

Reduction of black spruce seed bank by spruce budworm infestation compromises postfire stand regeneration

Martin Simard and Serge Payette

Abstract: In the southern boreal forest of eastern Canada, black spruce (*Picea mariana* (Mill.) BSP) is subjected to both defoliating insect and fire disturbances. As black spruce depends on its aerial seed bank for postfire regeneration, reduction of cone crop during a spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreak opens a vulnerability window during which stand regeneration could be hindered in the event of a fire. To assess the long-term effect of spruce budworm outbreak on black spruce reproductive potential, cone production and viable seed bank were estimated using cone crop surveys and germination trials in black spruce – lichen woodland stands that sustained different levels of defoliation during the 1980s. Black spruce cone crop was significantly related to the defoliation history of the stands ($R^2 = 0.89$), but not to stand age, basal area, or tree density. Black spruce stands damaged by severe defoliation showed a smaller number of cones, a higher incidence of insect-damaged cones, and a viable seed bank 3 to 17 times smaller than a lightly defoliated stand. The vulnerability window for black spruce regeneration following a spruce budworm outbreak may be as long as 20 years in the study area because black spruce seed bank in heavily defoliated stands has not yet replenished. Our work supports conclusions from stand reconstruction studies that suggest closed-crown spruce–moss stands convert to open lichen woodlands as a result of weak postfire regeneration caused by successive insect and fire disturbances.

Résumé : Dans le sud de la forêt boréale de l'est du Canada, l'épinette noire (*Picea mariana* (Mill.) BSP) est affectée à la fois par les insectes défoliateurs et les incendies de forêts. Puisque l'épinette noire dépend de sa banque de graines aérienne pour assurer sa régénération après feu, la réduction de la quantité de cônes lors d'une épidémie de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* (Clem.)) ouvre une fenêtre de vulnérabilité pendant laquelle la régénération pourrait être compromise en cas de feu. Afin d'évaluer l'effet à long terme d'une épidémie de tordeuse sur le potentiel reproducteur de l'épinette noire, nous avons estimé la production de cônes et la banque de graines viables avec des inventaires de cônes et des tests de germination dans des pessières noires à lichens qui ont subi différents degrés de défoliation dans les années 1980. La quantité de cônes d'épinette noire était significativement reliée à l'historique de défoliation des peuplements ($R^2 = 0,89$), mais non à leur âge ou à leur surface terrière, ni à la densité des tiges. Les pessières noires qui ont été sévèrement défoliées montraient un plus petit nombre de cônes, une plus grande incidence de cônes endommagés par les insectes et une densité de graines viables de 3 à 17 fois inférieure à celle d'une pessière légèrement défoliée. La fenêtre de vulnérabilité pour la régénération de l'épinette noire à la suite d'une épidémie de tordeuse des bourgeons de l'épinette pourrait donc être aussi grande que 20 ans dans la région étudiée puisque la banque de graines des pessières noires sévèrement défoliées ne s'est toujours pas reconstituée. Ce travail appuie les conclusions des études de reconstitutions de peuplements qui suggèrent que les pessières à mousses fermées peuvent se transformer en pessières à lichens ouvertes à la suite d'une mauvaise régénération après feu causée par l'impact successif des insectes défoliateurs et du feu.

Introduction

The zone of continuous lichen woodland reaches its southern range limit at 52°N in eastern Canada. This subarctic vegetation type is also distributed in scattered patches as far

as 500 km further south, near the transition zone between the southern boreal forest and the mixedwood forest (48°N) (Payette 1992). The southernmost lichen woodland patches are embedded in a matrix of closed-crown forests, in the heart of the balsam fir (*Abies balsamea* (L.) Mill.) bioclimatic

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zone (Robitaille and Saucier 1998). Even though the floristic composition of the lichen woodlands is approximately the same at both ends of its distribution zone (<40% black spruce (*Picea mariana* (Mill.) BSP) cover and continuous lichen mat with dwarf birch (*Betula glandulosa* Michx.) and ericaceous shrubs), the factors responsible for their origin and maintenance differ (Payette 1992). While the northern lichen woodland originates from postfire regeneration failure driven by climate change (Payette and Gagnon 1985; Sirois and Payette 1991; Arseneault and Payette 1992), the southern lichen woodland is thought to be a regressive forest type resulting from the detrimental impact of compounded disturbances (Payette et al. 2000; Jasinski and Payette 2005). Stand reconstructions suggest that these once closed forests suffered weak postfire regeneration after successive disturbances, such as consecutive fire events, or insect outbreak followed shortly by fire (Payette et al. 2000), or the combination of logging, insect outbreak, and fire (Payette and Delwaide 2003). It has been proposed (Payette 1992; Payette et al. 2000; Payette and Delwaide 2003) that if black spruce is affected by a disturbance that temporarily reduces its aerial seed bank and that a stand-destroying fire occurs before the seed bank has been replenished, then postfire regeneration would be compromised.

Black spruce is adapted to fire, bearing semi-serotinous cones that shed seeds under the heat of crown fires (Viereck and Johnston 1990). Old cones stay attached to the trees and retain viable seeds that contribute to the seed bank (Schooley et al. 1979). Because cone production is proportional to tree basal area (Pinard 1999; Sirois 2000; Greene et al. 2004), the heaviest cone crops are in mature (>100-year-old) stands (Black and Bliss 1980; Pinard 1999), precisely the most susceptible to several types of disturbance, such as spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks (Sanders et al. 1985). Spruce budworm's impact on black spruce stands is mainly through the destruction of current-year foliage, which causes growth reduction and eventually tree death (MacLean 1985). The spruce budworm also affects black spruce seed production by feeding directly on female flowers, cones, and seeds (Schooley 1980; Prévost et al. 1988), killing mature cone-bearing trees and causing death of tree-tops (top killing) (MacLean 1985; Raske and Sutton 1986), where the majority of cones are located (Bégin and Filion 1999). Cone production might even be suppressed for some years after an outbreak (Shearer 1980), a period during which wildfire ignition and spread is enhanced by surface fuel accumulation and vertical continuity of "ladder" fuel, i.e., dead broken tops (Stocks 1985, 1987; McCullough et al. 1998; Fleming et al. 2002).

