

Factors influencing black spruce reproductive potential in the northern boreal forest of Quebec

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Abstract

The reproductive ecology of the semi-serotinous species black spruce (*Picea mariana* (Mill.) BSP) in northern boreal forests remains poorly understood. There is a general lack of data on cone/seed production and viability as a function of biotic tree-level characteristics and abiotic variables. No studies currently exist to quantify these differences over a large gradient in temperature, elevation, and precipitation. Extensive physical, ecological, dendrometric, and reproductive data were collected from young to very old black spruce stands in northern Quebec. ANOVA and general linear mixed models were used to examine interannual cone production, and the relative importance of the biotic and abiotic explanatory factors in determining total cone production; length of the cone-bearing zone; filled seeds per cone; proportion of filled seeds; and seed viability. The results illustrate that the reproductive ecology of black spruce in northern cold forests is mainly explained by biotic variables such as age and diameter at breast height, and by abiotic variables related to temperature such as elevation, length of the growing season, and growing degree-days. Black spruce exhibits a lower reproductive potential in northern cold forests, making it possibly less resilient to increased fire frequency, particularly in unproductive and very young or very old stands.

Key words: black spruce, reproductive ecology, cone production, seed production, germination, boreal forest, forest fire, seed viability, resilience, adaptation

Résumé

L'écologie de la reproduction de l'espèce semi-serotineuse, l'épinette noire (*Picea mariana* (Mill.) BSP) dans les forêts boréales froides est encore peu documentée. Il existe un manque général de données sur la production des cônes/graines et leur viabilité en fonction des caractéristiques biotiques au niveau de l'arbre et des variables abiotiques. Aucune étude n'existe actuellement pour quantifier ces différences sur un large gradient de température, d'altitude, et de précipitations. De nombreuses données physiques, écologiques, dendrométriques et reproductives ont été recueillies dans des peuplements d'épinette noire jeunes à très âgés dans le nord du Québec. Des ANOVA et des modèles mixtes linéaires généraux ont été utilisés pour examiner la production annuelle de cônes et l'importance relative des facteurs explicatifs biotiques et abiotiques dans la détermination de la production totale de cônes; la longueur de la cime comportant des cônes; le nombre de graines pleines par cône; la proportion de graines pleines; et leur taux de germination. Les résultats indiquent que l'écologie de la reproduction de l'épinette noire dans les forêts boréales nordiques est expliquée par des variables biotiques telles que l'âge et le DHP, et des variables abiotiques liées à la somme thermique régionale telles que l'altitude, la durée de la saison de croissance, et les degrés-jours de croissance.

L'épinette noire présente un potentiel reproductif plus faible dans les forêts froides du nord, ce qui la rend moins résistante à l'augmentation de la fréquence des feux, particulièrement dans les peuplements improductifs et très jeunes ou très vieux.

Mots-clés : épinette noire, écologie de la reproduction, production des cônes, production des graines, germination, forêt boréale, feu de forêt, taux de germination, résilience, adaptation

1. Introduction

Black spruce (*Picea mariana* (Mill.)) is one of the most common and commercially important conifer species in the boreal forest of eastern North America (Viereck and Johnston 1990), where fire is the main disturbance agent (Bergeron et al. 2002, 2010; Stocks et al. 2002). Above the northern limit of commercial forests in Quebec, black-spruce-dominated stands dominate northern boreal forest landscapes (Payette 1992; MNR 2013a). The reproductive strategy of this species includes serotiny, the tendency to retain seeds in cones, long after maturation is completed (Lamont et al. 1991). This strategy often results in monospecific tree regeneration following fires, which, combined with layering, engenders self-replacement dynamics over time (Viereck and Johnston 1990; Lamont et al. 1991; Greene et al. 1999; Ilisson and Chen 2009; Johnstone et al. 2010b; Keeley et al. 2011).

Black spruce is considered semi-serotinous. The matured cones of black spruce delay opening for several years, and thus there are far fewer cone cohorts on the tree at any one time relative to serotinous *Pinus* (Greene et al. 1999). As with other serotinous species, black spruce has one of the lowest coefficients of variation of temporal seed production of any tree species (cf. Koenig and Knops 2000) as well as relatively lower coefficients of variation of temporal seed dispersal (Rossi et al. 2016). Therefore, there are always viable seeds in the aerial multi-cohort seed bank once sexual maturity has been reached. However, it has relatively small cones with thin ovuliferous scales and thus seeds are susceptible to necrosis caused by the passage of the flaming front (Michaletz et al. 2013; Splawinski et al. 2019b). Even-aged stands initiated by fire also can modestly infill a stand via the asexual reproductive mode of layering. On productive sites, black spruce takes much longer (30 vs. 5–10 years) than serotinous pine species to reach reproductive maturity (Viereck and Johnston 1990; Viglas et al. 2013). On unproductive sites typical of northern boreal forests where climate exerts a strong limiting effect on growth, attaining reproductive maturity can take significantly longer (Van Bogaert et al. 2015b). The species can therefore be extirpated from stands affected by short fire intervals (Keeley et al. 1999; Johnstone and Chapin 2006; Johnstone et al. 2010a; Brown and Johnstone 2012; Pinno et al. 2013). Given this sensitivity to both a short fire return interval and an increase in fire intensity in the context of climate warming, black spruce is vulnerable to regeneration failure following fires, as shown by comparative (e.g., Johnstone and Chapin 2006; Baltzer et al. 2021) and modelling studies (Splawinski et al. 2019a, 2019c; Cyr et al. 2021). This process has the potential to decrease forest resilience and stand productivity over time.

