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ARTICLE

Age and size effects on seed productivity of northern black spruce

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Abstract: Slow-growing conifers of the northern boreal forest may require several decades to reach reproductive maturity, making them vulnerable to increases in disturbance frequency. Here, we examine the relationship between stand age and seed productivity of black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) in Yukon Territory and Alaska. Black spruce trees were aged and surveyed for cone production and seed viability across 30 even-aged stands ranging from 12 to 197 years old. Logistic regression indicated that individual trees had a ~50% probability of producing cones by age 30 years, which increased to 90% by age 100 years. Cone and seed production increased steadily with age or basal area at both the tree and stand level, with no evidence of declining seed production in trees older than 150 years. Using published seed:seedling ratios, we estimated that postfire recruitment will be limited by seed availability in stands for up to 50 years (on high-quality seedbeds) to 150 years (low-quality seedbeds) after fire. By quantifying these age and seed productivity relationships, we can improve our ability to predict the sensitivity of conifer seed production to a range of disturbance frequencies and thus anticipate changes in boreal forest resilience to altered fire regime.

Résumé : Les conifères à croissance lente de la forêt boréale nordique peuvent nécessiter plusieurs décennies pour atteindre la maturité reproductive, les rendant vulnérables aux hausses de fréquence de perturbation. Nous examinons ici la relation entre l'âge des peuplements forestiers et la productivité en graines de l'épinette noire (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) au territoire du Yukon et en Alaska. Nous avons déterminé l'âge des épinettes noires et relevé leur production en cônes, ainsi que la viabilité de leurs graines dans 30 peuplements équiennes âgés de 12 à 197 ans. Une analyse par régression logistique indique que les arbres pris individuellement avaient une probabilité de produire des cônes d'environ 50 % lorsqu'ils atteignaient 30 ans, probabilité augmentant à 90 % pour les arbres atteignant 100 ans. La production en cônes et en graines a augmenté graduellement avec l'âge et la surface terrière au niveau individuel et au niveau du peuplement forestier, sans évidence d'un déclin en production de graines pour les arbres âgés de plus de 150 ans. En utilisant des ratios graine : semis publiés, nous avons estimé que dans les peuplements le recrutement suivant la perturbation sera limité par la disponibilité en graines pour une période allant jusqu'à 50 ans pour les terreaux d'ensemencement de haute qualité, et jusqu'à 150 ans pour les terreaux de faible qualité. En quantifiant les relations entre l'âge et la productivité des peuplements forestiers, nous pouvons améliorer notre habileté à prédire la sensibilité de la production en graines des conifères à une variété de fréquences de perturbation. Nous pouvons ainsi anticiper des changements dans la résilience de la forêt boréale en réponse à la variation dans le régime des feux.

Introduction

Changes to disturbance regimes associated with climate change and human activities are likely to have dominant and far-reaching effects on natural ecosystems (Turner 2010). In the northern boreal forest, increased summer temperatures and growing season length, changes to precipitation patterns, and a higher frequency of lightning are currently driving increases in fire activity (Kasischke and Turetsky 2006; Parisien et al. 2011; Flannigan et al. 2013). As climate change progresses, we anticipate that fire activity will continue to increase, in the form of longer fire seasons with larger, more severe, and more frequent fires (Balshi et al. 2009; Krawchuk et al. 2009; Flannigan et al. 2013). The boreal forest is dominated by species that have adapted to reproduce in synchrony with historic fire regimes (Greene et al. 1999). An increase in fire activity poses a real risk to the continuation of postfire self-replacement of stands dominated by these historically fire-adapted coniferous species. Immaturity risk (i.e., individuals are killed before reaching reproductive maturity; Keeley et al. 1999) is particularly tangible in northern boreal forest stands, where growth is slower and reproductive maturity delayed relative to southern boreal forest populations (Black and Bliss 1980; Sirois 2000).

Black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) stands are the dominant cover type in the northern boreal forest, extending over about 40% of the forested area in interior Alaska and northern Yukon Territory (Van Cleve et al. 1983). These forests are typically disturbed by stand-replacing fires at return intervals of 80–120 years (Johnson 1992; Johnstone et al. 2010*a*). Patterns of postfire regeneration often lead to the same species composition and spatial distribution as the prefire stand (Van Cleve and Viereck 1981; Johnson 1992). There are several properties that ensure the long-term success of these self-replacing black spruce stands. Black spruce accumulates semiserotinous cones in an aerial seed bank, allowing for a large amount of seed to be stored until fire triggers the cones to open by melting the sealing resin (Zasada et al. 1992). The large quantity of seed typically released after fire compensates for the risk of poor seedbed quality and low seed survivorship on a partially combusted forest floor (Johnstone and Chapin 2006*a*). This strategy results in the postfire establishment of even-aged stands; thus, northern black spruce stands tend to have tight age cohorts. In combination, these factors help to support stable cycles of black spruce dominance after fire across much of the northern boreal forest (Johnstone et al. 2010*a*).

While black spruce forests have historically maintained a stable regeneration cycle, unusual disturbances, such as two closely timed fires, could interrupt the equilibrium of these northern

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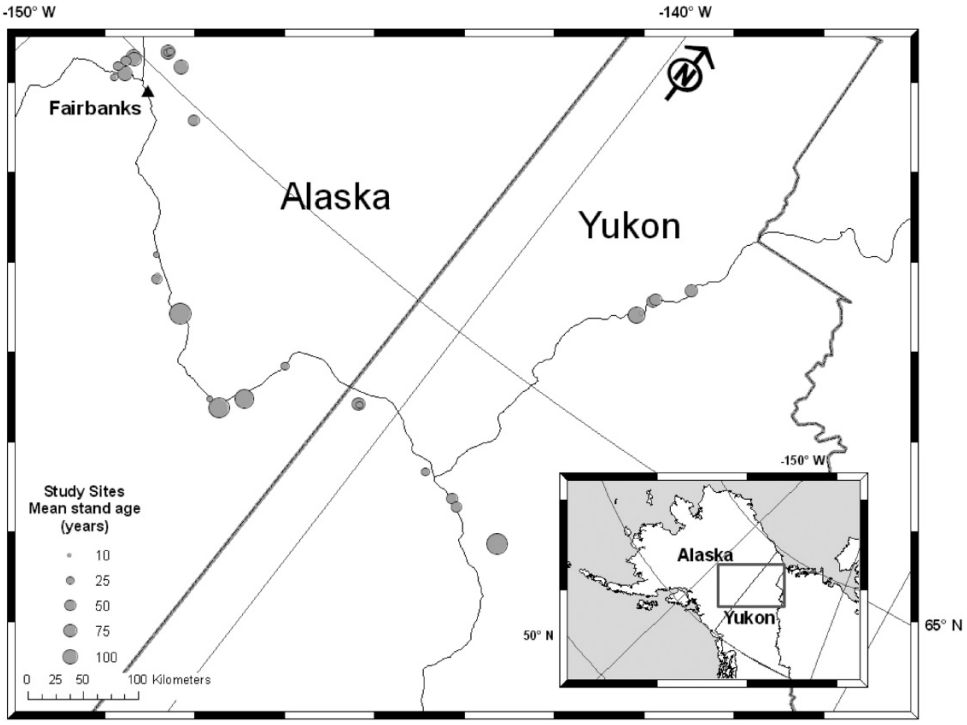
Fig. 1. Map of the study sites located in Yukon Territory, Canada, and Alaska, USA. Insert shows the larger region of the study area. Grey circles represent study sites, where the size of the circle corresponds to the stand mean age as illustrated in the legend.



