



Fire and forest recovery on seismic lines in sandy upland jack pine (*Pinus banksiana*) forests[☆]

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ABSTRACT

Networks of narrow linear (~3–12 m wide) forest disturbances used for petroleum exploration (seismic lines) are common throughout Alberta's boreal forest. These 'seismic' lines have often failed to recover trees decades after their initial disturbance, especially within treed peatland and jack pine (*Pinus banksiana*) forests. This has led to regional increases in forest fragmentation contributing to declines in threatened woodland caribou. Restoration of seismic lines to forests is now a top priority for conservation and recovery of woodland caribou, but are expensive and often ignore the occurrence of wildfires that may destroy restoration investments (planted trees), yet also recruit trees. This is especially relevant to jack pine forests that burn more frequently than other forests and depend on moderate to high intensity fires to release seeds *en masse* from their serotinous cones. Although much is known about jack pine tree recruitment following fire, little is known about patterns of tree recovery on seismic lines and how this varies with fire severity, line width (forest gap size), and line orientation. Here we examine natural tree recovery across a gradient in fire severity (defined as percent overstory tree mortality) with different seismic line characteristics (forest gap width and orientation), as compared to adjacent forest stands, in jack pine forests 5-years post-fire in northeast Alberta, Canada. Overall, jack pine regeneration was consistently 2-fold higher on seismic lines compared to adjacent burned forests with stem density increasing with fire severity in both sites, especially when fire severity was greater than 40%. We suggest that the observed increases in tree regeneration on seismic lines may be due to (1) removal of biomass and exposure of mineral soils on seismic lines creating more favorable conditions for jack pine seeds and seedlings; and/or (2) increases in available light resulting in better growing conditions and survival for this shade-intolerant species. Finally, we suggest that natural recovery (passive restoration) of seismic lines should be expected post-fire in jack pine stands and thus active restoration of these sites through silviculture and tree planting may not be the wisest use of limited restoration dollars if fires are locally common.

1. Introduction

Oil sands exploration and extraction in northern Alberta, Canada have affected the boreal forest in a number of ways, particularly through fragmenting forests with roads, pipelines, transmission lines, and drilling well pads. However, the largest anthropogenic contributor of forest fragmentation is seismic lines (Arienti et al., 2009; Schneider et al., 2010) often reaching densities of 10 km/km² (Lee and Boutin, 2006). Seismic lines are narrow (3–12 m) linear corridors (Fig. 1) designed in a network of repeating corridors where trees are removed for the purpose of petroleum exploration (seismic assessments). These disturbances can simplify microtopography and compact the soil surface leading to failures in tree regeneration (Lee and Boutin, 2006; Caners and Liefvers, 2014; van Rensen et al., 2015; Liefvers et al., 2017).

This has contributed to changes in wildlife populations and more broadly biodiversity (Timoney and Lee, 2001; Hooper et al., 2005; Lee and Boutin, 2006; Kemper and Macdonald, 2009a; 2009b; Caners and Liefvers, 2014). The most high-profile species-at-risk in Canada's boreal forest are woodland caribou (Environment Canada 2012). Although seismic lines are generally avoided by caribou (James and Stuart-Smith, 2000; Dyer et al., 2001, 2002), they are favored by wolves increasing their movement efficiency in caribou habitat (James and Stuart-Smith, 2000; Latham et al., 2011). This can reduce survival rates of caribou and as a consequence contribute to caribou population declines (James and Stuart-Smith, 2000; Dyer et al., 2001, 2002; Latham et al., 2011). Mitigation efforts are now extensively being used to address this issue by restoring tree growth on seismic lines or, over shorter periods, reducing wolf use of lines by adding structural barriers to movement.

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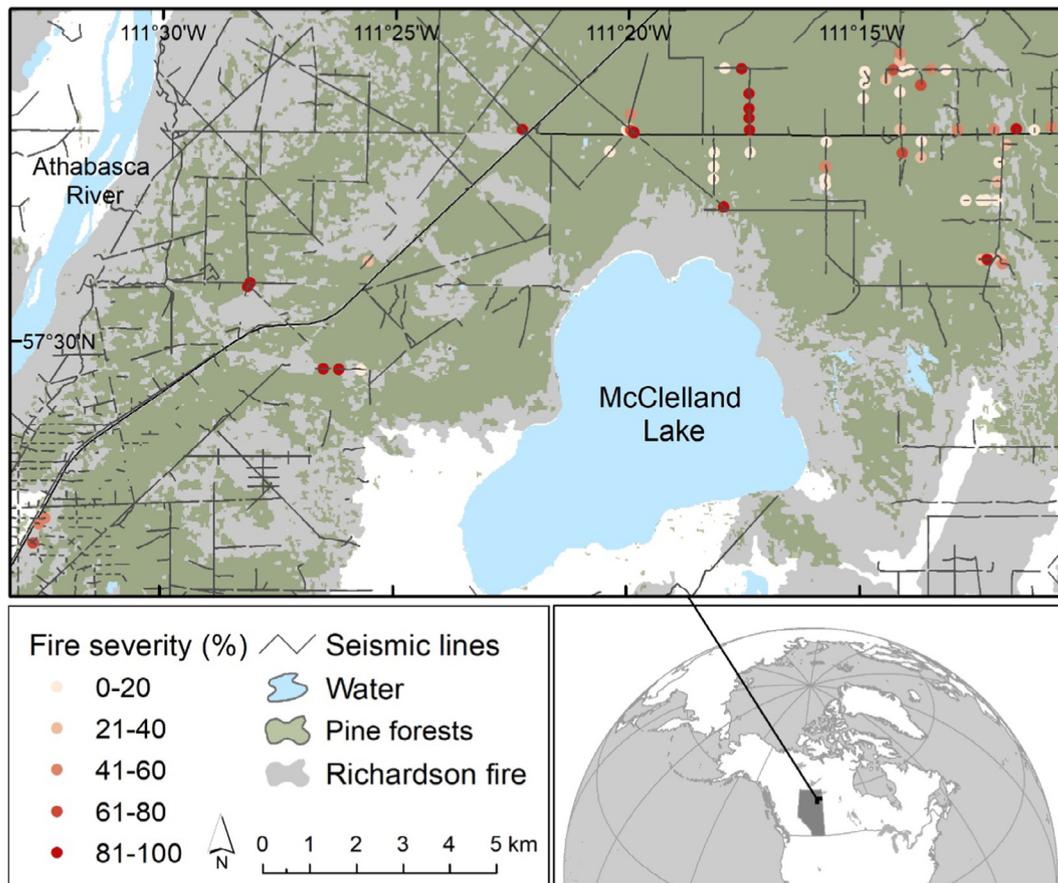


