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Ecological impact of clear-cutting on black spruce-moss forests in southern Québec[1]

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Abstract: Clear-cutting has been the most common harvesting method used in the Canadian boreal forest during the past century. However, its impact on forest dynamics and environmental change remains largely unknown. In this paper we have examined the dynamics of black spruce-moss forests logged between the 1940s and the 1960s in the Parc des Grands-Jardins, southern Québec. We have evaluated the potential of self-replacement of closed-crown forests 40 to 60 years after clear-cutting, and the interactions between tree harvesting, natural disturbances, and environmental factors. Clear-cutting can lead to the long-lasting opening of black spruce-moss forests. Several clear-cuts took place during or just after insect infestations. The spruce-moss forests regressed to shrub-moss woodlands showing little potential to revert to mature, pre-logged conditions. The main factors responsible for the shift to woodlands were the low density of advance growth, which was not compensated for by seedling establishment after the cut, and weak growth performance of black spruce. Stem growth slower than predicted for low site-class black spruce populations was likely caused by clumped distribution of layers, competition by dense ground vegetation, insect damage and reduction of site fertility after clear-cutting. The future of the post-logged woodlands relies heavily on the frequency and severity of natural disturbances that will certainly recur again in the area.

Keywords: clear-cutting, disturbance, dendroecology, *Picea mariana*, fire, insect infestations, regeneration.

Résumé : La coupe à blanc est la méthode de récolte forestière la plus commune au Canada. Cependant, ses conséquences sur la dynamique végétale et l'état des conditions environnementales restent mal connues. Dans ce travail, nous avons examiné la dynamique de pessières noires à mousses hypnacées, coupées entre 1940 et 1970 dans le parc provincial des Grands-Jardins au Québec. Notre objectif a été d'évaluer le potentiel de récupération de forêts fermées 40 à 60 années après leur coupe à blanc, ainsi que les interactions de cette méthode de récolte avec les perturbations naturelles et les facteurs du milieu. Nos résultats montrent que la coupe à blanc peut mener à l'ouverture de pessières noires à mousses hypnacées. Une partie des opérations de coupe s'est réalisée pendant ou juste après des épidémies d'insectes défoliateurs. Les forêts originelles ont régressé en formations ouvertes, qui ne semblent pas évoluer vers leur fermeture à maturité. Les principaux facteurs responsables de ce changement ont été la faible densité en régénération préétablie non compensée par l'établissement de plantules après coupe, ainsi que la faible croissance des épinettes noires. La croissance des tiges de cette espèce, inférieure à celle prédite même pour des sites de faible qualité, a été vraisemblablement affectée par leur distribution en bouquets de marcottes, la compétition avec les strates inférieures de la végétation, les épidémies d'insectes défoliateurs, ainsi que la réduction de la fertilité des sites après coupe. L'avenir de ces formations dépend fortement de la fréquence et la sévérité des perturbations naturelles qui reviendront certainement dans cette région.

Mots-clés : coupe à blanc, dendroécologie, feux, *Picea mariana*, perturbations, régénération, épidémies d'insectes défoliateurs.

Introduction

Black spruce (*Picea mariana* [Mill.] BSP.)-moss stands dominate much of the North American boreal forest, and their present exploitation represents a most valuable resource for the Canadian pulp and wood industry. Timber harvesting in the boreal forest began during the 20th century, mainly by clear-cutting, *i.e.,* the removal of all trees from an area at one time (Jeglum & Kennington, 1993). The use of this method, which includes a number of variants, is currently increasing in size and frequency and appears now as a new major disturbance at the landscape scale (Carleton & MacLellan, 1994; Grondin, 1996). In Canada, about 80% of the nearly one million ha of forests harvested annually are defined as clear-cut (Youngblood & Titus, 1996).

Earlier studies on clear-cutting of spruce-moss forests suggested that the impact of this practice is generally minor and short-lived at the stand scale (Keenan & Kimmins, 1993). In Ontario, Brumelis and Carleton (1988) showed that spruce regeneration in post-logged sites previously dominated by *Picea mariana* is linked to a combination of nutrient status of the site, maintenance of advance growth, and post-logging establishment. In Québec, black spruce regeneration left in cutovers originates primarily from layering. After release from over-story competition by clear-cutting, uneven-aged layer stems may develop like even-aged stands from seed origin (Lussier, Morin & Gagnon, 1992; Paquin & Doucet, 1992; Pothier, Doucet & Boily, 1995).

Layer abundance and stocking are generally sufficient to provide adequate regeneration after logging (Doucet, 1988). Growth performance of these second-growth stands may be satisfactory, depending on density of advance regeneration, height structure, and site quality (Morin, Gagnon & Frisque, 1991; Lussier, Morin & Gagnon, 1992; Paquin & Doucet, 1992). The latter studies reflect the common forestry practice, following which properly managed second-growth stands will look much like their original cover once mature (Rogers, 1996).

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Black spruce-moss forests have successfully adapted their regenerative power over the millennia to a natural disturbance regime including wildfires, insect attacks, and windthrows (Jeglum & Kennington, 1993). These factors interact at different spatiotemporal scales to maintain a landscape composed of stand patches at various successional states of the closed-crown forests, coexisting in some cases with open woodlands. It has been shown that two natural events, such as insect infestation and fire, can lead in this way to the development of confined black spruce-lichen woodlands in the southern part of the closed-crown forest, if they occur at about the same time in a stand (Payette *et al.,* 2000). A major new disturbance such as clear-cutting is also very likely to change the current pattern of tree recovery in the boreal zone in interaction with natural disturbances. Open, second-growth stands of black spruce can be found nowadays on the Charlevoix Highlands, in the heart of the closed-crown boreal forest zone. These stands, which are sometimes older than 60 years, do not seem to develop towards canopy closure.

The main objective of this study was to assess the long-term impact of clear-cutting in virgin, post-fire black spruce-moss stands. To do so, we have studied black spruce stands not disturbed by human activities before cutting and not affected by post-logged soil treatment, planting, or other silvicultural practices. After clear-cutting, sometimes called "cut and walk away" (Jeglum & Kennington, 1993), the resilience of forest stands depends solely on their natural regenerative power and the sequence of disturbance events that may affect the second-growth. With this in mind, we have addressed the following questions: *i*) Do virgin, closed-crown forests recover to similar stand structures after clear-cutting? *ii*). What are the interactions between natural disturbances, local environmental factors, and clear-cutting and their cumulative impact on canopy and potential regeneration of black spruce-moss stands? These questions may be relevant in the context of forest stability and renewal of the wood resource in one of the largest harvesting areas of boreal North America.

