

CANADA'S NATURAL RESOURCES
NOW AND FOR THE FUTURE

www.nrcan.gc.ca

Effect of seed production and soil scarification on the natural regeneration of a second-growth fir stand in the Lower St. Lawrence region

Richard Zarnovican



Laurentian Forestry Centre
Information Report LAU-X-127E

2003



Natural Resources
Canada
Canadian Forest
Service

Ressources naturelles
Canada
Service canadien
des forêts

Canada

**Effect of seed production and soil scarification on the
natural regeneration of a second-growth fir stand
in the Lower St. Lawrence region**

Richard Zarnovican

Information Report LAU-X-127E

2003

Natural Resources Canada, Canadian Forest Service
Laurentian Forestry Centre

**NATIONAL LIBRARY OF CANADA CATALOGUING IN
PUBLICATION DATA**

Zarnovican, Richard

Effect of seed production and soil scarification on the natural
regeneration of a second-growth fir stand in the Lower
St. Lawrence region

(Information report, ISSN 0825-1570; LAU-X-127)

Issued also in French under the title: Effet de la production
semencière et de la scarification du sol sur la régénération
naturelle d'une sapinière de seconde venue du Bas-Saint-
Laurent.

ISBN 0-662-34109-0

Cat. No. Fo46-18/127E

1. Balsam fir – Quebec (Province) – Bas-Saint-Laurent –
Growth.
 2. White spruce – Quebec (Province) – Bas-Saint-Laurent –
Growth.
 3. Forest regeneration – Quebec (Province) –
Bas-Saint-Laurent.
- I. Laurentian Forestry Centre.
 - II. Title.
 - III. Series: Information report (Laurentian Forestry Centre);
LAU-X-127.

SD397.B2Z47 2003 634.9'75456'0971476 C2003-980175-6

Cover photo:

Seed collection (R. Zarnovican).

© Her Majesty the Queen in Right of Canada 2003

Catalog Number Fo46-18/127E

ISBN 0-662-34109-0

ISSN 0835-1570

Limited additional copies of this publication are available at no charge from:

Natural Resources Canada

Canadian Forest Service

Laurentian Forestry Centre

1055 du P.E.P.S., P.O. Box 3800

Sainte-Foy, Quebec G1V 4C7

LFC Web Site: <http://www.cfl.scf.mcan.gc.ca>

Copies or microfiches of this publication may be purchased from:

Micromedia Ltd.

240 Catherine St., Suite 305

Ottawa, Ontario K2P 2G8

Tel.: (613) 237-4250

Toll free: 1-800-567-1914

Fax: (613) 237-4251

Cette publication est également offerte en français sous le titre « Effet de la production semencière et de la scarification du sol sur la régénération naturelle d'une sapinière de seconde venue du Bas-Saint-Laurent » (Numéro de catalogue Fo46-18/127F).



TABLE OF CONTENTS

ABSTRACT	v
RÉSUMÉ	v
INTRODUCTION	1
MATERIALS AND METHODS	1
Stand	1
Experimental design	2
Data analysis	3
RESULTS	4
Seed production	4
Seedling establishment and survival between 1997 and 2001	6
Balsam fir	6
White spruce	7
Status of regeneration in 2001	9
Balsam fir seedling density	9
White spruce seedling density	10
Height of dominant seedlings	10
DISCUSSION	11
Seed production	11
Seedling establishment and survival	12
Seedling height in 2001	13
CONCLUSIONS	13
ACKNOWLEDGEMENTS	14
REFERENCES	14

LIST OF TABLES

Table 1.	Mensuration characteristics of the 400 m ² plots	2
Table 2.	Number of seeds/m ² (mean \pm standard error) by species and period	5
Table 3.	Balsam fir seedling density in 2001, by soil treatment	9
Table 4.	White spruce seedling density in 2001, by soil treatment	10
Table 5.	Seedling height in 2001, by species and soil treatment	11

LIST OF FIGURES

Figure 1.	Seed production (mean \pm standard error) by period and species	5
Figure 2.	Mean density of viable seeds and seedlings by period and soil preparation – balsam fir	6
Figure 3.	Mean density of viable seeds and seedlings by period and soil preparation – white spruce	8

Zarnovican, R. 2003. Effect of seed production and soil scarification on the natural regeneration of a second-growth fir stand in the Lower St. Lawrence region. Nat. Resour. Can., Can. For. Serv., Laurentian For. Cent., Sainte-Foy, Que. Inf. Rep. LAU-X-127E.

ABSTRACT

This study examines the relationship between seed production, soil scarification and seedling establishment in balsam fir (*Abies balsamea* [L.] Mill.) and white spruce (*Picea glauca* [Moench] Voss). It was conducted as part of a trial of natural regeneration following shelterwood cutting in a second-growth fir stand in the Lower St. Lawrence region. In fir, relatively good seed production occurs on a two-year cycle, whereas the seed production cycle of white spruce varies. In the absence of a buried seed bank, seed production plays a critical role in the success of natural regeneration. Scarification, and particularly the presence of the mineral soil component of the seedbed, has a very significant effect during seedling establishment in the two species. The seedling recruitment process is active for the first three years; this is followed by a high rate of seedling mortality and seedbed deterioration. Canopy opening, expressed by canopy transmittance, does not have a significant effect on seedling density or the height of dominant seedlings in the two species. The experiment shows that it is possible to increase the proportion of white spruce in the stand by synchronizing scarification with seed production.

Zarnovican, R. 2003. Effet de la production semencière et de la scarification du sol sur la régénération naturelle d'une sapinière de seconde venue du Bas-Saint-Laurent. Ressour. nat. Can., Serv. can. for., Cent. for. Laurentides, Sainte-Foy, Qc. Rapp. inf. LAU-X-127.

RÉSUMÉ

L'étude examine les relations entre la production semencière, la scarification du sol et l'installation des semis du sapin baumier (*Abies balsamea* [L.] Mill.) et de l'épinette blanche (*Picea glauca* [Moench] Voss). Elle a été réalisée dans le cadre d'un essai de la régénération naturelle par la coupe progressive dans une sapinière de seconde venue du Bas-Saint-Laurent. La production semencière plus ou moins abondante suit un cycle de deux ans chez le sapin, alors que le cycle de l'épinette blanche est variable. En l'absence d'une réserve de graines enfouies, la production semencière joue un rôle capital dans la réussite de la régénération naturelle. L'effet de la scarification, en particulier la présence de la composante minérale du lit de germination, est très important lors de l'installation des semis des deux essences. Le processus de recrutement des semis est actif pendant les trois premières années; par la suite, il y a un fort taux de mortalité des semis et une détérioration des lits de germination. L'ouverture du peuplement exprimée par la transmittance du couvert n'a pas d'effet significatif sur la densité des semis, ni sur la hauteur des semis dominants des deux essences. L'expérience démontre que la synchronisation de la production semencière et de la scarification permet d'augmenter la proportion de l'épinette blanche dans la composition du peuplement.

INTRODUCTION

Since the 1940s, logging, insect outbreaks and birch dieback have profoundly altered the composition of the balsam fir—yellow birch stands of the Lower St. Lawrence and Gaspé Peninsula regions (Hatcher 1960; Hatcher 1963; Majcen and Gagnon 1976; Archambault et al. 1997; Laflèche et al. 2000). Balsam fir has been favoured to the detriment of other species and existing second-growth stands are generally dominated by balsam fir (Bérard and Côté 1996). Some authors believe that logging has contributed significantly to the development of balsam fir, particularly by means of a more abundant advance regeneration of fir (Hatcher 1960; Hatcher 1963; Frisque et al. 1978; Harvey and Bergeron 1989). The current dominance of fir in balsam fir—yellow birch stands contrasts with the pre-1940s stand composition, when balsam fir made up only 46% of the stand volume in this bioclimatic domain (Gobeil 1938), with white spruce accounting for over 30% and deciduous species accounting for over 15% of the stand volume.

Because this bioclimatic domain is very productive, it is believed necessary to increase the proportion of other species, particularly white spruce (Ministère des Ressources naturelles du Québec 1994; Bérard and Côté 1996). Such a strategy would increase the resistance of the stands to spruce budworm (*Choristoneura fumiferana* [Clem.]) and red rot or improve wood quality at harvest (Jessome 1977; MacLean 1984; Gagnon and Chabot 1988; Zarnovican 1998).