The aim of this study was to determine whether black spruce stands affected by a spruce budworm outbreak 15 years ago showed reduced cone crop and seed bank compared with stands that were lightly defoliated. We estimated cone production and viable seed bank of black spruce stands that sustained different levels of defoliation by the spruce budworm, using cone crop surveys and germination trials. The identification of a depleted seed bank in budworm-damaged stands would support retrospective studies that have shown that successive insect and fire disturbances can transform closed-crown spruce-moss stands into open lichen woodlands at the southern limit of the boreal forest.

Methods

Study area

The study was carried out in the Parc des Grands-Jardins (47°40'N, 70°50'W), 120 km northeast of the city of Québec (Québec, Canada). The park lies in the Laurentian Highlands (mean altitude 800–900 m a.s.l.), a rise in the Precambrian Shield that represents the southern limit of the boreal forest (Robitaille and Saucier 1998). The highlands form a barrier to humid westerly air masses, creating a rainshadow that results in drier conditions in the park (annual mean precipitation of 1000 mm) and, consequently, in higher fire frequency compared with the surrounding region. The balsam fir forest type that dominates the highlands is locally replaced, in the park, by a mixture of black spruce – feathermoss forests and black spruce – lichen woodlands, the latter being at their southern range limit. These forests grow under a cold (annual mean temperature of 0 °C) climate and are subjected to two main disturbances: fire and outbreaks of the spruce budworm. The last budworm infestation to occur in the park lasted from 1976 to 1985 (Gouvernement du Québec, ministère des Ressources naturelles, Direction de la conservation des forêts, unpublished defoliation maps) and affected several lichen woodland stands (Simard and Payette 2001).

Epiphytic lichens as markers of spruce budworm defoliation

Most lichen woodland stands in the park are characterized by unusually high biomass of epiphytic lichens of the genus *Bryoria* growing on black spruce trees. These lichens show a patchy distribution on individual trees and occur mainly on the dead tops and branches of trees, a distribution pattern unlike what is usually observed (Liu et al. 2000). According to recent analyses, epiphytic *Bryoria* lichens are restricted to those parts of the trees defoliated during the last spruce budworm outbreak (Simard and Payette 2003). Consequently, all the lichen-covered tree parts were formed before or during the outbreak, while postoutbreak tree parts were typically free of lichens, with a sharp transition in lichen cover between the two parts. At the stand level, lichen cover was more closely related to the severity of budworm defoliation, shown by ring-width patterns, than to stand age (Simard and Payette 2001). In the study area, the epiphytic lichen *Bryoria* is a marker of spruce budworm defoliation at both tree and stand levels (Simard and Payette 2003). In this study, cone sampling was stratified according to the epiphytic lichen cover to distinguish cones produced before or during the outbreak (lichen-covered cones) from postoutbreak cones (lichen-free cones).

Study sites

Black spruce cone production was studied in seven black spruce – lichen woodlands of different age and defoliation history (Table 1). All stands were affected by the last spruce budworm outbreak, but to different degrees, according to aerial defoliation surveys (Gouvernement du Québec, ministère des Ressources naturelles, Direction de la conservation des forêts, unpublished maps). We could not find a postfire stand that was not defoliated, as the outbreak was regionally severe (Gray et al. 2000). All stands were of postfire origin,

Table 1. Characteristics of black spruce – lichen woodland stands.

Site	Stand origin	Stand age (years)	Growth reduction (%) ^a	Incomplete growth rings (%) ^b	Top kill (%) ^{cd}	Tree mortality (%) ^c	Tree density (trees·ha ⁻¹) ^{cd}	Basal area (m ² ·ha ⁻¹) ^{cd}
1	Fire	59	29	0	0	0	656	3.8
2	Fire	78	88	100	47	25	1152	7.2
3	Fire	135	83	71	46	21	1092	3.9
4	Clearcut	40	56	28	0	3	2552	8.8
5	Fire	83	89	na	na	18	1036	4.7
6	Fire	107	77	80	66	24	872	4.3
7	Fire	134	87	76	26	27	1612	5.7

Note: At sites 1, 2, and 3, cones were sampled for verification of cone count estimates, germination trials, and signs of insect predation. na, not available.

^aMaximum radial growth reduction, calculated as the difference between the mean index (1.0) and the minimum index value during an outbreak.

^bMaximum frequency of incomplete growth rings for a single year.

^cTrees >3 m in height only.

^dLive trees only.

except one that originated from a clearcut. Except for their age and defoliation history, all sites were similar in terms of altitude (710–750 m a.s.l.), topography (flat), surficial deposits (fluvioglacial sands), soil drainage (class 2, according to the Canadian System of Soil Classification (Soil Classification Working Group 1998)), and ground-cover vegetation (mainly lichens of the genus *Cladina*, interspersed with ericaceous shrubs (*Vaccinium* sp., *Ledum groenlandicum* Retzius, *Kalmia angustifolia* L.) and dwarf birch.