forests (Johnstone et al. 2010*a*). Under a shortened disturbance interval, black spruce stands may be burned prior to reaching reproductive maturity. Reduced levels of postfire conifer recruitment have been linked in several instances to closely timed disturbance events, including fire and insect outbreaks, across a broad spectrum of spruce-dominated forest (e.g., Payette et al. 2000; Simard and Payette 2005; Johnstone and Chapin 2006*b*; Brown and Johnstone 2012). The decline in conifer recruitment after repeat disturbances is associated with low seed production of the younger black spruce stands (Simard and Payette 2005; Brown and Johnstone 2012). This suggests that the potential regeneration of black spruce after disturbance strongly depends on the amount of seed stored in the aerial seed bank. In black spruce forests, poor regeneration success after repeat disturbances appears to be an important factor that initiates alternate successional trajectories, such as open lichen woodlands (Simard and Payette 2005) or deciduous forest (Johnstone and Chapin 2006*b*).

Our objective was to assess how the size of the aerial seed bank and, thus, postfire seed availability, changes with stand age and size attributes in northern black spruce forests. Data on how seed production varies with age and tree size will improve our estimates of several reproductive parameters for black spruce including age and size requirements to reach stages of (*i*) sexual maturity, (*ii*) consistent cone production, (*iii*) peak seed productivity, (*iv*) seed productivity decline, and (*v*) changes in seed viability across cone cohorts. Furthermore, we aimed to develop equations to estimate seed production and early seedling density based on known stand attributes, including stand age and stand basal area. Such estimates provide a foundation for predicting changes in the reproductive potential of black spruce over time and thus anticipating the impacts of altered disturbance frequency on forest composition.

Methods

Study area

Study sites were located in black spruce forests of the Taiga Cordillera ecozone in northern Yukon Territory, Canada, and interior Alaska, United States (Fig. 1). With short, cool summers and long, cold winters, the mean annual temperatures range from –10 °C at the northern limit (~68°N) to –4.5 °C at the southern limit (~61°N) of the ecozone (Smith et al. 2004). Snow and ice cover the region for up to eight months of the year. Mean annual precipitation is low, ranging from 250 to 500 mm·year^{-1}. This region is dominated by black spruce forest, growing on Cryosolic, Gleysolic, and Organic soils characterized by widespread permafrost and shallow drainage (Canada Soil Survey Committee 1987; Smith et al. 2004).

We sampled a total of 30 black spruce sites in June 2009, with 20 located in central Alaska and 10 located in northern Yukon Territory. Sixteen sites were selected based on fire history maps and eight sites were chosen based on known estimates of stand ages (Hollingsworth et al. 2006; Brown and Johnstone 2011). The remaining six sites were selected to maximize geographic and stand age dispersion. We used fire history maps of Yukon Territory (Government of Yukon 2009) and Alaska (Alaska Interagency Coordination Center 2009) to locate fire perimeters dating back to the 1940s. These maps provided fire year, fire perimeter, and information on road access into the burned areas. Each study site was located in a well-defined burned patch or a visually homogeneous stand of black spruce. Sites were selected to be representative of mesic, black spruce forests based on the following criteria: tree stems composed of at least 80% black spruce, an understory dominated by feathermoss (*Hylacomium* spp. or *Pleurozium* spp.) or *Sphagnum* spp. and mesic drainage conditions. Sites were located a minimum of 100 m from roads in otherwise undeveloped land.

We sampled forest stands using the point centre quarter method (PCQ) to measure tree density and total basal area (m^2·ha^{-1}) (Mueller-Dombois and Ellenberg 1974). PCQ is one of several plotless methods used to estimate density and its performance falls in the middle of the range of these estimators when tested across a range of simulated distribution patterns (Engeman et al. 1994). Although we did not measure the spatial distribution of black spruce trees in this study, we assume this was roughly similar across the sampled stands. Sample points were distributed

along a 100 m transect with points at 25 m intervals, and measurements made on 20 trees (>1.4 m in height) per stand (five PCQ points, each point divided into four quarters). Ten black spruce trees were randomly selected (two from each sample point) to be sectioned at the ground level for stem disk collection and cone counts. Of those 10 trees, five trees were randomly selected for cone collection. Environmental variables characterizing surface organic layer depth, mineral soil pH and texture, thaw depth, elevation, slope, and aspect were measured at the same time but are not presented here (for more details see Viglas 2011).

Cone and tree sampling

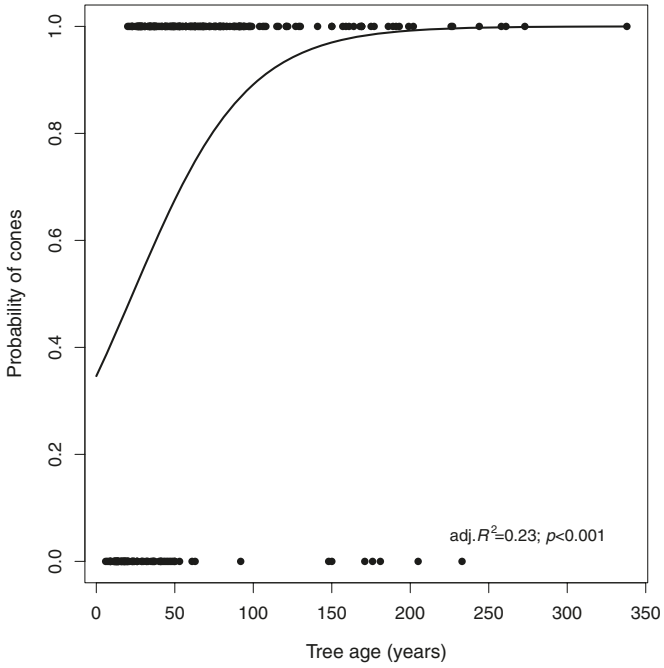
Cones were separated into four cohorts, representing different periods of seed production. As black spruce cones mature, they lose moisture and change colour from a purplish-green to brown to grey (Eremko et al. 1989). Therefore, we were able to distinguish between the different cohorts using cone color and canopy placement. The newest cones were positioned at the top of the tree and were bright purple, whereas the older cones farther down the stem were brown, and the oldest cones were the farthest down the stem and were a grey color. Exact aging of brown and grey cones is approximate. We classified cone cohorts based on relative age as current year's cones (2009), one-year-old cones (2008), approximately two-year-old cones (2007), and cones three years old or older (2006+).