In the context of even-aged management, shelterwood cutting is considered to be an effective regeneration method (Blum 1973; Hannah 1988; Perala and Alm 1989; Matthews 1994; Burschel and Huss 1997). Various experiments have shown that it creates conditions favourable to seedling establishment in various species, particularly white spruce (Baldwin 1977; Zasada and Grigal 1978; Childs and Flint 1987; Hannah 1988; Frank 1990; Youngblood 1990; Man and Lieffers 1997; Wurtz and Zasada 2001). In brief, this natural regeneration method consists of preparatory and seedling cuttings, proper soil preparation and, once the young crop is well established in the desired composition and density, final cutting (Matthews 1994; Burschel and Huss 1997). This approach is based on detailed and specific knowledge of the site and, if natural regeneration is to succeed, the forest manager must consider the stand condition, site quality and the autoecology of the species to be regenerated (Brand 1988; Matthews 1994; Burschel and Huss 1997). However, little information is available on shelterwood cutting or on seed dynamics in relation to natural regeneration in the balsam fir—yellow birch climatic domain of the Lower St. Lawrence region (Bérard and Côté 1996).

In this context, an experiment was carried out between 1996 and 2001 with natural regeneration in a second-growth fir stand in the balsam fir—yellow birch climatic domain of eastern Quebec. The objectives of the five-year experiment were: 1) to assess seed production and its variations for the main species; 2) to assess the seedling establishment process in balsam fir and white spruce and its temporal variations; and 3) to evaluate the effect of soil scarification on balsam fir and white spruce seedling establishment.

MATERIALS AND METHODS

Stand

The study was carried out in the Lower St. Lawrence Model Forest (lat. 48°17'N, long. 67°50'W, alt. 310 m). The stand is a 60-year-old regular high forest dominated by balsam fir and resulting from clearcuts performed in the 1940s (Hatcher 1963). The stand has a density of 1590 stems per hectare, a basal area of 35.6 m²/ha, a softwood merchantable volume of 260 m³/ha, and an average dominant and codominant height of 16.5 m. On the basis of site index and production, the stand corresponds to stand class 1, using the tables of Vézina and Linteau (1968).

According to Thibault (1986), the stand is part of the southern portion of the balsam fir—yellow birch climatic domain. It is located at the centre and base of a moderate slope (16%) balsam with southwest exposure. Surficial material consists of moderately to well drained loamy till. The climate is subpolar subhumid continental (Proulx et al. 1987). The mean annual temperature is 2.3°C and annual precipitation totals 950 mm.

The stand has been affected by spruce budworm outbreaks (Hatcher 1963), and two significant balsam fir growth reductions occurred between 1949 and 1964, and between 1971 and 1985 (Zarnovican and Laberge 1998). In large-diameter trees, balsam fir has a high rate of red rot (Zarnovican 1998). Preparatory cutting of four different intensities was carried out in the stand in 1994 (Zarnovican et al. 2001).

Experimental design

The study of natural regeneration was carried out using an experimental design established to study the effect of preparatory cutting on residual stand growth (Zarnovican et al. 2001). Six of the 16 plots (Table 1) were randomly selected and a square area measuring 20 m x 20 m was delineated at the centre of each. This area was in turn divided into 100 2 m x 2 m squares and, in August 1996, an area of 1 m x 1 m was delineated at the centre of each square.

Table 1. Mensuration characteristics of the 400 m² plots.

Plot	Species	dbh (cm)	Number of stems	dbh _{min} (cm)	dbh _{max} (cm)	Basal area (m ²)
1	BF	19.1±0.7	31	14.1	32.6	0.926
1	RM	14.0±0.0	1	14.0	14.0	0.015
1	CP	16.9±0.0	1	16.9	16.9	0.022
4	BF	20.0±0.8	24	13.0	30.7	0.778
4	RM	15.7±1.4	4	12.2	18.9	0.079
4	WS	15.3±2.3	2	13.0	17.6	0.038
9	BF	16.3±0.4	53	11.5	25.6	1.144
9	WB	8.4±0.9	2	7.5	9.4	0.011
9	RM	8.5±0.3	2	8.2	8.8	0.011
9	WS	21.5±3.5	3	14.9	26.9	0.115
9	YB	26.0±0.0	1	26.0	26.0	0.053
10	BF	17.9±0.6	31	13.4	25.2	0.804
10	WB	12.7±0.0	1	12.7	12.7	0.013
10	RM	16.4±4.2	3	11.9	24.7	0.071
13	BF	16.1±0.6	29	10.0	22.4	0.610
13	WS	22.3±2.5	4	17.1	28.7	0.162
18	BF	15.3±0.4	58	9.9	21.6	1.099
18	WB	10.8±1.2	4	8.0	13.6	0.038
18	WS	22.5±2.3	9	13.2	30.4	0.387

BF – Balsam fir; WS – White spruce; RM – Red maple (*Acer rubrum* L.); CP – Pin cherry (*Prunus pensylvanica* L.); WB – White birch (*Betula papyrifera* Marsh.); YB – Yellow birch (*Betula alleghaniensis* Britton); dbh: mean ± standard error; dbh_{min} – minimum dbh; dbh_{max} – maximum dbh.

Given the beneficial impact of some scarification techniques on natural regeneration (Spittlehouse and Childs 1992; Fleming et al. 1994; Lieffers and Beck 1994), four soil surface treatments were carried out. These treatments are: “control”, with no surface treatment; “humus”, with removal of the living organic layer; “mineral”, with removal of the organic layer to the mineral soil; and “mixed”, with removal of the living organic layer and the AH layer mixed with the mineral soil. Given that we wished to determine the effect of the treatments on natural regeneration at the stand level, each

treatment was randomly assigned to the 1 m x 1 m squares, with five replicates in each plot. It is a completely randomized experiment with repeated measurements over time. In the establishment of the design in 1996, all seedlings were removed from the 1 m x 1 m squares, and the squares selected for treatment were manually scarified using a rake. Seedling density was noted at the end of August between 1997 and 2001. The inventory was conducted on 30 cm x 30 cm microplots set in the centre of the 1 m x 1 m squares by means of permanent markers; these microplots correspond to the experimental units. In August 2001, the total number of seedlings in the microplots and the seedlings of the last year (2001) were counted and the height of two dominant seedlings was measured. We consider that the height of dominant seedlings in 2001 represents the height of the seedlings after five years. The number of 2001 seedlings was compared with the number of seedlings counted in the six microplots of a neighbouring experimental design established by Dr. J.-M. Lussier in 2000. These microplots were scarified in 2000 and the seedbed corresponds to mixed organic/mineral soil.

Seed dynamics were studied using seeds collected in traps (60 cm x 40 cm x 7 cm) between 1995 and 2001. A seed trap was placed on a horizontal support in the centre of each 400 m² plot and covered with wire mesh to protect the seeds from pests. Seeds were collected with the litter in early November of the current year and late May of the following year; e.g., the winter collection of 1996/1997 is identified "May 1997". To determine the effect of the stand on seed collection in the traps, the dbh and the position of trees near the trap were noted by species.

In the laboratory, the collected seeds were identified, separated into intact seeds (no visible defects) and altered seeds (empty seeds or seeds damaged by seed-eating insects), and counted. The intact seeds of November were weighed and exposed to stratification under cool conditions (temperature of 2°C) for 30 days before the germination test; the intact seeds of May were subjected directly to the germination test. The germinative capacity of the seeds was evaluated at a day temperature of 27°C and night temperature of 20°C, with a relative humidity of 90% and a 16-h day length, for 28 days. Germination was considered successful when the young cotyledon of the germinant reached a minimum length of 5 mm. Multiplying the germination rate by the number of intact seeds gives the number of viable seeds. The litter collected in the traps was air dried, weighed and separated into percentages of leaves, needles, inflorescences, bracts and others.

To take account of the effect of the preparatory cutting of 1994 on natural regeneration, physiologically active radiation (PAR) was measured in June 2000 using two ceptometers (model SF-80, Decagon Devices Inc., Pullman, WA). Simultaneous readings were taken between 11:00 a.m. and 1:00 p.m. on a sunny day, one in full sun (PAR_{SU}) and the other above the 30 cm x 30 cm microplots (PAR_{PL}). The ratio of the two readings (PAR_{PL}/PAR_{SU}), or canopy transmittance, reflects the light environment of the seedlings (Carter and Klinka 1992; Brown and Parker 1994) and, consequently, the effect of canopy opening by the preparatory cutting of 1994 on seedling density and height.