Tree-ring analysis

We constructed tree-ring chronologies to document the specific impact of the spruce budworm outbreak at each individual stand. At each site, 25 black spruce trees were randomly selected and sampled (increment cores or cross sections) 30 cm above the ground (Simard and Payette 2001). Samples were sanded to 600 grit and cross-dated (Stokes and Smiley 1968) using a frost-ring chronology, under 40× magnification. Tree-ring widths were measured along three radii using a Velmex moving table (precision of 0.002 mm) interfaced with a computer, and dating was checked with COFECHA (Holmes 1983). Individual series were detrended using straight lines, negative exponentials, or second-degree polynomial functions, then averaged to construct seven site chronologies. An additional chronology was constructed for jack pine (*Pinus banksiana* Lamb.) using 21 trees from across the study area. The comparison of tree-ring series between spruce budworm host (black spruce) and non-host (jack pine) species allows the identification of growth declines associated with insect defoliation (Swetnam et al. 1985). A digital low-pass (9 years) filter (Swetnam et al. 1985) was applied to the chronologies to highlight radial growth variations caused by spruce budworm outbreaks, which usually last 5–15 years (Royama 1984; Gray et al. 2000). Tree-ring growth reductions are known to be proportional to defoliation levels (Piene and Little 1990). To quantify the impact of spruce budworm on black spruce stands, maximum growth reduction was calculated for each stand chronology (Swetnam et al. 1985). This corresponds to the largest growth reduction for a single year during a budworm outbreak and is calculated as the difference between the chronology's mean index (1.0) and the minimum index value during the outbreak.

Cone crop survey

Cone production was surveyed in 1999 (sites 1–3) and 2004 (sites 4–7). A 2500-m² quadrat (100 m × 25 m) was randomly positioned at each site. All trees (dead and live) taller than 3 m were censused, their diameter at breast height measured, and living trees showing top kill were recorded. The number of seed cones was assessed on all black spruce trees >3 m in height within the quadrat, according to the following abundance classes: no cones, low (1–50), moderate (51–500), and high abundance (500+). All cone counts were made atop a 3.5-m stepladder, using 7× binoculars when necessary. In addition to cone abundance, the proportion of cones covered by epiphytic lichens was assessed to the nearest 5% for each tree. This distinction was done because lichen-covered cones were expected to have less seeds than cones devoid of lichens (see Epiphytic lichens as markers of spruce budworm defoliation). The assessment of cone abundance and lichen cover was facilitated by the fact that lichen woodlands are open stands (10% to 40% spruce cover) where tree-tops can be easily observed from different viewpoints. Also, the slow growth of black spruce in the study area (Dussart and Payette 2002) results in trees of low stature (site index, i.e., height at 50 years, of 6 to 8 m), which further facilitates the estimation of cone crops in older stands. Additionally, because tree density is low in these open stands, all tree crowns are in full light, and it is thus unlikely that cone production will be adversely affected by low light levels reaching treetops (Greene et al. 2002). To verify the accuracy of the estimates of the number of cones, 10 randomly chosen trees were cut down in three sites (sites 1, 2, and 3), and all their cones were brought back to the laboratory. As only one tree was sampled in the high abundance class, two additional trees were randomly selected within this group, for a total of 32 trees. Lichen-covered and lichen-free cones were then counted in the laboratory.

Cone sampling and germination trials

Cones were sampled only at sites 1, 2, and 3, which showed contrasting defoliation history. Site 1 was only lightly defoliated, whereas sites 2 and 3 were severely impacted by the last budworm outbreak, as shown by tree-ring series (Table 1). At each site, 10 black spruce trees taller than 3 m

were randomly selected, on which 10 lichen-covered and 10 lichen-free cones were collected (avoiding cones of the current year). Because not all selected trees had a sufficient number of cones, additional trees were sampled until 100 lichen-covered cones and 100 lichen-free cones were collected in each site. Sampling was conducted at the end of June 1999. Cones were promptly stored in the refrigerator and were only taken out for the time needed for seed extraction, germination, and viability tests. Cones were put in an oven at 80 °C for 4 h, after which time all cones were opened. Seeds were extracted manually from the cones by removing cone scales with tweezers. Cones were carefully checked for signs of insect predation such as coarse frass, partially eaten seeds and cone scales, hollowed cone axis, emergence holes, hypertrophied seeds, and cone deformities. Insects found in the cones or seeds were collected and identified. Seeds were then put in Petri dishes over two filter papers soaked with a 1% Benomyl (Benlate, DuPont Canada) solution, a systemic fungicide. The Petri dishes were sealed with parafilm and placed in Conviron growth chambers under a daily cycle of 14 h of light at 30 °C and 10 h of darkness at 20 °C to germinate (Farmer et al. 1984; Edwards 1987; Young and Young 1992). The number of germinated seeds (radicle >2 mm; Haavisto and Winston 1974) was noted every week for 5 weeks without opening the Petri dishes. Ungerminated seeds were dissected, and those showing a sound embryo were tested for viability in a 1% tetrazolium chloride solution (Edwards 1987). Viability estimates included both germination and staining trials.

Statistical analyses

The accuracy of the estimation of the number of cones in the field was tested with two statistics: Bowker's test of Symmetry (S) (Bowker 1948) and the weighted Kappa statistic (K_w) (Landis and Koch 1977), which are both adequate for ordered class data. The first test measures the symmetry of the estimated–observed number matrix and gives an associated probability level under a null hypothesis of symmetry. The Kappa statistic (dimensionless coefficient between –1 and 1, expressing total disagreement to total agreement, respectively) measures the interrater agreement, as if the estimated and observed number of cones were classified by two independent persons. The weighted Kappa takes into account that with ordered class data, misclassification by one class is a lesser error than misclassification by two or three classes, etc. Landis and Koch (1977) proposed that interrater agreement was good when $0.61 > K > 0.80$, and excellent when K exceeded 0.80.