Exact cone counts were performed on the 10 trees felled for stem disk collection. The entire stem disk of the tree was collected from just above the moss layer. Of the 10 trees felled for disks, five trees were randomly selected for collection of cones from 1-, 2-, and ≥3-year-old cohorts to determine seed counts. The current year's cone crop was still immature and was not collected.

In the lab, seeds were extracted from black spruce cones by soaking the cones in hot tap water for 24 h, drying them for 24 h, heating them in an oven at 60 °C for 16 h, and then agitating the cones to release the seeds (Leadem et al. 1997; D. Greene, personal communication, 2008). We repeated this procedure 3–4 times until most of the seeds had fallen out of the cones. We assumed that all of the seeds that would have been released in a natural fire would be released after each sample had undergone 3–4 seed-extraction cycles. We made this assumption because black spruce cones usually have a small number of seeds remaining in the cones for several years after a fire (Zasada et al. 1992). After counting the total number of seeds released per sample (grouped by cohort and tree), we performed a germination test on a random subsample of 0.100 g of seed (approximately 100 seeds) from each sample. Seeds were placed on filter paper in Petri dishes and kept moist with de-ionized water for 28 days when germination activity had largely ceased. The germination trials took place at room temperature (18–23 °C) with 20 h of growing light provided by artificial lighting. A seed was considered germinated once the hypocotyl was twice the length of the seed (Leadem et al. 1997).

Tree age was determined from counts of annual rings on sampled tree disks that were air-dried and cut using a band saw to create a level surface. Disks were then sanded with progressively finer sand paper (up to 400 grit) until they had a smooth finish with visible growth rings (Stokes 1968). Sections with very faint growth rings were sanded with an additional 600 grit paper. Once prepared, stem disks were scanned and aged using the WinDENDRO software program (WinDENDRO, Regent Instruments Inc. 2008). Each disk was aged twice with two radii that extended from the pith to the bark. Radii were oriented at least 90° apart to try and capture all of the rings present. The oldest radius was used as the minimum tree age, ignoring potential aging errors associated with missing rings. Estimates of stand age were calculated as the mean age of trees measured in that stand (n = 10). For stands up to 100 years of age, the correlation between the mean and maximum age of trees was close to 1:1, whereas mean ages of older stands increasingly underestimated the maximum observed tree age (Viglas 2011). We used mean tree age rather than maximum tree age as our best estimate of stand age since the last fire to balance between negative bias arising from increased underestimation of age with stand development (DesRochers and Gagnon 1997) against a positive bias arising from occasional individual trees surviving the most recent stand-replacement fire.

Fig. 2. Logistic regression between tree age and the probability of a tree having cones. Each point represents an individual tree (n = 288).



Data analysis

We examined bivariate relationships between two predictor variables, stand mean age and stand basal area, and three response variables, cones·m^{-2}, seeds·m^{-2}, and viable seeds·m^{-2} using linear regression with $\log_{10}$-tranformed data. We calculated these response variables using our data on cone and seed production, seed viability, and stand density. We first calculated the mean number of cones·tree^{-1} in a stand by summing the mean number of cones of the four cone cohorts for each site. Cones·m^{-2} was calculated by multiplying site-level cones·tree^{-1} and stand density (stems·m^{-2}). Seeds·tree^{-1} was calculated by multiplying the mean number of seeds·cone^{-1} by the mean number of cones·cohort^{-1} (= seeds·cohort^{-1}), which was then transformed to seeds·m^{-2} by summing the four cohorts (= seeds·tree^{-1}) and multiplying by stand density (stems·m^{-2}). Viable seeds·m^{-2} was calculated in the same manner as seeds·m^{-2}, with the additional step of multiplying seeds·cohort^{-1} by the proportion of viable seeds·cohort^{-1} before summing the four cohorts (= viable seeds·tree^{-1}).

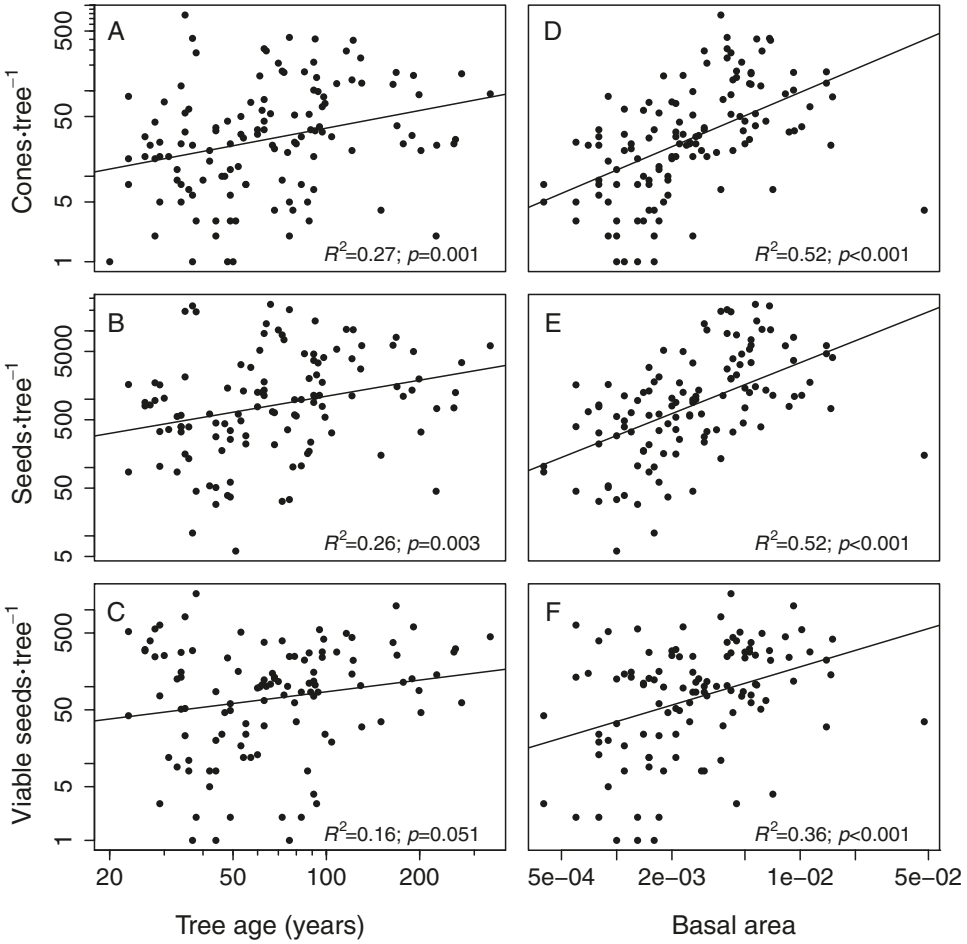
To include all of the data in the analysis, we used a two-stage process that first modeled the probability of observing cones or seeds (i.e., sexual maturity) and then modeled the observed density of cones or seeds when the density was >0 (Heilbron 1994). We used logistic regression to fit the response data based on presence or absence of cones and seeds. A similar binomial model with a log-link function was used to fit the relationship between stand mean age and the proportion of trees with cones. In the second part of the two-stage analysis, we used generalized linear regression to model nonzero observations of cone and seed densities. Response data were $\log_{10}$-transformed prior to analysis to meet assumptions of homoskedasticity and normality of residuals assumed by the linear regression models. All analyses were performed in R version 2.15.2 (R Core Team 2012).

