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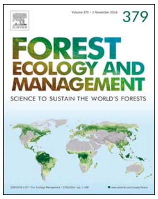

Early white spruce regeneration treatments increase birch and reduce aspen after 28 years: Toward an integrated management of boreal post-fire salvaged stands

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ABSTRACT

Post-harvest regeneration failure of white spruce (*Picea glauca* Moench [Voss]), has led to concerns of "de-coniferization" on productive site in the Alaskan boreal forest. Forest management in the region sought historically to increase spruce composition after harvest through silvicultural practices such as site preparation and assisted regeneration; however, successful reforestation requires the effects of these practices to persist over time and control non-target tree species. In order to identify the enduring effects of silvicultural regeneration practices, we sampled a large (26.7 ha) white spruce regeneration trial established immediately following a stand-replacing wildfire and subsequent salvage harvest in a productive upland forest. The original regeneration treatments followed a split-split plot experimental design on two landform types (LF), four ground scarification treatments (GST) plus a non-scarified control, and five artificial white spruce regeneration treatments (WSRT) plus a natural seedfall control (Densmore et al., 1999). Here we analyze the total biomass, stand density, and basal area for all tree species within each of the regeneration treatments 28 years post-establishment, and calculate seed dispersal distances. Our results show that compared to natural seedfall control plots, white spruce basal area was six times greater in planted seedling plots, and white spruce stem density (dbh ≥ 1.0 cm) was nearly three times greater in broadcast seeding plots. White spruce stem density from natural seedfall averaged 944 stems ha^{-1}, but was dependent on both topographic position and distance to wind-dispersed seed sources. Our results also indicate that GST had few significant effects on white spruce basal area or stem density. However, scarification nearly doubled Alaska birch (*Betula neoalaskana* Sarg.) stem density and basal area compared to non-scarified control plots. Planted white spruce plots supported 19% less birch basal area, except in the most intensive scarification treatments in which birch basal area did not differ. Intensive scarification reduced quaking aspen (*Populus tremuloides* Michx.) basal area by half on slope plots. Our results demonstrate that early regeneration practices profoundly influence stand development beyond the stem initiation stage, but pre-fire stand type, post-fire configuration of unburned seed sources, and topographical variation play a mediating role in determining species assemblages and competitive relationships. A fire-killed stand must be considered within its ecological and landscape context to determine the probable success of a management action such as salvage and tree regeneration.

1. Introduction

Silvicultural practices employed in slow-growing northern forests aim to influence future forest composition by emulating typical post-disturbance successional processes (Drever et al., 2006). Stand-replacing wildfire, the principal disturbance in the boreal forest, kills most sexually mature trees and initiates secondary succession (Heinselman, 1981). Boreal forest communities have adapted to particular fire frequencies, sizes, and severities (Weber and Flannigan, 1997), and individual tree species display reproductive strategies suited to post-wildfire conditions (Greene et al., 1999). Wildfires combust forest floor organic layers that hinder seedling establishment (Johnstone and Chapin, 2006), remove competing vegetation (Zasada et al., 1992), and leave a heterogeneous burn mosaic that permits remnant trees and legacy rootstocks to reproduce (Greene et al., 2006). Following a disturbance, seedling recruitment is especially constrained by propagule availability and seedbed receptivity to a short period of time (Zasada, 1986). Successful reforestation, whether natural or actively managed,

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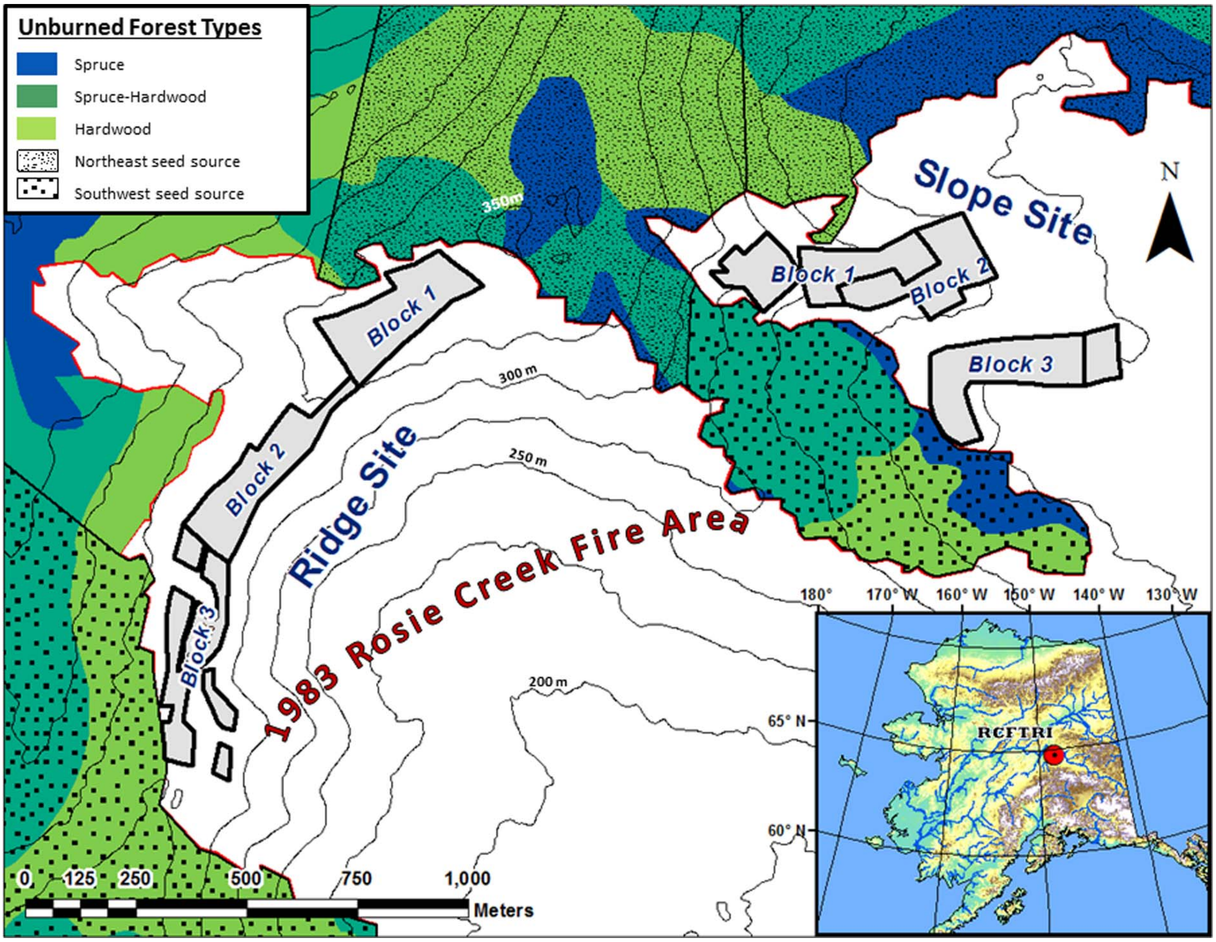

Fig. 1. Overview map of RCFTRI with unburned forest types and GIS-classified wind-dispersed seed sources. Pre-fire forest types classified by AHAP (1988). Seed source regions and burned area classified by authors using ArcMap 10.1 (ESRI, Redlands, CA). Prevailing wind during fall seed abscission comes with equal likelihood from the northeast and southwest (Youngblood and Max, 1992).

must be achieved during the boreal forest's brief stem initiation stage before canopy closure and organic layer accumulation significantly reduce the probability of further tree establishment (Johnstone et al., 2004; Johnstone and Chapin, 2006).

Boreal forest management activities not only aim to reestablish tree seedlings after a stand-replacing disturbance, but also to channel site productivity into preferred species and reduce rotation length (Hawkins et al., 2006; Cortini et al., 2010). Similar to post-fire effects, site preparation such as mechanical scarification reduces overtopping vegetation and exposes mineral soil, which increases rooting zone temperatures and reduces competition faced by small tree seedlings (Zasada and Grigal, 1978; Bella, 1986). Another common boreal silvicultural practice is the introduction of seed or planted seedlings to re-establish desired tree species (Youngblood and Zasada, 1991), which may otherwise decline in abundance or growth. The addition of seed or seedlings to a site post-harvest can be similar to the effect that residual seed trees produce in a patchy post-fire mosaic. Silvicultural practices which reliably produce the desired lasting effects on forest composition are especially critical in boreal forest ecosystems, where low productivity and thin economic margins place great importance on efficient, low-intensity management (Wurtz et al., 2006).

Boreal silvicultural research historically addressed the regeneration challenges of non-serotinous conifers following harvest (see Gärtner et al., 2011; Juday et al., 2013), focusing especially on the stem initiation stage of forest development for a single tree species: white spruce (*Picea glauca* Moench [Voss]) (see for example Zasada and Grigal, 1978; Wurtz et al., 2006). However, the stem exclusion stage that follows, during which trees grow into saplings and the canopy closes, involves intense competition between individuals and species for light, moisture, and nutrients (Zasada and Packee, 1995), has not been well evaluated. Ingrowth of non-crop species may compromise the effectiveness of silvicultural practices meant to foster a single species, for example the reversion of cutover spruce sites in Alberta to high-density hardwoods (Henderson, 1988).

Within minimally tended boreal mixed forests, crop tree characteristics measured early in a stand's development may not account for future stand conditions for three reasons. First, early regeneration treatments may attenuate over time as the competitive environment changes (see for example Bedford et al., 2000, Boateng et al., 2006). Second, unintended results of treatments may become apparent later in stand development (see for example Wurtz and Zasada, 2001). Third, boreal mixedwood stands may experience extended recruitment periods of shade-tolerant conifers, including continued recruitment on decomposing logs further into the life of the new stand. For example, quaking aspen (*Populus tremuloides* Michx.) canopies can let in sufficient light to permit continued white spruce establishment, typically reaching maximum stem density more than 20 years post-fire (Youngblood, 1995; Lieffers et al., 1996). Confirming truly effective regeneration practices in the boreal mixed forest requires an examination of the durability of initial results in later stages of stand development for all tree species present.

The goal of this study was to reevaluate whether early assisted regeneration practices typically used in western North American boreal forests meet two objectives: increase forest composition of target tree species and decrease non-target species in the stem exclusion stage. We analyzed an assisted regeneration trial established following a stand-

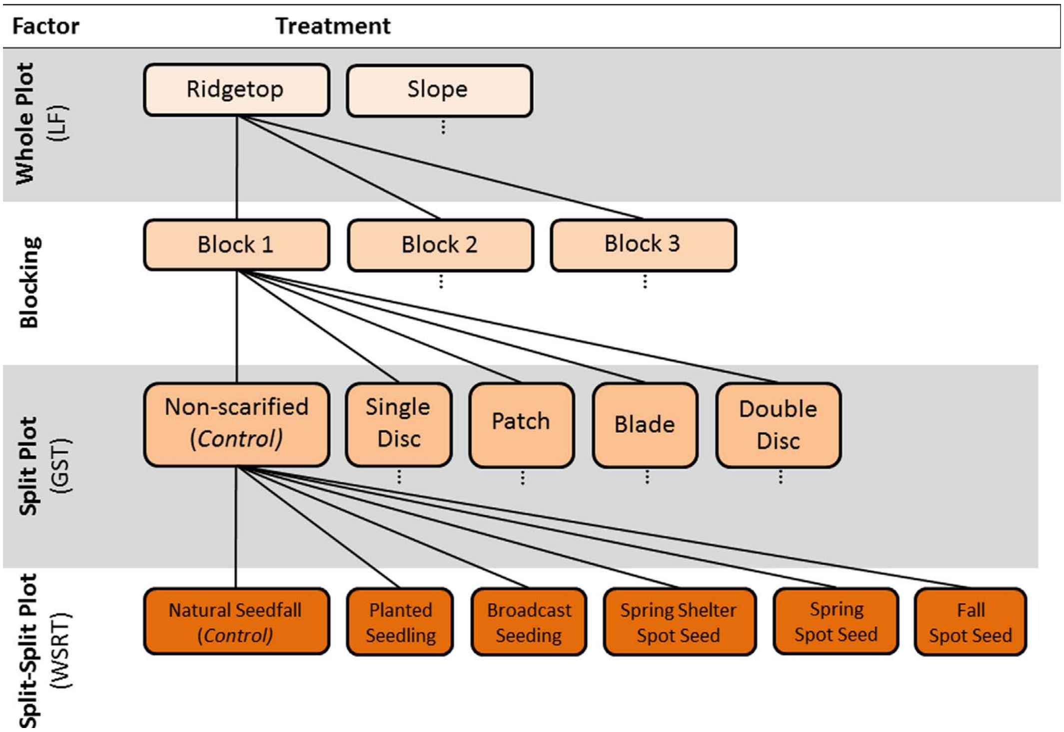

Fig. 2. RCFTRI experimental design, consisting of four hierarchical levels organized in a blocked split-split plot design. LF = landform, GST = ground scarification treatment, WSRT = white spruce regeneration treatment. Each ellipsis represents an identical array of nested treatments as treatments at the same level.

replacing wildfire in 1983, which was subsequently salvage harvested (Densmore et al., 1999). The regeneration trial, the Rosie Creek Fire Tree Regeneration Installation (RCFTRI), was designed to examine “the survival, distribution, and growth of white spruce seedlings…among five site preparation methods and six regeneration methods” (Densmore et al., 1999). The RCFTRI is the largest operational comparison of silvicultural practices in boreal Alaska known to the authors, with a well-replicated and controlled experimental design (Juday et al., 2013). The post-fire salvage sites comprising the RCFTRI present a relatively homogeneous environment to test differing practices while minimizing confounding factors. The initial RCFTRI study located white spruce seedlings one year after treatment, and reported subsequent growth and stocking up to 12 years post-treatment (Densmore et al., 1999). In the present study, we extend these results to 28 years post-treatment and examine basal area and stem density for all dominant tree species in Interior Alaska’s productive upland forest type. We also analyze spatially explicit topographic and seed dispersal measures to understand the contribution of geographic position to regeneration outcomes. In addition to individual tree species performance, we also examine whether regeneration treatments resulted in significant differences in total aboveground live woody biomass. Biomass as a forest product was not envisioned at the time of the experimental design, but now represents an important part of the demand in Alaska (Nicholls et al., 2010).

