EPISODIC RECRUITMENT OF THE SEEDLING BANKS IN BALSAM FIR AND WHITE SPRUCE

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- Premise of the study: In ecosystems where seed production is low and masting years are sporadic, or with species that have short-lived seeds, regeneration is assured by seedling banks rather than seed banks. Seedling establishment and survival play a critical role in determining the composition of these plant communities by supplying new individuals for their maintenance. Seedling emergence and mortality were investigated to test the hypothesis that recruitment into the seedling bank is periodic.

- Materials and methods: Seed production and seedling emergence and survival were monitored during 1994-2007 in balsam fir (Abies balsamea) and white spruce (Picea glauca) in four pristine stands of the boreal forest of Quebec, Canada. Measurements were collected twice per month by sampling one permanent plot of 20 x 20 m per stand.

- Key results: Seed-rain abundance reached 9 x 10³ seeds m⁻² year⁻¹, and was characterized by synchronous sequences of low and high seed production. New seedlings appeared only during the year following a seed production of at least 1 x 10³ and 1.5 x 10³ seeds m⁻² year⁻¹ for balsam fir and white spruce, respectively. Seedlings emerged in July and survived 34-52 d on average, with balsam fir showing a longer lifespan and lower mortality, although 85–99% of seedlings died before completing one year of life.

- Conclusions: The emergence of young seedlings was coupled with massive seed rains, which allowed synchronous replenishment of the seedling banks among stands and species, and generated different cohorts, yielding a discontinuous age structure.

Key words: Abies balsamea; boreal forest; demography; masting; mortality; Picea glauca; recruitment; reproduction; seed rain; survival

Among the factors structuring plant communities and driving the spatio-temporal dynamics of vegetation, strategies of plant reproduction and mechanisms of seedling establishment play the most important role in determining species composition and distribution. A key factor in the process of stand regeneration is the pool of individuals in the form of seeds stored in the soil (seed bank) or advance regeneration in the understory (seedling bank). They represent a persistent stage that can survive environmental extremes and respond to disturbances (Parker et al., 1989). The seed bank is formed by the ungerminated seeds present on a site that are potentially able to produce seedlings (Zasada et al., 1993). Once in the soil, viable seeds can germinate, or be subjected to death or predation. Thus, the preservation of the seed population relies on the duration of seed viability and has to be assured by a periodic addition of new seeds, mainly produced during masting years (Kelly and Sork, 2002). According to Kelly (1994), mast seeding is defined as the intermittent production of large seed crops by a plant population.

Differences in seed production and viability can be at the origin of divergent reproductive strategies. Species that have massive productions of small and light seeds can exhibit a post-embryonic dormancy extending beyond nine months and a long-lasting germination capacity (Qi and Scarratt, 1998; Greene et al., 1999; Rossi et al., 2012). A high proportion of the seeds remain viable for years after dispersal, allowing these species to successfully maintain persistent seed banks in the soil (Zasada et al., 1993; Ibarzabal, 1994). On the contrary, in ecosystems where seed production is low and masting years are more irregular and sporadic, or with species that have seeds with shorter longevity, regeneration is assured by seedling banks rather than seed banks (Payette et al., 1982; Zasada et al., 1993). In these species, the critical step consists in seeds germinating within a few months after dispersal, as this reduces seed mortality and increases the probability of recruitment into the overstory.

Seedling banks are generally formed by long-living and slow-growing individuals patiently waiting for release and ascendency to the dominant layer after a canopy opening (Antos et al., 2000). High shade-tolerance and the ability to modify the growth form for survival in dense shade are key traits for the long-term persistence of species in the understory (Antos et al., 2005). In some ecosystems, recruitment into the seedling bank is episodic, occurring as a response to disturbances, climatic variation, or internal stand dynamics (Antos et al., 2000). However, a fairly continuous recruitment has also been observed (Hett and Loucks, 1971). Although turnover of seedling banks should be directly assessed on the emerging individuals, this information is usually deduced from the age structure of individuals. At fine-scale resolution, results based on age structures are strongly affected by unavoidable aging inaccuracy and undetected early mortality of seedlings that would not be taken into account with this procedure (DesRochers and Gagnon, 1997; Parent et al., 2002). Currently, our findings are species-specific, and the data available on age structure of seedlings are