Data analysis

Changes in seedling density between 1997 and 2001 at the stand level were evaluated using profile analysis, a repeated-measures analysis of variance method (SAS Institute Inc. 1999). This analysis looks at seedling density (response) in four soil treatments (groups) sampled in five observation periods (conditions). Profile analysis is based on three tests: 1) the first (parallelism test) studies whether the temporal profiles of the mean density of the four soil treatments are parallel. A rejection of the hypothesis of parallelism implies an interaction between the observation period and the soil treatment, and indicates that the effect of the soil treatment is not the same at all observation periods; 2) the second (level test) studies the changes in the number of seedlings in time. Rejection of the hypothesis of equal levels indicates significant changes in the number of seedlings in time; 3) the third test compares mean densities between soil treatments. Rejection of the hypothesis of equal conditions indicates different seedling densities between at least two soil treatments. In the presence of a significant interaction between the observation period and the soil treatment, tests of the effect of the

soil treatments are performed for each observation period. The study of periods comprising two successive years is another option used to explain the results in the presence of interaction, and allows for a study of annual regeneration and mortality. All treatments are carried out using the GLM procedure of SAS; in the case of the profile analyses, the REPEATED option is used.

To determine the outcome of the experiment, the state of regeneration was evaluated in 2001. To this end, the effect of scarification and transmittance on all seedlings counted in the microplots in 2001, on the average height of two dominant seedlings measured in 2001, and on seedling mortality between 1999 and 2001, was studied. This study was conducted by analysis of covariance and the means were separated using the Games-Howell test. The latter was used for its robustness to violations of the hypotheses of normality of residuals and homogeneity of variance (Games and Howell 1976).

Normality of residuals was tested using the Kolmogorov-Smirnov test and homogeneity of variance was tested using the Levene test. In the absence of homogeneity of variance or normality of residuals, the conclusions were tested using transformed data based on the procedure of Anderson and McLean (1974), or using a non-parametric analysis using ranks.

RESULTS

Seed production

Seed production varied in time and by species between 1994 and 2001 (Table 2). With the exception of very small crops of other species (red maple, pin cherry and yellow birch), relatively good seed production in balsam fir occurs in a 2-year cycle (Figure 1). Seed production in spruce does not follow a two-year cycle; in the seven years of the study, only two good crops were observed (1995 and 1997). The 1997 crop (following the establishment of the regeneration experimental design in 1996) was particularly good with a mean germination rate of 86% for the experimental design. The production cycle of birch is similar to that of spruce, with very small crops, undoubtedly due to the small number of birch trees in the stand. The production cycle of cedar (WC – Eastern white-cedar (*Thuja occidentalis* L.)) cannot be described on the basis of the negligible quantities of seeds produced by the few solitary trees present in the stand. During the study period, fir accounted for 81% of the seeds produced, spruce accounted for 15%, white birch for 3% and other species for 1%. This distribution no doubt reflects the stand composition in basal area (balsam fir: 84%; white spruce: 11%; red maple: 3%; white birch: 1%; others: 1%).

Table 2. Number of seeds/m² (mean \pm standard error) by species and period.

Species	Period	Traps	Collected	Intact	Viable	Germination rate (%)
BF	1994/1995	6	2,863 \pm 110	2,774 \pm 95	1,012 \pm 56	36.5 \pm 1.5
BF	1995/1996	6	0 \pm 0	0 \pm 0	0 \pm 0	0.0 \pm 0.0
BF	1996/1997	6	1,074 \pm 235	524 \pm 127	192 \pm 51	33.4 \pm 3.2
BF	1997/1998	6	0 \pm 0	0 \pm 0	0 \pm 0	0.0 \pm 0.0
BF	1998/1999	6	1,290 \pm 133	1,290 \pm 133	386 \pm 62	29.7 \pm 2.6
BF	1999/2000	6	48 \pm 15	15 \pm 8	2 \pm 2	3.8 \pm 3.8
BF	2000/2001	6	2,031 \pm 294	999 \pm 109	260 \pm 44	28.2 \pm 7.3
WS	1994/1995	6	419 \pm 109	417 \pm 109	127 \pm 39	31.2 \pm 4.6
WS	1995/1996	6	0 \pm 0	0 \pm 0	0 \pm 0	0.0 \pm 0.0
WS	1996/1997	6	799 \pm 257	569 \pm 197	488 \pm 166	86.2 \pm 2.7
WS	1997/1998	6	0 \pm 0	0 \pm 0	0 \pm 0	0.0 \pm 0.0
WS	1998/1999	6	12 \pm 7	12 \pm 7	3 \pm 1	18.8 \pm 10.1
WS	1999/2000	6	0 \pm 0	0 \pm 0	0 \pm 0	0.0 \pm 0.0
WS	2000/2001	6	148 \pm 31	148 \pm 31	57 \pm 21	35.1 \pm 7.3
WB	1994/1995	6	101 \pm 42	101 \pm 42	37 \pm 14	44.1 \pm 5.2
WB	1995/1996	6	0 \pm 0	0 \pm 0	0 \pm 0	0.0 \pm 0.0
WB	1996/1997	6	72 \pm 43	67 \pm 42	22 \pm 12	37.8 \pm 9.9
WB	1997/1998	6	0 \pm 0	0 \pm 0	0 \pm 0	0.0 \pm 0.0
WB	1998/1999	6	2 \pm 1	2 \pm 1	1 \pm 1	8.3 \pm 8.3
WB	1999/2000	6	2 \pm 1	0 \pm 0	0 \pm 0	0.0 \pm 0.0
WB	2000/2001	6	97 \pm 73	97 \pm 73	22 \pm 18	8.9 \pm 5.7
WC	1994/1995	6	21 \pm 7	21 \pm 7	15 \pm 5	65.4 \pm 14.6
WC	1995/1996	6	0 \pm 0	0 \pm 0	0 \pm 0	0.0 \pm 0.0
WC	1996/1997	4	17 \pm 6	17 \pm 6	6 \pm 4	25.5 \pm 11.8
WC	1997/1998	6	0 \pm 0	0 \pm 0	0 \pm 0	0.0 \pm 0.0
WC	1998/1999	6	10 \pm 6	10 \pm 6	7 \pm 4	42.6 \pm 20.2
WC	1999/2000	5	2 \pm 2	2 \pm 2	0 \pm 0	0.0 \pm 0.0
WC	2000/2001	6	13 \pm 5	13 \pm 5	2 \pm 1	16.7 \pm 10.5

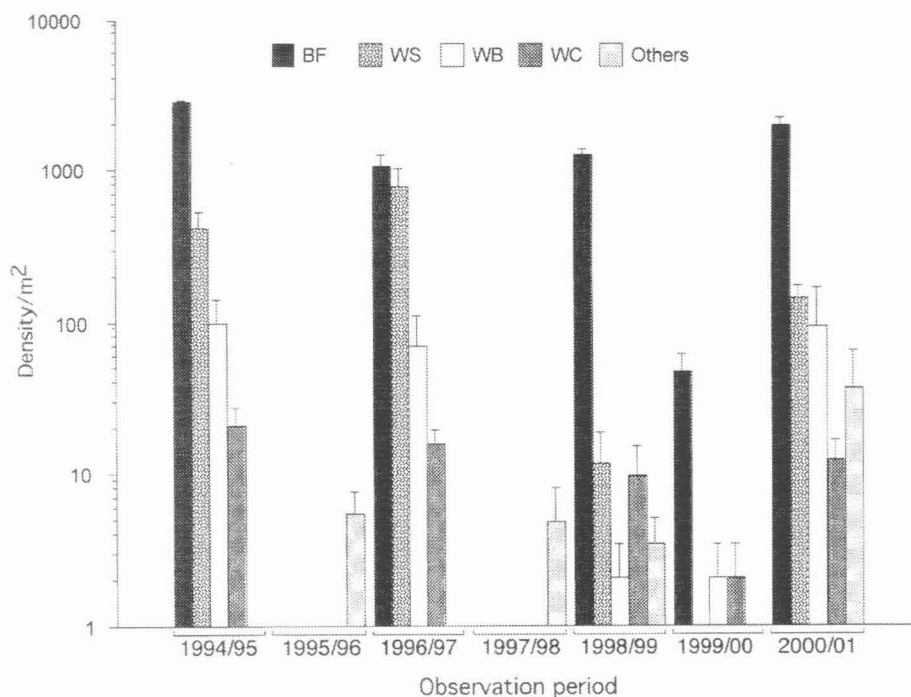


Figure 1. Seed production (mean \pm standard error) by period and species.

