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Clearcutting and high severity wildfire have comparable effects on growth of direct-seeded interior Douglas-fir

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ABSTRACT

The degree to which harvesting can achieve comparable beneficial effects to wildfire on seedling establishment is a key factor in understanding regeneration dynamics in dry interior forest ecosystems. We compared the capacity of harvesting versus wildfire to support establishment of directly-seeded interior Douglas-fir over a three-year period in the interior Douglas-fir biogeoclimatic zone of British Columbia. The mixed-severity McLure Fire of August 2003 affected over 26,000 hectares in the central British Columbia, Canada. Within the fire-affected area, we assessed growth performance in five disturbance types: High Severity Burn, Low Severity Burn, Clearcut, Screefed Clearcut, and Undisturbed Forest. Seedlings in the High Severity Burn had the significantly greater shoot biomass and root biomass than those in the Low Severity Burn and Undisturbed Forest in the first year. Additionally, seedlings in the High Severity Burn had significantly higher foliar N and P content than those in both clearcut treatments in year one. Foliar nitrogen concentrations remained above critical deficiency levels (1.4%) in both clearcut treatments and the High Severity Burn treatment in all three years. Overall, seedling growth performance in Screefed Clearcut was the most comparable with High Severity Burn treatment, indicating the potential for harvesting with site preparation to produce comparable effects to wildfire on aspects of seedling establishment, particularly growth and nutrition.

1. Introduction

Wildfire has historically been a key disturbance creating the necessary conditions for natural tree regeneration in the dry interior forests of North America. Interest has been growing in incorporating natural disturbance emulation into management strategies to increase forest recovery after wildfire and other disturbances, in part by creating forest structures and environmental conditions to facilitate tree regeneration (McRae et al., 2001; Long, 2009). In forests dominated by interior Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var glauca (Mayr)), the historic wildfire regime was mixed severity wildfire, which, when combined with both natural (insect outbreaks e.g.) and human-caused disturbances (logging e.g.), produce a heterogeneous forest landscape (Heyerdahl et al., 2006; Klenner et al., 2008). The degree that harvesting emulates wildfire depends on wildfire severity variation and the type of harvesting technique employed (Haeussler and Kneeshaw, 2003; Nitschke, 2005).

Given the mixed-severity regime in dry interior Douglas-fir forests, any attempt to improve regeneration success from seed must assess the growth potential of seedlings under a wide range of post-disturbance environments. A key comparison between harvesting and wildfire is their relative ability of disturbances to create favorable conditions for forest regeneration from seed. Both harvesting and wildfire can enhance interior Douglas-fir seedling growth by exposing mineral soil and reducing the abundance of competing vegetation (Greene et al., 1999; Flannigan et al., 2000). Wildfire appears to have greater potential to stimulate growth through increased nutrient availability than harvesting due to combustion of the forest floor (McRae et al., 2001). However, harvesting and site preparation can be applied to maximize forest floor disruption (e.g., through mechanical site preparation following logging) or remove competing vegetation, and thereby improve seedling growing conditions in temperate and boreal forests (Haeussler et al., 1999; Sutherland and Foreman, 2000).

The McLure Fire occurred in August of 2003 near Kamloops, British Columbia, and burned 26,420 hectares. This mixed-severity wildfire occurred within a forest area with active harvesting, and resulted in a mosaic of low, medium and high severity burns inter-mixed with clearcuts. This presented an opportunity to

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experimentally compare seed regeneration potential following different severities of wildfire and clearcutting disturbances on comparable sites. Our objective was to compare the ability of high and low severity wildfire vs clearcut harvesting to facilitate establishment of directly-seeded interior Douglas-fir by assessing seedling growth and foliar nutrient dynamics. First, we hypothesized that seedling growth would be higher under either type of stand-replacing disturbance than in control (undisturbed) or lightly burned forests, mainly as a result of increased resource availability (light, soil water and nutrients). Second, we hypothesized that nutrient availability to seedlings would increase with disturbance severity. We predicted that seedlings growing in the high severity burns and harvesting-with-screefing disturbance types would be associated with the highest seedling nutrient content. Taken together, we predicted that the clearcut harvesting-with-screefing and High Severity Burn disturbance types would have the best growth performance of seeded interior Douglas-fir.

2. Methods

2.1. Study area

The study was conducted in the vicinity of Barriere, British Columbia, Canada (51°00N, 120°00W). The sites were located between 400 m and 1400 m elevation within the Interior Douglas-Fir (IDF) biogeoclimatic zone, which is characterized by mean annual precipitation ranging from 300 to 850 mm (Lloyd et al., 1990). Soils at the study area were Brunisols and Luvisols of silty or sandy loam texture (Soil Classification Working Group, 1998).

Prior to disturbance, the forests were dominated by mature interior Douglas-fir with increasing amounts of subordinate lodgepole pine (*Pinus contorta* var. *latifolia* (Engelm.) Critchfield) at higher elevations. Common understory species included *Arctostaphlos uva-ursi* (L.) Spreng., *Linnaea borealis* L., *Lupinus arcticus* S. Watson, and *Calamagrostis rubescens* Buckl. (Lloyd et al., 1990).