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The observed lengthening of the fire cycle in northern ecosystems is increasing the proportion of northern boreal forests with a substantial component of old individuals (Lesieur et al., 2002). Thus, smaller-scale, secondary disturbances are expected to become an important component of the stands in unmanaged forests (Rossi et al., 2009c; Tremblay et al., 2011). This raises questions about when and how the tree species exploit the newly opened gaps. Stand persistence in the long term depends on tree recruitment, which is the result of interconnected processes, such as seed dispersal and germination, seedling establishment, and survival. Accordingly, investigations need to define the temporal dynamics of tree recruitment at all sequential stages of development to identify the patterns of tree regeneration occurring in stands of the boreal forest (Schupp and Fuentes, 1995; Duchesnau and Morin, 1999).

For this paper we analyzed the spatial and temporal variability in the number of individuals at different stand-development stages to assess the dynamics of establishment and replenishment of the advance regeneration in species characterized by seedling banks. According to Houle (1995), acknowledgment of consequences of seed production on the demographic structure of a stand is essential for understanding the patterns of recruitment of the new individuals over time. Thus, monitoring was performed from 1994 to 2007 by collecting data of seed production and seedling emergence and survival in balsam fir [Abies balsamea (L.) Mill.] and white spruce [Picea glauca (Moench) Voss], two sympatric mating species in the boreal forest of Quebec, Canada, characterized by a lack of long-lasting seed banks and low seed dormancy (Zasada et al., 1993). Their variation in seed production and viability were more extensively analyzed and discussed in a previous paper (Rossi et al., 2012). Here, the chronologies of seed-rain abundance are reported to compare seed production with the emergence and survival of seedlings.

The survival of these two species is assured by the presence of an abundant seedling bank, which guarantees the regeneration and long-term survival of the stand (Morin and Laprise, 1997). However, as well as growing into taller saplings, well-established seedlings are assumed to be susceptible to death from disease, disturbance, or consumption by animals. This clearly requires a renewal of the pool of seedlings to balance the incessant loss of individuals from the seedling bank (Morin and Laprise, 1997). This paper addresses the question of whether seedling banks are supplied by new individuals replacing the older ones through a sporadic or fairly continuous process.

MATERIALS AND METHODS

Stand selection and description—The study was conducted close to the 50° North parallel, in the region belonging to the black spruce [Picea mariana (Mill.) B.S.P.]-feather moss bioclimatic domain, 100 km north of Lac-Saint-Jean in the boreal forest of Quebec, Canada. Four balsam fir stands were selected within an area of 20 km in diameter, representing a chronosequence at different developmental stages (i.e., timings of occurrence of the last major disturbance by spruce budworm outbreak). The sites had been affected by the spruce budworm [Choristoneura fumiferana (Clem)] outbreaks dated by Morin (1994). The defoliation had killed some of the previously established trees and opened large gaps in the canopy that were subsequently filled by the advance regeneration of the understory trees (Rossi and Morin, 2011). According to Morin (1994), stand 1 showed the most recent canopy openings associated with a spruce budworm outbreak in the 1980s. Stand 2 had been affected by an outbreak around 1944, with most defoliated and weakened trees subjected to a blowdown in 1947. In stand 3, most serious damage was caused by two outbreak events that occurred around 1910 and 1944. The major disturbance in stand 4 was due to older outbreaks, occurring between 1815 and 1850. Because of their remote location and the absence of evidence of human impact, the stands were considered to have developed under the influence of natural disturbances. Analyses of fire scars and charcoal discounted the occurrence of fires in the stands during the last 300 yr (Morin, 1994).

Data collection—The regeneration dynamics were investigated by collecting data from trees, saplings, seedlings, and seeds from 1994 to 2007 and on sampling areas of different sizes, to obtain estimations as representative of the stand as possible. In 1994, one plot of 20 × 20 m with buffer zones of 3 m was delimited in each stand, and all living trees (i.e., individuals with diameter at breast height (DBH) greater than 9 cm) and saplings (i.e., individuals taller than 3 m and with DBH less than 9 cm) were measured and mapped. Within the plots, fixed points were assessed on a grid at intervals of 5 m using a double prism optical square (black dots in Appendix 1). Seed rain was measured using 25 seed traps systematically located at the nodes of the grid and fixed to a stake at 40 cm above the ground. The seed traps were inverted galvanized steel cones with an opening of 4.0 dm², so that the total sampling area was 1 m² per plot. The sampling design led to relative errors in the estimations of seed rain ranging between 5 and 15% with seed rain abundances greater than 1000 seeds m⁻² y⁻¹ (Rossi et al., 2012). Within each trap, a 0.1 mm mesh netting was draped to form a deep pouch, while a 12 mm mesh netting over the top prevented seed dispersers (e.g., rodents) from removing seeds from the traps. During the snow-free period, traps were emptied monthly in late spring and summer, and every 2 wk in autumn. There was no seed collection in winter and early spring because the stands were inaccessible from November to May.