2. Methods

2.1. Study area

The boreal forest of Interior Alaska supports only a few tree species, whose distribution are strongly influenced by disturbance history, regional climate, parent material, topography, and local biota (Van Cleve et al., 1991; Chapin et al., 2006; Kurkowski et al., 2008). South-facing uplands support some of the most productive forest ecosystems, particularly white spruce, mixed white spruce-hardwood, and hardwood stands (Viereck et al., 1983). These forest types comprise 63% of state-managed forest lands in Interior Alaska (Crimp et al., 1997), but only 15% of Interior Alaska forest (Hammond, 1996). Upland forests are the focus of much harvest activity, in which the principal commercial tree species are white spruce, Alaskan birch (*Betula neoalaska* Sarg), and quaking aspen (*Populus tremuloides* Michx.) (Wurtz et al., 2006).

The Rosie Creek Fire Tree Regeneration Installation (RCFTRI) is a 26.7 ha experiment established in 1985–6 to examine white spruce seedling recruitment under a variety of stand initiation practices within two distinct upland topographic types (Densmore et al., 1999). RCFTRI is located 30 km southwest of Fairbanks, Alaska at 64.74 °N 148.31 °W, in the Bonanza Creek Experimental Forest (Fig. 1). The area is comprised of the interior forested lowlands and uplands ecoregion of the boreal forest (Gallant et al., 1995). Rolling hills and valleys marked by a cold continental climate, discontinuous permafrost, and high wildfire frequency form a mosaic of ecosystems (Beget et al., 2006). The RCFTRI extends across mostly south-facing uplands above the Tanana River, and has deep, permafrost-free, silt-loam soils of aeolian origin (Soil Survey Staff, 2011). The site experiences an average July temperature of 16.1 °C, an average January temperature of −19.0 °C, and annual rainfall of 200 mm (Van Cleve et al., 2013a,b). An estimated 35% of annual precipitation falls as snow (Viereck and Slaughter, 1986). RCFTRI experienced stand-replacing high severity crown fire on 2 June 1983 as part of the greater 3482 ha Rosie Creek wildfire (Juday, 1985). Subsequent clearcut salvage logging operations took place on the entire installation during the snow-free season ending in August 1985 (Densmore et al., 1999).

2.2. Experimental design

The RCFTRI was designed as a blocked split-split plot experiment, comprising four hierarchical nested levels (Fig. 2) (Densmore et al., 1999). The first level involved two upland landform types (LF), Ridge and Slope, corresponding to the whole plot factor (approximately 13.3 ha each). Each LF whole plot was partitioned into three blocks (approximately 4.4 ha each). Each block was further divided into five equal split plots (approximately 0.9 ha each) where one of five ground

Table 1
Summary of landform (LF) whole plot characteristics across 180 S/SPs. The slope and ridge LFs represent a number of topographical gradients that typify Alaska's upland boreal forest. Standard deviation indicated in parentheses.

	Ridge	Slope	Whole experiment
Area	13.3 ha	13.4 ha	26.7 ha
Pre-fire Forest Type (AHAP, 1988)	White Spruce-Birch-Aspen, Birch-Aspen	White Spruce-Black Spruce-Birch-Aspen	Mixed spruce-Hardwood
Soil Type (Soil Survey Staff, 2011)	Gilmore Silt Loam 3–7% slope	Minto-Chatanika Complex 3–7% slope, Steese Silt Loam 20–30% slope	mod.-deep silt loam
Distance from Fire Edge	119.2 m *(49.4)*	151.6 m *(85.9)*	135.4 m
Southwest Seed Shadow Mean distance from wind-dispersed seed source	408.6 m *(306.7)*	163.7 m *(85.9)*	286.1 m
Northeast Seed Shadow Mean distance from wind-dispersed seed source	482.8 m *(342.8)*	297.7 m *(169.0)*	390.2 m

scarification treatments (GST) were randomly assigned. Each GST split plot was subsequently further divided into six equal split-split plots (S/SP; approximately 0.15 ha each, or 40 × 40 m) where one of six white spruce regeneration treatments (WSRT) were randomly assigned (Densmore et al., 1999). Each unique combination of the three factor levels represented by a split-split plot (S/SP) was replicated three times (n = 3).

Though only one kilometer apart, the Ridge and Slope LF have distinct topography and spatial configurations with important silvicultural implications typical of managed sites. The Ridge split-split plots (S/SPs) are higher in elevation and more uniform (311–344 m) than those on the Slope (194–291 m). On the Ridge, 59 of 90 S/SPs have a slope angle < 5°, compared to only 10 of 90 Slope S/SPs. The Ridge and Slope LFs have similar cumulative growing season solar radiation (ridge = 624,622 ± 2117 watt-hours m^{-2}, slope = 625,475 ± 4282). However, the Slope site contained the 13 S/SPs with the highest incoming solar radiation values, while the Ridge experienced a narrower range of solar input. Within both LFs, S/SPs have similar distances to the unburned forest edge, but many Ridge S/SPs are much further from wind-dispersed seed sources (Table 1). Prevailing wind direction during autumn seed dispersal was quantified for a nearby floodplain site with equal frequency from northeast and southwest (Youngblood and Max, 1992).

The ground scarification treatments (GST) involved mechanical disturbance of the residual organic layer of the forest floor and exposure of mineral soil seedbeds. Establishment of the five GSTs within each block occurred in August/September 1985: one non-scarified control and four types of mechanical scarification. Control S/SPs were not scarified, and mineral soil exposure was estimated at 0% in 1985 (Densmore et al., 1999). Organized from most to least mineral soil exposed, the four scarification types included: (1) bulldozer blading in parallel strips (29% mineral soil exposed), (2) double-disc trenching with a TTS-35 Disc Trencher in perpendicular passes (25%), (3) single-disc trenching in parallel passes (15%), and (4) patch scarification with a Bracke-type scarifier (10%). The mineral soil exposed within each of the GSTs did not significantly differ between the Ridge and Slope, nor did the percent of vegetation cover or treatment depth (for details see Densmore et al., 1999).

The white spruce regeneration treatments (WSRT, see Fig. 2) introduced white spruce propagules collected in 1983 from nearby unburned stands. Each of the six different WSRTs were carried out during 1986 on every split plot, and these included: natural seedfall (control), planted seedlings, broadcast seeding, spring unsheltered spot seed, fall unsheltered spot seed, and spring sheltered spot seed. The control WSRT was stocked by natural white spruce seed dispersal, which is highly episodic (Greene et al., 1999). Two-year-old containerized seedlings were planted at 2.4-m spacing (one tree every 6 m^2) in June 1986; seed was collected from mature trees located adjacent to planting sites and grown at the Alaska State Forest Nursery in Palmer, Alaska. The planted seedling stock in Ridge Blocks 2 and 3 were stunted due to contamination with a common greenhouse fungus (Densmore et al., 1999). Broadcast seeding occurred at a rate of 1 kg ha^{-1}.

2.3. Data collection

Sampling took place from July to September 2013, with supplemental sampling in early June 2014. The dataset consists of the three most commonly practiced WSRTs – natural seedfall, broadcast seeding, and planted seedlings – balanced across all six blocks (90 S/SPs). We did not examine the three spot seeding methods from the original experiment.

Each S/SP was systematically sampled by establishing a two-by-two crosscutting pattern of four 1-m wide belt transects on each S/SP to account for of heterogeneous forest composition within each plot. Key site characteristics may demonstrate gradients or a patchy distribution even at small scales (Reed et al., 1993). A robust sampling pattern is necessary to minimize heterogeneity due to variations in light environment (Deutschman et al., 1999), burn severity (Johnstone and Chapin, 2006), soil nutrient characteristics (Lechowicz and Bell, 1991), legacy effects such as sprouting from birch or aspen root stock (Greene et al., 1999), differential vegetative competition within patches (Cater and Chapin, 2000), or the orientation of ground scarification treatments in parallel strips.

Transect layout (Fig. 3) was established by (1) identifying the plot boundary on an azimuth of between 0 and 90°, and dividing it into thirds, (2) along the selected boundary at the one-third and two-thirds positions, transects one and two were placed perpendicular to the selected plot boundary, (3) the northernmost transect was then divided into thirds, and transects three and four were placed perpendicular to transects one and two. On average, we sampled 10.1% of a S/SP's total area with this method. Validation of this transect method was conducted by a complete census on one S/SP within each block (n = 6), representing each of the five GSTs and four of the six WSRTs.

Within the 1-m belt transects, we recorded species and diameter-at-breast-height (dbh = 1.37 m) for every live tree or shrub where (1) ≥50% of root collar was within the belt transect, and (2)

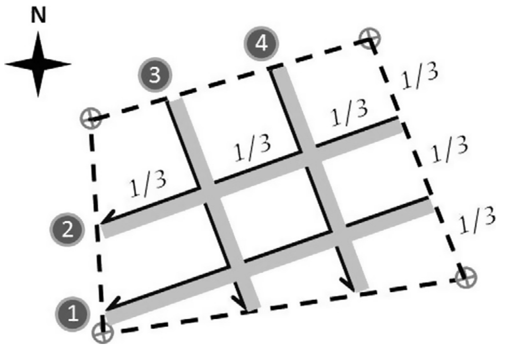

Fig. 3. Depiction of typical 1-m width belt transect layout. This layout procedure provided a representative sample of the entire S/SP. Note that diagram is not to scale.

dbh ≥ 1.0 cm. Shrubs were identified to genus and included willows (*Salix* spp.) and alders (*Alnus* spp.). Measurement protocols followed those previously established within the region (Malone et al., 2009).

In order to account for the effects of topography on tree growth and stand composition (Viereck et al., 1986; Kurkowski et al., 2008), we derived elevation, slope, and aspect from a 5-m pixel size digital elevation model (Alaska, 2010) in ArcMap 10.1 (ESRI, 2012). At high latitudes like the RCFTRI, forest community types are significantly influenced by aspect, with east- and west-facing slopes hosting different tree assemblages than south-facing aspects (Kurkowski et al., 2008). However, this experiment had almost exclusively east- or south-facing aspects, with only four north-facing S/SPs and six west-facing (and those in one block only). Since the experiment does not include a balanced representation of aspects, we incorporated the influence of aspect by deriving cumulative growing season solar radiation. Solar radiation aggregates the effects of latitude, slope angle, and slope aspect into a single figure: the amount of usable energy in watt-hours m^{-2} (Hinzman et al., 2006). We calculated cumulative solar radiation in ArcMap 10.1 using the 'Area Solar Radiation' tool for the period 1 April – 30 September (calculated at 14-day intervals, using 0.5 h interval during sampled days, and with 30% cloud cover) (ESRI, 2012).

Seed dispersal distance is also an important factor controlling sexual regeneration of boreal tree species, and total dispersal distance is a function of prevailing wind direction (Zasada, 1985; Greene et al., 1999). Seed sources for this experiment were defined as mature unburned forest downwind of the study areas. We classified a 22 August 1986 color infrared image into burned and unburned areas (USGS, 1986), then partitioned unburned areas into northeast and southwest seed sources relative to each LF whole plot in line with previously established prevailing wind directions (Youngblood and Max, 1992). Wind-dispersed seed sources were further classified as containing hardwoods only, or mixed spruce/hardwood communities (AHAP, 1988). We calculated several measures of seed dispersal distance to S/SP centroid: (1) distance to nearest unburned seed source, (2) mean distance from southwest and northeast seed sources, (3) minimum distance to closest wind-dispersed seed source, and (4) minimum distance to closest spruce seed source.

2.4. Data analysis

To assess the validity of our transect method, we used paired t-tests to evaluate the presence of mean bias in the sample transect estimates compared to the census results, similar to methods employed by Huang et al. (2000). Given no systematic bias in the transect method, we then evaluated the effects of the experimental factors in three ways. First, a blocked split-split plot design ANCOVA (Analysis of Covariance) model was constructed and the effects of the three experimental factors – LF, GST, WSRT – as well as the two- and three-way interactions were tested (Kuehl, 2000). Second, we evaluated the differences between treatment means using Dunnett's test (Dunnett, 1955). Third, we selected a set of relevant treatment contrasts (e.g., scarified vs. non-scarified) and tested whether the assembled groups demonstrated a significant difference in the response variables (i.e., stem density). We carried out two linear contrasts for each response variable, and used the Bonferroni method to control Type 1 error rates (significance level: $p = 0.05/k$ for k contrasts) (Kuehl, 2000). Statistical analysis was performed within SAS software, Version 9.3, using Proc GLM (SAS, 2012).

We assessed the inclusion of split-split plot covariates in the final model in three steps: (1) the covariate is independent of the experimental treatments, (2) a simple linear regression between the response variable and the covariate indicates a significant linear relationship, and (3) the covariate term achieves significance in the overall ANCOVA (Kuehl, 2000). We tested eight spatial covariates: (1) elevation, (2) slope angle, (3) cumulative solar radiation, (4) distance to unburned seed source, (5) natural logarithm of distance to unburned seed source, (6) distance to nearest wind-dispersed seed source, (7) mean distance to wind-dispersed seed sources, and (8) natural logarithm of spruce distance to spruce seed source. We used log-transformed variables to test seed dispersal relationships found by Densmore et al. (1999). All S/SP response variables were calculated on a per hectare basis, and values are reported as mean ± 1 SE unless noted otherwise. All response variables were power-transformed using the Box-Cox method (Box and Cox, 1964) and constant variance was evaluated using the Brown-Forsyth Test (Brown and Forsythe, 1974). We analyzed eight response variables: stem density (stems ha^{-1}) and basal area ($m^2\ ha^{-1}$) individually for aspen, birch, and white spruce; total stem density for all species; and total aboveground woody plant biomass (kg ha^{-1}) for all species. We calculated aboveground biomass dry weight using national allometric equations from Jenkins et al. (2003) for all species except alder. Alder biomass was derived from locally calibrated equations (Wurtz, 1995).

Table 2
P-values of census and transect estimates by ten response variables.

	Stem density	Basal area
All species	0.583	0.757
Alder	0.082	0.095
Aspen	0.439	0.186
Birch	0.736	0.534
White Spruce	0.431	0.667

3. Results

3.1. Census and transect comparisons

No significant difference was detected between transect versus census data in terms of stem density and basal area for all the different tree species ($p > 0.05$) (Table 2). However, five of the six census S/SPs contained fewer alder stems ha^{-1} than the transect estimates, though differences between the two methods were not significant ($p = 0.082$ for alder stem density, and $p = 0.095$ for alder basal area). Alders accounted for 0.8% of estimated total biomass across the measured S/SPs.

3.2. Spatial covariates

3.2.1. Effects of topographical covariates on experimental results

Though each response variable was significantly correlated with some spatial covariates in a simple linear regression, none of the S/SP covariates were significant in the ANCOVA model. However, cumulative growing season solar radiation was significantly related to both birch and aspen basal area, and explained about 5% of the variation. Birch basal area was negatively correlated with solar radiation while aspen was positively correlated. White spruce basal are was not significantly related to radiation. A simple linear regression comparing birch and aspen biomass to each other excluding planted seedling S/SPs indicates a significant negative relationship ($F_{1,103} = 113.81$, $p < 0.0001$), with 52% of the variation in aspen biomass explained by birch biomass (Fig. 4a).