Methods

STUDY AREA

The study area is located in the Charlevoix Highlands, 120 km north-east of Québec City (Canada), in the Parc des Grands-Jardins (PGJ) provincial park, at 47° 40' N and 70° 50' W. The topography is characterized by hills of moderate slopes (15%-30%), at an altitude ranging from 700 to 875 m above sea level. Mean annual temperature in the PGJ is -0.07°C (Boisclair, 1990). Mean monthly temperature of the warmest and coldest months are 14°C and -15°C in July and January, respectively. Mean annual precipitation totals about 1000 mm, of which 40% is snowfall. The snow cover lasts from November to May.

The vegetation of the PGJ is representative of the southern boreal zone (Grandtner, 1966), and closed-crown forests composed of black spruce-moss stands are the most common vegetation type (Payette *et al.,* 2000). These stands coexist with patches of lichen spruce woodlands, which cover about 10% (30 km^2) of the park area. Black spruce stands are subjected to a disturbance regime including outbreaks of the spruce budworm (*Choristoneura fumiferana* [Clem.]), fires, and logging (Boisclair, 1990; Payette, Delwaide & Dussart, 2000). The spruce budworm is the most important insect defoliator in eastern North America. Its larvae have the capacity to defoliate and kill balsam fir (*Abies balsamea* [L.] Mill.) and spruce (*Picea* spp.) trees over large areas (MacLean, 1980). Historical evidence shows that outbreaks of the spruce budworm have occurred at an average interval of 30 years since 1704 in northeastern North America (Blais, 1983). Several infestations of the spruce budworm occurred in the study area during the 20th century (Simard & Payette, 2001).

During the last century, 13 fires were recorded, covering about 40% (120 km^2) of the PGJ. Fire disturbance leads usually to self-replacement of even-aged black spruce stands, through seedling establishment, soon after the fire. Open woodlands replace the burnt moss forests, however, in cases of failures in post-fire regeneration (Payette, 1992). Clear-cutting was also an important disturbance before the creation of the park in 1981. Logging activities covered about 39% of the PGJ and were carried out between 1942-1948, 1955-1958, and 1961-1967 (Payette, Delwaide & Dussart, 2000). Harvesting techniques changed between these periods, from hand-felling and horse-skidding in the 1940s to mechanized logging and transport in the 1960s (J. C. Ruel, pers. comm.). No tree planting was done after logging of the spruce-moss stands.

LARGE-SCALE SURVEY OF LOGGED CLOSED-CROWN FORESTS

A set of representative sites were surveyed to evaluate canopy response of spruce-moss stands to logging (Figure 1). Potential sites were first identified following analysis of the available data on the spatiotemporal distribution of logging, fires, and other perturbations during the 20th century in the PGJ (Payette, Delwaide & Dussart, 2000) and field surveys. All selected stands had to be accessible (by road), merchantable black spruce-moss forests before the cut. We rejected stands where all merchantable trees were not obviously removed in one cutting, as well as overcuts dominated by balsam fir. Thirteen sites were finally selected to obtain the greatest diversity in terms of post-logging regeneration and date of cutting: 4 sites were cut during the 1940s, 4 during the 1950s, and 5 during the 1960s.

At each site, 8 parallel, rectangular transects (50 m × 1 m) were used, with the first transect located at random and the others placed systematically at an interval of 15 m. The density of felled trees (recorded as saw-cut stumps) and living stems was determined by counting the number of stumps (per tree species) in each transect, using 3 size categories based on basal stem diameters (regeneration: < 3 cm; intermediates: 3-10 cm; and dominants: > 10 cm). Mean densities were compared using a one-way ANOVA random effects model. Analyses were run using the General Linear Model procedure of SAS (SAS Statistical System software, v. 6.12, SAS Institute Inc., Cary, North Carolina, U.S.A.). The vegetation cover (percentage), including tree overstory, shrub understory, and ground vegetation (lichens and mosses), was evaluated by the line-intercept method (Mueller-Dombois & Ellenberg, 1974) at every meter along eight 50-m-long transects.

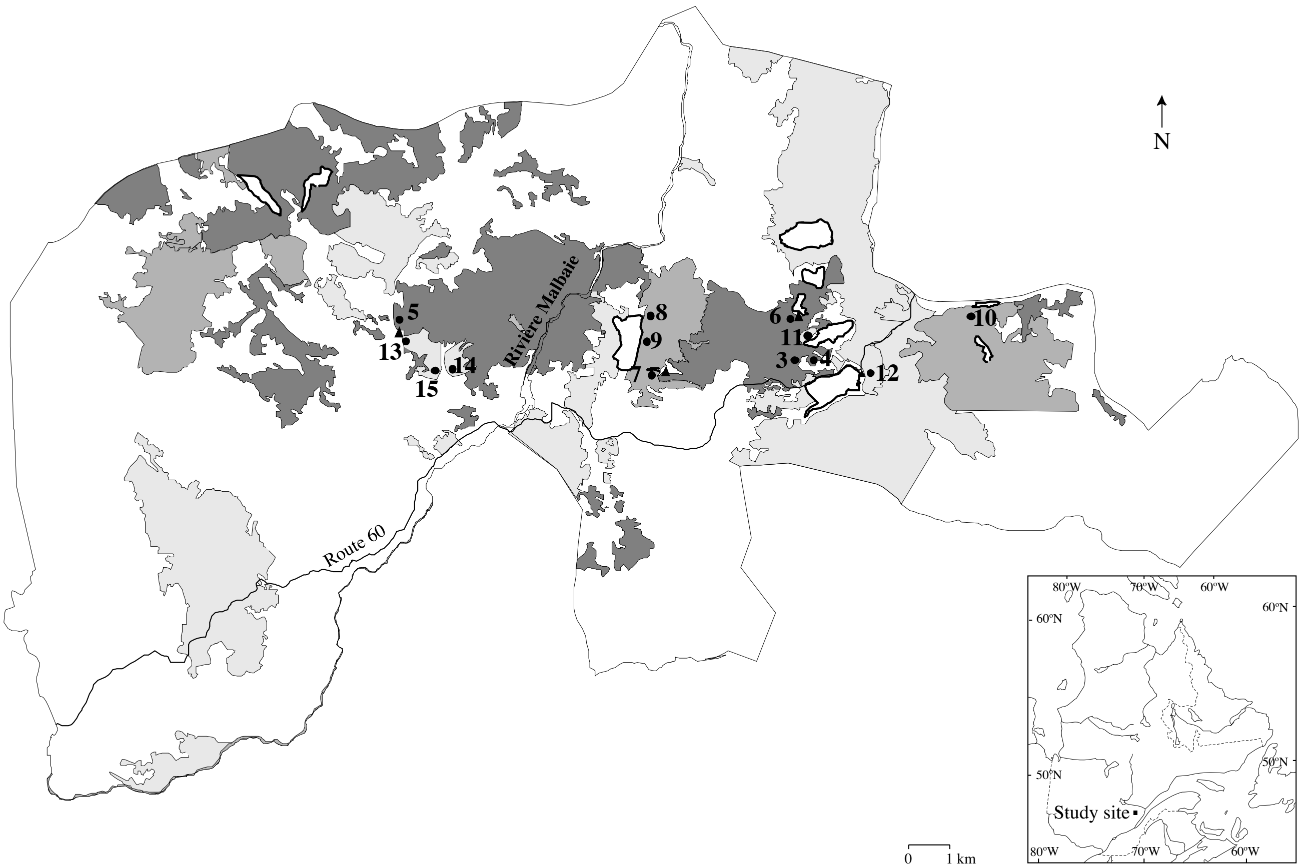

FIGURE 1. Location of the surveyed sites (circles with numbers in bold), reference populations (triangles), and clear-cutting areas in the Parc des Grands-Jardins (grey areas). Light grey refers to 1940s cuts, middle grey to 1950s cuts, and dark grey to 1960s cuts. Inset map shows location of the study area in eastern Canada.

