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Black spruce (*Picea mariana*) seed availability and viability in boreal forests after large wildfires

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Abstract

Key message Black spruce (*Picea mariana* (Mill.) B.S.P.) has historically self-replaced following wildfire, but recent evidence suggests that this is changing. One factor could be negative impacts of intensifying fire activity on black spruce seed rain. We investigated this by measuring black spruce seed rain and seedling establishment. Our results suggest that increases in fire activity could reduce seed rain meaning reductions in black spruce establishment.

Context Black spruce is an important conifer in boreal North America that develops a semi-serotinous, aerial seed-bank and releases a pulse of seeds after fire. Variation in postfire seed rain has important consequences for black spruce regeneration and stand composition.

Aims We explore the possible effects of changes in fire regime on the abundance and viability of black spruce seeds following a very large wildfire season in the Northwest Territories, Canada (NWT).

Methods We measured postfire seed rain over 2 years at 25 black spruce-dominated sites and evaluated drivers of stand characteristics and environmental conditions on total black spruce seed rain and viability.

Results We found a positive relationship between black spruce basal area and total seed rain. However, at high basal areas, this increasing rate of seed rain was not maintained. Viable seed rain was greater in stands that were older, closer to unburned edges, and where canopy combustion was less severe. Finally, we demonstrated positive relationships between seed rain and seedling establishment, confirming our measures of seed rain were key drivers of postfire forest regeneration.

Conclusion These results indicate that projected increases in fire activity will reduce levels of black spruce recruitment following fire.

Keywords Seed rain, Non-linear relationships, Fire return interval, Combustion severity, Fire size, Postfire regeneration

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1 Introduction

Wildfire is the primary large-scale disturbance in the boreal forest where it is a major determinant of forest age structure, species composition, and carbon stocks and fluxes (Bond-Lamberty et al. 2007; Beck et al. 2011). As a result of a changing climate and associated warming and drying at high northern latitudes (Johannessen et al. 2016), the frequency of extreme fire weather is projected to increase (Wang et al. 2017), altering the historic fire regime outside the norms to which biota are adapted (Flannigan et al. 2009; Seidl et al. 2017). Consequently, an increase in the frequency of large, severe crown fires is projected through the twenty-first century (Wotton et al. 2017), leading to an increase in the mean annual area burned (Wang et al. 2022). Many of these predicted changes are already apparent; for example, annual area burned in Canada surpassed the 31-year average for 6 years of the 11-year period 2010–2020 (Canadian Forest Service 2018). Understanding the impacts of large, severe fires on the population dynamics of tree species is essential to predict the structure and composition of boreal forests and the ecosystem services that they provide.

Black spruce (*Picea mariana* (Mill.) B.S.P.) is one of the most widespread and abundant tree species in boreal forests of North America. This species is adapted to boreal fire regimes through its semi-serotinous cones which maintain an aerial seedbank in the tree crowns. Fire is the main trigger for seed release, which is relatively low in unburned trees (Zasada et al. 1992; Arseneault 2001). The majority of black spruce seed dispersal occurs in the first 2 years following fire (Charron and Greene 2002; Greene et al. 2013). This initial seed rain results in a large recruitment pulse (Greene et al. 1999), which supports black spruce self-replacement after fire (as reviewed in Johnstone et al. 2010). The supply of viable seeds is an important factor limiting postfire seedling establishment and subsequent patterns of stand development (Greene et al. 1999; Johnstone et al. 2004; Brown and Johnstone 2012; Day et al. 2022).

Following Whelan (1995), by “fire regime”, we mean the quantified characteristics of the fires that occur in a region, including frequency, size, intensity, severity, cause, season of burning, and type (i.e. ground, surface, or crown). Of these, increases in the severity, frequency, or size of fires could reduce both the rate and viability of postfire black spruce seed rain, thereby reducing seedling recruitment through several processes. First, high fire intensity or severity can increase canopy combustion and reduce recruitment by heat-induced damage to embryos within seeds or by partially or completely combusting the seedbank (Arseneault 2001; Johnstone et al. 2009; Splawinski et al. 2019). Second, because the production of viable seeds is positively related to tree

age and basal area (Greene and Johnson 1999; Viglas et al. 2013), we expect that increases in fire frequency should result in a higher proportion of younger stands burning; this would tend to reduce postfire seed availability and recruitment in the long run. Third, as fire size increases, the distances from burned to unburned areas on the perimeter of or within the burn may also increase. Although seed fall rates from unburned black spruce are thought to be relatively low, and mean seed dispersal distance is also low (Payandeh and Haavisto 1982; McCaughey et al. 1986), the contribution from these sources may not be negligible. For example, Johnstone et al. (2009) found significant decreases in seed rain with distance from unburned edges for black spruce in interior Alaska. Therefore, an increase in fire size may reduce postfire seed availability and recruitment rates.

Environmental constraints may also mediate patterns of seed rain following fire via site productivity. For species with an aerial seedbank, such as black spruce, the size of the seedbank is positively correlated with site productivity (Greene and Johnson 1999; Turner et al. 2007). Conditions that lead to decreased black spruce productivity can also reduce postfire recruitment rates (Harper et al. 2005). For example, productivity and hence seed availability are expected to be highest on mesic sites (i.e. sites with moderate soil moisture), where moisture and/or nutrient limitations are less acute than on very dry or very wet sites (Bridge and Johnson 2000).

In 2014, wildfires burned 2.85 million hectares of forest in the NWT (Walker et al. 2018b); this was the largest annual area burned on record for the territory (Canadian Interagency Forest Fire Centre 2014). These wildfires provided an opportunity to assess the implications of a changing fire regime for postfire black spruce regeneration under conditions that, however extreme relative to the recent historical record, may be indicative of what may be expected later in this century (Wang et al. 2022). Based on the current state of knowledge, we hypothesized that higher levels of total black spruce seed rain and viability would occur at burned locations that (i) have relatively low levels of canopy combustion; (ii) have experienced longer fire-free intervals (i.e. older stand ages); (iii) are closer to unburned edges; (iv) have higher black spruce productivity; (v) have greater prefire basal area of black spruce; and (vi) have moderate soil moisture conditions (mesic). To test these hypotheses, we established a network of 250 seed traps deployed in 25 plots within three large 2014 fire scars in the Taiga Plains ecozone in the NWT (Fig. 1). This work will help support predictions of future responses and regeneration trajectories of boreal tree species to ongoing changes in fire activity.

