

Prolonged Absence of Disturbance Associated with Increased Environmental Stress May Lead to Reduced Seedbank Size in *Picea mariana* in Boreal Eastern North America

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ABSTRACT

Disturbance plays an important role in the distributional range of species by affecting their colonization potential and persistence. Short disturbance intervals have been linked to reduced seedbank sizes of some species, but the effects of long intervals are largely unknown. To explore the potential existence of seedbank sizes that may also be limited by long disturbance intervals, we studied an area in boreal eastern North America where time since fire (TSF) coincides with an increase in

environmental stress (accumulating organic matter measured as depth of the soil organic layer (SOL)). Along a chronosequence dating back about 710 years, we counted the number of seeds cone⁻¹ of black spruce (*Picea mariana*) and then estimated the number of seeds tree⁻¹ and site⁻¹ by upscaling. Younger sites [TSF 60–150 years] with mature first regeneration trees had average-sized seedbanks for black spruce [12.0–17.9 (10⁵) seeds ha⁻¹], whereas subsequent pulse trees that established in SOL depths greater than 35 cm showed highly reduced seed numbers. Sites with second- to fourth-regeneration pulse individuals [TSF c. 350–710 years] had exceptionally small seedbanks of 0.90 (10⁵) and 0.46 (10⁵) seeds ha⁻¹, respectively. Radial tree growth rate showed a similarly negative response to SOL depth and could potentially be used as an indicator of seed output in plant species. Because the decline in seedbank size was possibly caused by more general environmental stress factors such as reduced nutrient availability, we suggest exploring

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whether other examples of ecosystems exist where long time since disturbance may lead to reduced seedbank sizes.

INTRODUCTION

The crucial role of natural disturbance in communities of competing sessile organisms, such as plants and rocky intertidal invertebrates, was first revealed in the 1970s and 1980s (Connell and Slatyer 1977; Sousa 1979; VanBlaricom 1982). Ecologists found that disturbance size, intensity, and frequency play an important role in the colonization and persistence of species (Noble and Slatyer 1980). Generally, ecosystems are well-adapted to cyclic disturbance regimes and the species composition after the disturbance event often resembles that of the one before (Hobbs and Huenneke 1992). However, unusual variability in the length of disturbance intervals may lead to abrupt changes in vegetation composition (Turner and others 1993). When the disturbance interval is short, some shrubs and tree species may not have had the time to reach sexual maturity and could be eliminated from the landscape (Hoffmann 1998; Keeley 1999).

In contrast, the prolonged absence of disturbance may also disrupt the stability of an ecosystem. For instance, the anthropogenic elimination of fire from the Swedish boreal forest has caused a significant decrease in the sexual regeneration capacity of early successional species such as silver birch (*Betula pendula* Roth.), aspen (*Populus tremula* L.), and pine (*Pinus sylvestris* L.) resulting in an important change in the forest composition (Linder and others 1997). For species that rely on post-disturbance regeneration from seed, long disturbance intervals have generally been associated with a reduced sexual regeneration capacity (Austrheim and Eriksson 2003; Coates and others 2006; Van Bogaert and others 2010). Whether this reduced capacity is mainly attributed to a decline in seedbank size, a lack of favorable seedbeds, increased environmental stress such as progressive nutrient depletion, or a combination of these factors, is uncertain because attribution is difficult due to entangled factors (see Fenner and Thompson 2005).

Therefore, when studying the sexual regeneration capacity of a species, it is important to distinguish between seedbank and seed production: seedbank refers to all seeds stored above- or belowground in a given area irrespective of year of crop and plant individual, whereas seed production rather refers to the annual seed output of a single

Key words: long disturbance intervals; seedbank size; fire cycle; tree growth rate; black spruce; life history of a species; environmental stress; paludification.

plant individual (Csontos 2007). Because early research in the 1970s and 1980s already showed that the length of disturbance intervals can strongly affect a species' sexual regeneration capacity (e.g. Noble and Slatyer 1980), it is surprising that the relationship between disturbance frequency and seedbank size has not been explored and quantified more often. More recent studies suggest that the relationship is species-specific as in some plant species frequent disturbance has been associated with increased seedbank size (Tardiff and Stanford 1998; Donato and others 2009), whereas in others short disturbance intervals have been linked with a reduced seedbank size (Brown and Johnstone 2012; Larsson and others 2013).

One of the main reasons for these apparent contradictions is our limited understanding of seed production variability with time. Not only do ecologists still struggle to accurately predict mast years in tree species (Smaill and others 2011), there is an ongoing debate on universal factors that best predict seed production in a plant species (Leck 2012). For instance, factors such as plant size (Shipley and Dion 1992) and temperature (in heat limited areas; Sirois 2000) are generally believed to positively affect a species' seedbank size, but other parameters such as plant age have been identified as both positive and negative drivers of seed production and seedbank size depending on the focal species (negative: Black and Bliss 1980; Auld and Myerscough 1986; positive: Witkowski and others 1991; Viglas and others 2013).

Recently, variability in environmental stress levels has attracted attention as potentially being the main driver of temporal variability in a species' seedbank size (Coates and others 2006; Valkó and others 2014). However, because few studies have focused on the long-term (decades to centuries) variability in seedbank size along successional gradients, little empirical evidence exists to support this claim.

Against this background, this study aims to explore if seedbank size may not only be limited by short disturbance intervals but also by long ones. Specifically, we hypothesize that the prolonged absence of disturbance leads to increased environmental stress that in turn causes a decline in the plant community's productivity (for example, growth rate, biomass) and seedbank size. We chose a specific area in the boreal forests of eastern North America where the prolonged absence of fire is

associated with a rapid accumulation of organic matter that could affect seedbank size. Further, by choosing black spruce as focal species, we complement the study by Browne and Johnstone (2012) that examined potential changes in the species' seedbank size as a function of short disturbance intervals. Conducting a similar study but focusing on long disturbance intervals will provide a rare opportunity to explore *if* and *how* a species' seedbank size may be affected by both sides of the time spectrum of disturbance intervals.

MATERIAL AND METHODS

Study Area

The study area ($49^{\circ}00'–50^{\circ}00'N$; $78^{\circ}30'–79^{\circ}20'W$) is situated in the boreal forest of western Québec, about 200 km south of James Bay (Figure 1).

Physio-geographically, the area is part of the Clay Belt area that covers 120,000 km² in Québec and Ontario, an area roughly the size of England or 2.1% of the total Canadian boreal forest area. The Clay Belt is characterized by a flat topography and thick deposits of early-Holocene varved clays resulting in poor drainage and a rapidly thickening soil organic layer (SOL) in the absence of fire. Half of the area is covered by organic deposits more than 60 cm thick. Although periglacial activity has been observed in the study area, permafrost is absent or extremely rare (Natural Resources Canada 2009).

