance to the southeast corner, with a 10-fold increase for water and bog cells to capture the increased road construction and maintenance costs associated with accessing islands in lakes and "tree islands" surrounded by bog (Fig. 1). Even though there are other mills in the region, our purpose of including a harvest cost surface was to explore how differential preference independent of stand age interacts with the harvesting regime. Note also that these harvest costs are different from the cost to timber supply that we identified in the various scenarios.

Submodel descriptions

We built submodels for management, wildfire, and succession processes, which interact through their links with the dynamic forest conditions, and all use an annual time step. Since our focus was on age-class structure effects, we were primarily interested in the processes of stand-replacing harvesting and fire and the stand aging component of succession. That is, disturbance resets stand age to 0, while aging increments stand age (up to 300 years). The succession

Table 1. Scenarios explored in this analysis (see text for scenario descriptions).

Scenario	Use harvest cost layer	AC target	Fire cycle
SQ	Yes	None	None, 100, 150, 200, 250, and 500 years
SQ (no cost)	No	None	None, 100, 150, 200, 250, and 500 years
AC Bergeron (hard)	Yes	Bergeron et al. 1999 or Fig. 3a	None, 100, 150, 200, 250, and 500 years
AC Bergeron (soft)	Yes	Bergeron et al. 1999 or Fig. 3a	None, 100, 150, 200, 250, and 500 years
AC Burton (hard)	Yes	Burton et al. 1999 or Fig. 3b	None, 100, 150, 200, 250, and 500 years
AC Burton (soft)	Yes	Burton et al. 1999	None, 100, 150, 200, 250, and 500 years
Wildfire	Not applicable	Not applicable	150 years

Note: SQ, status quo; AC, age-class.

submodel includes a semi-Markov-based species transition model, but since species does not influence the results presented, we do not discuss this here. Although our analysis concentrated on the aspatial age-class distribution, the spatially explicit aspects of fire and harvesting interact through the patchy structure of stand age.

We based our landscape-level fire model on disturbance history information for the neighbouring Abitibi region, which indicated a mean fire return interval (or “fire cycle”) of 122 years for the period 1850–1920 and 283 years post-1920 (Bergeron et al. 2001). Owing to uncertainty in the future fire regime, we investigated the effects of fire cycles by modelling cycles between 100 and 500 years but used 150 years as a reference level (Table 1). To model fire size, we used an exponential distribution with a mean of 1500 ha. A given fire cycle then determines the mean number of fires, which we also assumed was distributed exponentially. Thus, a 150-year cycle implies a mean of 10.37 fires/year. Since our focus was on the age-class structure, our results do not critically depend on the distribution of the expected area burned among fire size-classes. At the start of each year during simulation, the model selects the number of fires. The start location of each fire is chosen at random from the forested cells, and a size for the fire is selected. The fire spreads from a burnt cell to a random number of adjacent cells (at least one) to produce irregularly shaped patches with unburned remnants in patterns similar to real fires for the region and continues until the selected fire size is reached. In a more complex version of the model, fire behaviour is influenced by spreading fire-front intensity, fire weather, fuel estimates, species tolerance, and soil moisture. For the purposes of this paper, we did not apply the complex model so that fires burned independent of age, a common simplifying assumption for studies in boreal forests (Van Wagner 1978; Boychuk and Perera 1997).

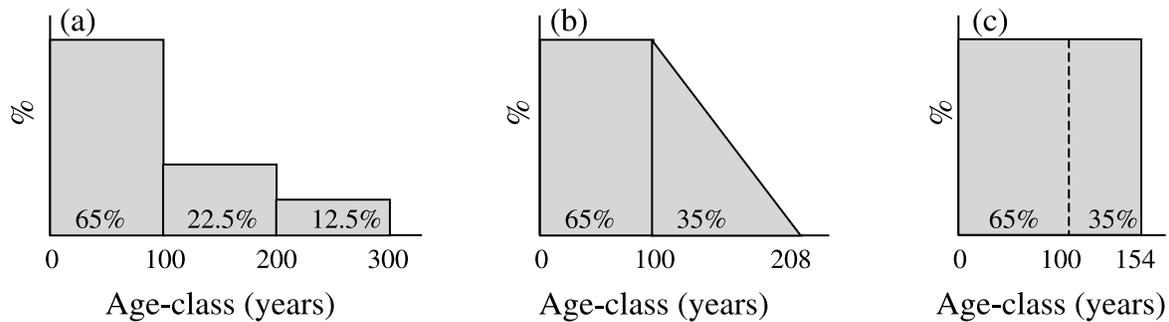
We used a number of scenarios (Table 1) to explore two main harvesting strategies. Status quo (SQ) harvesting is driven by a target annual percentage of the landscape to harvest. It is limited only by the minimum harvest age (MHA), which we set at 100 years for stands of all species mixes based on information from the Quebec ministry of natural resources (Pothier and Savard 1998). (MHA depends on site and species and can vary in the boreal forest of Quebec from 30 to 145 years. To simplify our analysis, we applied a single MHA across the landscape.) Although annual harvest targets are often volume based, our SQ scenario uses constant annual area and hence, volume may vary over time. We chose to use an area-based harvest target to facilitate the comparison of harvesting and fire for which data exist on an

area basis, to clarify the interactions between harvesting and fire, and to keep the model as simple as possible. The selection of starting locations for cutblocks was based on the harvest probability, generated within the model as the square of stand age divided by the harvest cost. Our goal was to reflect the trade-off between stand value and access cost when selecting the starting location for blocks. Block shape emerges based on a target size selected from a uniform distribution and landscape pattern surrounding the cutblock start location. We ran scenarios using size distributions of 60–120 and 250–1000 ha, typical lower and upper ranges for the region, and found that the results that we present are not sensitive to block size.

“Age-class targeted” harvesting includes the characteristics of the SQ strategy and additionally uses a target age-class (AC) distribution that specifies the desired proportion of the landscape in each 20-year age-class up to 300 years, which is considered very old in this forest type (Fig. 3). Achieving a target AC distribution can either take precedence or be secondary to achieving the annual harvest target, so we modelled this strategy in two different ways. First, as a hard constraint, the model attempts to reach the target AC structure as a primary goal, and so the annual harvest target may not be met if stands are “locked up” to maintain an age-class. That is, if the amount of forest in an age-class is less than or equal to the target, then no harvesting may take place in such stands. Second, as a soft constraint, the target AC structure is a secondary goal after assuring that the annual harvest target is met. For a cell from a given age-class, the age-class preference increases linearly with the amount of area that exceeds the target for that age-class. This age-class preference is combined with the age and harvest cost preference through multiplication. Our goal was simply to ensure that harvesting would tend to avoid areas that do not meet the target, unless such areas are needed to meet the harvest target. The distinction between the hard and soft constraints is meant to capture policy priorities: a higher priority is placed on biodiversity values using a hard constraint and on timber harvest values using a soft constraint.