Although the fir seed crop may seem high (Table 2), the proportion of seeds likely to germinate and to produce seedlings is much lower. During the five seed years, balsam fir produced on average 1461 seeds/m², but only 25.3% were viable. In spruce, birch and cedar (Table 2), average seed production for the same period was 344, 55 and 13 seeds/m², respectively, with a viable seed rate of 49, 30 and 48%, respectively. The viable seed crop for the stand therefore consisted of 66% fir, 30% spruce, 3% birch, and 1% cedar.

For the study period, the average germinative capacity of the species based on viable seeds was 26, 43, 20 and 30% for fir, spruce, birch and cedar, respectively. The correlation between seed production and germination rate is significant for fir ($p < 0.000$) and spruce ($p = 0.026$), but not significant for birch ($p = 0.82$) and cedar ($p = 0.66$).

The study of the relationships between the number of seeds per trap, the average distance, mean dbh and maximum dbh of the trees around the trap revealed only one significant relationship, i.e., between the maximum dbh of firs located west of the traps and the number of fir seeds ($p = 0.01$).

Seedling establishment and survival between 1997 and 2001

Balsam fir

Balsam fir seedling density varied by year and soil treatment (Figure 2). After moderate seed production in 1996/1997 (192 viable seeds/m²), there were between 7 and 83 seedlings/m² (depending on the soil treatment) in 1997. There was no recruitment in 1998. After good seed production in 1998/1999 (386 viable seeds/m²), recruitment peaked in 1999 with between 67 and 233 seedlings/m². In 2000, there was no recruitment, but there was mortality, as there was in 2001. Mortality in 2001 occurred despite good viable seed production (260 viable seeds/m²).

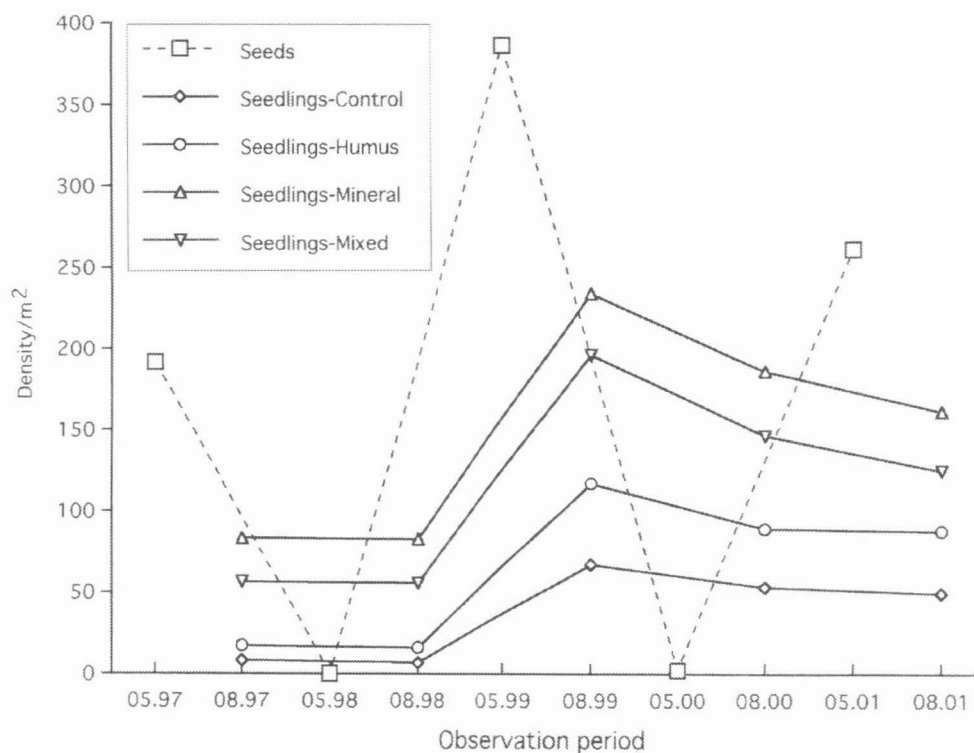


Figure 2. Mean density of viable seeds and seedlings by period and soil preparation – balsam fir.

These observations were confirmed by the profile analysis, which indicated that annual changes in seedling density were not the same between soil treatments, since there was a significant interaction between observation periods and soil treatments ($p = 0.019$). Moreover, despite the significant interaction, overall tests indicate that the period ($p < 0.0001$) and soil treatment ($p < 0.0001$) have highly significant effects on seedling density.

In order to clearly describe the presence of interaction between observation periods and soil treatments, the study of the variations in seedling density between the two consecutive years is presented. The study indicates that between 1997 and 1998, the number of seedlings did not change significantly ($p = 0.68$ for the level test) in any of the soil treatments ($p = 0.999$ for the parallelism test). These results suggest that seedling establishment in 1997 was controlled by the seedbed, and seedling density remained virtually unchanged in 1997 and 1998. Analyses of variance by year indicate that the soil treatments were significantly different in 1997 ($p < 0.0001$) and 1998 ($p < 0.0001$). For the two years, the mineral soil and mixed organic/mineral soil resulted in greater seedling recruitment than the humus or control.

In 1999, the number of seedlings increased significantly ($p < 0.0001$) compared with 1998. Seedling recruitment is significantly affected by the seedbed ($p < 0.0001$) and the highest number of seedlings was found in the mineral soil and in the organic/mineral soil. The profile analysis indicates a substantial reduction in the number of seedlings between 1999 and 2000 ($p < 0.0001$); this reduction varies significantly ($p = 0.0118$) between soil treatments. For the period 2000 and 2001, the profile analysis indicates a considerable decline in seedling density ($p = 0.0011$), with no significant difference in the decline in density between soil treatments ($p = 0.068$).

In the last three years, i.e. between 1999 and 2001, balsam fir seedling mortality was 9% on the control, 3% on humus, 26% on the mineral soil, and 34% on the mixed organic/mineral soil.

In the analyses of variance by year, the normality of the residuals and the homogeneity of the variance are rejected. The $1/x$ transformation corrects the non-homogeneity of variance, whereas the non-parametric analysis takes account of the two restrictive characteristics (non-normality and non-homogeneity). In all cases, the conclusions are identical to the conclusions on raw data. It can therefore be concluded that the non-normality of the residuals and the non-homogeneity of variance do not influence the conclusions on raw data.

The analyses of variance by year indicate that the mineral and organic/mineral treatments continue to yield a significantly higher number of seedlings than the other treatments, despite a higher mortality rate.

White spruce

Seedling establishment in white spruce (Figure 3) is different from that of balsam fir (Figure 2), and this difference is undoubtedly the result of the specific seed production cycle. During the study period, there were three viable balsam fir seed crops and only one good spruce seed crop (488 seeds/m²), in 1996/1997. Moreover, following massive white spruce establishment in 1997, there was virtually no recruitment of new seedlings (Figure 3).