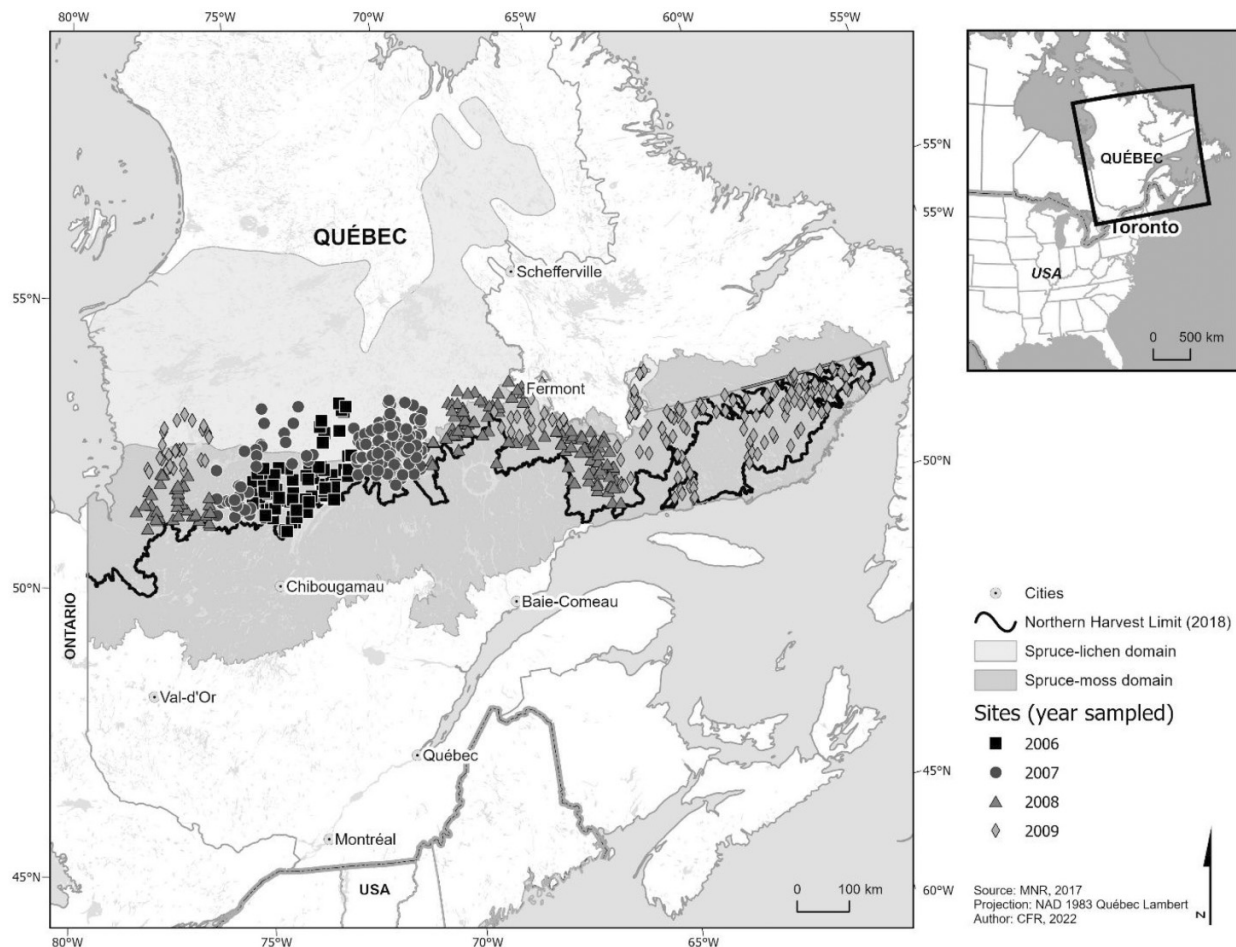
The amount of viable seeds available at the time of burning, which is ultimately the main determinant of postfire success, is potentially limited by diverse biotic and abiotic factors, including stand age (Skeates and Haavisto 1987; Viereck

and Johnston 1990; Viglas et al. 2013; Van Bogaert et al. 2015a), interannual cone production (Haavisto 1975; Skeates and Haavisto 1987), position of the tree within the canopy (Atkinson and Haavisto 1996), site productivity (Skeates and Haavisto 1987; Viglas et al. 2013; Van Bogaert et al. 2015a, 2015b), aspect (Skeates and Haavisto 1987), and temperature/growing degree-days (GDD; Sirois 2000; Meunier et al. 2007). However, these studies are mostly unifactorial and limited in geographical extent. Therefore, any attempt to tease out the effect of these potential drivers of the species' response to stand-replacing fire is hampered by the general lack of data on cone and seed production in the vast array of ecological conditions of northern black spruce forests in eastern Canada. Additionally, the relative importance of factors limiting reproductive potential may differ between northern cold forests and populations located in the central and southern portions of this species range. Apart from Sirois (2000), who examined the production of cones and seeds in four sites along a latitudinal and thermal gradient between the northern boreal forest and the tree line in Quebec, no studies currently exist that quantify these differences along a large continuous gradient of temperature, elevation, or precipitation.

A better understanding of the reproductive ecology and life history traits of black spruce in northern cold forests will improve modelling and forecasting of regeneration and succession in the context of global changes in climate and associated disturbance regimes, environmental stressors, and forest management. These forcing stressors (climate warming, fire, insect epidemic, harvest) have the capacity to induce regeneration failure and productivity loss, thereby leading to a decline in forest resilience and cover over time (Simard and Payette 2005; Splawinski et al. 2019a; Baltzer et al. 2021; Cyr et al. 2021). Such knowledge will prove particularly useful in the development of sustainable forest management, restoration, and adaptive strategies aimed at minimizing or reversing such changes (Raulier et al. 2013; Gauthier et al. 2014, 2015a, 2015b; Splawinski et al. 2019a, 2019c; Cyr et al. 2021).

The general objective of this study was to examine the relative importance of the biotic and abiotic factors limiting the reproductive potential of black spruce trees found across a wide longitudinal gradient of temperature and precipitation in the northern boreal forest of Québec. Specifically, we examined the relative importance of these factors in determining (1) total cone production, (2) length of the trees' cone-bearing zone, (3) filled seeds per cone, (4) proportion of filled seeds, and (5) seed viability. We hypothesized that biotic variables will play a greater role in cone production and length of the cone-bearing zone, whereas abiotic variables will exert a more significant influence on filled seeds per cone, proportion of filled seeds, and seed viability. We hypothesized that biotic factors will play a greater role in cone production and length of the cone-bearing zone, whereas abiotic factors will

Fig. 1. Study area and location of the 564 sites examined in this study (shapes correspond to year sampled). Light- and medium-grey regions represent the black spruce feather moss and balsam fir white birch domains, which make up the continuous boreal forest; dark grey represents the black spruce lichen domain (Taiga). The black continuous line refers to the northern limit of the commercial forest.



exert a more significant influence on filled seeds per cone, proportion of filled seeds, and seed viability.

2. Materials and methods

2.1. Study area

The study area covers 242 000 km², spanning over 2 degrees of latitude (50.39° to 53.00° lat. N.) and 21 degrees of longitude (−57.87° to −78.18° long. W.), from James Bay area in the west to the shore of the Saint Lawrence Gulf in the east (Fig. 1). This region is characterized by glacial (predominantly till) and organic surficial deposits. The forest landscape is dominated (~77% of the land area) by black spruce stands with a mixture of closed forest, peatlands, and open woodland (Jobidon et al. 2015). A longitudinal gradient in GDD and precipitation and latitudinal gradient in annual mean temperature and total/available precipitation exist within the study area (Table 1). These geographic gradients are associated to an average fire cycle that ranges from 44 to 94 years in the James Bay region in the west, to 272 to 8167 years near the shore of the St. Lawrence Gulf to the east (Gauthier et al. 2015b). A de-

tailed description of the study area can be found in Jobidon et al. (2015).