3.2.2. Effects of distance to seed source on experimental results

Log distance to nearest wind-dispersed spruce seed source was the best predictor, in terms of R^2, for white spruce stem density on the 30 natural seedfall S/SPs (Table 3). The 30 natural seedfall S/SPs averaged 944 white spruce stems ha^{-1}, but the 12 natural seedfall S/SPs within 200 m of a wind-dispersed white spruce seed source averaged 1512 stems ha^{-1}. The seven natural seedfall S/SPs with no recorded white spruce seedlings averaged only 111 m from the unburned forest edge, well within typical spruce dispersal distances (Greene et al., 1999), but were located an average of 649 m from wind-dispersed spruce seed sources Fig. 1). The strongest predictor of birch stem density as

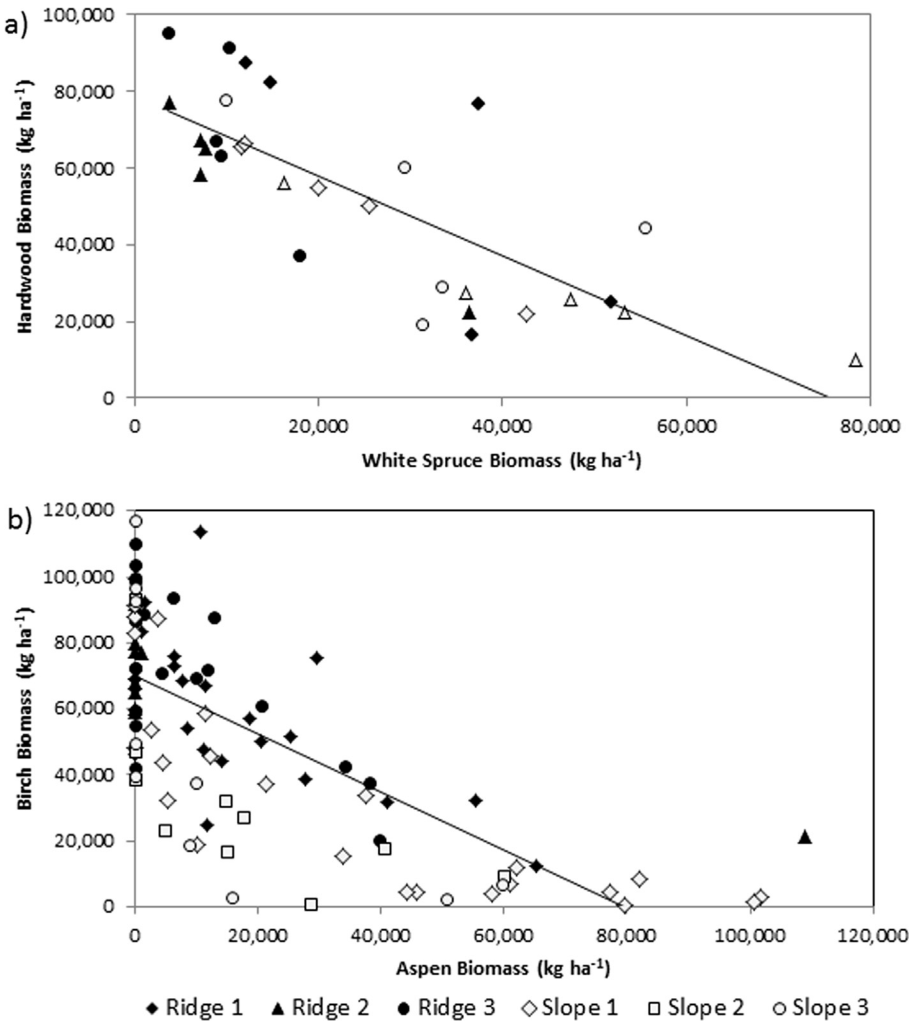

Fig. 4. Biomass trade-offs between tree species, by block. (a) Hardwood (aspen + birch) biomass as a linear function of white spruce biomass for 30 planted seedling S/SPs ($Y = 78,761 - 1.041 * X$; $R^2 = 0.61$, $p < 0.0001$). Planted seedlings in R2 and R3 were stunted due to infection with a greenhouse fungus. (b) Aspen biomass as a linear function of birch biomass for 105 unplanted S/SPs ($Y = 70,014 - 0.88 * X$; $R^2 = 0.52$, $p < 0.0001$).

Table 3
P-values for the linear relationship between distance to seed source and stem density, by species. White spruce figures calculated only with the subset of S/SPs receiving natural seedfall WSRT (n = 30). Birch and aspen calculated with all sampled plots (n = 90). All distances log-transformed except for mean distance to wind-dispersed seed source (R^2 in parentheses).

Species	Ln (Dist. to Nearest Unburned Forest)	Mean Dist. to Wind-Dispersed Seed Source	Ln (Dist. to Nearest Wind-Dispersed Seed Source)	Ln (Dist. to Nearest Wind-Dispersed Spruce Source)
White Spruce	0.6661 (0.01)	**0.0200**[*] (0.18)	0.0789 (0.11)	**0.0056**[*] (0.24)
Birch	**0.0001**[*] (0.23)	**0.0235**[*] (0.06)	**0.0023**[*] (0.10)	n/a
Aspen	0.0518 (0.04)	0.1258 (0.03)	0.2371 (0.02)	n/a

[*] Significant result ($\alpha < 0.05$). Bold values represent Bonferroni-adjusted significant result at 97.5% confidence level ($\alpha = 0.05/2 = 0.025$).

measured by R^2 was log distance to the unburned forest (Table 3, Fig. 1). The 79% of S/SPs within 200 m of the unburned edge supported an average of 6958 stems ha^{-1}, compared to the 21% of S/SPs that were further than 200 m and supported only 1586 birch stems ha^{-1}. While for aspen, there was no significant relationship found for any of the distance to seed source measures.

3.3. Biomass and stem density of all species combined

The LF factor had a marginally significant influence on total biomass ($p = 0.0737$, Table 4), where values were on average less on the Slope (72,146 ± 2782 kg ha^{-1}, n = 45) than on the Ridge (81,582 ± 2422, n = 45). The LF factor had no significant influence on total stem density.

Total aboveground biomass was significantly influenced by the GST factor (Table 4). Biomass was greater (30%) on scarified S/SPs compared to non-scarified S/SPs (Table 5; 80,607 kg ha^{-1} compared to 61,890 kg ha^{-1}). Total biomass from every type of scarification treatment was significantly greater than the non-scarified control with the exception of blade scarification (Fig. 5a). Ground scarification affected biomass differently based on hardwood composition: S/SPs established greater birch basal area (a correlate to biomass) with scarification (Fig. 5c), while aspen basal area responded neutrally (Fig. 5d). Excluding blade scarification, birch had 70% more biomass on scarified S/SPs compared to non-scarified S/SPs, while aspen had 14% less. Biomass in blade scarification treatments was not significantly different from controls, largely because of a 63% reduction in aspen and a simultaneous 82% increase in birch biomass compared to non-scarified controls.

The WSRT factor did not have a significant effect on total biomass (Table 4), nor did we detect a significant effect of the planted seedling treatment on total biomass (Table 5). However, two countervailing trends were observed: the planted seedling treatment was associated with an increase in white spruce biomass by a factor of 7 but decreased

Table 4
ANOVA table. LF = landform whole plot factor, GST = ground scarification split plot factor, and WSRT = white spruce regeneration split-split plot factor.

		All species				White spruce			
		Biomass		Stem density		Basal area		Stem density	
	df	F	p	F	p	F	p	F	p
LF	1	12.09	0.0737	0.66	0.5014	4.48	0.1686	10.10	0.0864
GST	4	4.15	**0.0171***	2.65	0.0719	0.52	0.7247	0.16	0.9541
GST * LF	4	0.34	0.8447	0.67	0.6207	1.63	0.2157	1.42	0.2732
WSRT	2	0.40	0.6714	3.99	**0.0262***	69.61	**0.0001***	21.61	**0.0001***
WSRT * LF	2	0.89	0.4170	1.11	0.3403	3.85	**0.0295***	6.16	**0.0046***
WSRT * GST	8	1.03	0.4304	0.35	0.9423	0.39	0.9188	0.44	0.8922
WSRT * LF * GST	8	1.49	0.1899	0.52	0.8330	1.06	0.4125	1.13	0.3635
		Birch				**Aspen**			
		basal area		**stem density**		**basal area**		**stem density**	
	df	F	p	F	p	F	p	F	p
LF	1	71.82	**0.0136***	5.51	0.1435	9.62	0.0901	13.2	0.0681
GST	4	2.05	0.1358	2.15	0.1215	0.82	0.5335	2.06	0.1336
GST * LF	4	0.98	0.4476	0.78	0.5526	2.46	0.0875	3.53	**0.0300***
WSRT	2	3.35	**0.0450***	1.45	0.2476	0.8	0.4546	0.05	0.9554
WSRT * LF	2	0.41	0.6693	1.52	0.2314	0.65	0.5280	0.55	0.5799
WSRT * GST	8	2.49	**0.0271***	1.69	0.1299	1.28	0.2815	0.76	0.6381
WSRT * LF * GST	8	1.34	0.2543	0.79	0.6111	0.81	0.5975	0.74	0.6559

* Significant result ($\alpha < 0.05$). Bold values represent Bonferroni-adjusted significant result at 97.5% confidence level ($\alpha = 0.05/2 = 0.025$).

birch biomass by 23% compared to natural seedfall S/SPs (Table 5) and decreased aspen biomass by 46%. A simple linear regression of white spruce to hardwood tree biomass in S/SPs receiving the planted seedling WSRT demonstrates a significant negative relationship (Fig. 4a), suggesting a tradeoff between hardwood and white spruce biomass.

The GST factor alone did not have a significant effect on total stem density ($p = 0.0719$, Table 4). However, when taken as group all scarified S/SPs (combination of all treatment types) exhibited

Table 5
Linear contrast results for all response variables. Group A corresponds to the first category listed in the contrast name, Group B the second. Where applicable, references that prompted a contrast are given. All values reported as mean ± 1 SE. 'scar' = all scarification treatments, 'nonscar' = non-scarified control treatment, 'intscar' = intensive scarification treatments (i.e., blade and double-disc), 'plant' = planted seedling WSRT, 'natseed' = natural seedfall control WSRT, 'others' = two WSRTs not named in group A.

Response variable	Contrast (group A vs group B)	Reference	F	P	Group A	Group B
Total biomass (kg ha^{-1})	Scar vs nonscar		26.63	**0.0001***	80,607 ± 1972 n = 72	61,890 ± 3623 n = 18
	Plant vs others	Man and Lieffers (1999)	0.59	0.4465	78,303 ± 2849 n = 30	76,144 ± 2481 n = 60
Total density (stems ha^{-1})	Scar vs nonscar		26.42	**0.0001***	9684 ± 473 n = 72	6415 ± 739 n = 18
	Broadcast vs others	Densmore et al. (1999)	7.24	**0.0103***	9942 ± 673 n = 30	8574 ± 540 n = 60
White spruce basal area (m^2 ha^{-1})	Scar vs nonscar		1.16	0.2871	3.79 ± 0.54 n = 72	3.80 ± 0.81 n = 18
	Plant: intscar vs nonscar	Boateng et al. (2009)	0.83	0.3672	7.22 ± 1.49 n = 12	7.80 ± 1.01 n = 6
White spruce density (stems ha^{-1})	Scar vs nonscar	DeLong et al. (1997)	0.18	0.6708	1712 ± 204 n = 72	1445 ± 257 n = 18
	Natseed: scar vs nonscar	Rupp (1997)	0.12	0.7312	916 ± 177 n = 24	1055 ± 656 n = 6
Birch basal area (m^2 ha^{-1})	Scar vs nonscar	Zasada (1980)	45.04	**0.0001***	13.29 ± 0.92 n = 72	7.60 ± 0.72 n = 18
	Plant: scar vs nonscar		23.34	**0.0001***	12.02 ± 1.47 n = 24	5.58 ± 2.18 n = 6
Birch density (stems ha^{-1})	Scar vs nonscar	Zasada et al. (1983)	104.39	**0.0001***	6454 ± 537 n = 72	3262 ± 679 n = 18
	Plant vs others		2.31	0.1364	5438 ± 816 n = 30	6014 ± 785 n = 60
Aspen basal area (m^2 ha^{-1})	Scar vs nonscar		2.10	0.1549	4.24 ± 0.85 n = 72	4.72 ± 1.40 n = 18
	Intscar vs nonscar	Peltzer et al. (2000)	4.95	0.0317	2.84 ± 0.91 n = 36	4.72 ± 1.40 n = 18
Aspen density (stems ha^{-1})	Scar vs nonscar	Stone and Elioff (1998)	4.20	0.0471	687 ± 162 n = 72	647 ± 228 n = 18
	Intscar vs nonscar	Peltzer et al. (2000)	7.12	**0.0109***	437 ± 178 n = 36	647 ± 228 n = 18

* Bonferroni-adjusted significant result ($\alpha = 0.05/2 = 0.025$). Bold values represent Bonferroni-adjusted significant result at 97.5% confidence level ($\alpha = 0.05/2 = 0.025$).