The climate of the study area is nearly subarctic with the two nearest weather stations La Sarre ($48^{\circ}47'N$, $79^{\circ}13'W$) and Matagami ($49^{\circ}46'N$; $77^{\circ}49'W$) having mean annual temperatures of +0.7 and $-0.7^{\circ}C$, respectively, for the normal period 1971–2000 (Environment Canada 2013). Mean annual precipitation for both places amounts to 950 and

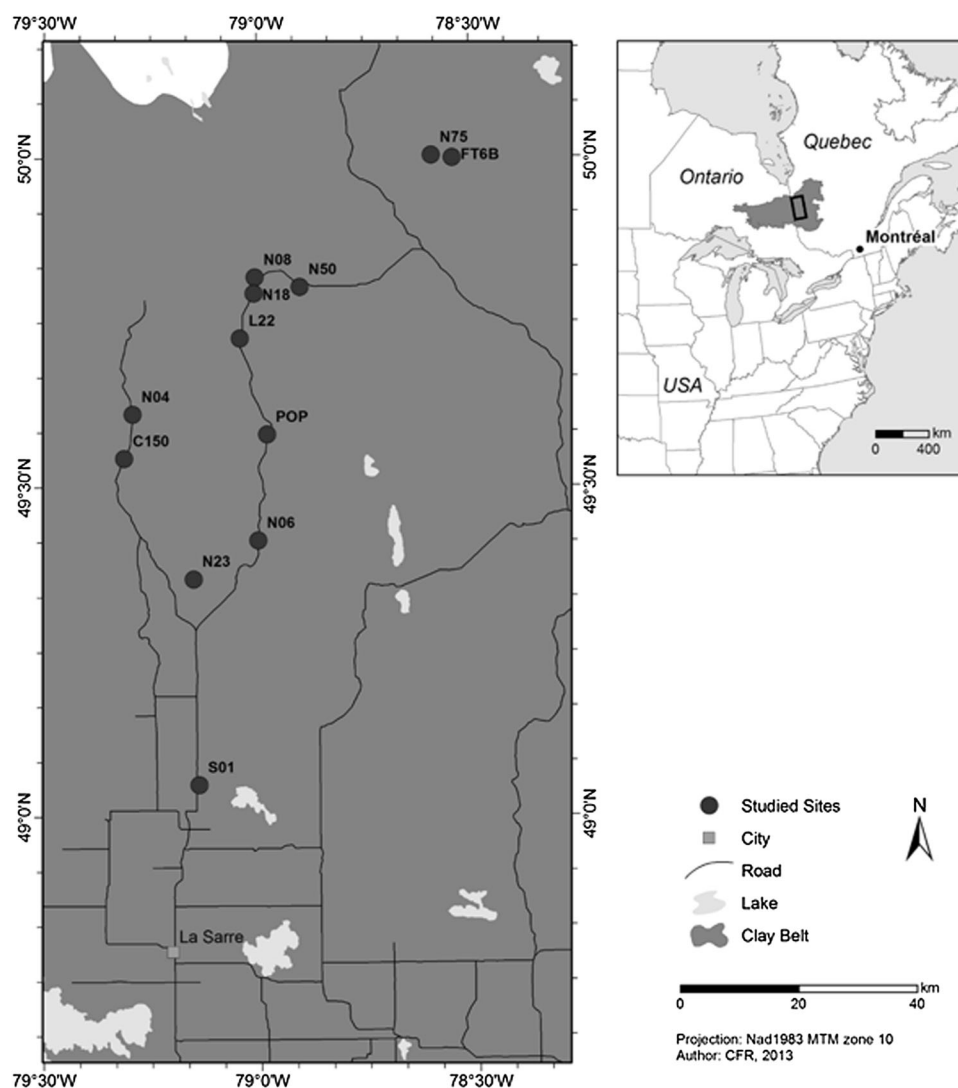


Figure 1. Study area with the 12 sites. The site names correspond to those listed in Table 1. Matagami (60 km to the east of site N50) and La Sarre are the closest towns, both having a meteorological station with a long-term record.

906 mm respectively, 35% of which falls during the growing season. The mean annual sum of degree days above 5°C amounts to 1287 for La Sarre and 1169 for Matagami.

The study area is located in the black spruce-feather moss bioclimatic zone that is mainly covered by monospecific *Picea mariana* stands. Scattered stands of jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.) also occur and more sporadically balsam fir (*Abies balsamea* (L.) Mill.) and paper birch (*Betula papyrifera* Marsh.) can be found. Stand dynamics are mainly controlled by large fires that kill most of the trees and aboveground vegetation. High-severity fires that kill both above- and below-ground stem organs of trees are common in the study area and are the focus of this study (Figure 2). Such fires usually consume the entire SOL, exposing the mineral soil layer that allows black spruce to rapidly re-establish from seed (Lecomte and others 2006a; Jayen and others 2006). When this first regeneration pulse breaks up, asexual layering forms second, third, and subsequent pulses that are more open and less productive as SOL depth and paludification become more important (Simard and others 2007). This retrogressive process continues until a new

high-severity fire occurs that consumes the entire SOL and resets the cycle (Figure 2).

Despite the relatively remote location of the study area, the recent fire history has been well-documented using dendrochronology and aerial photographs. Fire cycle length increased from 101 years before 1850 to 398 years since 1920 and the mean stand age is estimated to be 148 years (Bergeron and others 2004). Besides fire and secondary disturbances such as spruce budworm (*Choristoneura fumiferana*) outbreaks, the study area is mainly disturbed by logging; industrial forest activities started in the area between 1940 and 1960 (Belleau and others 2011).

Site Selection, Establishment, and Dating

Twelve sites were selected that were largely based on a previously established chronosequence (Lecomte and others 2006a; Table 1 and Online Appendix 1). For the purpose of this study, we aimed to select sites with a wide TSF range, but without including those with a TSF less than 50 years as it may take black spruce that much time to build up its aerial seedbank (Viglas and others 2013). However, TSF range was limited because of (i) ubiquitous logging activities in the Canadian black spruce-feather moss bioclimatic zone, and (ii) a