Table 1. Bivariate relationships between reproductive output variables and individual tree characteristics, using $\log_{10}$-transformed nonzero data.

Model									
Response variable	Predictor variable	n	a	SE_a	b	SE_b	r	p	AIC
Cones·tree^{-1}	Tree age	124	0.19	0.21	0.69	0.21	0.27	0.001	238.92
	Tree basal area	124	3.8	0.35	0.91	0.13	0.52	<0.001	209.94
Seeds·tree^{-1}	Tree age	116	1.49	0.47	0.78	0.26	0.26	0.003	261.53
	Tree basal area	116	5.67	0.42	1.07	0.16	0.52	<0.001	232.5
Viable seeds·tree^{-1}	Tree age	110	0.92	0.47	0.51	0.26	0.16	0.051	243.73
	Tree basal area	110	3.68	0.45	0.71	0.17	0.36	<0.001	231.41

Note: Data were $\log_{10}$-transformed; thus, the resulting equation to estimate reproductive output (y: cones per tree, seeds per tree, or viable seeds per tree) is $y = (10^a)(x^b)$, where x represents the individual tree characteristic (tree age (years) or tree basal area (m^2)), and a and b represent the equation coefficients for the intercept and slope, respectively. n, sample size; a, intercept; SE_a, standard error associated with a; b, slope; SE_b, standard error associated with b; r, correlation coefficient; p, p value for the bivariate relationship; AIC, Akaike's information criterion. Sample size varies as the number of samples with zero values increased from cones per tree to viable seeds per tree.

Fig. 3. All bivariate relationships between the two predictor variables, tree age and tree basal area (m^2), and the three response variables, number of cones·tree^{-1} (A and D; n = 124), the number of seeds·tree^{-1} (B and E; n = 116), and the number of viable seeds·tree^{-1} (C and F; n = 110). Points represent individual trees and all axes are plotted on a $\log_{10}$ scale.

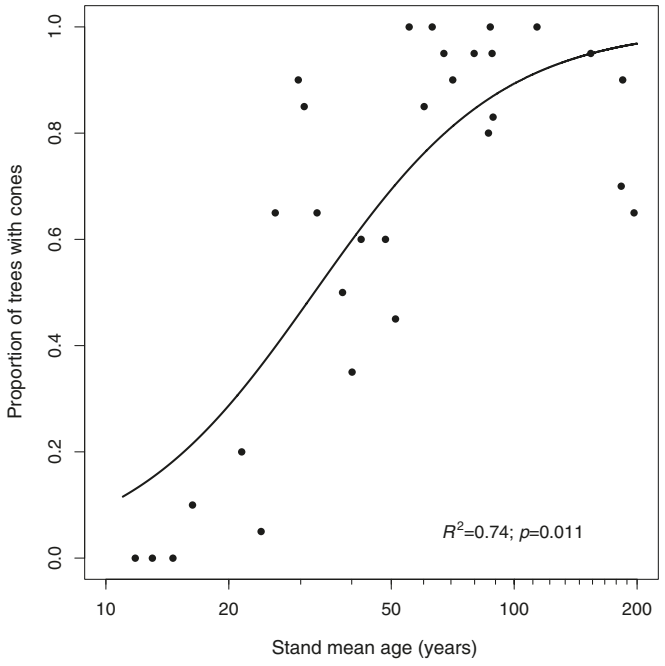


We analyzed reproductive output across cone cohorts using contigency table analysis. Pearson's χ^2 statistic was used to test for significant differences between expected and observed frequencies of cones·cohort^{-1}, seeds·cone^{-1}·cohort^{-1}, and proportion of viable seeds·cohort^{-1}, among the three separate cohorts. The χ^2 test was used to assess significant effects of cohort on each variable, as well as for pairwise comparisons between the different cohorts.

Results

Most of the sampled black spruce stands supported a ground layer dominated by the feathermosses *Hylocomium splendens* (Hedw.) Schimp. and *Pleurozium schreberi* (Brid.) Mitt., along with *Cladonia* spp. and *Cladina* spp. lichens. The vascular plant understory was usually dominated by ericaceous species such as *Vaccinium vitis-idaea* L., *Vaccinium uliginosum* L., *Ledum palustre* L. subsp. *decumbens* (Aiton) Hultén, and *Ledum groenlandicum* Oeder. Black spruce stem densities ranged from 517 to 10 370 stems·ha^{-1}, with basal areas ranging from 0.04 to 15.40 m^2·ha^{-1}, individual tree basal diameters ranging from 0.1 to 24.6 cm, and minimum tree ages ranging from 6 to 338 years old. Estimated mean stand ages ranged from 11.8 to 196.6 years across the 30 sampled sites, with 19 sites ≤80 years old and 6 sites estimated to be older than 150 years.

Fig. 4. Binomial regression between $\log_{10}$-transformed stand mean age and the proportion of trees with cones. Each dot represents a site (n = 30) and stand mean age is on a $\log_{10}$ scale.



Cone production ranged from 0 to 1138 cones·tree^{-1}. Of the trees randomly selected for cone collection, the youngest tree observed with cones was 20 years old. Sixty-five percent of the black spruce trees in our sample were producing cones. The probability of an individual tree producing cones reached 50% at an age of approximately 30 years (Fig. 2). Trees >100 years old had a 90% probability of producing cones (Fig. 2).

At the individual tree level, tree age (years) was positively associated with the number of cones·tree^{-1} and the number of seeds·tree^{-1} (Table 1 and Figs. 3A and 3B). Tree age was more weakly associated with the number of viable seeds·tree^{-1} (Table 1 and Fig. 3C). In general, tree basal area was a better predictor than tree age of the number of cones, seeds, or viable seeds per tree (Table 1 and Figs. 3D–3F). The steeper slope of the log-linear relationships with basal area compared with tree age indicates a greater sensitivity of the reproductive variables to tree size versus tree age. None of these relationships showed compelling evidence of a change in slope across the observed ranges of tree sizes and ages (Fig. 3), and fitting relationships with a polynomial curve showed no significant improvement over the log-linear model ($p > 0.1$). Finally, neither tree age nor basal area appeared to have an influence on seed viability or the proportion of germinated seeds observed in lab trials (data not shown; $p > 0.1$).