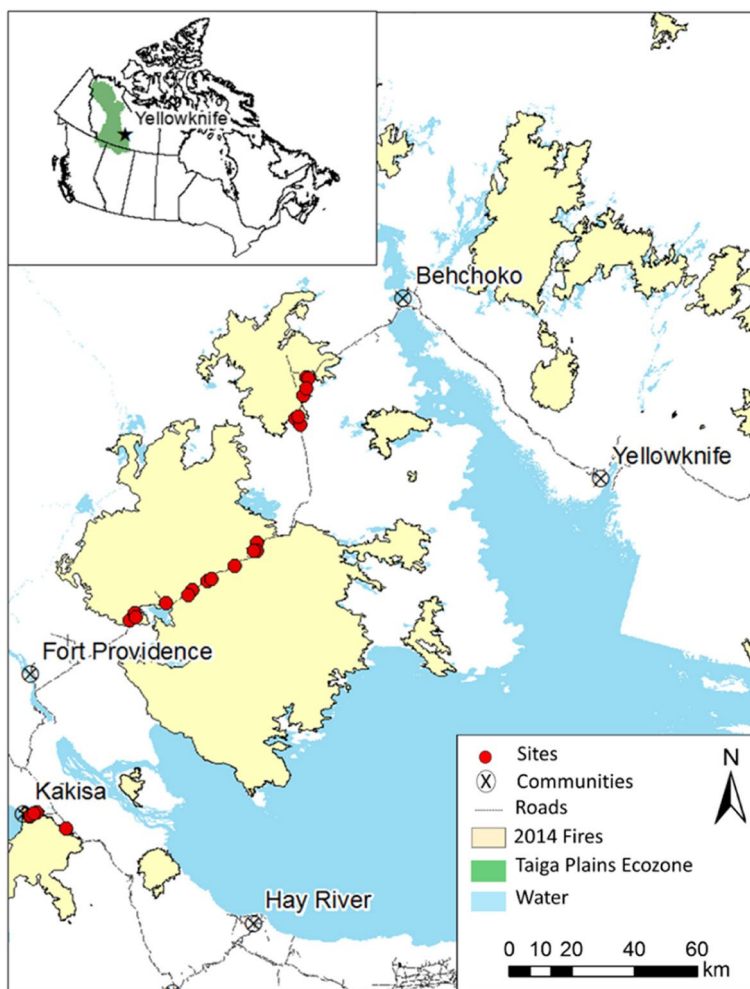


Fig. 1 Locations of black spruce-dominated sampled plots that burned in 2014 and where seed traps were deployed, and seedling counts performed. Plots are located in three burn complexes (yellow shading) along the road corridor between Behchoko and Hay River, Northwest Territories, Canada and are within the Taiga Plains ecozone (green shading in the inset)

2 Material and methods

2.1 Study region

This study took place in the Taiga Plains ecozone (Ecosystem Classification Group 2007) in the NWT, Canada (Fig. 1). The Taiga Plains is 45% forested, 32% wetlands/waterbodies, and 23% barren lands and grasslands (Environment and Natural Resources 2015). Forests are composed of closed to open canopies of mixed and pure stands of black spruce, jack pine (*Pinus banksiana* Lamb.), white spruce (*Picea glauca* (Moench) Voss), trembling aspen (*Populus tremuloides* Michx.), and paper birch (*Betula papyrifera* Marshall and *Betula neoalaskana* Sarg.). The Taiga Plains ecozone is mainly flat with extensive peatland coverage, level to undulating uplands, and is underlain by glacial till (Ecosystem Classification Group 2007). This region is within the zone of

discontinuous permafrost (Heginbottom et al. 1995). Mean annual air temperature (1981–2010) for the Yellowknife and Hay River weather stations was $-4.3\text{ }^{\circ}\text{C}$ and $-2.5\text{ }^{\circ}\text{C}$, respectively (Environment Canada 2017). The mean January and July air temperatures were -25.6 and $17.0\text{ }^{\circ}\text{C}$ for Yellowknife and -21.8 and $16.1\text{ }^{\circ}\text{C}$ for Hay River. Mean annual precipitation (1981–2010) was 289 mm for Yellowknife and 336 mm for Hay River (Environment Canada 2017).

2.2 Estimation of seed rain

Seed rain was measured at 25 black spruce-dominated plots within three burn scars (Fig. 1). We selected burned plots from a larger set of plots with road access to represent areas that were black spruce-dominated

before fire and captured gradients of fire severity and site drainage (Walker et al. 2018a). Each plot was a 2 × 30 m belt transect. At each plot, 10 traps were positioned at 3 m intervals along the transect (Figure 5 in Appendix) and secured with a large nail in each corner (250 traps in total). Traps were rectangular garden flats (52 cm × 22.5 cm) with drainage holes, lined with synthetic turf to trap the seeds. Turf was approximately 6 mm high and was used to prevent seeds from being blown out of traps by wind (Zasada et al. 1979); this design follows Johnstone et al. (2009). Traps were deployed in June 2015, and the order of deployment and collection was consistent for each sampling period to standardize sampling lengths. Seed traps were left out from June 2015 to August 2016 and emptied three times: first summer after fire (late June to late August 2015), second winter after fire (late August 2015 to mid-May 2016), and second summer after fire (mid-May 2016 to late August 2016). The timing of these collections was meant to ensure that seeds were not left in the field too long which could compromise viability. Upon collection, the contents of each seed trap were stored on ice in the field, frozen at a base camp in Fort Providence to prevent germination, and then shipped by air in coolers to Wilfrid Laurier University. In the lab, seeds from each trap were separated from organic debris, classified by tree species, and the total number of seeds by species per trap was recorded, providing an estimate of total seed rain per trap. Sorted seeds were stored at −2 °C until germination trials. There was no evidence of seed predation in the field or of fungal infection in the field or the lab.

The number of viable black spruce seeds was measured per trap, following Leadem et al. (1997). Seeds were surface disinfected by immersing in 3% H₂O₂ for 5 min, rinsed three times with de-ionized water, and then stratified at 4 °C for 3 weeks. Seeds were placed on moist filter paper in parafilm-sealed Petri dishes to germinate in a greenhouse for 21 days. Greenhouse photoperiod and temperature were 16/8 h day/night and 23/19 °C day/night, respectively. Seeds from each trap and period were germinated in separate petri dishes. Dishes were checked daily to ensure sufficient moisture, and water was added as necessary. Germinants were counted after 21 days. No seeds were lost to fungal infection or rot over the course of the germination trials. Viability of a subsample of ungerminated seeds (up to 10 seeds per sample) was assessed by sectioning and staining with tetrazolium chloride following (Leadem 1984) (see Appendix for additional details). We detected no viable ungerminated seeds, indicating that our germination assay was a good estimate of seed viability.

2.3 Plot-level attributes

We measured or calculated the following variables at each plot: soil moisture class, distance to the nearest unburned edge, time after previous fire in years (stand age), tree productivity index, canopy combustion, pre-fire standing black spruce basal area (m² ha⁻¹), density of prefire black spruce stems, and postfire black spruce seedling counts. Plot soil moisture class was assessed in the field following Johnstone et al. (2008). Our plots fell within three moisture categories: wet (mesic-subhygric, $n = 8$), with considerable surface moisture associated with depressions or concave toe slopes; mesic ($n = 7$), with moderate surface moisture on flat terrain or shallow depressions, including toe slopes; and dry (mesic-subxeric, $n = 10$), with less surface moisture on flat to gently sloping terrain. To estimate distance from the centre of each plot to the nearest unburned edge, we found the nearest edge by helicopter and took GPS coordinates while directly overhead.

All prefire trees that reached breast height (1.3 m) were identified, and diameter at breast height (DBH) measured within the 2 m × 30 m belt transect. Trees that were alive prefire consistently retained their bark, and there was no combustion of the bole allowing for distinction between trees that were standing dead prefire and those that were alive prefire. Basal area of each tree in the transect was calculated as $BA = \pi (DBH/2)^2$, and plot basal area was estimated by summing stem basal area over all black spruce stems within plots. We used standing black spruce basal area rather than total black spruce basal area (standing + downed) as a predictor variable in the models because standing basal area was more strongly related to total seed rain than was total black spruce basal area (data not shown), supporting previous findings (Johnstone et al. 2009). From this, we could also determine prefire stem density (stems ha⁻¹) for the stand and for each species individually.