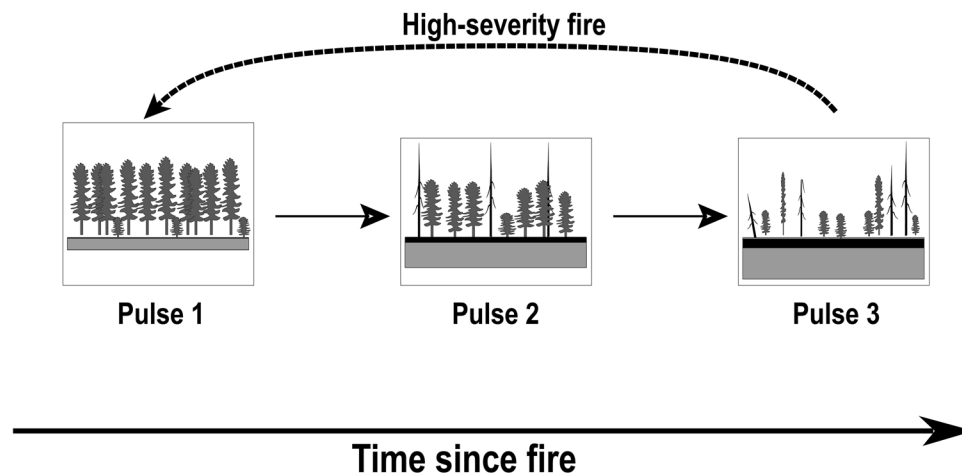


Figure 2. Stand development in black spruce as a function of time since fire (TSF). The process illustrated in this figure has previously been identified by Lecomte and others (2006a) and Simard and others (2007) in the same study area. High-severity fires usually consume all organic matter that accumulated since the previous fire. The elimination of this SOL (shown as a *black line*) exposes the mineral soil layer and allows black spruce to rapidly re-establish from seed. The first regeneration pulse usually has a high density of fast-growing even-aged trees. With increasing TSF, the first regeneration pulse starts to break up and the forest gaps trigger abundant asexual layering that forms the second regeneration pulse. In the prolonged absence of fire, SOL thickens and new slow-growing pulses replace older faster-growing ones. Stands become more open with an uneven age structure as tree mortality and regeneration occur more episodically. Generally, already when the third regeneration pulse establishes, distinction between tree individuals of different pulses becomes more difficult. This retrogressive process continues until a new high-severity fire occurs that resets the cycle by consuming the accumulated organic matter, killing all stems and roots, and forcing black spruce to re-establish from seed.

relatively short fire cycle in this part of the boreal forest, causing the mean stand age to be 148 years and implying that only 36% of stands in the area have a TSF greater than 150 years (Harper and others 2002). Yet, we succeeded in having a relatively wide TSF range by ensuring a significant proportion of older sites: that is, 6 sites, or 50% of our sample set, were at least 150 years old (Table 1). A second selection criterion was that sites needed to be characterized by high-severity fires that had left very little residual organic matter (ROM). For all 12 sites, the charcoal layer was positioned within 3.2 cm of the mineral soil layer, indicating that almost all organic matter had been consumed (Online Appendix 1; see below for identification of charcoal layers and determination of SOL and ROM depths).

Thirdly, species composition was carefully analyzed when selecting sites: we ensured that all sites were either pure black spruce stands (10 out of 12 cases), or the basal area of the co-existing species (*Pinus banksiana*, *Abies balsamea*, and *Larix laricina*) amounted to less than 5% of that of black spruce. In addition, micro-topography was studied because little depressions tend to have higher rates of organic matter accumulation. Therefore, all twelve sites were selected to have a slope between 1.0° and 3.0°, implying that drainage and organic matter accumulation rates should be very similar among sites. Finally, even though nine out of twelve sites were located relatively close (80–300 m) to a small road for reasons of accessibility (Figure 1), sites were strictly selected to show no signs of human impact. For similar reasons, the seven sites that start with the letter 'N' refer to the original sites established by Lecomte and others (2006a; see Table 1). These sites were sampled 20–50 m away from the original sites as some trees had been felled there by Lecomte. Also in sites S1 and L22, ecological sampling had been done prior to this study. Our sampling was therefore conducted at about 30 m distance from the original site. However, in every case, site conditions (SOL depth, ROM depth, soil texture, slope, species composition (basal area > 95% black spruce)) were verified to be consistent among sites and to strictly correspond to those of the original sites (Online Appendix 1).

Sites were set up by establishing a circular plot of 400 m² (radius of 11.28 m). In each plot, we recorded the total number of trees, DBH (0.1 cm accuracy), and tree species identity (>99% of all individuals were black spruce). To study if SOL depth affected seedbank size, we dug in each site 15 soil pits (25 × 25 cm) that extended to the mineral soil. In case of soil mixing, the lower end of the

organic layer was determined as the depth at which mineral soil content reached 25% (Lecomte and others 2006b). SOL depth was defined as the distance between the surface and the charcoal layer. Similarly, ROM depth was defined as the distance between the charcoal layer and the mineral soil. For the SOL and ROM depths at each site, we used the means of the measurements from the 15 soil pits. In all soil pits ($n = 180$; 12×15), charcoal layers were easily identifiable by their distinct color and texture. All pits had one charcoal layer that was located almost directly above the mineral soil layer (< 3.2 cm, Online Appendix 1).

Site dating or stand age (TSF) was obtained from tree-ring analysis and, in case of potentially older sites, also by radiocarbon dating. We identified the decade of establishment for each of the 12 trees that were sampled per site (see below for tree sampling strategy). Briefly, a site was attributed a given decade as TSF when at least five trees, showing rapid initial growth and no fire scars, had been established in that decade. Because of previous tree sampling and dating in the immediate vicinity of our twelve sites (Lecomte and others 2006a, b), the number of sampled trees that could be used to identify stand age was generally much higher (mean $n = 43$; Online Appendix 1). Although our sites were established at a distance of 20 to 50 m from these sites, for six out of seven 'N' sites, the presumed stand ages (TSF) determined by Lecomte and others (2006a) corresponded exactly to those we obtained from using our 12 tree samples per site (see discussion in Online Appendix 1). Similarly, our TSF identification for sites S1 and L22 corresponded exactly to the original dating obtained by Fenton and others (Online Appendix 1). Because of all these previous sampling efforts in the vicinity of our sites, in only three cases site dating was limited to 12 tree samples. Furthermore, for each of these three sites, a minimum of eight out of twelve trees had established within a period of five years, showed rapid initial growth and no fire scars, strongly reducing the risk of an erroneous TSF-determination.

Apart from site L22, sites with tree individuals more than 200 years old (sites N50 and N06) were radiocarbon dated by IsoTrace Laboratory (Toronto, Canada) using a sample of carbonized plant remains found in the charcoal layer of the organic layer (see Online Appendix 1). The obtained radiocarbon years for both sites were calibrated in calendar years (SD 50 years) using INTCAL98 (Stuiver and others 1998; but see Online Appendix 1 for a discussion on the calibration). Sites N50 and N06 were dated to have a TSF of 350 and 710 years,

Table 1. Site Conditions and Reproductive Parameters for the 12 Studied Sites

Site name	Independent ¹ variables				Dependent variables											
	Site	Cone	Tree	Site	Site	Tree	Cone	Site								
	TSF (years)	SOL depth (cm)	Normalized tree growth rate	Number of seeds cone ⁻¹	Number of filled seeds cone ⁻¹	Number of cones tree ⁻¹	Number Cone size (mm ²) tree ⁻¹	Number of seeds tree ⁻¹ (10 ³)	Mean tree age (years)	Mean DBH ² of trees ha ⁻¹ (cm)	Number of trees ha ⁻¹	Basal area (m ²) ha ⁻¹	Number of seeds ha ⁻¹ (10 ⁶)	Number of filled seeds ha ⁻¹ (10 ⁶)		
N-04	1st	60	12	0.796	18.0	11.9	134.5	276.7	3.421	1.601	57	8.7	800	55.5	1.584	0.718
N-23	1st	90	19	0.845	18.6	12.5	126.2	290.9	3.201	1.278	85	10.1	795	53.0	1.512	0.689
S-01	1st	90	7	1.000	26.7	17.5	168.3	325.5	4.494	2.945	84	10.8	399	59.1	1.793	0.793
N-18	1st	130	23	0.621	18.9	14.1	164.1	306.2	3.801	2.314	127	14.6	485	52.2	1.504	0.661
N-75	1st	130	22	0.633	20.9	13.5	192.8	315.8	4.030	2.603	124	14.3	404	55.3	1.630	0.700
N-08	1st	130	30	0.578	19.5	10.2	226.4	278.1	4.415	2.309	128	16.2	300	49.6	1.326	0.644
FT6B	1st	150	25	0.662	19.5	10.8	295.9	240.6	4.765	3.196	147	16.8	207	49.0	1.196	0.570
C-150	1st-2nd	170	52	0.344	14.4	6.4	175.4	190.4	2.526	1.123	103	12.5	200	35.9	0.504	0.261
POP	1st-2nd	180	36	0.366	11.5	4.4	213.6	157.8	2.456	0.940	119	13.5	236	33.1	0.579	0.231
L-22	1st-2nd	270	51	0.186	7.3	2.8	189.3	83.7	1.382	0.530	161	11.6	161	20.6	0.222	0.073
N-50	2nd	350	35	0.196	3.8	1.3	177.8	69.8	0.676	0.231	166	15.5	133	9.2	0.090	0.035
N-06	3rd-4th	710	58	0.001	1.6	0.8	111.0	40.5	0.178	0.089	192	15.9	72	3.0	0.046	0.018