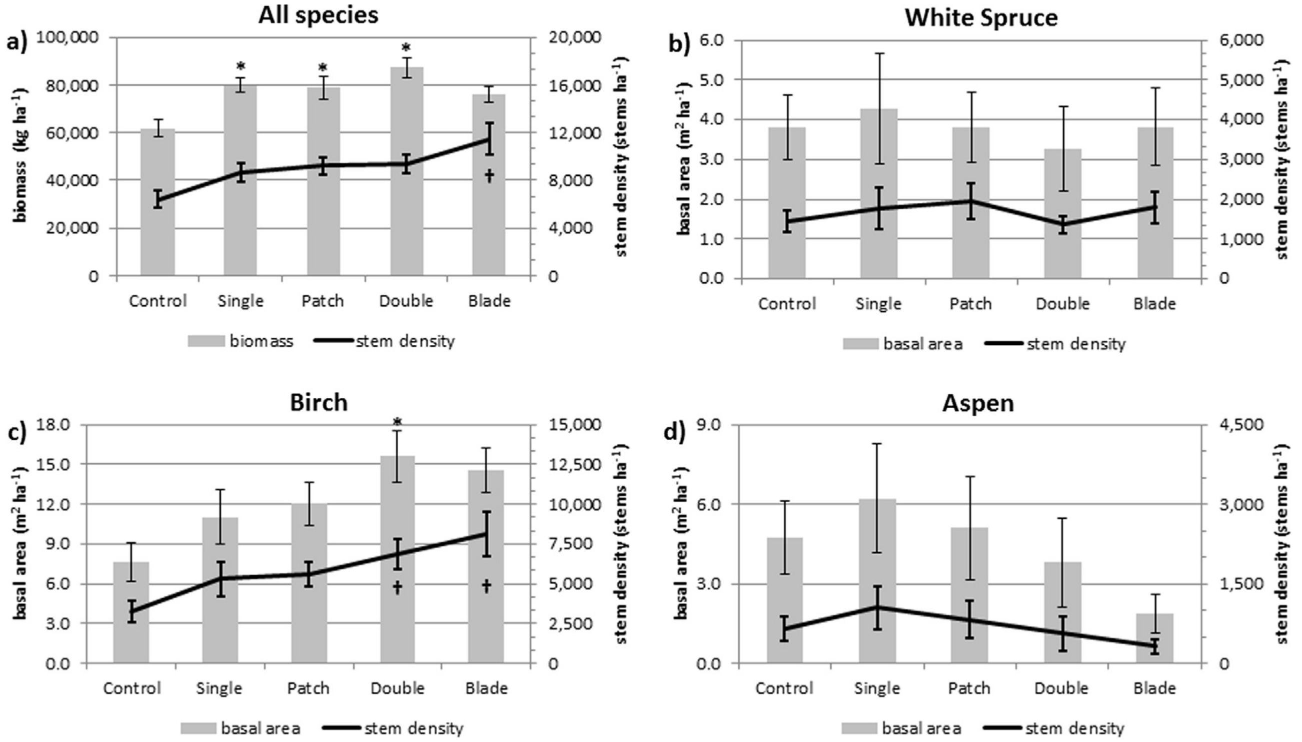

Fig. 5. Untransformed ground scarification treatment (GST) group means for all species (a), white spruce (b), birch (c), and aspen (d). Error bars are ± 1 SE. *Basal area significantly different from non-scarified control using Dunnett ($p < 0.05$). †Stem density significantly different from non-scarified control using Dunnett ($p < 0.05$).

significantly greater stem density (an increase of 51% from 6415 stems ha^{-1} to 9684 stems ha^{-1}) when compared to non-scarified S/SPs (Table 5). Blade-scarified S/SPs in particular supported significantly greater stem density (78%) compared to non-scarified S/SPs (Fig. 5a).

Total stem density was significantly influenced by the WSRT factor (Table 4). Total stem density on broadcast seed S/SPs was greater (9943 ± 673 stems ha^{-1}, n = 30) compared to the combination of planted seedling and natural seedfall S/SPs (8574 ± 540, n = 60) (Table 5). The higher total stem density (all species) on broadcast S/SPs compared to natural seedfall treatments appears to be accounted for largely by the 1234 stem ha^{-1} increase in white spruce stems in broadcast seeded S/SPs.

3.4. Shrub and other tree species biomass and stem density

Averaged across all study plots, willows comprised 1.4% of stems and 0.1% of biomass. Alders comprised 8.9% of stems and 0.8% of biomass. None of the experimental treatment factors had a significant effect on biomass or stem density for either shrub species. In addition, we recorded 11 balsam poplar (*Populus balsamifera* L.) among the 12,216 trees that were tallied in the 90 sampled S/SPs, a negligible fraction of total stem density and basal area. Poplars were included in the total biomass figures for all species combined, but did not receive additional analysis.

3.5. White spruce basal area and stem density

The LF factor by itself did not significantly influence either white spruce basal area or stem density, but LF had a significant interaction with WSRT (Table 4). In general, there was greater magnitude of white spruce basal area and stem density on Slope S/SPs compared to Ridge S/SPs, although the rank-ordering of WSRTs within both LF types was the same (Fig. 6b). Stem densities of planted seedling S/SPs on both Ridge and Slope were comparable, but white spruce stem density in absolute terms was more than three times greater on the Slope for both broadcast seeding and natural seedfall S/SPs. However, on both the Ridge and Slope, the broadcast seed WSRT resulted in proportionally similar increases in stem density compared to natural seedfall (152% increase on the Ridge, 159% increase on the Slope).

The GST factor alone did not have a significant impact on white spruce stem density (Table 4, Fig. 5b), nor did we detect any differences between scarified and non-scarified GSTs (Table 5). However, broadcast seeding following any type of scarification treatment produced significantly higher stem densities than the non-scarified natural seedfall controls (Fig. 7b). Broadcast seeding of non-scarified S/SPs resulted in similar white spruce stem densities compared to the natural seedfall control (Fig. 7b). The positive response of white spruce stem density to the combination of broadcast seeding and scarification was especially pronounced on the Slope, where broadcast seeding following scarification resulted in nearly three times the stem density than on non-scarified S/SPs (4355 ± 655 stems ha^{-1}, n = 12, versus 1727 ± 449, n = 3). However, the same trend did not occur on the Ridge, where broadcast seeded, scarified S/SPs averaged 925 ± 284 (n = 12) compared to non-scarified S/SPs with 1465 ± 740 (n = 3).

The GST of double-disc scarification was associated with reduced white spruce basal area on non-planted S/SPs. Broadcast seeded S/SPs supported less white spruce basal area (29%) on double-disc scarified sites compared to the non-scarified controls, and natural seedfall S/SPs receiving the double-disc treatment supported 54% less basal area compared to the non-scarified controls, although the effect was not significant in either case Fig. 7b).

White spruce basal area was significantly influenced by the WSRT (Table 4). Broadcast seeding and planted seedling treatments significantly increased basal area relative to the natural seedfall control (Dunnett, $p < 0.0001$). Planted seedling S/SPs supported an average of 7.44 ± 0.93 m^2 ha^{-1} (n = 30) white spruce basal area, broadcast seeding resulted in 2.67 ± 0.52 (n = 30), while natural seedfall had the lowest basal area at 1.25 ± 0.25 (n = 30) (Fig. 6b). The planted seedling S/SPs located in the two blocks impacted by greenhouse fungus at the time of planting (Densmore et al., 1999) supported only 38% of the white spruce basal area compared to planted seedling S/SPs in the four unaffected blocks.

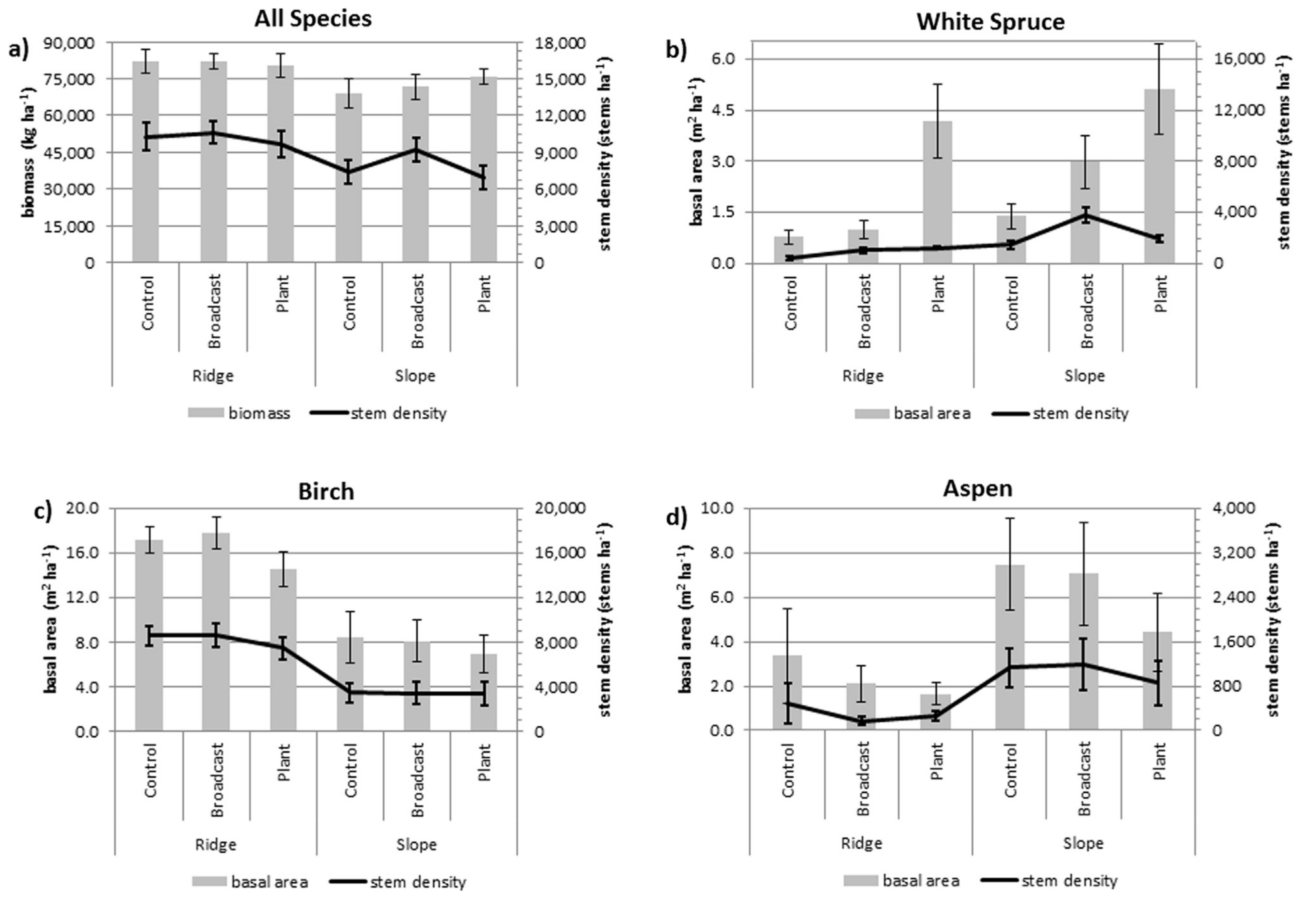

Fig. 6. Untransformed plant by landform group means for all species (a), white spruce (b), birch (c), and aspen (d). Error bars are ± 1 SE.

WSRT had a highly significant effect on white spruce stem density (Table 4), with both planted seedling and broadcast WSRTs producing significantly greater white spruce stem densities compared to natural seedfall (Dunnett, $p < 0.0001$). Broadcast seeding resulted in 2431 ± 412 stems ha^{-1} ($n = 30$), compared to planted seedling S/SPs with 1601 ± 161 ($n = 30$) and natural seedfall with 944 ± 187 ($n = 30$) (Fig. 6b).

3.6. Birch basal area and stem density

All three levels of experimental factors influenced birch basal area and stem density (Table 4). The LF effect on basal area was consistent (no interaction) regardless of GST and WSRT. Slope S/SPs supported less birch basal area (7.82 ± 1.12 m^2 ha^{-1}, $n = 45$) than Ridge S/SPs (16.48 ± 0.81, $n = 45$).

The WSRT factor significantly influenced birch basal area in the overall ANOVA (Table 4). The planted seedling WSRT resulted in lower birch basal area overall (10.74 ± 1.33, $n = 30$) compared to broadcast seeding (12.93 ± 1.48, $n = 30$) and natural seedfall (12.78 ± 1.49, $n = 30$) treatments (Fig. 6c). Birch basal area was significantly lower (19%) on S/SPs receiving the planted seedling WSRT compared to the combination of broadcast and natural seedfall (Table 5).

Although the GST factor alone did not significantly influence birch basal area, the effect of GST was mediated by a significant interaction with WSRT (Table 4). Scarified S/SPs had significantly greater (75%) birch basal area than non-scarified S/SPs (Table 5). More intensive scarification was associated with greater birch basal area, particularly the double-disc S/SPs which supported significantly greater (105%) birch basal area compared to non-scarified controls (Fig. 5c).

Birch stem density tended to be higher on the Ridge LF (8208 ± 3587 stems ha^{-1}, $n = 45$) than on the Slope (3439 ± 3507, $n = 45$), though the LF factor was not significant in the overall ANOVA (Table 4). Although GST was not significant in the overall ANOVA (Table 4), the contrast of all scarification treatments combined compared to the non-scarified treatment was significant; scarification of any kind increased birch stem density by 98% (Table 5). Intensive GSTs were associated with significantly more birch stems than the non-scarified control (Fig. 5c), but the less intensive scarification methods of patch and single-disc were not significantly different from the non-scarified control. WSRT was not a significant factor influencing birch stem density in the overall ANOVA (Table 4).

The presence of a significant interaction between GST and WSRT interaction indicated that scarification treatments produced different effects based on the WSRT (Table 4). In particular, birch basal area on planted seedling S/SPs depended on the intensity of scarification Fig. 7c). Non-scarified planted seedling S/SPs supported less than half the birch basal area of scarified planted seedling S/SPs (Table 5). On the planted seedling S/SPs, only the double-disc treatment produced significantly greater birch basal area than the non-scarified, natural seedfall controls (Fig. 7c). In addition, on planted seedling S/SPs, the intensive GSTs (i.e., blade and double-disc) were associated with greater birch basal area (13.86 ± 2.06 m^2 ha^{-1}, $n = 36$) than on moderate GSTs (i.e., patch and single-disc; 10.19 ± 2.05, $n = 18$). Although intensive scarification produced the greatest birch basal area on planted seedling S/SPs, white spruce did not show any concomitant reduction in basal area (Table 5).

