Reproductive limitation mediates the response of white spruce (*Picea glauca*) to climate warming across the forest–tundra ecotone

Trevor C. Lantz, Nina D. Moffat, Robert H. Fraser, and Xanthe Walker

Abstract: Shifts in the extent of the boreal forest during past warm intervals and correlations between climate and the position of the forest–tundra ecotone suggest that recent temperature increases will facilitate forest expansion into tundra ecosystems. In this study, we used a unique set of high-resolution repeat photographs to characterize white spruce (*Picea glauca* (Moench) Voss) populations in 1980 and 2015 at 52 sites across the forest–tundra transition in the Northwest Territories, Canada. We also conducted field inventories at eight sites to examine mapping accuracy, construct age distributions, and assess cone production and seed viability. Our analysis shows that stand density in the forest–tundra has increased significantly since 1980 but that the density of spruce at sites in the tundra has not changed. Age distributions constructed from field sampling also indicate that recent recruitment has occurred in the forest–tundra but not at tundra sites. The nonlinear relationship between summer temperature and seed viability suggests that recent warming has facilitated recruitment in the northern Subarctic but that cold temperatures still limit recruitment at higher latitude tundra sites. Additional research to determine the extent of changes in forest density across the northern Subarctic should be conducted to determine if similar changes are occurring across this ecotone.

Key words: treeline, vegetation change, air photographs, climate change, Arctic, boreal, Subarctic, tundra.

Résumé : Les changements au niveau de l'étendue de la forêt boréale au cours des dernières périodes chaudes et les corrélations entre le climat et la position de l'écotone forêt–toundra semblent indiquer que les augmentations récentes de la température faciliteront l'expansion du couvert forestier dans les écosystèmes de la toundra. Dans le cadre de cette étude, nous avons utilisé un ensemble unique de photographies répétées à haute résolution pour caractériser les populations d'épinettes blanches (*Picea glauca* (Moench) Voss) en 1980 et en 2015 à 52 sites dans l'ensemble de la zone de transition forêt–toundra dans les Territoires du Nord-Ouest, au Canada. Nous avons également effectué des inventaires sur le terrain à huit sites afin d'examiner la précision de la cartographie, de construire les répartitions selon l'âge et d'évaluer la production de cônes et la viabilité des semences. Notre analyse montre que la densité de peuplement dans la zone forêt–toundra a augmenté considérablement depuis 1980, mais que la densité de l'épinette dans la toundra n'a pas changé. Les répartitions selon l'âge établies à partir de l'échantillonnage sur le terrain indiquent également que des recrutements récents ont eu lieu dans zone de transition entre la

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forêt et la toundra, mais pas sur les sites de la toundra. La relation non linéaire entre la température estivale et la viabilité des semences semble indiquer que le récent réchauffement a facilité le recrutement dans la région subarctique du Nord, mais que les températures froides limitent encore le recrutement dans la toundra des latitudes plus élevées. D'autres recherches visant à déterminer l'ampleur des changements de la densité forestière dans la sous-région nordique devraient être menées pour déterminer si des changements semblables se produisent dans cet écotone. [Traduit par la Rédaction]

Mots-clés : limite forestière, changement de végétation, photographies aériennes, changement climatique, arctique, boréal, subarctique, toundra.

Introduction

Global climate change is expected to alter the structure and composition of vegetation in the Arctic and Subarctic (Epstein et al. 2004; ACIA 2005; Raynolds et al. 2008; Pearson et al. 2013). At regional scales, changes in vegetation are likely to impact wildlife habitat quality, ground temperatures, wildfire risk, and the stability of northern infrastructure (Blok et al. 2010; Cahoon et al. 2012; Lantz et al. 2013; Kokelj et al. 2017; Rickbeil et al. 2018). At the global scale, changes in vegetation structure and composition will feed back to the climate system by altering surface energy balance and carbon sequestration and storage (Chapin et al. 2000; Harding et al. 2002). One of the most dramatic shifts in northern vegetation structure and composition is predicted to occur where forested ecosystems transition to Arctic tundra (Epstein et al. 2004; ACIA 2005). This broad transition zone begins at the limit of continuous forest, consists of a mosaic of open woodlands and upland tundra, and is referred to as the forest–tundra ecotone. Moving northward across this area, the portion of the landscape occupied by trees declines until it reaches <0.1% at the southern boundary of the Low Arctic (Timoney et al. 1992; Payette et al. 2001).

Several lines of evidence suggest that recent temperature increases at high latitudes (Comiso and Hall 2014) are likely to cause increases in stand density and result in a northward shift of the forest–tundra boundary. Biogeographic studies show a strong association with the position of the forest–tundra transition and summer temperature (Hare 1950; Timoney et al. 1992; Epstein et al. 2004), and most global vegetation models project the northward expansion of forest with increasing temperatures (Harding et al. 2002; Kaplan and New 2006; Pearson et al. 2013). Paleoecological studies across the Subarctic also show that past temperature increases have been associated with shifts in the position of the forest–tundra ecotone (Spear 1993; MacDonald et al. 2000; Seppa et al. 2002). Despite these predictions, evidence from previous field research is mixed. A few regions show small shifts in response to warming (Suarez et al. 1999; Lloyd et al. 2002; Payette 2007; Mamet and Kershaw 2012), but the majority exhibit stability (Morin and Payette 1984; Payette and Filion 1985; Scott et al. 1987; Lescop-Sinclair and Payette 1995; Szeicz and Macdonald 1995; Lavoie and Payette 1996; MacDonald et al. 1998, 2008; Gamache and Payette 2005; Wilmking et al. 2012). Studies at sites across the circumpolar also show that climate warming following the Little Ice Age and during the early to mid–20th century increased stand density at the northern edge of the Subarctic forest but did not change the position of northern boundary of the forest–tundra (Morin and Payette 1984; Payette and Filion 1985; Scott et al. 1987; Lescop-Sinclair and Payette 1995; Szeicz and Macdonald 1995; Lavoie and Payette 1996; MacDonald et al. 1998, 2008; Wilmking et al. 2012).

Observations of low cone production and seed viability at the forest–tundra boundary suggest that expansion may be limited by a lack of viable seed (Elliott 1979; Black and Bliss 1980; Lescop-Sinclair and Payette 1995; Wilmking and Juday 2005; Walker et al. 2012; Wilmking et al. 2012; Brown et al. 2019). Other factors that have been invoked to explain

Fig. 1. Map showing the location of the four aerial photograph flight lines across the study area. Each of these flight lines is shown as a solid grey line and is lettered alphabetically from north to south. The dashed line with a thick white border represents the boundary between the northern forest–tundra and the tundra (Timoney et al. 1992). Twenty-four aerial photograph pairs (1980 and 2015) across the study area were used to establish 13 plots along each flight line. The inset map shows the position of our study area in the western Arctic.
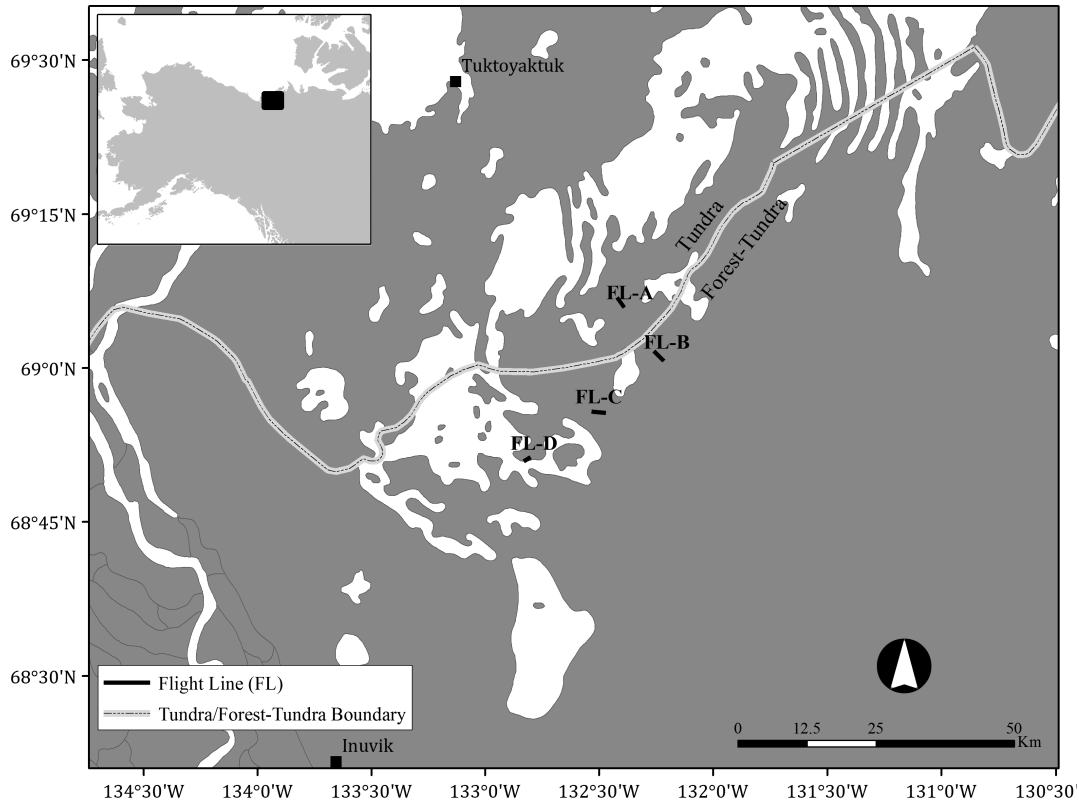