In the AC-targeted harvesting strategy, we modelled two different target AC distributions (Fig. 3). The first was derived from Bergeron et al. (1999) and the second from Burton et al. (1999). We contrasted these with the uniform age-class structure that results if the forest is harvested in order of age (i.e., oldest stands first; Davis and Johnson 1987). The AC target proposed by Burton et al. (1999) was based on combining the exponential distribution produced by fires with the regular distribution better suited to timber production. After the MHA, the proportion in each age-class de-

Fig. 3. Targeted forest age-class (AC) distributions (in terms of percentage of total forest area): (a) Bergeron et al. (1999) and (b) Burton et al. (1999) contrasted with (c) a uniform distribution.



clines linearly. In the case of a 100-year MHA and a 0.65% annual harvest rate, this leads to a maximum age of just over 200 years.

While the SQ regime implicitly targets a uniform distribution (the so-called normalized or regulated forest; Davis and Johnson 1987), it does not directly target an age-class structure. In general, the resulting age-class structure is uniform up to the MHA but unspecified for older stands. A fully uniform distribution only results if the harvest rate is set to 1/MHA, which in our case would be a rate of 1%/year. For a harvest rate less than 1/MHA, the distribution of stands older than MHA emerges as a result of harvest preference, which in this case is based on age and harvest cost. The uniform distribution in Fig. 3 can also be viewed as the structure that results if the forest is managed using an SQ regime with an MHA of 154 years.

Since MHA is 100 years, the theoretical maximum sustainable rate of harvest is 1% of the total forested area per year. However, this level of harvest does not allow for alternatives other than SQ. We chose a harvest level of 0.65%/year (Fig. 3) based on the MHA, as suggested by Burton et al. (1999), resulting in a rotation of about 150 years. The method of Bergeron et al. (1999) suggests a harvest rate of approximately 0.49%/year for fire cycles of 150 years but 0.65%/year for fire cycles of 100 years. So an alternative motivation of our choice of harvest rates was to effectively apply MHA as a “target natural disturbance cycle” for these ecosystem management proposals instead of a maximum stand age according to the maximum sustained harvest level. This provides an important step towards integration of ecological values in management regimes and is consistent with our goal of showing the amplitude of the risk that follows from planning according to results of maximum yield without accounting for the natural cycle of fire. Didion (2002) explored the effects of varying this rate. The target ACs have mean stand ages of about 98, 79, and 77 years, respectively, for the distributions in Figs. 3a, 3b, and 3c.

The implication of a harvest rate below the theoretical maximum is that there is some flexibility in the system assuming that the only disturbance is logging. At this harvest level, 65% of the forest will be uniformly distributed between 0 and 100 years, as shown in all distributions in Fig. 3. One of our goals was to explore how the remaining 35% is distributed among age-classes under different logging regimes as well as interactions with fire. If we assume no fire disturbance, then this entire 35% will be distributed in age-classes over 100 years. At one extreme, 65% of the

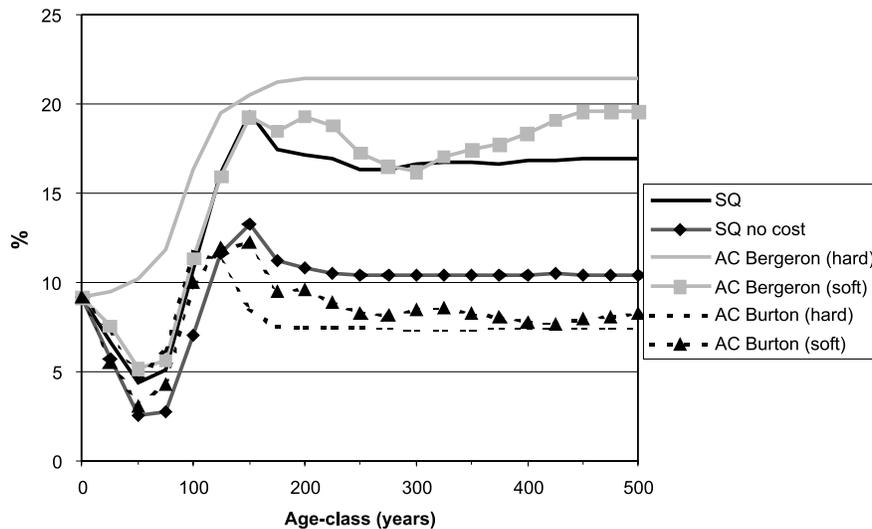
forest could be managed on a 100-year rotation with no harvesting in the remaining 35%, while at the other extreme, the entire forest could be managed on a 154-year rotation. When fire is included, it interacts with harvesting to distribute this 35% across a wide range of age-classes.

Model implementation, verification, and validation

We developed and implemented the Mauricie landscape model using the SELES (spatially explicit landscape event simulator) spatiotemporal modelling tool (Fall and Fall 2001). SELES combines a spatial database for a landscape with a high-level declarative modelling language used to specify key processes and a discrete-event simulation engine that interprets and executes such models.

We define “verification” as an assurance that the model is implemented as specified and “validation” as an assurance of the appropriateness of the model for its intended use (Rykiel 1996). That is, validation relates to the level of certainty that one can place in model outputs (i.e., the degree to which model results differ from expectations). The SELES modelling language creates transparent models that facilitate verification. We undertook a range of experimental tests and sensitivity analysis to ensure that the implemented model matched the conceptual model described (data not shown). Validation is often assessed as the degree to which model output matches an independent data set (Rykiel 1996). Although very useful, such empirical, or data, validation for a spatiotemporal model is only possible in cases with short time lags in system response or for which suitable replicates exist (e.g., for chronosequence type comparisons). Neither of these hold for situations involving regional-scale systems and long time horizons such as in the model we present. The exact conditions encountered within this system cannot be found outside the system (Levin 1992), and the long time lags inherent in the evolution of the age-class structure prohibit using a future state of the study area. In addition, observational data are not available for assessing hypothetical management alternatives. In the present study, it was more appropriate to rely on conceptual and logical validation (Rykiel 1996), where we viewed the model as a hypothesis and model output as a consequence of the hypothesis. That is, the purpose of the model was to make a clear link between the initial conditions, parameter values, and process behaviour and the consequences of those assumptions, which are projected via simulation (which in this sense is akin to theorem proving), and not to predict the real state of the future forest. Our approach to validation was extensive

Fig. 4. Time series showing mean percentage of forest older than 160 years (percentage of 2 332 624 ha total forest area) over the 10 replicates of 500 years under different scenarios. SQ, status quo; AC, age-class.



use of sensitivity analysis to ensure that this link between cause and effect can be clearly explained. For example, the fire-only scenario that we present effectively shows the expected consequence on age-class of the assumption of a fire regime driven by an input fire cycle with burning independent of age or species. Thus, logical validation inherently relies on the adequacy of the input information regarding initial conditions, model processes, and appropriate parameter values. Refinement of these will occur over time as ecological knowledge is refined as part of adaptive management.