3.7. Aspen basal area and stem density

Aspen distribution was extremely variable across the study area. On the Ridge LF, no aspen were recorded in the sample transects for 21 of

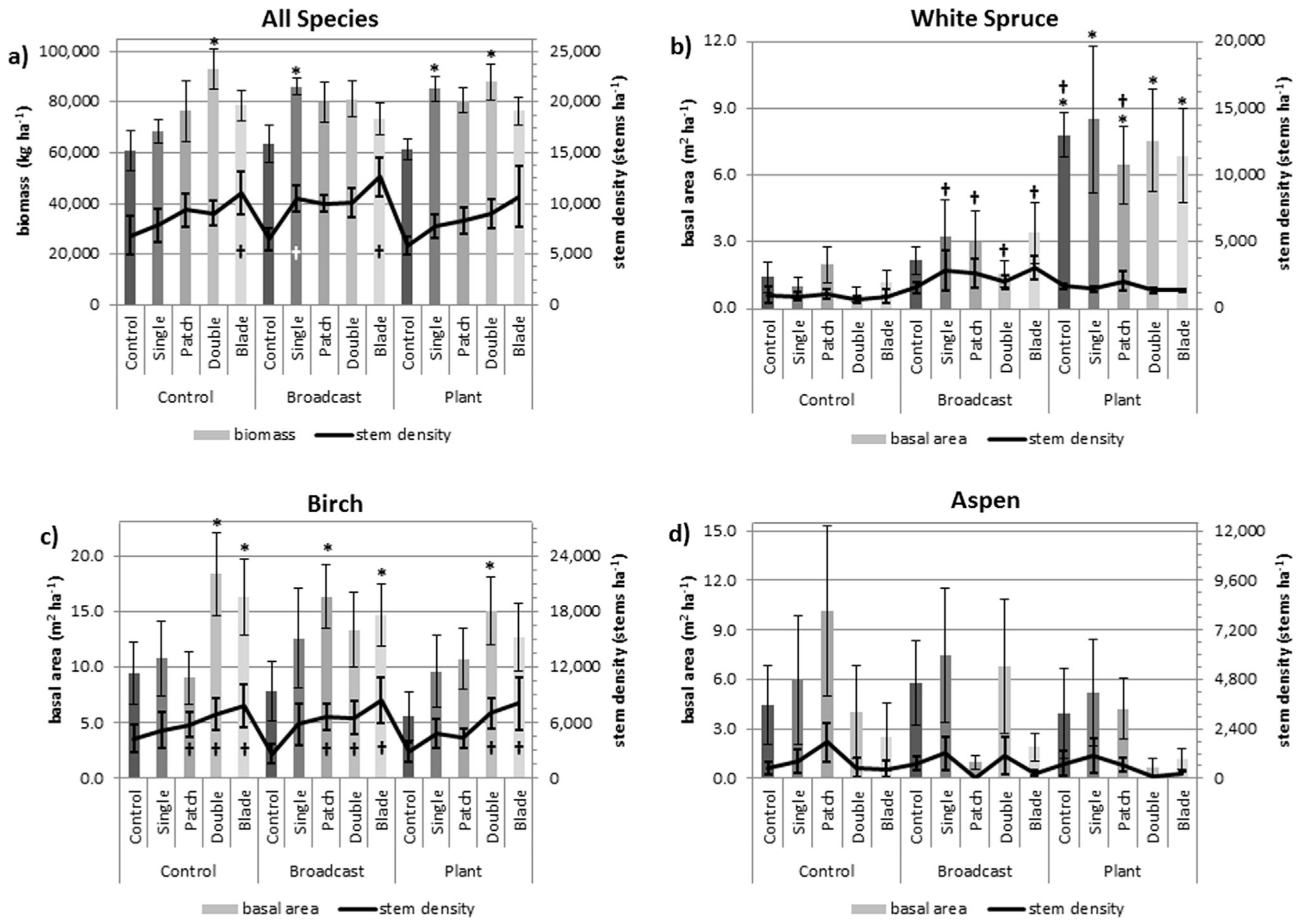

Fig. 7. Untransformed WSRT by GST group means for all species (a), white spruce (b), birch (c), and aspen (d). Error bars are ± 1 SE. *Basal area significantly different from non-scarified, natural seedfall control using Dunnett ($p < 0.05$). †Stem density significantly different from non-scarified, natural seedfall control using Dunnett ($p < 0.05$).

45 S/SPs, and on the Slope 15 of 45 lacked aspen. The data for both aspen stem density and basal area were highly right skewed, with 20 of 90 S/SPs exceeding mean stem density (5 of which were on the ridge) and 22 of 90 S/SPs exceeding mean basal area (6 of which were on the ridge). Nonetheless, transformed data conformed to parametric assumptions.

The experimental factors had limited impacts on aspen basal area and density. The LF factor was a marginally significant predictor of aspen basal area (p = 0.0901, Table 4). The Ridge LF supported less aspen basal area (2.37 ± 0.76 $m^2\,ha^{-1}$, n = 45) than the Slope (6.31 ± 1.18, n = 45).

The GST factor did not significantly influence aspen basal area (Table 4), though some trends merit reporting. Intensive GST (i.e., blade and double-disc scarification) tended to reduce aspen basal area by 40% on average compared to non-scarified controls, though these effects were not significant possibly due to limitations of the dataset (Table 5). Intensively scarified S/SPs on the Slope supported less than half the aspen basal area (3.61 ± 1.68 $m^2\,ha^{-1}$, n = 18) compared to non-scarified S/SPs (8.00 ± 2.28, n = 9).

Aspen basal area on natural seedfall S/SPs (5.41 ± 1.51 $m^2\,ha^{-1}$, n = 30) tended to be nearly twice the level of planted seedling S/SPs (3.03 ± 0.93, n = 30). However, the WSRT factor did not exert significant influence over aspen basal area (Table 4). In addition, when compared directly, aspen basal area on planted seedling S/SPs was not significantly different from the natural seedfall control (Dunnett, $p > 0.05$).

Aspen stem density was affected by similar experimental factors as basal area. Stem density was higher on Slope S/SPs (1055 ± 230 stems ha^{-1}, n = 45) than on Ridge S/SPs (303 ± 129, n = 45), and the difference was marginally significant (p = 0.0681, Table 4). GST alone was not a significant predictor of aspen stem density, but a significant interaction term indicated GST effects depended on LF type (Table 4). Intensive GST decreased aspen stem density significantly on both LFs together (Table 5). Slope S/SPs receiving intensive scarification had approximately half the aspen stem density (665 ± 345, n = 18) of non-scarified S/SPs (1204 ± 378, n = 9). The effect appeared to be reversed on the Ridge, with intensively scarified S/SPs (209 ± 75, n = 18) compared to non-scarified S/SPs (90 ± 27, n = 9).

4. Discussion

4.1. Strengths and limitations of the experimental design

The belt transect sampling method provided unbiased estimates of tree species density and basal area. To evaluate such a large experiment with confidence, it was a key pre-condition to establish the unbiased nature of our sampling method.

Lack of significance for spatial covariates indicated the original experimental design of Landform (LF) whole plots and blocks accounted for topographical and seed dispersal variables efficiently, indicating that within-whole plot and within-block variances of these variables were much smaller than those over the entire experiment. RCFTRI was designed to explicitly test specific assisted regeneration silvicultural treatments, and the original researchers minimized exogenous factors through careful temporal control of treatment implementation, spatially-sensitive blocking, and precise survey techniques to delineate treatment boundaries (Juday et al., 2013).

The inherited experimental design had some limitations for our analysis. There was only one replicate of a LF on a slope and one on a ridge, so hypothesis testing about LF was limited to 1 degree of freedom. However, it was important to include this variable because blocks in the same whole plot have a correlated error variance. Otherwise, blocks in the same whole plot (LF) would be treated as independent replicates, constituting a case of pseudo-replication resulting in unjustifiably narrower confidence intervals (Hurlbert, 1984). Furthermore, the parent experiment was not explicitly designed to test a balanced, continuous distribution of topographic gradients (e.g., elevation, slope angle, and distance from seed sources), and therefore generalizations cannot be made about how topographic variation would affect treatment outcomes. The original experimental design also did not control for legacy effects, such as root sprouting from aspen clones and the widely variable proximity to wind-dispersed seed sources. Finally, the experiment was not tended after establishment, so that natural reproduction and successional processes complicated the effects of treatments on recruitment. Still, a lack of tending activities, such as precommercial thinning or ongoing vegetation management, typifies forest practices in Alaska's boreal forest (Morimoto, 2016).

4.2. Biomass

The moderate positive effect on total biomass from ground scarification treatments (GST) may be understated by the opposite response of birch- and aspen-dominated forest types, both present in RCFTRI. Scarified S/SPs dominated by birch were associated with much higher basal area (a correlate of biomass) than controls (Table 5), while aspen-dominated S/SPs tended to show less basal area in response to increasingly intensive scarification (Fig. 5d). We found the biomass of these two upland hardwood species was significantly negatively correlated (Fig. 4b), and though they may co-occur, differences birch and aspen abundance is naturally driven by a preference for different site types and the legacy of pre-fire stand composition. In general, in Interior Alaska birch tolerates lower levels of insolation than aspen, and is more prevalent on cooler, moister sites (Chapin et al., 2006), which can be reinforced through subsequent competition. On severely burned sites, small-seeded species such as birch are at a competitive disadvantage compared to re-sprouting aspen connected to an established legacy root system (Johnstone and Chapin, 2006). Birch regeneration is very sensitive to reduced light levels from vegetative competition (Perala and Alm, 1990), and overtopping by fast-growing aspen shoots can prove deleterious (LaBonte and Nash, 1978). High levels of initial aspen abundance may have constrained birch recruitment from seed. We conclude that all types of scarification continued to influence total stand biomass 30 years after fire and salvage harvest, but a stand's composition of hardwood species determines whether the biomass will increase or decrease.

Although WSRT had a neutral effect on total biomass, there appeared to be a trade-off between hardwood biomass and white spruce biomass on planted seedling S/SPs (Fig. 4a). Establishing well-positioned seedlings soon after a disturbance while suppressing competition channels more of a site's productivity into the preferred species (Wagner et al., 2005). White spruce seedlings are quite shade-tolerant compared to aspen or birch, and as sapling size increases the mortality due to competition also rises (Kneeshaw et al., 2005). The successful establishment and growth of planted seedlings may have decreased hardwood vigor through competition. We interpret our result to indicate that planting seedlings shifts biomass production from hardwood seedlings to white spruce, but does not increase aggregate biomass (Fig. 4a).

Biomass of all species combined was marginally greater on the Ridge LF than the Slope (Fig. 6a). This apparent tendency would require testing in another study due to lack of replication of the LF whole plots in this design. One explanation for the productivity difference between LFs is that ridgetop sites may be buffered against high evaporation associated with decreased tree growth (Yarie, 2008).

4.3. White spruce crop Trees: Basal area and stem density

4.3.1. Effects of ground scarification treatments

The initial results which spanned a 12 year period at RCFTRI suggested a positive trend in seedling survival with scarification (Densmore et al., 1999). In our data, spanning 28 years, this trend for increased white spruce recruitment (as measured by stem density) by scarification did not hold: scarification alone appeared to exercise no influence over white spruce recruitment from either natural seedfall or planted seedling treatments (Fig. 7b). However, scarified S/SPs did respond positively to broadcast seeding with significantly elevated white spruce stem density (Fig. 7b), similar to white spruce results from Yukon Territory (Gardner, 1983). We conclude that scarification substantially increased stem density provided that a large, even distribution of seed occurs after canopy removal.

White spruce did not accumulate significantly more basal area on scarified plots compared to the non-scarified controls, consistent with the results found after 12 growing seasons (Densmore et al., 1999) and on a nearby experiment in northern British Columbia 15 years post-treatment (Bedford et al., 2000). Scarification apparently did not provide a lasting vegetative control on natural ingrowth of hardwood seedlings, which compete with white spruce seedlings for site resources. White spruce increases in height more slowly than birch or aspen, so competing vegetation must be suppressed for a longer time period to increase its growth significantly over hardwood competitors (Cole et al., 2003; Thiffault et al., 2003; Wiensczyk et al., 2011). On harvest-only sites, mechanical scarification seldom suppresses competing vegetation sufficiently to allow spruce growth rates to increase (Cole et al., 1999; Boateng et al., 2009). Initial blade scarification across Interior and south-central Alaska has been shown to increase planted seedling growth for some locations (Youngblood et al., 2011), but percentage of mineral soil exposed in those treatments was double that of the most intensive (blade) treatment in this experiment, suggesting that the stronger disturbance controlled of competition longer than in our study.

The more intensive scarification treatments applied in our study may have stimulated hardwood competition with white spruce. Double-disc scarification had a neutral effect on white spruce basal area compared to no scarification, while double-disc scarification increased birch basal area significantly (Fig. 5c). Stands with a substantial regenerating birch component, especially stands in which the initial accumulation of birch basal area was accelerated by early scarification treatments, will almost certainly support lower levels of white spruce basal area due to the early birch canopy dominance and reduced light transmittance (MacIsaac and Navratil, 1995; Comeau et al., 2003). Early establishment of planted white spruce seedlings appears to be an effective way to avoid early birch competition in burned and salvaged stands. The relative dominance of birch versus white spruce in young stands as mediated by scarification merits additional research, especially given the considerable expense of scarification.

4.3.2. Effects of white spruce regeneration treatments

The superior growth and initiation of dominance by white spruce seedlings within planted S/SPs compared to all other WSRTs was one of our clearest results (Fig. 6b). We found that planted seedling S/SPs accumulated substantially more basal area than any other WSRT regardless of GST or LF type (Fig. 6b), even allowing for the stunted growth due to fungal infection of spruce planting stock in two of the six blocks. Strong growth of planted white spruce at 28 years is consistent with observation after 10 years (Densmore et al., 1999). Other studies have established that the success of planting white spruce seedlings on unburned sites depends on a number of factors, especially the type and amount of ground cover (Eis, 1981; DeLong et al., 1997), which can be managed through site preparation such as herbicide or mechanical scarification (Boateng et al., 2009; Youngblood et al., 2011). Our study establishes that planted white spruce seedlings consistently succeeded in establishing a substantial basal area advantage on this burned and salvaged site, which may approximate the advantages of scarification seen on unburned harvested sites.

Broadcast seeding also succeeded in establishing large numbers of white spruce on the study area compared to natural seedfall Fig. 6b). We observed many small tree seedlings on broadcast S/SPs that did not meet the measurement inclusion criteria (dbh ≥ 1.0 cm), suggesting particularly high stem density. It appears that there will be a substantial time lag for these seedlings to reach the canopy, if they are able to at all. These results are similar to a nearby upland experiment, in which scarification following a mast-seeding year resulted in a high input of viable seed in conjunction with suitable seedbeds, ultimately resulting in severely overstocked stands (Wurtz and Zasada, 2001). The broadcast seeding WSRT appears prone to establishing overly dense stands on fire-prepared seedbeds, resulting in a crowded, slow-growing white spruce understory. By contrast, planting compared to broadcast seeding channels site productivity into fewer preferred stems and accelerates a stand's basal area accumulation of white spruce (rather than non-crop species).