Fig. 1. Location of study area in northeast Alberta, Canada (inset map), the location of study sample sites relative to fire severity as measured by overstory tree mortality (light red to red circular symbols representing the fire severity gradient), location of seismic lines, location of 2011 Richardson fire in gray, and pine forests in dark green for where it burned (most places) or in very few location light green where unburned. Each site represents a pair of plots with one being on the seismic line and the other in the adjacent forest stand. Note that some sites were within 200–400 m of each other when fire severity levels differed, stands varied, or there were gaps in the seismic line disturbance.

Long-term restoration goals hinge, however, on recovery of trees on seismic lines.

Costs of these active restoration treatments are high averaging \$12,000 (CAD) or more per km of seismic line with treatments involving site preparation (mounding, ripping) and tree planting. Conversely, passive restoration strategies for seismic lines that rely on natural rates of reforestation (i.e., leave-for-natural) have no direct costs, but depend on extended timeframes of recovery (Lee and Boutin, 2006; van Rensen et al., 2015). Understanding where reforestation is occurring is therefore a priority in planning and prioritizing the location of restoration activities. Wildfires, the largest contributor to boreal forest disturbance, are one possible leave-for-natural passive form of restoration, but also represent a risk to investments in active restoration treatments where tree planting occurs. Much less is known, however, on how wildfires affect recovery rates of seismic lines despite being a major driver of successional changes in the boreal forest and a risk or opportunity for restoration.

Seismic line disturbances in xeric sandy jack pine (*Pinus banksiana*) forests are one of the two forest-types in northeast Alberta characterized by being in a state of arrested succession (van Rensen et al., 2015). Yet this may be an overgeneralization that is dependent on the time scale examined since jack pine cones are serotinous and typically release their seeds *en masse* only after moderate to high intensity fires (Ahlgren and Ahlgren, 1960; Cayford and McRae, 1983; Lamont et al., 1991) with fire return intervals for jack pine forests in northeast Alberta typically being 28–54 years (Carroll and Bliss, 1982; Larsen, 1997; Larsen and MacDonald, 1998). A more informed test of whether these seismic lines will naturally regenerate is to therefore examine patterns of post-fire recovery. If fires promote recovery of seismic lines in conditions similar to adjacent stands (a form of passive restoration), it

would have major implications for planning restoration activities in the boreal forest even if fires are not directly used as active restoration treatments.

In this paper we examined recovery dynamics on seismic lines and adjacent paired forest controls in jack pine forests by fire severity (percent overstory tree mortality), forest stand conditions (age, height, and basal area), and seismic line characteristics (forest gap width and orientation). Specifically, we tested whether fire naturally recovers seismic lines or whether other factors (small gap widths, simplified microtopography, etc.) restrict regeneration compared to adjacent paired forest controls. On the one hand, seismic lines post-fire may provide more exposed mineral soil, sunlight, and wind (seed dispersal), as well as less competition thus favoring tree regeneration for shade-intolerant species like jack pine. On the other hand, micro-terrain on seismic lines may be simplified during construction of seismic lines offering fewer microsites for conditions that would favor tree recruitment following fire, especially under drier post-seed dispersal conditions. We address these questions by examining jack pine and other tree regeneration 5-years post fire on seismic lines compared to adjacent forests in northeast Alberta, Canada.

2. Methods

2.1. Study area

The study area consists of 100 km² of boreal forests within the Regional Municipality of Wood Buffalo and the Athabasca Oil Sands of northeastern Alberta. It is approximately 115 km north of Fort McMurray and within a 15-km radius of the west and north ends of McClelland Lake (57°31'56"N, 111°21'40"W, Fig. 1). The area lies on

the south end of the Athabasca Plain where the dominant soil is dystric brunisols with surface topography characterized by plains and sandy dunes deposited by eolian forces (Downing and Pettapiece, 2006; Smith et al., 2011). In most areas, including the focus of this study, the former glacial dunes and sand plains are stabilized with vegetation. Jack pine is by far the dominant tree species with other trees and tall shrubs including trembling aspen (*Populus tremuloides*), saskatoon (*Amelanchier alnifolia*), green alder (*Alnus crispa*), and pin cherry (*Prunus pensylvanica*).