the stability of this ecotone in response to warmer temperatures include a lack of suitable microsites, topographic constraints, low nutrient availability, herbivory, and competition (Rupp et al. 2001; Sullivan and Sveinbjornsson 2010; Aune et al. 2011; Dufour-Tremblay et al. 2012; Mamet and Kershaw 2013b; Jameson et al. 2015). To assess the response of the forest–tundra ecotone to temperature increases in the last several decades, case studies exploring recent changes are required. In this study, we take advantage of an exceptional collection of high-resolution repeat photographs (1980 and 2015) to explore the population dynamics of white spruce (*Picea glauca* (Moench) Voss) across the forest–tundra ecotone in the Northwest Territories, Canada. We combine aerial photograph analysis with field sampling to meet two specific objectives: (1) determine if recent increases in temperature have altered spruce stand density across the forest–tundra ecotone and (2) test the hypothesis that cone production, seed viability, and growth across this ecotone are limited by temperature.

Methods

Study area

This study focussed on the forest–tundra ecotone across the Tuktoyaktuk Coastlands in the Northwest Territories (Fig. 1). Moving northward across this region, white spruce woodlands quickly transition to shrub- and graminoid-dominated tundra (Lantz et al. 2010a; Ecosystem Classification Group 2012). The boundary between the forest–tundra and tundra, as mapped

Fig. 2. Air temperature record for the Inuvik area from 1926 to 2017. The solid lines show the least squares regressions for (A) mean annual temperature ($F_{[1,90]} = 57.4$, $P < 0.001$, $r^2 = 0.39$) and (B) mean summer (June–August) temperature ($F_{[1,89]} = 21.9$, $P < 0.001$, $r^2 = 0.20$). The dashed lines show the 95% confidence interval. Temperature data are from Environment Canada and can be obtained at http://climate.weather.gc.ca/historical_data/search_historic_data_e.html. Data from 1957 to 2017 are from Inuvik and data from 1926 to 1957 are from Aklavik.
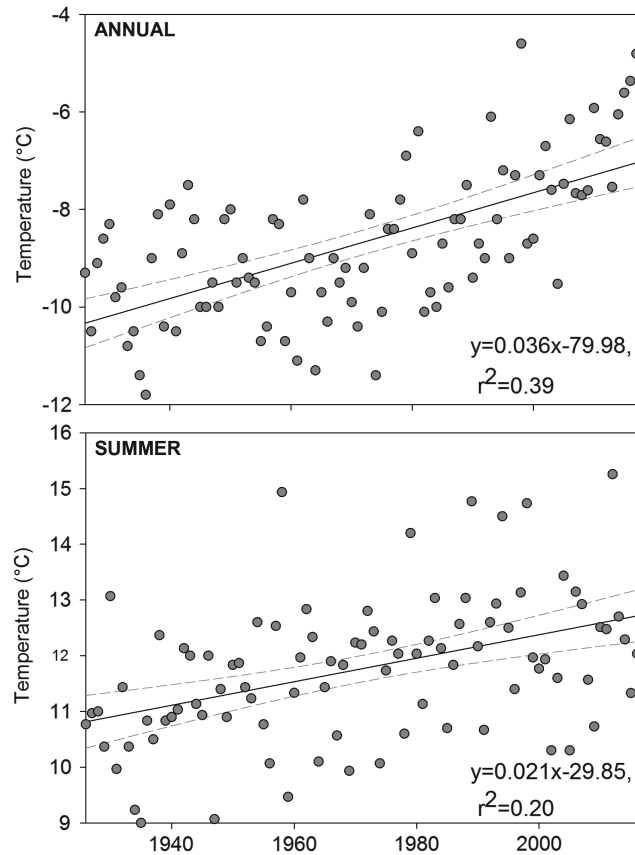
by Timoney et al. (1992), passes through the centre of our study area, but small stands of white spruce and white spruce tree islands occur up to 60 km north of this line (Walker et al. 2012). This gently rolling landscape is underlain primarily by clayey silts and ice-rich tills (Aylsworth et al. 2000; Agriculture and Agri-Food Canada 2011), but organic soils are also commonly found in the polygonal terrain that has developed in drained lake basins (Kokelj et al. 2014; Steedman et al. 2017). The climate of this region is cold, with mean temperatures <0 °C from October through April. During the short summer, the mean temperatures in Inuvik and Tuktoyaktuk are 12.2 and 8.8 °C, respectively (Environment Canada 2006). Data from multiple locations show that there is a linear decline in summer air temperature of approximately 3 °C/degree latitude across the study area (Lantz et al. 2010*b*). Mean annual and summer air temperatures in this region have warmed by 3.1 and 1.9 °C, respectively, since 1926 (Fig. 2) and permafrost temperatures have increased by approximately 2 °C (Kokelj et al. 2017).

Repeat photographs

To estimate changes in spruce density and height across the study area, we compared high-resolution aerial photographs from 1980 and 2015. The 1980 photographs were taken

between 6 and 8 August 1980 using using two Vinten 492 S/N cameras with 76.2 mm lenses attached to the wingtips of a Cessna 180. These images were captured in colour-infrared using Kodak Aerochrome Type 2443 film (Sims 1983). In 2013, an original set of film positives were scanned at 2400 dpi. These images were recaptured using a Nikon D7000 with a 35 mm lens mounted beneath a Bell 206LR helicopter in the summers of 2013 and 2015. The spatial resolution in both photograph sets is equivalent to 1:2000 scale or ~2–4 cm (Sims 1983; Moffat et al. 2016). Both the 1980 and 2015 photographs were captured under sunny conditions and clearly show the shadows of trees and shrubs. The flight lines analyzed in this paper ranged in length from 1.6 to 2.7 km, were located near the northern limit of forest–tundra, and were all captured on 30 June 2015 (Fig. 1). These flight lines did not overlap with fires documented by previous research (Fraser et al. 2014b; GNWT 2016) and sites visited in the field did not show evidence of recent fire (charcoal, fire scars, etc.).

Along the flight lines, we selected 24 photo pairs (between five and eight per flight line) that included spruce trees in one or both years. Each photo pair covered an area of approximately 1 ha. Since the terrain in the study area is relatively flat, photographs were georeferenced in ArcMap 10.3 using linear transformation and nearest neighbour resampling methods. In the first part of this process, we georeferenced the 1980 CIR images to 2004 orthophotographs. The resulting images had an average RMS error of 0.52 m (range: 0.08–1.22 m) and used the same coordinate system as the 2004 orthophotographs (NAD 1983 UTM 8N). Subsequently, we georeferenced the 2015 images using the geotifs from 1980 as a reference. The images produced during this process had an average RMS error of ~0.33 m (range: 0.11–0.83 m).

To examine changes in spruce population dynamics in the stands covered by the repeat images, we created 13 circular plots (radius = 20 m, area = 1256.6 m^2) along each flight line for a total of 52 plots across the entire study area. Along flight lines where spruce woodlands were less common, multiple plots were sometimes established on a single image pair. In these instances, plots were positioned so they did not overlap. On each image, spruce trees were identified using two criteria: (1) presence of a distinct triangular shadow and (2) foliage colour (yellow–green in RGB imagery and pale pink–orange in colour-infrared imagery). For each plot and sampling time, we mapped the position of each stem, assigned a tree identification number, assessed if it was living or dead, and recorded the length of its shadow. Trees were classified as dead if they were not associated with living foliage or fell over between 1980 and 2015. The relatively open canopy conditions at our sites also allowed us to use shadow length and solar altitude to estimate the height of each tree in 1980 and 2015. Solar altitude was determined using sun altitude/azimuth charts (United States Naval Observatory 2015). These look-up tables require shadow azimuth, photograph location (latitude, longitude), date of capture, and time zone. Shadow azimuth was calculated by averaging the orientation of 6–10 shadows on each image. We assumed that trees were growing on flat terrain and calculated tree height (h_e) as $h_e = s \times \tan(a)$, where s is tree shadow length (centimetres) and a is the solar altitude of the photograph in degrees. Only trees that had a clearly visible shadow in both 1980 and 2015 imagery were included in this analysis. Subsequently, these height data was used to calculate the relative annual growth rate: (($height_{2015}$ − $height_{1980}$)/$height_{1980}$)/35 years.