Canopy combustion for each tree measured within this transect was categorized in the field on a four-point scale: 0 — alive (no combustion); 1 — low combustion (only needles combusted); 2 — moderate combustion (many small branches remaining); and 3 — high combustion (only central trunk and branch stubs remaining). We used the modal value of tree-level canopy combustion for black spruce trees within plots as our plot-level measure of canopy combustion.

Stand age at time of burning in 2014 (i.e. time after previous fire) was determined at each plot using tree ring counts. Five trees representative of the size and species of trees found before the fire in each plot were determined by taking either a cross-sectional sample (tree disk) or an increment core as close to the base as possible. Tree disk and core samples were sanded with a progressively finer

grit until all rings were visible. The samples were then scanned and rings counted using Cybis CooRecorder v.7.8 (Larsson 2006) or WinDendro 2009 (Regent Instruments, Quebec City, Quebec, Canada). Tree ages within a plot were inspected for clustering, since it was expected that tree age would cluster around the date of postfire recruitment. When most trees (> 50%) fell within 10–20 years of a central date, we assumed this to indicate the most recent fire, and the age of the oldest tree in the cluster was used to represent stand age (see Walker et al. 2018a); 21 of 25 plots showed this clustered age distribution. In the absence of such clusters, we used the age of the oldest stem to represent stand age.

We used an index derived from tree size and age as a proxy for average tree productivity within a plot. Tree-level productivity was estimated as the deviance from a linear regression of basal diameter versus tree age for our sample of black spruce trees aged using basal ring counts described above. Trees with a positive or negative deviation were interpreted as indicating relatively above or below average growth, respectively, for their age. The mean of tree-level deviances for each plot was calculated to produce a plot-level productivity index.

2.4 Estimation of total seedling recruitment

Total seedling recruitment was sampled in five 1 m² vegetation sampling quadrats spaced at 6 m intervals along one transect in each plot (Figure 5 in Appendix). Seedling counts took place in June 2016, 1 year after our seed traps were established (Table 1), approximately 2 years postfire. The seedling counts reflected cumulative black spruce regeneration from immediately postfire, up to the date of seed trap deployment, and continuing past the end of the second seed trapping period.

2.5 Statistical analysis

All statistical analyses were performed using R version 3.6.2 (R Core Development Team 2017). Data were organized, and graphs were created using tidyverse,

plyr, and ggplot2 R packages. All traps were established within black spruce-dominated plots, and most trapped seeds were black spruce (see Section 3), so this was the only species modelled. Traps that were directly below the cone ball of a fallen black spruce tree had abnormally high seed counts and were excluded from analyses. Traps that were lost or destroyed in one or more of the three collection periods were also excluded. Our total sampling effort was 247 traps within 25 plots across the three sampling periods. For analysis, we summed trap-level seed counts in each trap across the three sampling periods, yielding total seed counts per trap over 60 consecutive weeks postfire. Data are available in Baltzer et al. (2020) and Reid et al. (2022).

We tested our hypotheses of factors affecting total number of seeds and viability by fitting two generalized linear or generalized linear mixed-effects models using lme4 R package (Bates et al. 2015). First, we modelled the total number of seeds per trap as overdispersed count data (model 1) using a generalized linear mixed effects model with a negative binomial distribution, logarithmic link, and a random intercept for plot to account for nonindependence of traps within plots. We included an offset term of $\log(\text{trap area} \times 60)$, where trap area is 0.117 m² and 60 is the total number of weeks of the three collection periods. With this offset, the model predicts mean seed-fall rates in units of seeds m⁻² week⁻¹. We used package lme4 (Bates et al. 2015) to fit this model. Model diagnostics testing for outliers, zero inflation, and overdispersion was performed using package DHARMA (Hartig 2020); these tests showed that model assumptions were not violated. Marginal R^2 (fixed effects only) and conditional R^2 (fixed and random effects) were calculated using package MuMIn (Bartoń 2019). Second, we modelled seed viability as the probability of germination per trap (model 2) using a binomial generalized linear mixed effects model with logit link and a random intercept for plot. The response variable was the proportion of viable seeds per trap over the three sampling periods. Only data from traps with a nonzero total seed counts were included ($n = 238$). We fitted model 2 using R package lme4 (Bates et al. 2015), with diagnostics and R^2 values derived as per model 1. For both models, predictors included distance to nearest unburned edge, standing black spruce basal area, stand age, plot productivity index, plot moisture class, and canopy combustion. Continuous predictors were standardized to a mean of zero and standard deviation of one, so that estimated coefficients and effect sizes were comparable across predictors. Moisture class was represented as a three-level factor using treatment contrasts, with the mesic class as the reference level. We characterized

Table 1 Summaries of continuous predictor variables measured in the 25 study plots 1 year after the 2014 fires. All plots were established in black spruce-dominated forests in the Taiga Plains region of the Northwest Territories, Canada. See Table 4 for plot-level values. SE: standard error

	Mean ± SE	Range
Distance to unburned edge (m)	153.80 ± 11.38	17–710
Stand age (years)	103.07 ± 2.63	71–232
Tree productivity index	$1.0 \times 10^{-4} \pm 0.002$	−0.05–0.06
Standing black spruce basal area (m ² ha ⁻¹)	8.94 ± 0.41	0–23.53

canopy combustion as a two-level factor using treatment contrasts, with the moderate combustion class as the reference level. Predictors were not strongly pairwise correlated ($r < 0.50$). To account for possible nonlinearities in the total and viable seed rain response, we compared alternative full-saturated models including linear or spline adjustments (with up to two degrees of freedom) for each continuous predictor. We selected the adjustment with the lowest Akaike Information Criterion (AIC) score as being the best supported model corrected for parsimony (Crawley 2013).

To test that our seed trap data were informative with respect to black spruce, we modelled black spruce seedling counts measured 2 years postfire. The seedlings were counted in five 1 m² quadrats along one 30 m transect at each of the sites where seed traps were established (see Day et al. 2022 for full details of seedling counts). It was not possible to pair seed traps with vegetation quadrats within sites, so we calculated plot-level means of black spruce seedlings per quadrat and of total and viable black spruce seeds per trap, standardized to counts per square meter. Equivalently, the three counts were standardized to sample mean densities. We then regressed seedling density against total seed density (model 3a) and viable seed density (model 3b). We used linear models with spline adjustments of up to three degrees of freedom to model possible nonlinear responses. We selected the adjustment with the lowest AIC score to determine the appropriate spline

adjustment. We calculated raw and adjusted R^2 for the selected models.

3 Results

The 247 seed traps collected a total of 3814 seeds over the 60 weeks. Most seeds (95%) were black spruce. Other tree species captured were trembling aspen (3.62%), jack pine (0.87%), and paper birch (0.16%). The mean number of black spruce seeds collected was 14.6 seeds per trap (range: 0–57, Table 4 in Appendix). Given the trap area of 0.117 m² and 60-week collection period, the mean black spruce seed rain was 2.2 seeds m⁻² week⁻¹. Of the 247 traps, 238 (74.8%) had nonzero total black spruce seed counts.