FOREST STAND DYNAMICS

Pre- and post-logging stand dynamics were evaluated from five sites. Results of the large-scale survey were used to select the five sites, according to their representativeness in terms of post-logging regeneration success and date of cut. Two sites were logged during the 1940s (sites 5 and 6), one site in 1956 (site 7), and two sites during the 1960s (sites 12 and 13). Lack of time available precluded the analysis of a second stand cut in the 1950s.

SOIL ANALYSIS

At each site, the soils were described and sampled following the Canadian system of soil classification (Commission canadienne de pédologie, 1978). Samples of the organic (FH) and mineral (B) horizons were taken for chemical analysis and texture determination, following McKeague's procedures (1978). Exchangeable bases (K, Ca, Na, and Mg), acidity (H + Al), $CaCl_2$-pH (0.01 M), organic carbon (loss on ignition) of the organic horizons, and nitrogen content (macroKjeldahl) were determined. Effective cation exchange capacity (ECEC) was measured as the sum of exchangeable cations, and base saturation (BS) was calculated by dividing exchangeable cations by ECEC.

REFERENCE POPULATIONS

As reference populations, at least 12 dominant black spruce trees were sampled in plots that were never logged near each of the five selected sites (maximum distance = 200 m, except for site 5 where distance was 500 m). The location of reference plots, confined between each logging area and the next lake border or forest road, as well as their shape and small size, allowed us to assume that they were formerly part of the mature spruce populations harvested next to them.

Total height of each tree was measured, and the stems were cut at the collar level to recover 2- to 5-cm thick cross-sections. All the sections were dried and sanded until xylem cells were clearly visible under a binocular microscope at 40X. The annual rings were counted and cross-dated by the skeleton plot method (Fritts, 1976) along two opposite radii. Annual ring width of each section was measured using a Velmex micrometer (± 0.002 mm). The dating of the tree-ring series was checked with COFECHA (Holmes, 1983) before the construction of the mean ring-width series (± SD) at each site.

Site indices (SI), *i.e.*, total height of dominant trees at 50 years, were determined from height and age data. We used Payandeh's site index curves for black spruce (Payandeh, 1991). SI are extensively used to quantify potential site productivity, because they integrate the influence of ecological factors (microclimate, soil quality, slope, drainage conditions) on the fertility of forest sites. We chose Payandeh's curves rather than yield tables established by Pothier and Savard (1998) because they provide better fit for height growth of black spruce, especially at young stages (J. Bégin, pers. comm.).

It can be argued that reference plots were not harvested because they did not include enough merchantable trees at the time of the cut. This in turn would be due either to disturbances having affected, in a very local way, the growth or the age structure of these otherwise fire-origin, even-aged populations or to microsite factors (soil conditions, drainage) which could locally affect site fertility. Such objections prevented us from using age of the sampled trees as an indication of the age of the harvested populations. Growth analyses were conducted, however, because they were very likely to provide solid information about growth conditions in each site before and after the cut. As for SI results, they were interpreted as minimum estimates of forest productivity in each neighbouring logged area. Finally, it is important to stress that no real reference stands are available in the studied area or elsewhere, because of the absence of post-logged black spruce-moss forests older than 100 years. In addition, it is worth noting that SI is calculated using age-height values only from post-fire stands, *i.e.,* site conditions not comparable to those of post-logged stands. As a result, one must consider SI values as gross approximations of the growth potential.

SECOND-GROWTH POPULATIONS

A systematic layout was superimposed on the sampling areas used in the previous large-scale survey, for the five selected sites. Ten parallel transects, each 100 m long, were positioned in each site at an interval of 10 m, with the first transect located at random. Ten sampling points were then systematically distributed in each transect, again at an interval of 10 m, in order to obtain 100 sampling points over 1 ha. Such sampling surfaces allow a reliable representation of heterogeneous vegetation covers, with dense spruce clusters distributed in large treeless gaps. The four closest living stems (irrespective of species identity) to each sampling point were spotted, following the point-centered quarter method (Cottam & Curtis, 1956). Distance to the central point, total height, basal diameter (at collar level), and diameter at breast height (DBH) were registered. Stand age structure was determined by sampling the individual nearest to the central point in each quarter (n = 100). Individual stems were carefully cut at the collar to reduce errors in age determination. In the case of black spruce, in particular, the root collar may be located below ground level in the mossy ground cover with adventitious roots along the buried stem (DesRochers & Gagnon, 1997). The age of basal cross-sections was determined as for those of the reference stands. Additional cross-sections were also sampled for dating purposes at every meter along these stems, to determine their height (by metric classes) at the time of the clear-cut.

STOCKING AT HARVEST TIME

The stumps of the four felled trees closest to each sampling point were spotted on the layout used for the living stems. Distance to the central point and basal diameter (at collar level) were registered. At each site, the value of stump DBH was inferred from basal diameter and mean (DBH/basal diameter) ratios of the second-growth, present-day living stems. The values of stump density and quadratic mean DBH were used to estimate the Relative Density Index (RDI) of each site at the time of the clear-cut. RDI measures the filling of an area by trees. RDI was obtained by dividing the measured stump density by the maximum density predicted by the black spruce Stand Density Management Diagram established by Smith (1994) for mean DBH values. Such diagrams are used to model the potential development of forest species in given areas, based on the relationship between plant size and stand density (Drew & Flewelling, 1979; Archibold, 1996).

Results

OPENING OF CLOSED-CROWN FORESTS AFTER CLEAR-CUTTING

The large-scale survey indicated that post-logged tree density at all sites was high, particularly black spruce, which had a mean value of 7,417 stems ha^{-1}. However, most individuals (90%) were from the small and intermediate regeneration categories. The original spruce populations always included more overstory adults (stem basal diameter > 10 cm) at the time of logging than the current second-growth populations (Table I). Black spruce was the dominant tree species (78% of all recorded stems) of the post-logged stands. Balsam fir was abundant in several sites. Tamarack (*Larix laricina* [DuRoi] K. Koch), paper birch (*Betula papyrifera* Marsh.), and quaking aspen (*Populus tremuloides* Michx.) were seldom present (Table I).