Extensive physical, ecological, and dendrometric data were collected in black spruce-dominated stands in the study area located north of the northern limit of commercial forests in Quebec over a 4-year period (2006–2009) (MNR 2013b) (Table 2). Sites were selected using a random stratified sampling design based on composition (forest type) and surficial deposit (Jobidon et al. 2015). Merchantable black spruce stems in sampled stands ranged in density from 25 to 2950 stems/ha (mean = 701). In each selected site, one circular 400 m² plot with a radius of 11.28 m was established to identify and measure all trees ≥9.1 cm diameter at breast height (DBH; 1.3 m). For all black spruce stems identified, those exhibiting the fourth and fifth largest DBH were retained for sampling (MRN 2013b). This approach yielded a total of 1015 living black spruce trees across 564 sites, representing dominant and co-dominant stems within the canopy, and with a DBH greater than 9.0 cm (Fig. 1). Each site was only sampled once over the 4-year study period, with 81, 153, 156, and 174 sites sampled in 2006, 2007, 2008, and 2009, respectively. In

Table 1. Range of abiotic variables observed among the 564 sites sampled within the study area.

Abiotic variable	Minimum	Mean	Maximum
Latitude	50.386	51.843	52.995
Longitude	-78.180	-69.330	-57.870
Elevation (m)	37	476	855
Mean temperature (°C)	-3.5	-1.6	1.2
Mean July temperature (°C) (2004–2008)	8.1	14.8	20.1
Degree-days above 5 °C	583.3	962.6	1267.4
Growing season (days)	95.3	122.9	150.5
Total annual precipitation (mm)	612.6	789.3	1038.0
Available precipitation during the growing season (mm)	273.9	374.5	447.1

Note: See Section 2.6 for details on climatic value timeframes.

Table 2. Range of biotic variables observed among the 1015 trees sampled between 2006 and 2009 within the study area.

Biotic variable	Minimum	Mean	Maximum
Age (years)	26	152	404
Diameter at breast height (cm)	9.1	15.1	36.5
Height (m)	4.66	10.68	22.46
Total cones per tree	10	262	2000
New cones (mature, sampled year) per tree	5	106	1000
Length of the cone-bearing zone (cm)	11	67	374
Filled seeds per cone	0.00	3.92	38.79
Filled seeds (%)	0	50	100
Seed germinability (%)	0	55	100
Mean filled seed mass (g)	0.00010	0.00097	0.00700

451 of the 564 sites, two trees were sampled for a total of 902 trees; in the remaining 113 sites only one tree per plot met the selection criteria to be sampled. All sampled trees were felled prior to data collection. Dominant and co-dominant stems were grouped together, since cones are primarily produced by trees forming the canopy (Greene et al. 1999). The age of each sampled tree was calculated using transversal discs cut from each individual just above the root collar. They were dried and sanded with up to 400 grit sandpaper. Age was determined using a binocular microscope by counting annual growth rings.

2.2. Cone production and collection

The total number of cones located within the cone-bearing zone (defined as the length of tree stem where 90% of female cones are located) of each sampled black spruce tree was estimated by classes of 10 when there were less than 100 cones, by classes of 100 when there were 100–1000 cones, and finally 1000+ (see MNR 2013b, table 31, p. 129). Estimates were corrected to indicate the mid-range value of each class (example: 0–10 yielded a corrected cone estimate of 5) except the largest, which remained fixed at 1000. Estimates were made for both cones from the sampling year and cones from previous years. Cones of the sampling year were easily distinguished from older cones by their purplish color and their position on the previous year's twig's growth units. Cones from previous years included all other cones that were de-

void of lichen and whose appearance suggested that they did not disperse yet the majority of their seeds (the scales were at most slightly ajar). Among the cones of previous years, two subgroups of cones were defined at the collection stage — last year's cones and older cones (MNR 2013b).

On each selected black spruce tree, 30 sampled cones that matured during the year prior to sampling that did not disperse the majority of their seeds were collected from the cone-bearing zone and combined together for each individual tree. Collection started with cones closest to the tree's apex and then continued progressively down the cone-bearing zone. When it was not possible to collect 30 cones from the previous year, older cones that had not dispersed the majority of their seeds were selected until a total of 30 cones was attained. Among older cones, the youngest were selected (those located on the youngest annual growth units).

2.3. Seed quality assessment

At the Berthier Forest Seed Centre (Québec) (Centre de semences forestières de Berthier) of the Ministère des Forêts, de la Faune et des Parcs (MFFP), sampled cones of each individual sampled tree were soaked in water in a 70 L bin for 65 h, then placed at -18 °C for 24 h. They were then dried in a MacPherson dryer at 70 °C, dew point 50 °C, for 20 h. This procedure was carried out because some of the sampled cones were highly serotinous and did not open under normal conditions (the standard procedure involves only the heating of the

cones without prior freezing). Seeds were then extracted by tumbling the cones, and seed wings were removed manually by rubbing the seeds together in a cotton bag. Empty seeds were then separated from filled seeds with a gravity separator, via introduction into a ventilation shaft along with air under controlled conditions. Filled seeds were subsequently verified by X-ray to confirm quality (Bioptics model Pixarray100) (Colas, Fabienne (Berthier Forest Seed Centre) personal communication). Filled seeds were then counted to determine the total number of seeds. Only lots with at least 40 total seeds per cone (prior to calculating filled seed proportion) were retained for analysis of filled seed proportion and germination proportion.

2.4. Calculating seed mass

The mean filled seed mass (g) was determined by calculating the mass of all filled seeds extracted per tree, then dividing the result by the total number of extracted seeds.

2.5. Germination tests

Germination trials were conducted on filled seeds combined for individual trees, with the germination percentage value of each retained seed lot determined according to the recommendations of the International Seed Testing Association (ISTA 1999). For lots larger than 400 seeds, four batches of 100 seeds were counted. For lots with between 200 and 399 seeds, two batches instead of four were carried out. For lots with less than 200 seeds, we tested germination for all seeds, without batches. The germination chamber was set according to the specifications outlined in the Supplementary Table S1 in Supplementary materials. Germination trays were then arranged randomly on shelves within the germination chamber. Germinated seeds were counted three times per week. To be considered germinated, a seed must have reached the second stage of germination (stage 2, Wang 1973), where cotyledons are easily distinguishable. Counted germinants were then removed from the germinating dish to facilitate subsequent counts, with average germination values taken for analyses.