Stand age showed a sigmoidal relationship with the proportion of trees with cones in a stand, with the steepest rate of increase occurring in stands <50 years old and relatively little change in stands >100 years old (Fig. 4). At 50 years of age, approximately 60% of the trees in a stand were predicted to have cones, whereas stands >100 years were predicted to have 90%–95% of the trees producing cones (Fig. 4). Cone production at the stand level, estimated as trees·ha^{-1} × cones·tree^{-1}, ranged from 0 to 78.86 total cones·m^{-2} (Fig. 5A). Estimates of the amount of seeds in the aerial seed bank ranged from 0 to 2044 seeds·m^{-2}, and viable seeds ranged from 0 to 273 viable seeds·m^{-2} (Figs. 5B and 5C). Positive relationships between cone production and black spruce age or basal area that were apparent at the level of individual trees were also apparent at the stand level, although these relationships were generally stronger for stands than for individual trees (Table 2 and Figs. 5A–5F). Mean age and stand basal area both can predict seed and cone production at the stand level. In contrast to the patterns observed for individual trees, stand mean age was a better predictor of cone and seed production than stand basal area (Table 2 and Fig. 5).

Cone production (cones·cohort^{-1}) did not differ among the four sampled cohorts (2009, 2008, 2007, and 2006; df = 3, χ^2 = 5.61, p = 0.132), but seed production varied significantly among cohorts (Table 3). Of the three cohorts tested, the highest number of seeds·cone^{-1} was in the 2008 cones and older cohorts progressively declined in seeds·cone^{-1} (Fig. 6). Although cones from the 2006 cohort were frequently encountered (in 51% of trees with cones), they typically held <10 seeds·cone^{-1}. The proportion of viable seeds also showed a significant decline with cohort age, with a mean of 22.27% in the 2008 cohort that declined to 0% in the 2006 cohort. The combination of fewer seeds per cone and lower viability in the older cohorts resulted in a significantly lower number of viable seeds that could be contributed from the ≥3-year–old cohort compared with the younger, 1- and 2-year-old cohorts (Table 3).

Discussion

Our study illustrates the strong relationships of age and basal area with cone and seed production of black spruce at both the tree and stand level. The data presented here clarify several key unknowns about the reproductive life history of northern black spruce: the timing of sexual maturity and consistent cone production in young trees, the continuous increase in seed productivity with age up to ~200 years, and the rapid decline in seed viability and number as cones age. Accurate life history information is essential for predicting regeneration and succession patterns after disturbance, an objective that is especially important within the context of changing climate and fire conditions across much of the North American boreal forest (Meunier et al. 2007; Balshi et al. 2009; Krawchuk et al. 2009; Flannigan et al. 2013; Boulanger et al. 2013).

In mature boreal forests of northwestern North America, regeneration after fire is highly correlated to the prefire composition, which provides a propagule source for postfire recruitment (Greene and Johnson 1999). Empirical evidence suggests that when forests are burned with an average fire return interval between 50 and 150 years, stand self-replacement typically occurs (Viereck 1983; Greene and Johnson 1999; Johnstone and Chapin 2006*b*). However, reductions in fire return interval can result in departures from the normal postfire species composition (Johnstone and Chapin 2006*b*; Brown and Johnstone 2012). Several studies have now documented low levels of conifer recruitment following disturbances that occurred at return intervals of less than 30 years, likely because of low availability of viable seed from aerial seed banks (Payette et al. 2000; Simard and Payette 2005; Johnstone and Chapin 2006*b*; Brown and Johnstone 2012). Similarly, evaluation of black spruce regeneration across a range of stand ages and postfire seedbeds found that black spruce recruitment was lower than expected in stands that burned at an age of less than 80 years (Johnstone et al. 2010*b*). These results suggest that the age at which a stand burns can be an important control on patterns of postfire recovery. However, individual case studies of short disturbance intervals can provide only general predictions of how regeneration potential will vary with stand age.

Here we present equations to estimate viable seeds·m^{-2} as a function of stand age or basal area of black spruce. Estimates of seed availability can be combined with published estimates of seed:seedling ratios required for successful conifer recruitment (Johnstone and Chapin 2006*a*) to predict the impacts of prefire stand age and structure on postfire seedling densities. Experimental seeding trials with black spruce on thick organic seedbeds estimate that an average of 383 viable seeds are required to

Fig. 5. All bivariate relationships between the two predictor variables, site mean age and site basal area (area·area^{-1}), and all three response variables, cones·m^{-2} (A and D), seeds·m^{-2} (B and E), and viable seeds·m^{-2} (C and F). Points represent individual sites (n = 30) and all axes are on a $\log_{10}$ scale.

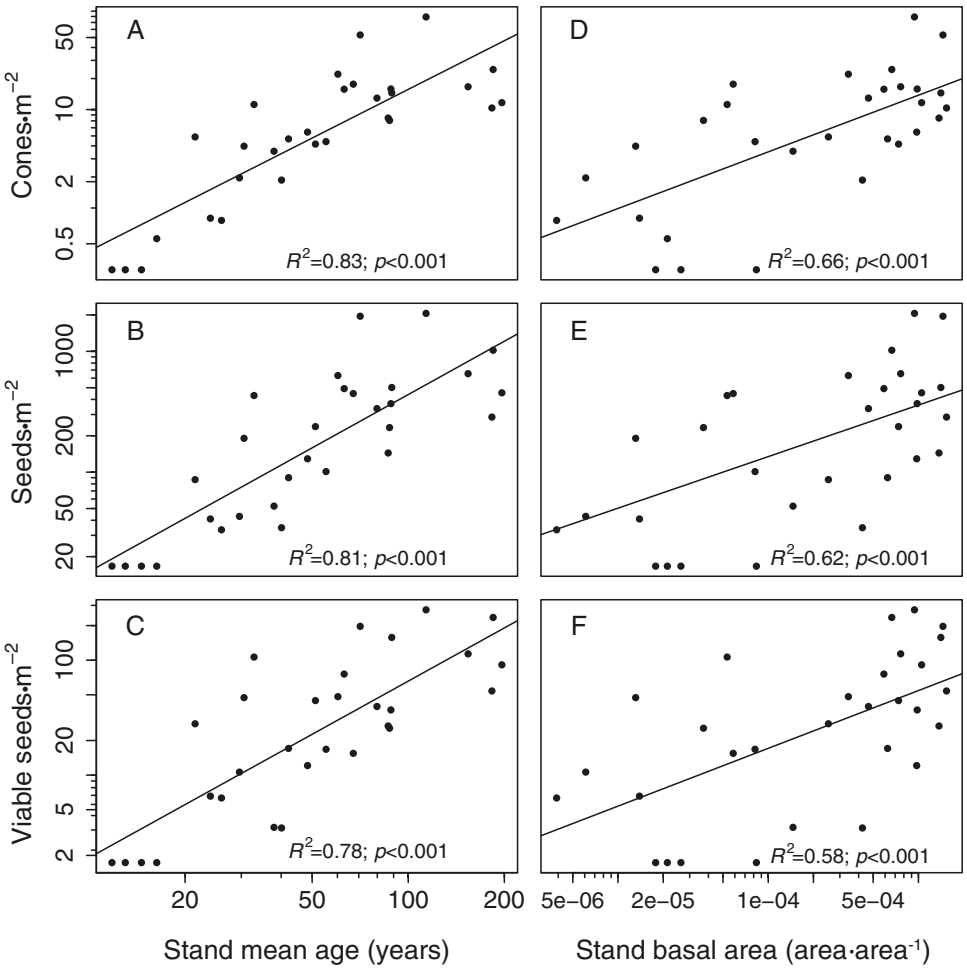


Table 2. Bivariate relationships between reproductive output variables and stand characteristics using using $\log_{10}$-transformed data.