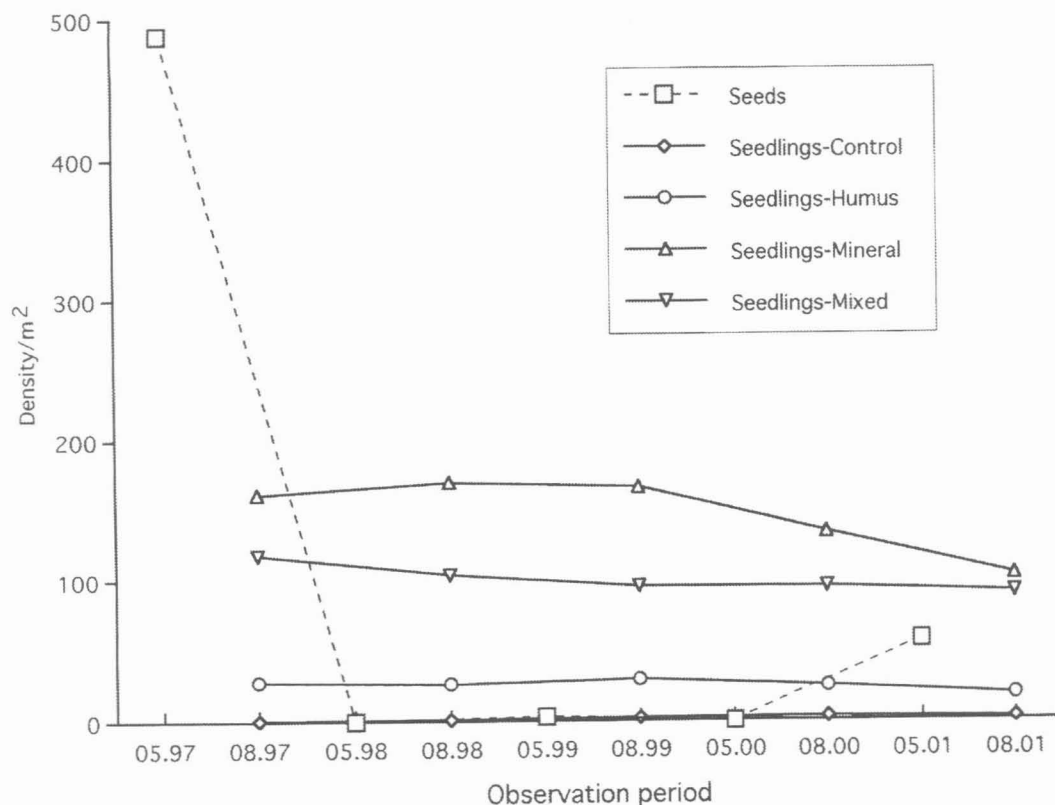


Figure 3. Mean density of viable seeds and seedlings by period and soil preparation – white spruce.

The results of the profile analysis indicate that annual changes in seedling density differ between scarification treatments. There is a significant interaction between these two factors ($p < 0.0001$ for the parallelism test). Despite the presence of a significant interaction term, the global tests lead to the conclusion that the soil treatments ($p < 0.0001$) and time ($p < 0.0001$) have a very significant effect on white spruce seedling density. In other words, white spruce seedling density per square metre varies significantly between years and between soil treatments, but annual variations are not the same for all types of scarification.

The study of variations between two consecutive years indicates that the number of seedlings (Figure 3) did not change between 1997 and 1998 ($p = 0.75$ for the level test) and density remained unchanged for the four scarification treatments ($p = 0.49$ for the parallelism test). On average, one seedling/m² was counted on the unscarified soil, 26 on humus, 165 on the mineral soil, and 110 on the mixed organic/mineral soil. According to the results of the level ($p = 0.59$) and parallelism ($p = 0.70$) tests, white spruce seedling density between 1998 and 1999 and between 1997 and 1998 was similar.

Between 1999 and 2000, white spruce seedling density declined significantly ($p = 0.0005$), and the decline varied significantly between scarification treatments ($p < 0.0001$). The substantial decline in seedling density continued between 2000 and 2001 ($p < 0.0001$), varying significantly between scarifications ($p = 0.0001$). In the last three years, i.e. between 1999 and 2001, average seedling mortality was 38% on the mineral soil, 2% on the mixed organic/mineral soil, 16% on humus, and 33% on the unscarified soil.

The study of the variations between two consecutive years indicates that the homogeneity of variance is rejected for some years, but no transformation makes it possible to improve the situation.

Normality of residuals is rejected and the non-parametric analyses yield the same conclusions as the analyses of raw data. It can therefore be concluded that the non-normality of the residuals and the non-homogeneity of variance do not affect the conclusions on raw data.

The one-way analyses of variance (scarification) by year indicates that the mineral and organic/mineral treatments result in the establishment of a larger number of seedlings than the other two treatments.

Status of regeneration in 2001

Balsam fir seedling density

The results of the analysis of covariance between soil treatments, transmittance as a covariable, and balsam fir seedling density in 2001 are based on the acceptance of the hypothesis of normality of residuals ($p = 0.237$) and the rejection of the hypothesis of homogeneity of variance ($p < 0.0001$). The logarithmic transformation provides the best transformation. However, the analysis of transformed data yielded the same results as the analysis of raw data; the results of the analysis of raw data were therefore retained.

The results of this analysis indicate that transmittance does not differ significantly between soil treatments ($p = 0.71$), that soil treatment had a significant effect ($p = 0.0005$) on balsam fir seedling density in 2001, and that there is no significant relationship between seedling density and transmittance ($p = 0.81$).

The Games-Howell test indicates that in order for natural regeneration of balsam fir to be successful, the best seedbed is the mineral layer, followed by the mixed organic/mineral layer and humus (Table 3). The lowest level of natural regeneration was obtained on the control.

Table 3. Balsam fir seedling density in 2001, by soil treatment.

Soil treatment	Number of seedlings/m ²
Mineral	160 a
Mixed	124 ab
Humus	87 bc
Control	49 c

According to the Games-Howell test ($p = 0.05$), means with the same letters do not differ significantly between soil treatments.

The data on viable seeds collected between 1997 and 2001, combined with the data on seedling density in 2001, support the conclusion that in order to establish one balsam fir seedling per square metre, 46 viable seeds are required for the unscarified surface, 24 seeds for humus, 12 seeds for the mineral soil and 16 seeds for the mixed organic/mineral soil.

The analysis showed no significant linear regressions between the mean seedling density in 2001 and the number of balsam fir stems per 400 m² plot (control: $p = 0.14$; humus: $p = 0.66$; mineral: $p = 0.67$; mixed: $p = 0.94$).

The number of new fir seedlings in 2001 is significantly higher ($p < 0.0001$, t test) on the mixed organic/mineral soil prepared in 2000, with 118 new seedlings/m², than on the mixed organic/mineral soil prepared in 1996, with only 28 new seedlings/m².

White spruce seedling density

For the analysis of covariance between soil treatments, canopy transmittance as a covariable, and white spruce seedling density in 2001, the hypothesis of normality of the residuals is accepted ($p = 0.056$) and the hypothesis of homogeneity of variance is rejected ($p < 0.0001$). The reciprocal transformation provides the best transformation. However, the analysis of transformed data yielded the same results as the analysis of raw data; the results of the analysis of raw data were therefore retained.

The results of this analysis show that transmittance does not differ significantly between the soil treatments ($p = 0.67$), that soil scarification has a significant effect ($p = 0.0004$) on spruce seedling density and that there are no significant relationships ($p = 0.49$) between seedling density and transmittance.

The multiple comparisons of seedling densities in 2001 between soil treatments using the Games-Howell test indicate that the best seedbeds for regenerating white spruce are the mineral layer and the mixed organic/mineral layer (Table 4); the organic layer is an average seedbed and the unscarified soil is the worst seedbed.

Table 4. White spruce seedling density in 2001, by soil treatment.

Soil treatment	Number of seedlings/m ²
Mineral	103 a
Mixed	90 a
Humus	18 b
Control	2 c

According to the Games-Howell test ($p = 0.05$), means with the same letters do not differ significantly between soil treatments.

The data on viable seeds collected between 1997 and 2001, combined with data on seedling density in 2001, support the conclusion that in order to establish one white spruce seedling per square metre, 126 viable seeds/m² are required on average for the unscarified surface, 49 seeds/m² for humus, 6 seeds/m² for the mineral soil, and 8 seeds/m² for the mixed organic/mineral soil.

Linear regressions between mean seedling density and the number of white spruce stems in 2001 per 400 m² plot show significant relationships for the soil treatments (mixed: $p = 0.006$; humus: $p = 0.03$; mineral: $p = 0.03$) and non-significant for the control ($p = 0.73$).

In 2001, we observed the establishment of one new white spruce/m² on the mixed organic-mineral soil prepared in 1996, and seven on a similar seedbed prepared in 2000. The t test suggests that these two densities are not significantly different ($p = 0.068$).

Height of dominant seedlings

The analysis looks at the mean height of two dominant seedlings per 30 cm x 30 cm microplot for balsam fir and white spruce in 2001, by soil treatment and canopy transmittance. The results of the linear regressions between canopy transmittance and mean fir seedling height indicate that there are no significant relationships between these two variables for the different soil scarifications (control: $p = 0.187$; humus: $p = 0.551$; mineral: $p = 0.089$; mixed: $p = 0.565$). Similar results were obtained for white spruce (control: $p = 0.642$; humus: $p = 0.987$; mineral: $p = 0.235$; mixed: $p = 0.205$).