Scenarios

We assessed the effects of a variety of scenarios, as summarized in Table 1. The name of the AC target scenarios indicates if the target was a hard or soft constraint. We ran each of the 37 scenarios 10 times for 500 years and analyzed the mean and variance of the age-class structure over time. We are interested in whether the harvest and AC targets can be met under various management alternatives and disturbance assumptions. To assess the impact of the harvest cost layer, we ran the SQ scenario with and without harvest cost. Given that AC-targeted harvesting will force dispersion of harvest activities to meet its objective, we expected that the impact of the harvest cost layer would be most evident with SQ logging.

Results

We graphed results to highlight changes in the age-class structure over time (as in Fig. 4) and at specific points in time (as in Fig. 5). The time series illustrates changes in the percentage of older forest (over 160 years) over time. We chose 160 years, as this is just above the effective rotation using a harvest rate of 0.65%/year. The time points highlight details of the transition from the starting to final age-class structure.

Management-only scenarios

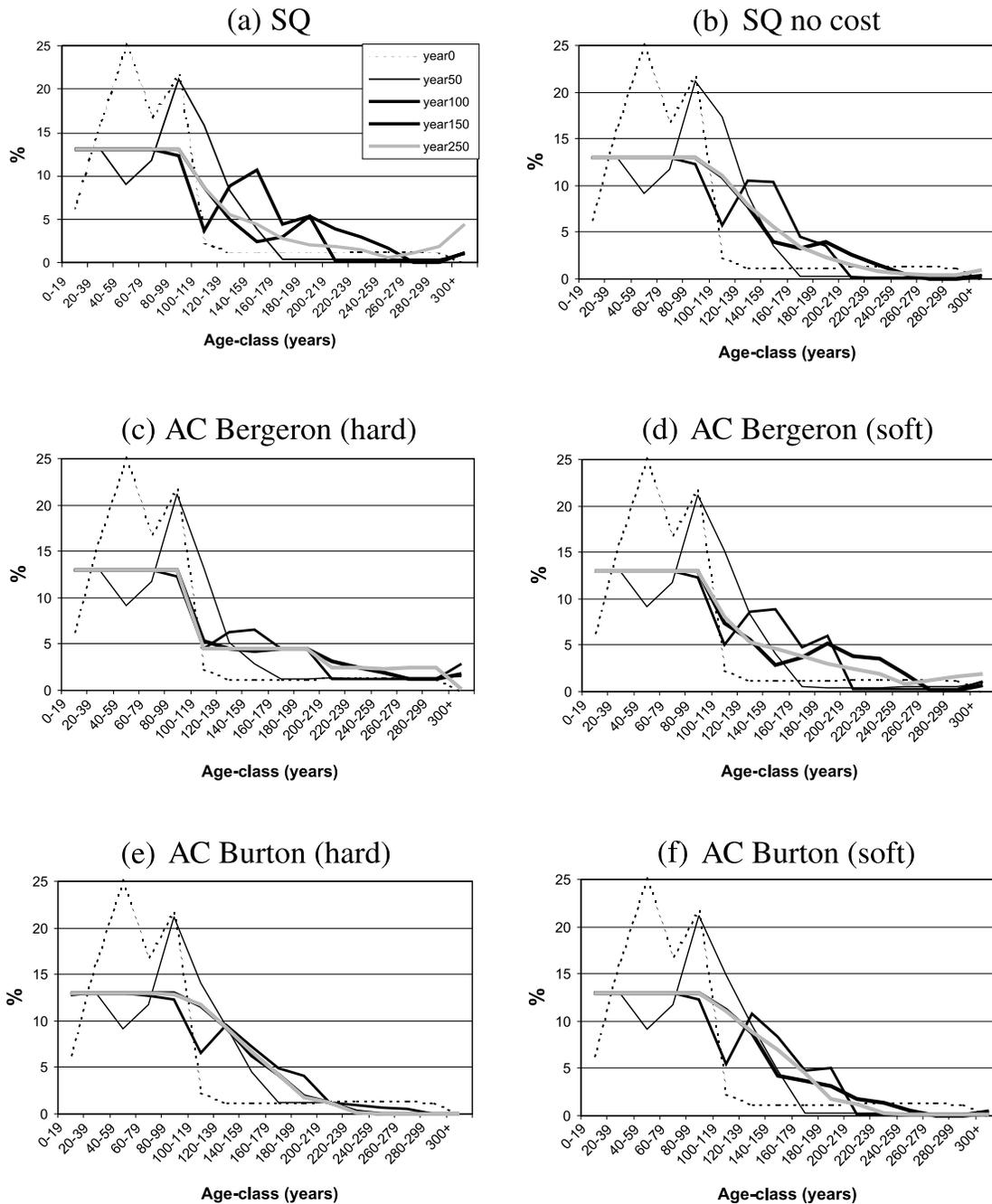
All scenarios take over a century to reach equilibrium,

ranging between 150 and 300 years (Fig. 4). Using a soft AC constraint for the AC Bergeron strategy, the system does not entirely stabilize in the 500-year time horizon. A bottleneck in forest over 160 years occurs around 50 years in all scenarios except for AC Bergeron with a hard constraint (Fig. 4).

In the SQ scenario, three zones emerge as a result of feedback between harvest target, age, and harvest cost (Fig. 2b): (I) a portion (approximately 23%) is harvested at the maximum rate according to the 100-year minimum rotation length, (II) a larger portion (approximately 72%) is harvested on increasingly longer rotations, lengthening with increasing cost, (III) a small portion (just under 5%) is not harvested at all (areas with very high cost). Thus, some full conservation (no harvest) areas may emerge under SQ harvesting provided that the harvest level is less than the theoretical maximum and that the managed area is large (see Discussion). The percentages depend on the strength of harvest cost relative to age in influencing harvest preferences. Disabling harvest cost significantly changes the results for older forest (Fig. 5b). The selection of harvest blocks based only on age in this scenario creates a declining age-class structure, with little forest over 240 years (<2.3%).