2.2. Experimental design and treatments

In May 2004, 16 sites were located across a continuum of wildfire and harvesting disturbance severities, ranging from undisturbed forests to high severity burns and Screefed Clearcuts. The sites included five disturbance types (hereafter referred to as 'treatments': (1) High Severity Burn, (2) Low Severity Burn, (3) Screefed Clearcut, (4) Clearcut (without screefing) and (5) Undisturbed Forest. These treatments were examined on four replicate sites each that were located at least 1 km apart, except for the Clearcut and Screefed Clearcut treatments, which were located in the same replicate clearcuts. Measured site characteristics and climatic information are given in Table 1. Mean annual precipitation (MAP) and mean annual temperature (MAT) were estimated using the ClimateWNA, which combines climate data and modeling with site longitude and latitude data to produce historical climate variable estimates (Wang et al., 2012).

Burn severity was defined as the amount of organic material consumed by the fire (Johnstone and Chapin, 2006). In this study, we assessed burn severity based on fire effects on tree boles and the forest floor. Residual forest floor status was determined post hoc based on depth of forest floor charring and exposure of mineral soil. At the High Severity Burn sites, the forest floor was completely consumed and the mineral soil exposed (residual depth of forest floor 0.7, se 0.2 cm). Only charred boles of fire-killed trees remained of the canopy and understory trees, which were removed prior to study initiation using a mechanical harvester. At the Low Severity Burn sites, at least 95% of the canopy survived (based on number of tree stems) the fire but 100% of the understory was killed (residual depth of forest floor 1.8, se 0.5 cm). We required that the High Severity Burn and Low Severity Burn conditions occurred uniformly over an area at least 50 m × 50 m to qualify as a replicate site.

The Undisturbed Forest and clearcut sites were located either within the overall perimeter or at the immediate periphery (within 4 km) of the McLure Fire. The Undisturbed Forests were dominated by mature Douglas-fir trees that were estimated to be 100–200 years old. Forest floor depth averaged 4.9, se 0.6 cm. The clearcut sites were harvested in the winter of 2003–2004 and were cleared of canopy cover over an area of at least 1.5 ha. In May 2004, two circular plots (see paragraph below) were located within each clearcut and randomly assigned the Clearcut or Screefed Clearcut treatment. In the Screefed Clearcut treatment, all vegetation and forest floor was removed (screefed) down to the mineral soil using shovels and rakes (depth of forest floor 0 cm). In the Clearcut treatment, the forest floor was left intact leaving an average depth of forest floor 3.8 (se 0.4 cm).

Treatment effects were assessed within a single 15-m circular plot at each replicate site. Within each plot area, five seed beds (120 cm × 140 cm) were located. Wooden stakes were driven into the ground to mark the four corners and center of each seedbed. Seeds of interior Douglas-fir (seedlot 48523, originating within 50 km of study sites, Tree Seed Center, Ministry of Forests and Range, Surrey, B.C., Canada) were stratified at 4 °C for 3 weeks and sown into the seedbeds during the first two weeks of May, 2004. At each seedbed, seven to eight narrow rows (<1 cm wide) were dug through the forest floor (where it remained) to expose bare mineral soil for sowing. The mineral soil was only disturbed 1–2 mm by the digging. The seedbeds were sown with 1000 seeds per replicate site, or 200 seeds per individual seedbed. Seeds were covered by a thin layer of mineral soil and organic matter (if present). All vegetation establishing within and adjacent to the seedbeds was clipped at the root collar and removed from the plots. There was little vegetation, except for some pinegrass (*Calamagrostis rubescens* Buckl. (Poaceae)) at the clearcut sites and fireweed (*Epilobium angustifolium* L.), at the High Severity Burn sites. Natural Douglas-fir regeneration was absent from the clearcut, Undisturbed Forest and High Severity Burn sites, but some occurred near the seedbeds in the Low Severity Burn sites, and were removed. The original goal of the study was to compare seedling growth and foliar nutrient status in all 5 treatments for three years after germination; however, poor survival in the Low Severity Burn and Undisturbed Forest treatments after the first growing season prevented a growth comparison with the stand-replacing treatments in 2005–2006. Additionally, one High Severity Burn site

Table 1
Range of site properties in each disturbance treatment. MAP = Mean Annual Precipitation. MAT = Mean Annual Temperature.

Treatment	Elevation range (m)	MAP (mm)	MAT (°C)	Slope range (%)	Aspect (# of sites)
High Severity Burn (HSB)	806–1179	449–514	3.6–5.3	0–6	NW (3), NE (1)
Low Severity Burn (LSB)	700–1176	427–508	4.3–5.6	2–24	NE (2), SE (1), SW (2)
Screefed Clearcut (SCC)	1000–1268	433–603	3.3–4.4	8–20	NW (2), NE (1) SW (1)
Clearcut (CC)	1000–1268	433–603	3.3–4.4	8–20	NW (2), NE (1) SW (1)
Undisturbed Forest (UF)	843–1176	423–487	3.9–5.2	0–11	NW (3), NW (1)

was not available for growth analysis because of seedling emergence failure.