The majority of the study area was burned in 2011 by the Richardson Fire (Fig. 1) which was one of the largest fires documented in western Canada burning an area of 576,000 ha. Understorey species were described for the area 4-years post fire by Pinno and Errington (2016) with species richness highest in low severity burns and plant cover lowest in high severity burns. Pinno et al. (2013) also examined jack pine recruitment in the Richardson fire 1-year post fire finding it to be highly variable depending on fire severity and stand age, but did not assess linear disturbances associated with seismic lines which is the objective of this study. Seismic lines varied in width from 3.5 to 9.5 m with initial disturbances occurring between 2005 and 2008 (3 to 6 years prior to the fire).

2.2. Site selection and field methods

Sampling locations were selected across the full gradient of fire severity, measured by overstorey tree mortality, with stratification to five categorical fire severity classes used to help allocate sampling effort across the area (Fig. 1): 0–20% ($n = 27$ sites), 21–40% ($n = 11$ sites), 41–60% ($n = 10$ sites), 61–80% ($n = 5$ sites), and 81–100% ($n = 17$ sites). Effort was also made to capture the range of forest stand conditions (height, density, age, etc., see Table 1). All sites were at least 90 m from any road or trail with a random toss of a metal stake on the seismic line used to designate the starting location of plots. As a single seismic line can stretch for kilometers, a single site per seismic line was used in most cases unless forest stand conditions and/or fire severity varied in which case additional sites at least 200 m apart were sometimes added.

In total, 70 sites were sampled in the summer of 2016 with each site consisting of a pair of plots for a total of 140 plots (see Fig. 2 for example site photograph). The paired plots were each represented by: (1) a plot on the seismic line; and (2) a plot in the adjacent forest. Each site (paired plots – seismic line and adjacent forest control) was selected based on the requirement of having uniform forest stand conditions (i.e., height, density, age) and fire severity for the pair of plots and each plot consisting of a 30 m transect. Seismic line transects were located in the center of the seismic line, while the adjacent paired control plots were located 25 m into the adjacent forest running parallel to the seismic line. A coin toss was used to randomize which side of the

Table 1

Stand characteristics and tree regeneration rates for 70 burned jack pine stands studied in northeast Alberta, Canada. Regeneration density is reported for both forest stands ($n = 70$) and adjacent disturbed seismic line corridors ($n = 70$).

Stand variable	Minimum	Median	Maximum	Mean (S.E.)
Overstorey tree mortality (%)	0	40	100	46.5 (4.3)
Stand age	33	77	135	77 (2.9)
Height (m)	3.6	15.4	23.2	14.8 (0.5)
Tree diameter (DBH)	1.4	14.1	38	14.5 (0.3)
Basal area (m ² /ha)	2	18	34	17.3 (0.9)
Trees/ha (belt plots)	333	3833	27,333	6248 (763)
<i>Jack pine regeneration (stems/ha)</i>				
Seismic line	0	18,500	535,333	62,419 (11,890)
Adjacent stand	0	3167	296,000	29,419 (6284)
<i>Non-jack pine regeneration (stems/ha)</i>				
Seismic line	0	1	137	14.2 (3.0)
Adjacent stand	0	0	92	12.0 (2.6)