The forest cover of post-logged stands ranged from 36% to 63%. Black spruce was the dominant tree species, though the canopy of balsam fir was also important in several sites (Table II). The broadleaf category (mostly located in the understory) in table II includes *Acer spicatum* Lam., *Alnus* sp., *Amelanchier* sp., *Betula* sp., *Populus tremuloides*, *Salix* sp., and *Sorbus americana* Marsh. These species were heavily grazed by herbivores (moose, snowshoe hare, beaver), as evidenced by conspicuous browsing scars at all sites. Ericaceous shrubs, mainly sheep laurel (*Kalmia angustifolia* L.), were generally abundant (cover ranging from 21% to 54%) and dominated open gaps. Mosses (particularly *Pleurozium schreberi* [Brid.] Mitt.) covered the shaded forest floor.

The overall mean cover of black spruce, lichen, and moss since logging showed no trend towards canopy closure with time (Figure 2). Such a trend would imply an increase in black spruce cover with time since clear-cut, which does not appear here. Whatever the date of logging, no significant differences (ANOVA) were found between mean cover of black spruce of the post-logged stands.

FOREST STAND DYNAMICS

SOIL ANALYSIS

Soil profiles of the 5 selected sites (sites 5, 6, 7, 12, and 13) corresponded to podzolic soils with FH, Ae, B, and C horizons developed from sandy loam till (Table III). All the soils were very acid (pH = 2.7 to 3.2 in FH, 3.9 to 4.9 in B) and nutrient-poor with low CEC (< 20 cmol[+] kg^{-1} in FH, < 5 cmol[+] kg^{-1} in B) and base saturation values (Table III). All soils were poor in nitrogen, and C/N ratios were high (> 30 in FH).

TREE STOCKING AT HARVEST TIME

The values of RDI for sites 5, 6, 7, and 13 suggested closed canopies, with corresponding minimal to weak stem

TABLE I. Stump density and living tree density (stems ha^{-1}) according to basal diameter category. Category 1: basal diameter > 10 cm. Category 2: 3 cm < basal diameter < 10 cm. Category 3: basal diameter < 3 cm. *: selected sites for the study of post-logged stand dynamics.

Site		3	4	5*	6*	7*	8	9	10	11	12*	13*	14	15
Stumps	1	1450	2825	1450	1900	1334	1750	2200	2257	1900	2425	1025	1175	1775
	2	75	775	500	250	88	225	300	429	1075	275	300	375	600
	3	0	0	0	0	0	0	0	0	250	0	0	25	0
Black spruce	1	650	975	700	675	510	700	500	1029	425	825	850	950	900
	2	950	3375	975	4125	4422	3950	2175	3629	4150	9975	1400	5350	3400
	3	675	2600	2225	1900	5422	2950	1150	1658	5300	5975	1275	5025	2700
Balsam fir	1	525	375	50	0	0	300	150	914	0	275	100	25	0
	2	2125	2200	100	50	44	1375	2550	2200	0	425	25	25	0
	3	1400	2925	225	100	0	475	2750	1029	100	350	50	0	0
Tamarack	1	0	0	0	25	156	0	0	0	25	50	25	25	0
	2	0	0	0	0	134	0	0	0	0	0	0	50	100
	3	0	0	0	0	44	0	0	0	25	0	0	75	0
Paper birch	1	0	0	0	0	0	0	125	29	0	0	0	0	0
	2	175	450	0	125	22	0	100	0	0	0	0	0	0
	3	750	400	0	0	0	0	275	0	0	0	0	0	0
Quaking apsen	1	0	0	0	0	0	75	0	0	0	0	75	50	0
	2	0	50	0	0	0	50	0	0	0	0	50	0	25
	3	0	0	0	0	0	0	25	0	0	0	0	0	0

TABLE II. Vegetation cover (% of linear cover) of the surveyed sites. The broadleaf category includes *Acer spicatum*, *Alnus* sp., *Amelanchier* sp., *Betula* sp., *Populus tremuloides*, *Salix* sp., and *Sorbus americana*. *: selected sites for the study of post-logged stand dynamics.

Site	Logging date	Litter	Feather-mosses	*Sphagnum* spp.	Lichens	Ericaceous shrubs	Black spruce	Balsam fir	Tamarack	Broadleaf trees
3	1948	9.47	81.27	7.75	2.12	21.17	23.62	22.1	0	10.95
4	1948	18.82	73.25	4.9	2.55	27.3	41.35	19.3	0	2.1
5*	1942	13.72	66.8	11.37	9.22	47.57	32.62	3.05	0.35	12.98
6*	1948	2.2	81.35	1.27	15.6	54.2	39.35	0.52	0.57	4.67
7*	1956	4.82	65.91	4.42	24.31	44.2	45.82	0.53	4	2.2
8	1958	12.35	80.85	2.6	5.05	38.95	41.7	12.02	0	7.12
9	1958	11.37	73.57	9.92	6.37	35.82	28.75	21.05	0	6.17
10	1958	10	75.6	10.27	4.5	23.85	37.5	24.75	0.02	11.67
11	1964	2.05	65.72	3.05	28.1	43.12	37.02	0.1	1.07	2.42
12*	1964	9.35	78.6	0.97	10.97	30.32	55.67	6.55	0.52	0
13*	1964	54.1	40.17	2.05	1.67	40.97	38.52	0.42	0.57	35.07
14	1964	23.27	61.17	5.4	10.5	39.6	52.12	0.02	1.22	14.52
15	1964	2.4	78.7	0.9	18.65	45.55	40.32	0	0.37	10.65

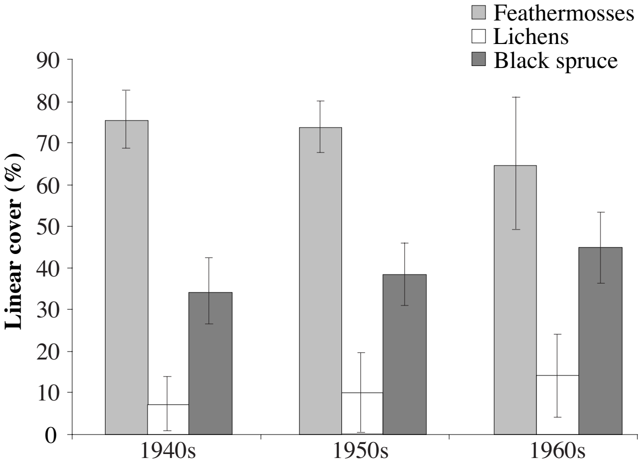

FIGURE 2. Mean (± SD) linear cover of black spruce, lichen, and moss in stands logged between the 1940s and 1960s.

competition (density class B and C) at the time of harvesting (Table IV). In site 12 RDI was excessive (density class D), which means that loss of individuals by self-thinning outweighs the growth of survivors (Drew & Flewelling, 1979; Archibold, 1996).