Field sampling

To compare population age structure across the forest-tundra ecotone and assess the accuracy of our aerial photograph mapping, we conducted field surveys in the summer of 2016. Along each flight line, we randomly selected two plots for field sampling. At these eight sites, we established a circular plot with a radius of 15 m (706.9 m^2). High-resolution georeferenced aerial photographs and georeferenced stem maps of each site were

consulted in the field using a GPS-enabled tablet to ensure that the plot centres of our ground and aerial photograph surveys corresponded exactly. Each plot area was thoroughly searched for seedlings and all spruce stems were mapped by annotating a paper copy of the 2015 aerial photograph and recording a GPS point. The height and diameter at breast height of each tree were recorded using a laser hypsometer (Haglöf VL5) and digital calipers (Haglöf Digitech Pro). For seedlings and saplings (≤1.4 m), we recorded height using a tape measure and basal diameter using calipers. The status of each tree (living or dead) was also recorded in the field. To estimate the age of each tree, we collected two increment cores for large trees and a cross section of the entire stem for smaller stems. Samples were collected above the root collar near the base of the tree. Increment cores and stem cross sections were dried, mounted (increment cores), and sanded before being examined using a dissecting microscope to record stem ages. At some sites, we encountered clonal individuals with multiple, interconnected stems. In these instances, we recorded the height and diameter and collected increment cores of all stems, but for the purposes of analysis, we treated them as single individual and used the height and diameter of the oldest stem in the clone.

To compare seed production and viability across our study area, between 28 and 30 August 2017, we visited eight additional sites along the flight lines and two additional sites near Inuvik, Northwest Territories (Fig. 1). At each site, we randomly selected 10 mature trees (>2 m tall) and collected up to 10 cones from each tree. On 27 August 2018, we returned to six of these sites and collected cones in the same manner. All cones were allowed to dry in paper bags at room temperature. Cones opened in approximately 3 weeks, at which time the seeds were extracted, dewinged, and weighed. Germination assays were completed using 25 seeds from each tree. Seeds were soaked in water for 24 h prior to mixing them with moist sand for cold stratification at 3 °C. After 15 days, seeds were placed on moistened filter paper in Petri plates. Petri plates were kept under 20 h of light at approximately 28 °C at the University of Victoria Forest Biology Greenhouse. Petri plates were monitored daily to record germination for 30 days.

Accuracy assessments

To assess the accuracy of stand inventories using aerial photographs, we compared our results with field data collected inside eight of the circular plots. These areas had the same plot centres as the aerial photograph surveys, but had a 15 m radius. We used a 15 m radius to ensure that we could survey all of the stems within a single plot within a 2 day period. For each plot, we calculated mapping accuracy by focussing on the mature stems (≥1.5 m tall) inside the plot with a 15 m radius (706.9 m^2):

$$\text{Mapping error} = \frac{\text{number of trees}_{(\text{field})} - \text{number of trees}_{(\text{mapped})}}{\text{number of trees}_{(\text{field})}} \times 100$$

To determine the accuracy of height estimates made from the lengths of tree shadows on aeriall photographs, we compared these estimates with the heights of 90 of the same trees measured in the field (h_f) using a laser hypsometer. For each tree, we used the difference between heights ($h_f - h_e$) to calculate the average overall difference.

Statistical analysis

To test for significant differences in spruce density between 1980 and 2015 and seed production and viability, we used the GLIMMIX procedure in the SAS software package to construct linear mixed effects models (Littell 2006). For models of stem density, we treated year (1980 and 2015) and flight line as fixed effects and photograph pair as a random effect and specified our repeated measures design using the subject option to indicate that individual plots were resampled. To test for significant differences in spruce growth,

Fig. 3. Least squares regression of average summer temperature (AST) by latitude (LAT) and mean summer temperature at Inuvik (YEV) for seven sites across the study area in 2005, 2006, 2007, and 2009 ($AST = 1.11986 \times YEV - 2.4931 \times LAT + 168.57954$) ($P < 0.001$, $r^2 = 0.95$).
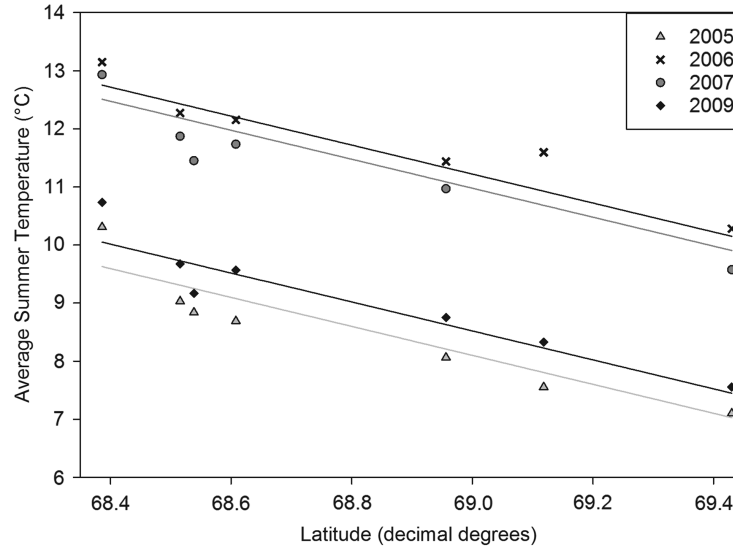
seed production, and viability across the study area, our mixed models included flight line as a fixed effect and photograph (i.e., site) as a random effect. In all models, pairwise comparisons were conducted using the adjusted P values provided by the LSMEANS option for multiple comparisons. Degrees of freedom were approximated using the Kenward–Roger method (Littell 2006).

To explore the impact of summer temperature on seed viability among years, we combined our findings with data reported by Walker (2010) for the same region in 2008 and 2009. In the first step of this analysis, we regressed air temperature data collected in 2005, 2006, 2007, and 2009 at seven sites by latitude and mean summer temperature recorded at Inuvik (Palmer et al. 2012; Environment Canada 2016). This analysis shows that there is a strong linear relationship between latitude and temperature. The slope of this relationship is consistent among years, but the severity of summer conditions varies among years (*y*-intercept) (Fig. 3). In the second step of this analysis, we used this regression model to estimate the average summer temperature at each sample site based on its latitude and the mean summer temperature at Inuvik in the year of sampling. To explore the relationship between average summer temperature and seed viability, we used a model selection approach to compare linear, lognormal, exponential, and logistic models using the lm and nls functions in R (R Development Core Team 2017). The best model was selected using AIC and AIC weights (Anderson et al. 2000).

Results

The density of the spruce woodlands that we mapped decreased with increasing latitude across the Tuktoyaktuk Coastlands in a manner consistent with previous descriptions of the forest–tundra transition (Timoney et al. 1992). In 1980, mean stand density was close to three times higher along the southernmost flight line than along the northernmost flight line (Figs. 1 and 4). Mapping from 2015 showed a similar spatial pattern but indicated that vegetation structure in this region changed significantly between 1980 and 2015.

Fig. 4. White spruce (*Picea glauca*) density in 1980 and 2015 at four flight lines across the treeline ecotone. The dashed line inside the box shows the mean, the solid line inside the box represents the median value, the ends of the boxes represent the 25th and 75th percentiles, and the whiskers show the 10th and 90th percentiles. Asterisks denote statistically significant differences between 1980 and 2015 for each flight line ($P < 0.01$).
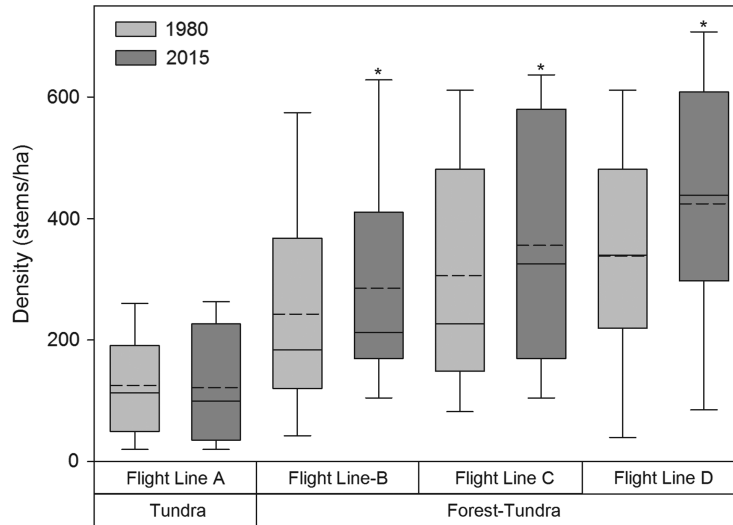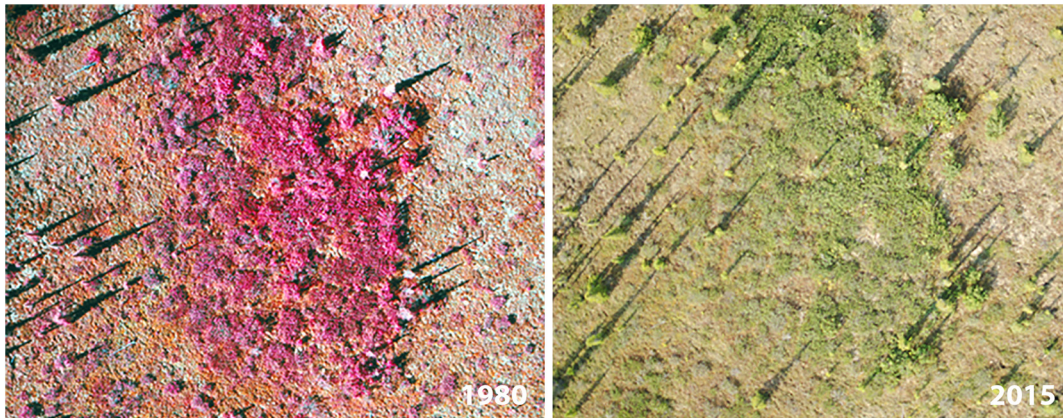

Fig. 5. Aerial photograph pair in the forest–tundra showing increasing white spruce (*Picea glauca*) density between 1980 and 2015. These images cover approximately 2700 m^2.