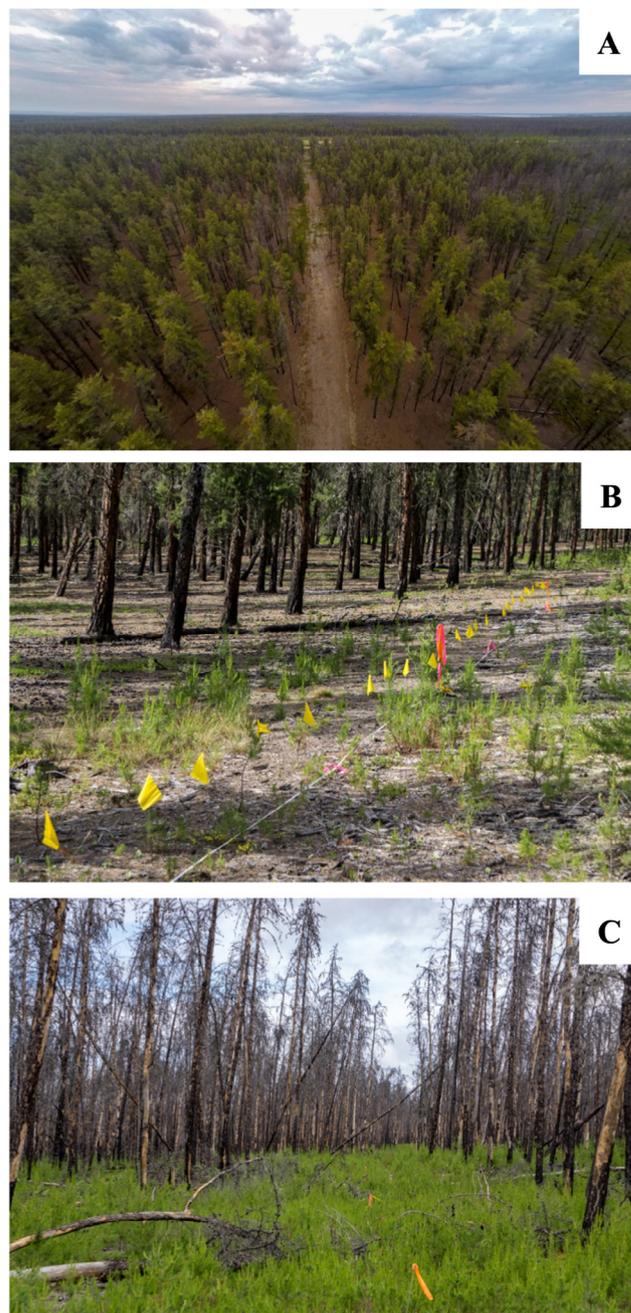


Fig. 2. Oblique aerial photograph (July 12, 2017) of a seismic line disturbance within a jack pine (*Pinus banksiana*) forest in northeast Alberta, Canada (A) and ground photographs depicting tree regeneration 5-years post-fire under low severity (B) and high severity (C) conditions (June 16, 2016). Photographs by S.E. Nielsen.

seismic line the adjacent forest control plot was located. Tree regeneration and forest stand conditions on seismic lines and adjacent forest stands were measured along 30 m transects with regenerating trees and shrubs counted in 1 m × 30 m ‘belt’ quadrats and trees (≥ 1 cm DBH) counted in 2 m × 30 m belt quadrats. Additional information was collected in the adjacent forest stand including stand basal area by species using a 2-factor metric prism at the midpoint of the forest transect (15 m), stand age of representative mature trees in the plot using dendrochronology via tree cores, and representative tree height using a Haglof Vertex IV (Sweden).

2.3. Analysis of seismic lines, fire severity, and stand characteristics on regeneration density

First, to visualize the main experimental effects, we plotted the mean and standard errors of regeneration density (per m²) for both jack pine and all other tall woody species (aspen, saskatoon, green alder, and pin cherry) against the two main experimental variables of fire severity (5 ordinal categories) and plot location (seismic line versus adjacent forest) for all 140 plots (70 pairs). We then used paired t-tests (*ttest* command in STATA 13.1/SE; StataCorp, 2013) to evaluate whether regeneration densities (log-transformed) were higher on seismic lines than adjacent plots by each fire severity class. Non-parametric Wilcoxon sign-rank tests on raw densities were also examined, but they did not differ with t-tests using log-transformed densities and were therefore not further reported.

Second, we used generalized linear mixed effects models (*xtreg* command in STATA 13.1/SE; StataCorp, 2013) to relate linear changes in jack pine regeneration and regeneration of other species (both log transformed with a constant of 1 added) to location treatment (seismic line versus adjacent control forest), fire severity measured on a continuous scale (% overstory tree mortality), and forest stand measures including tree height, stand basal area, and stand age. Models were fit separately for jack pine and all other species grouped together. Site was used as a random effect to account for the paired nature of the seismic line and adjacent control forest plots. The location variable was dummy (binary) coded as 1 for seismic lines and 0 for adjacent control forests. Responses on seismic lines were therefore relative to reference conditions (changes) in the adjacent forest stand.

Model selection was as follows: (1) all main treatment variables (fire severity [continuous scale] and the binary seismic line location variable) were included regardless of their significance; (2) non-linear effects of fire severity and an interaction between fire severity and seismic line location were tested and added only if significant; and (3) variables for stand characteristics (including quadratic terms for non-linear responses and interaction terms with main treatment variables) were tested and included only if significant. Significance in linear terms was considered at $\alpha = 0.05$ or $\alpha = 0.10$ if it related to a quadratic non-linear response. Collinearity among continuous variables were assessed using Pearson correlations with no variables considered colinear when $|r| = > 0.7$ (highest correlation was between height and age at $r = 0.64$). For the final model we report model parameters for treatment variables and other significant variables, as well as model goodness of fit using the 'overall' R² value that is based on the combination of 'between' R² (representing variance between sites such as fire severity and stand conditions) and 'within' R² (representing variance within sites or in this case the binary seismic line variable) components.

2.4. Analysis of line (forest gap) width, orientation, and stand conditions on regeneration density

Here we isolated the responses of tree regeneration (jack pine and other species) on seismic lines to line (forest gap) width and line orientation. In doing so, we removed all adjacent paired forest plots since they did not represent discrete forest gaps. This resulted in a total sample size of 70 plots. Because plots were no longer paired with the forest controls, we used simple linear regression (*reg* command in STATA 13.1/SE; StataCorp, 2013). Model selection was similar to that of the prior models using linear mixed effects regression with the exception of the exclusion of the location treatment variable since it was no longer relevant and the inclusion of line width (forest gap size) and line orientation as fixed variables since we were specifically interested in whether these line characteristics affected regeneration responses on seismic lines. Line width varied between 3.5 m and 9.5 m (mean of 6.1 and SE = 0.1), while line orientation represented the compass bearing of seismic lines transformed to an index between 0 (east-west orientation) and 1 (north-south orientation) following the methods of van

Rensen et al. (2015). Most lines in the area were on north-south and east-west axes. As in the prior section, forest stand measures of tree height, stand basal area, and stand age were considered including their interaction with other factors such as seismic line (forest gap) width.