Model								
Response variable	Predictor variable	a	SE$_a$	b	SE$_b$	r	p	AIC
Cones·m^{-2}	Mean age	–1.94	0.34	1.57	0.20	0.83	<0.001	29.04
	Basal area	2.79	0.43	0.55	0.11	0.66	<0.001	45.78
Seeds·m^{-2}	Mean age	–0.29	0.34	1.47	0.19	0.81	<0.001	28.03
	Basal area	4.04	0.43	0.49	0.11	0.62	<0.001	45.63
Viable seeds·m^{-2}	Mean age	–1.26	0.39	1.54	0.23	0.78	<0.001	36.94
	Basal area	3.24	0.48	0.50	0.13	0.58	<0.001	52.75

Note: Data were $\log_{10}$-transformed; thus, the resulting equation to estimate reproductive output (y: cones per m^2, seeds per m^2, or viable seeds per m^2) is $y = (10^a)(x^b)$, where x represents the stand characteristic (mean age (years) or basal area (dimensionless; e.g., m^2/m^2)), and a and b represent the equation coefficients for the intercept and slope, respectively. a, intercept; SE$_a$, standard error associated with a; b, slope; SE$_b$, standard error associated with b; r, correlation coefficient; p, p value for the bivariate relationship; AIC, Akaike's information criterion. Models included all of the study sites (n = 30).

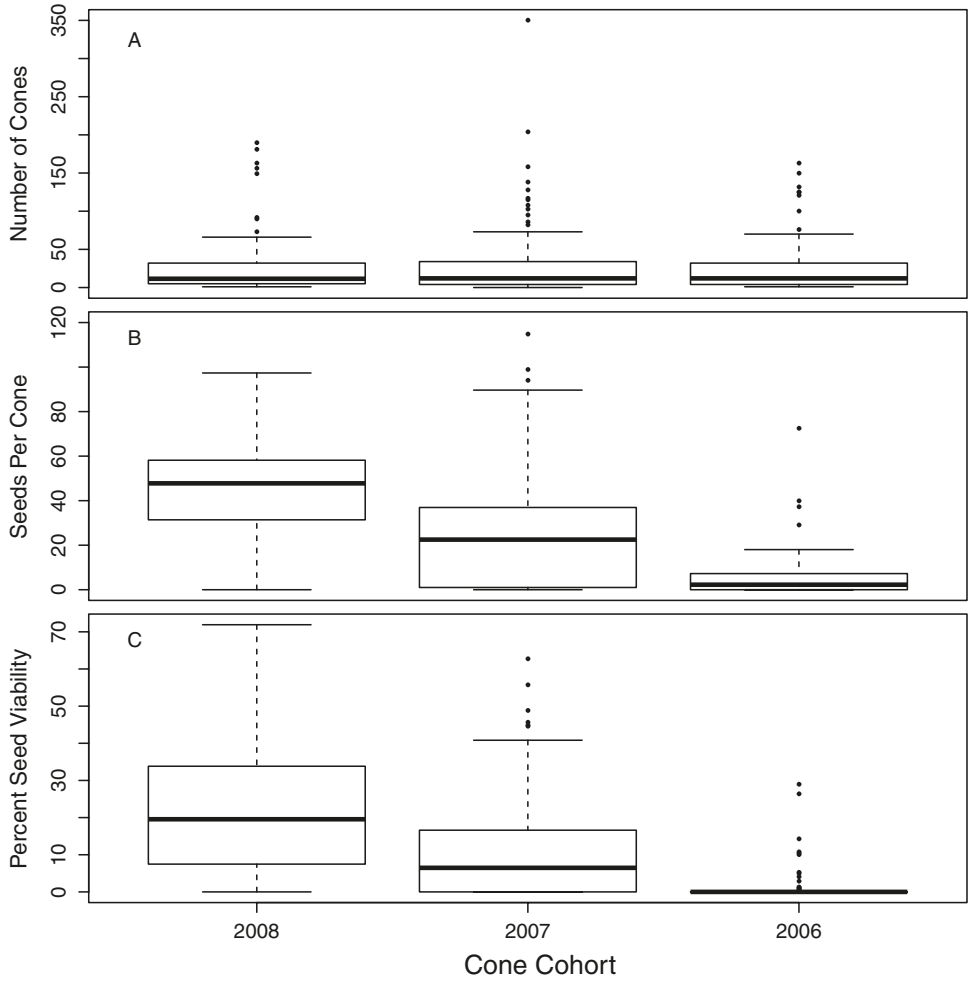
Table 3. Contingency table results comparing cones·cohort^{-1}, seeds·cone^{-1}, and proportion of viable seeds·cohort^{-1} across three cone cohorts (2008, 2007, and 2006), with the results from pairwise comparisons included for models that were significant.

Variable	Cohort	df	χ^2	p
Seeds·cone^{-1}	2008, 2007, 2006	2	27.11	<0.001
	2008–2007	1	4.86	0.027
	2008–2006	1	27.17	<0.001
	2007–2006	1	10.88	<0.001
Percent viability	2008, 2007, 2006	2	18.25	<0.001
	2008–2007	1	3.16	0.075
	2008–2006	1	18.24	<0.001
	2007–2006	1	8.24	0.004
Viable seeds·cone^{-1}	2008, 2007, 2006	2	8.06	0.018
	2008–2007	1	1.21	0.271
	2008–2006	1	8.21	0.004
	2007–2006	1	3.86	0.049

Note: Variable, the variable under analysis; cohort, years of cone production being compared in the analysis; df, degrees of freedom for the analysis; χ^2, Pearson's χ^2 statistic; p, p value obtained from the analysis.

produce a single two-year-old seedling of black spruce, compared with 61 viable seeds required to produce a seedling on severely burned seedbeds with exposed mineral soil (Johnstone and Chapin 2006*a*). Based on a target stocking density of 4000 trees·ha^{-1} (the mean stem density observed across our 30 study sites), we estimate that stands are likely to produce sufficient seed to restock following a high-severity fire when they reach >50 years in age. In contrast, this age requirement is likely to be closer to 150 years for restocking after a low-severity fire (Fig. 7). One of the main conclusions of this study is that fire return intervals of less than 50 years are very likely to result in reduced black spruce densities after fire, regardless of seedbed quality. The size of the aerial seed

Fig. 6. Boxplots summarizing the reproductive output between cone cohorts. (A) Comparison of the number of cones across cone cohorts (2006–2008). (B) Comparison of the number of seeds per cone across cone cohorts. (C) Comparison of percent seed viability across cone cohorts (2006–2008). Statistical comparisons are shown in Table 3. The line in the centre of the boxes represents the median of the data, with the boxes encompassing the 25%–75% quartiles of the data. The whiskers extending beyond the boxes represent the 95% quartiles, and extreme values are beyond the whiskers shown as filled circles.