Given these results, canopy transmittance is not used as a covariable and the analysis considers only the effect of the soil treatment. In the case of balsam fir, the hypothesis of normality of residuals is accepted ($p = 0.425$) and the hypothesis of homogeneity of variance must be rejected ($p < 0.0001$). The logarithmic transformation provides the best transformation. However, the analysis of

transformed data yielded the same results as the analysis of raw data; the results of the analysis of raw data will therefore be retained. In the case of white spruce, the hypothesis of normality is accepted ($p = 0.669$) as is the hypothesis of homogeneity of variance ($p = 0.313$).

The results of the analysis indicate that soil treatment has a significant effect on the height of dominant seedlings, both in balsam fir ($p < 0.0001$) and white spruce ($p = 0.005$). The multiple comparison of fir heights (Table 5) indicates that the best terminal growth is achieved on mineral soil and mixed organic/mineral soil (similar mean heights), and that it is significantly greater than the mean height observed on humus and unscarified soil (similar mean heights). In the case of spruce (Table 5), this comparison indicates that the best terminal growth is obtained on mixed organic/mineral soil, followed by mineral soil, humus and unscarified soil.

Table 5. Seedling height in 2001, by species and soil treatment.

Soil treatment	Mean height (mm)	
	Fir	Spruce
Mineral	83.1 a	82.3 ab
Mixed	80.5 a	85.6 a
Humus	54.9 b	56.6 bc
Control	43.5 b	46.8 c

According to the Games-Howell test ($p = 0.05$), means with the same letters do not differ significantly between soil treatments.

The comparison of the height of the fir and spruce seedlings using a paired t test indicates that the mean heights of the two species are similar between the various scarification treatments (control: $p = 0.973$; humus: $p = 0.305$; mineral: $p = 0.731$; mixed: $p = 0.443$).

DISCUSSION

Seed production

Between 1994 and 2001, seed production in the stand varied in time and by species. In balsam fir, relatively good seed production occurs in a 2-year cycle; this cycle seems to be consistent with that generally observed in the literature (Bakuzis and Hansen 1965; Godman and Mattson 1976; Owens and Molder 1977; Edwards 1986; Burns and Honkala 1990; Grenier 1995).

The seed production cycle of spruce is not clearly defined; in the seven years of observation, there were only two good seed years (1995 and 1997). Moreover, the temporal variability of viable seed production (between 2 and 6 years or more) seems to be characteristic of white spruce (Bean and Prielipp 1961; Dobbs 1972; Cavers 1983; Bell 1991).

While the periodicity of good seed years depends on water and nutrient distribution between the tree's reproductive and vegetative organs (Godman and Mattson 1976; Edwards 1986; Fenner 1991), the abundance of viable seeds is governed by the prevailing climatic conditions during flowering (Cavers 1983; Fenner 1991). The results obtained with respect to viable seed production and germination rates in fir and white spruce are comparable to provincial averages (Grenier 1995) and to published data for fir (Bakuzis and Hansen 1965) and white spruce (Hennessey 1970; Dobbs 1976; Bell 1991).

It is reported in the literature that abundant seed dispersal is favoured by tree height, seed weight and wind velocity (Bakuzis and Hansen 1965; Alexander and Edminster 1983; Bell 1991). Our

results show that only tree vigour, combined with dominant westerly winds, promotes balsam fir seed dispersal.

A number of authors have suggested that seed trees that are well formed by preparatory cutting and that produce viable seeds make it possible to shorten the interval between seed years (Edwards 1986; Burschel and Huss 1997; Matthews 1994).

Seedling establishment and survival

The success of seedling establishment is directly dependent on the quantity of viable seeds and proper soil preparation. Given that the germinative capacity of buried conifer seeds is nil after the first year (Frank and Safford 1970; Archibold 1989; Hills and Morris 1992; Zarnovican and Laberge 1997), it is critical, if we wish to increase the proportion of white spruce, to synchronize soil preparation with good viable seed production.

The significant effect of the seedbed on fir and spruce seedling recruitment in the first three years confirms the conclusions of Davis and Hart (1961), Bakuzis and Hansen (1965), Frank (1990), McLaren and Janke (1996), and Raymond et al. (2000). Soil scarification improves the conditions for seedling establishment (relative humidity and air temperature near the soil surface) (Man and Lieffers 1999; Roberts and Zwiazek 2001). On the other hand, the unscarified surface, comprised mainly of feathermoss and litter, has a low water-retention capacity and an extreme thermal range, and it resists radicle penetration (Jablanczy and Baskerville 1969; Bell 1991; Kabzems and Lousier 1992; Man and Lieffers 1999). In some cases, the allelopathic effects of some litters can prevent or hinder seedling establishment (Fischer 1980; Ahlgren and Ahlgren 1981).

It has been estimated that between 2 and 26 viable seeds are required to ensure the establishment of one spruce (Dobbs 1976; Putman and Zasada 1986). Our results show that between 6 and 8 viable seeds are needed to ensure the establishment of one spruce and that between 12 and 16 viable seeds are required to ensure the establishment of one fir on scarified surfaces with the mineral soil component. Over time, the number may increase to between 15 and 37, even on scarified soils (Lees 1970; Stewart et al. 2000), due primarily to deterioration of the seedbed (Davis and Hart 1961; Lees 1970; Perala and Alm 1989; Stewart et al. 2000). This is confirmed by the comparison of the number of seedlings established in 2001 on seedbeds scarified in 1996 and in 2000.

Despite these results, a high rate of seedling mortality was observed between 1999 and 2001, both in fir (between 3 and 33%) and white spruce (between 8 and 36%). Although comparable to the data of Stewart et al. (2000) for white spruce (16 and 35% after 3 years), this rate of mortality raises questions. On the basis of a 27-year follow-up, Wurtz and Zasada (2001) believe that, despite its immediate effects on white spruce seedling establishment, the mineral soil surface seedbed can be counterproductive at the sapling stage. In this perspective and taking account of the white spruce mortality, the removal of the organic layer to the point of contact with the mineral layer may not be the best method of scarification.

In the last two years, mortality exceeded recruitment both in fir and spruce, regardless of the type of scarification. In 2001, the mean density observed on the mineral and mixed soils was 120 and 160 seedlings/m² for fir and 103 and 90 seedlings/m² for white spruce. Although these data are highly variable, they are much higher than the data reported in the literature on regeneration in boreal fir stands. Côté and Bélanger (1991) estimate the density of spontaneous regeneration of fir to be between one and nine seedlings/m². Raymond et al. (2000), after seed cutting and soil scarification, estimate seedling density on scarified soils at between 8 and 37 seedlings/m² for fir, and between 1 and 6 seedlings/m² for spruce. Raymond et al. (2000) estimate the proportion of white spruce relative to fir at 14.4% following this experiment on scarified soil. Our results indicate that white spruce accounted for 39% of the established conifer seedlings; in this perspective, the experiment was conclusive. Is

seedling density in natural regeneration sufficient to ensure the establishment of a future stand? There are no standards on which to judge the experiment. Bella and DeFranceschi (1978) estimate that between two and three well developed seedlings per 10 m² are required.

Although the density and proportion of white spruce are acceptable, the high mortality rate observed raises questions concerning the deterioration of the seedbed and the invasion of the area by competing vegetation. The presence of cover during shelterwood cutting reduces the risk of invasion of the area by competing vegetation. Moreover, the cover produces on average 1100 kg of new litter per hectare per year, over 50% of which is comprised of needles. The accumulation of litter and the invasion of the area by moss are undoubtedly the main causes of the rate of mortality observed.

In the absence of germination of buried seeds and given the irregular production of viable seeds in spruce, should longer regeneration periods with several soil scarifications be considered? Probably, particularly in view of sustainable development, whereby tending operations will have to be tailored to the stands not only to ensure as much high quality wood as possible, but also to conserve a climatic composition to ensure biodiversity.

Seedling height in 2001

Scarification has a positive effect on seedling height after 5 years in both spruce and fir. The mean height of the dominant seedlings is higher on the mixed organic/mineral soil and mineral soil than on the controls or humus. These results are similar to those of other studies (Raymond et al. 2000; Stewart et al. 2000). However, after 5 years, the height of spruce is not inferior to that of fir. Can seedling height be considered sufficient to proceed with harvesting the residual stand? If so, at what rate and in how many years? If we apply the standard used by the Alberta Forest Service (1992), white spruce regeneration is not acceptable because it has not reached the minimum height of 50 cm. Moreover, these aspects affect the seedling development phase and should be the subject of further research.