The Slope LF appeared to be more hospitable to white spruce recruitment arising from seedfall than the Ridge, with a threefold greater stem density coming from both natural seedfall and broadcast seeded S/SPs (Fig. 6b). White spruce survival, measured five years after establishment, was slightly greater on the Slope than the Ridge for the direct seed treatments, and the difference increased on the subset of S/SPs measured after 10–12 years (Densmore et al., 1999). One reason for differential spruce survival by LF appears to have been the greater cover and persistence of the grass *Calamagrostis canadensis* across the ridge. Two years after treatment, disc scarification was not as effective at reducing vegetation on the Ridge compared to the Slope (Densmore et al., 1999). *C. canadensis* grows vigorously after disturbance, cools the soil, and may suppress spruce seedling recruitment and growth (Hogg and Lieffers, 1991; Collins and Schwartz, 1998). Conversely, the slope had greater herb cover, which is positively correlated with spruce survival and growth (Cater and Chapin, 2000). The differences in topography between the two LFs are consistent with environmental factors that facilitate the different ground cover vegetation types. These two different vegetation covers are associated with micro-scale differences in soil temperature and light environment (Cater and Chapin, 2000; Purdy et al., 2002), and we infer that these factors reduced white spruce establishment from seed on the Ridge. Hypothesized boreal forest succession processes, in which slow-growing conifers eventually replace same-aged hardwood associates (Awada et al., 2004; Chapin et al., 2006; Kurkowski et al., 2008), appear unlikely to occur on the Ridge due to the very low levels of spruce recruitment (Fig. 6b).

4.3.3. Natural regeneration considerations

The simplest method to recruit spruce stems is from natural seedfall. However, regeneration from natural seedfall requires both a significant seed source input and suitable seedbeds for germination (Gärtner et al., 2011). Our study area had high levels of both factors favoring white spruce establishment: historically large mast-seeding episodes immediately following fire, which provided a strong seed source (in 1983 and 1987; see Zasada, 1985; Roland et al., 2014), and highly favorable seedbed conditions compared to nearby unburned and harvested sites (Densmore et al., 1999). We infer that the combination of these factors favored substantial white spruce recruitment throughout RCFTRI at distances up to 265 m downwind from unburned stands with a mature spruce component (see Section 3.2.2), in line with local prevailing winds (Youngblood and Max, 1992).

Even though the Slope and Ridge LFs are similar in distance to unburned edge (Table 1), the Slope whole plot is oriented perpendicular to the prevailing wind direction within a burned finger bordered on three sides by unburned mature spruce-hardwood forest (Fig. 1). By contrast, the Ridge is parallel to the prevailing wind and less of its area is within the wind-dispersed seed shadow. As a result, the less favorable position of the Ridge S/SPs with respect to surviving white spruce seed sources and prevailing winds appears to have contributed to lower average spruce density compared to the Slope (Fig. 6b).

Depending on wind-dispersed seed sources for natural regeneration also requires timely seed masting events, but the timing of salvage harvest is tied to the fire season and not the masting cycle per se. White spruce masting in Interior Alaska is both infrequent (Juday et al., 2003) and irregular (Zasada and Viereck, 1970; Fox et al., 1984). Environmental factors that control the initiation, viability, and magnitude of periodic white spruce seed crops in Interior Alaska apparently maximize the probability that seeds, and especially mast crops, will be released into landscapes in which fires have recently occurred (Juday et al., 2003; Roland et al., 2014). In addition, seedbed receptivity to white spruce seedling establishment is considerably improved by fire consumption of the upper organic layer of the forest floor (Purdy et al., 2002). However, established white spruce seedling density following fire is not necessarily explained by masting events alone, because factors such as immediate post-fire weather and fire severity effects on the seedbed may also exert a controlling influence (Peters et al., 2006). Overall, because of post-fire seedbed receptivity and the synchrony of large seed crops to fire, burned stands are likely to experience higher natural white spruce regeneration success than stands originating from arbitrarily scheduled harvest of green stands. As a result, natural regeneration is often a robust regeneration strategy in post-fire salvage stands.

4.4. Birch ingrowth: Basal area and stem density

The experimental regeneration treatments of the RCFTRI were designed to increase white spruce establishment and early growth. However, all the factors we analyzed continued to exert a large influence on birch basal area and stem density into the stem exclusion stage of development, with implications for white spruce establishment and growth. Birch dominated the Ridge, contributing 84% of total basal area compared to only 44% on the Slope. Birch establishment likely did not generally face a seedbed limitation on either landform, because the thick organic layers that typically inhibit birch recruitment (Densmore and Page, 1992) were greatly reduced by the combined effects of severe burning and salvage logging. Nonetheless, birch basal area was doubled with any form of ground scarification (Table 5), which would constitute direct competition with a white spruce crop. Birch density and basal area also did not appear to be limited by the higher levels of *C. canadensis* on the Ridge measured after initial treatment (Densmore et al., 1999), even though birch stem density has been inversely related to *C. canadensis* cover (Densmore and Page, 1992). Apparently, organic layer thickness on a burned and salvaged site exercises greater control over birch abundance than grass cover.

Birch stem density decreased with greater distance from the nearest unburned edge (Table 3). Birch seed is typically wind-dispersed with peak dispersal occurring in the fall (Safford et al., 1990). However, variation in birch stem density in our study was not improved by incorporating the prevailing wind direction during the fall months. Birch seed dispersal may be less reliant on fall winds to reach suitable seedbeds than white spruce in our study area: birch seeds have been recorded up to 200 m from the seed source irrespective of wind direction (Zasada, 1985), may be latent in soil seedbanks even in burned sites (Archibold, 1979), and continue to abscise from the parent at reduced rates throughout the winter (Safford et al., 1990). Though birch can also reproduce asexually from root collar sprouting, sprouting ability begins to decline after a stem reaches 55 years (Safford et al., 1990), the burned stands that comprise the study area originated between the late 18th and early 19th centuries (Juday et al., 2013). As a result, we believe that birch largely reproduced in our study area from seed, and that birch seedfall was not as wind-dependent as white spruce. Forest managers should expect birch regeneration in post-fire salvage sites if unburned birch stands are nearby.

4.5. Aspen sprouting: Basal area and stem density

In order to make statistically robust inferences about aspen in a silvicultural installation such as RCFTRI, the experiment would need to be applied on post-fire sites that had a more even pre-fire aspen component than the patchy distribution which characterized our site (for example, Paragi and Haggstrom, 2007). Nevertheless, we observed strong tendencies that are highly indicative of aspen's probable response to the experimental treatments. Aspen was more prevalent on the Slope LF, with approximately three times as much aspen basal area and stem density compared to the Ridge. Although both landforms had the same average amount of insolation (see Section 2.2), the Slope site had a much greater variance in incoming solar radiation during the growing season, and contained those S/SPs with the highest incoming solar radiation, which relatively favors aspen establishment.

Aspen stem density was not correlated significantly with any seed dispersal measure, which suggests that many aspen in the study area sprouted asexually. Alternatively, aspen's plumose seeds, which are capable of long-distance dispersal (Perala, 1990), may have allowed for a more uniform distribution across the study site. Generally, sexual reproduction of aspen is less effective than asexual sprouting in Interior Alaska due to stringent mineral seedbed and microclimatic germination requirements (Johnstone and Chapin, 2006; Paragi and Haggstrom, 2007). Surveys conducted following the Rosie Creek fire found aspen self-replacement to be the norm, due in part to the early spring timing of the fire and the availability of unused root carbohydrate reserves at that time of year (Foote and Viereck, 1985). Within the burn scar of the Rosie Creek Fire, aspen regenerated in all pre-fire forest types, but regenerated aspen stem density was up to two orders of magnitude greater in pre-fire aspen stands (MacCracken and Viereck, 1990). Certain site types are more suitable to aspen growth due to earlier snow melt, higher solar radiation, and higher rates of evapotranspiration that put potential competitors at a disadvantage (Chapin et al., 2006; Kurkowski et al., 2008). Site types inherently favorable to aspen often have high levels of aspen basal area that readily regenerate following a disturbance. These adaptive mechanisms for aspen persistence suggest that when considering silvicultural regeneration treatments in stands dominated by aspen prior to disturbance, a significant legacy effect can be expected.

Fire or moderate forms of ground scarification have the potential to increase aspen basal area and stem density via the reduction of thick moss layers or slash removal which increases soil warmth and stimulates aspen sprouting (Bella, 1986; Paragi and Haggstrom, 2007). However, scarification methods that cause deep disturbance to the soil can damage the shallow root systems which subsequently reduces aspen density and growth (Haeussler and Kabzems, 2005). For example, in northern Saskatchewan, disc and blade scarification reduced aspen biomass and stem density by over 70% compared to non-scarified sites, likely due to the elimination of regenerating shoots rather than decreasing the vigor of remnant shoots (Peltzer et al., 2000). Vigorous competition from birch and quick-growing shrub species has also been observed to reduce aspen sprouting densities (Paragi and Haggstrom, 2007). Similarly in our study, competition from the prolific establishment of birch following scarification have further reduced aspen regeneration already weakened by scarification-induced soil disturbance. In evaluating our results at the RCFTRI, it is noteworthy that the Rosie Creek Fire significantly reduced the organic layer before site preparation or regeneration treatments. As a result, we believe that lower aspen recruitment on S/SPs receiving an intensive GST was likely a function of elimination of below-ground buds, compacted soil that reduced the growth potential of surviving buds, and vigorous competition. Aspen stem density was negatively related to the intensity of scarification, suggesting that seedbed at the time of treatment was not a key limitation, and therefore the majority of reproduction was from clonal root suckering. Intensive scarification works against renewal of vigorous aspen stands in Interior Alaska.

4.6. Management implications

4.6.1. Large dimension white spruce

The findings from this study can be summarized in a synthesis of key decision points that incorporate multiple species management potentials (Fig. 8a). Traditionally, one of the most common forest management goals in Interior Alaska was producing large dimension white spruce (Wurtz et al., 2006). However, meeting this goal following fire and salvage harvest requires both establishing vigorous spruce regeneration and suppressing other competitors from the earliest years of stand establishment. Among the practices evaluated in this study, the single most effective way to establish spruce and increase early basal area and biomass was to plant white spruce seedlings. Planted seedlings succeeded on sites even where the grass *C. canadensis* apparently suppressed direct seeding efforts. Planted white spruce seedlings also experienced reliably high survival on a nearby floodplain study site (Youngblood and Zasada, 1991), and our finding now demonstrate similar high survival on upland landforms. In addition, our results demonstrate that although several techniques for initial establishment of spruce were successful (Densmore et al. 1999), planted seedlings subsequently obtained a significant advantage in early growth.

Some studies have suggested scarification as an effective way to reduce grass competition and enhance spruce establishment (Collins and Schwartz, 1998), but the scarification methods employed in the RCFTRI were not intensive enough to increase white spruce basal area on sites with substantial pre-existing grass cover. Achieving increased basal area growth of white spruce usually requires suppression of hardwood competitors over a more extended period than the initial mechanical site preparation provides (Thiffault et al., 2003; Wiensczyk et al., 2011). In fact, a British Columbia study found that patch scarification stimulated an increase in vegetative competition and reduced spruce seedling growth (Bedford et al., 2000), and based on our results we expect that a similar competitive mechanism following scarification will favor birch regeneration and reduce white spruce on similar sites. Fire-thinned forest floor organic layers likely are sufficiently suitable seedbeds to establish white spruce from seed, provided grass cover is low to minimal. Where grass cover is vigorous and dense, for example on the Ridge landform, even scarification apparently did not improve spruce establishment due to rapid grass regrowth. Broadcast seeding, although it represents less investment than planted seedlings, resulted in many smaller stems that undoubtedly will have delayed entry into the canopy (and thus longer rotation lengths) if they are able to at all.

The least-cost method to recruit spruce stems is from natural seedfall. Nonetheless regeneration from natural seedfall requires both a significant seed source input and suitable seedbeds for germination (Alden, 1985; Rupp, 1997). Our study area had both factors, and we found white spruce recruitment sufficient to meet statutory requirements of 1111 stems ha^{-1} for stocking under the Alaska Forest Practices Act (DOF, 2007) at distances up to 265 m downwind from unburned stands with a mature spruce component. However, several factors likely elevated the natural recruitment above what could be reliably expected in other post-fire salvage situations. First, the study area experienced multiple masting episodes within a few years of disturbance, including the 1987 record high seedfall in 60 years of measurement. Second, all spruce seed sources were uphill at higher elevation than the study area, which may increase horizontal glide path distance travelled before a seed reaches the ground. Finally, even mortally injured trees, which might be salvaged logged in other circumstances, contributed viable seed (Zasada, 1985). Other literature suggests a reliable downwind dispersal distance for effective seed rain is approximately 100 m (Greene and Johnson, 2000). In sum, the unique factors of this study area suggest managers may not be able to depend on the long dispersal distances we found.

In addition to establishing white spruce seedlings, management for large dimension white spruce must also reduce the effects of hardwood competition on white spruce volume and height growth in order to

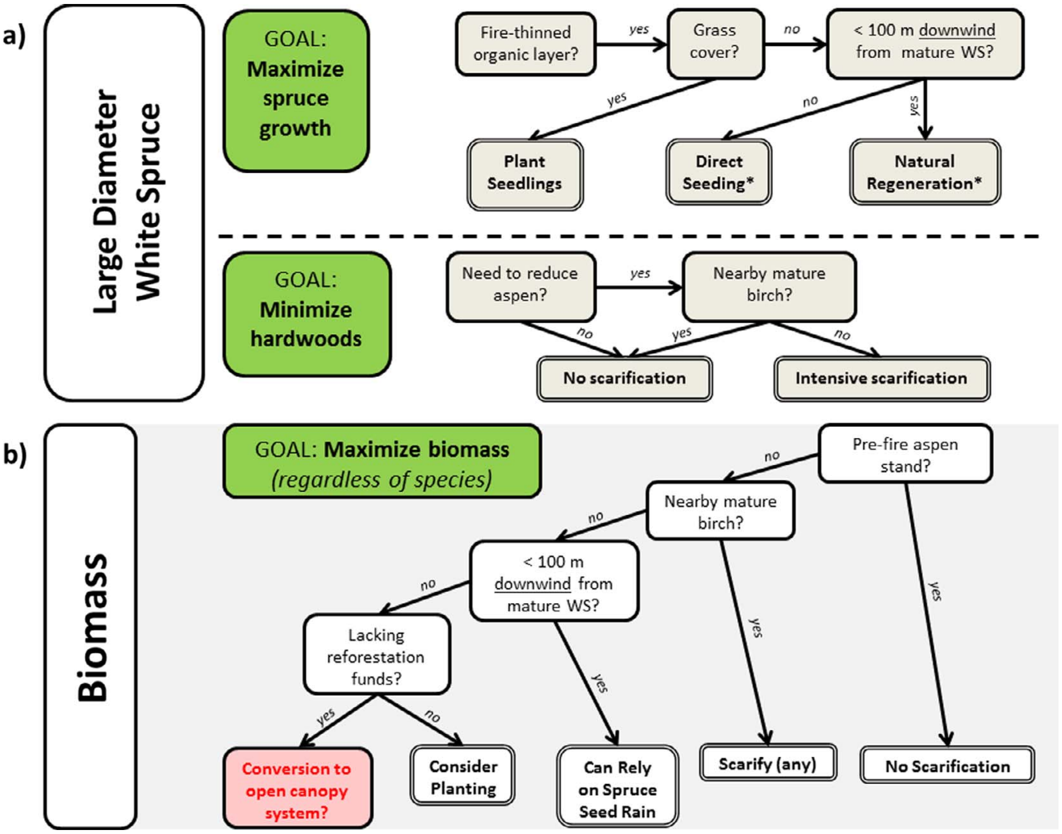

Fig. 8. Decision trees for (a) producing large diameter white spruce, and (b) maximizing on site biomass production.* represents a management decision that may lead to slower-growing crop trees and longer rotation lengths compared to planting seedlings.

minimize rotation length. Stands with a substantial regenerating birch component, especially stands in which the initial accumulation of birch basal area was accelerated by early scarification treatments, will almost certainly support lower levels of white spruce basal area (originated from seed) due to the early birch canopy dominance. If mature birch seed trees are nearby, care must be taken not to stimulate birch regeneration through intensive scarification methods. Similarly, an aspen overstory can decrease white spruce growth (Wright et al., 1998), but intensive forms of ground scarification may disrupt the aspen clonal root systems sufficiently to enhance early white spruce growth. Depending on hardwood reproduction potential, mechanical ground scarification may facilitate birch and reduce aspen competition.