SI OF REFERENCE STANDS

Mean age and height of tree samples taken as reference populations are given in Table IV together with their SI. The same group of trees was used for sites 5 and 13, due to their proximity. Growth analysis (see below) showed that all the samples had always been free to grow, so age-height values could be combined to determine SI of each site following Payandeh's (1991) site index curves. SI values at 50 years ranged from 6 to 8 m, which are the lowest values for merchantable black spruce forests in Quebec.

SECOND-GROWTH POPULATIONS

All second-growth stands were uneven-aged, despite a high frequency of stems established shortly after clear-cut (Figure 3). The proportion of advance regeneration older than the dates of the clear-cuts ranged from 3% to 39%. This proportion was lower than reported elsewhere (Morin & Gagnon, 1991; Lussier, Morin & Gagnon, 1992; Paquin & Doucet, 1992). Most individuals established 10 to 30 years after logging. Recruitment seemed to have peaked around 1970 in the oldest clear-cuts (sites 5 and 6). The noticeable absence of young black spruce could be due to an overestimation of the age of young layers. Layers of black spruce developed from living basal branches may be

TABLE III. Physical and chemical characteristics of the studied soils.

Site	Drainage class	Horizon	Thickness (cm)	OC[a] (%)	N (%)	C/N	pH	ECEC[b] (*)	BS[c] (%)
5	4	FH	10.5	16.50	0.44	37.38	3.21	14.80	55.6
		B	12-53	2.83	0.09	31.44	3.97	2.88	29.2
6	3	FH	22	20.40	0.44	46.27	3.14	16.70	27.4
		B	25-54	1.91	0.07	27.28	4.06	2.99	13.2
7	3	FH	26	9.92	0.23	43.13	2.83	9.90	25.6
		B	40-116	3.53	0.12	29.41	3.88	3.57	22.5
12	2	FH	9	8.94	0.22	40.63	3.18	8.78	23.8
		B	13.5-84	3.67	0.14	26.21	4.33	1.38	16.0
13	2	FH	6.5	9.91	0.31	31.96	2.71	9.11	12.9
		B	16-40	1.87	0.07	26.71	4.92	0.20	97.4

* cmol (+) kg^{-1}

[a] Organic Carbon

[b] Effective Cation Exchange Capacity

[c] base saturation

TABLE IV. Stocking at harvest time, age and height of reference populations, Site Index, and height of advance growth in comparison with predicted values for each Site Index in the five sites selected for the study of post-logged stand dynamics. (B), (C), and (D) refer to density categories according to RDI values, following Drew and Flewelling (1979). Class B (0.15 < RDI < 0.4): median density, with gross production roughly proportional to stand density. Class C (0.4 < RDI< 0.55): optimal density, with gross production remaining constant whatever stand density. Class D (RDI > 0.55): excessive density, with significant losses due to self-thinning.

Site	Stumps density (Stems. ha^{-1})	Mean stump DHP (cm)	RDI*	Mean age ± SD of reference populations	Mean height ± SD of reference populations	SI**	Number of years after cutting	Predicted height (m) of advance regeneration	Height ± SD (m) of advance regeneration
5	2209.5	12.00	0.47 (C)	105 ± 6	14.7 ± 0.8	8	56	8.75	4.84 ± 0.92
6	2063	10.10	0.34 (B)	146 ± 11	15.4 ± 1.5	8	50	8.00	5.32 ± 2.00
7	1530	11.33	0.29 (B)	120 ± 20	13.2 ± 2.0	7	40	5.84	2.82 ± 2.02
12	2065	14.25	0.55 (D)	160 ± 20	13.9 ± 1.8	6	34	4.36	3.60 ± 1.91
13	2375	11.22	0.24 (B)	105 ± 6	14.7 ± 0.8	8	34	5.12	2.94 ± 2.09

* Relative Density Index

** Site Index (height in meters at 50 years) following Payandeh's curves (1991).

several years old (Bégin & Filion, 1999; Laberge, Payette & Bousquet, 2000) before being embedded in the organic horizon (Stanek, 1961).

Figure 4 shows height and age values of all living black spruce on the post-logging sites together with height-age curve based on the SI of their corresponding reference stands. Following Payandeh (1991), height may be calculated as a function of age and SI with the expression

$$\text{Height (m)} = 4.294 \times SI^{0.670} (1-e^{-0.021.Age})^{1.762} \qquad [1]$$

Most black spruce established after clear-cut were smaller than predicted by this formula. For individuals older than the age of the clear-cut, dating of tree sections at every meter indicated that fewer than 3% of living stems had reached a height of 1 meter at the time of clear-cutting, at all sites. This means that almost all individuals forming the advance growth population were small (< 1 m high) and suppressed at the time of logging. Thus, height growth of advance regeneration did not correspond to their real age. Some stems were released and developed well after the clear-cut. Nevertheless, mean height of the advance growth was also well under the values predicted by Payandeh's curves (Table IV), with the exception of site 12, which had the lowest SI of all stands.

Figure 5 shows the relation between age and basal diameter of the living stems. The main sub-group in all sites was always the small regeneration (basal diameter < 3 cm), representing more than half of the second-growth populations, except in site 12. As for height values, basal diameter of the advance growth showed much variability. Overstory adults were a small part of the total population, except in site 5. Whereas advance growth is particularly scarce in this site, an important cohort of black spruce (21% of the population) established after logging and made its way to the tallest size category.

RADIAL GROWTH PATTERNS OF REFERENCE VERSUS SECOND-GROWTH STANDS

Canopy opening following clear-cut accelerated the growth of suppressed stems forming the advance regeneration (Figure 6). Before the cut, radial increment was in the order of 0.5 mm year^{-1}. During the years that followed the clear-cut, this value increased by 300% to 800% in all the studied sites. Afterwards, their growth patterns became roughly similar to those of reference populations. Several growth depressions occurred during the last decades. The first growth decrease extended from the late 1930s to the early 1940s. This was followed by sharp drops between 1951 and 1953, in 1978-1979, and finally during the mid-1980s. Annual SD were not included on the mean ring-width series for reasons of legibility. Variable pre-logged growth patterns are likely attributable to unequal forest age and structure before the cuts and to the reduced size of advance growth. This highlights the fact that a diversity of forest stands was analyzed, all affected similarly by the clear-cuts.