2.6. Climatic data

Climatic variables for each site were interpolated from 71 weather stations from the Réseau météorologique coopératif du Québec using Biosim version 11.5.10.6. (Régnière et al. 2017). These weather stations were located in and around our study area. With the exception of July mean temperature ($^{\circ}\text{C}$), which was projected annually for 2004–2008, all other climatic variables were averaged over the 1981–2010 reference period due to the limited number of weather stations across the study area/surrounding region, and by extension, the possible imprecision of local projections. Biosim projections of annual mean temperature ($^{\circ}\text{C}$), July mean temperature ($^{\circ}\text{C}$), annual GDD (defined as the heat sum of days where the mean daily temperature was $>5^{\circ}\text{C}$), length of growing season (defined as the period between the last 3 consecutive days with frost ($T_{\min} < 0$) in the spring and the first 3 consecutive days with frost ($T_{\min} < 0$) in the fall), and total precipitation during growing season (mm) were calculated by spatial regressions

between georeferenced weather stations and study sites, adjusted for differences in latitude, longitude, and elevation.

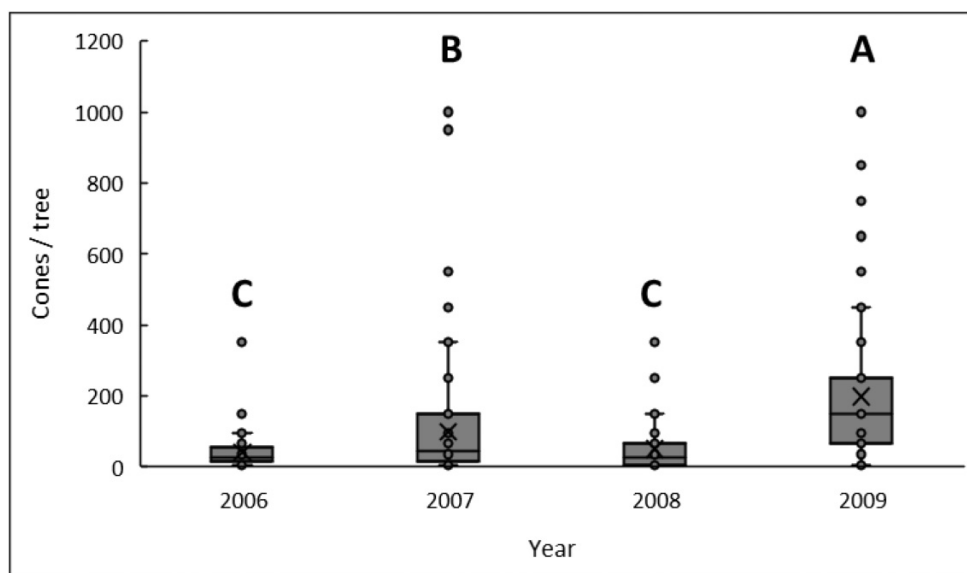
2.7. Data analysis

To evaluate variation in annual (i.e., current-year cone crop) black spruce cone production between sampling years, we used an Analysis of variance (ANOVA) with sampling year as a fixed effect factor, and site as a random effect. Pairwise comparison between years was then assessed a posteriori using Tukey's honest significant difference (HSD) method. This analysis was performed with JMP statistical software (v 7.0.; JMP 1989–2019). In addition, we used ΔT ($^{\circ}\text{C}$) as a predictor of annual cone production (Kelly et al. 2013) according to LaMontagne et al. (2020). This predictor is merely the July mean temperature 1 year preceding the cone crop minus the July mean temperature ($^{\circ}\text{C}$) 2 years before the crop. That is, the reproductive buds of the 2009 cone crop were initiated in the summer of 2008; if that summer was warmer than 2007, the 2009 crop should be large (i.e., crop size is proportion to the magnitude of a positive value of ΔT). To account for the effect of individual tree size, we modified the predictor as the product of ΔT and the length of the cone-bearing zone. A linear regression was then implemented to evaluate the effect of ΔT on annual black spruce cone production.

Linear regressions were performed to evaluate the importance of biotic and abiotic explanatory variables on each of the following five dependent variables, and for the development of predictive models, with individual trees being the effective sample unit: (1) total cone production (i.e., the sum of current and previous years cones) ($n = 1015$); (2) the length of the cone-bearing zone (length of the cone cluster) ($n = 995$) (20 trees were excluded from the analysis due to erroneous data on the length of the cone-bearing zone—outliers); (3) the mean number of filled seeds per cone ($n = 1014$) (1 tree was excluded as it had missing data on the number of cones sampled); (4) the proportion of filled seeds ($n = 856$) (159 trees were excluded as they did not meet the 40-seed threshold for calculating the filled seed proportion); and (5) seed viability ($n = 673$) (342 trees were excluded as they did not meet the 40 filled-seed threshold for calculating the germination proportion, mentioned above).

We built five model groups (cone production, length of the cone-bearing zone, number of filled seeds per cone, filled seed proportion, and seed viability), where age, DBH, tree height, elevation, mean annual temperature, growing season length, precipitation available during the growing season, and GDD were considered as independent variables. Multicollinearity among explanatory variables was first assessed using the variance inflation factor (VIF) function of the car package (v 3.0-10). Only combinations of explanatory variables with a VIF < 2 were retained (Hair et al. 2009; Dormann et al. 2013). Therefore, due to high multicollinearity, only one of either DBH or tree height and only one of either elevation, mean annual temperature, or growing season length was included at the same time in a candidate model. Candidate models were then built within each model group to assess the relative importance of biotic and abiotic factors in determining reproductive potential. To ensure a robust and

Fig. 2. Annual cone production by year of sampling (ANOVA). Box and whisker plots represent the 10th and 90th percentiles, along with the first, second (median), and third quartiles, and the "X" represents the mean. Letters represent significant differences between years (Tukey's HSD) ($n = 1015$ trees); $n = 145, 284, 283,$ and 304 in 2006, 2007, 2008, and 2009, respectively.



through comparative analysis, all possible combinations of explanatory factors were explored. A total of 95 candidate models were built for cone production, length of the cone-bearing zone, and number of filled seeds per cone, respectively; 191 candidate models were built for filled seed proportion and seed viability, respectively. The larger number of models built for filled seed proportion and germination proportion relative to the other three analyses reflects the addition of seed mass as a predictor variable, as it has been identified as an important predictor of germination and early survivorship of tree species due to the greater availability of maternal resources in seeds with a greater mass (Greene and Johnson 1998).

A square root transformation was applied to response variables (cone production, length of the cone-bearing zone, and the number of filled seeds per cone) to meet assumptions of normality and homoscedasticity. For each model, we estimated conditional R^2 (proportion of variance explained by both fixed and random effects, which included year and site) and marginal R^2 (proportion of variance explained by the fixed effects alone). Linear regressions were performed using the R software (v 3.4.3.; R Development Core Team 2015), with the lmer function in the lme4 stats package (v 1.1-26), and the multilevelTools package (v 0.1.0) to obtain the p value and R^2 parameter values.