Sites are ranked according to TSF. Independent variables that potentially drive variability in seedbank size with TSF are listed on the left side of the table (site scale), whereas dependent variables are shown to the right and are classified into three scales (cone, tree, and site), similar to the classification that has been used for the seedbank upscaling (number of seeds ha⁻¹).

¹Note that in the regression analysis presented in Online Appendix 6, the variables SOL depth and normalized tree growth rate are also considered dependent variables (regressed against the independent variable TSF), but are listed only once in this table as independent variables.

²Also note that mean DBH calculation only includes tree-size (DBH > 8.0 cm) individuals because smaller individuals may not be relevant for seedbank analysis.

respectively (but see Online Appendices 1 and 2), values which correspond well to the observed trends in SOL depth and tree growth rate with increasing TSF (Table 1 and see Simard and others 2007). Site L22 was not radiocarbon dated, but its stand age is likely to correspond to the age of its oldest tree (272 years) because all five 268 to 272-year-old trees found in either L22 ($n = 2$) or its two neighboring stands ($n = 3$) showed no fire scars but rapid initial tree growth, indicating establishment after a high-severity fire (the age of the three neighboring individuals was obtained from the stand initiation map created by Bergeron and others (2004); not presented in this study, see Online Appendix 1 for discussion).

Sampling

Trees

To study the effect of TSF on seedbank size while controlling for DBH variability between sites, 12 individuals per site (referred to as sampled trees hereafter, $n = 144$) were randomly selected to be felled within four DBH-classes (three trees per class): 8.1–12.0, 12.1–16.0, 16.1–20.0, and >20.0 cm. These classes represented well the documented variability in DBH of the adult black spruce trees in the study area (Online Appendix 3). The lower DBH limit was set at 8.0 cm to ensure that no tree individuals younger than 50 years, which had not yet reached sexual maturity, would be included.

Cones

From all sampled trees ($n = 144$), all cones were counted irrespective of their age. However, cones produced in different years likely experienced different abiotic and biotic conditions such as weather, seed predation, tree growth performance, and competition. To control for these factors, we only selected mature cones of the most recent 2005 growing season. This crop year could be distinguished by a slightly lighter purplish color compared with the darker brown and grayish older cones (Eremko and others 1989). All 2005 cones were put in a non-transparent bag to avoid a tendency to select for bigger cones during laboratory analyses. Ten cones per tree were randomly taken out for seed analysis, giving a total of 1367 cones. In case a tree individual did not have ten cones from 2005, all available cones of that year were used.

Lab Measurements of Sampled Trees: Determination of Tree Age, Tree Growth, Cone Size, and the Number of Total and Filled Seeds

Trees

Tree age was determined by counting the number of annual rings on the cross-sections taken at the root collar of the tree. The cross-sections were sanded until xylem cells were visible and tree rings were counted under $\times 40$ magnification. For 13 out of 144 individuals, tree age could not accurately be determined, generally because initial tree growth was so low that annual rings were too small to see and the risk of multiple missing rings was high. In a few other cases, we were not sure to have cut the stem at the exact root collar position. The failure to do so can easily result in erroneous dating, particularly in the case of black spruce where as many as 20 annual rings may be missing if the tree is cut as little as a few cm above the true root collar (DesRochers and Gagnon 1997). As a result, 13 individuals were removed from analyses that involved tree age (leaving 131 trees).

To control for the presumed decrease in tree growth rate with increasing TSF and with the establishment of every new regeneration pulse (Figure 2), both sampled and non-sampled trees were classified according to pulse class. Sites with a TSF no more than 150 years only had first regeneration pulse individuals and trees did not need to be classified. The four sites with a TSF between 170 and 270 years had both first and second regeneration pulse individuals and distinction between the two pulse classes was easy because a pronounced DBH gap (>8.0 cm, that is, exceeding 2 DBH-class intervals, Online Appendix 3) existed between the younger second-pulse and the older first-pulse individuals (Online Appendices 3 and 4). Also for site N50 with a TSF of about 350 years, the regeneration pulse of individuals could still be determined because second-pulse trees showed a pronounced DBH (Online Appendix 3) and age gap (data not shown) with the smallest (DBH < 8.0 cm) third-pulse individuals. However, with increasing TSF, the distinction between pulses became more difficult (see Figure 2) and individuals in the oldest site with a TSF of around 710 years could no longer be accurately classified into third or fourth regeneration pulse and were therefore labeled “third-to-fourth pulse” trees (Online Appendix 4).

To study if recent tree growth rate affected cone or seed production, we measured the 15 most re-

cent annual ring widths (1991–2005) on two radii with a Velmex measuring stage with a precision of 0.01 mm (Velmex Incorporated, Bloomfield, New York, USA). By the time of tree sampling, ring formation had been completed for the growing season of 2005. To compare growth rate values with other studies on tree growth performance, the 15-year cumulative ring widths obtained for each tree were converted into basal area increments (BAI) via the formula:

$$\text{BAI} = \pi (R_n^2 - R_{n-1}^2),$$

where R is the tree radius and n is the year of tree-ring formation (LeBlanc 1990). Because short-term climate fluctuations, rather than tree growth performance, are likely to attribute for significant variability in annual growth, we grouped the BAI-values for each tree into 5-year cumulative values (one value for the period 1991–1995, one for 1996–2000, and one for 2001–2005). The mean 5-year cumulative BAI was used to represent recent tree growth rate in each individual, similar to previous studies (for example, Zhang and others 2004).

In study areas characterized by rapidly changing environmental conditions such as SOL depth, growth rate standardization (that is, correcting for the age trend in BAI that is observed in almost every plant individual, Fritts 1976) is challenging as both stand age and SOL depth increase with time since disturbance. To eliminate the age-effect but retain the presumed effect of SOL depth on tree growth rate, we selected only individuals that grew on sites with similar SOL depth values (Figure 3). Further, to ensure no bias resulting from pooling trees of different regeneration pulses showing potentially different growth rates, we only selected first-pulse individuals. By plotting 5-year BAI against tree age for these individuals, we found that the common age trend in black spruce was best represented by a 150-year cubic spline with a 50% frequency cut-off (Figure 3). This function highly resembled age trend functions of black spruce obtained by other studies in boreal Quebec (Hofgaard and others 1999; Rossi and others 2009) and was used to normalize the BAI into age-independent growth rate indices using the program ARSTAN (Cook 1985).