To determine which factor or set of factors best explained the abundance of cones, multiple regression analyses were performed between cone abundance (response variable) and maximum growth reductions in tree-ring chronologies (stand-level spruce budworm impact), stand basal area, tree density, and stand age (explanatory variables) using data from all seven stands. Variables that were not significant ($\alpha = 0.05$) were eliminated from the model until only significant ones remained. Three separate regressions were performed for the abundance of lichen-covered cones, lichen-free cones, and the total (lichen-covered + lichen-free). All regressions were done with the SAS/STAT® statistical software package (PROC REG, SAS Institute Inc. 2000).

To test the effect of lichen (lichen-covered vs. lichen-free) and site on the incidence of lepidopteran insect damage on cones, we used logistic regressions with the GLIMMIX macro (SAS Institute Inc. 2000), which allows the inclusion of random effects (tree effect). Logistic regression models best fit binary response variables, in our case, presence or absence of insect damage. Because logistic regressions were performed five times on the same data set (for the five types of insect damage), the significance level was lowered from 0.05 to 0.025 to keep the overall type I error rate relatively low.

The effect of lichen cover and site on the number of extracted seeds was tested with a Poisson regression corrected for overdispersion, with the GLIMMIX macro to include random effects (tree effect) (SAS Institute Inc. 2000). The number of viable seeds was tested with the same method, with the exception that the lichen effect could not be tested because of the absence of viable seeds in lichen-covered cones. Therefore only site effect was tested among lichen-free cones. For the same reason, only site effect was tested for the proportion of viable seeds, using a logistic regression with the GLIMMIX macro (SAS Institute Inc. 2000).

Results

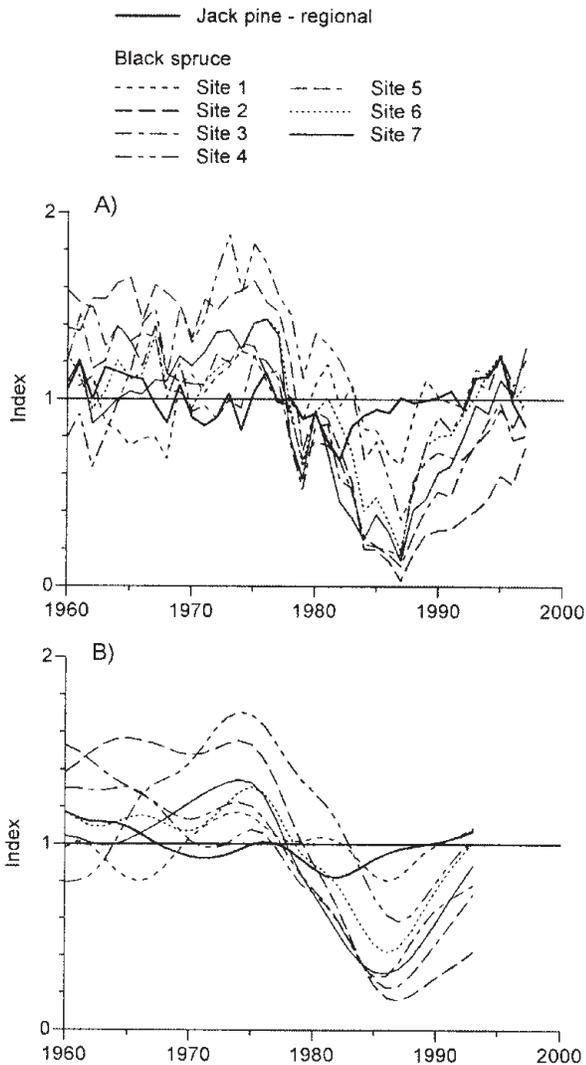
All sites were affected by spruce budworm infestation in 1976–1985, as indicated by airborne defoliation surveys (Gouvernement du Québec, ministère des Ressources naturelles, Direction de la conservation des forêts, unpublished maps), field surveys (Forest Insect and Disease Survey National Database, Canadian Forest Service), and tree-ring chronologies (Fig. 1). However, the impact of spruce budworm differed among stands, as shown by tree-ring growth reductions ranging from 29% (light defoliation) to 89% (severe defoliation) (Table 1). Growth reductions, frequency of incomplete growth rings, percent top kill, percent tree mortality, and proportion of cones covered with lichens, which are all influenced by spruce budworm defoliation (MacLean 1985), were all strongly intercorrelated (Table 2), suggesting that maximum growth reduction is a good estimator of spruce budworm defoliation.

Cone survey

Cone abundance class estimation was accurate ($K_w = 0.737$, $n = 32$), with 60% to 100% of trees successfully classified (Fig. 2). Cone counts for misclassified trees were systematically underestimated, although not at a significant level ($S = 9.00$, $df = 6$, $p = 0.1736$). Therefore, to compute the number of cones and seeds per hectare, we used the observed mean cone abundance for each class (1, 45, 327, and 3647) instead of the estimated abundance class median (0, 25, 250, and 2500). Both set of values yielded the same relative quantity of cones among sites, but the observed values were thought to be more representative of the absolute number of cones per hectare. The proportion of cones covered with epiphytic lichens was well predicted from field estimates ($R^2 = 0.98$, $F = 1119$, $df = 22$, $p < 0.0001$; $\text{Prop}_{\text{obs}} = 1.018(\text{Prop}_{\text{est}}) + 1.985$; slope not significantly different from 1).