Overall, we found there were different significant predictors for total and viable seed rain. Total black spruce seed rain (scaled to m² week⁻¹; model 1) was significantly associated with standing black spruce basal area (Table 2; Fig. 2). Model selection supported a hump-shaped relationship between seed rain and basal area (spline adjustment of two degrees of freedom) rather than a linear relationship (Table 5 in Appendix). Total seed rain increased with basal areas up to ~12 m² ha⁻¹, after which this increase did not continue in plots with larger basal areas. There was also a significant positive association of total seed rain with the productivity index. Plots with moderate combustion appeared to have greater total seed rain compared to high combustion, but this factor was not significant. There were no significant effects for time

Table 2 Negative binomial mixed-effects model of total black spruce seed rain (seeds m⁻² week⁻¹; model 1) and binomial mixed-effects model of black spruce seed viability (germination probability; model 2) with estimated coefficients, standard errors (SE), p -values and variance explained by marginal and conditional R^2 . Significant predictors are presented in bold. Mesic plots were the reference level of the contrast against which both wet and dry plots were compared. Moderate combustion was the reference level of the contrast of moderate vs. high combustion

Predictors	Model 1: total seed rain			Model 2: seed viability		
	Coefficient est.	SE	P	Coefficient est.	SE	p
(Intercept)	-0.39	0.34	0.259	-1.71	0.17	<0.001
Stand age	0.02	0.12	0.885	0.21	0.09	0.018
Combustion (high)	-0.26	0.23	0.251	-0.32	0.17	0.060
Productivity index	0.21	0.11	0.046	-0.00	0.10	0.978
Basal area (1st degree)	2.25	0.52	< 0.001	0.03	0.09	0.767
Basal area (2nd degree)	-0.48	0.46	0.301			
Moisture (wet)	0.23	0.23	0.307	0.66	0.19	0.001
Moisture (dry)	0.30	0.26	0.250	-0.04	0.19	0.817
Distance to edge (1st degree)	-0.10	0.10	0.354	-1.02	0.48	0.033
Distance to edge (2nd degree)				1.03	0.42	0.014
Random effects						
σ^2	0.26			3.29		
Marginal R^2 /conditional R^2	0.42/0.65			0.23/0.29		

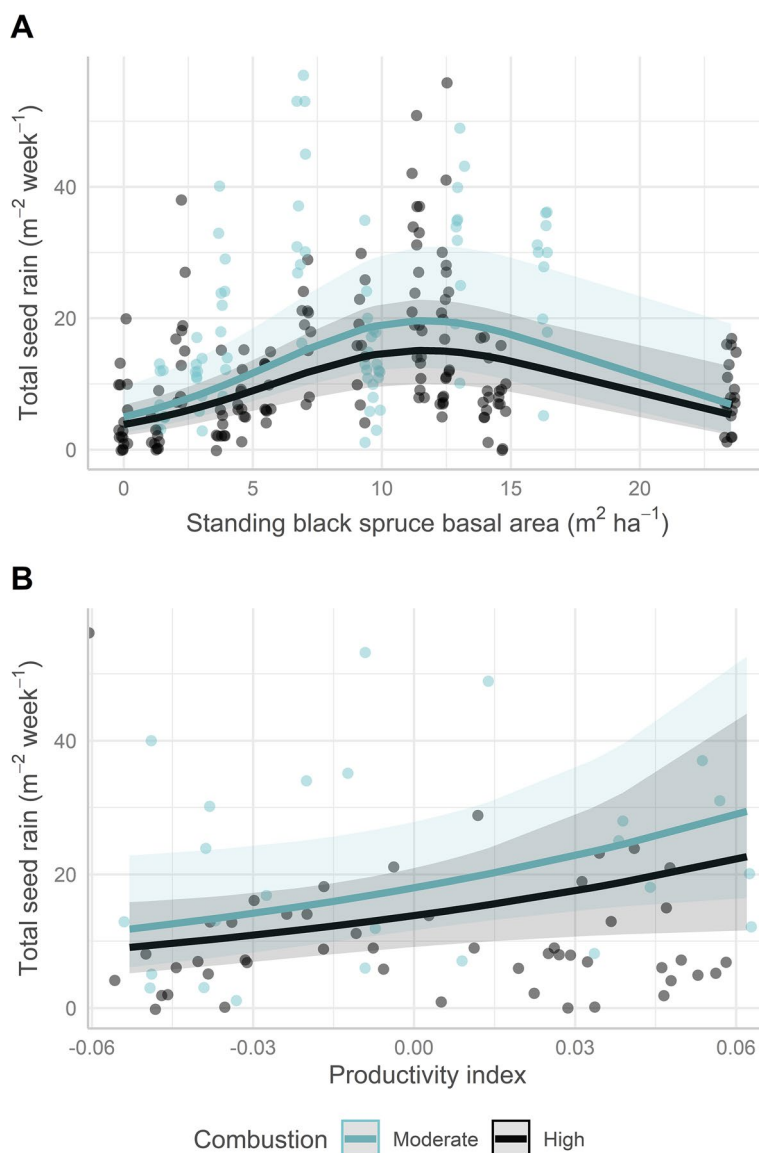


Fig. 2 Predicted total black spruce seed rain as a function of prefire black spruce basal area (**A**) and productivity index (**B**), at two canopy combustion levels (model 1, Table 2). Shaded areas represent 95% confidence intervals. Values of other continuous covariates were held constant at their mean or reference levels

after fire, site moisture class, or distance to edge, on total seed rain. Model 1 R^2_m (marginal R^2 ; fixed effects only) was 0.42, and the R^2_c (conditional R^2 ; fixed and random terms) was 0.65.

Our germination trials showed that 498/3637 black spruce seeds were viable (13.7%). The number of viable seeds per trap ranged from 0 to 15 (mean \pm standard deviation: 2.02 ± 2.29 , Table 4 in Appendix), and the proportion of viable seeds per trap ranged from 0 to 1.0 (mean \pm standard deviation: 0.17 ± 0.21). Germination probability increased with stand age, but

not with standing black spruce basal area (model 2; Table 2, Fig. 3). Model selection supported a hump-shaped relationship between seed viability and distance to edge (spline adjustment of two degrees of freedom) rather than a linear relationship (Table 5 in Appendix). Thus, seed viability was greater in plots closer to an unburned edge ($\sim 100\text{--}200$ m; Fig. 3B). Soil moisture was also a significant predictor with seed viability being highest on wet compared to mesic or dry sites. There was a marginally significant negative effect of canopy combustion on seed viability with higher