In the forest–tundra, average stand density increased significantly between 1980 and 2015 along all flight lines, but no change was observed in the tundra (Fig. 4). In the forest–tundra, 36 of the 39 plots that we inventoried using aerial photographs showed increased stand density. Visual inspection of these images and distance calculations show that changes were the result of recruitment in open areas (Fig. 5). Trees recruited between 1980 and 2015 were an average distance of 4 m from trees taller than 1.5 m and 71% of them were located between 1 and 7 m from trees taller than 1.5 m. The magnitude of the increase in density in the forest–tundra was higher at flight lines farther from the forest–tundra boundary. Along the southernmost flight line (D), average spruce density increased by 100 stems/ha,

Fig. 6. Aerial photograph pair in the tundra showing stable white spruce (*Picea glauca*) density between 1980 and 2015. These images cover approximately 3600 m^2.
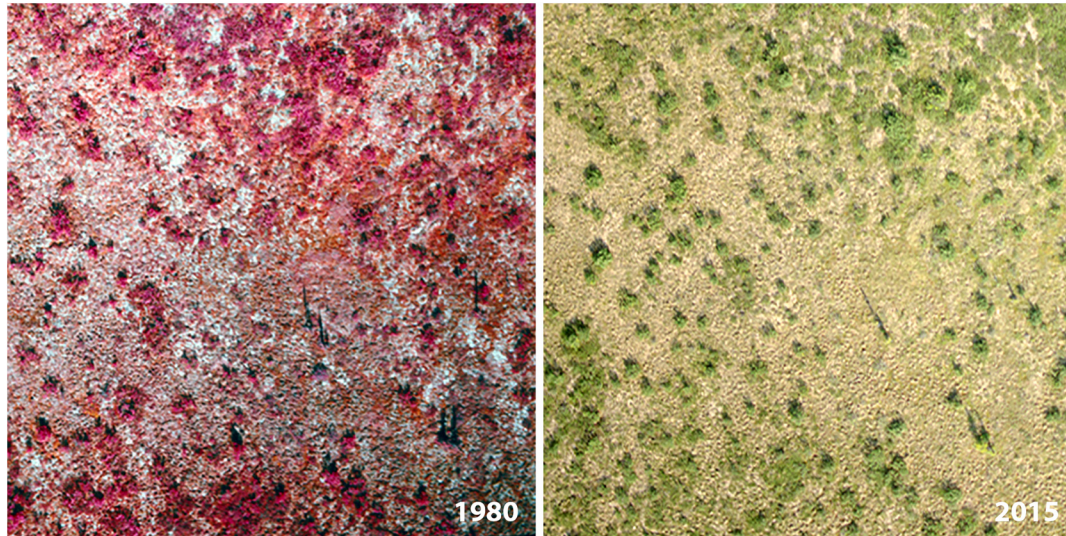
while the flight line immediately south of the tundra (B) showed an average increase of 42.1 stems/ha (Fig. 4). Spruce stands in the tundra showed little evidence of change between the two observation periods and average stem density did not change significantly over time (Figs. 4 and 6). Four of the six sites where we conducted detailed field inventories in the forest–tundra had age distributions dominated by individuals that were recruited between 1985 and 2015 (Fig. 7). Ten of the 13 plots sampled in the tundra were stable over time or showed decreases of one to four trees. Age distributions from the two tundra sites where we conducted field inventories were uneven and showed no evidence of recent recruitment (Figs. 6 and 7). Trees in the southernmost forest–tundra showed significantly greater vertical growth rates compared to trees along all other flight lines (Fig. 8).

Comparisons of field and aerial photograph inventory data showed that average mapping accuracy was 80% and indicated that our aerial photograph analysis identified the majority of trees in our sample plots (Table 1). The centimetre-scale resolution of the images from both time periods meant that we could easily identify spruce in open canopy conditions (Figs. 5 and 6). Although we could not characterize the accuracy of mapping using the 1980s photographs, based on their quality, we are confident that our stand mapping in 1980 also had high accuracy. Identifying spruce trees relied on crown colour and the presence of a shadow. It is therefore likely that we were unable to identify seedlings <10 cm tall in both time periods because they did not cast a visible shadow. Consequently, our estimates of changes are likely conservative. With the exception of one extremely dense stand, where clustering made it difficult to identify individual trees, mapping accuracy was similar across the study area. The fact that we measured increased density in forest tundra stands also indicates that our mapping is suitable for detecting change in the more open conditions at tundra sites. The average difference between tree height measured using shadow length on aerial photograph and a laser hypsometer was 0.34 m (Table 2) and indicates that this method is an effective means to estimate tree height.

Seed production was lower at more northern sites, but these differences were only significant between tundra sites and the two southernmost forest–tundra sites (Flight Line C, Flight Line D) (Fig. 9A). Flight lines A, B, C, and D all produced significantly less

Fig. 7. Age distributions of the eight white spruce (*Picea glauca*) stands sampled in the field. Each plot shows the number of stems in 5 year age classes. The dashed horizontal line shows 1980. Numbers in parentheses show the photograph and plot number. Histograms are organized with the northernmost sites at top and the southernmost sites at the bottom.
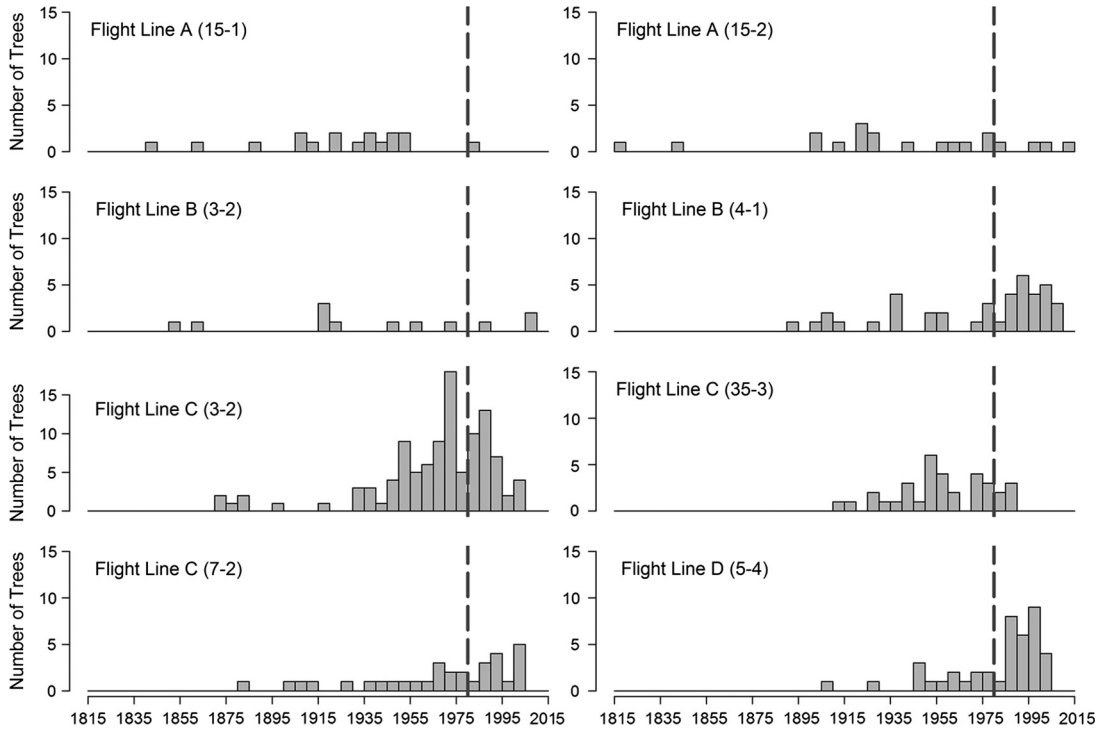

Fig. 8. Relative annual growth rate (metres per metre per year) from 1980 to 2015 measured using aerial imagery. The line inside the box represents the median value, the ends of the boxes represent the 25th and 75th percentiles, and the whiskers show the 10th and 90th percentiles. Boxes labelled with different letters are statistically different from each other ($P < 0.05$).
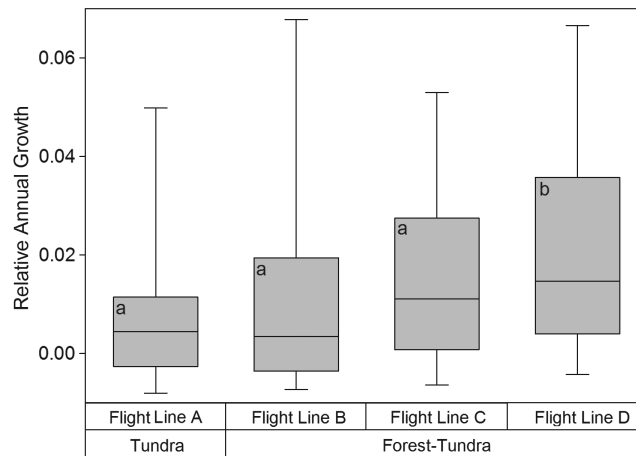
Table 1. Mapping accuracy of aerial photograph inventories estimated by comparison with field surveys.