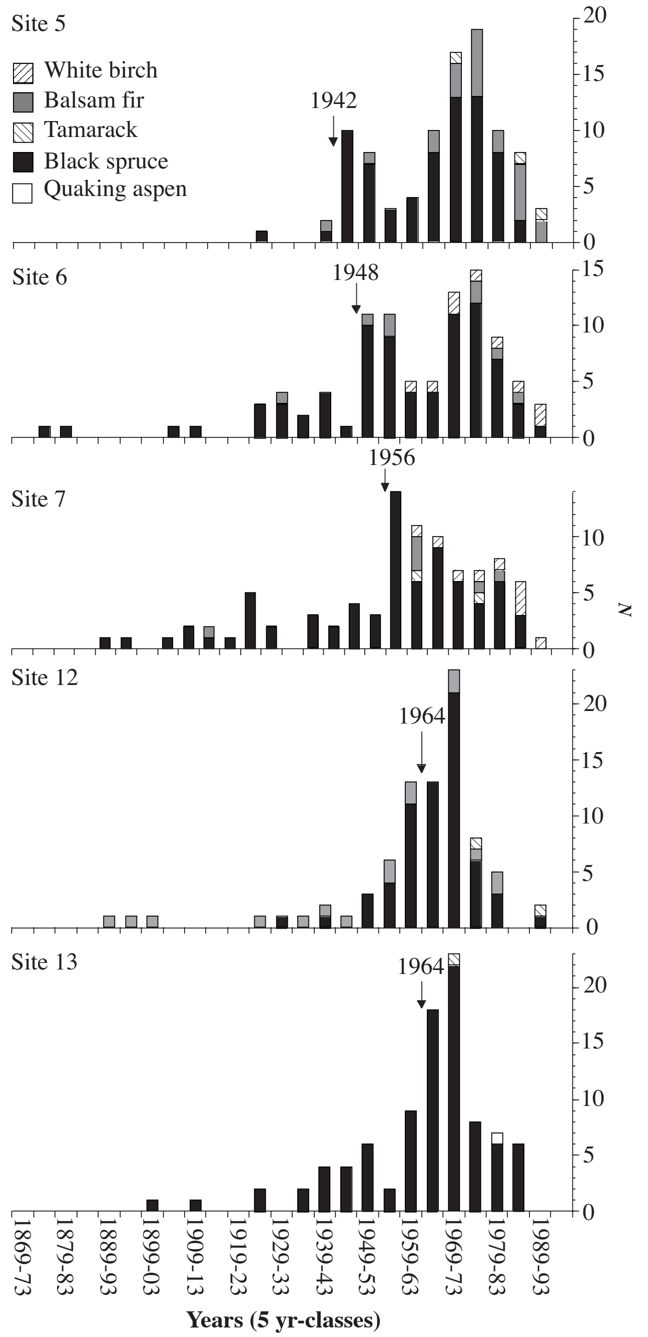

FIGURE 3. Date of tree establishment in each of the five sites selected for the study of post-logged stand dynamics. Arrows indicate date of clear-cutting.

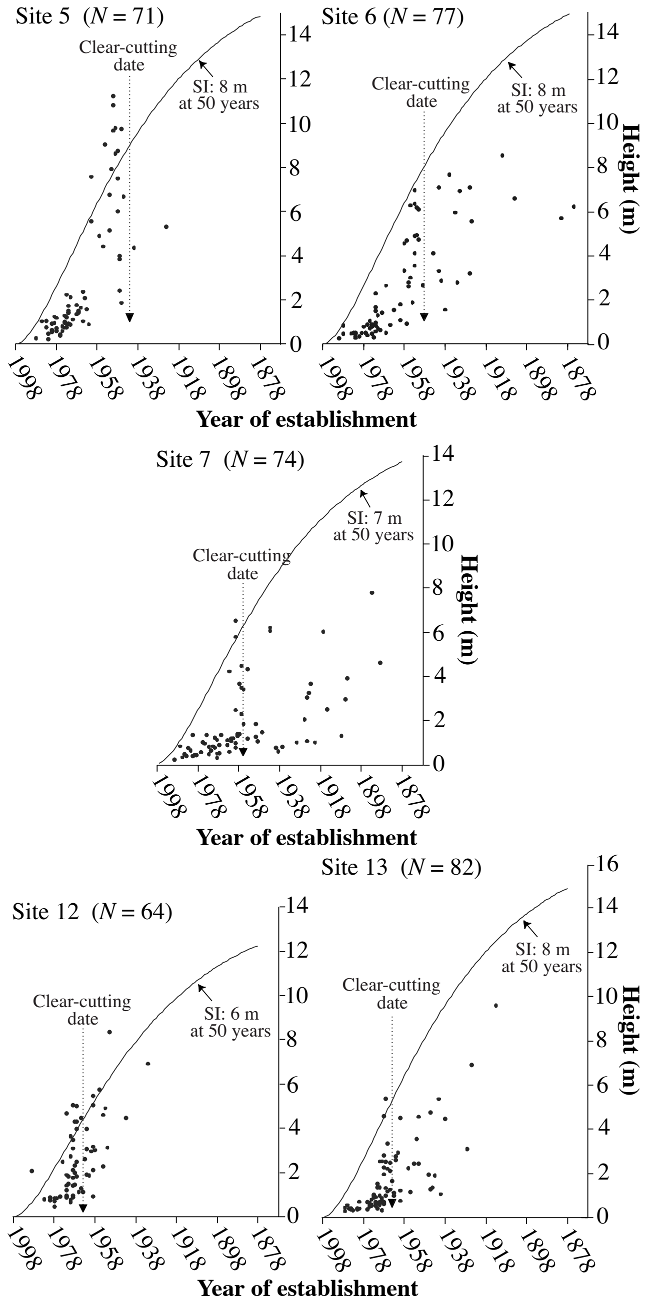

FIGURE 4. Relationship between age and height in second-growth black spruce and height-age curves based on each Site Index, following Payandeh (1991).

Discussion

PRESENT FOREST COVER

Our large-scale survey reveals a landscape of open post-logged forests 40 to 60 years after logging. Although stem densities are high, trees are small or medium-sized and tend to form clusters between large gaps occupied by lichens, mosses, and ericaceous shrubs. These results are in accordance with those of other studies, showing second-growth black spruce distributed either in aggregates or at random (Doucet, 1988; Groot & Horton, 1994). It is unlikely that these gaps will close with time. Establishment of black spruce seedlings does not succeed on such seedbeds (Jeglum & Kennington, 1993), and layering alone does not seem enough to take over large clearings (Riverin & Gagnon, 1996; Payette *et al.,* 2000). In addition, the growth of black spruce advance regeneration in gaps is severely hampered by sheep laurel, the main post-logged invading shrub in the area (Yamasaki *et al.,* 1998).