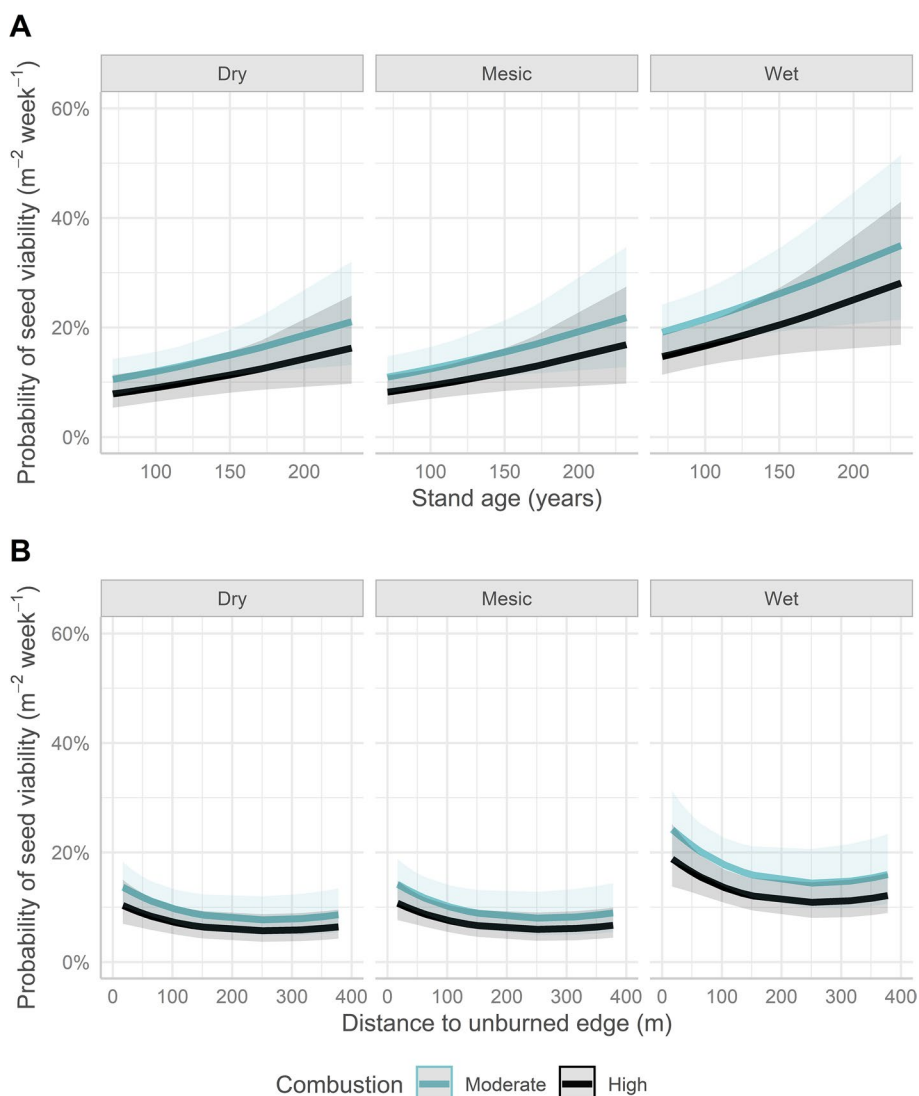


Fig. 3 Predicted probability of black spruce seed viability as a function of prefire stand age (**a**) and distance to unburned edge (**b**) at two levels of canopy combustion levels and three levels of moisture regime (model 2; Table 2). Values of other continuous covariates were held constant. Shaded areas represent 95% confidence intervals

canopy combustion trending toward lower seed viability compared to moderate combustion. Model R^2_m for the seed viability model (marginal R^2 ; fixed effects only) was 0.23, and the R^2_c (conditional R^2 ; fixed and random terms) was 0.29.

The analysis of plot-level seedling regeneration showed that density of black spruce seedlings was positively related to both total and viable seed rain (model 3; Table 3, Fig. 4). However, the variation explained by the model including total seed rain as a predictor was higher than the model including viable seed rain (Table 3). Both models displayed a concave relationship (spline adjustment with 2 degrees of freedom, Table 6 in Appendix);

seedling densities increased with total or viable seed rain up to ~ 200 seeds m^{-2} or ~ 20 seeds m^{-2} , respectively, after which further increases in both seed rain variables led to no further significant increases in seedling establishment (Table 3; Fig. 4).

4 Discussion

Our models of black spruce seed rain and seed viability in boreal forests of the Northwest Territories (NWT), Canada, confirmed expected positive relationships between standing black spruce basal area and postfire total seed rain. However, these relationships were non-linear: this increase in postfire seed availability is not

Table 3 Linear models of plot-level black spruce seedlings per m² (model 3) against total (A) and viable (B) seeds per m² showing estimated coefficients, standard errors (SE), *p*-values, and variance explained by marginal and conditional R squared. Significant predictors are in bold

Predictors	Estimates	SE	<i>p</i>
A			
(Intercept)	-0.07	2.17	0.975
Total seeds (1st degree)	19.22	5.76	0.003
Total seeds (2nd degree)	-6.09	3.41	0.089
R ² /R ² adjusted	0.43/0.38		
B			
(Intercept)	2.16	2.25	0.349
Viable seeds (1st degree)	11.62	5.55	0.049
Viable seeds (2nd degree)	-6.30	4.71	0.196
R ² /R ² adjusted	0.26/0.18		

maintained at high basal areas. Contrary to our expectations, high canopy combustion was not a significant predictor of total seed rain and only had a marginal negative effect on postfire seed viability. As expected, seed viability rates were greater in older sites and closer to unburned edges and, surprisingly, were higher in wet than in dry or mesic sites. Finally, seedling densities were related to both total and viable seed rain, with the highest levels of recruitment corresponding with moderate levels of total and viable seed counts, suggesting that beyond a certain level of seed rain, other factors become limiting to establishment.

The concave relationship between site black spruce basal area and total seed rain has not previously been reported to our knowledge. Basal area has been shown to be a principal mechanism supporting black spruce self-replacement after fire across North America (Greene and Johnson 1999; Johnstone et al. 2009; Splawinski et al.

2016). In serotinous conifers, greater prefire basal area translates into larger aerial seedbanks (Greene and Johnson 1999), thus supporting ample seed rain following fire. This is an example of a positive neighbourhood effect that promotes stand self-replacement and regeneration after disturbance (Frelich and Reich 1999), which may be particularly important for seeds with low dispersal distances such as black spruce. Our findings support this mechanism; however, our data also suggest that when basal area gets too high, reproductive outputs can be negatively impacted. The lack of continued increase in seed rain at basal areas greater than ~12 m² ha⁻¹ could be due to negative effects of competition on reproductive outputs (e.g. Rossi et al. 2012). To evaluate this, we investigated relationships between our site productivity index, density of black spruce stems, and basal area (Figure 6 in Appendix). While stem density was significantly negatively correlated with the productivity index, a concave relationship existed between basal area and both stem density and site productivity. This meant that the plots with highest productivity had both moderate stem densities and basal areas, which corresponded with the plots with the greatest reproductive outputs (Fig. 2). It is noteworthy that our range of sampled sites included many with high basal areas compared to other studies (range: current study, 1.4–37.1 m² ha⁻¹; Johnstone et al. 2009, 0.1–28 m² ha⁻¹; Zasada et al. 1979, 1.8–6.9 m² ha⁻¹), which may explain why a concave response was not detected in previous studies. Thus, our study has added knowledge of basal area relationships in seed rain that have not been captured previously.

Although seeds may be directly destroyed by high severity fire in the tree canopy (Arseneault 2001; Splawinski et al. 2019) leading to reduced total or viable seed rain, we did not find evidence of reduced total seed rain in the present study. However, our models indicate that severe canopy combustion marginally reduced seed

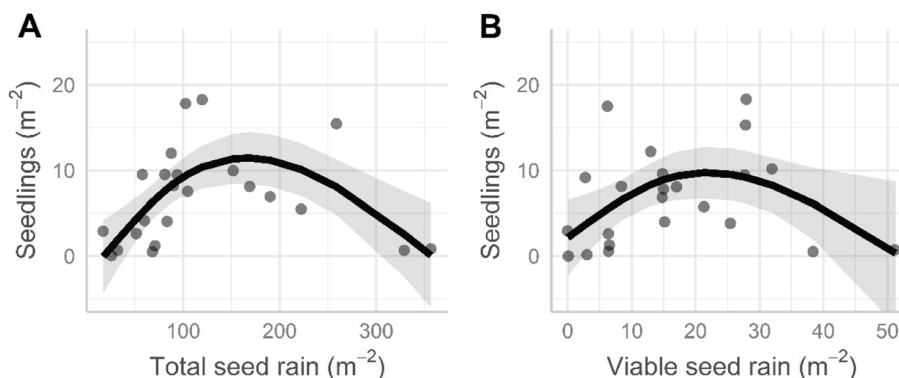


Fig. 4 Predicted black spruce seedlings (m⁻²) as a function of total seed rain (A) and viable seed rain (B) for 25 plots. Shaded areas represent 95% confidence intervals. Model fits are presented in Table 3

viability. This finding supports previous studies from other regions in North America that greater combustion results in lower seed viability either at the individual level (Johnstone et al. 2009) or in response to within-crown variability in combustion (Splawinski et al. 2019). Other studies have also found that severe canopy combustion may reduce viable seed rain with no apparent impact on total seed rain (e.g. Johnstone et al. 2009), suggesting that loss of seed viability due to heating associate with greater canopy combustion may be a more common mechanism of reduced reproductive potential than complete combustion of seeds or cones.

