

Forest Ecology and Management 155 (2002) 369-385

Forest Ecology and Management

www.elsevier.com/locate/foreco

# Stand-landscape integration in natural disturbance-based management of the southern boreal forest

Brian D. Harvey<sup>a,\*</sup>, Alain Leduc<sup>b,1</sup>, Sylvie Gauthier<sup>c,2</sup>, Yves Bergeron<sup>d,1</sup>

<sup>a</sup>Unité de recherche et de développement forestiers de l'Abitibi-Témiscamingue,

Université du Québec en Abitibi-Témiscamingue, 445, boulevard de l'Université, Rouyn-Noranda, Que., Canada J9X 5E4

<sup>b</sup>Groupe de recherche en écologie forestière, Interuniversitaire (GREF-I),

Université du Québec à Montréal, C.P. 8888, succursale Centre-ville, Montréal, Que., Canada H3C 3P8 <sup>c</sup>Ressources naturelles Canada, Service canadien des forêts, Centre de foresterie des Laurentides,

1055 rue du P.E.P.S., Sainte-Foy, Que., Canada G1V 4C7

<sup>d</sup>NSERC-UQAT-UQAM Industrial Chair in sustainable forest management, C.P. 8888, succursale Centre-ville,

Montréal, Que., Canada H3C 3P8

#### Abstract

Forest ecosystem management, based partly on a greater understanding of natural disturbance regimes, has many variations but is generally considered the most promising approach to accommodating biodiversity concerns in managed forested regions. Using the Lake Duparquet Forest in the southeastern Canadian boreal forest as an example, we demonstrate an approach that attempts to integrate forest and stand-level scales in biodiversity maintenance. The concept of cohorts is used to integrate stand age, composition and structure into broad successional or stand development phases. Mean forest age (MFA), because it partly incorporates historic variability of the regional fire cycle, is used as a target fire cycle. At the landscape level, forest composition and cohort objectives are derived from regional natural disturbance history, ecosystem classification, stand dynamics and a negative exponential age distribution based on a 140 year fire cycle. The resulting multi-cohort structure provides a framework for maintaining the landscape in a semi-natural age structure and composition. At the stand level, the approach relies on diversifying interventions, using both even-aged and uneven-aged silviculture to reflect natural stand dynamics, control the passage ("fluxes") between forest types of different cohorts and maintain forest-level objectives. Partial and selective harvesting is intended to create the structural and compositional characteristics of mid- to late-successional forest types and, as such, offers an alternative to increasing rotation lengths to maintain ecosystem diversity associated with overmature and old-growth forests. The approach does not however supplant the necessity for complementary strategies for maintaining biodiversity such as the creation of reserves to protect rare, old or simply natural ecosystems. The emphasis on maintaining the cohort structure and forest type diversity contrasts significantly with current even-aged management in the Canadian boreal forest and has implications for stand-level interventions, notably in necessitating a greater diversification of silvicultural practices including more uneven-aged harvesting regimes. The approach also presents a number of operational challenges and potentially higher risks associated with multiply stand entries, partial cutting and longer intervals between final harvests. There is a need for translating the conceptual model into a more quantitative silvicultural framework. Silvicultural

\* Corresponding author. Tel.: +1-819-762-0971/ext. 2361; fax: +1-819-797-4727.

*E-mail addresses*: brian.harvey@uqat.uquebec.ca (B.D. Harvey), r13064@er.uqam.ca (A. Leduc), sgauthier@exchange.cfl.forestry.ca (S. Gauthier), bergeron.yves@uqam.ca (Y. Bergeron).

<sup>&</sup>lt;sup>1</sup>Tel.: +1-514-987-3000x4872; fax: +1-514-987-4647.

<sup>&</sup>lt;sup>2</sup> Tel.: +1-418-648-5829; fax: +1-418-648-5849.

trials have been established to evaluate stand-level responses to treatments and operational aspects of the approach. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Natural disturbance; Boreal forest; Silviculture; Management; Biodiversity

# 1. Introduction

The concept of ecosystem management in which regional natural disturbance regimes serve as a template for forest management has received considerable attention in many regions (Attiwill, 1994; Hunter, 1999). At the landscape level, maintaining ecosystem integrity implies maintaining structural and compositional patterns within the limits of historical variability of the regional mosaic produced under the natural disturbance regime (Mladenoff et al., 1993; Landres et al., 1999). At the stand level, ecosystem management promotes the use of silvicultural systems which are inspired by or closely resemble natural stand dynamics and in which maintaining structural and biotic attributes or legacies of natural stands is of primary importance (Franklin, 1993; Seymour and Hunter, 1999). In the boreal mixedwood forest where stand composition and structure change over time through canopy succession (Bergeron and Dubuc, 1989; MacDonald, 1995; Bergeron, 2000), the use of uneven management (partial and selective cutting) to mimic canopy succession and gradual stand break-up, and clear-cutting to reinitiate even-aged stands as an analogue to severe fire has been proposed by Bergeron and Harvey (1997). Similar "natural" silvicultural systems have been proposed for the mixedwood forest of the boreal plain by Lieffers and Beck (1994) and Lieffers et al. (1996).

Assuming that the historical natural disturbance regime for a region can be reconstructed and stand dynamics within that region can be determined, the objective of maintaining forest composition over the landscape under a management regime, while posing a considerable challenge to foresters, could constitute a primary component of a strategy for biodiversity maintenance. Gauthier et al. (1996) have demonstrated how regional site classification and an understanding of natural stand dynamics under varying fire cycles can provide forest composition targets for management. However, as even-aged forestry is the most common management approach applied in the Canadian boreal forest, maintaining an age-class structure under management similar to that under a fire-driven disturbance regime could be more problematic for two main reasons (Seymour and Hunter, 1999; Bergeron et al., 1999a). First, commercial rotation ages are generally shorter than mean length of natural disturbance cycle in the eastern boreal forest of Canada (Bergeron et al., 1999b). Full regulation of age class structure under a traditional even-aged forest regime has the potential effect of eliminating virtually all stands over the rotation age and reducing average stand age to somewhere between 40 and 60 years. Second, many boreal foresters have mistakenly equated rotation age with natural fire cycle, and assumed that, if not harvested, entire forest regions will inevitably burn before they reach over-mature or old-growth stages. However, if all forest stands share the same probability of burning, over one-third of a forested region should be occupied by stands older than the mean disturbance cycle (Johnson and van Wagner, 1985). Fire history studies in the boreal mixedwood region of northwestern Quebec and northeastern Ontario demonstrate that a significant portion of the forest in the region originates from fires dated to over 100 years B.P. (55%) and even to over 200 years B.P. (27%) (Bergeron et al., 1999b; Gauthier et al., 2000). An initial reading of this difference in age structure between a fully regulated forest and a boreal forest region driven by the natural fire regime would suggest that the latter is completely incompatible with conventional sustained-yield management under an even-aged regime. Faced with this problem, some ecologists (see Harris, 1984; Burton et al., 1999; Seymour and Hunter, 1999) have suggested zoning forest management areas into areas or units with different rotation ages, for example, ranging from 50 to 300 years. Bergeron et al. (1999a) have proposed, as an alternative solution, in which silvicultural treatments are varied in order to preserve composition and structure of over-mature and old-growth forests. It has become apparent that maintaining a significant proportion of the forest landscape in age classes that exceed conventional rotation ages, or creating assemblages of older stands through silvicultural interventions, without compromising allowable cut, constitutes the crux of the problem of sustainable forest management in the eastern boreal zone. Here we propose an approach that relies on diversifying silvicultural practices to maintain and promote compositional and structural forest diversity while keeping rotation ages similar to current values.