The AC Bergeron scenario results in an increased amount of forest over 200 years and a concomitant reduction in forest between 100 and 200 years (Fig. 5c). This strategy effectively results in the emergence of zones with different rotations: 100 years in low-cost areas, 200 years in intermediate-cost areas, and 300 years in high-cost areas. Since there is an initial deficit of older forest in the study area, all forest older than 200 years is locked up from the start, with more stands being recruited over time to meet the target. All hard AC scenarios had low variability between runs with a coefficient of variation of less than 0.1%. Using the target AC structure as a soft constraint results in more variability between replicates (coefficient of variation of about 2.5%). At years 150 and 250, there is a strong deviation from the target AC structure (Fig. 5d), and, as with the SQ scenarios, there is less older forest in the early part of the model runs (year 50) than in the long term.

Fig. 5. Mean percentage of forest by age-class (percentage of 2 332 624 ha total forest area) over 10 replicates for management-only scenarios at initial conditions and after 50, 100, 150, and 250 years of simulation. SQ, status quo; AC, age-class.



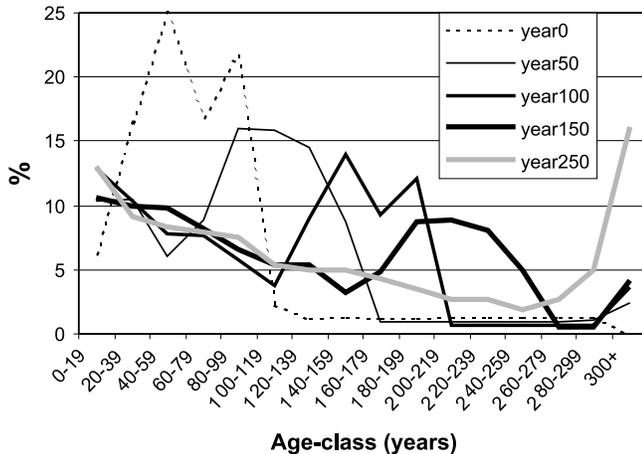
The AC Burton scenario produces significantly more forest between 100 and 200 years old than the SQ scenario but very little over 200 years (Fig. 5e). Owing to the gradually declining AC target for stands over 100 years, much less of the forest is harvested on a 100-year rotation (about 6.5%, with the balance managed on gradually increasing rotations), but the entire forest land base must be managed to meet the target. Unlike AC Bergeron, using a soft constraint for AC Burton gives results very similar to those for the hard constraint (Fig. 5f). The only significant difference is in the first few decades. Using a hard constraint reserves some forest up to 208 years, as shown by the age-class at year 50 in Fig. 5e.

Using a soft constraint, these older forests are harvested in the early decades, and by year 50, there is almost no forest over 160 years old. By year 100, conditions recover to those very close to the hard constraint.

Wildfire scenario

As designed, the fire model with a 150-year cycle produces an approximately exponential distribution with a mean age of 150 years (Fig. 6). Approximately 40% is over 160 years, with about 45% younger than 100, about 25% between 100 and 200, and 30% over 200. Since the fire model uses spatial spreading, the pattern of age patches across the

Fig. 6. Mean percentage of forest by age-class (percentage of 2 332 624 ha total forest area) over 10 replicates for wildfire-only scenario at initial conditions and after 50, 100, 150, and 250 years of simulation. The large percentage of forest in the oldest age-class is a result of not extending the tail of the distribution. This becomes even more pronounced after 500 years, as in Fig. 7a.



landscape is not random, with relatively more old stands in areas less connected to the forest matrix: on tree islands in bogs and on islands. Also, fires initiating in isolated patches (e.g., on islands) may not grow to the selected fire size. As a result, the actual fire cycle in this scenario, and in the other scenarios that include fire, is on average about 6%–8% longer than specified. In addition, the variability between runs is significantly higher than in the management-only scenarios (with a mean coefficient of variation of just over 20%). It takes about 300 years to reach equilibrium. Younger forest area diminishes through time (Fig. 6). Also, this figure contrasts starkly with the trends in all of the management-only scenarios shown in Fig. 5.

Combined management and fire scenarios

At long fire cycles (e.g., 500 years), the effect of how fire interacts with the SQ scenario is relatively minor, resulting in an increase in young age-classes at the expense of older age-classes (Fig. 7). This effect is amplified at shorter fire cycles, and little forest over 240 years remains even for a 250-year fire cycle. Harvesting and fire interact to produce an emergent age-class structure that combines the effects of these processes.

At long fire cycles (e.g., 500 years), interactions between fire and the AC Bergeron scenario produce an increase in the amount of young and intermediate-age forest at the expense of forest older than MHA (Figs. 8a and 8b). Old forest declines gradually as the fire cycle shortens. Using the AC target as a hard constraint maintains more forest in older age-classes than when the AC target is a soft constraint. This also leads to a significant harvest impact, as described in the next section. At fire cycles of 250 years and shorter, using a soft constraint results in an age-class structure similar to the SQ scenario (Fig. 7).

The effect of combining the AC Burton scenario with fire at long cycles (e.g., 500 years) is a reduction in forest of intermediate age (Figs. 8b and 8c). This effect is amplified at

shorter fire cycles. As with the AC Bergeron scenario, using a hard constraint maintains some degree of older forest, but at a cost to harvest levels (described in the next section), while using a soft constraint gives results almost identical to the SQ scenario.

Impacts on harvest target and older forest

Most of the scenarios were able to maintain the 0.65% annual harvest level over the entire time horizon in all runs without fire (Table 2). One exception is that the AC scenarios with hard constraints sometimes had periods when all merchantable forest was locked up, leading to a harvest deficit. Interestingly, the most constraining scenario, AC Bergeron, was always able to achieve the harvest target, whereas AC Burton maintained a mean level of 99.8% of the harvest target, with a low point of 72%.

When fire was combined with management, harvest shortfalls occurred in all scenarios with a fire cycle of 100 years and most scenarios with a fire cycle of 150 years. Combining the 154-year rotation specified by the harvest level with a 200-year fire cycle results in an overall disturbance cycle of about 87 years, which is under the MHA. The SQ and AC (soft constraint) scenarios were able to absorb a fire cycle of 200 years and still maintain the harvest level, since fires were assumed to burn independent of age. Enough forest aged beyond MHA of 100 years to satisfy the harvest request. At fire cycles of 100 years, harvest levels for these scenarios dropped to about 92%. Using the AC target as a hard constraint led to harvest shortfalls for all fire cycles.