The positive relationship between stand age and seed viability suggests that shortened fire return intervals may negatively impact postfire regeneration of black spruce in the NWT. Our study provides an underlying mechanism for previous findings of reduced black spruce seedling density in areas experiencing more frequent stand replacing fires in the NWT (Whitman et al. 2019, Day et al. 2022) and Yukon (Brown and Johnstone 2012). With the increased fire activity predicted for the boreal biome (de Groot et al. 2013; Wang et al. 2022), the average age at which stands burn must necessarily decrease, which will have wide-ranging impacts in these forests. As stands age, the accumulation of black spruce basal area slows and can even decrease as uneven age- and size-class structures develop (Miquelajauregui et al. 2016). This decoupling between age and basal area may explain the differential responses we observed for total and viable seed rain to these predictors. Specifically, our results suggest that basal area is an important determinant of total seed rain, but that the age of the stand is more relevant for determining how much of this seed will be viable, a critical component of regeneration.

The greater viability rate of seeds on wet plots was unexpected. Wet sites with thick organic soils are stressful locations from a growth perspective, meaning trees may increase allocation to reproductive output. Indeed, greater reproductive efforts in trees are favoured in response to other resource-related mechanisms, such as shade (Paz and Martínez-Ramos 2003; Quero et al. 2007) and intraspecific resource competition (Lebrija-Trejos et al. 2016). Indirectly, it is possible that differences in fire behaviour and cone heating amongst plot moisture classes not captured in our canopy combustion estimates explain this finding. Other things being equal, elevated soil moisture is associated with lower rates of fuel consumption (Forestry Canada Fire Danger Group 1992) and hence with lower fire intensity. Lower fire intensity would reduce scorch height (Van Wagner 1973), and presumably the amount

of heating experienced by cones, thereby helping to maintain seed viability.

Distance to unburned edge was a significant positive predictor of seed viability, but not of seed rain. These findings align with previous studies of seed rain in interior Alaska (Johnstone et al. 2009). We found that seed viability declined up to distances of ~100–200 m from an edge, after which it remained constant (Fig. 3B); this is consistent with the previously measured dispersal distances of approximately 100–120 m (Payandeh and Haavisto 1982; McCaughey et al. 1986). This implies that contributions of viable seed from relatively distant unburned sources can affect regeneration of this species. Large fires are common in the NWT and are expected to become even more common under climate warming (Amiro et al. 2004; Burton et al. 2008). Our findings suggest a moderate negative impact of large fire complexes on postfire regeneration in black spruce.

It is notable the models of total seed rain and of seed viability identified different significant covariates. Seed rain and viability are only the first of multiple limiting factors in postfire regeneration; actual germination of viable seed on suitable substrate, seedling establishment, and survival to maturity is also important (Greene et al. 2007; Brown et al. 2015). The concave relation of seedlings to seed rain implies that seed supply is not limiting on all sites. Our results address the initial stages of this complex chain of processes and provide novel information regarding postfire regeneration in the extensive black spruce forests of the NWT. The implications are that regeneration depends on fairly local properties of stand structure (i.e. both stand age and basal area), on stand-level moisture/drainage, and also on the level of canopy combustion, which interacts with stand structure in boreal black spruce forests (Miquelajauregui et al. 2016). Vegetation dynamics models that do not consider these local phenomena may be inadequate to forecast future forest conditions in these regions.

Our data and models are of ecological relevance insofar as they inform on drivers of black spruce regeneration postfire. However, we may also have missed temporal variation in seed rain and seed viability due to constraints in our experimental design. The period of postfire seed dispersal from black spruce is brief; a large majority of seed rain occurs in the first two growing seasons following fire (Charron and Greene 2002), resulting in a large recruitment pulse (Greene et al. 1999). In addition, seeds released in the first months after fire may come preferentially from cones at the periphery of tree crowns. These seeds might have lower viability than later-falling seeds from more protected,

interior cones (Splawinski et al. 2019). Earlier seed trap deployment and more regular seed trap emptying would indicate the timing of release of the 'most' and 'least' viable seed and reduce seed loss or viability reduction by shortening the length of time seeds are left in traps. Data from earlier seed trap deployments might also reveal whether there is an absolute difference in number of seeds released from coneballs experiencing high vs. low combustion. To capture all postfire seed rain, traps would need to be deployed immediately after late-burning fires are extinguished by the onset of winter snow, which creates logistical challenges difficult to overcome in any study (e.g. Johnstone et al. 2009). By starting in June 2015, our study may have missed upwards of 50% of the total seed rain attributable to the 2014 fires (Greene et al. 2013). However, despite missing this early period of seed rain, our data show significant relationships between black spruce seedling establishment and both total and viable seed rain, suggesting that our estimates of seed rain are meaningful from an ecological perspective.

5 Conclusion

Our findings both support and extend previous work in the North American boreal forest showing that total and viable black spruce seed rain are driven by various combinations of standing basal area, distance to an unburned edge, stand age, and canopy combustion severity (Zasada et al. 1979; Arseneault 2001; Johnstone et al. 2009). Importantly, we also show the relevance of these measures for natural seedling establishment. Taken together, these results suggest that black spruce recruitment after fire may decline under projected increases in fire activity in this region (Wotton et al. 2017), most notably fire frequency and to a lesser extent fire size. Indeed, there is already evidence of changing regeneration patterns in black spruce across much of boreal North America (Baltzer et al. 2021). The non-linear nature of several of the modelled relationships highlights the importance of capturing broad environmental, stand structural, and climatic gradients to better reflect complex ecological relationships. Further exploration of non-linearities between key measures of forest recovery and environmental or stand characteristics, such as those identified here, will help to refine projections of postfire forest recovery. As the fire regime continues to change, there is an increased need for detailed and generalizable understanding of the responses of dominant boreal forest species to such changes, to support

predictive modelling of the future state of this vast and globally important biome.

Appendix

Seed viability determination

To determine viable seed rain, germination trials were conducted using the sorted seeds from the seed traps. The protocol for the germination trials follows Leadem et al. (1997). Specifically, all seeds were surface sterilized by immersing them in H₂O₂ for 5 min and rinsed three times with de-ionized water. All seeds were then stratified by soaking for 24 h in 20–25 °C de-ionized water, following which the seeds were placed in plastic bags or vials for 21 days at 2–5 °C. Seeds were then placed on moist filter paper on Petri dishes to germinate in a greenhouse for 21 days where conditions were 23 °C for 16 h of light and 19 °C for 8 h of dark. Dishes were set up in a randomized blocking design with 10 independent blocks and dishes distributed randomly amongst blocks. Samples from each trap were tested separately unless there were more than 100 seeds in a sample in which case the sample was separated into subsamples. Dishes were checked daily to ensure sufficient moisture. At the end of the 21-day germination period, the number of germinated seeds was counted.