2.3. Seedling responses

In July 2004, seedlings were assigned a number based on location in the seedbed. Samples were chosen by selecting numbers from a list created by a random number generator. Starting in July, 2004, seedlings from the May 2004 direct-seeding cohort were sampled each September for shoot and root biomass, shoot height, and foliar nutrients. Five seedlings per treatment replicate (one per seedbed) were sampled each year. In September 2004, a grand total of 90 seedlings were collected from 18 experimental units. In September 2005–2006, a grand total of 110 seedlings were collected (55 from each year) from 11 experimental units."Samples were oven-dried at 72 °C and weighed after reaching a constant mass. From each sampled seedling, all needles were removed for analysis of foliar N and P concentration, and foliar biomass was measured to estimate nutrient content. The samples were sent for analysis to the Analytical Laboratory in Victoria, British Columbia (B.C. Ministry of Forests and Range, Research Branch). Foliar N was analyzed by dry combustion with the Leco CHN-600 analyzer (LECO Corp., St. Joseph, MI). Foliar P was analyzed by inductively coupled plasma-atomic emission spectroscopy following microwave digestion (Kalra and Maynard, 1991).

Seedling wood was assessed for natural abundance of $\delta^{13}C$ for a seasonally integrated proxy measure of relative water use efficiency (WUE) (Farquhar and Richards, 1984). In September 2004, 2005 and 2006, the most recent year's growth was sampled by removing the terminal bud from the shoot and cutting out a small (approximately 1-cm long) piece of wood tissue. The samples were weighed and placed in tin capsules. The samples were then combusted, CO_2 was liberated, and the gas was analyzed for $^{13}C/^{12}C$ ratio with a continuous-flow isotope-ratio mass spectrometer. In 2004, the samples were sent to the Pacific Center for Isotopic and Geochemical Research at UBC for analysis. In 2005 and 2006, they were sent to the UC Davis Stable Isotope Laboratory (Davis, CA, USA). The C ratio ($\delta^{13}C$) was calculated as: δ^{13}Csample ‰ = ([$^{13}C/^{12}$Csample]/[$^{13}C/^{12}$Cstandard] $-1) \times 1000$. The standard used was Vienna-PeeDee Belemnite (V-PDB).

2.4. Soil nutrients, water and temperature

Mineral soils were sampled for soil nutrients to a depth of 10 cm using a hand-held soil corer. Mineral soil and soil organic layer were collected in October 2004, and analyzed for total N, mineralizable N (as NH_4–N), available P (Bray), pH (water) and total C. Percentage total N was determined using the colormetric method (Bremner, 1996). Mineralizable N was determined after a two-week anaerobic incubation (Bremner, 1996). Soil analysis methods followed Kalra and Maynard (1991). All samples were sent to the Analytical Laboratory in Victoria, British Columbia for analysis (B.C. Ministry of Forests and Range, Research Branch).

Volume for soil bulk density was determined by inserting glass beads into the holes created by the hand-held soil corer. The volume of the glass beads was determined by water displacement in the laboratory. Mass was determined by oven-drying the fine fraction (<2 mm) at 105 °C. Soil C and N contents were determined by multiplying each nutrient concentration by bulk density. Volumetric soil water content (%) was measured monthly from May to September in 2004, 2005 and 2006 using a time-domain reflectometry probe (Hydrosense CS620, Campbell Scientific). At each measurement time, water content was sampled at three locations in each seedbed (center and each end of the seedbed) by inserting the probe to 20-cm depth in the mineral soil. The three samples were then averaged to produce a value for seedbed volumetric soil water content.

Growing season light availability (400–700 nm) was assessed in at each replicate site using hemispherical canopy photography. The photographs were taken in July 2006, during homogeneous clear sky conditions. Each photograph was taken at 1-m height using a Nikon digital camera with an attached Nikon FC-E8 fisheye converter lens set on a tripod. One photograph was taken in the center of each seedbed and the five values were averaged per replicate site. The growing-season light availability (direct and diffuse light sources) was expressed as a percentage of full sun and was calculated from each photograph using the Gap Light Analyzer (GLA) 2.0 software, following Frazer et al. (2000).

Soil temperature was measured using Stowaway Tidbit (Onset Computers) temperature loggers. The temperature loggers were placed at 10-cm depth in the mineral soil in the center of the experimental plots (outside of the seedbeds) in July, 2004, and retrieved one year later. The data were downloaded and the temperature logger replaced into the soil; this procedure was repeated in 2005 and 2006. The data loggers were finally retrieved and the data were downloaded in September, 2006. Only 14 data loggers were available for use and assigned to site replicates as follows: four sites each in the High Severity Burn and the Undisturbed Forest treatments, and three sites each in the Clearcut and Low Severity Burn treatments. Soil temperature was recorded at 20-min intervals. For statistical analysis, monthly average, minimum, and maximum temperatures were calculated. Data recorded during the first two weeks after datalogger instalment were not included in the analysis.

2.5. Statistical analysis

Statistical analysis was carried out using SAS ver. 9.1 (SAS Institute 2002). A maximum likelihood approach (Proc Mixed) was used for analysis of treatment effects on soil nutrients, foliar nutrients, soil water content, $\delta^{13}C$, canopy openness and seedling growth responses. The effect of time on soil water content and growth was assessed by including time as a main effect in the model. Subsamples were included as random factors for analysis of seedling growth, $\delta^{13}C$, and foliar nutrients. For analysis of temperature data, repeated measures analysis was used, where the temperature probe identity was included in the mixed model as a random factor. Where significant treatment effects were found, differences between means were detected using the Tukey–Kramer multiple comparison test.