Although the effect of the light environment on seedling establishment and height development is considered important (Carter and Klinka 1998; Raymond et al. 2000), our results agree with the findings of Perala and Alm (1989), Man and Liefvers (1999), and Wurtz and Zasada (2001), which indicate that canopy transmittance at the seedling establishment stage did not have a significant effect on the density or mean height of the seedlings of 2001.

CONCLUSIONS

Seed production in the stand between 1994 and 2001 varied in time and by species. Relatively good balsam fir seed production occurs in a 2-year cycle. Good seed production in spruce does not follow a clearly defined cycle and its production of viable seeds is characterized by a temporal variability specific to the species.

The success of seedling recruitment depends largely on the quantity of viable seeds and proper soil preparation. Given that the germinative capacity of buried seeds of conifers is nil after the first year, it is critical, if we wish to increase the proportion of white spruce, to synchronize soil preparation with good viable seed production. In comparison with other results, our experiment of regeneration with shelterwood cutting and soil preparation appears to be conclusive.

After a period of sustained seedling recruitment at the outset of the study, the high rate of seedling mortality in the last 2 years raises serious questions about the regeneration period and the

number of scarification treatments to be carried out. The deterioration of the seedbed may be a significant factor in the establishment of white spruce; this problem requires more detailed studies.

Although the light environment of the seedlings does not have a significant effect during the seedling establishment period, its effect could be a determining factor during the seedling development period and could be used in determining the timing of the final cutting, i.e. the time required to reach a height of 50 cm.

ACKNOWLEDGEMENTS

The author thanks Jean Breton, Gilles Bélanger and Joseph Seres, CFS-LFC, for the field work, Claude Laberge, Statex, for the data analysis, and Louis Archambault, CFS-LFC, and Guy Lessard, CERFO, for their constructive comments on the manuscript. Without their cooperation, this study would not have been possible.

REFERENCES

- Ahlgren, C.E.; Ahlgren, I.F. 1981. Some effects of different forest litters on seed germination and growth. *Can. J. For. Res.* 11:710-714.
- Alberta Forest Service. 1992. Alberta forest regeneration survey manual. Alberta Forestry, Lands and Wildlife, Forest Service, Edmonton, AB.
- Alexander, R.R.; Edminster, C.B. 1983. Engelmann spruce seed dispersal in the central Rocky Mountains. USDA For. Serv., Rocky Mt. For. Range Exp. Stn., Fort Collins, CO. Res. Note RM-424.
- Anderson, V.L.; McLean, R.A. 1974. Design of experiments: a realistic approach. Marcel Dekker Inc., New York.
- Archambault, L.; Morissette, J.; Bernier-Cardou, M. 1997. Succession forestière après feu dans la sapinière à bouleau jaune du Bas-Saint-Laurent, Québec. *For. Chron.* 73:702-710.
- Archibold, O.W. 1989. Seed banks and vegetation processes in coniferous forests. Pages 107-122 in M.A. Leck, V.T. Parker and R.L. Simpson, eds. *Ecology of soil seed banks*. Academic Press Inc., San Diego.
- Bakuzis, E.V.; Hansen, H.L. 1965. Balsam fir - a monographic review. University of Minnesota Press, Minneapolis, MN.
- Baldwin, V.C. 1977. Regeneration following shelterwood cutting in a New Brunswick softwood stand. *Environ. Can., Can. For. Serv., Maritimes For. Res. Cent., Fredericton, NB. Inf. Rep. M-X-76*.
- Bean, J.L.; Prielipp, D.O. 1961. Insect damage to white spruce cones and seeds - a factor in white spruce regeneration. USDA For. Serv., Lake States For. Exp. Stn., St. Paul, MN. Tech. Note 602.
- Bell, F.W. 1991. Critical silvics of conifer crop species and selected competitive vegetation in northwestern Ontario. *For. Can., Ontario Region and Ont. Minist. Nat. Resour., Northwestern Ont. For. Tech. Dev. Unit, Thunder Bay, ON. NWOFTDU Tech. Rep. 19. COFRDA Rep. 3310*.
- Bella, I.E.; DeFranceschi, J.P. 1978. Assessment of regeneration stocking standards used in Alberta: a follow-up. *Environ. Can., Can. For. Serv., Northern For. Res. Cent., Edmonton, AB. Inf. Rep. NOR-X-211*.
- Bérard, J.; Côté, M. (Coords.). 1996. Manuel de foresterie. Les Presses de l'Université Laval, Québec, QC.
- Blum, B.M. 1973. Some observations on the age relationships in spruce-fir regeneration. USDA For. Serv., Northeastern For. Res. Stn., Upper Darby, PA. Res. Note NE-169.
- Brand, D.G. 1988. A systematic approach to assess forest regeneration. *For. Chron.* 64:414-420.
- Brown, M.J.; Parker, G.G. 1994. Canopy light transmittance in a chronosequence of mixed-species deciduous forests. *Can. J. For. Res.* 24:1694-1703.
- Burns, R.M.; Honkala, B.H. 1990. *Silvics of North America. Vol. 1, Conifers*. USDA For. Serv., Washington, DC. USDA Agric. Handb. 654.
- Burschel, P.; Huss, J. 1997. *Grundriss des Waldbaus. Ein Leitfaden für Studium und Praxis*. Parey Buchverlag, Berlin.
- Carter, R.E.; Klinka, K. 1992. Variation in shade tolerance of Douglas fir, western hemlock, and western red cedar in coastal British Columbia. *For. Ecol. Manag.* 55:87-105.
- Cavers, P.B. 1983. Seed demography. *Can. J. Bot.* 61:3578-3590.