Using the southern boreal mixedwood forest as an example, this paper presents (1) the application of an approach used to set regional-level targets for forest composition and cohort proportions based on natural disturbance regime, forest ecosystem classification, stand dynamics and species life traits; (2) the development of silvicultural regimes that integrate natural stand dynamics as a means of maintaining regional-level objectives and certain stand-level ecological processes. Although we recognize the importance of the spatial aspects of natural disturbance-based management, our discussion here is limited to non-spatial elements.

# 2. Study area

The core area of application for the study is the  $80 \text{ km}^2$  Lake Duparquet Research and Teaching Forest (Harvey, 1999), located in the southern boreal forest of northwestern Quebec ( $48^{\circ}30'$ N,  $79^{\circ}20'$ W, altitude ca.300 m). The Lake Duparquet Forest is divided into two principal zones: a management zone, covering approximately 75% of the land base, in which a natural disturbance-based forest management plan is being implemented and a conservation zone (25%), containing a forest mosaic formed by a variety of site conditions and a disturbance history which includes eight major fires in the last 240 years (see map, Bergeron and Harvey, 1997). This zone, although only ca. 2000 ha, provides a reference for natural stand and, to a lesser extent, certain landscape features.

An ecological classification of a 350 km<sup>2</sup> area encompassing the Lake Duparquet Forest was undertaken by Bergeron et al. (1983). The area is characterized by the presence of extensive clay deposits originating from the proglacial Lake Barlow–Ojibway, and includes low rocky hills covered with reworked tills, as well as humid, organic soils and a variety of moisture class conditions. The climate is cold (annual average temperature 0.6 °C) and continental (annual average precipitation 822.7 mm). The Lake Duparquet Forest is located in Rowe's (1972) Missinaibi-Cabonga forest section, also classified as the Abitibi Lowlands Ecological Region (5a) in Quebec's western balsam fir-white birch bioclimatic domain (Robitaille and Saucier, 1998) Balsam fir (Abies balsamea (L.) Mill.) is the dominant species in mature forests and is associated with white spruce (Picea glauca [Moench] Voss), black spruce (Picea mariana [Mill.] B.S.P.) and white birch (Betula papyrifera Marsh). Northern white cedar (Thuja occidentalis L.) is also a late successional associate of balsam fir on mesic sites and is found on shorelines and rich organic sites in the Lake Duparquet area. Following fire, jack pine (Pinus banksiana Lamb.), trembling aspen (Populus tremuloides Michx.), balsam poplar (Populus balsamifera L.) and white birch form extensive monospecific or mixed stands. Eastern larch (Larix laricina [Du Roi] K. Koch.) grows on wet, organic sites in pure stands or in association with black spruce. Red pine (Pinus resinosa Ait.) is limited to isolated populations on islands and shorelines, occasionally mixed with white pine (Pinus strobus L.). Scattered white pine, remnants of larger populations that occurred between 6800 and 2200 B.P. (Bergeron et al., 1998), are associated with old black spruce stands on summits and escarpments.

#### 3. Conceptual framework and approach

Based on our understanding of landscape- and stand-level dynamics, we developed landscape-level objectives and silvicultural scenarios that integrate these two scales. Specifically, the method can be divided into five parts: (1) characterization of the historic natural disturbance regime; (2) forest ecosystem classification, characterization of stand-level dynamics and partitioning of stand development stages and forest types into three "cohorts" or phases; (3) establishment of forest-level objectives of composition and cohort structure; (4) development of a forest-level model that tracks age structure changes of dominant forest types and fluxes between forest types of different cohorts; and (5) employment of a variety of silvicultural treatments to attain landscape-level objectives of maintaining forest type diversity and cohort structure.

#### 4. Natural disturbance cycle

The regional fire regime is characterized by intense crown fires that cover large areas. Using charcoal analysis of pond sediment cores, Bergeron et al. (1998) have shown that large fluctuations in fire interval have occurred over the last 7000 years. These differences in fire cycle have been demonstrated, through pollen studies, to influence regional forest cover: late-successional species such as white cedar and white pine register higher pollen counts during periods of long fire intervals and early successional (post-fire) species such as white birch and jack pine show the opposite tendency. Using dendroecology and mapping, Bergeron (1991) and Dansereau and Bergeron (1993) estimated fire cycle in the area of the Lake Duparquet Forest at 63 year before 1870 and over 99 year since 1870. Although eight major fire events have occurred in the Lake Duparquet Forest since 1760, the fire cycle continued to increase during the 20th century. Recent studies covering a 16,000 km<sup>2</sup> area that includes the Lake Duparquet Forest have shown large temporal variations in fire cycle (Bergeron et al., 1999b; Bergeron, unpublished results). Nonetheless, mean forest age (MFA), as evaluated by time since fire, is estimated around 140 years and, at scales  $> 5000 \text{ km}^2$ , has remained relatively constant during the past three centuries.

The spruce budworm (Choristoneura fumiferana [Clemens]) is the other dominant natural disturbance agent in the southern boreal region. The budworm is a defoliator that feeds primarily on fir and, to a lesser extent, on spruce. The occurrence of three budworm outbreaks in this century has been documented for the area by Morin et al. (1993). The interrelationships between fire cycle, forest composition and spruce budworm outbreaks have been treated by Bergeron and Leduc (1998). Because longer fire intervals tend to increase the proportion of later successional stands over the landscape, stands which are generally dominated by budworm-susceptible fir and spruce, low fire frequency will tend to create a forest cover that is more vulnerable to the spruce budworm. Outbreaks of the budworm in the southeastern boreal forest have the

regional-scale effect of reducing the softwood component and increasing the mixedwood proportion of the forest (Bergeron and Dansereau, 1993).

#### 5. Forest classification and successional patterns

Forest ecosystem classification and natural canopy succession following fire have been extensively studied in the region (Bergeron et al., 1983; Bergeron and Dubuc, 1989; DeGrandpré et al., 1993; Bergeron and Charron, 1994; Leduc et al., 1995; Paré and Bergeron, 1995; Grondin et al., 1999; Bergeron, 2000). Post-fire succession on sites having a potential vegetation of balsam fir-white birch is characterized by pioneer stands of intolerant hardwoods, primarily trembling aspen and balsam poplar although jack pine and white birch stands also occur, especially on coarser textured soils and thin tills (Fig. 1A-D). Shade-tolerant fir and spruce usually seed in either at the same time as the faster growing pioneer species or regenerate under these developing stands by seed from proximate sources (Galipeau et al., 1997; Greene et al., 1999). As a result, stands of shade-intolerant species are gradually replaced, over a period of 75-125 years, by mixedwood stands as mortality creates gaps and the softwood understory attains the canopy. These stands eventually develop into balsam fir-spruce-white cedar associations, with a certain hardwood component maintained in local gaps and by relatively long-lived birch (Kneeshaw and Bergeron, 1998). As tree mortality during budworm outbreaks tends to be greatest in these late-successional, fir-dominated stands, stand structure and composition are radically altered in the event of a severe outbreak as the fir component is transformed over a period of 5-10 years into standing and fallen coarse debris (Bergeron et al., 1995). In the absence of fire, fir-spruce stands with heavy budworm-induced mortality can either develop a mixedwood composition or rebuild into softwooddominated stands.

On poorer sites, the potential vegetation is characterized by late-successional stands of black spruce. Xeric sites are characterized by pioneer stands of seedorigin jack pine and black spruce that will initially form pure or mixed, even-aged stands. Short fire intervals favor recurring jack pine (or white birch) where pine is present with or without black spruce.