4.6.2. Wood biomass in Alaska

An emerging alternative to the production of large dimension white spruce is production of above ground biomass, irrespective of species or dimension of the woody material (Nicholls et al., 2010). If biomass is to be produced from post-fire salvage harvested stands under a constrained budget, effective management decisions will need to account for legacy effects following fire (Fig. 8b). Legacy effects of particular importance for upland forests include the post-fire configuration of unburned stands near the salvaged stand, the autumn prevailing wind direction, as well as the pre-fire basal area of asexual sprouting species (e.g., aspen).

The least cost management approach to reforest a site would involve neither scarification nor artificial stocking. On sites with a substantial pre-fire aspen component, doing nothing appears to maximize stand biomass (particularly avoiding intensive scarification methods such as bulldozer blading or multiple passes with a disc-trencher). However, this management approach requires selecting sites that are conducive to aspen (Kurkowski et al., 2008), particularly with substantial pre-disturbance root systems (Frey et al., 2003). Warmer forest floors following the removal of logging slash were correlated with an increase in aspen sucker reproduction (Bella, 1986). High-severity wildfire similarly reduces ground-cooling organic layers, ground layer vegetation cover, and woody debris while killing the aspen canopy that suppresses root-sprouting (Ilisson and Chen, 2009). Aspen regenerated prolifically after the Rosie Creek Fire, with estimates between 71,600 and 138,150 stems ha^{-1} on pre-fire quaking aspen sites (Foote and Viereck, 1985; MacCracken and Viereck, 1990). However, the highly intensive scarification methods employed in this experiment reduced aspen stem density, and high-severity fire alone is likely sufficient to regenerate aspen (Paragi and Haggstrom, 2007).

By contrast, on sites with a large pre-fire birch component and nearby birch seed sources, scarification will increase total biomass (specifically birch biomass). Birch abundance in our study was related to distance to unburned edge (with autumn prevailing wind direction not significant), emphasizing the need for a proximate seed source before considering scarification. Increasing scarification intensity, as measured by mineral soil exposed, likely increases birch on a site up to a critical point where overcrowding may occur. Double-disc plowing (which initially exposed 25% mineral soil) increased birch basal area the most (Fig. 5c), an effect that may be related to the depth of scarification and the soil horizons exposed (Densmore and Page, 1992). Scarification for birch reproduction may also increase moose browsing activity due to the increase of young trees (Cole et al., 1999), and should therefore be undertaken with full knowledge of local wildlife dynamics.

Though planting white spruce seedlings had a neutral effect on total biomass in this study after 28 years, this practice may increase total woody biomass over a longer period by creating a multi-species stand. Some boreal silviculture systems actively cultivate a spruce understory beneath a birch canopy (Navratil, 1996), which protects young spruce from frost and herbivory as well as improves soil qualities (Simard and

Hannam, 2000; Wurtz and Zasada, 2001). Small spruce seedlings do not impact birch growth, and eventual removal of the birch overstory releases the shade-tolerant spruce (Simard and Hannam, 2000). White spruce and aspen mixed stands in Alberta also show higher gross productivity when considered for rotation ages over 80 years due to partitioning of site resources in space and time (Man and Lieffers, 1999). Our results indicate that planting white spruce seedlings shifts more of a site's early productivity from hardwood to white spruce growth, but could be a viable strategy to produce more biomass over a long period.

5. Conclusions

- Early silvicultural treatments targeted in this study to improve white spruce survival continue to have profound effects on the density and growth of boreal tree species, even after nearly three decades without tending.
- Contrasting with green-harvest management findings, ground scarification on this burned and salvaged site had a neutral effect on white spruce growth, while planted white spruce seedlings was particularly successful regardless of landform type or groundcover vegetation.
- Treatment effects did not attenuate over time for white spruce, and we found statistically significant effects that the original researchers could only describe as tendencies.
- Total biomass was increased on birch dominated areas that received scarification, but planting spruce merely shifted site biomass away from hardwoods largely into canopy-dominant spruce.
- Site differences, such as we found between the Slope and Ridge landforms, are a key consideration for implementing effective silvicultural practices. Statistically significant interactions between the regeneration treatments and landform types proved to be critical to meet specific reforestation objectives, likely through the mechanism of differing herbaceous vegetation cover types, presence/absence of aspen clonal rootstocks, and spatial configurations regarding seed sources.
- Reforesting mixed species stands, which are common in the lightly managed portions of the boreal forest, requires not only the consideration of the future crop tree, but also the interacting effects of silvicultural practices on all tree species.

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References

AHAP, 1988. Vegetation classification for Bonanza Creek Experimental Forest. In: Alaska High-Altitude Aerial Photography Program GeoData Center, Geophysical Institute, University of Alaska Fairbanks, Fairbanks AK.

Alaska, S.o., 2010. SDMI IFSAR N64W148 DTM. In: Geographic Information Network of Alaska, University of Alaska Fairbanks.

Alden, J., 1985. Early surival and growth of white spruce on natural sites. In: Dyrness, C. T., Juday, G.P. (Eds.), Early Results of the Rosie Creek Fire Research Project-1984. University of Alaska, Agricultural and Forestry Experiment Station, Misc. Publ. 85-2, Fairbanks, AK, pp. 40–43.

Archibold, O.W., 1979. Buried viable propagules as a factor in postfire regeneration in northern Saskatchewan. Can. J. Bot. 57, 54–58.

Awada, T., Henebry, G.M., Redmann, R.E., Sulistiyowati, H., 2004. Picea glauca dynamics and spatial pattern of seedlings regeneration along a chronosequence in the mixedwood section of the boreal forest. Ann. For. Sci. 61, 789–794.

Bedford, L., Sutton, R.F., Stordeur, L., Grismer, M., 2000. Establishing white spruce in the Boreal White and Black Spruce Zone. New For. 20, 213–233.

Beget, J.E., Stone, D., Verbyla, D.L., 2006. Regional overview of Interior Alaska. In: Chapin, F.S., Oswood, M.W., Cleve, K.V., Viereck, L.A., Verbyla, D.L. (Eds.), Alaska's Changing Boreal Forest. Oxford University Press, New York, pp. 12–20.

Bella, I.E., 1986. Logging practices and subsequent development of aspen stands in east-central Saskatchewan. Forest. Chron. 62, 81–83.

Boateng, J.O., Heineman, J.L., Bedford, L., Harper, G.J., Linnell-Nemec, A.F., 2009. Long-term effects of site preparation and postplanting vegetation control on Picea glauca survival, growth and predicted yield in boreal British Columbia. Scand. J. For. Res. 24, 111–129.

Boateng, J.O., Heineman, J.L., McClarnon, J., Bedford, L., 2006. Twenty year responses of white spruce to mechanical site preparation and early chemical release in the boreal region of northeastern British Columbia. Can. J. For. Res. 36, 2386–2399.

Box, G., Cox, D., 1964. An analysis of transformations. J. Royal Stat. Soc. Ser. B (Methodological) 26, 211–252.

Brown, Morton B., Forsythe, Alan B., 1974. Robust tests for equality of variances. J. Am. Stat. Assoc. 69, 364–367.

Cater, T.C., Chapin, F.S., 2000. Differential effects of competition or microenvironment on boreal tree seedling. Ecology 81, 1086–1099.

Chapin, F.S., Hollingsworth, T.N., Murray, D.F., Viereck, L.A., Walker, M.D., 2006. Floristic diversity and vegetation distribution in the Alaskan boreal forest. In: Chapin, F.S., Oswood, M.W., Van Cleve, K., Viereck, L.A., Verbyla, D.L. (Eds.), Alaska's Changing Boreal Forest. Oxford University Press, New York, pp. 81–99.

Cole, E., Youngblood, A., Newton, M., 2003. Effects of competing vegetation on juvenile white spruce (Picea glauca (Moench) Voss) growth in Alaska. Ann. For. Sci. 60, 573–583.

Cole, E.C., Newton, M., Youngblood, A., 1999. Regenerating white spruce, paper birch, and willow in south-central Alaska. Can. J. For. Res. 29, 993–1001.

Collins, W.B., Schwartz, C.C., 1998. Logging in Alaska's boreal forest: creation of grasslands or enhancement of moose habitat. Alces 34, 355–374.

Comeau, P.G., Wang, J.R., Letchford, T., 2003. Influences of paper birch competition on growth of understory white spruce and subalpine fir following spacing. Can. J. For. Res. 33, 1962–1973.

Cortini, F., Comeau, P.G., Boateng, J.O., Bedford, L., 2010. Yield implications of site preparation treatments for lodgepole pine and white spruce in northern British Columbia. Forests 1, 25–48.

Crimp, P.M., Phillips, S.J., Worum, G.T., 1997. Resources on State Forestry Lands in the Tanana Valley. In: Division of Forestry, Alaska Department of Natural Resources, p. 80.

DeLong, H.B., Lieffers, V.J., Blenis, P.V., 1997. Microsite effects on first-year establishment and overwinter survival of white spruce in aspen-dominated boreal mixedwoods. Can. J. For. Res. 27, 1452–1457.

Densmore, R.V., Juday, G.P., Zasada, J.C., 1999. Regeneration alternatives for upland white spruce after burning and logging in interior Alaska. Can. J. For. Res. 29, 413–423.

Densmore, R.V., Page, J.C., 1992. Paper birch regeneration on scarified logged areas in Southcentral Alaska. North. J. Appl. Forest. 9, 63–66.

Deutschman, D.H., Levin, S.A., Pacala, S.W., 1999. Error propagation in a forest succession model: the role of fine-scale heterogeneity in light. Ecology 80, 1927–1943.

DOF, 2007. Alaska Forest Resources & Practices Regulations. In: Division of Forestry, Alaska Department of Natural Resources, p. 68. < http://forestry.alaska.gov/pdfs/2009AFResourcesPracticesRegulations_June2007.pdf > .

Drever, C.R., Peterson, G., Messier, C., Bergeron, Y., Flannigan, M., 2006. Can forest management based on natural disturbances maintain ecological resilience? Can. J. For. Res. 36, 2285–2299.

Dunnett, C.W., 1955. A multiple comparison procedure for comparing several treatments with a control. J. Am. Stat. Assoc. 50, 1096–1121.

Eis, S., 1981. Effect of vegetative competition on regeneration of white spruce. Can. J. For. Res. 11, 1–8.

ESRI, 2012. ArcMap GIS. In: Enivronmental Systems Research Institute, Inc., Redlands, CA.

Foote, J., Viereck, L., 1985. Burn severity: its impact on the natural revegetation process following the Rosie Creek Fire. In: Dyrness, C.T., Juday, G.P. (Eds.), Early Results of the Rosie Creek Fire Research Project-1984. University of Alaska, Agricultural and Forestry Experiment Station, Misc. Publ. 85-2, Fairbanks, AK, pp. 26–29.

Fox, J.D., Zasada, J.C., Gasbarro, A.F., Van Veldhuizen, R., 1984. Monte Carlo simulation of white spruce regeneration after logging in interior Alaska. Can. J. For. Res. 14, 617–622.

Frey, B.R., Lieffers, V.J., Landhäusser, S.M., Comeau, P.G., Greenway, K.J., 2003. An analysis of sucker regeneration of trembling aspen. Can. J. For. Res. 33, 1169–1179.

Gallant, A.L., Binnian, E.F., Omernik, J.M., Shasby, M.B., 1995. Ecoregions of Alaska. In: US Geological Survey, Washington.

Gardner, A.C., 1983. White Spruce Regeneration Options on River Floodplains in the Yukon Territory. Pacific Forest Research Centre, Canadian Forestry Service 24.

Gärtner, S.M., Lieffers, V.J., Macdonald, S.E., 2011. Ecology and management of natural regeneration of white spruce in the boreal forest. Environ. Rev. 19, 461–478.

Greene, D.F., Gauthier, S., Noël, J., Rousseau, M., Bergeron, Y., 2006. A field experiment to determine the effect of post-fire salvage on seedbeds and tree regeneration. Front. Ecol. Environ. 4, 69–74.

Greene, D.F., Johnson, E.A., 2000. Tree recruitment from burn edges. Can. J. For. Res. 30, 1264–1274.

Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I., Simard, M.-J., 1999. A review of the regeneration dynamics of North American boreal forest tree species. Can. J. For. Res. 29, 824–839.

Haeussler, S., Kabzems, R., 2005. Aspen plant community response to organic matter removal and soil compaction. Can. J. For. Res. 35, 2030–2044. http://dx.doi.org/10.1139/X05-133.

Hammond, T.O., 1996. Mapping Interior Alaska forest types with satellite imagery. In: School of Agriculture and Land Resources Management. University of Alaska, Fairbanks, Fairbanks, AK, p. 136.

Hawkins, C.B.D., Steele, T.W., Letchford, T., 2006. The economics of site preparation and the impacts of current forest policy: evidence from central British Columbia. Can. J. For. Res. 36, 482–494.

Heinselman, M.L., 1981. Fire and succession in the conifer forests of northern North America. In: West, D.C., Shugart, H.H., Botkin, D.B. (Eds.), Forest Succession. Springer, New York, pp. 374–405.