Site and plot number	Stem density (per hectare, 2015)	% accuracy (overall)
12-1-15, 1	212	92
12-1-15, 2	42	75
12-2-3, 2	156	92
12-2-4, 1	99	78
13-1-3, 2	467	40
13-1-35, 3	184	100
13-1-7, 2	156	100
13-2-5, 4	127	60
Average		80

Table 2. Average accuracy of height estimates calculated using shadow length on aerial photographs.

Height group (m)	Number of trees	Average height difference (m) (field measurement – aerial photograph calculation)
0–1	15	0.037
>1–2	15	0.23
>2–4	32	0.45
>4–6	18	0.57
>6–8	7	0.33
>8–10	1	0.41
Average		0.34

seed than reference sites near Inuvik, approximately 70 km to the south (Fig. 9A). Seed viability was higher at more southern sites but increased variability meant that not all pairwise differences were significant (Fig. 9B). Seed viability data from multiple years (2008, 2009, 2017, and 2018) showed a strong, nonlinear relationship with mean summer temperature (MST) (Fig. 10, $P < 0.001$, $\Delta AIC = 0$, $AICw = 0.95$) (Tables 3 and 4). No viable seed was produced below 9 °C, and between 10.1 and 12 °C, viability increased from 1% to 53% (Fig. 10).

Discussion

Our analysis of a unique set of high-resolution repeat photographs shows that white spruce recruitment is altering the structure of the forest–tundra transition in the Tuktoyaktuk Coastlands but that the position of forest–tundra ecotone in this region has not changed in recent decades. This finding is consistent with the majority of studies at the latitudinal limit of trees, which show that multiple warm episodes over the last 200 years have not displaced the northern boundary of the forest–tundra ecotone (Morin and Payette 1984; Payette and Filion 1985; Scott et al. 1987; Lescop-Sinclair and Payette 1995; Szeicz and Macdonald 1995; Lavoie and Payette 1996; MacDonald et al. 1998, 2008; Wilmking et al. 2012). Observed increases in stand density at forest tundra sites in the Tuktoyaktuk Coastlands are also consistent with previous research showing that recent and historic warming episodes have been associated with increased spruce density within the northern forest tundra (Morin and Payette 1984; Payette and Filion 1985; Scott et al. 1987; Lavoie and Payette 1994; Szeicz and Macdonald 1995; MacDonald et al. 1998, 2008; Mamet and Kershaw 2012; Wilmking et al. 2012; Frost and Epstein 2014). Taken together, these observations raise the possibility that the density of Subarctic woodlands is

Fig. 9. White spruce (*Picea glauca*) reproductive effort across the study area: (A) seed production and (B) seed viability. The dashed line inside the box shows the mean, the solid black line inside the box represents the median value, the ends of the boxes represent the 25th and 75th percentiles, and the whiskers show the 10th and 90th percentiles. Boxes labelled with different letters are statistically different from each other ($P < 0.05$).
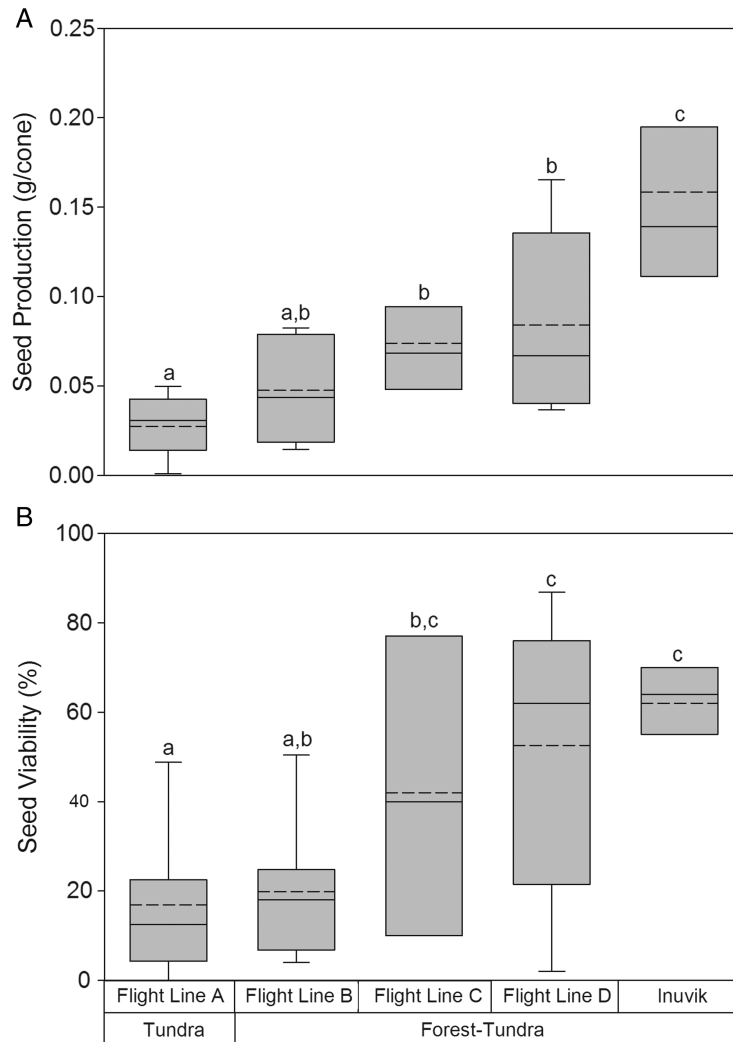
increasing across the circumarctic and highlights the need for additional research to determine the extent and magnitude of change.

While historical Landsat data have proven valuable to study Arctic shrub proliferation (McManus et al. 2012; Raynolds et al. 2013; Fraser et al. 2014a), the dominance of shrub and graminoid vegetation cover across the forest–tundra in northwestern Canada makes it difficult to use Landsat to discern the fine-scale, decadal changes in spruce density documented in this analysis. A global archive of high-resolution (1–4 m) optical satellite imagery has been expanding since the IKONOS and Quickbird satellites were launched in 1999 and 2001. These images can provide an almost 20 year baseline for change studies, but using them to detect early shifts in the density of juvenile spruce trees within a matrix of expanding tall shrub vegetation (Lantz et al. 2013; Moffat et al. 2016) is likely to be

Fig. 10. Relationship between mean summer temperature (June–August) and white spruce (*Picea glauca*) seed viability. Points show seed viability in 2008 (■), 2009 (▲), 2017 (●), and 2018 (♦), the solid line shows the logistic model fit, and the dashed lines show the 95% confidence interval. Residual deviance for this model is 7.6 and null deviance is 21.4 (Table 3).
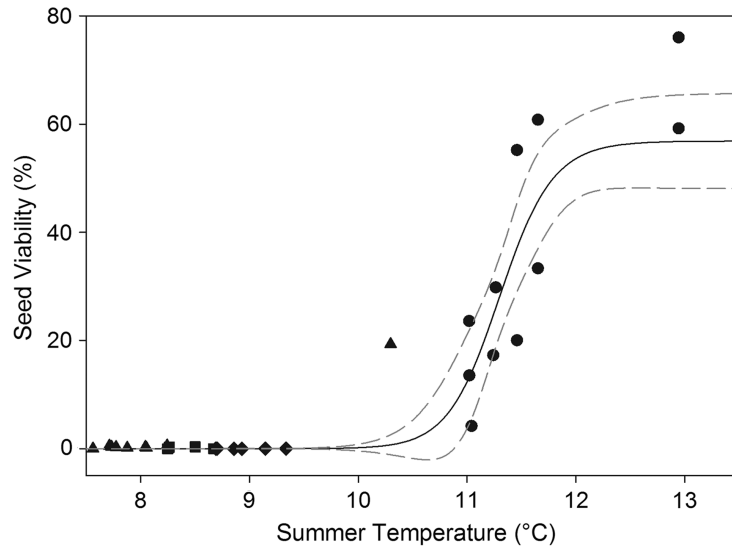

Table 3. Model selection results for seed viability (*v*) as a function of mean summer temperature (*t*) in the Tuktoyaktuk Coastlands.

Model	Equation	AIC	ΔAIC	AIC weight	Residual deviance	Residual df	Log likelihood
Linear	$v = at + b$	250.3	24.9	0	11.4	30	−122.1
Quadratic	$v = at + bt^2 + c$	231.6	6.2	0.04	8.4	29	−111.8
Exponential	$v = e^{ax + b}$	236.3	10.9	0	9.1	30	−115.2
Logistic	$v = \frac{a}{1+e^{\frac{b-t}{c}}}$	225.4	0.0	0.953	7.6	29	−108.7

Note: Null model deviance was 21.4 on 31 degrees of freedom (df).