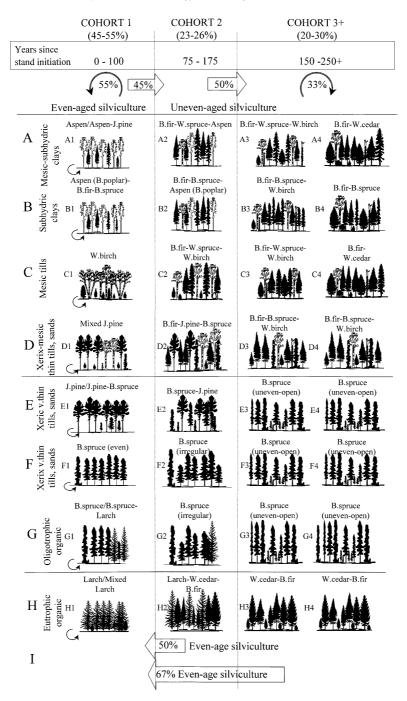


Fig. 1. Schematic profile of dominant forest types applied to the cohort system. Stand development and uneven-aged silviculture on a given site type (A–H) progresses from left to right whereas severe disturbance and even-aged silviculture; (I) revert stands to cohort 1 on left. Refer to Table 2 for treatment explanations.

Longer intervals result in jack pine or mixed pine– spruce stands developing into uneven-aged black spruce (Bergeron and Dubuc, 1989) (Fig. 1E and F).

Pure or mixed, even-aged stands of black spruce and eastern larch establish after fire on hydric soils. Possibly because of its superior growth after establishment, larch often forms the dominant layer in a twolayer canopy with black spruce. In the absence of fire, these sites tend to develop into uneven-aged stands, and eventually open black spruce stands (Fig. 1G). Northern white cedar is found on richer hydric soils and on mesic to subhydric sites in association with balsam fir in late-successional stands (Fig. 1A–C and H). The use of decayed nurse logs for seedling establishment and an avoidance of deciduous litter may explain why white cedar is most frequently found in mid- to late-succession stands on these latter sites (Simard et al., 1998).

#### 6. Cohort characterization

Because disturbance history and site conditions influence the forest landscape composition, speciesspecific attributes need to be put in context with these factors. An understanding of species life traits such as reproductive modes, shade tolerance, soil and site requirements and longevity, provides a partial explanation of not only the spatial distribution of tree species and associated forest types but a temporal portrait of their presence through time since disturbance (Table 1).

While recognizing that within-site stand dynamics can be highly variable, we subjectively classified dominant forest types, identified from inventory, into one of three successive cohorts, roughly corresponding to early-, mid- and late-successional phases of stand development (Bergeron et al., 1999a). In their present form, cohorts are more an ecological concept, based primarily on stand age, composition and structure, rather than strict mensurational or silvicultural units. Nonetheless, they are based on a number of previously cited ecological studies undertaken in the Lake Duparquet Forest area, and others (Lavertu et al., 1994; Kneeshaw and Bergeron, 1999) as well as on regional forest ecological classification work by the Quebec Ministry of Natural Resources (Grondin et al., 1999).

Stands of fire-adapted, pioneer species constitute the first cohort. These include stands of jack pine, trembling aspen, balsam poplar and white birch which tend to dominate over the first 100 years following fire (Fig. 1A-E). On mesic sites spruce and fir that have either regenerated immediately after fire or have gradually seeded in following stand establishment are more abundant in the understory than in the canopy of the first cohort. Black spruce and larch are considered first-cohort species on humid, organic sites (Fig. 1F-H). The middle part of this first phase is characterized by self-thinning mortality and the latter part by initiation of stand break-up. In the second cohort, stands generally consist of two components: surviving canopy stems from the first cohort and either (1) tolerant softwoods that were present in the understory in the first cohort, or (2) other softwood or hardwood stems that have been recruited into the understory and gaps. Consequently, the second cohort represents a mid-successional phase of 75-175 years where mixed stands dominate on mesic and mesic-hydric sites. The second cohort of seed-origin black spruce stands are characterized more by a change in stand structure, typically changing from an even-aged to an irregular structure, than by a change in stand composition. The conjuncture of the second and third cohorts (conceptually, the passage from mid- to late-successional phases) is less evident than that of the first and second. Certainly, by the beginning of the third cohort at about 150 years, virtually all first-cohort canopy trees should have been eliminated through natural mortality. Cedar, a late successional species found in second-cohort understories, is associated with fir and, to a lesser extent spruce, in third cohort canopies on mesic to subhydric sites. The third cohort time interval is not inherently discrete and, for conceptual purposes, incorporates stands at the tail end on the age structure curve. At any moment throughout succession, an intense crown fire will have the effect of reverting most stands to first-cohort forest types because of the fire adaptations of the tree species making up this cohort (Table 1).

# 7. Setting forest-level objectives based on the natural disturbance cycle

A principal forest-level objective for the Lake Duparquet Forest is to maintain an approximation of forest composition and cohort structure similar to

	White birch	Trembling aspen	Jack pine	Eastern larch	Balsam fir	White spruce	Black spruce	Northern white cedar
Primary reproductive mode after fire <sup>a</sup>	Seed, stump sprouts	Root suckers	Seed	Seed	Seed	Seed	Seed	Seed
Regeneration time after fire <sup>a</sup>	Rapid	Rapid	Rapid	Rapid	Variable (gradual)	Variable (gradual)	Rapid or gradual	Long
Reproductive mode in absence of fire <sup>a</sup>	Seeding in gaps	Suckers in gaps, seed	Little regeneration	Little regeneration	Seeding in understory	Seeding in understory	Layering	Seeding and layering
Shade tolerance <sup>a</sup>	Intolerant	Very intolerant	Very intolerant	Very intolerant	Very tolerant	Intermediate	Tolerant	Tolerant
Dominant site types <sup>b</sup>	A–D	A–C	A, C–F	B, G, H	A–D, H	A–C	B–G	А–С, Н
Rotation age (maximum tree age) (years) <sup>c</sup>	60–90 (235)	50-90 (170)	50-90 (240)	70–120 (180)	50-90 (145)	70–110 (230)	80-130 (240)	80-160 (920)
Importance <sup>d</sup>								
First cohort	•	•	•	•			●, ▲	
Second cohort	0		•	0	<b>O</b> , <b>A</b>	<b>O</b> , <b>A</b>	<b>O</b> , <b>A</b>	<b>)</b> , <b>(</b>
Third cohort	•				●, ▲	D, 🔺	●, ▲	●, ▲

Table 1 Life traits of the major tree species of the southeastern boreal region and their relation in the cohort structure

<sup>a</sup> Source: Burns and Honkala (1990).

<sup>b</sup> Refer to Fig. 1.

<sup>c</sup> Maximum tree age (rounded to nearest 5) from studies undertaken in the Lake Duparquet region. Note: values are intended to provide an indication of potential species longevity, rather than maximum stand longevity. Values may differ from those reported elsewhere.

<sup>d</sup> Each cohort refers to a broad temporal phase in stand succession (see text). •: Dominant in canopy; O: sub dominant in canopy; ): present in canopy; A: present in understory.

conditions that, theoretically, would be observed under the influence of the natural disturbance regime and historical legacies and in the absence of management.

### 7.1. Cohort objectives

Because of the historic variability in the regional fire cycle (Bergeron et al., 1998, 1999b) and the fact that current forest composition is a product of both the disturbance regime and climatic and disturbance factors that have prevailed over previous centuries, targeting a particular fire cycle, as a forest-level objective, is highly questionable (Armstrong, 1999). As a case in point, at least three major changes have occurred in fire cycle in the study region during the last three centuries. However, the time periods during which these changes have occurred are so short that regional forest age structure does not have time to reach equilibrium with each fire cycle. In contrast to aiming for a specific fire cycle, targeting a regional mean forest age (MFA of ca. 140 years) at least partially incorporates historical variations in disturbance cycle. Thus, to some extent, MFA provides a means of incorporating the variability of both past and present fire cycles and its use in defining forest-level age structure objectives assures inclusion of older stands in the forest mosaic. Targeting a fully regulated, even-aged forest age-class structure with a mean age of 140 years is not, however, a realistic option in the eastern boreal forest because of the relatively short biological rotations of the commercial tree species. Rather, we propose that MFA serve as a target fire cycle for the negative exponential age structure model (Fig. 2A). The proportion of the forest mosaic to be targeted for each of the three cohorts is then derived from the fire cycle and the mean maximum age at harvest (Bergeron et al., 1999a).