Viability tests were then run on a subsample of seeds that did not germinate to determine whether they are viable to germinate (i.e. filled seeds) or not. Ten ungerminated seeds from each site were tested for viability ($n = 250$ seeds). Protocol for the viability test follows Leadem (1984). Seeds were soaked overnight in 20 °C water to soften the tissues. A thin layer of the endosperm was sliced off, and the cut seeds were placed in Petri dishes and covered with 1% tetrazolium (TZ) solution (pH = 6.5–7). Seeds were then incubated for 2–8 h and removed when staining is complete. To determine when staining is complete, an additional dish of seeds was stained, and seeds were cut periodically to assess how far the staining has progressed and to ensure that the staining did not get too dark. When staining was complete, the TZ solution was drained, and the seeds were rinsed 2–3 times with water. Seeds were then cut in half to view the embryo. The protocol by Leadem (1984) provides figures which were then used to assess the make-up of inside of the seed and assess viability. None of the seeds that were tested for viability was viable, indicating that all seeds that were viable had germinated during the preceding experiment.

Table 4 Summary of studied variables from each of the 25 study plots

Plot	Burn date (Julian days in 2014)	Total seed rain count ^a	Viable seed rain count ^a	Distance to unburned edge (m)	Stand age (years)	Moisture regime	Canopy combustion	Tree productivity index	Standing black spruce basal area (m ² ha ⁻¹)	Black spruce stem count
SS33-01B	189	165	35	17	171	Mesic	High	0.0025	9.2	38
SS33-03C	183	60	10	315	232	Dry	High	0.0035	23.5	53
SS33-06C	183	70	14	105	72	Wet	Moderate	0.0080	1.4	32
SS33-09A	183	183	27	378	90	Wet	High	-0.0346	7.1	134
SS33-11B	183	105	14	56	163	Dry	High	0.0019	23.5	105
ZF20-04A	203	107	13	23	150	Dry	Moderate	0.0139	2.9	53
ZF20-06B	196	271	18	354	110	Dry	High	0.0060	12.4	37
ZF20-09C	193	75	8	34	85	Wet	High	-0.0505	4.5	139
ZF20-10C	194	92	28	66	84	Wet	High	0.0011	5.6	55
ZF20-11C	196	72	4	44	83	Mesic	High	0.0036	14.7	158
ZF20-12B	197	145	16	575	73	Mesic	High	0.0354	11.5	58
ZF20-34B	211	268	42	39	87	Dry	Moderate	0.0388	16.2	36
ZF20-40A	212	40	10	710	167	Dry	High	-0.0179	3.8	97
ZF20-43C	210	104	10	133	74	Wet	High	-0.0084	12.5	124
ZF20-52C	212	89	11	135	93	Mesic	High	-0.0382	14.0	171
ZF20-59B	211	26	0	55	74	Dry	High	-0.0033	0	35
ZF20-64A	209	31	3	62	75	Dry	High	0.0624	0	18
ZF46-01B	203	325	43	51	72	Wet	High	0.0125	11.3	85
ZF46-15B	203	377	62	51	116	Dry	Moderate	-0.0023	6.9	43
ZF46-18B	220	169	16	153	71	Wet	High	-0.0146	2.2	36
ZF46-21B	213	155	31	55	72	Wet	Moderate	0.0142	9.5	88
ZF46-30B	205	110	22	60	102	Wet	Moderate	-0.0222	9.8	160
ZF46-35C	205	322	38	31	110	Mesic	Moderate	0.0103	13.0	39
ZF46-48A	225	22	0	251	71	Mesic	High	-0.0530	1.2	88
ZF46-51A	214	224	23	71	71	Mesic	Moderate	0.0330	3.9	30

^a Sums over all traps over the entire sampling period

Table 5 Comparison of AIC values in negative binomial mixed-effects model of total black spruce seed rain (model 1) and binomial mixed-effects model of black spruce seed viability (model 2), using linear and nonlinear relationships (nl) of 2 degrees of freedom (df) for the continuous predictors, i.e. Stand age, productivity index, basal area, and distance to edge. The lowest AIC for each model is highlighted in bold

Fixed effects	Model 1	Model 2
	AIC	AIC
Stand age + combustion + productivity index + basal area + moisture + distance to edge	1687	835
nl(Stand age, df = 2) + combustion + productivity index + basal area + moisture + distance to edge	1679	831
Stand age + combustion + nl(productivity index, df = 2) + basal area + moisture + distance to edge	1687	836
Stand age + combustion + productivity index + nl(basal area, df = 2) + moisture + distance to edge	1676	832
Stand age + combustion + productivity index + basal area + moisture + nl(distance to edge, df = 2)	1689	829

Table 6 Comparison of AIC values in linear models of plot-level black spruce seedlings per m² (model 3) against total (a) and viable (b) seeds per m² showing estimated coefficients, standard errors (SE), using linear and nonlinear relationships (nl) of 2 degrees of freedom (df) for the continuous predictors, i.e. total and viable seeds per m². The lowest AIC for each model is highlighted in bold.

Fixed effects	Model 3a	Model 3b
	AIC	
Total seeds	149	
nl(total seeds, df = 2)	138	
Viable seeds		148
nl(viable seeds, df = 2)		144

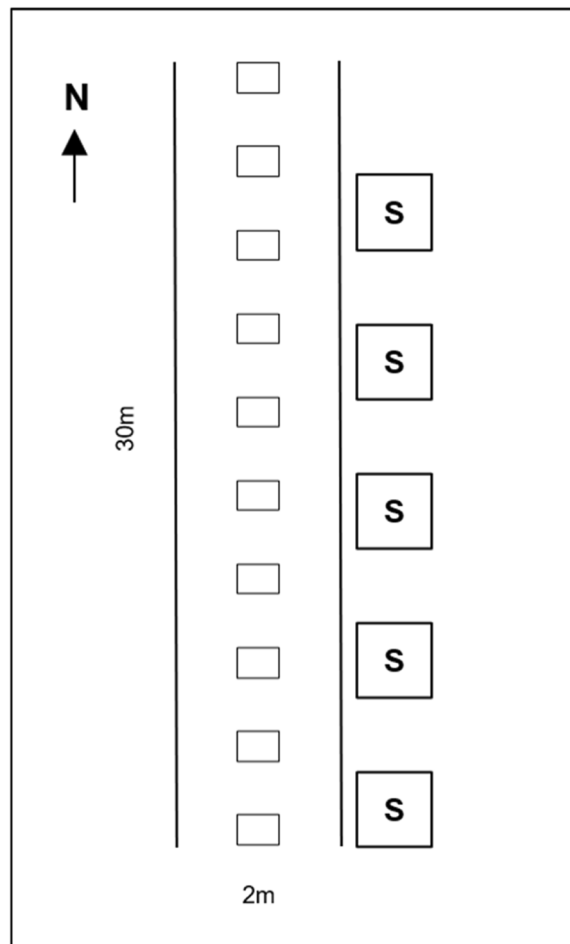


Fig. 5 Schematic of plot design. Each plot was a pair of parallel 30 m belt transects, 2 m apart. Ten seed traps were positioned at 3 m intervals along the center line. Traps were rectangular garden flats (52 cm × 22.5 cm) with drainage holes and lined with synthetic grass turf to trap the seeds. Five of the traps were collocated with five 1 m² quadrats where all seedlings were counted in June 2016 (squares marked S, adjacent to the right hand transect)