The living individuals were identified using permanent tags with unique alphanumeric codes. The tagged individuals that were found dead in a successive monitoring were not remeasured. Specimens less than 3 m in height were considered seedlings, and were monitored annually in autumn on a total of 11.5, 27.5, and 77.5 m² for seedlings of: (i) up to 0.25; (ii) between 0.25 and 0.75; and (iii) between 0.75 and 3 m, respectively. The sampling design with the distribution of subplots is presented in Appendix 1. Seedlings less than 0.25 m in height were monitored twice per month from June to October to assess the dynamics of emergence and lifespan of the germinating individuals belonging to the two conifer species.

Statistical analyses—The cumulative distribution of the dates of emergence and death of the germinating seedlings was superimposed with the normal probability curve using the CDF function in SAS 9.2 (SAS Institute, Cary, North Carolina, USA). The proportions of seedlings surviving the first winter after germination were computed at plot level for each year and stand, and modeled as binomial ratios in generalized linear mixed models with logit-link functions (GLIMMIX procedure in SAS), where the response variable was implemented as the ratio between number of events (i.e., number of surviving seedlings) and number of trials (number of germinated seedlings). The differences among stands were examined using contrasts. The amount of seeds, emerging seedlings, and one-year-old seedlings was assessed for each species, year, and stand. The resulting chronologies were compared using the nonparametric Spearman rank-order correlation. Relationships between seed-rain abundance of the previous year, emerging seedlings, and one-year-old seedlings of the following year were tested for each species with linear regressions.

Survival of balsam fir was calculated for the period 1994-2007, the longest chronology available from this study, for individuals occurring in the form of seed in 1994. Mortality was given as mortality per year (m), calculated according to the equation recommended by Sheil et al. (1995),

\[
m = 1 - \frac{N_0}{N_t}
\]

where \(N_0\) and \(N_t\) were the number of individuals counted at the beginning and end of the measurement interval \(t\), which in this study corresponded to one year.

RESULTS

Trees and saplings—A total of 210 trees were identified and mapped at plot establishment in 1994. Plots contained between 17 and 84 trees, which indicated a high variability in density, from 425 to 2100 trees ha⁻¹, with the densest plot being in stand 2 (Table 1). The dominant height varied between 16.2 and 20.8 m.
with a mean DBH of 12.2–20.1 cm, which produced a basal area ranging between 15.3 and 31.2 m² ha⁻¹. Balsam fir formed a monospecific plot in stand 4, and was the dominant species in the other plots, where it represented more than 70% of the trees. White spruce and white birch [Betula papyrifera Marsh.] were also present but only accounted for a percentage of trees ranging between 2.3 and 17%.

Of the 344 saplings mapped in 1994, 88% were balsam fir and only 9% were white birch. White spruce was observed only in stand 2 with 7 individuals. The mean DBH of the saplings was similar among the stands except in stand 1 where saplings had smaller mean diameters, while the mean height varied greatly, between 3.6 and 9.0 m (Table 1). Density varied between 100 and 6125 saplings ha⁻¹, observed in stands 4 and 2, respectively. During the 14 yr of monitoring, the number of saplings decreased in all stands except in the most recently opened stand 1, where saplings increased from 25 to 176 over the first 10 yr, corresponding to 378 new individuals ha⁻¹ year⁻¹ (data not shown). Mortality of saplings was mainly concentrated in stands 2 and 3, although it was also occasionally observed in stands 1 and 4.

**Emerging seedlings**—Between 73 and 95% of seedlings in the stands were balsam fir, while only 0.5–4% were white spruce and mountain maple (Acer spicatum Lamb.). White birch accounted for 1.6–3.2% of seedlings, although no individuals of this species were found in the plots of stand 2. Other species were present, but only occasionally and in some stands: they totaled less than 2–3%.