3. Results

3.1. Seedling growth and light availability

Disturbance of any type or severity increased seedling shoot and root biomass compared with the Undisturbed Forest in 2004 (Table 2). Furthermore, seedlings in the Clearcut and High Severity Burn treatments had significantly greater shoot height than those in the Undisturbed Forest (Table 2). In 2005–2006, seedlings in the High Severity Burn had significantly greater shoot biomass (Fig. 1) ($P = 0.0004$), root biomass (Fig. 2) ($P = 0.0007$), and shoot height (Fig. 3) ($P = 0.0043$) than those in the Clearcut and Screefed Clearcut treatments, which did not significantly differ each other. Shoot biomass, root biomass, and height increased from 2005 to 2006 ($P < 0.0001$ in each case).

Disturbance had a small effect on seedling foliar N concentration and no effect on foliar P concentration in 2004 (Table 2). Seedlings had significantly higher N and P contents in 2004 in the High Severity Burn than the other treatments (Table 2). When

Table 2
Comparison of seedling growth and nutrient responses among disturbance treatments in September 2004. Standard errors are in brackets. Means with different letters are significantly different at $\alpha = 0.05$.

Treatment[1]	HSB	LSB	SCC	CC	UF	*P*-values
Shoot biomass (g)	0.077[a] (0.01)	0.043[b] (0.01)	0.059[ab] (0.01)	0.043[b] (0.01)	0.016[c] (0.003)	$P < 0.0001$[*]
Root biomass (g)	0.018[a] (0.002)	0.011[b] (0.002)	0.015[ab] (0.002)	0.015[b] (0.001)	0.004[c] (0.002)	$P = 0.0005$[*]
Shoot height (cm)	5.1[a] (0.30)	4.7[ab] (0.27)	4.2[ab] (0.30)	4.8[a] (0.30)	3.8[b] (0.50)	$P = 0.0068$[*]
Foliar N (%)	2.6[ab] (0.12)	2.9[a] (0.11)	2.6[ab] (0.11)	2.2[b] (0.11)	na	$P = 0.023$[**]
Foliar N content (g)	0. 16[a] (0. 13)	0.05[b] (0.011)	0.081[c] (0.011)	0.053[bc] (0.011)	na	$P < 0.0001$[**]
Foliar P (%)	0.29[a] (0.019)	0.30[a] (0.017)	0.31[a] (0.017)	0.28[a] (0.016)	na	$P = 0.52$[**]
Foliar P content (g)	0.018[a] (0.015)	0.0053[b] (0.0013)	0.0010[c] (0.0013)	0.0062[b] (0.0013)	na	$P < 0.0001$[**]

na = Not applicable because foliar biomass in the Undisturbed Forest was too small to conduct foliar nutrient analyses.
[1] Treatments: HSB = High Severity Burn; LSB = Low Severity Burn; SCC = Screefed Clear-cut; CC = clearcut; UF = undisturbed.
[*] $n = 90$.
[**] $n = 110$.

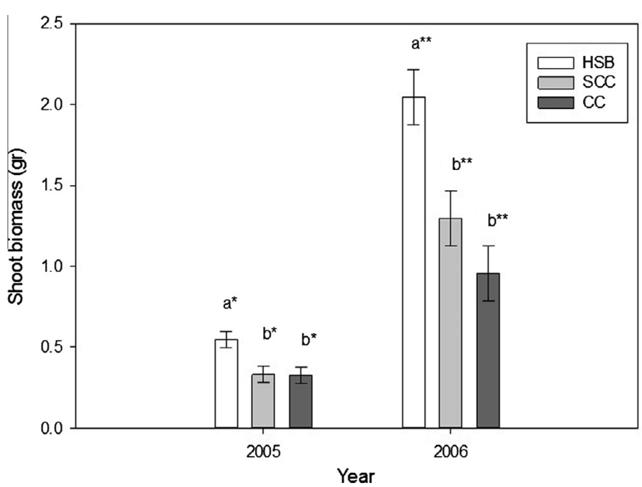

Fig. 1. Comparison of September shoot biomass among treatments from 2005 to 2006. Treatment means with different letters are significantly different within a year at $\alpha = 0.05$. $n = 110$.Treatment means with different numbers of asterisks are significantly different between years at $\alpha = 0.05$. HSB = High Severity Burn; SCC = Screefed Clear-cut; CC = clearcut.

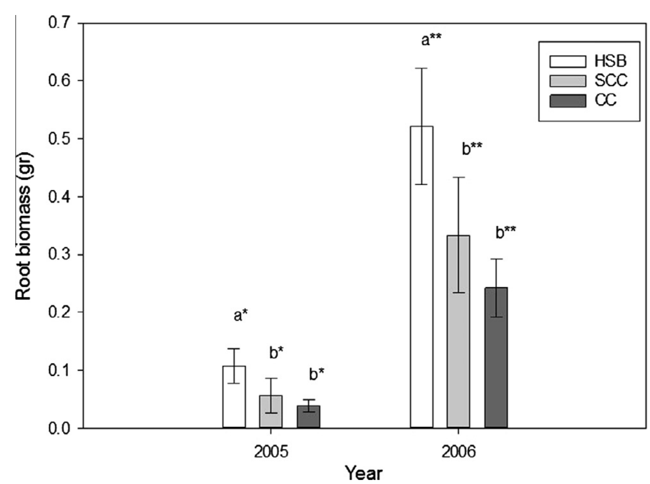

Fig. 2. Comparison of September root biomass among treatments from 2005 to 2006. Error bars = ±1 s.e., $n = 110$. Treatment means with different letters are significantly different within a year at $\alpha = 0.05$. Treatment means with different numbers of asterisks are significantly different between years at $\alpha = 0.05$. HSB = High Severity Burn; SCC = Screefed Clear-cut; CC = clearcut.