Impacts on the age-class distribution are harder to summarize because of the difference in targets between scenarios. Table 3 shows the mean percentage, across all years and replicates, of forest over 160 years. We chose 160 years for illustration, although similar trends appear for other age thresholds. As these values are means over the entire horizon, the percentages reflect the transition from initial to equilibrium conditions. When fire is not included, the amount of older forest is driven by interactions between harvest cost, harvest rate, and the AC target. When fire is included, the amount of older forest declines rapidly as the fire cycle shortens for the SQ and soft AC constraint scenarios but much less so for the scenarios that apply a hard AC constraint. Even a long fire cycle of 500 years leads to a dramatic reduction in older forest in cases that do not enforce its maintenance.

Discussion

Options to shape the age-class distribution to achieve landscape-scale goals of ecosystem management are constrained by the legacy of past disturbance and harvesting (Wallin et al. 1994) and by the desired balance of costs and risks to timber production and ecological integrity. Since we used the same constant annual harvest rate (0.65%/year) and MHA (100 years) for all scenarios, the strategies effectively differed only in the preference criteria for selecting stands for harvest. The results give insight into interactions that are common for forests subjected to both management and natural disturbance and provide some general guidance on how management and fire regimes interact to produce an emergent age-class structure.

Fig. 7. (a) Mean percentage of forest by age-class (percentage of 2 332 624 ha total forest area) between simulation years 400 and 500 and over 10 replicates for status quo (SQ) harvesting with fire cycles of 100, 150, 200, 250, and 500 years and with fire alone (with a 150-year fire cycle). (b) The same distributions as an inverse cumulative (i.e., the percentage of forest in a given age-class and older).

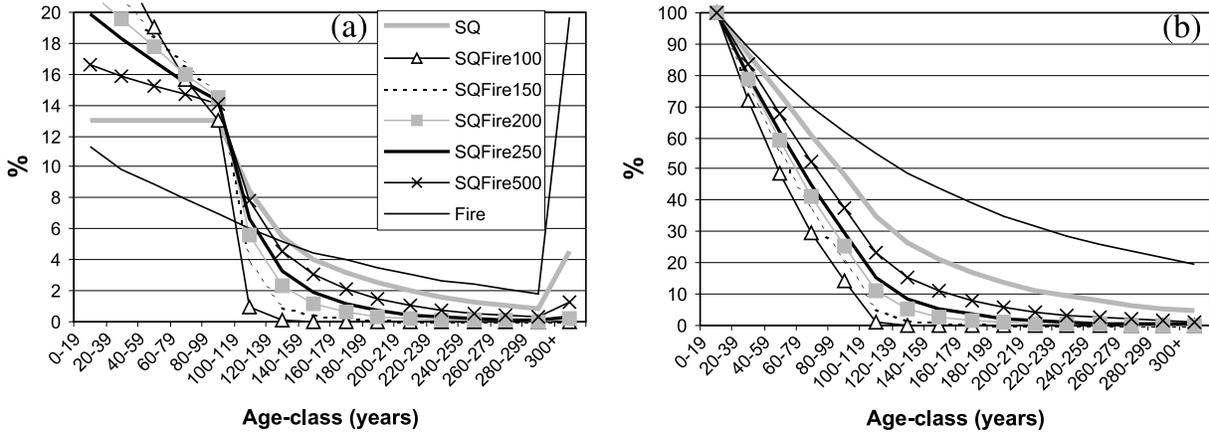
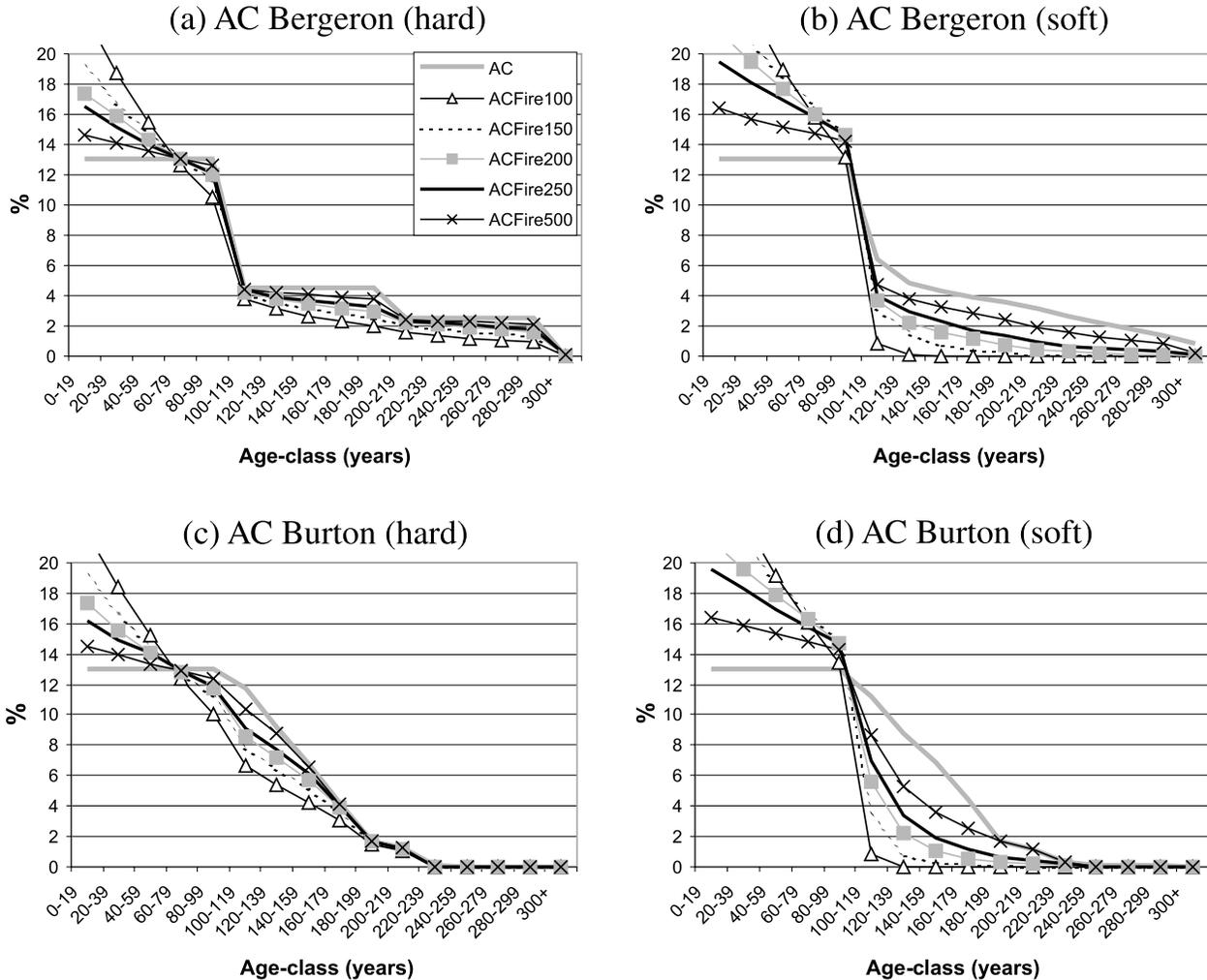


Fig. 8. Mean percentage of forest by age-class (percentage of 2 332 624 ha total forest area) between simulation years 400 and 500 and over 10 replicates for age-class (AC) targeted harvesting scenarios with fire cycles of 100, 150, 200, 250, and 500 years.