The period of emergence and death of seedlings followed a normal distribution, and lasted 80 and 100 d, respectively (Fig. 1). On average, seedlings appeared in mid-July, although the first individuals were observed in mid-June. Dead seedlings were detected from the end of June to mid-October, with an average date of death being estimated as the end of August. Earlier emergences occurred in stands 1 and 2, while dead seedlings were observed later in stands 2 and 3. This resulted in longer and shorter lifespans of seedlings being calculated for stands 1 and 3, respectively (Fig. 1). On average, the seedlings dying the same year as their emergence exhibited a lifespan ranging between 34 and 52 d. In general, balsam fir emerged earlier and died later than white spruce, thus achieving a longer lifespan (46 vs. 39 d, respectively).

The proportion of seedlings that survived the first year of life varied widely among years. On average, 62–96% of seedlings died before the first winter; balsam fir had higher survival rates than white spruce (Table 2). Survival differed significantly among stands (p < 0.0001), and was higher for seedlings of balsam fir growing in stands 1 and 4, while 85% of seedlings in stand 2 died during the first year of life. Substantial differences in survival among stands were also observed for white spruce, but were not statistically different (p > 0.05, Table 2) probably

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**Table 1.** Stand characteristics at plot establishment in 1994 concerning all tree species detected in the plots. Methods for assessing the mean age in the studied stands are described in Rossi and Morin (2011).

<table>
<thead>
<tr>
<th>Stand</th>
<th>Dominant height (m)</th>
<th>Mean DBH (cm)</th>
<th>Density (trees ha⁻¹)</th>
<th>Mean age (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>16.8</td>
<td>20.1</td>
<td>425</td>
<td>109</td>
</tr>
<tr>
<td>2</td>
<td>20.8</td>
<td>12.2</td>
<td>2100</td>
<td>58</td>
</tr>
<tr>
<td>3</td>
<td>16.2</td>
<td>15.1</td>
<td>1450</td>
<td>120</td>
</tr>
<tr>
<td>4</td>
<td>20.0</td>
<td>18.5</td>
<td>1275</td>
<td>151</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Stand</th>
<th>Height (m)</th>
<th>Mean DBH (cm)</th>
<th>Density (saplings ha⁻¹)</th>
<th>Mean age (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>3.6</td>
<td>4.1</td>
<td>625</td>
<td>108</td>
</tr>
<tr>
<td>2</td>
<td>5.6</td>
<td>5.8</td>
<td>6125</td>
<td>52</td>
</tr>
<tr>
<td>3</td>
<td>4.5</td>
<td>5.5</td>
<td>1750</td>
<td>59</td>
</tr>
<tr>
<td>4</td>
<td>9.0</td>
<td>5.8</td>
<td>100</td>
<td>96</td>
</tr>
</tbody>
</table>

**Fig. 1.** Cumulative distributions of the dates of germination (black dots) and death (gray dots) of seedlings in four stands of the boreal forest of Quebec, Canada. Solid lines correspond to normal probability curves.
balsam fir and white spruce, respectively. Accordingly, one-year-old seedlings were observed only in 1998 and 2005 for both species, and in 1996 for balsam fir (Fig. 2). Emerging seedlings were highly correlated with one-year-old seedlings with coefficients ranging between 0.73 \((p < 0.01)\) and 0.99 \((p < 0.0001)\), confirming that germination and appearance of new seedlings was similar among stands.

Significant linear regressions were observed for both species between seed rain abundance of the previous year, emerging seedlings, and one-year-old seedlings of the following year (Fig. 3). Seed rain suitably explained both emerging and one-year-old seedlings, with high variation accounted for and R-square ranging between 0.58 and 0.75. In balsam fir, the slope of the regression estimated between seed rain and emerging seedlings was statistically different from 1 \((F = 10.71, p < 0.01)\), suggesting that high amounts of seed production led to proportionally higher densities of emerging seedlings.

**Survival**—The monitoring on balsam fir allowed a survival curve to be calculated of the seeds produced in 1994 and germinating as seedlings in 1995 (Fig. 4). The higher mortality rates were observed at seed germination (95–99\%) and during the first year of emergence of the seedlings (85–96\%). In all stands, the mortality rates fell drastically to 3–21\% in one-year-old seedlings, and gradually decreased attaining annual values of ca

### Table 2. Proportion of seedlings surviving the first winter after emergence and F-value and significance of generalized linear mixed models comparing the four stands of the boreal forest of Quebec, Canada. Values with the same letters are not statistically different \((p > 0.05)\). Results are reported as mean ± SD.