examining the stand-replacing disturbances in 2005/2006, there was no evidence for a treatment effect on foliar N and P concentrations ($P = 0.25$ and $P = 0.59$, respectively). Similarly, there was no treatment effect on N content ($P = 0.54$) or P content ($P = 0.90$) in 2005/2006. Further, foliar nutrient content did not change from 2005 to 2006 ($P = 0.88$ for N content and $P = 0.45$for P content). Mean 2005/2006 foliar N content was 0.26 g (se 0.0062). However, there were significant time effects on foliar concentrations. Both foliar N and P concentrations declined from 2005 to 2006 ($P = 0.0018$ and $P = 0.010$, respectively). Seedling N concentration fell from 2.4% (se 0.08) in 2005 to 1.2% (se 0.08) in 2006. Seedling P concentration fell from 0.30% (se 0.08) in 2005 to 0.18% (se 0.08) in 2006.

Canopy openness was 100% in the ‘stand-replacing’ treatments. There was no significant difference in canopy openness between the Low Severity Burn and Undisturbed Forest treatments ($P = 0.19$). Mean canopy openness was 45% (se 15%) in the Low Severity Burn treatment and 33% (se 9.5%) in the Undisturbed Forest treatment.

Stem natural abundance $\delta^{13}C$ was affected by the presence of canopy cover during the first growing season. Low Severity Burn and Undisturbed Forest seedlings had significantly lower $\delta^{13}C$ values than seedlings in the stand-replacing treatments ($P < 0.0001$) (Fig. 4). When comparing the three ‘stand-replacing’ treatments only from 2005 to 2006, we found no effect of disturbance ($P = 0.29$) or time ($P = 0.32$) on stem $\delta^{13}C$. Average $\delta^{13}C$ values for the three ‘stand-replacing’ treatments were −26.0‰ (se 0.30) in 2005 and −26.2‰ (se 0.26) in 2006.

3.2. Soil nutrients and environment

Mineral soil total C and N content, Bray P, and bulk density did not vary significantly among the five treatments in 2004 (Table 3). Disturbance had a small effect on C:N ratio, which was significantly higher in the Clearcut than the other four treatments (Table 3). In addition, there were significant treatment effects on mineralizable N and pH (Table 3). Mineralizable N was higher in the Clearcut and

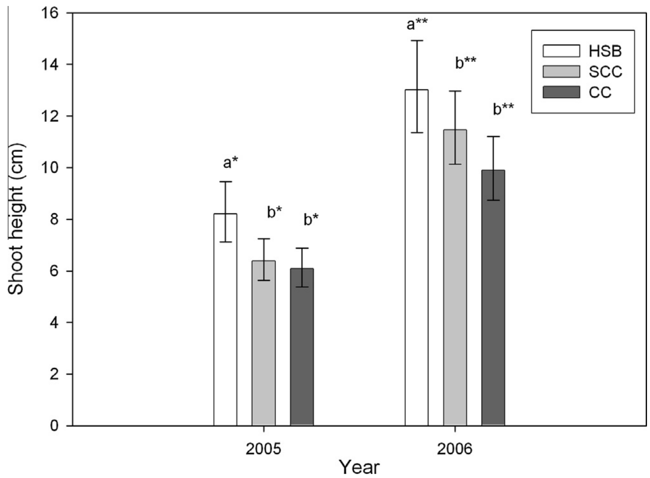

Fig. 3. Comparison of September shoot height among treatments from 2005 to 2006. Error bars = ±1 s.e., $n = 110$. Treatment means with different letters are significantly different within a year at $\alpha = 0.05$. Treatment means with different numbers of asterisks are significantly different between years at $\alpha = 0.05$. HSB = High Severity Burn; SCC = Screefed Clearcut; CC = clearcut.

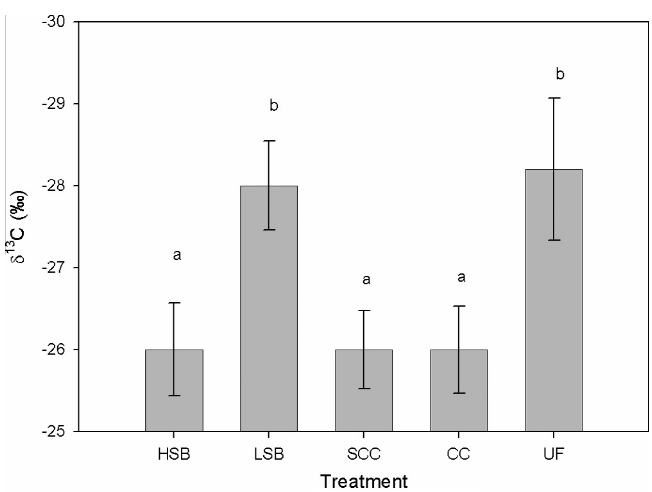

Fig. 4. Comparison of $\delta^{13}C$ values among treatments in 2004. Error bars = ±1 s.e., $n = 90$. Treatment means with different letters are significantly different at $\alpha = 0.05$. HSB = High Severity Burn; LSB = Low Severity Burn; SCC = Screefed Clearcut; CC = clearcut; UF = Undisturbed Forest.