Assuming a spatially varying harvest cost, we show that an SQ regime in the absence of fire may produce an emergent age-class structure that maintains older age-classes without requiring additional rules. This is possible because

of the large management area plus the existence of a harvest cost gradient. The critical requirement is a reduction in harvest levels (i.e., to less than the theoretical maximum of 1/MHA) to provide enough flexibility to allow some stands

Table 2. Mean percentage of the annual harvest target (0.65%/year, 0.65% = 15 176 ha) achieved over the 10 replicates of 500 years under different scenarios (see text for scenario descriptions).

Scenario	Fire cycle (years)					No fire
	100	150	200	250	500	
SQ	91.9	99.9	100	100	100	100
AC Bergeron (hard)	54.6	65.9	72.3	78.0	88.8	100
AC Bergeron (soft)	92.2	100	100	100	100	100
AC Burton (hard)	44.6	59.7	68.7	74.0	86.0	99.8
AC Burton (soft)	92.1	99.9	100	100	100	100

Note: SQ, status quo; AC, age-class.

Table 3. Mean percentage of forest older than 160 years (percentage of 2 332 624 ha total forest area) over the 10 replicates of 500 years under different scenarios (see text for scenario descriptions).

Scenario	Fire cycle (years)					No fire
	100	150	200	250	500	
SQ	0.6	1.2	2.3	3.7	7.8	14.9
AC Bergeron (hard)	9.8	12.5	14.1	15.1	17.0	19.4
AC Bergeron (soft)	0.6	1.5	3.3	5.6	10.3	16.0
AC Burton (hard)	5.5	6.2	6.5	6.6	6.9	7.6
AC Burton (soft)	0.4	0.9	1.8	2.8	5.3	8.2

Note: SQ, status quo; AC, age-class.

to reach ages beyond the MHA. The emerging “no-harvest” areas are a result of applying management planning over large areas with spatial harvest cost. Hence, by the time harvesting commences in more costly regions, stands closer to the mill have reached the MHA. It is crucial to note that in smaller management areas, these no-harvest areas may not emerge. However, the high-cost areas that are not harvested tend to be in poorly accessible areas such as on islands in lakes and “forest islands” surrounded by bogs. While these forests are old, such forests may not meet all biodiversity objectives. In addition, these areas only emerge in the long run: there is less older forest in the early part of the horizon (year 50) than in the long term, possibly indicating a constrained period for wood supply. If we do not assume a harvest cost surface, stands are managed in the SQ scenario closer to the “effective rotation” specified by the harvest rate (e.g., $1/0.65\% = 154$ years), harvesting stands close to an “oldest-first” order. In this case, without additional constraints, few older stands are likely to persist on the landscape, which may lead to a significant loss of biodiversity (Berg et al. 1995). To achieve more old forest requires explicit management constraints for maintenance and recruitment of older age-classes that provide habitat for a range of species (e.g., pine marten; Thompson 1991).

The target ACs proposed by Burton et al. (1999) and Bergeron et al. (1999) both require a drop from the maximum theoretical harvest level, partly because we only considered the area harvested using conventional clear-cutting. Extended rotations result in an increased mean age harvested, which generally results in increased mean volume harvested and increased piece size. In addition, there is potential for selective partial harvest in older stands (Bergeron et al. 1999; Burton et al. 1999), creating opportunities to cre-

ate or enhance some stand structure attributes (Graham and Jain 1998). Together, these may offset the reduced annual harvest target. Our findings can also be viewed in terms of the TRIAD approach (Hunter 1990; Hunter and Calhoun 1996), in which a relatively small portion of the land is managed intensively to meet the reduced wood supply from protected areas and ecosystem management zones.

The AC Bergeron and AC Burton scenarios modify preferences to guide the AC towards the target distribution. Hard AC rules “lock out” stands required to meet the AC target, while soft AC rules apply an objective rather than a constraint. In these cases, the evolving age-class structure largely dominates the process. The AC Bergeron scenario initially reduces harvest of older stands and instead focuses effort on stands that are just over 100 years old. It is only after 300 years of simulation that there is any surplus of stands in the older age-classes. The AC Burton scenario follows a similar pattern, although actual age-class values change.

The issue of “landscape legacies” (Wallin et al. 1994) is highlighted by our findings. The cumulative impacts of past disturbance and management (logging, fire suppression, etc.) have resulted in the present age-class structure. This legacy may pose challenges and (or) opportunities for management objectives (Östlund et al. 1997). In all of the AC scenarios, there is a time lag of over a century before the targeted AC structure is reached, as there is a large discrepancy between the initial age-class structure and any of the target distributions. This long time lag required to shape the age-class structure implies a need for proactive management, since it has significant consequences for the stand ages and spatial pattern of harvest and may lead to a potential conflict between the harvest flow and target AC structure objectives. Given the uncertainty of changes in climate, economics, and social values over such a long time frame (Kaufmann et al. 1994; Chapin and Whiteman 1998), the focus should be on the transition period and how the current forest state can be shaped into a desired condition. If short-term costs (economic or ecological) are too significant, a plan is unlikely to be acceptable regardless of the long-term benefits. In the study area, the period 50 years in the future is most critical to conservation objectives, since all scenarios that do not specify hard AC targets pass through a phase of very little old forest on the landscape as the current old forest is depleted before the young crop ages into older classes.