The number of lichen-covered and lichen-free cones per hectare was estimated for each of the seven stands. The abundance of cones devoid of lichens decreased with increasing budworm impact ($R^2 = 0.89$, $F = 41.7$, $df = 5$, $p =$

Fig. 1. Detrended tree-ring chronologies (1960–1997) of jack pine (thick solid line; $n = 21$ trees; three radii per tree) and black spruce (thin lines; $n = 25$ trees per site; three radii per tree) in the study area (A). Series were filtered with a 9-year low-pass digital filter to highlight radial growth decline caused by spruce budworm outbreak (B). Data modified from Simard and Payette (2001) with additional data.



0.0013), whereas stand basal area, tree density, and stand age did not significantly ($\alpha = 0.05$) add more strength to this relationship (Table 3, Fig. 3). The number of lichen-covered cones per hectare was also best explained by tree-ring growth reductions, but the relationship was positive ($R^2 = 0.70$, $F = 11.5$, $df = 5$, $p = 0.0195$). Again, there was no significant relationship between lichen-covered cone abundance and basal area, tree density, or stand age. The total number of cones (lichen-free + lichen-covered) was not related to either of these variables (Table 3).

Insect predation

Seeds were extracted from the cones sampled in sites 1 (lightly defoliated) and 2 and 3 (severely defoliated) and were checked for signs of insect predation. Although several types of insect damage were found on cones and seeds, only

damage associated with lepidopteran larvae (Hedlin et al. 1980; Turgeon and de Groot 1993) is presented, as it was more frequent and obvious than the other types. Lepidopteran predation signs included partially eaten seeds, coarse frass, deformed cones, and hollowed cone axis (overwintering site of *Cydia strobilella* L., a seed predator) (Hedlin et al. 1980; Turgeon and de Groot 1993). Overall, cones covered with lichens consistently showed a higher frequency of insect damage than did lichen-free cones (Fig. 4). Partially eaten seeds were more frequently observed (up to 73%) than the other types of insect damage (26% maximum). Insect predation data are not independent, however, as some cones showed several types of lepidopteran damage. During seed extraction, a few insects were found and identified: one larva of the spruce seed moth (*C. strobilella*) was found in lichen-covered cones at site 3, and adults of the deathwatch cone beetle were also found in lichen-covered cones at both site 3 (two adults of *Ernobius bicolor* White) and site 2 (one adult of *Ernobius nigrans* Fall).

Seed viability

In all three sites, a greater number of seeds were found in lichen-free cones ($F = 43.3$, $df = 4$, $P = 0.0028$), which contained, on average, eight times more seeds than lichen-covered cones (Fig. 5). No site or site \times lichen effect was detected ($\alpha = 0.05$). Stain trials improved total viability by 1% to 4%, on average, compared with germination alone. Viability ranged between 29% and 40% for seeds extracted from lichen-free cones, whereas it was zero for seeds found in lichen-covered cones (Fig. 5). A P value could not be calculated for this obvious lichen effect, however, because the absence of viable seeds in lichen-covered cones precluded the inclusion of the lichen effect in the logistic regression model. No site effect was detected ($\alpha = 0.05$) for both the number or the proportion of viable seeds in lichen-free cones.

The number of viable seeds per hectare was calculated for each of the three sites using cone crop surveys (Fig. 3) and viability trials (Fig. 5). Site 1 (lightly defoliated stand) showed the largest seed bank, with about 1 500 000 viable seeds \cdot ha $^{-1}$, while sites 2 and 3 (severely defoliated stands) had considerably smaller seed bank, with about 485 000 and 85 000 viable seeds \cdot ha $^{-1}$, respectively (Fig. 6). The number of viable seeds per hectare in site 1 was thus 3 times and 17 times greater than that of site 2 and 3, respectively. The large difference among the sites' seed bank was mostly influenced by the number of lichen-free cones (Fig. 3a), because lichen-covered cones produced no viable seeds, and the number of viable seeds from lichen-free cones was approximately the same in all sites (Fig. 5).

Discussion

Spruce budworm and black spruce seed bank

The cone crop and viable seed bank of black spruce were clearly smaller in stands severely damaged by spruce budworm defoliation (Figs. 3, 6). Our data show that cone crop is closely and only related to the defoliation history of the stands, determined from tree-ring growth reductions. Increasing budworm impact results in a lower quantity of lichen-free cones and consequently in lower viable seed density, but also in a higher quantity of lichen-covered cones, which pos-

Table 2. Correlation matrix of stand-level estimators of spruce budworm impact.

	Growth reduction ^a	Incomplete rings ^b	Top kill ^{cd}	Tree mortality ^c	Lichen-covered cones ^c
Growth reduction	—	0.96	0.75	0.91	0.90
Incomplete rings	0.0023	—	0.85	0.96	0.89
Top kill	0.0882	0.0338	—	0.83	0.84
Tree mortality	0.0047	0.0027	0.0386	—	0.96
Lichen-covered cones	0.0052	0.0176	0.0357	0.0008	—

Note: The upper right portion of table shows Pearson’s correlation coefficients, while the lower-left portion shows *p* values.