This forest cohort structure objective is in effect a compromise between full regulation and the negative exponential age structure (Fig. 2C). Using a fire cycle of 140 years, corresponding to mean forest age, and a range of stand break-up varying from 80 to 110 years, we estimate that roughly 45–55% of the management zone should consist of first-cohort forest types, 23–26% of second cohort types and 20–30% of third+ cohort forest types (The "+" indicates that a minor portion of third cohort stands should be treated by selection cuts (or left untreated) to generate fourth

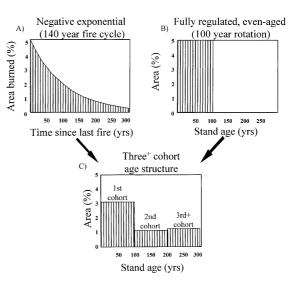


Fig. 2. Comparison of three theoretical forest age structures: (A) negative exponential under natural disturbance regime; (B) full regulation even-aged management on 100 year rotation; (C) targeted age structure comprised of third+ cohorts. (Adapted from Bergeron et al., 1999a).

cohort stands). While the fire cycle target should remain relatively stable, the ranges for each cohort are meant to provide some flexibility in implementing management. These percentages do not include the conservation zone (25% of the total forest area) or riparian buffers, unproductive and inaccessible zones which will not be harvested.

#### 7.2. Forest composition objectives

The method of developing forest composition objectives based on natural fire regime has been described in detail by Leduc et al. (1995) and Gauthier et al. (1996). Based on regional site classification, forest dynamics and age structure modeling, the approach produces forest composition models under different fire cycles and regional site conditions. Moreover, using the Shannon diversity index and a coarse forest classification containing four types (hardwood, mixed hardwood, mixed softwood and softwood), these authors estimated that maximum forest type diversity would occur at fire cycles between 100 and 150 years in the study area. While recognizing that forest types do not necessarily incorporate all the complexities of forest ecosystems, the objective of maintaining forest type diversity represents a manageable surrogate to maintaining ecosystem diversity.

The forest-level composition objective for all dominant forest types consists of the proportion of forested area to be occupied by each type. Having established the cohort objectives for the management zone, the proportion that should be occupied by each forest type is determined by weighting by dominant site types. For example, having established that approximately 50% of the management zone should be occupied by the first cohort, and given that about 57% of the zone is occupied by mesic and hydric clays (Fig. 1A and B), then, at first glance, roughly 28.5% of the management zone should be occupied by the aspen-dominated forest types associated with the these site types. However, because we know that other firstcohort forest types are found on these sites, including jack pine and white birch associations, this value is intended to provide a general objective rather than a strict target. Maintaining forest type diversity is dependent on assuring that (1) all representative forest types are continually present on the landscape and (2) the relative area occupied by each forest type (all age classes combined) approximates the forest-level objective. Given the limited area of the Lake Duparquet Forest, it is virtually impossible to integrate forest-level spatial configuration of fire disturbance into harvest planning. (In the surrounding region, over 50% of the area burned has occurred from fires that were larger than the entire Lake Duparquet Forest (Bergeron et al., 1999b) and Johnson et al. (1998) have reported similar fire size distributions for the western Canadian boreal forest). Because attaining the theoretical equilibrium of landscape composition and age structure may be possible only at larger spatial scales (e.g.  $>5000 \text{ km}^2$ ), the Lake Duparquet Forest is meant to serve as a small-scale demonstration of the approach.

Maintaining forest type diversity by this approach requires regulating the forest such that each firstcohort forest type eventually becomes fully regulated (even-aged) up to harvest age according to the target proportion for the forest, and that second- and thirdcohort forest types also become proportionally distributed in terms of time since last fire or clear-cut. The reason for this distinction between stand age for the first cohort and time since fire or clear-cut for forest types of the succeeding cohorts is that the age structure in older stands does not necessarily correspond to time in years since disturbance. In maintaining a resemblance to "natural" forest age structure, "age" thus refers to the number of years since clear-cut or other even-aged harvest or fire. Notwithstanding biophysical differences that exist between the impacts of fire and clear-cut harvesting (Keenan and Kimmins, 1993), notably in terms of standing and fallen residuals, the point here is that clear-cutting (and its variations), contrary to partial cutting, have the effect of reinitiating secondary forest succession.

# 8. Favoring fluxes between forest types of different cohorts

Managing for all forest types on the landscape is probably impossible without exploiting natural stand dynamics. Having determined the relative importance of dominant site types and established forest composition objectives for the entire management area, it is necessary to define the "rate of flow" between cohorts of the various site types. This step underlines the concern for maintaining ecological processes associated with succession (Kimmins, 1997), notably non-catastrophic disturbances, species replacement, mortality, and recruitment (Kneeshaw and Bergeron, 1998, 1999) and soil processes involved in organic matter accumulation and nitrogen dynamics (Brais et al., 1995; Paré et al., 1993).

Globally, fluxes between cohorts are determined as a function of composition and age structure objectives, average harvest age and fire cycle. Because harvesting and recruitment rates of different forest types are interdependent, we developed an area-based forest model that simulates fluxes within and between forest type matrices (Harvey and Leduc, 1999). The nonspatial, forest-level model consists of a series of transition matrices (one for each forest type) that track change in age-class structure (% area per age class), in 5 year increments, over a 150 year simulation period. For a given forest type, initial values of percent area represent current age class structure. End values aim for roughly equal area of that type in all age classes, the sum of which should equal the forest type's total area objective. The matrices indicate at what period harvesting and recruitment should occur and over how

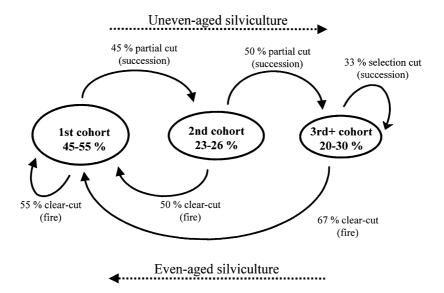


Fig. 3. Conceptual forest model of cohorts and fluxes. See Fig. 1 for forest types included in each cohort and Table 2 for treatments proposed to control fluxes.

much area in order to move from the present age structure and area to the desired conditions for each forest type. Each matrix also identifies fluxes between forest types, that is, periods at which (1) area in the 0–5 year age class of one forest type is generated by the harvesting of another forest type and (2) area harvested in a mature age class of one type generates a corresponding area in the 0-5 year age class of another forest type.

The cohort structure determines the rate of recycling of the first cohort and of the other fluxes between cohorts. The shorter the targeted fire cycle, the greater the proportion of the first cohort on the landscape and the more generalized is the application of even-aged management. With a longer fire cycle target, a greater portion of the landscape should be occupied by forest types of cohorts second and third+ and more uneven-aged silviculture is necessary to generate the fluxes between succeeding cohorts. For the management zone of the Lake Duparquet Forest, roughly 55% of first-cohort forest types (30% of this zone) should be "recycled" through even-aged management and 45% (25% of management zone) should be treated to develop toward second-cohort forest types; half of harvested second-cohort forest types should be recycled into the first cohort and half into the third cohort; and 67% of third cohort forest

types should be recycled into the first cohort and 33% should be treated to maintain third+ cohort characteristics (Fig. 3). These inter-cohort fluxes and recycling rates provide the means of controlling proportions of each cohort around target values.