To evaluate model performance, we used the Akaike information criterion (Akaike 1974) using the AICcmodavg package (v 2.2-2), which allows the ranking of the candidate models (Burnham and Anderson 2002). For each of the five analyses, the top-ranking candidate models, those within a $\Delta AICc$ range of <2 were retained. Retained models had R^2 parameter values assessed with and without random factors (site and year). A full list of candidate models, the complete code to reproduce regression analyses, and statistical results for all

parsimonious models not included in the results section can be found in the Supplementary Materials. An α value of 0.05 was used for all the statistical analyses.

3. Results

3.1. Annual variation in cone production

Annual cone production varied greatly between sampling years (p value < 0.0001) and between individual trees/sites within individual years (Fig. 2). All pairwise comparisons between years were significant, with relatively low cone production in 2006 (range: 5–350 cones/tree; mean \pm standard error (SE): 41.12 cones/tree \pm 13.13) and 2008 (range: 5–350 cones/tree; 50.00 cones/tree \pm 9.43), followed by moderate production in 2007 (range: 5–1000 cones/tree; mean \pm SE: 97.44 cones/tree \pm 9.46), and high cone production in 2009 (range: 5–1000 cones/tree; mean \pm SE: 196.82 cones/tree \pm 9.02).

Prediction of new cone production by the ΔT ($^{\circ}$) model explained 15% of the variance in cone production ($p < 0.001$). Including the effect of tree size, the predictor became the product of ΔT ($^{\circ}$) and length of the cone-bearing zone, which yielded an R^2 of 0.19 ($p < 0.001$).

3.2. Factors affecting cone and seed production

3.2.1. Total cone production

Two top-ranking models predicting black spruce cone production were retained (Table 3). For the most parsimonious model, the effects of age, DBH, and elevation on the total number of cones were highly significant (Table 4, $p < 0.0001$, conditional $R^2 = 0.54$, marginal $R^2 = 0.22$, $n = 1015$ trees). The second-most parsimonious model of black spruce cone

Table 3. Top-ranking models retained with a $\Delta AICc$ range of <2 from among the 95, 95, 95, 191, and 191 candidate models that were built for cone production, length of the cone-bearing zone, number of filled seeds per cone, filled seed proportion, and germination proportion, respectively, as assessed by Akaike information criterion (AICc).

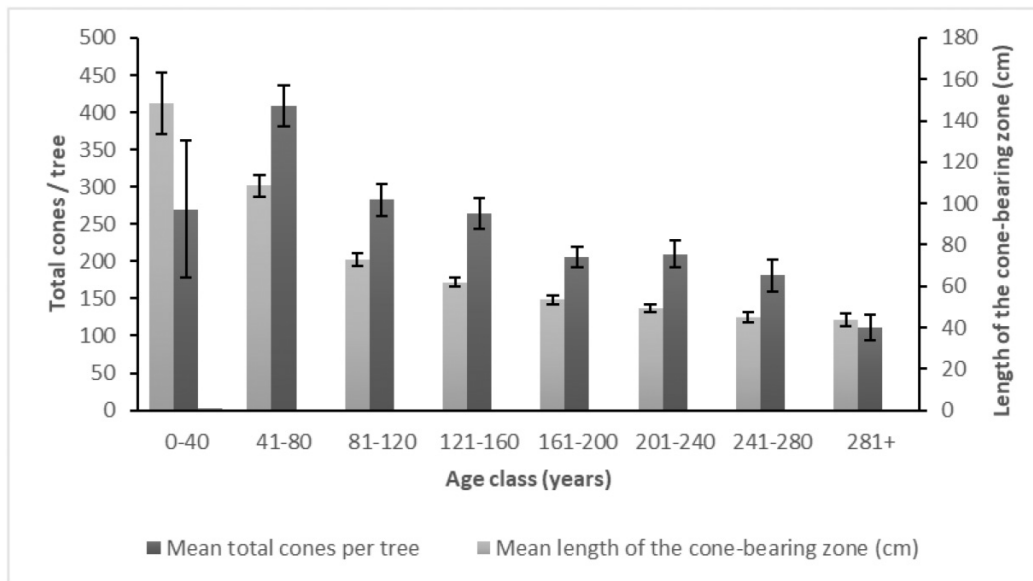
Response variable	Model rank	Models	K	AICc	$\Delta AICc$	AICcwt
Cone production	1	Age + DBH + Elevation	7	6527.23	0.00	0.51
	2	Age + DBH + Elevation + Available precipitation	8	6529.22	1.99	0.19
Length of the cone-bearing zone	1	Age + DBH + Growing season + Degree-days	8	4114.71	0.00	0.44
	2	Age + DBH + Growing season	7	4115.81	1.10	0.25
	3	Age + DBH + Available precipitation + Growing season + Degree-days	9	4116.67	1.96	0.17
Filled seeds per cone	1	Age + DBH + Elevation + Degree-days	8	2392.45	0.00	0.26
	2	Age + Height + Elevation + Degree-days	8	2393.06	0.61	0.19
	3	Age + Elevation + Degree-days	7	2393.19	0.75	0.18
Filled seed proportion	1	Age + DBH + Degree-days + Mean temperature + Seed mass	9	7382.35	0.00	0.23
	2	Age + DBH + Degree-days + Available precipitation + Mean temperature + Seed mass	10	7384.28	1.93	0.09
Seed germination proportion	1	Elevation + Seed mass	6	6184.82	0.00	0.12
	2	Elevation + Available precipitation + Seed mass	7	6185.37	0.54	0.09
	3	Age + Elevation + Seed mass	7	6185.98	1.16	0.06
	4	Elevation + Degree-days + Seed mass	7	6186.01	1.19	0.06
	5	DBH + Elevation + Seed mass	7	6186.46	1.64	0.05
	6	Age + Elevation + Available precipitation + Seed mass	8	6186.51	1.68	0.05

Table 4. Multiple regression results and estimated coefficient (standard error, SE) of the fixed effects for the most parsimonious model (rank 1) for cone production, length of the cone-bearing zone, number of filled seeds per cone, filled seed proportion, and germination proportion as a function of biotic and abiotic variables.