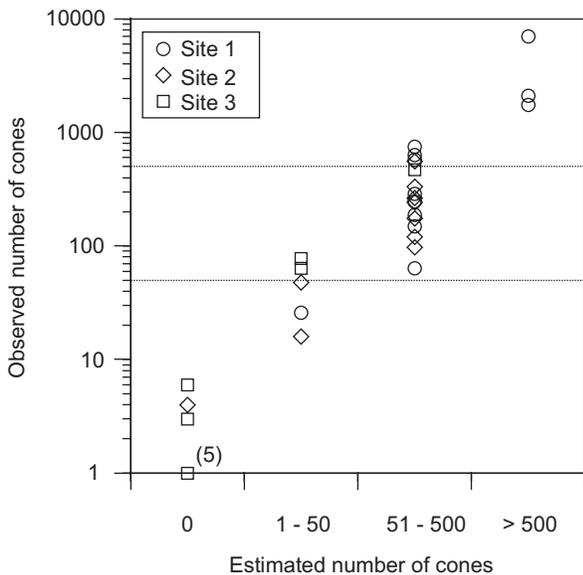
^aMaximum radial growth reduction, calculated as the difference between the mean index (1.0) and the minimum index value during an outbreak.

^bMaximum frequency of incomplete growth rings for a single year.

^cTrees >3 m in height only.

^dLive trees only.

Fig. 2. Estimated cone abundance class versus observed number of cones (*n* + 1 for use of logarithmic scale) of sampled trees (*n* = 32). Broken lines correspond to class limits. Number in brackets beside the symbol indicates number of superposed observations.



sess no viable seeds and show a high occurrence of insect damage. Stand age, basal area, and tree density were not significantly related to the abundance of lichen-free cones, which bear the viable seeds (Table 3). This is somewhat surprising, since black spruce cone crop and viable seed bank have been shown to be most strongly related to basal area and stand age. Pinard (1999) used stand age and stem diameter to accurately predict the number of black spruce cones and viable seeds in the James Bay area, while Sirois (2000) and Greene et al. (2004) both found a significant relationship between basal area and black spruce cone production for the James Bay area and the northern Abitibi area, respectively. However these studies were conducted in regions that are near or north of the northernmost range limit of spruce budworm, where spruce budworm outbreaks are weaker. Our study was done in the core of the spruce budworm’s range, where its effects on cone production are likely to be stronger and probably override the basal area – cone production relationship.

Spruce budworm can affect the seed bank in two ways. First, defoliation of the upper crown by budworm larvae causes death of treetops (MacLean 1985; Raske and Sutton 1986), where the majority of young cones are located (Bégin and Fillion 1999). Top kill frequency in live trees increased with increasing budworm impact (Table 2). As death of cone-bearing branches probably reduces seed viability in black spruce, as it does in jack pine (S. Gauthier, unpublished data), the viable seed bank was likely diminished in stands with heavy top kill. Furthermore, top kill likely reduces post-outbreak cone production (Shearer 1980) by altering tree architecture (Simard and Payette 2003) and starch reserves (Webb and Karchesy 1977). Second, spruce budworm reduces the black spruce seed bank by feeding directly on the megastrobili that mature into cones. Budworm larvae feed on the female reproductive structures of black spruce at all development stages (female flowers, immature cones, and mature cones) preferring them to vegetative buds or current-year foliage (Hedlin et al. 1980; Schooley 1980; Syme 1981; Bonneau et al. 1986; Prévost et al. 1988; Turgeon and de Groot 1993; Miller et al. 1995). Budworm feeding results in female flower mortality, abnormal cone development, and a drastic reduction in the number of viable seeds (Schooley 1980), leaving partially eaten cones filled with abundant coarse frass (Hedlin et al. 1980; Turgeon and de Groot 1993). This feeding behavior of the spruce budworm also has been documented for balsam fir (Powell 1973; Schooley 1978), white spruce (*Picea glauca* (Moench) Voss) (Tripp 1950), and eastern larch (*Larix laricina* (Du Roi) Koch) (Amirault and Rae Brown 1986; Prévost 2002), as well as for its western relative, the western spruce budworm (*Choristoneura occidentalis* Free.) on Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Dewey 1970). This cone feeding habit could benefit spruce budworm on black spruce by providing food for newly hatched larvae until bud break, which is delayed compared with balsam fir and white spruce, the main hosts of the insect.

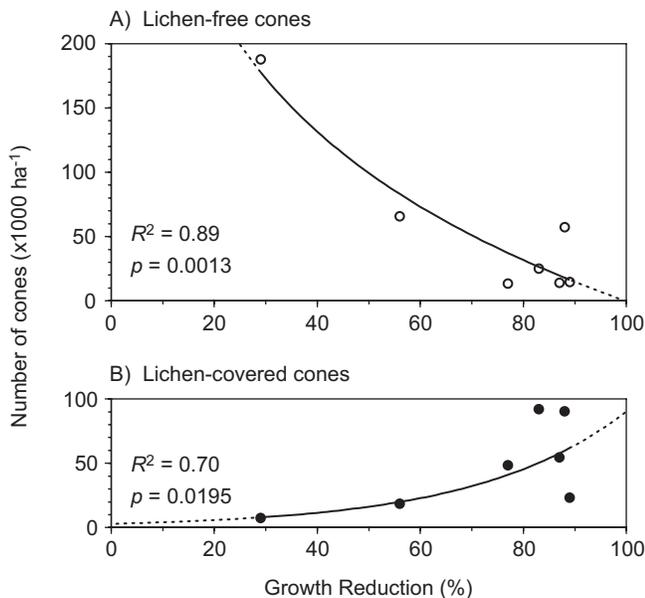
At all sampled sites, lichen-covered cones showed higher incidence of insect damage (Fig. 4), lower number of seeds, and lower seed viability (Fig. 5). That lichen-covered cones yielded no viable seeds is no surprise, as these cones were probably formed before the outbreak and are therefore older than lichen-free cones, formed after the outbreak (see Epiphytic lichens as markers of spruce budworm defoliation). However, lichen-covered cones also showed significantly higher oc-

Table 3. Results of regression analyses with cone abundance (lichen-free, lichen-covered, and total) as the response variables, and tree-ring growth reduction, stand basal area, tree density, and stand age as explanatory variables.