Henderson, C.J., 1988. Managing aspen in the mixedwood forest. In: Samoil, J.K. (Ed.), Management and utilization of northern mixedwoods. Northern Forestry Centre, Canadian Forestry Service, Edmonton, AB, pp. 50–52.

Hinzman, L.D., Viereck, L.A., Adams, P.C., Romanovsky, V.E., Yoshikawa, K., 2006. Climate and permafrost dynamics of the Alaskan boreal forest. In: Chapin, F.S., Oswood, M.W., Van Cleve, K., Viereck, L.A., Verbyla, D.L. (Eds.), Alaska's Changing Boreal Forest. Oxford University Press, New York, pp. 39–61.

Hogg, E.H., Lieffers, V.J., 1991. The impact of Calamagrostis canadensis on soil thermal regimes after logging in northern Alberta. Can. J. For. Res. 21, 387–394.

Huang, S., Price, D., Titus, S.J., 2000. Development of ecoregion-based height-diameter models for white spruce in boreal forests. For. Ecol. Manage. 129, 125–141.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54, 187–211.

Ilisson, T., Chen, H.Y.H., 2009. Response of six boreal trees species to standreplacing fire and clearcutting. Ecosystems 12, 820–829.

Jenkins, J.C., Chojnacky, D.C., Heath, L.S., Birdsey, R.A., 2003. National-scale biomass estimators for United States tree species. For. Sci. 49, 12–35.

Johnstone, J.F., Chapin, F.S., 2006. Effects of soil burn severity on post-fire tree recruitment in boreal forest. Ecosystems 9, 14–31.

Johnstone, J.F., Chapin, F.S., Foote, J., Kemmett, S., Price, K., Viereck, L., 2004. Decadal observations of tree regeneration following fire in boreal forests. Can. J. For. Res. 34, 267–273.

Juday, G.P., 1985. Preface: the Rosie Creek Fire and its research opportunities. In: Juday, G.P., Dyrness, C.T. (Eds.), Early Results of the Rosie Creek Fire Research Project-1984. University of Alaska, Agricultural and Forestry Experiment Station, Misc. Publ. 85-2, Fairbanks, AK.

Juday, G.P., Barber, V., Rupp, T.S., Zasada, J.C., Wilmking, M., 2003. A 200-year perspective of climate variability and the response of white spruce in Interior Alaska. In: Greenland, D., Goodin, D.G., Smith, R.C. (Eds.), Climate Variability and Ecosystem Response at Long-term Ecological Research Sites. Oxford University Press, New York, NY, pp. 226–250.

Juday, G.P., Densmore, R.V., Zasada, J.C., 2013. White spruce regeneration silviculture techniques 25 years after wildfire: the Rosie Creek Fire Tree Regeneration Installation. In: Camp, A.E., Irland, L.C., Carroll, C.J.W. (Eds.), Long-term Silvicultural & Ecological Studies: Results for Science and Management, Volume 2. Yale University School of Forestry and Environmental Studies, pp. 49–65.

Kneeshaw, D., Kobe, R., Coates, K.D., Messier, C., 2005. Sapling size influences shade tolerance ranking among southern boreal tree species. Ecology 94, 471–480.

Kuehl, R.O., 2000. Design of Experiments: Statistical Principles of Research Design and Analysis. Duxbury Thomson Learning, Pacific Grove, CA.

Kurkowski, T.A., Mann, D.H., Rupp, T.S., Verbyla, D.L., 2008. Relative importance of different secondary successional pathways in an Alaskan boreal forest. Can. J. For. Res. 38, 1911–1923.

LaBonte, G.A., Nash, R.W., 1978. Cleaning and weeding paper birch – a 24-year case history. Forestry 4, 223–225.

Lechowicz, M.J., Bell, G., 1991. The ecology and genetics of fitness in forest plants. II. Microspatial heterogeneity of the edaphic environment. Ecology 79, 687–696.

Lieffers, V.J., Stadt, K.J., Navratil, S., 1996. Age structure and growth of understory white spruce under aspen. Can. J. For. Res. 26, 1002–1007.

MacCracken, J.G., Viereck, L.A., 1990. Browse regrowth and use by moose after fire in Interior Alaska. Northwest Sci. 64, 11–18.

MacIsaac, D.A., Navratil, S., 1995. Competition dynamics in juvenile boreal hardwood-conifer mixtures. In: Comeau, P.G., Thomas, K.D. (Eds.), Silviculture of Temperate and Boreal Broadleaf-conifer Mixtures. BC Ministry of Forests, Richmond, BC, pp. 23–34.

Malone, T., Liang, J., Packee, E.C., 2009. Cooperative Alaska forest inventory. In: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, p. 42.

Man, R., Lieffers, V.J., 1999. Are mixtures of aspen and white spruce more productive than single species stands? Forest Chron. 75, 505–513.

Morimoto, Miho, 2016. Past, current, and future forest harvest and regeneration management in interior Alaska boreal forest: adaptation under rapid climate change. Doctoral Dissertation, University of Alaska Fairbanks.

Navratil, S., 1996. Silvicultural systems for managing deciduous and mixedwood stands with white spruce understory. In: Comeau, P.G., Thomas, K.D. (Eds.), Silviculture of Temperate and Boreal Broadleaf-conifer Mixtures. BC Ministry of Forestry, Richmond, BC, pp. 35–46.

Nicholls, D.L., Brackley, A.M., Barber, V., 2010. Wood energy for residential heating in Alaska: current conditions, attitudes, and expected use. In: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, p. 30.

Paragi, T.F., Haggstrom, D.A., 2007. Short-term responses of aspen to fire and mechanical treatments in Interior Alaska. North. J. Appl. Forest. 24, 153–157.

Peltzer, D.A., Bast, M.L., Wilson, S.D., Gerry, A.K., 2000. Plant diversity and tree responses following contrasting disturbances in boreal forest. For. Ecol. Manage. 127, 191–203.

Perala, D.A., 1990. Populus tremuloides Michx. quaking aspen. Silvics of North America: Volume 2, Hardwoods 34.

Perala, D.A., Alm, A.A., 1990. Regeneration silviculture of birch: a review. For. Ecol. Manage. 32, 39–77.

Peters, V.S., Macdonald, S.E., Dale, M.R.T., 2006. Patterns of initial versus delayed regeneration of white spruce in boreal mixedwood succession. Can. J. For. Res. 36, 1597–1609.

Purdy, B.G., Macdonald, S.E., Dale, M.R.T., 2002. The regeneration niche of white spruce following fire in the mixedwood boreal forest. Silva Fennica 36, 289–306.

Reed, R.A., Peet, R.K., Palmer, M.W., White, P.S., 1993. Scale dependence of vegetation-environment correlations: a case study of a North Carolina piedmont woodland. Veg. Sci. 4, 329–340.

Roland, C.A., Schmidt, J.H., Johnstone, J.F., 2014. Climate sensitivity of reproduction in a mast-seeding boreal conifer across its distributional range from lowland to treeline forests. Oecologia 174, 665–677.

Rupp, T.S., 1997. A geographic model of landscape-level post-disturbance forest establishment patterns of Interior Alaska white spruce ecosystems. In: School of Natural Resources. University of Alaska, Fairbanks.

Safford, L.O., Bjorkbom, J.C., Zasada, J.C., 1990. Betula papyrifera Marsh. paper birch. Silvics of North America: Volume 2, Hardwoods 19.

SAS, 2012. SAS Software for Windows, Release 9.3. In: SAS Institute, Inc., Cary, NC.

Simard, S.W., Hannam, K.D., 2000. Effects of thinning overstory paper birch on survival and growth of interior spruce in British Columbia: implications for reforestation policy and biodiversity. For. Ecol. Manage. 129, 237–251.

Soil Survey Staff, N.R.C.S., U.S. Department of Agriculture, 2011. Web Soil Survey. < http://websoilsurvey.nrcs.usda.gov/ > .

Stone, D.M., Elioff, J.D., 1998. Soil properties and aspen development five years after compaction and forest floor removal. Can. J. Soil Sci. 78, 51–58.

Thiffault, N., Jobidon, R., Munson, A.D., 2003. Performance and physiology of large containerized and bare-root spruce seedlings in relation to scarification and competition in Québec (Canada). Ann. For. Sci. 60, 645–655.

USGS, 1986. 22 August 1986 Color Infrared Photo: ID AR5860035821810. In: Earth Resources Observation and Science Center, U.S.G.S. (Ed.), Sioux Falls, SD.

Van Cleve, K., Chapin, F.S., Dyrness, C.T., Viereck, L.A., 1991. Element cycling in taiga forests: state-factor control. Bioscience 41, 78–88.

Van Cleve, K., Chapin, F.S., Ruess, R.W., 2013a. Bonanza Creek Experimental Forest: Hourly Precipitation data, 1988 to Present. In: Bonanza Creek LTER – University of Alaska Fairbanks.

Van Cleve, K., Chapin, F.S., Ruess, R.W., 2013b. Bonanza Creek Experimental Forest: HourlyTemperature (sample, min, max) at 50 cm and 150 cm from 1988 to Present. In: Bonanza Creek LTER – University of Alaska Fairbanks.

Viereck, L.A., Dyrness, C.T., Van Cleve, K., Foote, M.J., 1983. Vegetation, soils, and forest productivity in selected forest types in interior Alaska. Can. J. For. Res. 13, 703–720.

Viereck, L.A., Slaughter, C.W., 1986. Climatic characteristics of the taiga in Interior Alaska. In: Van Cleve, K., Chapin, F.S., Flanagan, P.W., Viereck, L.A., Dyrness, C.T. (Eds.), Forest Ecosystems in the Alaskan Taiga. Springer Verlag, New York, pp. 9–21.

Viereck, L.A., Van Cleve, K., Dyrness, C.T., 1986. Forest ecosystem distribution in the taiga environment. In: Van Cleve, K., Chapin, F.S., Flanagan, P.W., Viereck, L.A., Dyrness, C.T. (Eds.), Forest Ecosystems in the Alaskan Taiga. Springer Verlag, New York, pp. 22–43.

Wagner, R.G., Little, K.M., Richardson, B., Mcnabb, K., 2005. The role of vegetation management for enhancing productivity of the world's forests. Forestry 79, 57–79.

Weber, M.G., Flannigan, M.D., 1997. Canadian boreal forest ecosystem structure and function in a changing climate: impact on fire regimes. Environ. Rev. 5, 145–166.

Wiensczyk, A., Swift, K., Morneault, A., Thiffault, N., Szuba, K., Bell, F.W., 2011. An overview of the efficacy of vegetation management alternatives for conifer regeneration in boreal forests. Forest. Chron. 87, 175–200.

Wright, E.F., Coates, K.D., Canham, C.D., Bartemucci, P., 1998. Species variability in growth response to light across climatic regions in northwestern British Columbia. Can. J. For. Res. 28, 871–886.

Wurtz, T.L., 1995. Understory alder in three boreal forests of Alaska: local distribution and effects on soil fertility. Can. J. For. Res. 25.

Wurtz, T.L., Ott, R.A., Maisch, J.C., 2006. Timber harvest in Interior Alaska. In: Chapin, F.S., Oswood, M.W., Van Cleve, K., Viereck, L.A., Verbyla, D.L. (Eds.), Alaska's Changing Boreal Forest. Oxford University Press, New York, pp. 302–308.

Wurtz, T.L., Zasada, J.C., 2001. An alternative to clear-cutting in the boreal forest of Alaska: a 27-year study of regeneration after shelterwood harvesting. Can. J. For. Res. 31, 999–1011.

Yarie, J., 2008. Effects of moisture limitation on tree growth in upland and floodplain forest ecosystems in interior Alaska. For. Ecol. Manage. 256, 1055–1063.

Youngblood, A., 1995. Development patterns in young conifer-hardwood forests of interior Alaska. Veg. Sci. 6, 229–236.

Youngblood, A., Cole, E., Newton, M., 2011. Survival and growth response of white spruce stock types to site preparation in Alaska. Can. J. For. Res. 41, 793–809.

Youngblood, A., Max, T.A., 1992. Dispersal of white spruce seed on Willow Island in Interior Alaska. In. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.

Youngblood, A., Zasada, J.C., 1991. White spruce artificial regeneration options on river floodplains in interior Alaska. Can. J. For. Res. 21, 423–433.

Zasada, J.C., 1980. Some considerations in the natural regeneration of white spruce in interior Alaska. In: Murray, M., Van Veldhuizen, R.M. (Eds.), Forest Regeneration at High Latitudes. Pacific Northwest Forest and Range Experiment Station, U.S. Department of Agriculture, Forest Service, Fairbanks, AK, p. 52.

Zasada, J.C., 1985. Production, dispersal, and germination of white spruce and paper birch and first year seedling establishment after the Rosie Creek Fire. In: Juday, G.P., Dyrness, C.T. (Eds.), Early Results of the Rosie Creek Fire Research Project-1984. University of Alaska, Agricultural and Forestry Experiment Station, Misc. Publ. 85-2, Fairbanks, AK, pp. 34–37.

Zasada, J.C., 1986. Natural regeneration of trees and tall Shrubs on forest sites in Interior Alaska. In: Van Cleve, K., Chapin, F.S., Flanagan, P.W., Viereck, L.A., Dyrness, C.T. (Eds.), Forest Ecosystems in the Alaskan Taiga. Springer Verlag, New York, pp. 44–73.

Zasada, J.C., Grigal, D., 1978. The effects of silvicutural system and seedbed preparation on natural regeneration of white spruce and associated species. In: Proceedings of the Fifth North American Forest Biology Workshop, 1978, Gainesville, Fla. Southern Forest Experiment Station, U.S. Department of Agriculture, Forest Service, Gainesville, FL, pp. 213–220.

Zasada, J.C., Norum, R., Van Veldhuizen, R.M., Tuetsch, C.E., 1983. Artificial regeneration of trees and tall shrubs in experimentally burned upland black spruce/feather moss stands in Alaska. Can. J. For. Res. 13, 903–913.

Zasada, J.C., Packee, E.C., 1995. The Alaska Region. In: Barrett, J.W. (Ed.), Regional Silviculture of the United States. Wiley, New York, pp. 559–606.

Zasada, J.C., Sharik, T.L., Nygren, M., 1992. The reproductive process in boreal forest trees. In: Shugart, H., Leemins, R., Bonan, G. (Eds.), A Systems Analysis of the Global Boreal Forest. Cambridge University Press, Cambridge, UK, pp. 85–125.

Zasada, J.C., Viereck, L.A., 1970. White spruce cone and seed production in interior Alaska, 1957-68. In: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR, p. 11.