<table>
<thead>
<tr>
<th></th>
<th>Stand 1</th>
<th>Stand 2</th>
<th>Stand 3</th>
<th>Stand 4</th>
<th>F-value</th>
<th>df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balsam fir</td>
<td>0.25 ± 0.32(^a)</td>
<td>0.15 ± 0.17(^b)</td>
<td>0.19 ± 0.07(^c)</td>
<td>0.38 ± 0.28(^a)</td>
<td>95.94</td>
<td>25</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>White spruce</td>
<td>0.18 ± 0.01(^b)</td>
<td>0.04 ± 0.10(^a)</td>
<td>0.20 ± 0.25(^a)</td>
<td>0.13 ± 0.12(^a)</td>
<td>1.02</td>
<td>13</td>
<td>0.41</td>
</tr>
</tbody>
</table>

Because of the low number of observations and wide variability. The massive emergence of white birch precluded an exhaustive quantification of this species at the stage of current-year seedlings. However, qualitative evaluations and observations on the older seedlings revealed that most specimens of this species survived less than one year.

**Regeneration dynamics**—Monitoring succeeded in representing the dynamics of seed production and emergence of seedlings of balsam fir and white spruce for the period 1994-2007 (Fig. 2). The chronologies were highly variable (by more than one order of magnitude) and were constituted by data showing marked exponential distributions (data not shown). Seed-rain abundance varied among years, with the highest values being observed in 1994, 1996, 2003, and 2006, attaining up to \(9 \times 10^3\) and \(1 \times 10^3\) seeds m\(^{-2}\) year\(^{-1}\) for balsam fir and white spruce, respectively. Seed production was lower in 1995, 1997, 2004, and 2007, with no seeds of white spruce found in stand 3 in 2007 (Fig. 2). The synchrony in seed production among stands was confirmed in both species by the highly significant correlations producing coefficients of 0.85-0.96 \((p < 0.0001)\).

Young seedlings appeared only during the year after massive seed productions (Fig. 2). Seedlings emerged only in 1995, 1997, 2004, and 2007, which corresponded to a previous year’s production of at least \(1 \times 10^3\) and \(1.5 \times 10^2\) seeds m\(^{-2}\) year\(^{-1}\) for balsam fir and white spruce, respectively. Accordingly, one-year-old seedlings were observed only in 1998 and 2005 for both species, and in 1996 for balsam fir (Fig. 2). Emerging seedlings were highly correlated with one-year-old seedlings with coefficients ranging between 0.73 \((p < 0.01)\) and 0.99 \((p < 0.0001)\), confirming that germination and appearance of new seedlings was similar among stands.

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Origin of the pulsing—Balsam fir and white spruce complete seed maturation in late summer, and dispersal occurs in autumn, mainly in September-October (Young and Young, 1992; Rossi et al., 2012). This allows seeds of both species to germinate in early summer, as soon as the seedbed conditions are favorable to germination and emergence of seedlings (Fig. 1). Despite the irregular and episodic process of establishment of new seedlings, and although only a minor proportion (1–5%) of seeds produced seedlings, more than 50 new seedlings m\(^{-2}\) year\(^{-1}\) of balsam fir appeared the year following a masting (Fig. 2). Germination in mosses and rotten wood, the most favorable seedbeds, is not normally considered to be a limiting factor to tree regeneration (Zasada et al., 1993; McLaren and Janke, 1996). Moreover, the dynamics of seed production and germination revealed that the emergence of seedlings was scarce or even absent during the years following a low seed production and seeds that did not germinate at the first opportunity had reasonably little or no chance of survival. This demonstrated either the short longevity of the seeds of the two studied species or that seed reserves are adequate to sustain the first stages of development of seedlings only during the year of dispersal (Morin, 1986). Moreover, these findings again confirmed the well-known reduced dormancy and viability of the seeds of balsam fir and white spruce, whose regeneration does not rely on seed banks (Zasada et al., 1993; Rossi et al., 2012).