Variable	Source	<i>t</i>	<i>p</i>
Lichen-free cones, $R^2 = 0.89$	Growth reduction	-6.46	0.0013
	Basal area	—	ns
	Tree density	—	ns
	Stand age	—	ns
Lichen-covered cones, $R^2 = 0.70$	Growth reduction	3.39	0.0195
	Basal area	—	ns
	Tree density	—	ns
	Stand age	—	ns
All cones	Growth reduction	—	ns
	Basal area	—	ns
	Tree density	—	ns
	Stand age	—	ns

Note: Variables that were not significant (ns; $\alpha = 0.05$) were removed from the model. For all regressions, $n = 7$ and $df = 5$.

Fig. 3. Black spruce cone crop in relation to maximum growth reduction in tree rings during the last spruce budworm outbreak. Stand age, stem density, and basal area were not significant in either regression ($\alpha = 0.05$). Each symbol represents a stand. The regression equation between growth reduction (GR) and number of lichen-free cones (C_{lf}) is $C_{lf} = -331\ 428 \log(\text{GR}) + 662\ 377$, and between growth reduction and number of lichen-covered cones (C_{lc}) is $\log(C_{lc}) = 0.0149\text{GR} + 3.4649$.



currence of insect feeding damage, indicating the impact of insects on the seed bank during the outbreak. It is thus impossible to separate the effects of cone age (Schooley et al. 1979) from that of insect feeding on the low viable seed yield of lichen-covered cones. In any case, the net result is that lichen-covered cones did not contribute at all to the aerial seed bank. On the other hand, the severity of the outbreak had a long-lasting effect on black spruce seed bank because severely defoliated stands showed a smaller number of lichen-free cones (Fig. 3a). Lichen-free cones were presumably produced after the outbreak, i.e., between ca. 1986

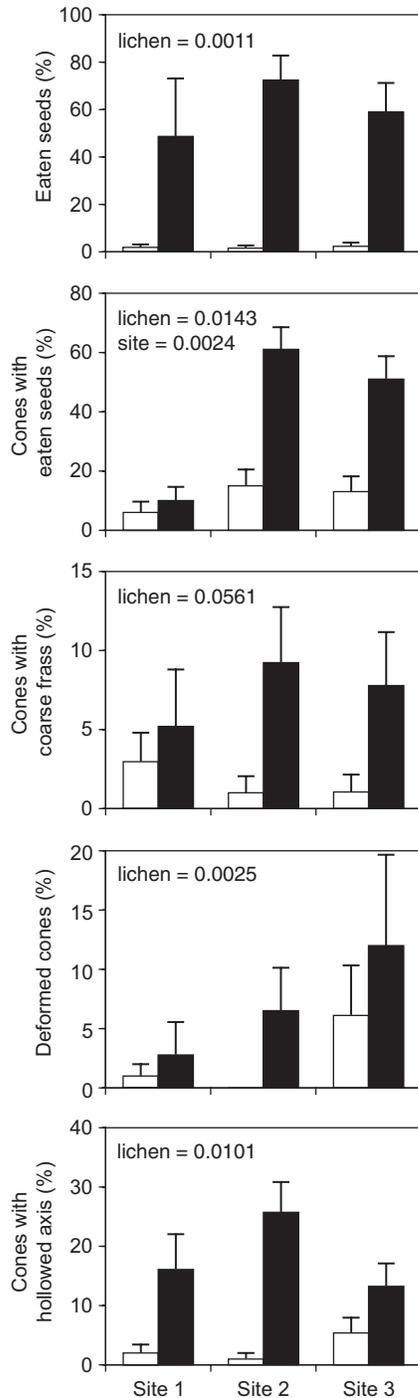
and 1999 (year of sampling), which is supported by the low incidence of insect feeding damage on these cones. Thus, postoutbreak recovery of the seed bank was poorer in the severely defoliated stands than in the lightly defoliated stands.

Although spruce budworm feeding probably accounts for most cones being deformed, filled with coarse frass, and containing partially eaten seeds, there is evidence for other insects being responsible for at least part of the damage. Some cones were found to have a hollowed cone axis (Fig. 4), which serves as overwintering site for both the spruce seed moth (*C. strobilella*); one larva found in lichen-covered cones) and the deathwatch cone beetle (*E. bicolor* and *E. nigrans*; three adults found in lichen-covered cones), two major seed predators that leave cones filled with frass (Hedlin et al. 1980; Schooley 1983; White 1983; Sweeney et al. 1993; Turgeon and de Groot 1993). Also, partially eaten seeds and coarse frass can be associated with feeding of the spruce cone maggot (*Strobilomyia neanthracina* Mchs.) and coneworms (*Dioryctria reniculelloides* Mut. & Mun. and *Dioryctria abietivorella* Grt.) (Hedlin et al. 1980; Turgeon and de Groot 1993), even though these species leave no characteristic feeding damage and that none was found. There is little doubt, however, that the majority of insect damage was caused by spruce budworm, as field surveys and airborne defoliation surveys showed that the study area was affected by a severe infestation in 1976–1985, and because damaged cones were covered by epiphytic lichens, which are markers of budworm defoliation (Simard and Payette 2003). Several species of insect pests abound in budworm-damaged stands and further contribute to their decline (Spies and Dimond 1985; Raske and Sutton 1986). Feeding damage of both spruce budworm and other obligate seed predators on the same lichen-covered cones suggests that during or immediately after outbreaks, black spruce cones are attacked by a variety of seed-eating insects that likely destroy the largest part of the cone biomass (Syme 1981; Spies and Dimond 1985; Bonneau et al. 1986; Prévost et al. 1988; de Groot et al. 1994; Turgeon et al. 1994).