3. Results

3.1. Stand characteristics

Total basal area (m²/ha) in adjacent forest stands, including recent dead snags from the fire, varied from 2 to 34 (mean of 17.3, SE = 0.9), stand age varied from 33 to 135 years (mean of 77, SE = 2.9), and tree heights varied from 3.6 to 23.2 m (mean of 14.8, SE = 0.5). Table 1 provides a more complete overview of basic stand characteristics of burned forests adjacent to seismic lines. Other species of trees and tall shrubs (e.g., aspen, saskatoon, green alder, and pin cherry) were found in approximately half of all plots (38 out of 70 seismic line plots, 34 out of 70 adjacent forest control plots, and thus 72 out of all 140 plots), but at a significantly lower density than jack pine. Overall, the composition of trees and shrubs across all plots were as follows: 92% jack pine, 2.2% saskatoon, 1.7% aspen, 1.5% green alder, and 1.1% pin cherry. Understory vegetation was dominated by bearberry (*Arctostaphylos uva-ursi*), blueberry (*Vaccinium myrtilloides*), and reindeer lichens (e.g., *Cladina rangiferina*, *C. mitis*, *C. stellaris*).

3.2. Seismic lines versus adjacent forest by fire severity class

Wildfires within jack pine forests promoted tree regeneration on seismic lines with 92% of regenerating stems being jack pine and the remaining 8% from aspen and three species of tall shrubs (saskatoon, green alder, and pin cherry). For jack pine itself, regeneration densities were positively related to fire severity, particularly when fire severity was > 40%, where densities were consistently 2-fold higher in seismic lines compared with adjacent forest stands (Fig. 3A). In fact, the highest rates of jack pine regeneration occurred at the highest fire severity (81–100%) with densities reaching 14.8 (SE = 3.7) trees/m² on seismic lines and 7.3 (SE = 1.8) trees/m² in adjacent forest stands (Fig. 3A). In contrast, at the lowest fire severity (0–20%) jack pine regeneration averaged only 1.0 (SE = 0.2) trees/m² in seismic lines and 0.08 (SE = 0.03) trees/m² in adjacent forests (Fig. 3A). Comparison tests by fire severity class supported significant differences ($p < .05$) in regeneration density of jack pine between seismic lines and adjacent forest for all fire severity classes, except for 61–80% severity where it was only marginally significant ($p < .078$), although it should be noted that this class also had the lowest statistical power with the fewest number of plots ($n = 5$ pairs).

In comparison to jack pine, regeneration for all other trees (and tall shrubs) was much lower in number and non-linearly related to fire severity (Fig. 3B). For this group, regeneration peaked at moderate levels of fire severity (41–60%) with 1.0 (SE = 0.5) trees/m² in seismic lines and 0.7 (SE = 0.4) trees/m² in adjacent forests (Fig. 1B). When comparing directly to jack pine, peak regeneration levels for non-jack pine species were at least 10-fold lower than that of jack pine. Comparison tests between seismic lines and adjacent forests for non-jack pine regeneration did not support differences among any fire severity class ($p > .226$) illustrating no obvious changes in regeneration within forest gaps from seismic lines.

3.3. Seismic lines (vs. forest), fire severity, and stand characteristics on regeneration density

The final generalized linear mixed effects model for jack pine included positive effects for seismic line treatment ($\beta = 0.573$, $p < .001$) and fire severity ($\beta = 0.021$, $p < .001$), and a non-linear relationship with forest stand height ($\beta_{\text{height}} = 0.314$, $p < .001$; $\beta_{\text{height}^2} = -0.010$, $p < .001$) (Table 2). Stand basal area and stand age were not