10% at the end of the monitoring. On average, the yearly reduction in seedlings was 15.3% for the period 1996-2007. Thus, a production of up to \(7 \times 10^3\) seeds m\(^{-2}\) year\(^{-1}\) in balsam fir resulted in 0.5-2 seedlings m\(^{-2}\) year\(^{-1}\) after 14 yr (Fig. 4). Except in stand 4, the decrease in the number of individuals was similar among stands. As a consequence, at the end of the monitoring few seedlings were detected in stand 1, where the seed rain abundance of 1994 had been minor.

DISCUSSION

This paper reports the short-term dynamics of establishment and replenishment of the seedling banks of balsam fir and white spruce in the boreal forest of Quebec, Canada. Seed-rain production was irregular, and showed several unusually large reproductive efforts. The dynamics of the emerging regeneration closely followed seed-rain abundance, with pulsing recruitments of new seedlings appearing the year after massive seed production. Thus, the question about the renewal of the seedling bank is answered: it is not continuously renewed. On the contrary, it is clearly episodic and irregular, and closely related to seed production. As a corollary to these findings, it can be deduced that the seedling bank is constituted of a pool of plants belonging to different cohorts and with discontinuous ages.
There was evidence that massive seedling emergence could occur only above a certain threshold of seed rain abundance, while no or very few new seedlings were observed after the low seed production of the intermast years (Fig. 2). Masting behavior is a critical driver in defining the fluctuations of the population density in seedling banks of several tree species (Frey et al., 2007). These findings confirmed the advantage of investing in larger and less frequent reproductive efforts, which is supposed to provide both an improved potential for regeneration and a reduced proportion of predation (Norton and Kelly, 1988; Rossi et al., 2012). On the one hand, in wind-pollinated plants like balsam fir and white spruce, larger and synchronized efforts of reproduction assure increased pollination and efficient fertilization, leading to greater proportions of viable seeds (Kelly et al., 2001). As a result, years with high seed production were observed to be followed by years with proportionally higher emergence of seedlings (Fig. 3). During the intermast years, when pollen density is scarce, self-pollination and ovule abortion due to degeneration of the embryo during early development occur more frequently, which produces empty seeds (Greene et al., 1999). On the other hand, with greater seed-rain abundance, the presence of both larval-infected and viable seeds increases, but the former increases proportionally less than the latter (Rossi et al., 2012). According to Silvertown (1980), the recurrence of high and low seed productions as observed in Fig. 2 allow (i) satiation of predators with more seeds than they can consume so that some seeds escape predation during mast years (1994, 1996, 2003, and 2006), and (ii) starvation of the increased population of predators during the intermast years. For the area examined in this work, seed predators were both generalists, such as mice and squirrels, and insects specialized in attacking cones and seeds that were described and identified by Cadieux (2010).

As a consequence of the recurrent high seed production, the emergence of new seedlings occurred in the same years for balsam fir and white spruce, and was significantly correlated among the four stands. Also, although seedling emergence was not monitored in white birch, a similar pattern could be expected, because of the synchronous masting years with the other two species observed by Rossi et al. (2012). Certain environmental conditions may act as a trigger for coordinating flowering and fruiting within a region (Schauber et al., 2002). Most likely, in communities with different masting species as those of the stands studied in this paper, a lack of synchrony in seed production among species may decrease seed survival by maintaining a large population of generalist seed predators (e.g., mice, squirrels, and some species of insects) during the intermast years. Asynchronous mast seeding may have detrimental effects on the survival of the species in multispecies assemblages through a mechanism similar to apparent competition and is expected to be discouraged (Schnurr et al., 2002). Consequently, the reproductive strategies and dynamics of recruitment into the seedling banks seem to be closely related to converging evolutionary forces and predation pressures due to the coexistence of the three sympatric species within the same plant community.