Table 4. Estimated parameters for the logistic model of seed viability (Table 3).

Parameter	Estimate	Standard error	t	P
a	69.01507	5.871	11.938	1.03×10^{-12}
b	11.44060	0.085	133.99	$<2 \times 10^{-16}$
c	0.32326	0.084	3.83	0.00063

challenging (Montesano et al. 2016; Loranty et al. 2018). The rarity of historical aerial photographs with comparable resolution makes it unlikely that analyses similar to this one could be completed in other regions. Nevertheless, the unique photographs analysed here point to the possibility of using UAV-based mapping and structure from motion photogrammetry to provide highly detailed photographic surveys and vegetation structural models within forest–tundra ecosystems (Fraser et al. 2016). This approach could be used to establish a baseline for monitoring small changes in spruce density and size. Monitoring changes in the northern forest–tundra is important because changes in vegetation structure have the potential to alter ecological processes with feedbacks to the climate

system including surface energy balance (Chapin et al. 2000, 2005), fire frequency and intensity (Higuera et al. 2009; Hu et al. 2015), carbon sequestration (Chapin et al. 2000), and animal habitat use (Joly et al. 2009; Rickbeil et al. 2018).

It is likely that increased spruce density in the forest–tundra of the Tuktoyaktuk Coastlands was caused by regional climate warming. White spruce reproduction is temperature limited (Figs. 9 and 10) (Elliott 1979; Walker et al. 2012), and our data indicate that recent changes in summer temperature in our study region have been large enough to significantly impact reproduction. Predictions of seed viability at our southernmost forest–tundra site using the model shown in Fig. 10 suggest that only eight of the summers between 1926 and 1970 (18%) were warm enough to yield average seed viability >2% (Supplementary Fig. S1[1]). Following 1970, 67% of summers (31/46) were warmer than the threshold associated with 2% seed viability (Supplementary Fig. S1[1]). Our field data also indicate that warmer temperatures are likely to have increased both the quality and the quantity of spruce seed (Fig. 9). Recruitment pulses in the spruce stands that we sampled in the field were concentrated between 1985 and 2000, an interval that included three of the five warmest summers in the last 92 years (Fig. 2). The conclusion that increased stand density was caused by warming is also consistent with our observation that changes in density were largest at warmer sites in the southern portion of the study area and previous research showing correlations between white spruce abundance, recruitment, and summer temperature (Szeicz and Macdonald 1995; Miller et al. 2017).

Our observations suggest that stand density at tundra sites in the Tuktoyaktuk Coastlands remained stable because temperature increases at these sites have not been large enough to facilitate recruitment. Although warming has almost certainly increased seed production at tundra sites, predictions using the model shown in Fig. 10 suggest that since 1970, 65% of summers at our northernmost sites were below the threshold associated with 2% viable seed (Supplementary Fig. S1[1]). Since germination, growth, and survival are all temperature limited, successful recruitment likely requires a succession of warm summers (Black and Bliss 1980; Szeicz and Macdonald 1995; Hobbie and Chapin 1998; Wolken et al. 2011; Wilmking et al. 2012; Brown et al. 2019), which have not occurred at sites in the tundra (Supplementary Fig. S1[1]). The lower relative growth rates of individuals along more northern flight lines are also indicative of temperature stress likely to limit seedling survival and growth.

Continued increases in temperature will likely result in spruce expansion at sites north of the forest–tundra boundary, but predicting the timing of this shift is not straightforward. Our observation that current summer temperatures are near a nonlinear reproductive threshold for white spruce, combined with evidence that the position of the forest–tundra ecotone is shifting at sites in Alaska (Suarez et al. 1999; Lloyd et al. 2002), Manitoba (Mamet and Kershaw 2012), and Labrador (Payette 2007), raises the possibility that this shift is imminent. Research at other sites also indicates that when viable seed is present, biotic and abiotic conditions can significantly impact population dynamics. Key factors include microsite availability and quality (Black and Bliss 1980; Hobbie and Chapin 1998; Sullivan and Sveinbjornsson 2010; Dufour-Tremblay et al. 2012; Sutinen et al. 2012; Mamet and Kershaw 2013a), seed predation (Jameson et al. 2015), and topography and snowpack (Mamet and Kershaw 2013a). As temperatures increase in the Tuktoyaktuk Coastlands, it is likely that these factors will begin to exert a growing influence on the population dynamics of white spruce. Understanding the relative influence of these processes on population dynamics will require additional field research.

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[1]Supplementary material is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/as-2018-0012.

Conclusions

Based on our analysis of the data presented in this paper we draw the following conclusions: (1) temperature-driven shifts in seed production and viability have facilitated increased white spruce density in the forest–tundra of the Tuktoyaktuk Coastlands, (2) spruce populations at higher latitude tundra sites have remained stable because cold temperatures still limit recruitment in this area, and (3) additional research is needed to characterize changes in forest density across the northern Subarctic.

Acknowledgements

References

ACIA (*Editors*). 2005. Impacts of a warming Arctic: Arctic Climate Impact Assessment. Cambridge University Press, Cambridge, UK.

Agriculture and Agri-Food Canada. 2011. Soil landscapes of Canada (SLC): version 3.2. Canadian Soil Information System, National Soil DataBase, Government of Canada [online]. Available from http://sis.agr.gc.ca/cansis/nsdb/slc/index.html [accessed 15 April 2015].

Anderson, D.R., Burnham, K.P., and Thompson, W.L. 2000. Null hypothesis testing: problems, prevalence, and an alternative. J. Wildl. Manage. **64**: 912–923. doi: 10.2307/3803199.

Aune, S., Hofgaard, A., and Söderström, L. 2011. Contrasting climate- and land-use-driven tree encroachment patterns of subarctic tundra in northern Norway and the Kola Peninsula. Can. J. For. Res. **41**: 437–449. doi: 10.1139/X10-086.

Aylsworth, J.M., Burgess, M.M., Desrochers, D.T., Duk-Rodkin, A., Robertson, T., and Traynor, J.A. 2000. Surficial geology, subsurface materials, and thaw sensitivity of sediments. *In* The physical environment of the Mackenzie Valley, Northwest Territories: a base line for the assessment of environmental change. *Edited by* L.D. Dyke and G.R. Brooks. Geological Survey of Canada Bulletin 547. Geological Survey of Canada, Ottawa, Ont. pp. 41–48.

Black, R.A., and Bliss, L.C. 1980. Reproductive ecology of *Picea mariana* (Mill.) BSP., at tree line near Inuvik, Northwest Territories, Canada. Ecol. Monogr. **50**: 331–354. doi: 10.2307/2937255.

Blok, D., Heijmans, M.M.P.D., Schaepman-Strub, G., Kononov, A.V., Maximov, T.C., and Berendse, F. 2010. Shrub expansion may reduce summer permafrost thaw in Siberian tundra. Glob. Change Biol. **16**: 1296–1305. doi: 10.1111/j.1365-2486.2009.02110.x.

Brown, C.D., Dufour-Tremblay, G., Jameson, R.G., Mamet, S.D., Trant, A.J., Walker, X.J., Boudreau, S., Harper, K.A., Henry, G.H., Hermanutz, L., Hofgaard, A., Isaeva, L., Kershaw, G.P., and Johnstone, J.F. 2019. Reproduction as a bottleneck to treeline advance across the circumarctic forest tundra ecotone. Ecography, **42**: 137–147. doi: 10.1111/ecog.03733.

Cahoon, S.M.P., Sullivan, P.F., Shaver, G.R., Welker, J.M., and Post, E. 2012. Interactions among shrub cover and the soil microclimate may determine future Arctic carbon budgets. Ecol. Lett. **15**: 1415–1422. doi: 10.1111/j.1461-0248.2012.01865.x. PMID: 22938383.

Chapin, F.S., McGuire, A.D., Randerson, J., Pielke, R., Baldocchi, D., Hobbie, S.E., Roulet, N., Eugster, W., Kasischke, E., Rastetter, E.B., Zimov, S.A., and Running, S.W. 2000. Arctic and boreal ecosystems of western North America as components of the climate system. Glob. Change Biol. **6**: 211–223. doi: 10.1046/j.1365-2486.2000.06022.x.

Chapin, F.S., Sturm, M., Serreze, M.C., McFadden, J.P., Key, J.R., Lloyd, A.H., McGuire, A.D., Rupp, T.S., Lynch, A.H., Schimel, J.P., Beringer, J., Chapman, W.L., Epstein, H.E., Euskirchen, E.S., Hinzman, L.D., Jia, G., Ping, C.L., Tape, K.D., Thompson, C.D.C., Walker, D.A., and Welker, J.M. 2005. Role of land-surface changes in Arctic summer warming. Science, **310**: 657–660. doi: 10.1126/science.1117368. PMID: 16179434.

Comiso, J.C., and Hall, D.K. 2014. Climate trends in the Arctic as observed from space. Wiley Interdiscip. Rev. Clim. Change, **5**: 389–409. doi: 10.1002/wcc.277.