Response variable	Variable	Coefficient	SE	t value	p value	Conditional R^2	Marginal R^2
Cone production	Intercept	7.200	1.459	4.93	0.0007*	0.54	0.22
	Age (years)	-0.288	0.034	-8.48	<0.0001*		
	DBH (cm)	0.649	0.050	12.98	<0.0001*		
	Elevation (m)	-0.006	0.001	-4.20	<0.0001*		
Length of the cone-bearing zone	Intercept	2.357	1.148	2.05	0.0408*	0.61	0.27
	Age (years)	-0.171	0.011	-15.17	<0.0001*		
	DBH (cm)	0.115	0.016	7.09	<0.0001*		
	Growing season (days)	0.037	0.009	3.99	<0.0001*		
	Degree-days ($>5^\circ\text{C}$)	-0.001	0.001	-1.73	0.0849		
Filled seeds per cone	Intercept	1.720	0.389	4.43	0.0002*	0.52	0.13
	Elevation (m)	-0.001	0.000	-5.98	<0.0001*		
	Degree-days ($>5^\circ\text{C}$)	0.001	0.000	3.73	0.0002*		
	Age (years)	-0.011	0.004	-2.41	0.0161*		
	DBH (cm)	-0.011	0.006	-1.66	0.0972		
Filled seed proportion	Intercept	25.232	7.832	3.22	0.0020*	0.39	0.11
	Degree-days ($>5^\circ\text{C}$)	0.035	0.005	6.48	<0.0001*		
	Age (years)	-0.293	0.112	-2.62	0.0090*		
	Seed mass (g)	-0.677	0.313	-2.16	0.0310*		
	DBH (cm)	-0.342	0.160	-2.15	0.0322*		
	Mean temperature ($^\circ\text{C}$)	-1.763	0.848	-2.08	0.0476*		
Seed germination proportion	Intercept	62.148	9.324	6.67	0.0003*	0.66	0.05
	Elevation (m)	-0.035	0.007	-5.18	<0.0001*		
	Seed mass (g)	1.334	0.524	2.54	0.0112*		

Note: Conditional R^2 includes year and site as random factors; marginal R^2 excludes random factors. *, denotes a significant effect.

Fig. 3. Mean total cones per tree and mean length of the cone-bearing zone by age class observed in our study. Error bars represent standard error.



production also included available precipitation as a fourth predictor (Table 3). Multiple regression results for the second-most parsimonious model can be found in Supplementary Table S2. Examining mean observed total cones per tree by age class, there was an initial increase until 80 years, followed by a progressive decline (Fig. 3).

3.2.2. Length of the cone-bearing zone

Three top-ranking models predicting the length of the cone-bearing zone in black spruce were retained (Table 3). For the most parsimonious model, the effects of age, DBH, and growing season duration on the length of the cone-bearing zone were highly significant, and GDD approached significance (Table 4; $p < 0.0001$, conditional $R^2 = 0.61$, marginal $R^2 = 0.27$, $n = 996$ trees). The second-most parsimonious model included age, DBH, and growing season duration as predictor variables, whereas the third included age, DBH, available precipitation, growing season duration, and GDD as predictor variables (Table 3). Multiple regression results for the second- and third-most parsimonious models can be found in the Supplementary Table S3. Examining mean observed length of the cone-bearing zone per tree by age class, the greatest length was observed in the youngest age class, followed by a progressive decline in subsequent classes (Fig. 3).

3.2.3. Filled seeds per cone

Three top-ranking models predicting the number of filled seeds per cone were retained (Table 3). For the most parsimonious model, the effects of elevation and GDD on the number of filled seeds per cone were highly significant, age was significant, and DBH approached significance (Table 4; $p < 0.0001$, conditional $R^2 = 0.52$, marginal $R^2 = 0.13$, $n = 1014$ trees).

All top-ranking models included age, elevation, and GDD as predictor variables, the second with tree height replacing DBH. The third included only age, elevation, and GDD (Table 3). Multiple regression results for the second- and third-most parsimonious models can be found in the Supplementary Table S4.

3.2.4. Filled seeds proportion

Two top-ranking models predicting filled seed proportion in black spruce were retained (Table 3). For the most parsimonious model, the effect of GDD on filled seed proportion was highly significant, and age, seed mass, DBH, and mean temperature were significant (Table 4; $p < 0.0001$, conditional $R^2 = 0.39$, marginal $R^2 = 0.11$, $n = 856$ trees).

In addition to age, GDD, mean temperature, and seed mass, the second-most parsimonious model also included available precipitation as a predictor variable (Table 3). Multiple regression results for the second-most parsimonious model can be found in the Supplementary Table S5.

3.2.5. Seed viability

Six top-ranking models predicting seed germination in black spruce were retained (Table 3). For the most parsimonious model, the effect of elevation on seed germination was highly significant, and seed mass was significant (Table 4; $p < 0.0001$, conditional $R^2 = 0.66$, marginal $R^2 = 0.05$, $n = 673$ trees).

All top-ranking models always included elevation and seed mass as predictor variables. Two of the six included age as a biotic predictor variable, and one included DBH. The second- and sixth-most parsimonious models included available precipitation as an abiotic predictor variable, while the fourth included GDD (Table 3). Multiple regression results for

the second- through sixth-most parsimonious models can be found in the Supplementary Table S6.

For the most parsimonious model (rank 1) in each analysis (cone production, length of the cone-bearing zone, number of filled seeds per cone, filled seed proportion, and germination proportion), details on the relative strength of each independent variable in predicting the dependent variable using regression estimates can be found in the Supplementary Fig. S1.

4. Discussion

Black spruce is a major component of the North American boreal forest whose postfire regenerative potential relies entirely on its viable seed production. Our study represents an integrated analysis of the diverse factors controlling the sexual regenerative capacity of this species. Being a semi-serotinous species with pronounced seed years occurring every 2–6 years (Viereck and Johnston 1990; Messaoud et al. 2007), we found significant interannual variation in cone production per tree (Fig. 2), although compared with non-serotinous species the variation is quite muted (Koenig and Knops 2000). Assuming a functional relationship between weather and subsequent cone production, the ΔT model (Kelly et al. 2013; LaMontagne et al. 2020) explained only 15% of the variation, a fraction much lower than that obtained by LaMontagne et al. (2020) when they applied the model to non-serotinous *Picea glauca* and *Picea engelmannii* (with typically about 50% of the variation explained). However, LaMontagne et al. (2020) used stand-level cone crop production averages rather than individuals, where the bulk of the variation in production resides (Sirois 2000; Koenig et al. 2003). Given the moderate interannual variation seen here (typical of serotinous species: Messaoud et al. 2007; Lamontagne et al. 2021), the response of serotinous individuals to a weather cue must be more muted than with non-serotinous species, and so a lower proportion of explained variance is to be expected among species displaying some serotinitism. This is the first time the ΔT ($^{\circ}\text{C}$) model has been applied to a serotinous species; one wonders if this cue — the difference in temperature in the two summers prior to the crop — will turn out to be general for the many conifer species (essentially all but *Pinus* spp.) with a 2-year reproductive cycle.