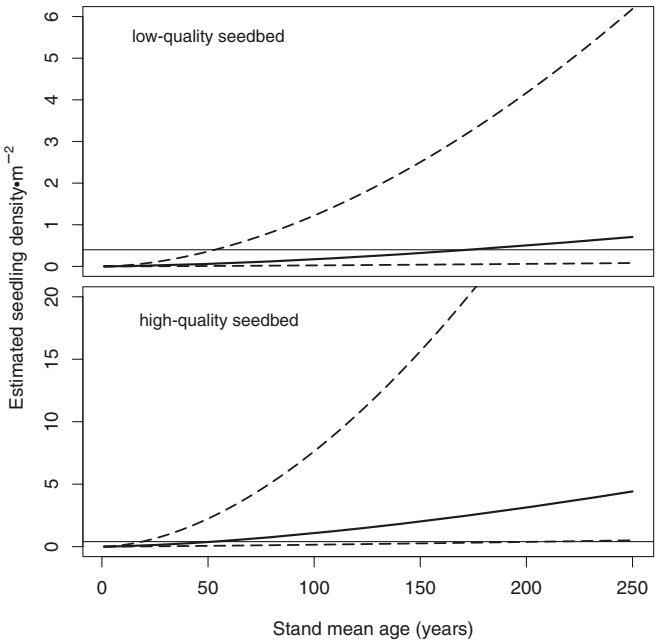


banks in stands younger than 50 years are simply too low to ensure adequate seedling recruitment even with high success rates on mineral seedbeds. In cases where postfire recruitment is limited to lower quality organic seedbeds, we expect the time span of vulnerability to seed limitation to be substantially longer. By quantitatively linking stand age with seed production, we can use empirical estimates of seed recruitment under a variety of postfire conditions to predict regeneration patterns after fire and link the life history traits of dominant conifers to patterns in disturbance regimes.

Climatic constraints on the production of mature seeds in conifer forests become more acute with increasing latitude and elevation, and can significantly reduce the availability of viable seed in northern forests (Henttonen et al. 1986; Zasada 1988; Sirois 2000). We estimated that northern black spruce stands between ages 50 and 100 years produce $2.27 \times 10^5 - 5.75 \times 10^5$ viable seeds·ha^{-1}. These values are an order of magnitude lower than what has been measured in black spruce stands in northern Ontario, central Saskatchewan, and Quebec ($2.90 \times 10^6 - 8.10 \times 10^6$ seeds·ha^{-1} and $\sim 4.5 \times 10^6$ filled seeds·ha^{-1}, respectively; Skeates and Haavisto 1987; Greene and Johnson 1999). However, our estimates are comparable to other northern black spruce populations in the Northwest Territories (6.28×10^5 seeds·ha^{-1}; Black and Bliss 1980). This difference in black spruce seed production from southern to northern Canada is similar to north–south gradients in the production of viable seed seen in Scots pine (*Pinus sylvestris* L.; Henttonen et al. 1986). It is important to note that this north–south gradient may occur not only across the entire range of black spruce, but also within our study area to a lesser magnitude, as it spans 3° latitude. The primary mechanism for a decrease in viable seed production of conifers in northern climates appears to be the reduction in the number of growing degree-days, which affects the maturation of developing seeds (Henttonen et al. 1986; Sirois 2000; Meunier et al. 2007). Furthermore, northern regions may have a lower proportion of viable pollen, which could increase the number of immature or unfilled seeds (Elliott 1979; Sirois 2000). Reduced seed productivity of northern black spruce could mean that northern populations of black spruce are particularly vulnerable to changes in disturbance regimes. However, the potential for fire disturbances to be compounded with other disturbances like insect outbreaks may increase in the south (Payette et al. 2000; Simard and Payette 2005). Thus, the regeneration of black spruce and other serotinous conifers is likely to be sensitive to time since disturbance across the range of the boreal forest, wherever disturbance frequencies approach the stand age required for adequate seed production.

Black spruce typically has three to four cone cohorts present on an individual tree in northern latitudes (Zasada et al. 1992), and as

Fig. 7. Estimated seedling density predicted by mean stand age. Lines are estimated based on the generated equation from the mean stand age – viable seeds·ha^{-1} relationship and the number of viable seeds required to produce a two-year-old seedling on moderately burned soils (upper panel) and severely burned soils (lower panel; Johnstone and Chapin 2006*b*). The solid thin line represents a target density of 4000 stems per hectare. The 95% confidence intervals for the estimates are represented by broken lines.



many as six or more cohorts in more southern locations (Chai and Hansen 1952; Greene and Johnson 1999). Even though multi-year cone production is held in the canopy of black spruce forests, the progressive opening of semiserotinous cones means that regeneration potential is highest in the youngest cone cohorts (Chai and Hansen 1952; Atkinson and Haavisto 1996). Based on the proportion of viable seeds in each cohort, we found that the two youngest cone cohorts provide approximately 94% of the available viable seed on an individual tree. These results are similar to other studies of black spruce seed production. In northern Ontario, black spruce cones three to seven years old had similarly low numbers of seeds per cone when compared with one- and two-year-old cones (Atkinson and Haavisto 1996). An early study of black spruce with 19 different cone cohorts in Minnesota found that viability was highest in the youngest cohorts and gradually diminished as the cones aged, with some viable seeds contained even in the oldest cones sampled (Chai and Hansen 1952). Black spruce seeds lose viability between 10 and 16 months after being released from the cones (Fraser 1975), thus, seeds stored in aerial cones are the principle source for postfire regeneration. The results of this study and the others cited previously suggest that the viable seed stores in a stand can be effectively estimated from the two youngest cone cohorts in black spruce.

Estimating the true age of black spruce individuals or stands is challenging, as slow rates of growth combined with harsh growing conditions generate many deformities that complicate aging from simple ring counts. For example, many black spruce develop adventitious roots along the basal part of the stem to stabilize the tree and provide better aeration of the roots within the rapidly accumulating moss layer (LeBarron 1945). This means that the true root collar of black spruce trees is underneath the adventitious roots (Telewski and Lynch 1991), and there can be as many as 20 additional growth rings in underground stem sections when compared with the age at ground level (DesRochers and Gagnon 1997). In addition, black spruce exhibit a reverse taper in ring formation, where rings formed in the crown of the tree may not always reach the base of the stem (Esau 1977). Therefore, studies using ground-level stem disks or cores like this will typically underestimate the true age of black spruce trees, particularly in older stands (LeBarron 1945; Gagnon et al. 1992). It is apparent that achieving an accurate age is very difficult, since nowhere along the stem is there an entire series of growth rings (DesRochers and Gagnon 1997). The difficulty of cross-dating of black spruce stems under slow-growing conditions thus creates a trade-off between high-precision aging versus sampling across multiple stands. Our models provide a framework for predicting reproduction using data on tree and stand age that match the precision of tree chronologies that are typical in studies of forest age structure (DesRochers and Gagnon 1997).