#### 9. Implementation at the stand level

Table 2 and Fig. 1 provide the conceptual silvicultural framework for applying the approach and illustrate how stand-level silviculture is used to attain forest-level objectives of forest type diversity and cohort structure. This model, as a first step, is meant to provide a general framework rather than strict guidelines based on stand and site inventory and precise silvicultural criteria. Globally, 55% of the management zone should be treated by even-aged silviculture and 45% by uneven-aged silviculture. Just as first-cohort forest types usually self-recruit following fire (e.g. jack pine and black spruce from seed or aspen from root suckers), about 55% of first-cohort forest types should be harvested using even-aged silviculture when stands reach maturity (Fig. 1, A1-H1). Although natural regeneration is preferred, harvesting and regeneration treatments may include clear-cutting, shelterwood and seed tree variations (Graham and Jain, 1998) Table 2

A1	Regeneration cut: clear-cut with 4-8% retention of intolerant hardwood (clumps or scattered) and clumps of softwood
4.2	regeneration; natural regeneration primarily by aspen suckering
A2	If tolerant softwood understory stocking <60%, plant white spruce in understory at 35–50 years; succession cuts (i) High partial cut 70–80% of intolerant hardwood stems with maximum protection of softwood component;
	(i) Figh partial cut 70–80% of intolerant hardwood stems with maximum protection of softwood component; residual hardwood stems are not harvested
	(ii) Low or free partial cut 40–50% of merchantable intolerant hardwood stems with maximum protection of
	softwood component; most residual hardwood stems are harvested in $10-20$ years
A3	Succession cut: late summer—fall group or individual selection cut favoring merchantable balsam fir over spruce;
AJ	site disturbance to enhance fir and spruce establishment
A4	Succession cut: selection cut spruce and fir
B1	Regeneration cut: clear-cut with 4–8% retention of intolerant hardwood (clumps or scattered) and clumps of
21	softwood regeneration; natural regeneration primarily by aspen suckering
B2	If tolerant softwood understory stocking <60%, plant white or black spruce in understory at 35–50 years; succession cut: as in A2
B3	Succession cut: late summer—fall group or individual selection cut favoring merchantable balsam fir over spruce; site
00	disturbance to enhance fir and spruce establishment
B4	Succession cut: selection cut spruce and fir
C1	Regeneration cut: clear-cut with 4–8% retention of birch (clumps or scattered) and clumps of softwood regeneration;
C1	natural regeneration primarily by stump sprouting of birch (coppice)
C2	If tolerant softwood understory stocking <60%, plant white spruce in understory at 35–50 years
02	Succession cut: thin stump sprouts to 1–3 dominant stems per stump at 35–50 years
C3	Succession cut: late summer—fall selection cut of birch sawlogs at 75–120 years; site disturbance to enhance fir and
00	spruce establishment
C4	Succession cut: selection cut spruce and fir
D1	Regeneration cuts
51	(i) Clear-cut and plant jack pine, black spruce (3:1 or 4:1)
	(i) Clear-cut with on-site delimbing and retention of 20 seed-tree stems/ha; control burn for jack pine regeneration;
	black spruce may be manually seeded; precommercial thin to 3000 stems/ha. (note: clear-cut may be preceded
	by commercial thinnings
D2	Succession cuts: modified shelterwood to favor spruce establishment and growth or low to free partial cuts (25–45% thinnings)
	of jack pine stems with maximum protection of shade-tolerant softwoods. Second thinning and final cut over 10–25 years
D3	Succession cut: final selection cut of jack pine and dominant fir and spruce
D4	Succession cut: selection cut spruce and fir and birch sawlogs
E1	Regeneration cut: summer clear-cut with on-site delimbing and 5-10% retention of dispersed clumps of jack pine;
	natural regeneration by seeding from limbed jack pine branches, or seed or plant
E2	Succession cut: same as D2; maximum protection of black spruce stems
E3	Succession cut: final selection cut of merchantable jack pine stems
E4	Succession cut: selection cut of merchantable black spruce stems
F1	Regeneration cut: summer strip or patch clear-cut with on-site delimbing; retention of 10% irregular clumps in cuts on very tills
F2	Succession cut: partial cut 35–45% of dominant stems
F3	Succession cut selection cut of merchantable stems
F4	Succession cut: selection cut of merchantable stems
G1	Regeneration cut: alternate careful logging for advance regeneration protection with clear-cutting, controlled burning
	or mechanical site preparation, planting or seeding
G2	Succession cut: partial cut 35–45% of dominant stems, favoring larch if present
G3	Succession cut: selection cut of merchantable larch and black spruce stems
G4	Succession cut: selection cut of merchantable black spruce stems
H1	Regeneration cut: alternate careful logging for advance regeneration protection with clear-cutting, controlled burning
	or mechanical site preparation, planting or seeding
H2	Succession cut: partial cut 35–45% of dominant stems, favoring larch if present
H3	Succession cut: final selection cut of merchantable larch and fir
H4	Succession cut: final selection cut of merchantable cedar and fir
I	Clear-cut (or other even-age treatment of) second and third+ cohort stands for recruitment into first cohort. If
	natural regeneration is inadequate, stand establishment is achieved by site preparation and seeding or planting

<sup>a</sup> (Refer to Fig. 1) note that treatments are intended as examples of possible interventions rather than precise silvicultural prescriptions.

with or without subsequent mechanical site preparation or prescribed fire and seeding or planting. Stands in this category are not geographically fixed; that is, a site on which a stand is clear-cut at age 60 may be managed through a longer subsequent rotation (and vice versa).

During periods through forest rotation when there is not enough area of a given first-cohort forest type to self-recruit, second- or third-cohort stands on the same site type serve as source-stands for regenerating the first cohort. This can be done naturally, for example, by clear-cutting mixed (second and third cohort) forest types on mesic clay sites with at least a minor aspen component to regenerate sucker-origin, aspen-dominated stands (Lavertu et al., 1994; Weber, 1990). Alternately, second- and third-cohort forest types that do not regenerate naturally into the first cohort after final harvest will require treatment for artificial stand establishment.

Certain mid- to late-successional forest types can not be "constructed" within a single normal rotation after fire but similar structural and compositional characteristics may be created by applying a series of interventions including partial and selection cutting, underplanting over an extended period and maintaining residual structures. Forest types of second and third+ cohorts are not intended to substitute for overmature and old-growth forest contained in reserves or conservation areas. Rather, they are meant to assure that structural and compositional approximations of these ecosystems are maintained on the managed landscape. Moreover, because a portion of first-cohort forest types are treated by partial cutting to develop into successive cohort forest types, inevitably forest types of the older cohorts have to serve as source stands for recruitment of first cohort types.

First and second-cohort forest types are sources for second- and third-cohort types. Under the natural disturbance regime, a portion of first-cohort forests escapes being killed by fire and evolves toward a second-cohort character. Similarly, under this management regime approximately 45% of first-cohort forest types are intended to be treated by partial cutting to permit their development into mixed, second-cohort stands. Partial cutting of shade-intolerant first-cohort species to generate second- and third-cohort stands should, to some extent, resemble natural dynamics (Kneeshaw and Bergeron, 1998) and lead to the creation of stand conditions similar to those

of over-mature and late-successional stages. For example, partial cuts of first-cohort stands simulate partial stand break-up of post-fire stands and increase stem diameter diversity by reducing the proportion of mature first-cohort stems (Buongiorno et al., 1994). Similar fluxes that are consistent with and reflect sitespecific natural dynamics can occur between secondand third-cohort stands. Partial succession cuts (Fig. 1, A2–H2) are prescribed for about 25% of forest area whereas selection succession cuts (Fig. 1, A3–H3, A4–C4), are prescribed for only about 19% of the forest.