Factors limiting the reproductive potential of black spruce in northernmost boreal forests remain poorly understood compared with the central and southern portions of its range. Therefore, although many of the same limiting factors may be at play, their order of importance may differ. Hustich (1966) suggested that a decrease in trees' regeneration capacity determines the zonation between the northern boreal forests and treeline. Supporting this, Sirois (2000) observed an inverse relationship between the percentage of filled seeds and germination and the regional variation in heat sum, although no south–north trend in cone crop was observed.

Considering the order of importance of significant limiting factors for the most parsimonious models in each of the five model groups, our results illustrate that for cone production and length of the cone-bearing zone, biotic variables such as tree age and DBH outweigh abiotic variables such as eleva-

tion, growing season length, and GDD. However, although biotic variables played a greater role, the indirect effects of climate on tree growth and associated fecundity cannot be discounted (Clark et al. 2021) as they directly affect site productivity. For the number of filled seeds per cone, the opposite trend was observed, with abiotic variables such as elevation and GDD outweighing the biotic variable tree age. For filled seed proportion, the abiotic variable GDD was most significant, followed by the biotic variables age, seed mass, and DBH, and finally the climatic variable mean temperature. For germination proportion, the abiotic variable elevation was most significant, followed by the biotic variable seed mass (Table 4; Supplementary Tables S2–S6). Seed mass was inversely correlated with filled seed proportion; conversely, seed mass was positively correlated with germination and establishment potential, due to the greater abundance of seed reserves before the germinant becomes fully rooted (Greene and Johnson 1998). It is important to note that although linear regression analyses found that the effects of seed mass were significant for both the proportion of filled seeds and viability, estimates of the relative impact of this explanatory variable on the dependent variable (Fig. S1, panels 4D and 5B) across its observed mass range reveal a practically non-existent effect, varying by only 0.005% for filled seed proportion and 0.009% for seed germination proportion. As observed by Messaoud et al. (2007), DBH was not a significant predictor of filled seed proportion or germination proportion. As argued by Sirois (2000), climatic limitations imposed by reduced heat sum in northern areas instead likely result in decreased success of gametophyte and embryo development, and possibly lower pollen viability. Projected increases in temperature therefore have the potential to directly and indirectly improve fecundity within our study area (Clark et al. 2021).

4.1. Comparison with Haavisto and Skeates (1995) and Skeates and Haavisto (1987)

To illustrate the potential differences in cone and seed production based on latitude, using the same age-class distribution, we compared our data on the number of seeds per cone (total and filled seeds), the number of cones per tree (current year, not total cones), and the number of seeds per tree (all data lumped), with combined current-year data from Haavisto and Skeates (1995) and Skeates and Haavisto (1987). These two studies summarize cone and seed yields from roughly 3500 black spruce trees sourced from unmanaged and managed stands across northern Ontario but located south of our study area (see fig. 1 in Skeates and Haavisto 1987). Although the authors mention the use of cleaned seeds, it is not specified whether this refers to filled seeds; therefore, we made a comparison using both total seeds and filled seeds per cone. Direct comparisons between current-year cones per tree and seeds per cone were possible. However, for comparison of seeds per tree, extrapolation was necessary since our data do not include seed counts per tree but instead seeds per cone. It was estimated by multiplying the mean number of cones (current year, not total cones) by age

Fig. 4. Comparison of current-year cones per tree with **Haavisto and Skeates (1995)** using a similar age-class distribution.

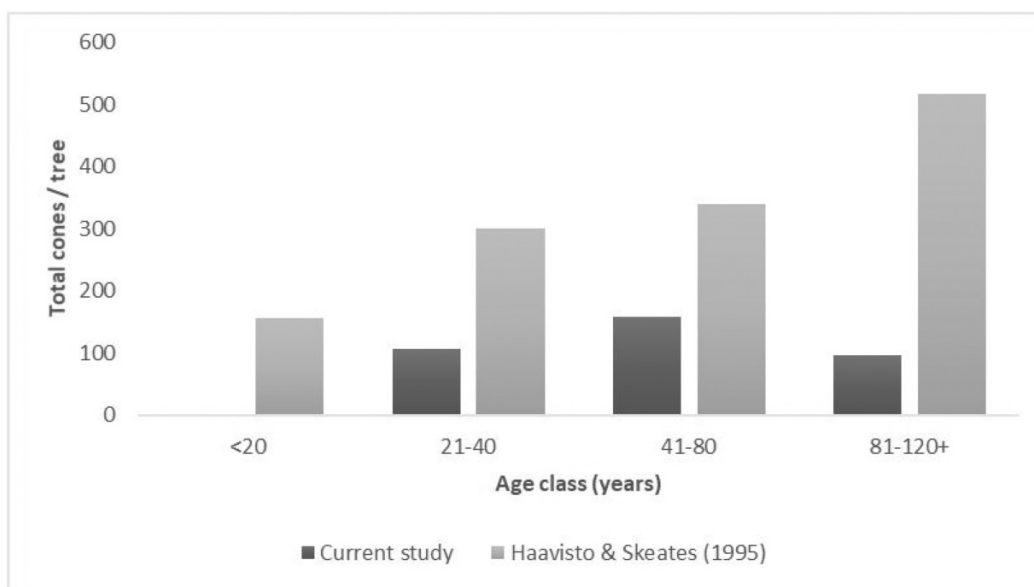


Table 5. Comparison of data on the number of seeds per cone (total and filled), the number of current-year cones per tree, and the number of seeds per tree (total and filled) between the current study and that of **Skeates and Haavisto (1987)** (S & H).

Age class	Current study (n)	Seeds/cone			Current-year cones/tree		Seeds/tree		
		S & H	Current study (all seeds)	Current study (filled seeds)	S & H	Current study	S & H	Current study (total seeds)	Current study (filled seeds)
21-40	11	22.70	14.71	9.83	350.00	107.27	8 050.00	1578.17	1054.07
41-80	171	24.10	8.98	5.27	460.00	158.13	12 700.00	1419.80	833.52
81-120	161	16.10	8.80	4.76	525.00	97.20	8 100.00	855.37	462.60
120+	671	N/A	6.87	3.28	N/A	94.97	N/A	652.90	311.05

class with the mean number of seeds observed per cone (both total seeds and filled seeds).

A significantly lower reproductive potential was observed when comparing our data on tree-level cone and seed production with that of **Haavisto and Skeates (1995)** (Fig. 4). The mean number of current-year cones produced by a tree was three to five times lower than that of **Haavisto and Skeates (1995)** (see fig. 3 in **Haavisto and Skeates 1995**), when examining a similar age-class distribution.