Cones and Seeds

To determine cone size, cone length and width were measured for all 1367 fresh cones (2005 crop) from 144 different trees. We multiplied cone length with cone width to obtain a proxy of cone size (Greene and others 1999). The total number of seeds \cdot cone⁻¹ was counted and split into filled and

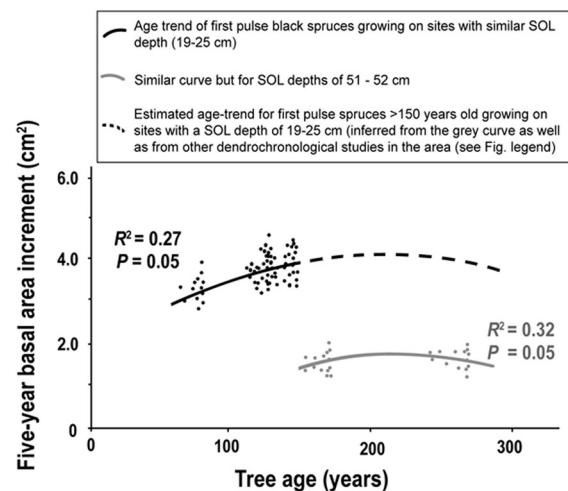


Figure 3. Standardization of tree growth (basal area increment) in black spruce. To identify the common age trend in our stands, 5-year basal area increments are plotted against tree age. To eliminate the age-effect but retain the presumed effect of increasing SOL depth on growth rate, we selected only tree individuals that grew on sites with similar SOL depth values. Further, to ensure no bias resulting from pooling trees of different regeneration pulses showing potentially different growth rates, we only selected first-pulse individuals. Two distinct groups of pooled tree individuals could be identified that satisfied both criteria: (i) a group of trees selected from sites with SOL depths ranging from 19 to 25 cm and TSF from 90 to 150 years: that is, sites N-23, N-75, N-18, and FT6B (see Table 1) and (ii) a second group of two sites for which SOL depth was 51 and 52 cm and TSF 170 and 270 years: that is, sites C-150 and L-22, respectively (Table 1). The age trend of both tree groups was best represented by a stiff 150-year cubic spline with 50%-frequency cut-off, plotted as a black solid line for the youngest group and a gray solid line for the older one. The vertical structure of the points reflects the even-aged nature of the first sexual regeneration pulse after a high-severity fire. The best estimate for the age trend of spruce for its entire lifespan is represented by fitting an identical cubic spline to that of the older group of trees onto the spline that represents the younger group (*broken gray line*). This age trend was similar to that found by other studies on black spruce in boreal Québec (Hofgaard and others 1999; Rossi and others 2009).

empty seeds using a separator machine from the Centre de semences forestières de Berthierville (Messoud and others 2007). This machine has a ventilation shaft with a controlled airflow. Seeds are introduced in the shaft, the lighter empty seeds are sucked into a pipe and deposited in a container, while the heavier filled seeds fall into another container. Results were verified on a subsample of seeds classified as empty or filled using X-rays. Although theoretically seedbank often refers to the

number of viable seeds (Harper 1977), we will focus in this study on the numbers of total and filled seeds. This interpretation has the advantage that our results should be easily comparable with most other seedbank size studies that use the same seed classes.

Upscaling Seedbank

To estimate the total number of seeds of the sampled trees, we (i) calculated the mean number of seeds counted per sampled cone for each tree ($n = 10$ cones, only crop 2005); and (ii) multiplied this mean value by the total number of cones (crop 2005 and earlier) counted on each tree. Although black spruce is a semi-serotinous species implying that older cones likely have fewer seeds than younger ones (Gauthier and others 1996), we preferred to count only the seeds of cones of the same year to allow for a better comparison of seed production per cone between the twelve sites as such that observed differences are unlikely to be attributed to annual variability in factors such as weather and seed predation. However, this methodology calls for some caution with respect to the obtained extrapolated values for the number of total and filled seeds ha^{-1} for each site, but also the possibility of comparing seedbank size values between sites that may have a different proportion of older vs. more recent cones (see discussion).

To estimate the total number of seeds tree^{-1} for the non-sampled trees, we regressed the number of seeds tree^{-1} against DBH for the 12 sampled individuals (Online Appendix 4). The resulting regression functions were then used to estimate total and filled seed numbers in the remaining trees with known DBH (0.1 cm accuracy, $\text{DBH} > 8.0$ cm) in each site. However, following our hypothesis, TSF may affect seed production, implying that a distinction should be made between trees of different regeneration pulses. Indeed, when we redid the regression analyses and controlled for regeneration pulse, we obtained stronger relationships between seed production per tree and DBH (compare R^2 values in Online Appendix 4 between Figures 4.1 and 4.2). These new regression functions were used to estimate seed production in all non-sampled trees in each site. The total number of seeds site^{-1} (400 m^2), including both sampled and non-sampled trees, was multiplied by 25 to obtain the total seedbank size ha^{-1} (including both filled and empty seeds). The same procedure was used to estimate the number of filled seeds ha^{-1} . Note that the terms ‘total number of seeds per tree (or per ha)’ or ‘number of filled seeds per tree (or per ha)’ used in

the “Results” section refer to numbers obtained by extrapolation and should be considered as approximate numbers (see “Discussion” section).

Analyses of Potential Drivers

We used regression to determine the direction and strength (via R^2) of the relationships between selected variables at the cone, tree, and site scale. To facilitate interpretation of the results, we chose between linear, logarithmic, and (more rarely) polynomial 2nd degree functions to describe the observed relationship between two variables. The following variables were considered for regression: TSF as independent variable, SOL depth and normalized tree growth rate as both dependent (against TSF) and independent variables, and mean number of seeds cone^{-1} , number of cones tree^{-1} , cone size, number of seeds tree^{-1} , number of trees ha^{-1} , basal area ha^{-1} , DBH and tree age as dependent variables. We only regressed variables that were either used in the seedbank upscaling process or that were important in identifying potential drivers. As the nature of the upscaling procedure involves some multiple comparisons (for example, seeds tree^{-1} is estimated using the mean number of seeds cone^{-1} and cones tree^{-1} so that the regression of seeds tree^{-1} vs. TSF is not independent of the regressions seeds cone^{-1} vs. TSF and cones tree^{-1} vs. TSF), we used Bonferroni corrections to verify if statistical relationships remained significant. Further, in case data were characterized by a skewed distribution, the variable was log-transformed to meet the assumptions of normality and homogeneity of the residuals.