# 10. Implications for management

#### 10.1. Forest-level planning

The approach developed for the Lake Duparquet Forest constitutes a significant departure from conventional boreal forest management at both the stand and forest levels. At the general management planning level, reference to the regional disturbance regime is increasingly expected of managers when identifying forest-level objectives and silvicultural systems to be employed. In terms of general management planning, however, the emphasis we place on maintaining a third+ cohort structure and forest types associated with early-, mid- and late-successional phases on the landscape contrasts with conventional objectives of regulating the forest toward an even-aged structure with mean forest age of 40-60 years. Moreover, clear definition of regional forest composition objectives based on the natural disturbance regime and regional ecological classification (Gauthier et al., 1996), is not yet standard practice for public forest land in Canada.

Using the natural disturbance regime as a template for forest management does of course present a number of challenges. Historical reconstruction studies of disturbance regimes in different regions have shown that natural disturbance cycles tend to vary widely over long time scales and that past conditions do not necessarily reflect those of the future (Millar and Woolfenden, 1999), a fact that has implications for the establishment of forest-level composition and age structure objectives. But although some authors would suggest that the very existence of historic variability undermines the natural disturbance-template paradigm (Armstrong, 1999), managers will generally be more comfortable with a cautious range of landscape-level objectives based on an understanding of historic natural variability in disturbance regime than a constantly moving target or a target situated outside the range of natural variability (Landres et al., 1999). The use of mean forest age appears to be a good compromise as a basis for a fire cycle target and subsequent cohort distribution in the southeastern boreal forest. MFA is easier to estimate than the fire cycle and potentially less variable in time. It partially incorporates natural variation in fire cycle (in our case, for a period covering about the last 300 years) and, as such, attempts to address the problem of selecting a "natural benchmark period" for the fire unq cycle objective. Moreover, in the context of an increasing fire cycle, due largely to anthropogenic effects on climate, the use of 140 years as a fire cycle succe objective represents a pondered adhesion to the concent Wa recognize howaver that although mean

(in our case, for a period covering about the last 300 years) and, as such, attempts to address the problem of selecting a "natural benchmark period" for the fire cycle objective. Moreover, in the context of an increasing fire cycle, due largely to anthropogenic effects on climate, the use of 140 years as a fire cycle objective represents a pondered adhesion to the concept. We recognize, however, that although mean stand age might be relatively constant over large areas (despite constant change in disturbance cycle), forest age structure does not necessarily follow a negative exponential distribution. Nonetheless, whatever the natural age distribution, over large areas in the eastern boreal forest it invariably includes stands of various ages-young, mature and old-and the cohort concept based on the negative exponential may constitute the best operational framework for maintaining all these parts in the managed forest.

The impacts of this approach on annual allowable cut have not been evaluated, but preliminary results from a similar cohort-based project north of Lake Duparquet conclude that the effect is not significant.<sup>3</sup> It should be emphasized, moreover, that forest types designated to be harvested in the first cohort can be intensively managed to maximize fiber production and compensate for reductions due to the creation of reserves as well as possible reductions due to the use of uneven-aged silviculture. In such a case, intensively managed first-cohort forest types could be considered to correspond to the high timber yield component of Seymour and Hunter's (1992) Triad concept, just as the conservation zone constitutes the reserve portion.

# 10.2. Stand-level management

The conceptual basis of this approach also demands a certain amount of innovation at the stand level. Although boreal silviculture in Canada has evolved over the last 30 years, from extensive management with minimal regeneration investment, to plantation silviculture, and later to "careful logging" aimed at protecting advanced natural regeneration, it has largely remained even-aged. Given the general severity of fire disturbance in the boreal forest, the fire adaptations of several commercial species, and the fact most boreal species have relatively short biological rotations, this has a reasonably sound, although unquestionably flawed ecological basis. The problem lies in not recognizing that: (1) significant portions of the eastern Canadian boreal forest do not inevitably succumb to fire within the period of a commercial forest rotation; (2) fire severity is in fact highly variable and that this has consequences for natural stand structure and composition; (3) over-mature and late-successional forest types constitute an integral component of boreal ecosystem diversity and can not be recreated within a single even-aged rotation; and (4) some tree species, forest types and possibly animal and plant species benefit from long intervals between catastrophic disturbances. Hence, both the key and one of the major challenges to this approach lie in diversifying silvicultural practices from those that are strictly even-aged (and consist primarily of careful logging and clear-cutting) to incorporate uneven-aged silvicultural systems, as well as other even-aged treatments involving some temporary or long-term retention, such as shelterwood and seed-tree systems.

Although a forest type does not necessarily constitute an ecosystem, maintaining regional forest type diversity does reflect the essence of the coarse filter approach to maintaining biodiversity. Diversifying silvicultural treatments constitutes part of a promising strategy for maintaining ecosystem diversity in the boreal forest where increasing rotation lengths, as proposed elsewhere (Seymour and Hunter, 1999), may not be possible due to the limitations of tree species longevity and effects on allowable cut. However, in targeting area ranges for each cohort and cover type, and in attempting to harness site-specific dynamics, it is also clear that the use of silvicultural interventions must go beyond the relatively straight-

<sup>&</sup>lt;sup>3</sup> Thuy Nguyen, personal communication (thuy.nguyen@uqat.uquebec.ca).

forward task of growing trees efficiently to harvest age. This has considerable implications for harvesting and regeneration regimes. Partial cutting requires more finesse in execution and thus greater investment in operator training and development of smaller machinery designed for multiple, low-impact stand entries. Uneven-aged silvicultural systems should also exploit the full ecophysiological elasticity of individual species (Messier et al., 1999), particularly in terms of the species' reproductive modes, shade tolerance and longevity.

Because partial and selection cutting probably present greater risks of treatment failure than conventional harvesting and regeneration, this approach is not without perils. High stocking levels and volumes generally achieved by plantation forestry provide a challenging reference for fiber production by unconventional methods. Moreover, alternative silvicultural approaches, involving repeated partial harvesting entries and extended rotations through the second and third cohorts, present a certain risk of increased volume losses due to stem and root damage, insects, fungal diseases, windthrow and natural mortality. This said, integrating high fiber yield silviculture in management of first cohort standsand even in partial cutting regimes-is not incompatible with this approach and could, in fact, compensate for potential losses incurred through the uneven-aged component of this management regime.

While ostensibly aimed at benefiting forest biodiversity, the approach does provide a number of other advantages that are not apparent under conventional management. Partial cuts are undertaken at intervals shorter than even-aged rotations and can have the positive effect of increasing unit log value, thus offsetting possible higher harvesting costs (Lämås et al., 1996). They can also increase non-timber values such as habitat for song bird populations (Norton and Hannon, 1997), recreation and other uses. Partial cutting in the boreal mixedwood forest maintains mixed stand types that might otherwise be partitioned into either hardwood or softwood trajectories (Bergeron and Harvey, 1997). Creating and maintaining a proportion of the landscape in mixed stands may have positive effects on renewal of seed banks and natural regeneration establishment (Kneeshaw and Bergeron, 1996, 1998) on site productivity (Longpré et al., 1994; Man and Lieffers, 1999) and soil nutrient quality (Paré et al., 1993; Brais et al., 1995; Paré and Bergeron, 1996). Forest-level quotas for mixedwood stands and retention of a portion of the intolerant hardwood component through second and even third cohorts may also have positive effects on epiphytic diversity as well as other components of biodiversity. Finally, using partial cutting to extend the interval between clear-cutting events permits the replenishment of soil nutrient capital (Kimmins, 1977) while clearcutting and site preparation of older, third cohort stands should have the effect of rejuvenating soil by increasing summer soil temperatures, soil microbial activity (Fox et al., 1986; Lundmark-Thelin and Johansson, 1997) and nutrient mineralisation (Vitousek and Matson, 1985; Prescott et al., 2000).