Undisturbed Forest than in the High Severity Burn, Low Severity Burn, and Screefed Clearcut treatments in 2004 (Table 3). Soil pH was higher in the High Severity Burn and Low Severity Burn treatments than the two clearcuts treatments and intermediate in the Undisturbed Forest (Table 3).

The stand-replacing disturbances (High Severity Burn and both clearcut treatments) had significantly higher average and minimum soil water contents than the Low Severity Burn and Undisturbed Forest disturbance types (Table 4). The High Severity Burn was the driest of the stand-replacing disturbance types (Table 4). Maximum soil water content also varied significantly by disturbance type, being higher in the clearcut than the burned or Undisturbed Forest treatments (Table 4). Average, maximum and minimum soil water content varied significantly among years ($P < 0.0001$ in each case). Average soil water content was lowest in 2004 (11%, se 0.90), highest in 2005 (18%, se 0.55) and intermediate in 2006 (15%, se 0.85). Maximum and minimum soil water content followed similar patterns (data not shown). Neither mean nor minimum soil temperature was affected by treatment; however, maximum temperature increased (though not significantly) following removal of canopy cover (Table 5). Monthly average, maximum, and minimum temperatures varied significantly over the growing season (Table 5). Temperature also varied significantly among years ($P = 0.018$). The average temperature was higher in 2004 (13.0 °C, se 1.1) than in 2005 (12.6 °C, se 1.1), but neither year was significantly different than 2006 (12.9 °C, se 1.1). There was no evidence of a yearly difference in maximum or minimum temperatures ($P = 0.083$ and $P = 0.42$, respectively) (data not shown).

4. Discussion

4.1. Disturbance effects on seedling growth and physiology

After germination has occurred, resource availability (light, water and nutrients) is considered to surpass microclimatic effects in limiting seedling growth (Newsome, 1998; Simard et al., 2003). Therefore, we expected seedlings in the stand-replacing disturbances, which had greater light and soil moisture availability, to have greater growth relative to the Low Severity Burn and Undisturbed Forest treatments. As expected, seeding in the stand-replacing disturbance types was associated with increased seedling growth, but not to the same degree in each treatment. From 2005 to 2006, seedlings growing in the High Severity Burn had significantly higher shoot height, shoot biomass and foliar nutrient content than those in the clearcut treatments, suggesting that

Table 3
Comparison of soil properties among disturbance treatments in 2004. Standard errors are in brackets. Means with different letters are significantly different at $\alpha = 0.05$. $n = 18$.

Treatment[1]	HSB	LSB	SCC	CC	UF	*P*-values
Total C (kg/ha)	54104[a] (33,580)	25720[a] (15,960)	15960[a] (8081)	55860[a] (28,280)	57750[a] (35,840)	$P = 0.054$
Total N (kg/ha)	2160[a] (1065)	1300[a] (641)	665[a] (270)	1710[a] (694)	2270[a] (1120)	$P = 0.059$
C:N	25[a] (2.4)	20[a] (2.4)	24[a] (2.0)	33[b] (2.0)	25[a] (2.4)	$P = 0.013$
Mineralizable N (kg/ha)	37.5[a] (16.2)	41.5[a] (21.9)	23.1[a] (8.60)	129[b] (67.8)	217[b] (93.6)	$P = 0.0008$
Bray P (kg/ha)	256[a] (37.8)	160[a] (38.2)	157[a] (43.2)	135[a] (40.3)	139[a] (37.3)	$P = 0.34$
pH	6.6[a] (0.21)	6.9[a] (0.21)	5.7[b] (0.28)	5.5[b] (0.26)	6.2[a] (0.208)	$P = 0.0013$
Bulk density (fine fraction) (kg/ha)	810[a] (40)	740[a] (40)	750[a] (70)	720[a] (35)	750[a] (36)	$P = 0.48$

[1] Treatments: HSB = High Severity Burn; LSB = Low Severity Burn; SCC = Screefed Clear-cut; CC = clearcut; UF = Undisturbed Forest.

Table 4
Comparison of average, maximum and minimum soil water content (%) among disturbance treatments from 2004 to 2006. Standard errors are in brackets. Means with different letters are significantly different at $\alpha = 0.05$. $n = 18$.

Treatment[1]	HSB	LSB	SCC	CC	UF	*P*-values
Average (%)	14^{a} (0.95)	12^{b} (1.1)	17^{a} (0.83)	18^{a} (0.82)	12^{b} (1.04)	$P < 0.0001$
Maximum (%)	17^{a} (1.3)	17^{a} (1.5)	23^{b} (1.1)	23^{b} (1.1)	17^{a} (1.4)	$P < 0.0001$
Minimum (%)	11^{a} (0.80)	8.0^{b} (0.93)	12^{a} (0.70)	13^{a} (0.69)	8.01^{b} (0.88)	$P < 0.0001$

[1] Treatments: HSB = High Severity Burn; LSB = Low Severity Burn; SCC = Screefed Clear-cut; CC = clearcut; UF = Undisturbed Forest.