The legacy effect and the value conflict are manifested in the hard versus soft AC constraints. Setting a target AC distribution as a hard constraint (i.e., a higher priority than the

harvest request) tended to reduce the time to equilibrium, but with an economic cost. The fact that harvest levels were even slightly below the target (above 99%) indicates difficulties in locating cutblocks. Given that the harvest target is already significantly below the theoretical maximum, further reductions may be unacceptable to industry and government. The differences between enforcing an AC target as a hard or soft constraint are highlighted when fire is included. At long fire cycles (which could occur if suppression is effective), fire has approximately the same impact on the two options. However, at shorter fire cycles, the soft constraint favours harvesting, with a dramatic reduction in older forest and resulting age-class structures for the AC scenarios that are very similar to the SQ scenario. The hard constraint, by affixing as an objective the transition of forest into old age-classes, may have an impact on timber supply but may also be essential to avoid extirpation of old forest dependent species.

A number of factors lengthen the time to reach a desired age-class structure. The closer a target AC is to the current conditions or to the conditions resulting from even-flow harvest, the shorter the time to equilibrium. The older the age-class is in a gap between current and target conditions, the longer it takes to fill. A deficit or surplus of young forest can be remedied in at most one rotation (100 years), but a deficit of 300-year old forest can take several rotations. This has serious implications for current harvesting strategies that call for the liquidation of "overmature" stands before other stands. Such a strategy not only seriously undermines a goal of sustainable resource use by eliminating a potential habitat type but also reduces future possibilities to reconstruct this habitat type.

Given the risk of fire in boreal forests (Payette 1992), planning forest management at the theoretical maximum harvest level poses a high risk to growing stock for future harvest as well as to ecological values, and so management plans should incorporate some flexibility to absorb natural disturbance (Boyчук and Perera 1997). A reduced harvest rate is the primary mechanism to do this. The scenarios that combine SQ harvesting with fire show that even a relatively low fire regime relative to the historical level can significantly reduce old forest. However, the burn rate can be quite substantial (close to the historical level in this case) before timber shortages occur. Given uncertainty in the long-term effectiveness of fire suppression and the consequent impact on fire cycles (Johnson 1992), selecting a fire cycle to use in planning should be done as part of a risk assessment. Assuming low values and ignoring variability inherent in a fire regime may indicate that management poses an unrealistically low risk to economic and ecological values.

We have also shown how SQ logging can cause significant departures from expected natural conditions for age-class structure, in particular a large reduction in older forests (Fig. 7b). Fire regimes at increasingly short cycles while leaving harvest rates constant move the age-class pattern further away from natural conditions. However, we did not include postfire salvaging in these models, clearly an important component of management in fire-prone ecosystems. Salvage could potentially offset this combined effect, provided that salvaged area is subtracted from green-tree harvest area. However, given that fires may burn stands too

young to be economically salvaged and that salvage is often a sporadic activity that may result in temporary increases in harvest areas to reduce unsalvaged loss, we suggest that the results presented provide a reasonable estimate of the expected interactions between fire and management regimes.

The inherent uncertainty in the timing or location of future fires implies a need for flexible policies. Two precautionary approaches can be taken. The first is to develop policies that explicitly incorporate and plan for wildfire. Explicitly incorporating uncertainty into a planning process is at odds with approaches commonly used for timber supply projections (Carson 1995) that only incorporate mean values. A second approach is to implicitly recognize that fire will occur and to set harvest targets that are below the theoretical maximum based at least in part on the past and present fire regimes. Ecological and economic risks must be weighed to determine how much flexibility should be incorporated into a management regime. Managing closer to the theoretical maximum may reduce short-term economic risk but increase long-term ecological, economic, and social risk. Using AC targets provides a means to incorporate coarse-filter landscape-level conservation objectives into management. Without these, old-growth forest will be reduced or disappear across much of the land base. Policies developed to integrate economic, social, and ecological values should be thoroughly assessed prior to implementation (e.g., using landscape simulation as we have done here) and ought to be linked to monitoring and adaptive management programs so that performance can be evaluated during implementation and refined if needed.

Acknowledgements

We would like to acknowledge support from the Natural Sciences and Engineering Research Council of Canada, the Simon Fraser University President grant (M.-J. Fortin), and the Sustainable Forest Management Network (part of the Networks of Centres of Excellence), the ministère des Ressources naturelles du Québec for providing the SIFORT_{MRN-DCF}, SIFORT_{SOPFEU}, SIFORT_{SOPFIM} data, and the use of facilities in the School of Resource and Environmental Management at Simon Fraser University.

References

- Attiwill, P.M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. *For. Ecol. Manage.* **63**: 247–300.
- Baker, W.L. 1989. Landscape ecology and nature reserve design in the Boundary Waters Canoe Area, Minnesota. *Ecology*, **70**: 23–35.
- Berg, Å., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M., and Weslien, J. 1995. Threat levels and threats to red-listed species in Swedish forests. *Conserv. Biol.* **9**: 1629–1633.
- Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. *Ecology*, **81**: 1500–1516.
- Bergeron, Y., Harvey, B., Leduc, A., and Gauthier, S. 1999. Forest management guidelines based on natural disturbance dynamics: stand- and forest-level considerations. *For. Chron.* **75**: 49–54.
- Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., and Lesieur, D. 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. *Can. J. For. Res.* **31**: 384–391.