#### 11. Research needs and development

As field application of this approach is only in its third year in the Lake Duparquet Forest, most of the proposed silvicultural scenarios have not been tested for all forest types and specific silvicultural guidelines have yet to be developed. One of the inherent problems with this approach in its current form is that the cohort system is based both on time since last major disturbance (or stand age) and stand composition and structure, as they reflect our understanding of broad seral stages (young, mature and old). Because of the natural variability in stand dynamics and composition, stands of a certain age do not always contain the corresponding structural and compositional attributes that we would expect. Clearly, the conceptual basis of this model and our understanding of the ecological processes involved in stand dynamics will have to be translated into a more quantitative, mensurational framework which provides silvicultural criteria for prescribing interventions.

As part of an adaptive management program in the Lake Duparquet Forest, a series of silvicultural field trials has been established in an interdisciplinary research program known as SAFE (*Sylviculture et aménagement forestier écosytémique*). Whereas general forest management planning targets the forestlevel composition and cohort objectives, the principal objective of SAFE is to evaluate species and standlevel responses to proposed silviculture treatments applied to various forest types and to improve understanding of treatment effects on stand-level ecological processes. Some aspects of landscape-level effects of natural disturbance-based management in the boreal forest are treated by Bergeron et al. (2001). In the short-term, these silvicultural trials will provide an indication of operational feasibility and costs while establishing a basis for long-term monitoring and calibration of SORTIE, a spatially explicit stand dynamics model, for the southeastern boreal mixedwood forest. Growth and yield information, regeneration and mortality dynamics, including possible volume losses due to partial cutting treatments, will constitute part of anticipated medium term results. Longer-term results will provide information on operational aspects of multiple entries, effects on log values and ecological impacts.

This natural disturbance-based management approach has been developed for the southeastern boreal forest where (1) the disturbance regime is characterized by large, catastrophic fires and smaller scale perturbations between fire events; (2) the negative exponential provides a reasonable model of natural age distribution; (3) stand composition and structure tend to change with time since disturbance; and (4) a significant proportion of the landscape is naturally occupied by stands older than normal harvest rotations. It is unclear whether this approach can be applied to other forest regions where disturbance regime is characterized by subcatastrophic gap dynamics and where uneven-aged silviculture can be employed to maintain most all-aged stands over the landscape. Nonetheless, the emphasis on diversifying silvicultural treatments as a means of generating and maintaining forest type diversity, will probably become a reality of forest management in those jurisdictions were there is concern about biodiversity.

### Acknowledgements

We gratefully acknowledge recommendations made by four anonymous reviewers and Guest editor Alison Dibble on a previous version of this paper. We also thank Martin Béland and Pierre Grondin for their suggestions for improvement to the original manuscript and Pierre Drapeau, Dan Kneeshaw, Christian Messier and Suzanne Brais (and others) who have contributed, through numerous discussions, to the content of this paper.

### References

- Armstrong, G.W., 1999. A stochastic characterisation of the natural disturbance regime of the boreal mixedwood forest with implications for sustainable forest management. Can. J. For. Res. 29, 424–433.
- Attiwill, P.M., 1994. The disturbance of forest ecosystems—the ecological basis for conservation management. For. Ecol. Manage. 63, 247–300.
- Bergeron, Y., 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. Ecology 72, 1980– 1992.
- Bergeron, Y., 2000. Species and stand dynamics in the mixedwoods of Quebec's southern boreal forest. Ecology 81, 1200– 1516.
- Bergeron, Y., Charron, D., 1994. Postfire stand dynamics in a southern boreal forest (Québec): a dendroecological approach. Ecoscience 1 (2), 173–184.
- Bergeron, Y., Dansereau, P., 1993. Predicting the composition of Canadian southern boreal forest in different fire cycles. J. Veg. Sci. 3, 827–832.
- Bergeron, Y., Dubuc, M., 1989. Forest succession in the southern part of the boreal forest. Can. Vege. 79, 51–63.
- Bergeron, Y., Harvey, B., 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. For. Ecol. Manage. 92, 235–242.
- Bergeron, Y., Leduc, A., 1998. Relationships between change in fire frequency and mortality due to spruce budworm outbreak in the southeastern Canadian boreal forest. J. Veg. Sci. 9, 492– 500.
- Bergeron, Y., Bouchard, A., Gangloff, P., Camiré, C., 1983. La classification écologique des milieux forestiers d'une partie des cantons d'Hébécourt et de Roquemaure. Études écologiques no. 9, Université Laval, Québec, p. 169.
- Bergeron, Y., Morin, H., Leduc, A., Joyal, C., 1995. Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. Can. J. For. Res. 25, 1375–1384.
- Bergeron, Y., Harvey, B., Leduc, A., Gauthier, S., 1999a. Basing forest management on natural disturbance: stand- and landscape-level considerations. For. Chron. 75 (1), 49–54.
- Bergeron, Y., Gauthier, S., Carcaillet, C., Flannigan, M., Prairie, Y., Richard, P.J.H., 1999b. Variability in fire frequency and forest composition in Canada's southeastern boreal forest: a challenge for sustainable forest management. In: Veeman, T.S., Smith, D.W., Purdy, B.G., Salkie, F.J. (Eds.), Proceedings of the 1999 Sustainable Forest Management Network Conference, pp. 74–80.
- Bergeron, Y., Richard, P.J.H., Carcaillet, C., Flannigan, M., Gauthier, S., Prairie, Y., 1998. Variability in Holocene fire frequency and forest composition in Canada's southeastern boreal forest: a challenge for sustainable forest management. Conservation Ecology (on-line), 2(2), art. 6. (On line: http:// www.consecol.org/Journal/vol2/iss2/art6/).
- Bergeron, Y., Leduc, A., Gauthier, S., Harvey, B., 2001. Natural fire regime: a guide for sustainable forest management of the boreal forest. Silva Fennica (accepted).

- Brais, S., Camiré, C., Bergeron, Y., Paré, D., 1995. Changes in nutrient availability and forest floor characteristics in relation to stand age and forest composition in the southern part of the boreal forest of northwestern Québec. For. Ecol. Manage. 76, 181–189.
- Buongiorno, J., Dahir, S., Lu, H.-C., Lin, C.R., 1994. Tree size diversity and economic returns in uneven-aged stands. For. Sci. 40 (1), 83–103.
- Burns, R.M., Honkala, B.H., 1990. Silvics of North America. Agriculture Handbook 654, Vol. 1 and 2. Forest Service, USDA, Washington, DC.
- Burton, P.J., Kneeshaw, D.D., Coates, K.D., 1999. Managing forest harvesting to maintain old-growth forest in the sub-boreal Spruce zone of British Columbia. For. Chron. 75, 623–631.
- Dansereau, P., Bergeron, Y., 1993. Fire history in the southern boreal forest of northwestern Quebec. Can. J. For. Res. 23, 25–32.
- DeGrandpré, L., Gagnon, D., Bergeron, Y., 1993. Changes in the understory of Canadian southern boreal forest after fire. J. Veg. Sci. 3, 803–810.
- Fox, T.R., Buger, J.A., Kreh, R.E., 1986. Effects of site preparation on nitrogen dynamics in the southern piedmont. For. Ecol. Manage. 15, 241–256.
- Franklin, J.F., 1993. Preserving biodiversity: species, ecosystems or landscapes. Ecol. Applic. 3, 202–205.
- Galipeau, C., Kneeshaw, D., Bergeron, Y., 1997. White spruce and balsam fir colonization of a site in the south eastern boreal forest as observed 68 years after fire. Can. J. For. Res. 27, 139– 147.
- Gauthier, S., Leduc, A., Bergeron, Y., 1996. Forest dynamics modelling under a natural fire cycle: a tool to define natural mosaic diversity in forest management. Environ. Monitor. Assess. 39, 417–434.
- Gauthier, S., Lefort, P., Bergeron, Y., Drapeau, P., 2000. Time since fire map, age-class distribution and forest dynamics in the Lake Abitibi Model Forest. Preliminary Information Report submitted to the LAMF, Iroquois Falls, Ont., Canada.
- Graham, R.T., Jain, T.B., 1998. Silviculture's role in managing boreal forests. Conservation Ecology, (on-line) 2(2), art. 8. (On line: http://www.consecol.org/Journal/vol2/iss2/art8/).
- Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I., Simard, M.-J., 1999. A review of the regeneration dynamics of North American boreal forest tree species. Can. J. For. Res. 29, 824–839.
- Grondin, P., Blouin, J., Racine, P., 1999. Rapport de classification écologique du sous-domaine bioclimatique de la sapinière à bouleau blanc de l'ouest. Ministère des Ressources naturelles du Québec. Direction des inventaires forestiers, Que., Canada, p. 220.
- Harris, L.D., 1984. The Fragmented Forest: Island Biogeography Theory and the Theory and the Preservation of Biotic Diversity. University of Chicago Press, Chicago, IL.
- Harvey, B., 1999. The Lake Duparquet research and teaching forest: building a foundation for ecosystem management. For. Chron. 75 (3), 389–393.
- Harvey, B., Leduc, A., 1999. Forêt d'enseignement et de recherche du Lac Duparquet: Plan général d'aménagement (1998–2023), Unpublished document, p. 144 +maps.