Dufour-Tremblay, G., Levesque, E., and Boudreau, S. 2012. Dynamics at the treeline: differential responses of *Picea mariana* and *Larix laricina* to climate change in eastern subarctic Québec. Environ. Res. Lett. **7**: 044038. doi: 10.1088/1748-9326/7/4/044038.

Ecosystem Classification Group. 2012. Ecological regions of the Northwest Territories — Southern Arctic. Department of Environment and Natural Resources, Government of the Northwest Territories, Yellowknife, N.W.T.

Elliott, D.L. 1979. The current regenerative capacity of the northern Canadian trees, Keewatin, N.W.T., Canada: some preliminary observations. Arct. Alp. Res. **11**: 243–251. doi: 10.2307/1550648.

Environment Canada. 2006. Canadian climate normals. Environment Canada [online]. Available from http://www.climate.weatheroffice.ec.gc.ca/climateData/monthlydata_e.html.

Environment Canada. 2016. National climate data and information archive [online]. Available from http://climate.weather.gc.ca/.

Epstein, H.E., Beringer, J., Gould, W.A., Lloyd, A.H., Thompson, C.D., Chapin, F.S., Michaelson, G.J., Ping, C.L., Rupp, T.S., and Walker, D.A. 2004. The nature of spatial transitions in the Arctic. J. Biogeogr. **31**: 1917–1933. doi: 10.1111/j.1365-2699.2004.01140.x.

Fraser, R.H., Lantz, T.C., Olthof, I., Kokelj, S.V., and Sims, R.A. 2014*a*. Warming-induced shrub expansion and lichen decline in the Western Canadian Arctic. Ecosystems, **17**: 1151–1168. doi: 10.1007/s10021-014-9783-3.

Fraser, R.H., Olthof, I., Kokelj, S.V., Lantz, T.C., Lacelle, D., Brooker, A., Wolfe, S., and Schwarz, S. 2014*b*. Detecting landscape changes in high latitude environments using landsat trend analysis: 1. Visualization. Remote Sens. **6**: 11533–11557. doi: 10.3390/rs61111533.

Fraser, R.H., Olthof, I., Lantz, T.C., and Schmit, C. 2016. UAV photogrammetry for mapping vegetation in the low-Arctic. Arct. Sci. **2**: 79–102. doi: 10.1139/as-2016-0008.

Frost, G.V., and Epstein, H.E. 2014. Tall shrub and tree expansion in Siberian tundra ecotones since the 1960s. Glob. Change Biol. **20**: 1264–1277. doi: 10.1111/gcb.12406.

Gamache, I., and Payette, S. 2005. Latitudinal response of subarctic tree lines to recent climate change in eastern Canada. J. Biogeogr. **32**: 849–862. doi: 10.1111/j.1365-2699.2004.01182.x.

GNWT. 2016. Fire history of the Northwest Territories [online]. Available from geomatics.gov.nt.ca.

Harding, R., Kuhry, P., Christensen, T.R., Sykes, M.T., Dankers, R., and van der Linden, S. 2002. Climate feedbacks at the tundra–taiga interface. Ambio, Special Report Number 12: 47–55. PMID: 12374059.

Hare, F.K. 1950. Climate and zonal divisions of the boreal forest formation in eastern Canada. Geogr. Rev. **40**: 615–635. doi: 10.2307/211106.

Higuera, P.E., Brubaker, L.B., Anderson, P.M., Hu, F.S., and Brown, T.A. 2009. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. Ecol. Monogr. **79**: 201–219. doi: 10.1890/07-2019.1.

Hobbie, S.E., and Chapin, F.S., III. 1998. An experimental test of limits to tree establishment in Arctic tundra. J. Ecol. **86**: 449–461. doi: 10.1046/j.1365-2745.1998.00278.x.

Hu, F.S., Higuera, P.E., Duffy, P., Chipman, M.L., Rocha, A.V., Young, A.M., Kelly, R., and Dietze, M.C. 2015. Arctic tundra fires: natural variability and responses to climate change. Front. Ecol. Environ. **13**: 369–377. doi: 10.1890/150063.

Jameson, R.G., Trant, A.J., and Hermanutz, L. 2015. Insects can limit seed productivity at the treeline. Can. J. For. Res. **45**: 286–296. doi: 10.1139/cjfr-2014-0385.

Joly, K., Jandt, R.R., and Klein, D.R. 2009. Decrease of lichens in Arctic ecosystems: the role of wildfire, caribou, reindeer, competition and climate in north-western Alaska. Polar Res. **28**: 433–442. doi: 10.1111/j.1751-8369.2009.00113.x.

Kaplan, J.O., and New, M. 2006. Arctic climate change with a 2 °C global warming: timing, climate patterns and vegetation change. Clim. Change, **79**: 213–241. doi: 10.1007/s10584-006-9113-7.

Kokelj, S.V., Lantz, T.C., Wolfe, S.A., Kanigan, J.C., Morse, P.D., Coutts, R., Molina-Giraldo, N., and Burn, C.R. 2014. Distribution and activity of ice wedges across the forest–tundra transition, western Arctic Canada. J. Geophys. Res.: Earth Surf. **119**: 2032–2047. doi: 10.1002/2014JF003085.

Kokelj, S.V., Palmer, M.J., Lantz, T.C., and Burn, C.R. 2017. Ground temperatures and permafrost warming from forest to tundra, Tuktoyaktuk Coastlands and Anderson Plain, NWT, Canada. Permafrost Periglac. Process. **28**: 543–551. doi: 10.1002/ppp.1934.

Lantz, T.C., Gergel, S.E., and Kokelj, S.V. 2010*a*. Spatial heterogeneity in the shrub tundra ecotone in the Mackenzie Delta region, Northwest Territories: implications for Arctic environmental change. Ecosystems, **13**: 194–204. doi: 10.1007/s10021-009-9310-0.

Lantz, T.C., Gergel, S.E., and Henry, G.H.R. 2010*b*. Response of green alder (*Alnus viridis* subsp. *fruticosa*) patch dynamics and plant community composition to fire and regional temperature in north-western Canada. J. Biogeogr. **37**: 1597–1610. doi: 10.1111/j.1365-2699.2010.02317.x.

Lantz, T.C., Marsh, P., and Kokelj, S.V. 2013. Recent shrub proliferation in the Mackenzie Delta uplands and microclimatic implications. Ecosystems, **16**: 47–59. doi: 10.1007/s10021-012-9595-2.

Lavoie, C., and Payette, S. 1994. Recent fluctuations of the lichen–spruce forest limit in subarctic Quebec. J. Ecol. **82**: 725–734. doi: 10.2307/2261438.

Lavoie, C., and Payette, S. 1996. The long-term stability of the boreal forest limit in subarctic Quebec. Ecology, **77**: 1226–1233. doi: 10.2307/2265591.

Lescop-Sinclair, K., and Payette, S. 1995. Recent advance of the arctic treeline along the eastern coast of Hudson Bay. J. Ecol. **83**: 929–936. doi: 10.2307/2261175.

Littell, R.C. 2006. SAS for mixed models. 2nd ed. SAS Institute Inc., Cary, NC, USA.

Lloyd, A.H., Rupp, T.S., Fastie, C.L., and Starfield, A.M. 2002. Patterns and dynamics of treeline advance on the Seward Peninsula, Alaska. J. Geophys. Res.: Atmos. **107**: ALT 2-1–ALT 2-15. doi: 10.1029/2001JD000852.

Loranty, M., Davydov, S., Kropp, H., Alexander, H., Mack, M., Natali, S., and Zimov, N. 2018. Vegetation indices do not capture forest cover variation in upland Siberian larch forests. Remote Sens. **10**: 1686. doi: 10.3390/rs10111686.

MacDonald, G.M., Szeicz, J.M., Claricoates, J., and Dale, K.A. 1998. Response of the central Canadian treeline to recent climatic changes. Ann. Assoc. Am. Geogr. **88**: 183–208. doi: 10.1111/1467-8306.00090.

MacDonald, G.M., Velichko, A.A., Kremenetski, C.V., Borisova, O.K., Goleva, A.A., Andreev, A.A., Cwynar, L.C., Riding, R.T., Forman, S.L., Edwards, T.W.D., Aravena, R., Hammarlund, D., Szeicz, J.M., and Gattaulin, V.N. 2000. Holocene treeline history and climate change across northern Eurasia. Quat. Res. **53**: 302–311. doi: 10.1006/qres.1999.2123.

MacDonald, G.M., Kremenetski, K.V., and Beilman, D.W. 2008. Climate change and the northern Russian treeline zone. Philos. Trans. R. Soc., B, **363**: 2283–2299. doi: 10.1098/rstb.2007.2200.

Mamet, S.D., and Kershaw, G.P. 2012. Subarctic and alpine tree line dynamics during the last 400 years in north-western and central Canada. J. Biogeogr. **39**: 855–868. doi: 10.1111/j.1365-2699.2011.02642.x.

Mamet, S.D., and Kershaw, G.P. 2013*a*. Multi-scale analysis of environmental conditions and conifer seedling distribution across the treeline ecotone of northern Manitoba, Canada. Ecosystems, **16**: 295–309. doi: 10.1007/s10021-012-9614-3.