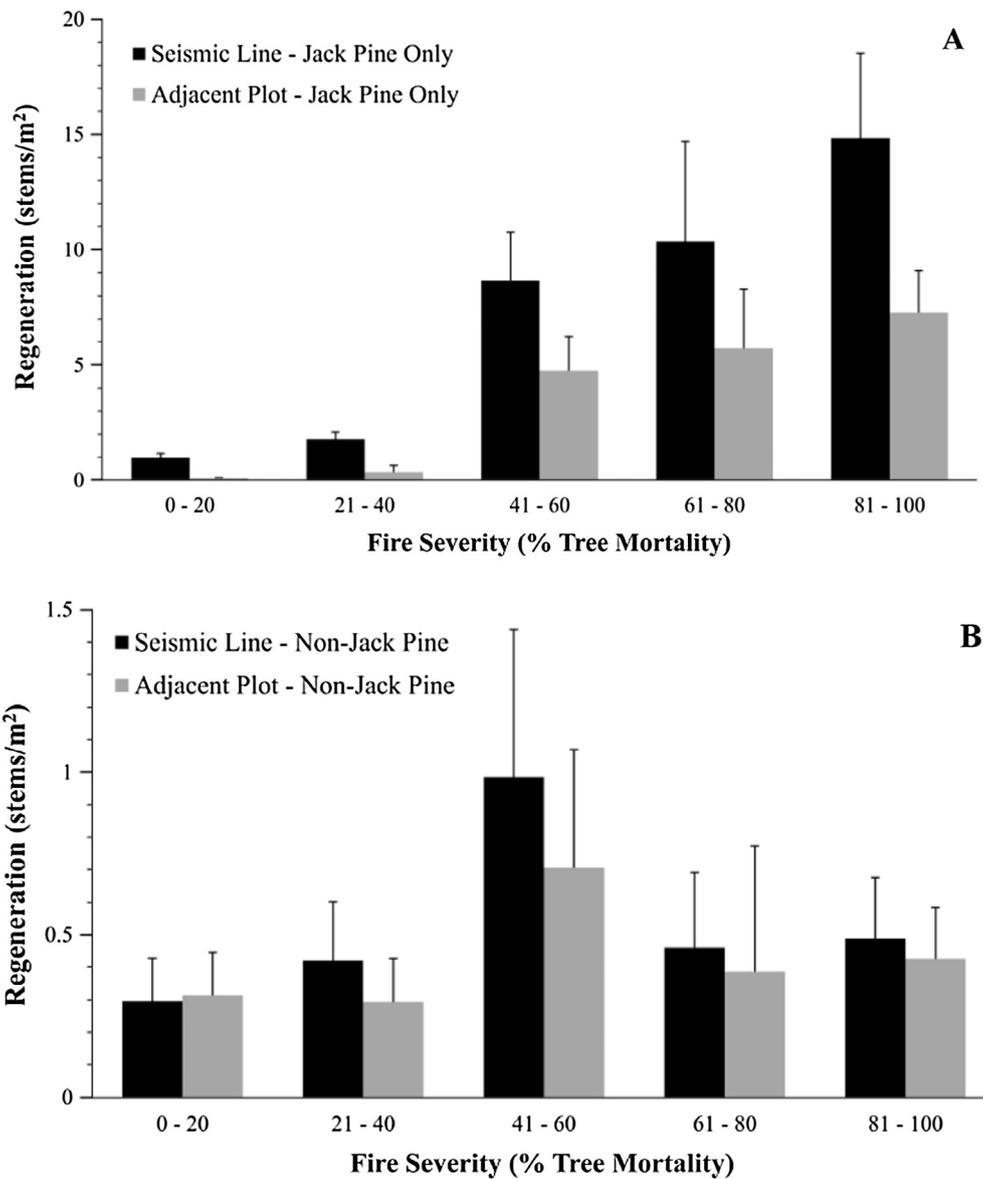


Fig. 3. Regeneration as a response to fire severity (overstory tree mortality): (A) jack pine regeneration increased with fire severity with a marked increase in sites where fire severity was > 40%; (B) regeneration densities of other tree and shrub species demonstrated increases until ~50% fire severity and thereafter declines. Note regeneration scale in (A) is ~12x greater than that in (B).

Table 2

Generalized linear mixed effect model parameters relating regeneration density of jack pine and other woody species to treatment variables of seismic lines (vs. adjacent control forests) and fire severity, as well as stand characteristics (forest stand height and stand age). No interaction terms were supported, while treatment variables were included regardless of significance.

Variable	Jack pine			Other species		
	β	S.E.	<i>p</i>	β	S.E.	<i>p</i>
Seismic line (binary)	0.573	0.092	< .001	0.036	0.041	.387
Fire severity (overstory tree mortality)	0.021	0.002	< .001	0.002	0.001	.034
Forest stand height	0.314	0.079	< .001	0.084	0.011	< .001
Forest stand height ²	-0.010	0.003	< .001			
Stand age (yrs.)				-0.037	0.010	< .001
Stand age ²				0.0002	0.00005	.001
Constant (intercept)	-2.510	0.561	< .001	0.637	0.326	.050
Model fit (R ²)	0.62			0.41		

significantly related to patterns in jack pine regeneration, nor were there further interactions between variables. Model predictions and observed data demonstrated that jack pine regeneration peaked when stand height was ~16 m and at 100% fire severity. Interestingly, there was no correlation in observed values between stand height and fire severity ($r = -0.099, p = .246$), nor interactions between these variables. Model fit was high with an ‘overall’ R² of 0.62, a ‘within’ R² of 0.36 for the seismic line treatment, and a ‘between’ R² of 0.69 that reflected site differences due to fire severity and stand characteristics.

In contrast to jack pine regeneration, the final model for other regenerating trees and tall shrubs was not affected by the seismic line treatment ($\beta = 0.036, p = .387$) and was positively and linearly related to forest stand height ($\beta = .084, p < .001$) (Table 2). Regeneration of these species was still positively related to fire severity, but much weaker in strength ($\beta = 0.002, p = .034$) and did not support non-linear effects as suggested in Fig. 3B once other factors were considered. This included a strong non-linear effect of stand age ($\beta_{age} = -0.037, p < .001; \beta_{age^2} = 0.0002, p = .001$; Table 2) whereby regeneration density that is initially highest in young, taller stands thereafter

Table 3

Linear regression model parameters relating regeneration density of jack pine and other woody species to fire severity, seismic line characteristics (width and orientation), and stand conditions (forest stand height) only on seismic lines. Note that seismic line width and orientation were included regardless of significance.