Implications for postfire regeneration

Although interruption of cone production during spruce budworm outbreaks has been documented (Ghent 1958; Powell

Fig. 4. Incidence of various types of insect damage on lichen-free (open bars) and lichen-covered (solid bars) cones in lightly (site 1) and severely defoliated (sites 2, 3) stands ($n = 100$ cones per site per cone type). Probability (p) values associated with site, lichen, or site \times lichen effects are shown (see Methods for p value threshold correction for multiple tests).



1973), it has never been considered a hazard for stand regeneration, since preestablished seedlings and layers usually replace dead overstory trees (Baskerville 1975; Morin 1994). However, in fire-prone sites, even a temporary reduction of the seed bank creates a window of vulnerability for repro-

Fig. 5. Number of seeds extracted from lichen-free (open bars) and lichen-covered (solid bars) cones ($n = 100$ cones per site per lichen cover type) and number of viable seeds (hatched bars) in lightly (site 1) and severely defoliated (sites 2, 3) stands. The resulting viability percentages are shown above bars. Viability includes germination and staining trials.

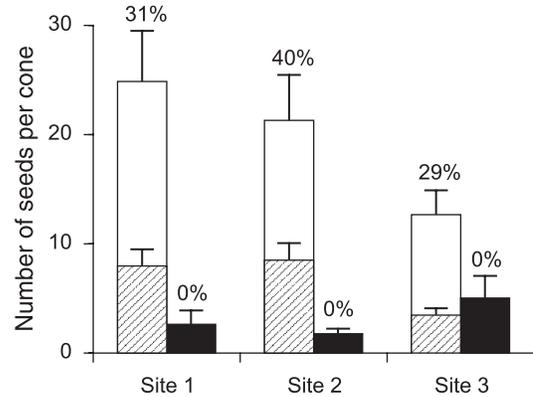
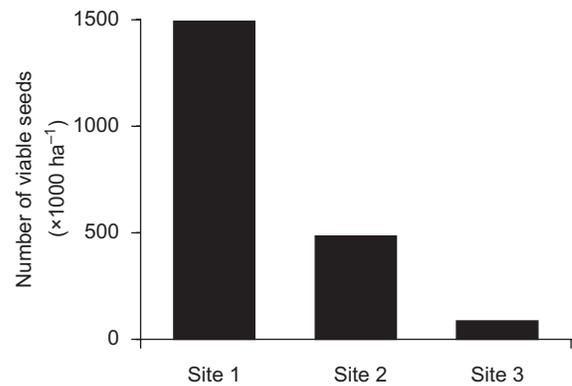


Fig. 6. Viable seed bank in lightly (site 1) and severely defoliated (sites 2, 3) stands, calculated with cone crop survey data (number of cones per hectare; Fig. 3) and germination trials (number of viable seeds per cone; Fig. 5).



duction of black spruce, which depends on its aerial seed bank for postfire regeneration. In the event of a fire, such seed-depleted stands could not provide enough seeds for adequate regeneration, resulting in stand opening. Because spruce budworm infestation causes a decrease of cone production for several years after an outbreak (Shearer 1980; this study), the vulnerability window is extended and the probability of having a stand-destroying fire resulting in reduced postfire regeneration is higher. Furthermore, fire probability itself could be increased because fine fuel accumulation enhances fire ignition and spread after spruce budworm outbreaks (Stocks 1985, 1987; McCullough et al. 1998; Fleming et al. 2002; Hummel and Agee 2003). In this study, even 15 years after the outbreak, the cone crop in heavily defoliated stands was still lower than that in lightly defoliated stands. Assuming that cone production is negligible in the third year of a heavy defoliation (Powell 1973), then the susceptibility window of black spruce may exceed 20 years (1978 to 1999, year of sampling). Successful stand establishment not only depends on the viable seed bank, but also on seedbed availability, germination success, and early survivorship. How-

ever, when stands show striking differences in their reproductive potential, like those observed in this study (3- and 17-fold), it is probable that these differences will be observed in the final stages of stand establishment.

Local high fire frequency in the park, along with recurrent spruce budworm outbreaks, increases the hazard of budworm–fire interactions resulting in reduced postfire regeneration. Many open lichen woodlands in the study area appear to be the result of such events, as retrospective studies have shown these stands to be closed-crown canopies prior to the last fire (Payette et al. 2000). Therefore, the spruce budworm – closed-crown conifer forest complex, described as a self-perpetuating system (Baskerville 1975; Morin 1994), can become highly unstable when a second disturbance such as fire occurs, shifting vegetation development towards an alternate successional pathway (Paine et al. 1998; Payette and Delwaide 2003). Although much information exist on both fire and spruce budworm disturbance regimes in the boreal forest and on their impact on timber yield (MacLean 1990; Bergeron et al. 2001; MacLean et al. 2002), little is known about the areas where budworm–fire interactions may compromise forest regeneration and thus produce unsuspected reductions in timber yield. Because the influence of spruce budworm gradually decreases as one goes north, we speculate that the probability of budworm–fire interactions should be highest at the southern limit of spruce–moss forests and lowest at the northern range limit of spruce budworm. There is clearly a need for such information, which could be incorporated to forest growth and yield models to prevent overestimation of timber supply. The impact of climate change on the probability of budworm–fire interaction events should also be addressed, as both spruce budworm and fire regimes are likely to be altered by global change (Fleming and Candau 1998; Flannigan et al. 1998; Bale et al. 2002; Logan et al. 2003).

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