Mamet, S.D., and Kershaw, G.P. 2013*b*. Age-dependency, climate, and environmental controls of recent tree growth trends at subarctic and alpine treelines. Dendrochronologia, **31**: 75–87. doi: 10.1016/j.dendro.2012.08.002.

McManus, K.M., Morton, D.C., Masek, J.G., Wang, D.D., Sexton, J.O., Nagol, J.R., Ropars, P., and Boudreau, S. 2012. Satellite-based evidence for shrub and graminoid tundra expansion in northern Quebec from 1986 to 2010. Glob. Change Biol. **18**: 2313–2323. doi: 10.1111/j.1365-2486.2012.02708.x.

Miller, A.E., Wilson, T.L., Sherriff, R.L., and Walton, J. 2017. Warming drives a front of white spruce establishment near western treeline, Alaska. Glob. Change Biol. **23**: 5509–5522. doi: 10.1111/gcb.13814.

Moffat, N.D., Lantz, T.C., Fraser, R.H., and Olthof, I. 2016. Recent vegetation change (1980–2013) in the tundra ecosystems of the Tuktoyaktuk Coastlands, NWT, Canada. Arct. Antarct. Alp. Res. **48**: 581–597. doi: 10.1657/AAAR0015-063.

Montesano, P.M., Neigh, C.S.R., Sexton, J., Feng, M., Channan, S., Ranson, K.J., and Townshend, J.R. 2016. Calibration and validation of landsat tree cover in the taiga–tundra ecotone. Remote Sens. **8**: 551. doi: 10.3390/rs8070551.

Morin, A., and Payette, S. 1984. Expansion récente du mélèze à la limite des forêts (Québec nordique). Can. J. Bot. **62**: 1404–1408. doi: 10.1139/b84-191.

Palmer, M.J., Burn, C.R., and Kokelj, S.V. 2012. Factors influencing permafrost temperatures across tree line in the uplands east of the Mackenzie Delta, 2004–2010. Can. J. Earth Sci. **49**: 877–894. doi: 10.1139/e2012-002.

Payette, S. 2007. Contrasted dynamics of northern Labrador tree lines caused by climate change and migrational lag. Ecology, **88**: 770–780. doi: 10.1890/06-0265. PMID: 17503604.

Payette, S., and Filion, L. 1985. White spruce expansion at the tree line and recent climatic change. Can. J. For. Res. **15**: 241–251. doi: 10.1139/x85-042.

Payette, S., Fortin, M.J., and Gamache, I. 2001. The subarctic forest–tundra: the structure of a biome in a changing climate: the shifting of local subarctic tree lines throughout the forest–tundra biome, which is linked to ecological processes at different spatiotemporal scales, will reflect future global changes in climate. BioScience, **51**: 709–718. doi: 10.1641/0006-3568(2001)051[0709:TSFTTS]2.0.CO;2.

Pearson, R.G., Phillips, S.J., Loranty, M.M., Beck, P.S.A., Damoulas, T., Knight, S.J., and Goetz, S.J. 2013. Shifts in Arctic vegetation and associated feedbacks under climate change. Nat. Clim. Change, **3**: 673–677. doi: 10.1038/nclimate1858.

R Development Core Team. 2017. R: a programming environment for data analysis and graphics. Version 3.4.3. R Foundation for Statistical Computing, Vienna, Austria [online]. Available from http://www.R-project.org.

Raynolds, M.K., Comiso, J.C., Walker, D.A., and Verbyla, D. 2008. Relationship between satellite-derived land surface temperatures, arctic vegetation types, and NDVI. Remote Sens. Environ. **112**: 1884–1894. doi: 10.1016/j.rse.2007.09.008.

Raynolds, M.K., Walker, D.A., Verbyla, D., and Munger, C.A. 2013. Patterns of change within a tundra landscape: 22-year landsat NDVI trends in an area of the northern foothills of the Brooks Range, Alaska. Arct. Antarct. Alp. Res. **45**: 249–260. doi: 10.1657/1938-4246-45.2.249.

Rickbeil, G.J.M., Hermosilla, T., Coops, N.C., White, J.C., Wulder, M.A., and Lantz, T.C. 2018. Changing northern vegetation conditions are influencing barren ground caribou (*Rangifer tarandus groenlandicus*) post-calving movement rates. J. Biogeogr. **45**: 702–712. doi: 10.1111/jbi.13161.

Rupp, T.S., Chapin, F.S., and Starfield, A.M. 2001. Modeling the influence of topographic barriers on treeline advance at the forest–tundra ecotone in northwestern Alaska. Clim. Change, **48**: 399–416. doi: 10.1023/A:1010738502596.

Scott, P.A., Hansell, R.I.C., and Fayle, D.C.F. 1987. Establishment of white spruce populations and responses to climatic change at the treeline, Churchill, Manitoba, Canada. Arct. Alp. Res. **19**: 45–51. doi: 10.2307/1550999.

Seppa, H., Nyman, M., Korhola, A., and Weckstrom, J. 2002. Changes of treelines and alpine vegetation in relation to post-glacial climate dynamics in northern Fennoscandia based on pollen and chironomid records. J. Quat. Sci. **17**: 287–301. doi: 10.1002/jqs.678.

Sims, R.A. 1983. Ground-truth and large-scale 70 mm aerial photographs in the study of reindeer winter rangeland, Tuktoyaktuk Peninsula Area, N.W.T. Ph.D. thesis, University of British Columbia, Vancouver, B.C.

Spear, R.W. 1993. The palynological record of Late-Quaternary arctic tree-line in northwest Canada. Rev. Palaeobot. Palynol. **79**: 99–111. doi: 10.1016/0034-6667(93)90040-2.

Steedman, A.E., Lantz, T.C., and Kokelj, S.V. 2017. Spatio-temporal variation in high-centre polygons and ice-wedge melt ponds, Tuktoyaktuk Coastlands, Northwest Territories. Permafrost Periglac. Process. **28**: 66–78. doi: 10.1002/ppp.1880.

Suarez, F., Binkley, D., Kaye, M.W., and Stottlemyer, R. 1999. Expansion of forest stands into tundra in the Noatak National Preserve, northwest Alaska. Écoscience, **6**: 465–470. doi: 10.1080/11956860.1999.11682538.

Sullivan, P.F., and Sveinbjornsson, B. 2010. Microtopographic control of treeline advance in Noatak National Preserve, northwest Alaska. Ecosystems, **13**: 275–285. doi: 10.1007/s10021-010-9318-5.

Sutinen, R., Narhi, P., Middleton, M., Hanninen, P., Timonen, M., and Sutinen, M.L. 2012. Advance of Norway spruce (*Picea abies*) onto mafic Lommoltunturi fell in Finnish Lapland during the last 200 years. Boreas, **41**: 367–378. doi: 10.1111/j.1502-3885.2011.00238.x.

Szeicz, J.M., and Macdonald, G.M. 1995. Recent white spruce dynamics at the subarctic alpine treeline of northwestern Canada. J. Ecol. **83**: 873–885. doi: 10.2307/2261424.

Timoney, K.P., La Roi, G.H., Zoltai, S.C., and Robinson, A.L. 1992. The high subarctic forest–tundra of northwestern Canada: position, width, and vegetation gradients in relation to climate. Arctic, **45**: 1–9. doi: 10.14430/arctic1367.

United States Naval Observatory. 2015. Sun or moon altitude/azimuth table: Form B — locations worldwide. Astronomical Applications Department, Naval Oceanography Portal [online]. Available from http://aa.usno.navy.mil/data/docs/AltAz.php [accessed 20 June 2016].

Walker, X. 2010. The reproduction, establishment, and growth of white spruce in the forest tundra ecotone of the Inuvik–Tuktoyaktuk Region. M.Sc. thesis, University of British Columbia, Vancouver, B.C.

Walker, X., Henry, G.H.R., McLeod, K., and Hofgaard, A. 2012. Reproduction and seedling establishment of *Picea glauca* across the northernmost forest–tundra region in Canada. Glob. Change Biol. **18**: 3202–3211. doi: 10.1111/j.1365-2486.2012.02769.x.

Wilmking, M., and Juday, G.P. 2005. Longitudinal variation of radial growth at Alaska's northern treeline — recent changes and possible scenarios for the 21st century. Glob. Planet Change, **47**: 282–300. doi: 10.1016/j.gloplacha.2004.10.017.

Wilmking, M., Sanders, T.G.M., Zhang, Y.X., Kenter, S., Holzkamper, S., and Crittenden, P.D. 2012. Effects of climate, site conditions, and seed quality on recent treeline dynamics in NW Russia: permafrost and lack of reproductive success hamper treeline advance? Ecosystems, **15**: 1053–1064. doi: 10.1007/s10021-012-9565-8.

Wolken, J.M., Landhausser, S.M., Lieffers, V.J., and Silins, U. 2011. Seedling growth and water use of boreal conifers across different temperatures and near-flooded soil conditions. Can. J. For. Res. **41**: 2292–2300. doi: 10.1139/x11-136.