Variable	Jack pine			Other species		
	β	S.E.	<i>p</i>	β	S.E.	<i>p</i>
Fire severity (overstory tree mortality)	0.022	0.002	< .001	0.012	0.005	.009
Fire severity ²				-0.0001	0.00004	.021
Forest stand height	0.371	0.092	< .001	-0.132	0.057	.023
Forest stand height ²	-0.013	0.003	< .001			
Line (forest gap) width	-0.035	0.074	.641	-0.306	0.148	.043
Line orientation (north index)	-1.346	0.635	.038	-0.202	0.093	.034
Line width × Stand height	0.102	0.040	.014	0.027	0.009	.004
Constant (intercept)	-1.883	0.820	.025	1.482	0.879	.097
Model fit (R ²)	0.64			0.46		

decreased with stand age until stabilizing around 80–105 years and then again increasing slightly in stands > 105 years old prior to the fire. However, this may reflect the fact that the two highest regeneration densities observed were for a 39-year old stand burned at a 60% severity having 4.6 stems/m² on seismic lines (much less in adjacent forest) and a 135-year old burned stand (oldest sampled) at a 20% fire severity with 2.8 stems/m² on both the seismic line and adjacent plot. The other plots generally had regeneration densities of < 2 stems/m² and a general trend towards peak regeneration densities in 60–80-year old burned stands. Model fit was moderate with an ‘overall’ R² of 0.41, a ‘within’ R² of 0.01 for the seismic line treatment demonstrating the lack of relationship for seismic line effects, and a ‘between’ R² of 0.50 that reflected site differences due to fire severity and stand characteristics that largely affected non-jack pine regeneration patterns.

3.4. Line (forest gap) width, orientation, and adjacent stand conditions on regeneration density

The final regression model for regeneration within only seismic lines was related to seismic line characteristics (width and orientation), fire severity, and adjacent stand conditions of stand height (see Table 3). For jack pine this included a positive relationship with fire severity ($\beta = 0.022$, $p < .001$) and a non-linear response to forest stand height ($\beta_{\text{height}} = 0.371$, $p < .001$; $\beta_{\text{height}^2} = -0.013$, $p < .001$). Both responses were similar to the prior model considering both seismic lines and adjacent forests, but with jack pine regeneration further related to line characteristics of line orientation and width. Specifically, jack pine regeneration decreased on north-south orientated lines ($\beta = -1.346$, $p = .038$), while not being significantly related to line width alone ($\beta = -0.035$, $p = .641$), but was significant when line width interacted with stand height ($\beta_{\text{height} \times \text{width}} = 0.102$, $p = .025$) (Table 3). Here jack pine regeneration increased in wider lines when adjacent stand heights were higher. Overall model fit was high with an adjusted-R² of 0.64 (Table 3).

In comparison to jack pine, the regeneration of other trees and tall shrubs was non-linearly related to fire severity ($\beta_{\text{severity}} = 0.012$, $p = .009$; $\beta_{\text{severity}^2} = -0.0001$, $p = .021$) peaking in density around 60% fire severity and negatively related to forest stand height ($\beta = -0.132$, $p = .023$) (Table 3). Additional responses to line characteristics included negative relationships in regeneration with line width ($\beta = -0.306$, $p = .043$) and north-south orientated lines ($\beta = -0.202$, $p = .034$) with again a positive interaction supported between stand height and line width ($\beta = 0.027$, $p = .004$) (Table 3). Thus, although regeneration on seismic lines for non-jack pine species declined in wider, north-south lines, it was much higher when in wider lines adjacent to taller forest stands.

4. Discussion

4.1. Regeneration post-fire on seismic lines versus adjacent forest stands

Wildfires within jack pine forests of northeast Alberta promoted jack pine regeneration (92% of stems) over regeneration of trembling aspen and three species of shrubs with fire severity positively related to total regeneration density, particularly for jack pine. Linear open corridors associated with seismic line exploration also resulted in higher jack pine regeneration, especially for moderate and higher severity (> 40% overstory tree mortality) fires where stocking density was twice as high in the most severe fires on seismic lines (14.8 trees/m²) than in adjacent stands (7.3 trees/m²). These results are somewhat contrary to Pinno et al. (2013) who found the highest seedling densities in moderate severity burns with the highest severity fires in young stands averaging only 1164 seedlings per ha (0.12 trees/m²). This compares to an average of 73,000 survived seedlings per ha 5-years post fire in the highest severity burned forests in our study. We did not, however, sample very young (< 30 years of age) stands as did Pinno et al. (2013) where they found low post-fire recruitment. Although cones can be present in young jack pine stands, their cone density may be lower and less serotinous (Gauthier et al., 1993a) and perhaps most problematic for recruitment are seed loss from direct burning of cones in shorter trees (de Groot et al., 2004). Indeed, when considering jack pine recruitment, the two most important factors are the number of viable seeds and the favorability of the seedbed (Sirois, 1993).