In contrast, basal area is a quick measurement that provides information on aboveground tree biomass, and has been previously linked to the seed productivity of boreal conifers (Greene and Johnson 1999). As tree size increases with age, it is not surprising that we found both were correlated with cone and seed production of black spruce. At the individual tree level, basal area was a better predictor of cone and seed production than age. However, at the stand level, mean age was a better predictor than stand basal area of cone and seed production. As both age and basal area were significantly related to cone and seed production at scales of individual trees and stands, the choice of which variable to use will depend on the specific objectives of a study. When seed production is to be estimated across many stands, basal area may be the best choice because it is much easier and quicker to measure. However, stand age has the advantage of being measured on the same scale as disturbance frequency, and thus can be easily linked to disturbance interval.

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Appendix

Tables A1 and A2 follow.

Table A1. Summary of stand (n = 30) environmental characteristics.

Site ID	Mean age	SOL depth (cm)	Soil pH	Elevation (m)	Thaw depth (cm)	Soil texture	Slope (°)	Aspect (°)	Latitude	Longitude
21	11.8	12.8	5.53	460	46	na	0	—	63.8019	–145.1085
26	13.0	10.8	4.87	652	59	Si	0	—	65.9935	–137.2866
6	14.6	3.8	5.73	506	66	Si	0	—	63.3276	–142.8950
8	16.3	7.8	4.93	408	65	GSi	0	—	63.9172	–145.4039
9	21.5	8.6	5.73	134	35	SiL	0	—	64.7145	–148.2959
24	24.0	15.6	5.95	668	32	SiL	3.5	175	64.0412	–140.6436
12	26.0	4.2	5.50	558	63	GSi	4	85	65.1827	–147.8734
13	29.6	6.2	4.50	460	58	GSiC	5	324	65.1704	–147.8922
4	30.6	11.2	6.23	616	27	Si	2	140	63.9172	–142.2050
3	32.9	7.2	5.57	587	46	SiL	14	290	63.9445	–138.8964
10	38.0	14.8	5.20	165	28	Si	4	350	64.8009	–148.3916
16	40.1	2.1	5.17	224	59	SiL	15	230	64.8836	–148.3574
22	42.2	27.0	5.80	528	38	GSiL	5	20	63.7749	–145.0805
2	48.4	4.6	5.60	623	52	SiL	5.5	110	63.8536	–138.0346
1	51.2	6.2	5.37	639	41	SiL	0	—	63.8903	–138.1985
15	55.3	24.2	4.70	242	32	n/a	2	310	64.9118	–146.6174
29	60.2	12.0	4.90	630	33	Si	6	292	66.1472	–137.2182
27	63.0	18.8	4.80	622	34	SiC	0	—	66.1240	–137.2430
28	67.3	12.4	4.05	721	45	SiL	9	254	66.3695	–136.7246
25	70.7	14.4	5.25	695	28	SiL	7	111	64.0424	–140.6652
18	79.8	24.0	3.87	594	34	GSiL	6	134	64.9443	–148.2681
19	86.5	15.6	4.43	244	39	GSiL	5	185	65.1569	–147.4894
17	87.4	17.0	4.30	677	38	GSi	8	330	64.9474	–148.3038
14	88.3	12.8	3.97	465	38	Si	1	20	65.1698	–147.8908
11	88.8	27.0	3.90	500	37	Si	9	20	64.8002	–148.1925
30	113.7	10.6	4.05	618	34	Si	3	75	65.9569	–137.3612
5	154.1	15.6	6.27	797	27	na	2	26	63.5019	–142.4071
23	182.9	24.4	5.90	496	36	Si	0	—	63.3150	–142.6531
20	184.5	31.0	4.80	449	32	SiL	0	—	63.8085	–144.9771
7	196.6	23.6	3.47	446	29	na	3	3	63.6962	–144.3301

Note: For soil texture: Si; Silt, GSi; Gravelly Silt, SiL; Silty Loam, GSiC; Gravelly Silty Clay, GSiL; Gravelly Silt Loam, SiC; Silty Clay. SOL, soil organic layer.

Table A2. Summary of age, density, cone production, seed production, and viable seed production in each of the study sites (n = 30).

Site No.	Mean age	Oldest age	BA (m^2 per hectare)	Black spruce density (stems·ha^{-1})	Total stand density (stems·ha^{-1})	Cones per m^2	Seeds per m^2	Viable seeds per m^2
21	11.8	13	0.84	6824	—	0.00	0.00	0.00
26	13.0	17	0.26	10370	—	0.00	0.00	0.00
6	14.6	18	0.18	5120	9707	0.00	0.00	0.00
8	16.3	20	0.21	3111	—	0.28	0.00	0.00
9	21.5	24	2.52	7305	8661	5.15	7.02	2.63
24	24.0	35	0.14	2944	—	0.60	2.43	0.48
12	26.0	29	0.04	517	519	0.56	1.67	0.46
13	29.6	35	0.06	636	762	1.90	2.64	0.89
4	30.6	37	0.13	969	—	4.14	17.40	4.50
3	32.9	38	0.53	1624	1775	10.90	41.45	10.47
10	38.0	41	1.46	3966	—	3.67	3.57	0.18
16	40.1	45	4.23	3412	5117	1.79	1.80	0.17
22	42.2	48	6.24	5986	6956	4.91	7.34	1.53
2	48.4	50	9.74	6830	9371	5.77	11.24	1.04
1	51.2	55	7.38	8784	—	4.35	22.17	4.28
15	55.3	79	0.82	1435	—	4.61	8.44	1.50
29	60.2	69	3.42	3422	3464	21.79	61.42	4.64
27	63.0	72	5.89	3899	—	15.48	47.45	7.40
28	67.3	99	0.59	975	—	17.36	43.04	1.37
25	70.7	79	14.57	7708	—	52.62	193.51	19.56
18	79.8	169	4.65	2946	—	12.65	31.92	3.78
19	86.5	94	13.71	6730	—	7.99	12.75	2.50
17	87.4	157	0.37	712	—	7.57	21.70	2.38
14	88.3	97	9.80	5670	—	15.57	35.17	3.52
11	88.8	98	14.11	4885	—	14.22	48.48	15.60
30	113.7	129	9.41	4195	—	78.86	204.42	27.26
5	154.1	232	7.62	3297	—	16.38	63.69	11.18
23	182.9	205	15.40	4938	—	10.09	26.89	5.22
20	184.5	338	6.65	3901	—	24.21	100.34	23.37
7	196.6	261	10.49	6452	—	11.39	43.74	8.96

Note: BA, basal area.