ESTABLISHMENT OF THE POST-LOGGED REGENERATION

Most living tree stems established after logging. Compared to other data (Lussier, Morin & Gagnon, 1992; Paquin & Doucet, 1992; Lussier, 1997), stand age structures

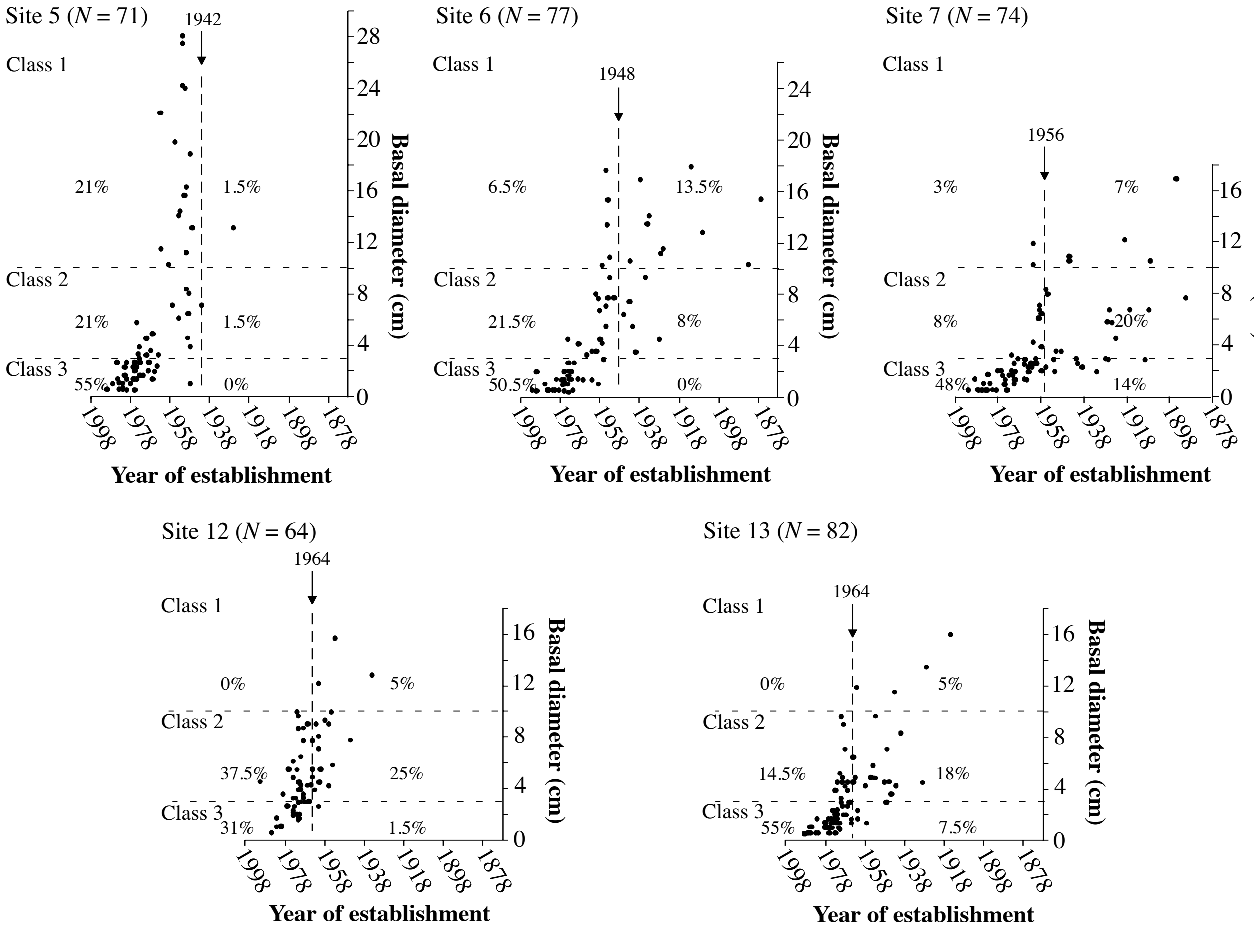

FIGURE 5. Relationship between year of establishment and basal diameter in second-growth black spruce stands. Arrows indicate date of clear-cutting. Size of clones are based on basal stem diameters (class 1: > 10 cm; class 2: 3-10 cm; class 3: < 3 cm). Percentage values indicate the population of individuals of each class that established before and after the cut.

show that present tree populations include only a few stems originating from advance regeneration. These stems were very small at the time of clear-cut. However, it must be stressed that our results report only present-day survivors. The small size of advance regeneration could be due, in part, to the loss of individuals, some having been wounded or killed during logging. Mechanized clear-cutting during the 1960s may have been more destructive than horse logging in the 1940s. Moreover, overstory removal always triggers drastic changes in environmental conditions for advance regeneration. After harvesting, survivors must cope quickly with large increases in light intensity and evapotranspiration and also with potential frost injury. These factors can cause high mortality of black spruce advance growth in the first few years following the clear-cut (Ruel *et al.*, 2000).

Particularly in young stands, black spruce is known to be generally less vulnerable than balsam fir and other spruce species to spruce budworm attacks (MacLean, 1990). However, in a study of merchantable black spruce populations from the Laurentides Highlands, Lussier (1997) found that most mortality occurred during the last spruce budworm outbreak in the 1970s and that the smallest stems (minimum DBH = 2.5 cm) were the most affected. It is possible that a proportion of advance growth in our sites could have disappeared during the infestations that affected the PGJ after the clear-cuts. Infestations that occurred just before some clear-cuts may also have been important, as a number of defoliated stems might have been too damaged to tolerate abrupt changes in light conditions. Spruce budworm defoliation may also change regeneration patterns through reduced cone and seed production. Virtually all flowers of black spruce are destroyed even when only a small population of budworm larvae are present, because the needles and vegetative buds of this species are less favorable feeding sites (Schooley, 1980).

The lack of abundant advance growth was responsible for post-logged canopy opening in the PGJ, a conclusion that accords with several earlier studies on the regeneration of post-logged black spruce stands (Morin & Gagnon, 1991; 1992; Lussier, Morin & Gagnon, 1992; Paquin & Doucet, 1992). These studies focused on the performance of second-growth stands compared to fire-origin stands. The growth of fire-origin stands is expected to be greater, at least during the first decades, as fire releases most nutrients that otherwise are retained in the accumulating litter and reduces thickness of the organic horizon, which affects vertical stem growth (Archibold, 1996, Lussier, Morin & Gagnon, 1992). However, results from these studies (Morin & Gagnon, 1991; 1992; Lussier, Morin & Gagnon, 1992; Paquin &