RESULTS

Seedbank Size of Black Spruce as a Function of TSF

The total number of seeds cone^{-1} initially increased with TSF, leveled off at 100–150 years, and strongly declined starting at 150–200 years. This decline continued with further increasing TSF although the rate of decline decreased as indicated by the negative logarithmic function (Figure 4A). The number of cones tree^{-1} did not show a clear trend with TSF, even though a small peak was observed at 150–200 years (Figure 4B). Cone size (Figure 4C) and the total number of seeds tree^{-1} (Figure 4D) showed a similar trend to the total number of seeds cone^{-1} with a maximum recorded at a TSF of 100–150 years followed by an important decline that gradually leveled off at further elevated TSF. At the site scale, the

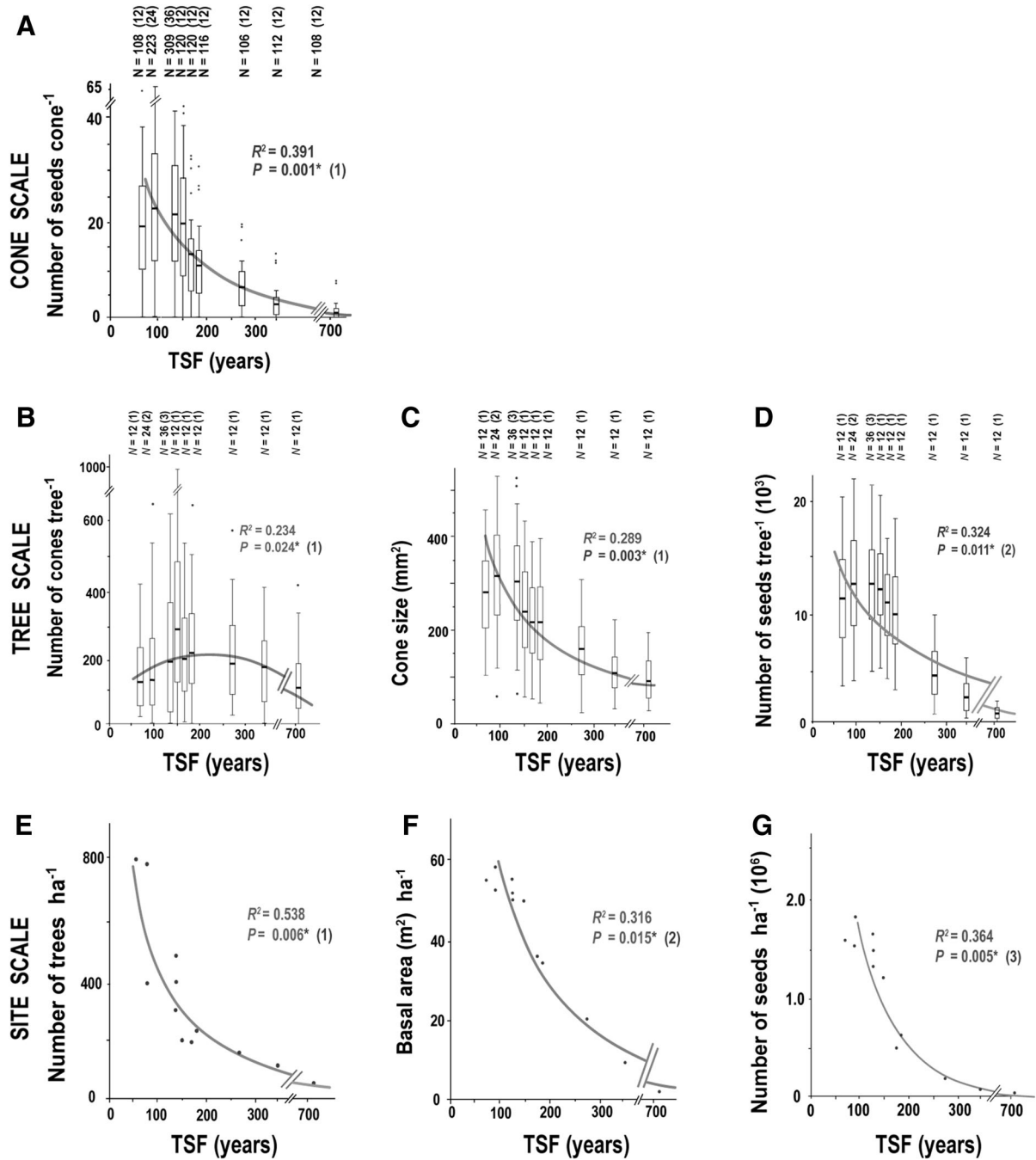


Figure 4. Seed production and reproductive parameters as a function of TSF. Trends were studied at three different scales: cone, tree, and site. Graphs (A) to (D) show the results of the sampled cones ($n = 1367$) and trees ($n = 144$), whereas the site scale represented by graphs (E) to (G) shows extrapolated values obtained from our upscaling procedure. At the cone and tree scale, there is more than one sample (cone or tree) for each TSF-value and sample points are therefore plotted as box plots with whiskers extending to the 10th and 90th percentile. Note that one boxplot sometimes represents more than one site as some sites have identical TSF-values (see Table 1). The linear, logistic, or polynomial (2nd degree) function that best described the relationship between the dependent and independent variable is plotted in dark gray. As the nature of the upscaling procedure involves some multiple comparisons, we used Bonferroni corrections to verify if statistical relationships remained significant. The number of interdependent variables is listed in brackets after each P -value ('1' means that there were no multiple comparisons). The adjusted significance threshold for each P -value is obtained by dividing the common threshold value (0.05) by the number of interdependent variables listed in between brackets. P -values that remained significant after the Bonferroni correction are marked by an asterisk.

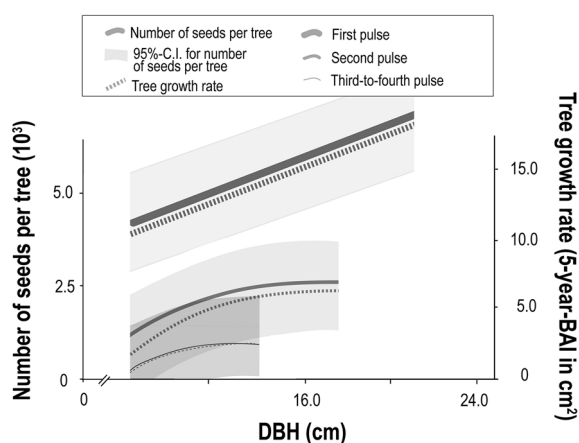


Figure 5. Seed production and tree growth rate in *black spruce* as a function of DBH. Tree individuals belonging to the same regeneration pulse are pooled. For each regeneration pulse, total seed numbers per tree and absolute tree growth rate are plotted as a *solid* and *broken line*, respectively. The 95%-confidence interval for seed production per tree is plotted as a *gray area*. TSF-values for the different pulses range from 60 to 270 years for the first one, from 170 to 350 years for the second one, and amount to 710 years for the third-to-fourth pulse (see Online Appendix 7).

number of trees ha^{-1} (Figure 4E), basal area ha^{-1} (Figure 4F), and most importantly, seedbank size (total numbers of seeds ha^{-1} ; Figure 4G) significantly decreased with increasing TSF showing a negative logarithmic trend. Similar to total seeds, the number of filled seeds strongly declined at all three levels (cone, tree and site) as TSF reached 150–200 years (Online Appendix 5). All trends for both total and filled seeds remained significant following Bonferroni corrections (Figure 4) and a sensitivity analysis of the chronosequence dating uncertainties (Online Appendix 2).