In our case, the number of viable seeds should not affect regeneration differences between seismic lines and adjacent forests since both plots were receiving approximately the same source and amount of seeds (25 m from each other) with stands all > 30 years of age (threshold from Pinno et al., 2013). In contrast, the seedbed between seismic lines and adjacent forests varied substantially with the mechanized creation of seismic lines resulting in removal of woody biomass, including stumps, 3–6 years prior to the fire and in many cases exposure of mineral soils that should favor jack pine regeneration (Ahlgren and Ahlgren, 1960; Chrosiewicz, 1974; Cayford and McRae, 1983). Although microtopography is often simplified on seismic lines reducing tree recruitment (Liefers et al., 2017), this was not to the detriment of jack pine regeneration in our study. Therefore, the process which originally removed jack pine forests as small linear openings for oil sands exploration was benefiting jack pine regeneration post-fire potentially due to increases in available mineral soil, but also potentially by increases in light on seismic lines. Although we did not directly measure light levels, jack pine is known to be shade intolerant (Ahlgren and Ahlgren, 1960; Cayford and McRae, 1983; Rudolph and Laidly, 1990; Weber and Stocks, 1998; Arseneault, 2001) and lines create forest openings that should increase light levels, especially for wider lines (see Section 4.2 for more discussion).

Jack pine regeneration was also affected by forest stand heights with peak regeneration occurring at sites where stand heights were approximately 16 m. In our study, ~16 m high forests ranged in age from 62-year-old stands to the oldest stands sampled of 135 years. Interestingly, stand height was not correlated with fire severity suggesting that the effects of stand height had more to do with cone density and seed viability, although cones positioned in lower parts of the canopy can be directly consumed by the fire thus reducing post-fire seed rain (de Groot et al., 2004).

In contrast to jack pine, other regenerating trees (trembling aspen) and tall shrubs (saskatoon, green alder, and pin cherry) were not affected by the presence of open linear corridors associated with seismic line disturbances, but were positively affected by fire severity and stand height, and non-linearly related to stand age (generally negative effect). Patterns of recruitment in these species therefore had more to do with characteristics of the stand conditions and fire and may reflect past distribution of plants since all four of species can root sucker following disturbance, particularly for aspen (Frey et al., 2003). Regardless,

regeneration density of these other species was quite small representing only 8% of total stems with jack pine being the dominant species in both seedlings and alive or dead overstory trees. This is typical for these sandy plain jack pine forests. In fact, in the 56 jack pine stands studied in the same area by Pinno et al. (2013), no other tree species were present.

4.2. Effect of seismic line width and orientation on post-fire regeneration

Forest gap size in boreal forests is known to affect regeneration patterns in trees (Kneeshaw & Bergeron, 1998), including jack pine (Gauthier et al., 1993b; Frelich and Reich, 1995), as it affects among other things competition for available light (Lieffers et al., 1999) and soil properties (Kuuluvainen, 1994). In our study, width of forest gaps associated with seismic lines varied between 3.5 and 9.5 m and was positively related to regeneration density in non-jack pine species and for jack pine when adjacent to taller forest stands. This suggests that resources, particularly for light, were limiting recruitment. This is further supported by lower jack pine recruitment in adjacent stands where snags and alive trees reduced light and availability of other resources. Although the seedbed may have been different between seismic lines and forests, the fact that line width affected recruitment suggests light is a limiting factor. However, competition for other resources (nutrients and moisture) may also play a role with width of seismic line likely relating to different intensities of initial soil disturbance. Further study is needed to assess resource competition among forest gaps that are much smaller than typically studied and for differences in soil disturbances and microsites.

A second factor that affects light levels and potentially seed dispersal on seismic lines is line orientation. East-west orientated lines are expected to have greater available light in the groundlayer compared with that of north-south lines (van Rensen et al., 2015), while wind conditions are dominantly from the west providing possible dispersal corridors for seed (Roberts et al., in preparation). In support of the light limitation and perhaps seed dispersal hypothesis, we found increases in recruitment of trees on east-west orientated lines over that of north-south lines. These results are similar to that of van Rensen et al. (2015) who found significantly higher probability of forest recovery on seismic lines orientated east-west than north-south in a region of treed peatlands south of our study area. Although you may expect a multiplicative effect on tree regeneration based on line orientation and width if light were limiting, there was no support for their interaction in our tests suggesting that conditions for regeneration were more suitable if in either wider lines or east-west orientated lines, as well as wider lines when adjacent stand height was taller.

5. Conclusions and management implications

Overall, our results support the suggestion that the inferred lack of tree regeneration on seismic lines in xeric jack pine forests is due to the timing of its measurement as it relates to stand replacing fires since jack pine cones are serotinous releasing their seeds *en masse* only after fires (Ahlgren and Ahlgren, 1960; Cayford and McRae, 1983; Lamont et al., 1991). Given that fire frequency in these areas range from 28 to 54 years (Carroll and Bliss, 1982; Larsen, 1997; Larsen and MacDonald, 1998), cost-benefits of active restoration projects of tree planting and site preparation to those of passive forms of restoration relying on natural regeneration following wildfire should be considered. Here we found no evidence for the need of site preparation for burned seismic lines in jack pine stands, while investments in tree planting in these sites may be short-lived if wildfires do occur. Indeed, jack pine regeneration following moderate to high severity fires on seismic lines were 2-fold higher than in adjacent forests, although these differences may lessen over time as the natural process of stand thinning progresses (Yarranton and Yarranton, 1975; Carroll and Bliss, 1982; Arseneault, 2001). The passive form of restoration of these sites through fire has the

potential to save significant amounts of restoration dollars and still contribute to the long-term conservation objectives, including caribou recovery. Future research should examine whether these patterns hold within other recently burned forest types including those with trees having semi-serotinous cones such as black spruce.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2018.01.027>.

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