Table 5
Comparison of mean, maximum and minimum soil temperature (°C) by month and treatment from 2004 to 2006. Standard errors are in brackets. Means with different letters are significantly different at = 0.05. $n = 13$.

	Month					*P*-values
	May	June	July	August	September	
Mean (°C)	9.83^{a} (1.06)	13.0^{b} (1.06)	16.1^{c} (1.06)	16.0^{c} (1.06)	10.1^{a} (1.06)	$P < 0.0001$
Maximum (°C)	18.0^{a} (1.07)	18.8^{b} (1.07)	20.9^{c} (1.07)	21.1^{c} (1.07)	15.1^{a} (1.07)	$P < 0.0001$
Minimum (°C)	3.88^{a} (1.10)	7.65^{b} (1.10)	11.3^{c} (1.10)	11.0^{c} (1.10)	5.17^{d} (1.10)	$P < 0.0001$
	Treatment[1]					
	HSB	LSB	CC	UF		
Mean (°C)	14.40^{a} (1.10)	12.3^{a} (1.08)	13.8^{a} (1.15)	10.7^{a} (1.10)		$P = 0.15$
Maximum (°C)	22.8^{a} (1.12)	17.04^{a} (1.10)	21.05^{a} (1.18)	14.80^{a} (1.12)		$P = 0.052$
Minimum (°C)	7.26^{a} (1.13)	7.45^{a} (1.10)	7.37^{a} (1.18)	6.67^{a} (1.13)		$P = 0.75$

[1] Treatments: HSB = High Severity Burn; LSB = Low Severity Burn; CC = clearcut; UF = Undisturbed Forest.

burning increased resource availability to seedlings through combustion of the forest floor.

Disturbance effects on seedling productivity appeared to influence WUE patterns, which reflect the balance between carbon assimilation and transpiration (Larcher, 2001). WUE trends were assessed through $\delta^{13}C$ values, with higher $\delta^{13}C$ values generally associated with higher WUE (Guy and Holowachuk, 2001). The $\delta^{13}C$ results indicated that light availability was the major driver in isotope depletion variation, followed in importance by nutrient availability. The least depleted $\delta^{13}C$ values corresponded with increased light availability and increased water availability in the stand-replacing disturbances, suggesting enhanced photosynthetic capacity was associated with increased WUE (Cregg et al., 2000; Guy and Holowachuk, 2001). The Low Severity Burn and Undisturbed Forest seedlings were more depleted in ^{13}C than those growing in the open in 2004, corresponding with lower WUE associated with low light and low water availability. Seedlings in the Low Severity Burn treatment grew faster yet had equivalent $\delta^{13}C$ values to those in the Undisturbed Forest, however, suggesting their productivity increased from a nutrient pulse. Even so, low light availability likely limited the benefits of increased nutrient availability, witnessed by the very high N concentration but relatively low N content of foliage in the Low Severity Burn seedlings. Increases in foliar N concentration have been associated with increasing WUE in Douglas-fir (Ripullone et al., 2004). In the three stand-replacing disturbances, the disparity between biomass and $\delta^{13}C$ patterns suggests the moderately drier conditions in the High Severity Burn treatments may have affected WUE. Though seedling productivity and resource availability appeared to drive $\delta^{13}C$ values, there may have also been a source effect on seedlings growing in close proximity to the forest floor because the air just above the forest floor is depleted ($\delta^{13}C \approx -29‰$) (Bauer et al., 2000), which can affect plant $\delta^{13}C$ values (Berry et al., 1997).

Overall, we found little correlation between soil nutrient measurements and seedling growth/foliar nutrients and, but soil nutrients do not always reflect plant-available nutrients (Turner et al., 2009). We also found very high nitrogen mineralization in the Clearcut and Undisturbed forests, levels which are well above in the upper range of levels found in forests (Chapman et al. 2013). The reason is unclear, but the other three treatments had levels comparable to levels found at other interior sites (Simard et al., 2003). Nevertheless, when comparing growth among the stand-replacing treatments, we found evidence to support that our second hypothesis that increased nutrient availability associated with burning would enhance growth. The higher foliar N and P contents in the High Severity Burn than the clearcut treatments suggest that combustion of the forest floor contributed to increased nutrient availability. In addition to the direct nutrient release from combustion, the elevated pH levels in the High Severity Burn relative to clearcuts likely contributed to the increase in nutrient availability, particularly P (Caccia and Ballare, 1998). Foliar N concentrations in 2004 and 2005 were well above the 1.4% critical value for limiting growth in Douglas-fir (Moore et al., 2004), but were approaching the critical level in 2006, suggesting that N limitation was starting to develop with time. Foliar P concentration and N:P ratio remained above critical levels throughout the study period (Ballard and Carter, 1986).

The higher foliar N concentration in the High Severity Burn treatment is consistent with other studies showing increased nutrient availability for the first several years following wildfire or clear-cutting in interior Douglas-fir forests (Hope et al., 2003). This assart effect is often short-lived (1 to 2 years after fire) and generally occurs after forest fires (Wan et al., 2001). In clearcuts, post-disturbance nutrient pulses are also expected but typically peak later than following wildfire (3–5 years after fire) (Keenan and Kimmins, 1993); thus, our study may have been completed too early to capture any short-term pulse in the Screefed Clearcuts.