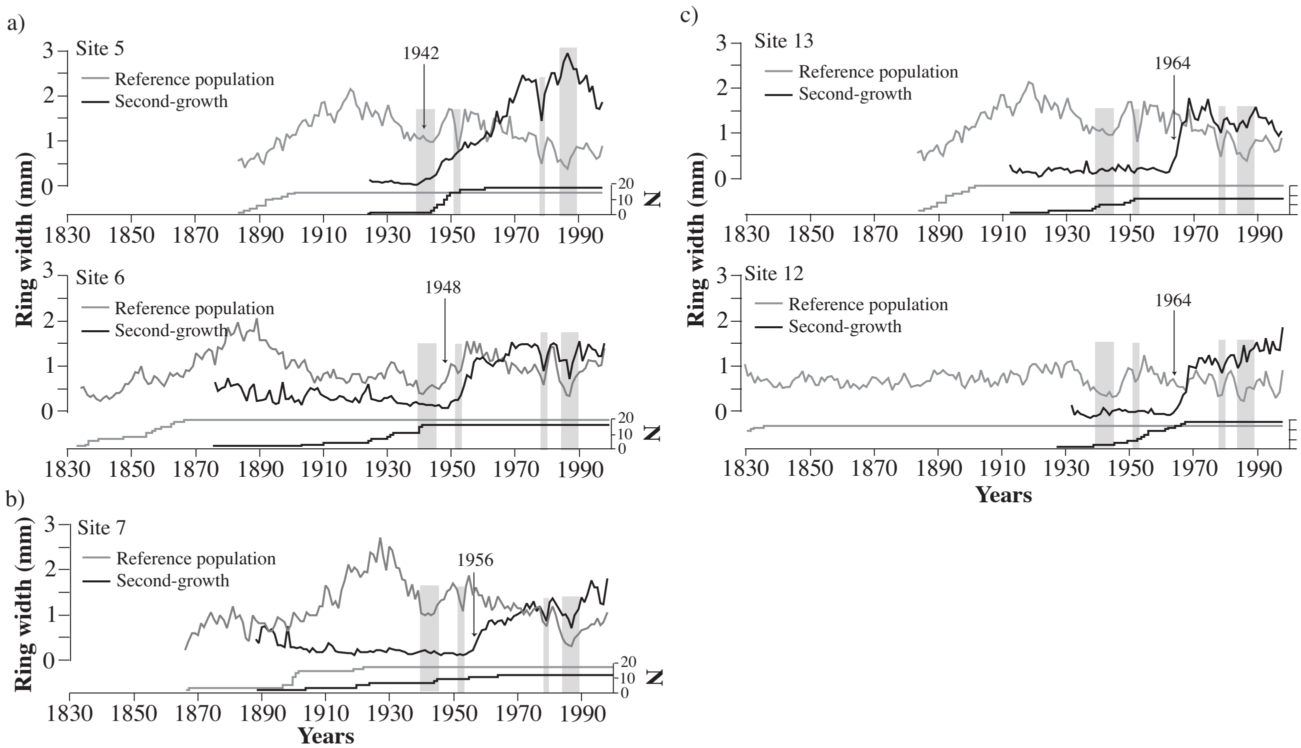

FIGURE 6. Tree-ring width series of black spruce of reference (grey) and second-growth (black) stands harvested during the 1940s (a), in 1956 (b), and the 1960s (c). Grey bars correspond to periods of insect infestation. Sampling depth is plotted below each graph. SD of mean series not shown.

Doucet, 1992) suggest that second-growth stands may recover and reach the state of fire-origin forests provided there is an abundance of well-distributed and tall advance growth left on the cutovers. This clearly was not the case at our sites and likely explains the weak performance of black spruce regeneration after clear-cutting.

GROWTH OF THE REGENERATION

Height-growth performance of most stems growing today in the post-logged sites was lower than predicted by the SI of reference populations. With SI values ranging from 6 m to 8 m at 50 years, forest productivity appears very low throughout the studied sites. Based on Pothier and Savard's local tables (1998), SI values should have extended between 9 to 12 m at 50 years, and differences between growth of the regeneration and predicted values should have been even greater. Low SI can be caused by nutrient-poor soil conditions (nutrient deficiency, extreme acidity) and local climatic conditions. The PGJ climate is cold to the point that the growing season lasts for no more than 80 days in mature black spruce stands (Boisclair, 1990).

The growth of post-logged stems is important because they represent the majority of current populations. However, most of these stems are small and suppressed in dense clusters under the cover of scarce taller trees. Only a few young stems are growing freely in large gaps. As for advance growth, some stems were released and developed well after clear-cut. Height growth remains variable, however, and lower than predicted by yield tables. Variability in height growth is common where small stems are distributed in clusters, as in black spruce layers forming advance regeneration left on cutovers. In this particular case, the whole cluster initially reacts well to opening until one individual becomes dominant and outcompetes its neighbors (Doucet & Boily, 1988; Paquin & Doucet, 1992).

All tree-ring chronologies show several synchronous growth reductions linked to a series of insect infestations that affected the area during the 20th century. Outbreaks of the spruce budworm were reported in the 1910s, 1946 to 1957, 1976-77, and 1981-85 (Blais, 1968; 1985). The European spruce sawfly (*Gilpinia hercyniae* Hartig.) also affected these populations at the end of the 1930s (Payette *et al.,* 2000). Stands 5, 6, and 7 were harvested during or just after a spruce budworm infestation. It is possible that logging was conducted in order to salvage the attacked timber, as was done elsewhere (Morin, Gagnon & Frisque, 1991). This could explain the low values of mean stem diameter and RDI in all sites (except in site 12). Although these stands were already closed crowned, trees in sites 5, 6, 7, and 13 were likely harvested before reaching maximum production. The second-growth populations were also clearly affected by the last outbreak and recorded a corresponding decrease in radial increment similar to reference trees.

Another explanation for the low growth performance of spruce regeneration in the PGJ could be the reduction of site fertility due to soil nutrient depletion after clear-cutting of low-site class black spruce stands. Results from a logged site in northeastern Quebec show that removal of the aboveground portion of trees can lead to severe macronutrient losses (Weetman & Algar, 1983). Also, clear-cutting may lead to changes in soil nutrients that are different from those induced by wildfire (Simard *et al.,* 2001).

Conclusion

The second-growth black spruce stands are today open forests that show little potential to produce mature closed-crown forests several decades after logging, despite having originated from merchantable stands. Advance growth did not succeed, either because there were no individuals left on the cutovers or because they did not survive to today. Some clear-cuts took place during or just after insect infestations, which might have damaged the small regeneration trees. It is possible that some clear-cuts were conducted in order to salvage the attacked timber. Most sites were harvested before attaining their maximum production. The lack of abundant and tall advance regeneration was not offset by any significant establishment of seedlings free to grow after clear-cut; this may explain the opening of the present second-growth black spruce populations.

The growth performance was lower than predicted for low-class black spruce populations. This may be explained, in part, by the large number of stems suppressed in clusters, together with the detrimental effects of the last spruce budworm outbreak. It is also possible that tree removal on such nutrient-poor sites resulted in a significant decrease of site fertility.

Our results show that clear-cutting can lead to the long-lasting opening of black spruce-moss forests. The future development of these stands will be determined by the sequence of natural disturbances (especially insect infestations and forest fires) that will certainly recur again in the area. This underlines the need for management strategies to take into account disturbance regimes, in order to achieve successful renewal of this type of forest. In Quebec, legal and economic reasons cause current forestry practices to favor preservation of advance growth rather than planting. Thus, considerable efforts are made to improve variants of the clear-cutting method that seek to protect advance regeneration while harvesting the overstory. These variants are usually called "careful logging". A better understanding of the impact of perturbations on forest dynamics is also needed, however, and preservation of a greater proportion of sensitive populations should be considered to ensure forest sustainability.

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