- Bissonnette, J. 2000. Cartographie matricielle réalisée à partir du système d'information forestier par tessellation (SIFORT) du ministère des Ressources naturelles. Ministère des Ressources naturelles, Québec, Que.
- Boyчук, D., and Perera, A.H. 1997. Modeling temporal variability of boreal landscape age-classes under different fire disturbance regimes. *Can. J. For. Res.* **27**: 1083–1094.
- Burton, P.J., Kneeshaw, D.D., and Coates, K.D. 1999. Managing forest harvesting to maintain old growth in boreal and sub-boreal forests. *For. Chron.* **75**: 623–631.
- Carson, D.M. 1995. Timber supply analysis: an industrial model from British Columbia. *For. Chron.* **71**: 735–738.
- Chapin, F.S., and Whiteman, G. 1998. Sustainable development of the boreal forest: interaction of ecological, social and business feedbacks. *Conserv. Ecol.* **2**(2). Available on line at <http://www.consecol.org/vol2/iss2/art12>.
- Cissel, J.H., Swanson, F.J., McKee, W.A., and Burditt, A.L. 1994. Using the past to plan the future in the Pacific Northwest. *J. For.* **92**: 30–31.
- Côté, M.-A., and Bouthillier, L. 2000. Analysis of the relationship among stakeholders affected by sustainable development and forest certification. *For. Chron.* **75**: 961–965.
- Daust, D. 1994. Biodiversity and land management: from concept to practice. M.Sc. thesis, The University of British Columbia, Vancouver, B.C.
- Davis, L.S., and Johnson, K.N. 1987. *Forest Management*. 3rd ed. McGraw-Hill, Inc., New York.
- Didion, M. 2002. Improving forest management decisions by modelling landscape disturbance impacts on forest age structure dynamics. M.Sc. thesis, School of Resource and Environmental Management, Simon Fraser University, Burnaby, B.C.
- Eng, M. 1998. Spatial patterns in forested landscapes: implications for biology and forestry. In *Conservation biology principles for forested landscapes*. Edited by J. Voller and S. Harrison. University of British Columbia Press, Vancouver, B.C.
- Fall, A., and Fall, J. 2001. A domain-specific language for models of landscape dynamics. *Ecol. Model.* **141**(1–3): 1–18.
- Franklin, J.F., and Forman, R.T.T. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. *Landsc. Ecol.* **1**: 5–18.
- Galindo-Leal, C., and Bunnell, F. 1995. Ecosystem management: implications and opportunities of a new paradigm. *For. Chron.* **71**: 601–606.
- Gauthier, S., Leduc, A., and Bergeron, Y. 1996. Vegetation modelling under natural fire cycles: a tool to define natural mosaic diversity for forest management. *Environ. Monit. Assess.* **39**: 417–434.
- Graham, R.T., and Jain, T.B. 1998. Silviculture's role in managing boreal forests. *Conserv. Ecol.* **2**(2). Available on line at <http://www.consecol.org/vol2/iss2/art8>.
- Hegan, R.L., and Luckert, M.K. 2000. An economic assessment of using the allowable cut effect for enhanced forest management policies: an Alberta case study. *Can. J. For. Res.* **30**: 1591–1600.
- Hunter, M.L., Jr. 1990. *Wildlife, forests and forestry. Principles for managing forests for biodiversity*. Prentice Hall, Englewood Cliffs, N.J.
- Hunter, M.L., Jr., and Calhoun, A. 1996. A triad approach to land-use allocation. In *Biodiversity in managed landscapes*. Edited by R.C. Szaro and D.W. Johnstone. Oxford University Press, Oxford, U.K. pp. 477–491.
- Johnson, E.A. 1992. *Fire and vegetation dynamics: studies from the North American boreal forest*. Cambridge University Press, Cambridge, U.K.
- Kaufmann, M.R., Graham, R.T., Boyce, D.A., Moir, W.H., Perry, L., Reynolds, R.T., Bassett, R.L., Mehlop, P., Edminster, C.B., Block, W.M., and Corn, P.S. 1994. An ecological basis for ecosystem management. U.S. For. Serv. Gen. Tech Rep. RM-246.
- Kneeshaw, D.D., and Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. *Ecology*, **79**: 783–794.
- Kneeshaw, D.D., Leduc, A., Messier, C., Drapeau, P., Paré, D., Gauthier, S., Carignan, R., Doucet, R., and Bouthillier, L. 2000a. Developing biophysical indicators of sustainable forest management at an operational scale. *For. Chron.* **76**: 482–493.
- Kneeshaw, D.D., Messier, C., Leduc, A., Drapeau, P., Carignan, R., Paré, D., Ricard, J.-P., Gauthier, S., Doucet, R., and Greene, D. 2000b. Towards a sustainable forestry: a proposal for indicators of SFM based on natural disturbances. Sustainable Forest Management Network brochure. Available from http://sfm-1.biology.ualberta.ca/english/pubs/PDF/SP-kneeshaw_en.pdf [cited 1 September 2002].
- Kneeshaw, D.D., Yamasaki, S., Fortin, M.-J., Leduc, A., and Messier, C. 2000c. Développement d'indicateurs et d'outils d'évaluation de GDF à une échelle opérationnelle: un défi d'intégration. Part 1. *Aubelle*, **134**: 20–22.
- Kneeshaw, D.D., Yamasaki, S., Fortin, M.-J., Leduc, A., and Messier, C. 2000d. Développement d'indicateurs et d'outils d'évaluation de GDF à une échelle opérationnelle: un défi d'intégration. Part 2. *Aubelle*, **135**: 19–20, 25.
- Landres, P.B., Morgan, P., and Swanson, F.J. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecol. Appl.* **9**: 1179–1188.
- Lertzman, K., Spies, T., and Swanson, F.J. 1997. From ecosystem dynamics to ecosystem management. In *The rain forests of home: profile of a North American bioregion*. Edited by P.K. Schoonmaker, B. van Hagen, and E.C. Wolf. Island Press, Washington, D.C. pp. 261–382.
- Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology*, **73**: 1943–1967.
- Messier, C., and Kneeshaw, D.D. 1999. Thinking and acting differently for sustainable management of the boreal forest. *For. Chron.* **75**: 929–938.
- Oliver, C.D. 1992. A landscape approach: achieving and maintaining biodiversity and economic productivity. *J. For.* **90**: 20–25.
- Östlund, L., Zackrisson, O., Axelsson, A.-L. 1997. The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Can. J. For. Res.* **27**: 1198–1206.
- Parminter, J. 1998. Natural disturbance ecology. In *Conservation biology principles for forested landscapes*. Edited by J. Voller and S. Harrison. University of British Columbia Press, Vancouver, B.C. pp. 3–41.
- Payette, S. 1992. Fire as a controlling process in the North American boreal forest. In *A systems analysis of the global boreal forest*. Edited by H.H. Shugart, R. Leemans, and G.B. Bonan. Cambridge University Press, Cambridge, U.K. pp. 144–169.
- Pothier, D., and Savard, F. 1998. Actualisation des tables de production pour les principales espèces forestières du Québec. Ministère des Ressources naturelles, Forêt Québec, Québec, Que.
- Rykiel, E.J., Jr. 1996. Testing ecological models: the meaning of validation. *Ecol. Model.* **90**: 229–244.
- Schoonmaker, P., and McKee, A. 1988. Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. *For. Sci.* **34**: 960–979.
- Spies, T., and M., Turner. 1999. Dynamics forest mosaics. In *Maintaining biodiversity in forest ecosystem*. Edited by M.L. Hunter, Jr. Cambridge University Press, Cambridge, U.K. pp. 95–160.
- Thompson, I.D. 1991. Could marten become the spotted owl of eastern Canada. *For. Chron.* **67**: 136–140.

- Van Wagner, C.E. 1978. Age-class distribution and the forest fire cycle. *Can. J. For. Res.* **8**: 220–227.
- Van Wagner, C.E. 1983. Simulating the effect of forest fire on long-term annual timber supply. *Can. J. For. Res.* **13**: 451–457.
- Wallin, D.O., Marks, B., and Swanson, F.J. 1994. Landscape pattern response to changes in pattern generation rules: landscape legacies in forestry. *Ecol. Appl.* **4**: 569–580.