- Hunter Jr., M.L. (Ed.). Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, Cambridge, UK, 1999, p. 698.
- Johnson, E.A., van Wagner, C.E., 1985. The theory and use of two fire history models. Can. J. For. Res. 15, 214–220.
- Johnson, E.A., Miyanishi, K., Weir, J.M.H., 1998. Wildfires in the western Canadian boreal forest: landscape patterns and ecosystem management. J. Veg. Sci. 9, 603–610.
- Keenan, R.J., Kimmins, J.P., 1993. The ecological effects of clearcutting. Environ. Rev. 1, 121–144.
- Kimmins, J.P., 1977. Evaluation of consequences for future tree productivity of the loss of nutrients in whole-tree harvesting. For. Ecol. Manage. 1, 169–183.
- Kimmins, J.P., 1997. Forest Ecology: A Foundation for Sustainable Management, 2nd Edition. Prentice Hall, New Jersey, p. 596.
- Kneeshaw, D., Bergeron, Y., 1996. Ecological factors affecting the abundance of advanced regeneration in Québec's southwestern boreal forest. Can. J. For. Res. 26, 888–898.
- Kneeshaw, D., Bergeron, Y., 1998. Canopy gap dynamics and tree replacement in the southeastern boreal forest. Ecology 79 (3), 783–794.
- Kneeshaw, D., Bergeron, Y., 1999. Spatial and temporal patterns of seedling recruitment within spruce budworm caused canopy gaps. Ecoscience 6 (2), 214–222.
- Lämås, T., Thuresson, T., Sören, H., 1996. A cost function estimating the loss due to extended rotation age. Scand. J. For. Res. 11, 193–199.
- Landres, P.B., Morgan, P., Swanson, F.J., 1999. Overview of the use of natural variability concepts in managed ecological systems. Ecol. Appl. 9 (4), 1179–1188.
- Lavertu, D., Mauffette, Y., Bergeron, Y., 1994. Suckering success of aspen (*Populus tremuloides* Michx.) in relation to stand age and soil disturbance. J. Veg. Sci. 5, 561–568.
- Leduc, A., Gauthier, S., Bergeron, Y., 1995. Prévision de la composition d'une mosaïque forestière naturelle soumise à un régime des feux: proposition d'un modèle empirique pour le nord-ouest du Québec. In: Domon, G., Falardeau, J. (Eds.), Méthodes et réalisations de l'écologie du paysage pour l'aménagement du territoire, Polyscience publication, Morin Heights, pp. 197–205.
- Lieffers, V.J., Beck Jr, J.A., 1994. A semi-natural approach to mixedwood management in the prairie provinces. For. Chron. 70, 260–264.
- Lieffers, V.J., Macmillan, R.B., MacPherson, D., Branter, K., Stewart, J.D., 1996. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. For. Chron. 72, 286–292.
- Longpré, M.-H., Bergeron, Y., Paré, D., Béland, M., 1994. Effect of companion species on jack pine growth. Can. J. For. Res. 24, 1846–1853.
- Lundmark-Thelin, A., Johansson, M.B., 1997. Influence of mechanical site preparation on decomposition and nutrient dynamics of Norway spruce (*Picea abies* (L.) Karst.) needle litter and slash needles. For. Ecol. Manage. 96, 101–110.
- MacDonald, B., 1995. The case for boreal mixedwood management: an Ontario perspective. For. Chron. 71, 725–734.

- Man, R., Lieffers, V.J., 1999. Are mixtures of aspen and white spruce more productive than single species stands? For. Chron. 75 (3), 505–513.
- Messier, C., Doucet, R., Ruel, J.-C., Claveau, Y., Kelly, C., Lechowicz, M., 1999. Functional ecology of advance regeneration in relation to light in boreal forests. Can. J. For. Res. 29 (6), 812–823.
- Millar, C.I., Woolfenden, W.B., 1999. The role of climate change in interpreting historical variability. Ecol. Appl. 9 (4), 1207–1216.
- Mladenoff, D.J., White, M.A., Pastor, J., Crow, T.R., 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes for biodiversity design and management. Ecol. Appl. 3, 293–305.
- Morin, H., Laprise, D., Bergeron, Y., 1993. Chronology of spruce budworm outbreaks in the Lake Duparquet region, Abitibi, Québec. Can. J. For. Res. 23, 1497–1506.
- Norton, M.R., Hannon, S.J., 1997. Songbird response to partial-cut logging in the boreal mixedwood forest of Alberta. Can. J. For. Res. 27, 44–53.
- Paré, D., Bergeron, Y., 1995. Above ground biomass accumulation along a 230 year chronosequence in the southern portion of the Canadian boreal forest. J. Ecol. 83, 1001–1008.
- Paré, D., Bergeron, Y., 1996. Influence of colonizing trees on soil properties following fire in the Canadian southern boreal forest. Can. J. For. Res. 26, 1022–1031.

- Paré, D., Bergeron, Y., Camiré, C., 1993. Changes in the forest floor of Canadian southern boreal forest after disturbance. J. Veg. Sci. 3, 811–818.
- Prescott, C.E., Maynard, D.G., Laiho, R., 2000. Humus in northern forests: friend or foe? For. Ecol. Manage. 133, 23–36.
- Robitaille, A., Saucier, J.-P., 1998. Paysages régionaux du Québec méridional. Les publications du Québec, Québec, p. 213.
- Rowe, J.S., 1972. Forest Regions of Canada. Environment Canada, Ottawa.
- Seymour, R.S., Hunter Jr., M.L., 1992. New forestry in eastern spruce–fir forests: principles and application to Maine. Maine Agricultural and Forestry Experiment Station, Miscellaneous Publication 716, p. 36.
- Seymour, R.S., Hunter Jr., M.L., 1999. Principles of ecological forestry. In: Hunter Jr., M.L. (Ed.), Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, Cambridge, UK, pp. 22–61.
- Simard, M.J., Bergeron, Y., Sirois, L., 1998. Conifer recruitment in the southeastern Canadian boreal forest: the importance of substrate. J. Veg. Sci. 9, 575–582.
- Vitousek, P.M., Matson, P.A., 1985. Disturbance, nitrogen availability, and nitrogen losses in an intensively managed Loblolly pine plantation. Ecology 66 (4), 1360–1376.
- Weber, M.G., 1990. Response of immature aspen ecosystems to cutting and burning in relation to vernal leaf flush. For. Ecol. Manage. 31, 15–33.