- Childs, S.W.; Flint, L.E. 1987. Effect of shadeboards, shelterwoods, and clearcuts on temperature and moisture environments. *For. Ecol. Manag.* 18:205-217.
- Côté, S.; Bélanger, L. 1991. Variations de la régénération préétablie dans les sapinières boréales en fonction de leurs caractéristiques écologiques. *Can. J. For. Res.* 21:1779-1795.
- Davis, G.; Hart, A.C. 1961. Effect of seedbed preparation on natural reproduction of spruce and hemlock under dense shade. USDA For. Serv., Northeastern For. Exp. Stn., Upper Darby, PA. Stn. Pap. 160.
- Dobbs, R.C. 1972. Regeneration of white spruce and Engelmann spruce: a literature review with reference to the British Columbia interior. *Environ. Can., Can. For. Serv., Pacific For. Res. Cent., Victoria, BC. Inf. Rep. BC-X-69.*
- Dobbs, R.C. 1976. White spruce seed dispersal in central British Columbia. *For. Chron.* 52:225-228.
- Edwards, I.K. 1986. Review of literature on fertilization and conifer seed production. *Can. For. Serv., Northern For. Cent., Edmonton, AB. For. Manag. Note 40.*
- Fenner, M. 1991. Irregular seed crops in forest trees. *Quart. J. For.* 85:166-172.
- Fisher, R.F. 1980. Allelopathy: a potential cause of regeneration failure. *J. For.* 78:346-348, 350.
- Fleming, R.L.; Black, T.A.; Eldridge, N.R. 1994. Effects of site preparation on root zone soil water regimes in high-elevation forest clearcuts. *For. Ecol. Manag.* 68:173-188.
- Frank, R.M. 1990. *Abies balsamea* – balsam fir. Pages 26-35 in R.M. Burns and B.H. Honkala, eds. *Silvics of North America. Vol. 1, Conifers.* USDA Agric. Handb. 654.
- Frank, R.M.; Safford, L.O. 1970. Lack of viable seeds in the forest floor after clearcutting. *J. For.* 68:776-778.
- Frisque, G.; Weetman, G.F.; Clemmer, E. 1978. Analyse, 10 ans après coupe de bois à pâte, des problèmes de régénération dans l'Est du Canada. *FERIC. Rap. Tech. RT-23.*
- Gagnon, R.; Chabot, M. 1988. Un système d'évaluation de la vulnérabilité des peuplements à la tordeuse des bourgeons de l'épinette : ses fondements, son implantation et son utilisation en aménagement forestier. *L'Aubelle* 67:7-14.
- Games, P.A.; Howell, J.F. 1976. Pairwise multiple comparison procedures with unequal *n*'s and/or variances: a Monte Carlo study. *J. Educ. Stat.* 1:113-125.
- Gobeil, A.R. 1938. Dommages causés aux forêts de la Gaspésie par les insectes. *Minist. Terres et Forêts, Serv. entomol. Bull. n° 2.*
- Godman, R.M.; Mattson, G.A. 1976. Seed crops and regeneration problems of 19 species in northeastern Wisconsin. USDA For. Serv., North Cent. For. Exp. Stn., St. Paul, MN. Res. Pap. NC-123.
- Grenier, J. 1995. Petit manuel des semences forestières au Québec. 4^e éd. *Minist. Ressour. nat. du Québec.*
- Hannah, P.R. 1988. The shelterwood method in northeastern forest types: a literature review. *North. J. Appl. For.* 5:70-77.
- Harvey, B.D.; Bergeron, Y. 1989. Site patterns of natural regeneration following clear-cutting in northwestern Quebec. *Can. J. For. Res.* 19:1458-1469.
- Hatcher, R. 1960. Croissance du sapin baumier après une coupe rase dans le Québec. *Minist. Nord can. Ressour. nat., Dir. for., Div. rech. sylvic. Mémo Tech. n° 87.*
- Hatcher, R.J. 1963. Effects of birch dieback and spruce budworm on forest development, Forest Section L.6, Quebec. *Dep. Forestry, For. Res. Branch. Publ. No. 1014.*
- Hennessey, G.R. 1970. Seedfall and litterfall in a mature white spruce stand in Manitoba. *Dep. Fish. For., Can. For. Serv., For. Res. Lab., Winnipeg, MB. Intern. Rep. MS-108.*
- Hills, S.C.; Morris, D.M. 1992. The function of seed banks in northern ecosystems: a literature review. *Ont. Minist. Nat. Resour., Ont. For. Inst., Sault Ste. Marie, ON. For. Res. Inf. Pap. 107.*
- Jablanczy, A.; Baskerville, G.L. 1969. Morphology and development of white spruce and balsam fir seedlings in feather moss. *Can. For. Serv., Maritimes For. Res. Lab., Fredericton, NB. Inf. Rep. M-X-19.*
- Jessome, A.P. 1977. Strength and related properties of woods grown in Canada. *Environ. Can., Can. For. Serv., East. For. Prod. Lab., Ottawa, ON. For. Tech. Rep. 21.*
- Kabzems, R.D.; Lousier, J.D. 1992. Regeneration, growth and development of *Picea glauca* under *Populus* spp. canopy in the boreal white and black spruce zone. *For. Can. and B.C. Minist. For., Victoria, BC. Canada/B.C. Partnership Agreement For. Resour. Dev. Rep. 176.*
- Laflèche, V.; Ruel, J.-C.; Archambault, L. 2000. Évaluation de la coupe avec protection de la régénération et des sols comme méthode de régénération de peuplements mélangés du domaine bioclimatique de la sapinière à bouleau jaune de l'est du Québec, Canada. *For. Chron.* 76:653-663.
- Lees, J.C. 1970. Natural regeneration of white spruce under spruce-aspen shelterwood, B-18a forest section, Alberta. *Dep. Fish. For., Can. For. Serv., Ottawa, ON. Publ. No. 1274.*
- Lieffers, V.J.; Beck, J.A. Jr. 1994. A semi-natural approach to mixedwood management in the prairie provinces. *For. Chron.* 70:260-264.

- MacLean, D.A. 1984. Effects of spruce budworm outbreaks on the productivity and stability of balsam fir forests. *For. Chron.* 60:273-279.
- Majcen, Z.; Gagnon, G. 1976. Description écologique et cartographie des groupements forestiers de la station forestière de la Baie-des-Chaleurs. Minist. Terres et Forêts, Serv. Rech. Rapp. int. n° 172.
- Man, R.; Lieffers, V.J. 1999. Effects of shelterwood and site preparation on microclimate and establishment of white spruce seedlings in a boreal mixedwood forest. *For. Chron.* 75:837-844.
- Matthews, J.D. 1994. *Silvicultural systems*. Clarendon Press, Oxford.
- McLaren, B.E.; Janke, R.A. 1996. Seedbed and canopy cover effects on balsam fir seedling establishment in Isle Royale National Park. *Can. J. For. Res.* 26:782-793.
- Ministère des Ressources naturelles du Québec. 1994. Une stratégie : aménager pour mieux protéger les forêts. Minist. Ressour. nat. du Québec.
- Owens, J.N.; Molder, M. 1977. Bud development in *Picea glauca*. II. Cone differentiation and early development. *Can. J. Bot.* 55:2746-2760.
- Perala, D.A.; Alm, A.A. 1989. Regenerating paper birch in the Lake States with the shelterwood method. *North. J. Appl. For.* 6:151-153.
- Proulx, H., Jacques, G.; Lamothe, A.-M.; Litynski, J. 1987. Climatologie du Québec méridional. Minist. Environ. Québec, Dir. Météorol. M.P. 65.
- Putman, W.E.; Zasada, J.C. 1986. Direct seeding techniques to regenerate white spruce in interior Alaska. *Can. J. For. Res.* 16:660-664.
- Raymond, P.; Ruel, J.-C.; Pineau, M. 2000. Effet d'une coupe d'ensemencement et du milieu de germination sur la régénération des sapinières boréales riches de seconde venue du Québec. *For. Chron.* 76:643-652.
- Roberts, J.J.; Zwiazek, J.J. 2001. Growth, morphology, and gas exchange in white spruce (*Picea glauca*) seedlings acclimated to different humidity conditions. *Can. J. For. Res.* 31:1038-1045.
- SAS Institute Inc. 1999. SAS/STAT guide for personal computers, Version 8.02. SAS Institute Inc., Cary, NC.
- Spittlehouse, D.L.; Childs, S.W. 1992. Evaluating the seedling moisture environment after site preparation. Pages 80-94 in S.P. Gessel, ed. Sustained productivity of forest soil. 7th North American Forest Soils Conference, Vancouver, BC. University of British Columbia, Faculty of Forestry.
- Stewart, J.D.; Lanhausser, S.M.; Stadt, K.J.; Lieffers, V.J. 2000. Regeneration of white spruce under aspen canopies: seeding, planting, and site preparation. *West. J. Appl. For.* 15:177-182.
- Thibault, M. 1986. Les régions écologiques du Québec méridional (2^e approximation). Carte synthèse. Minist. Énerg. Ressour. Québec, Serv. rech. et Serv. cartographie.
- Vézina, P.E.; Linteau, A. 1968. Growth and yield of balsam fir and black spruce in Quebec. *Can. Dep. For. Rural Dev., For. Branch, For. Res. Lab., Sainte-Foy, Quebec. Inf. Rep. Q-X-2*.
- Wurtz, T.L.; Zasada, J.C. 2001. An alternative to clear-cutting in the boreal forest of Alaska: a 27-year study of regeneration after shelterwood harvesting. *Can. J. For. Res.* 31:999-1011.
- Youngblood, A.P. 1990. Radial growth after a shelterwood seed cut in a mature stand of white spruce in interior Alaska. *Can. J. For. Res.* 21:410-413.
- Zarnovican, R. 1998. Observations on windfall and decay in a second-growth balsam fir stand in the Lower St. Lawrence Model Forest. *Nat. Resour. Can., Can. For. Serv., Laurentian For. Cent., Sainte-Foy, QC. Res. Note No. 3*.
- Zarnovican, R.; Laberge, C. 1997. Seed production in a second-growth balsam fir stand in the Lower St. Lawrence Model Forest. *Nat. Resour. Can., Can. For. Serv., Laurentian For. Cent., Sainte-Foy, QC. Res. Note No. 1*.
- Zarnovican, R.; Laberge, C. 1998. Radial growth of balsam fir [*Abies balsamea* (L.) Mill.] associated with past spruce budworm [*Choristoneura fumiferana* (Clem.)] outbreaks in Quebec, Canada. *Lesnictvi-Forestry* 44:481-487.
- Zarnovican, R.; Lussier, J.-M.; Laberge, C. 2001. Coupe préparatoire et croissance en surface terrière d'une sapinière de seconde venue à la forêt modèle du Bas-Saint-Laurent, Québec. *For. Chron.* 77:685-695.
- Zasada, J.C.; Grigal, D.F. 1978. The effects of silvicultural system and seed bed preparation on natural regeneration of white spruce and associated species in interior Alaska. Pages 213-220 in C.A. Hollis and A.E. Squillace, eds. *Proc. Fifth North American Forest Biology Workshop*, 13-15 March 1978, Gainesville, Florida. School of For. Resour. and Conserv., University of Florida, Gainesville.