Other Factors Related to TSF or Seedbank Size

With increasing TSF, we recorded a logarithmic increase in SOL depth and decrease in normalized tree growth rate ($R^2 = 0.292$ and 0.358 , $P = 0.038$ and 0.011 , respectively, $n = 12$ sites; Table 1 and Online Appendix 6). The total number of seeds tree^{-1} and normalized tree growth rate were found to be strongly linearly related ($R^2 = 0.481$, $P < 0.001$, $n = 131$ trees; Online Appendix 6). Trees with the highest radial growth rates had the highest number of seeds and generally also the biggest DBH (Figure 5). This observation was particularly true for first-pulse individuals, but was less clear for trees of subsequent pulses as the relationship shifted

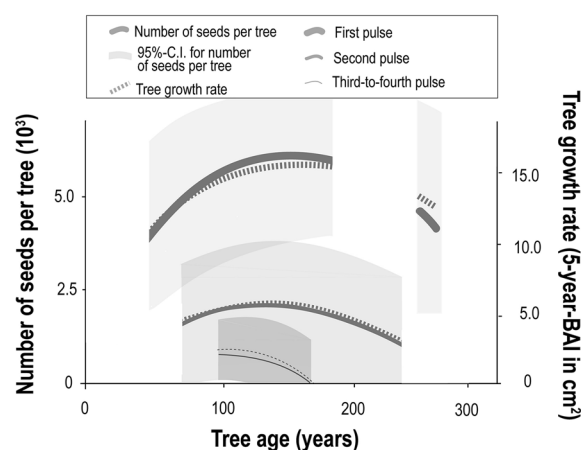


Figure 6. Seed production and absolute tree growth rate of black spruce with increasing tree age. Similar to Fig. 5, both seed production and absolute tree growth rate trends were best represented by a 2nd degree polynomial function. Because no site was sampled with a TSF between 180 and 270 years (see Table 1), first-pulse individuals—that tend to be the same age as the site's TSF-value—showed a corresponding age gap. Such a gap was not documented for subsequent pulses because tree establishment periods did not correspond any longer to TSF and were more spreadout in time: for example, second-pulse individuals of site N50 (TSF c. 350 years) established 120 to 200 years after fire resulting in tree ages between 150 and 230 years. Note that the increase in minimum tree age with every new pulse is the result of a decline in tree growth rate: whereas first-pulse individuals may reach tree-size (DBH > 8.0 cm) at 60 years, it takes an individual of the second and third-to-fourth pulse at least 75 and 95 years, respectively (see Online Appendix 7).

from a linear function to a logistic one. In other words, tree growth rate and the total number of seeds tree^{-1} leveled off at smaller DBH-values with increasing TSF.

Not only did the type of relationship change between different regeneration pulses, also the magnitude of the two dependent variables decreased with ongoing succession. Second and subsequent pulse trees showed highly reduced tree growth rates and number of seeds tree^{-1} (Figure 5). For instance, the absolute tree growth rate of 160-year-old first-pulse trees was nearly 30 times higher than that of equally old third-to-fourth-pulse individuals [20 vs. 0.75 5-year-BAI (cm^2), respectively]. Similarly, a 160-year-old first-pulse tree held on average 6.1 (10^3) seeds compared with 0.2 (10^3) seeds for third-to-fourth-pulse individuals (Figure 6). Furthermore, with ongoing succession, the type of relationship changed again: whereas for first- and second-pulse individuals, growth rate and seed numbers ini-

tially increased with tree age, no such trend was documented for third-to-fourth-pulse individuals (Figure 6). Although this observation could at least in part be related to a lack of young individuals in the latter pulse class (no individuals <95 years old), the overall age-trends also differ suggesting that with each new regeneration pulse, both absolute tree growth rate and the total number of seeds tree⁻¹ start declining at a progressively younger tree age (Figure 6). Whereas for first-pulse individuals this decline started around the age of 150 years, for second and third-to-fourth-pulse individuals, a reduced number of seeds was already observed at tree ages of around 120 and 100 years, respectively (Figure 6).

DISCUSSION

Observed Decline in Seedbank Size

This study provides new evidence that a species' seedbank size may in some cases be limited by both short and long disturbance intervals. Whereas previous studies have shown that black spruce suffers reduced seed availability when disturbance events follow each other closely (Simard and Payette 2005; Brown and Johnstone 2012), we documented the same development in the prolonged absence of disturbance. Sites with mature first-pulse individuals, corresponding to TSF-values of about 50–150 years (Table 1), still had a seedbank size of 12.0 to 17.9 (10⁵) seeds ha⁻¹; that is, average values for black spruce (LeBarron 1948; Greene and Johnson 1999). However, older sites with second- and subsequent pulse individuals had 5.8 down to 0.5 (10⁵) seeds ha⁻¹, numbers even lower than those reported at the arctic treeline (13.2 down to 6.0 (10⁵) seeds ha⁻¹; Black and Bliss 1980).

Similar to the number of total seeds, the number of filled seeds ha⁻¹ strongly decreased for sites with second- or subsequent pulse individuals (Table 1). We recorded numbers down to 0.2 (10⁵), exceptionally low values for most parts of the Canadian boreal forest (see Black and Bliss 1980; Haavisto and others 1988; Greene and others 1999; Meunier and others 2007; Viglas and others 2013).

Potential Effect of SOL Depth on Tree Growth Rate and Seedbank Size

In large parts of the circumboreal forest, and particularly in the Canadian Clay Belt, the absence of fire coincides with an increase in SOL depth, a factor that has the potential to significantly reduce tree growth (Drobyshev and others 2010) and other productivity parameters such as stand bio-

mass (Simard and others 2007). However, for black spruce, a species that prefers moist soils and can tolerate waterlogged soils (Van Cleve and Viereck 1981; Pollock and Payette 2010), such effects seem less likely. Yet, when SOL depth reaches a level of around 30–40 cm, growth rates of black spruce are known to decline. Because spruce has a superficial root network, such thick SOL hampers access to the mineral soil layer and forces roots to concentrate in the nutrient-poor and cooler upper organic layer (Simard and others 2007; Lafleur and others 2011). At our sites, normalized mean tree growth rate particularly decreased as SOL depth exceeded 35 cm (Table 1 and Online Appendix 6) and suggests that this process is indeed ongoing.

Furthermore, this initial stage of paludification could be an important driver of the observed decline in seeds cone⁻¹ in black spruce by hampering the allocation of a constant annual proportion of photosynthate for sexual reproduction. The coinciding reduction in tree growth rate, a factor that often reflects the productivity level of an ecosystem (Simard and others 2007), could therefore possibly be regarded as an indicator, rather than driver, of trees' current seed production levels.