**Strategy of survival in the understory**—In general, the higher losses of individuals were concentrated in the first two years after seed dispersal, at seed germination and during the first growing season of seedlings, with each year accounting for between 85 and 99% of mortality (Fig. 4), confirming the results reported by Zasada et al. (1993). Survival drastically increased in seedlings older than one year, which, however, still showed an annual mortality of 10–20%. The lower density of trees and saplings in stands 1 and 4 allowed seedlings to emerge earlier in the year and to have more probability of surviving the first growing season (Fig. 1 and Table 2). In stands 2 and 3, seedlings exhibited reduced stem sizes and growths of apical and lateral buds (data not shown). As observed in other shade-tolerant
species (Rossi et al., 2009a), the advance regeneration of balsam fir is well-known for its high resistance and tenacity (Greene et al., 1997; Rossi et al., 2009a, 2009b), and its ability to survive at light intensities of 5–6% full sunlight, by maintaining low production rates and drastically reducing height and diameter growth (Côté and Bélanger, 1991; Parent et al., 2002; Wang and Kemball, 2005). This strategy allows seedlings growing in suppressed conditions to avoid construction costs for new tissues, reduce outlay for nonphotosynthetic organs, and wait with slow growth until a small-scale disturbance occurs to open the dominant canopy (Parent and Messier, 1995). In this way, seedlings can survive insect outbreaks and exploit the new microclimatic conditions after gap opening. Even after prolonged periods of suppression, the older seedlings of balsam fir are able to rapidly reactivate vigorous growth and successfully reach the canopy (Ghent 1958; Bergeron and Dubuc, 1989).

Ecological relevance of the seedling bank—An outbreak of spruce budworm is the disturbance that most frequently creates canopy openings in balsam fir stands. This insect is a native defoliator widely distributed in northeastern North America whose populations periodically reach outbreak densities and cause growth reductions and mortality of single trees or entire stands (MacLean, 1985; De Grandpré et al., 2000; Harper et al., 2003). Within the stands, trees show different sensitivities to defoliation according to age and size, with the younger and smaller individuals being more resistant and having lower mortality rates (MacLean, 1980; Bergeron et al., 1995; Rossi et al., 2009a). Insect outbreaks cause mainly the death of the older and larger trees of the stand, creating gaps in the canopy. In addition, spruce budworm consumes the reproductive tissues and repeated defoliations deplete the reserves of trees, thus reducing the quality and quantity of seed production and the consequent numbers of young recently emerged seedlings during and after an outbreak. The strategy of maintaining a dense and vital seedling bank integrated into the tree community is the key to species persistence and regeneration following natural disturbance, allowing balsam fir to rapidly and successfully replace dead dominant trees with other shade-tolerant, long-lived individuals of the same species previously established in groups in the understory (Kneshaw and Bergeron 1999; Rossi and Morin, 2011). Within a wider ecological context of interaction between plants and insects, this finding supports the hypothesis of Baskerville (1975) that balsam fir and spruce budworm could form an interdependent self-regulating system, with insect outbreaks driving the cyclical regeneration and long-term survival of balsam fir stands.

Conclusions—Survival and regeneration of several tree species are assured by the presence of an abundant seedling bank, which forms a dynamic pool of individuals waiting in the understory for improved growing conditions. The unavoidable aging inaccuracies and undetected early mortality of seedlings prevent the measured age structure adequately representing the dynamics of mortality and recruitment of new individuals in the seedling bank. This paper described a monitoring of the spatial and temporal variability in seed production and number of individuals to assess causes and dynamics of replenishment of the advance regeneration in balsam fir and white spruce. Emergence of seedlings closely followed seed-rain abundance, with pulsing recruitments of new individuals appearing the year after a massive seed production. Our findings clearly demonstrate by direct observation that the seedling bank is periodically and irregularly replenished with new individuals according to the episodes of mast seeding. The dynamics of emergence and mortality of the young individuals are related to the ecological requirements of the species, contribute to shaping the age structure of the seedling bank of balsam fir and white spruce, and determine the final composition of a stand after natural disturbances.

LITERATURE CITED


Cadieux, É. 2010. L’entomophaune des cônes de sapin baumier (Abies balsamea (L.) Mill.) et son impact sur la régénération, Ph.D. dissertation, Université du Québec à Chicoutimi, Chicoutimi, Québec, Canada.


Houle, G. 1995. Seed dispersal and seedling recruitment: The missing link(s). Ecoscience 2: 238–244.


APPENDIX 1. Sampling design for monitoring seed rain (dots) and seedlings (squares) within the permanent plots. In black squares, all seedlings were measured, while in dark and light gray squares, only seedlings taller than 0.25 and 0.75 m were measured. This resulted in sampling areas of 11.5, 27.5, and 77.5 m² for seedlings with heights of: (i) up to 0.25; (ii) between 0.25 and 0.75; and (iii) between 0.75 and 3 m, respectively. One plot was located in each stand.