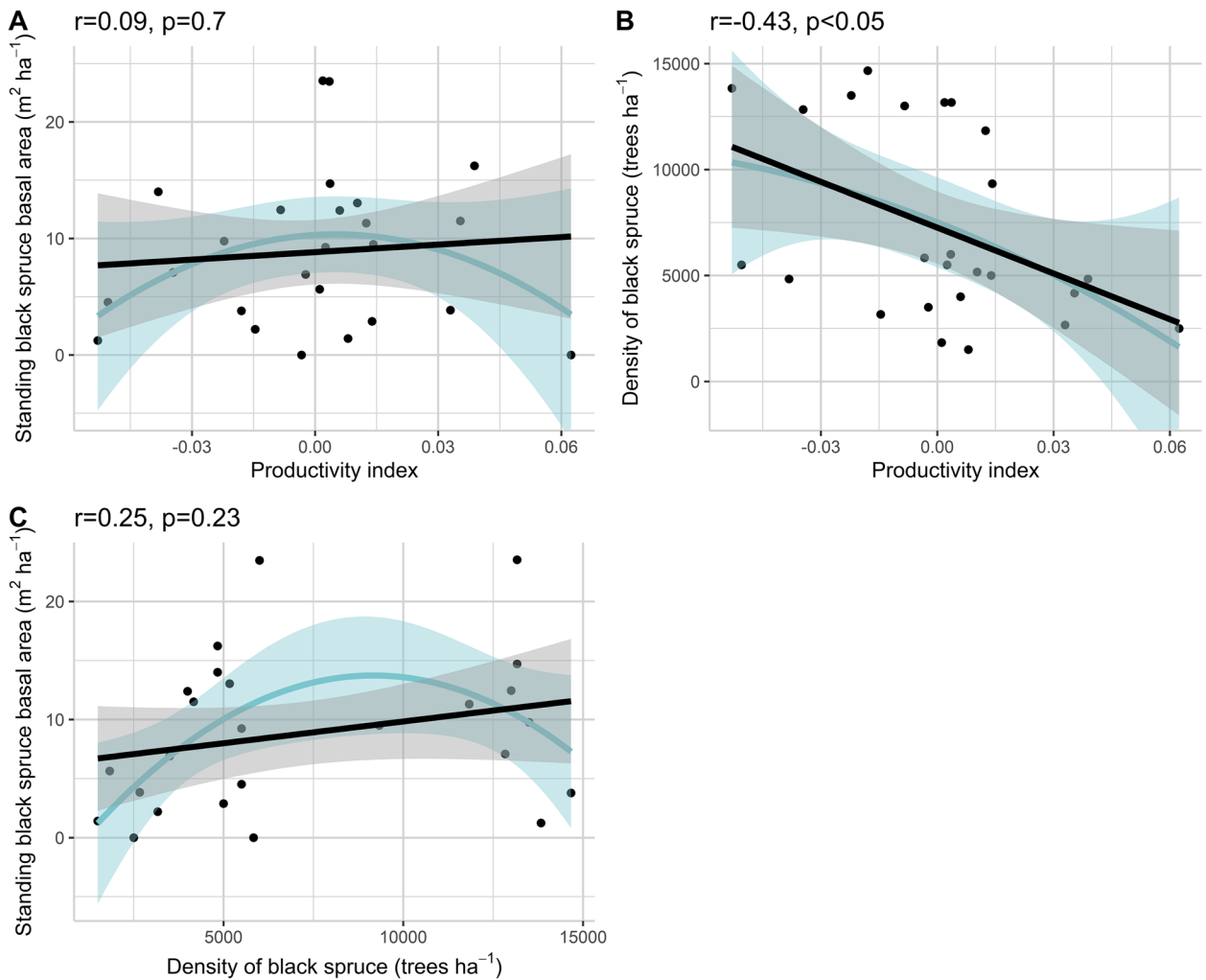


Fig. 6 Relationships between standing black spruce basal area and tree productivity index (a), density of black spruce stems and tree productivity index (b), and standing black spruce basal area and density of black spruce stems (c). Regression lines are shown as black lines and cubic polynomial lines as blue lines. Insets in the panels show Pearson correlation coefficients between plotted variables

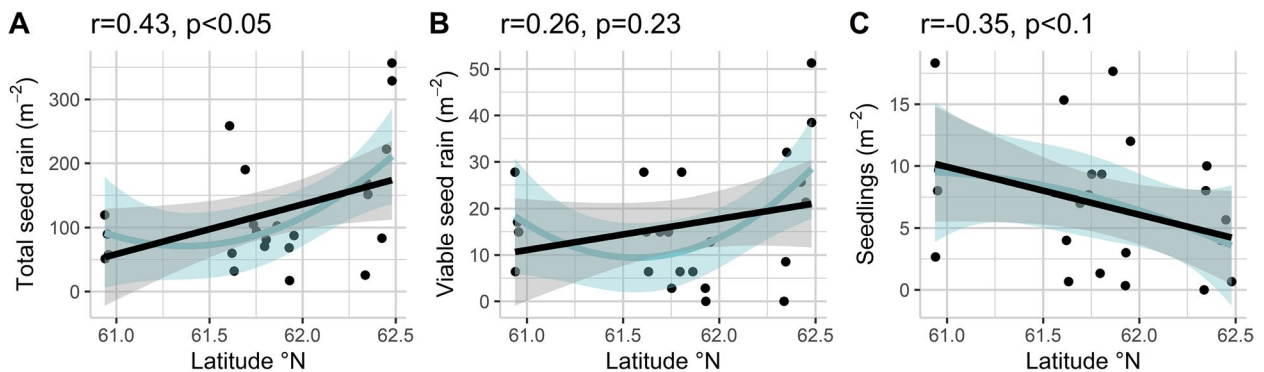


Fig. 7 Relationships between total seed rain (a), viable seed rain (b), and seedling recruitment (c) with latitude. Regression lines are shown as black lines and cubic polynomial lines as blue lines. Insets in the panels show Pearson correlation coefficients between plotted variable

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Code availability

Not applicable. We used existing R code for all analysis.

Authors' contributions

Conceptualization, JLB, JFJ, MCM, and MRT with support from NJD, SGC, and XJW; methodology, all authors contributed; formal analysis and investigation, KAR, NJD, XJW, and RAS with support from JLB, JFJ, and SGC; writing — original draft preparation, KAR with support from JLB, NJD, JFJ, RAS, and SGC; writing — review and editing, all authors contributed; funding acquisition, JLB, JFJ, SGC, MRT, and MCM; resources, JLB, MCM, and MRT; supervision, JLB and ND. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets generated during and/or analysed during the current study can be found in Reid et al. (2022) <https://doi.org/10.5061/dryad.z8w9ghxg4> and Baltzer et al. (2020) <https://doi.org/10.5061/dryad.76hdr7sth>.

Declarations

Ethics approval and consent to participate

The authors declare that they obtained the approval of the Government of the Northwest Territories Aurora Research Institute (Research Licenses 15879 and 16018) in consultation with the Ka'a'gee Tu First Nation, the Tłı̄chǫ Government, and the Wek'èezhii Renewable Resources Board for conducting this study on their traditional territories.

Consent for publication

All authors gave their informed consent to this publication and its content.

Competing interests

The authors declare that they have no competing interests.

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