Overall, the process of a continued accumulation of organic matter and increased waterlogging with TSF could be assumed to cause progressively lower seed production in spruce trees as succession proceeds. As the timing of the initial decline in the number of seeds cone⁻¹ (Figure 4A) highly corresponds to the break-up of the first-pulse generation at a TSF of c. 150 years (Lecomte and others 2006a and this study), this hypothesis seems plausible.

Excessive SOL accumulation (>c. 35 cm) may thus affect the seedbank size of black spruce by operating synchronously at two levels: (i) number of trees ha⁻¹: progressively reduced regeneration with ongoing succession due to decreased establishment and survival rates of new recruits, and (ii) tree growth rate: progressively reduced growth performance with increasing tree age and regeneration pulse (Figure 6).

However, a reduction in the number of trees ha⁻¹ with increasing TSF could be caused by self-thinning; that is, mortality due to intra-specific competition. But since only trees with a DBH greater than 8 cm were accounted for in our seedbank size analysis, self-thinning should have been mostly completed by this stage. Furthermore, the already low tree densities in the youngest sites having only first-pulse individuals (median = 404 trees ha⁻¹) suggest that the role of self-thinning was likely not important in further reducing tree density with ongoing succession.

Therefore, SOL depth increase remains the primary explanation for the observed decline in seedbank size with TSF. Still, most likely this driver did not entirely account for the decline. Previous research suggests that the conditions associated with elevated SOL depth (reduced soil temperature, nutrient availability, and soil aeration), rather than SOL depth itself, are generally identified to be responsible for reduced recruitment and tree growth rate in tree species such as black spruce (Lavoie and others 2005). Furthermore, even if rapid accumulation of organic matter appears to be the most remarkable change in the absence of disturbance, other factors likely change too with increasing TSF and may contribute to increased environmental stress. For instance, irrespective of SOL depth accumulation that hampers root access to nutrients in the mineral soil, nutrient levels themselves are known to decline in the long-term absence of disturbance (Peltzer and others 2010). Also increased interspecific competition in the absence of disturbance (for example, increases in Ericaceae and Sphagnum, see Online Appendix 1) could be a factor that contributes to reduced growth rates in new pulse individuals. However, irrespective of their exact type, it appears that changes in environmental stress levels play an important role. Westoby and others (1996) and Lázaro and Traveset (2008) previously showed that environmental stress in the form of gradual changes in microclimatic conditions and competing vegetation highly determined variability in seed mass.

In addition to local-scale environmental stress, external factors such as macroclimate and seed predation may have affected our findings. However, long-term climate variability, a critical factor in chronosequence studies, cannot explain why older sites would have such significantly lower seedbank size. The study area is located more than 800 km south of the black spruce arctic treeline (Payette and Gagnon 1979) and even during the Little Ice Age (AD 1300–1910), most growing seasons at this latitude should have well-exceeded 800 degree days ($> 5^{\circ}\text{C}$) (cfr. Esper and others 2002), the threshold value associated with temperature-related decline in seed production in black spruce (Meunier and others 2007). Similarly, seed predation, a common factor determining annual variability in seed production (Côté and others 2005), has unlikely caused the pattern of seedbank decline with increasing TSF. Independent studies that made use of aerial photographs, historical documents, and tree-ring analysis showed low overall incidence of spruce budworm outbreaks in our

study area in all age classes with less than 2% of stands affected (Gray and others 2000; Harper and others 2002; Simard and others 2007).

Potential Biases and Uncertainties

Although we considered factors such as DBH and regeneration pulse to obtain a more accurate estimate of seedbank size, some uncertainties remain related to the seedbank upscaling process. As black spruce is only semi-serotinous, this characteristic could have affected our estimates because old cones likely carry fewer seeds than young ones (Buma and others 2013).

Because we only counted seeds of 2005-crop cones for the upscaling, no bias is expected in this initial step. Nevertheless, if tree individuals in older sites were to show a significantly different proportion of young *versus* older cones, this pattern would affect upscaling and our comparative seedbank analysis between sites. However, we verified the sampled trees of all sites and did not observe any clear pattern (data not shown). Assuming that all trees have a similar proportion of young versus older cones, semi-serotiny may still cause an overestimation of the number of seeds $\cdot \text{cone}^{-1}$ as we extrapolated seed numbers from young 2005 cones to all other cones. This extrapolation should not have caused any bias in comparative analyses between sites, but implies that actual seedbank sizes are probably even lower than our estimated values. This overestimation may be counterbalanced by the fact that trees with a DBH below 8.0 cm were not included in the seedbank upscaling. Although generally few or no cones were observed on these smaller individuals, this exclusion likely resulted in some underestimation of the actual seedbank size values.

In addition to upscaling uncertainties, chronosequence studies inherently imply some uncertainties related to initial site conditions and site dating. Although we cannot exclude that these types of uncertainties affected our results, numerous measurements of site conditions and sensitivity analyses of site dates (Online Appendices 1, 2, and 5) should have reduced their impact.

Implications

The significant decline in seedbank size of black spruce stands in the prolonged absence of fire may have implications for the persistence of these stands. Following a long fire-free period, the occurrence of a new high-severity fire that kills all above- and belowground stem organs prevents further asexual regeneration and causes re-estab-

ishment to rely entirely on seed availability. As a result, the risk of a reduced forest density after a new high-severity fire is increased considering our very small seedbanks (cfr. Viglas and others 2013). Even without knowing whether seedbanks will continue to decline with further increasing TSF, the low number of seeds ha^{-1} that we observed for sites with a TSF approaching 200 years and beyond, could affect the long-term persistence of these stands.

However, it is important to recognize that the Canadian Clay Belt is an area where SOL depth increases rapidly in the absence of disturbance and this type of ecosystem likely represents an exception rather than a generality. Yet, as there are many other types of environmental stresses that may increase in the absence of disturbance such as long-term nutrient depletion of soils or interspecific competition, we suggest further exploration of the effect of long absence of disturbance on key factors such as seedbank sizes that may affect population dynamics.

CONCLUSIONS

Many animal and plant species are adapted to some type of disturbance with a specific recurrence interval. However, an exceptionally short disturbance interval period may alter the successional pathway of a community and cause a change in dominance or even a total degradation of the ecosystem. This study suggests that in areas where prolonged absence of disturbance coincides with increased environmental stress, the seedbank of some species may, in addition to a lower limit, potentially also show an upper limit for the disturbance interval that allows for sexual regeneration. The length of this upper time interval is less easy to determine and depends on parameters including the rate of changing site conditions such as a thickening SOL, the species' plasticity, and its longevity. The sudden occurrence of a new disturbance event after the long-term depletion of a species' seedbank may induce a shift from a closed to a more open landscape area, similar to the outcome of areas that have suffered too short disturbance intervals. Even though such a potential vegetation shift occurs likely less frequently and drastically than in the case of very short disturbance intervals, our findings suggest that species that are able to regenerate in both the presence and absence of disturbance may surprisingly fail to re-establish subsequently to a disturbance event following a very long interval. Having identified this mechanism of declining seed numbers with

increasing time since disturbance, future studies should now explore whether this process is a more general phenomenon in nature and can possibly explain the remarkable retrogression, densification, or elimination of some disturbance-adapted species in the past.

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