Next, we compared our data on the number of seeds per cone, the number of current-year cones per tree, and the number of seeds per tree (total and filled), with combined current-year data from **Skeates and Haavisto (1987)** (tables 1 and 3 in **Skeates and Haavisto 1987**), again using the same age-class distribution. In general, we observed a lower reproductive potential in our data set: 2–3 times lower total seeds per cone, 3–5 times lower current-year cones per tree, and a difference in total seeds per tree approaching one order of magnitude; when total seeds are replaced with filled seeds, the difference becomes even greater (Table 5).

Comparison of our data on cone and seed production with that of **Haavisto and Skeates (1995)** and **Skeates and Haavisto (1987)** from unmanaged stands in northern Ontario illustrates the potential contrasting effects of latitude on re-

productive potential. Estimates of seed counts (total and filled) per tree were made for comparative purposes only. Besides regional differences in climate and site-level differences in productivity and tree density (our data were gathered from more northern populations and across a wide range of site productivity and tree density), discrepancies observed (particularly for seeds per cone) could also potentially be affected by differences in sampling design and seed extraction methods between studies (**Skeates and Haavisto 1987; Haavisto et al. 1988**). The overall comparison nevertheless illustrates a significantly lower reproductive potential of northern black spruce populations compared with those located further south.

4.2. Resilience to fire

This species has one of the smallest ovulate cones among the conifers, and thus the proportionally thinner scales, the main barrier to heat penetration, only provide minor protection in an intense fire (**Splawinski et al. 2019b**). Black spruce compensates to some degree by limiting cone production to clusters of cones in the upper crown of older trees (**Black and Bliss 1980; Viereck and Johnston 1990; Greene et al. 1999**) where temperatures are lessened and the exterior cones in a cluster can provide some protection for interior cones. This

clustering retards heat penetration, thus maintaining the viability of seeds found in cones from interior of clusters (Splawinski et al. 2019b). Although Splawinski et al. (2019b) only examined a narrow range of cone-bearing zone lengths, tree ages, and tree sizes, all from a single mature black spruce stand following a low-intensity crown fire, we assume that low cone density within clusters and smaller clusters (e.g., young or over-mature trees, as illustrated in Fig. 2) and (or) higher intensity fires would significantly decrease available viable seed number following fires.

Maximum black spruce cone and seed production occurs between 100 and 200 years of age, with the main cone-bearing period extending to 250 years (Black and Bliss 1980; Viereck and Johnston 1990; Van Bogaert et al. 2015a; Clark et al. 2021). Our results for total cone production and the length of the cone-bearing zone (Fig. 3) suggest an even shorter temporal window in these high latitude stands.

In young black spruce stands, seed production is limited by the species-specific age of reproductive maturity. Black spruce growing on productive sites typically attains reproductive maturity at about 30 years (Viglas et al. 2013) but may require between 50 and 150 years to produce the seed supply necessary to adequately regenerate a stand following high-severity fire (Viereck and Johnston 1990; Viglas et al. 2013). The resilience of this species to fire is therefore significantly limited in juvenile stands, when the interval between successive stand-replacing disturbances is shorter than this initial regenerative temporal window (Payette and Delwaide 2003, 2018; Jasinski and Payette 2005; Johnstone and Chapin 2006; Girard et al. 2009; Johnstone et al. 2010b; Brown and Johnstone 2012; Pinno et al. 2013; Splawinski et al. 2019a). Presumably, warming could increase black spruce growth rates (D'Orangeville et al. 2018; Clark et al. 2021; Pau et al. 2021) and thus hasten the advent of reproductive maturity, increase cone production, and improve gametophyte and embryo development. However, warming could also create more severe and shorter fire interval and increase the frequency and duration of drought, which could decrease reproductive and regeneration potential (Brown and Johnstone 2012; Stevens-Rumann et al. 2018; Splawinski et al. 2019b; Clark et al. 2021). This interaction is not presently understood.

With the exception of Black and Bliss (1980) and Van Bogaert et al. (2015a, 2015b), little attention has been given to seed and cone production in over-mature and old-growth stands (>100 years). However, as illustrated by the results in this study and that of Van Bogaert et al. (2015a, 2015b), production declines as trees age (Fig. 3), in the low productivity conditions typical of northern forests, with productivity declining due to paludification (Simard et al. 2007), and due to the mortality of dominant stems.

Black spruce stands exhibiting limited reproductive potential are at greater risk of natural regeneration failure following fire and may result in the fragmentation of continuous forest cover, leading to changes in successional patterns and forest composition, and a potential shift from closed-crown forest to open lichen woodland (Sirois and Payette 1989; Sirois and Payette 1991; Girard et al. 2008, 2009; Côté et al. 2013; Splawinski et al. 2019a, 2019c; Baltzer et al. 2021; Cyr et al. 2021). Projections of a more frequent and intense

fire regime under climate change (Flannigan et al. 2005, 2009, 2013; Bergeron et al. 2010; Boulanger et al. 2014) will make both young and over-mature stands even more vulnerable to regeneration failure, although vegetation feedbacks may dampen the effect (Boulanger et al. 2017). Such a shift in disturbance regime therefore has the potential to decrease the overall resilience of black spruce to fire over time, leading to declines in forest productivity and potentially compromising regional wood production potential.

4.3. Study limitations

As outlined in the methods, individual sites and trees were only sampled once during the 4-year study period, and as illustrated in Fig. 1, annual sampling occurred in distinct regions rather than homogeneously over the entire study area. Therefore, overall results and comparisons made with data from Skeates and Haavisto (1987) and Haavisto and Skeates (1995) could be impacted by regional and interannual variations in black spruce cone production. However, due to the large annual sample size, we believe that our results painted an accurate portrait of the reproductive ecology of black spruce in northern cold forests.

5. Conclusion

Overall, our results illustrated that reproductive potential of black spruce varied significantly across our study area due to tree-level biotic variables such as age and DBH, and the regional variation in temperature and elevation. A decrease in cone production and length of the cone-bearing zone was observed in young, over-mature, and smaller (DBH) individuals, at higher elevations, and shorter growing season. The number of filled seeds per cone was positively influenced by the number of GDD, but inversely correlated with age, DBH, and elevation. For filled seed proportion, a positive relationship was observed with GDD, but age, DBH, seed mass, and mean temperature exhibited an inverse relationship. Seed viability exhibited a positive relationship with seed mass but an inverse relationship with age and elevation.

The results presented here on cone and seed production and viability can be used to improve model projections of short- and long-term forest regeneration and succession patterns in northern boreal forests exhibiting similar climatic limitations, thereby facilitating the development of sustainable forest management, restoration, and adaptive strategies aimed at maintaining forest resilience, cover, and productivity.

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Data availability

Data available upon request. Data generated or analyzed during this study are available from the corresponding author upon reasonable request. The data used in this study were collected by and belong to the Québec MFFP.

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Competing interests

The authors declare there are no competing interests.

Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjfr-2022-0092>.

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