Based on previous research, we expected a stronger positive seedling response to screefing, but the sparse vegetation ingress after harvest likely contributed to the lack of differences in seedling response. Stark et al. (2006) examined seedbank and post-disturbance vegetation in three of the High Severity Burn and two of the Clearcut sites used in the present study, and found that re-vegetation was sparse, with <25% of subplots occupied by vegetation in the first year after disturbance (2004). By contrast, Simard et al. (2003) found that mechanical removal of pinegrass increased survival and growth of lodgepole pine seedlings by increasing soil water availability, but in their study, pinegrass cover was very high. In our study, ingress of herbaceous vegetation outside the seedbeds increased in the clearcuts and high severity burns from 2004 to 2006, but it was purposefully removed from all of the experimental seedbeds. Removal of competing vegetation, particularly grasses, likely stimulated seedling survival and/or growth in all of the treatments. Regenerating grasses can often be N-limited after fire (Romme et al., 2009), and their absence or removal may allow conifer seedlings to take advantage of nutrient pulses.

In the first growing season, regeneration in the Low Severity Burn appeared comparable to the clearcuts, but declined thereafter. In the longer-term, without sufficient light, seedlings establishing will perform poorly, and thus contribute to regeneration failure (Vyse et al., 2006). Interior Douglas-fir can initiate regeneration under as little as 5–10% openness (Williams et al., 1999; Lochhead and Comeau, 2012), but exposure to above 40% of full sun is considered optimal for growth (Carter and Klinka, 1992, Mailly and Kimmins, 1997).

4.2. Connecting direct seeding to natural regeneration

Interior Douglas-fir forests have historically naturally regenerated from seed over extensive areas characterized by a patchwork of wildfire severities, which typically occur under mixed severity wildfire regimes (Marshall and Wang, 1996; Klenner et al., 2008). Interior Douglas-fir regenerating from seed can grow well in burned, mineral, or mixed organic/mineral seedbeds (Ryker, 1975; Oswald et al., 1998; Klinka et al., 2000). In a Northern Idaho study, Oswald et al. (1998) found better growth of directly seeded Douglas-fir in burned than bare mineral soil or mixed seedbeds. However, the optimal seedbed for establishment varies with the environmental conditions (e.g., aspect and slope) (Oswald et al., 1998). Natural regeneration continues to be an important pathway of forest regeneration in western conifer forests (Shatford et al., 2007; Kopra and Feller, 2007). Mixed severity wildfires can provide both adequate seed sources and suitable conditions for germination and establishment (Donato et al., 2009). At the same time, high levels of patchiness and poor growth performance of natural regeneration are often cited as the rationale for extensive post-disturbance planting (Newton et al., 2006; Shepperd et al., 2006). In interior forests sampled after the 2003 Stark et al. (2006) found that scattered conifer regeneration wildfires on High Severity Burn sites but conifer regeneration was significantly lower after clearcuts. From a regeneration perspective, a key question is whether silvicultural techniques can also facilitate regeneration in circumstances were faster regeneration is desired, such as for timber production and erosion control. Managers seeking to use harvesting to emulate natural disturbances in forests within the Interior Douglas-fir biogeoclimatic zone will have to balance the need to create diverse stand characteristics with creating favorable regeneration environments. Harvesting does not always produce sufficient disruption to the forest floor to facilitate regeneration, necessitating site preparation to enhance regeneration success (Kimmins, 2004). In terms of growth, clearcutting with site preparation produced the most comparable short-term growth most comparable to the high severity wildfires treatment. Our results provide further impetus to explore the use of site preparation techniques to mimic some of the beneficial effects growth and foliar nutrition of high severity wildfires.

Direct-seeding experiments on establishment should also be expanded to include a wider range of conditions than was possible in this study. Factors such as slope and aspect are important in wildfire severity and regeneration success (Oswald et al., 1998) and should be more closely studied than was done in this study. Further, Douglas-fir seedlings can in fact regenerate under relatively low light levels. For example, Lochhead and Comeau (2012) found that selection harvesting with basal areas below 24 m^2/ha created favorable growth and survival conditions for Douglas-fir with light levels as low as 15%. They noted that although light levels were a strong indicator for regeneration success, others factors, such as better accounting of understory vegetation and seedbed conditions, were needed to better predict regeneration success. Although wide-spread use of direct seeding in interior forests to promote regeneration is largely limited due to seed predation (Zwolak et al., 2010; Sullivan and Sullivan, 1982), our results indicated a targeted direct seeding approach combine with site preparation can produce comparable effects on seedling growth and nutrition to high severity wildfire as well as a baseline for comparing artificial versus natural regeneration from seed. We note in terms of evaluating growth performance of artificial versus natural regeneration that direct-seeded seedlings are much smaller during early establishment than planted seedlings, as planted seedlings are grown for at least one year with fertilizer before planting. As a result, early growth performance of the seedlings in this study are more similar to newly germinated natural regeneration than planted seedlings. Our experimental approach did not directly address creation of landscape heterogeneity by wildfire that is an important feature of natural regeneration in interior forests. This aspect of mixed-severity wildfires is important because the pattern of surviving trees can strongly influence regeneration success (Donato et al., 2009). Our low severity wildfire treatment only represented one dimension of a continuum of the conditions that arise between seedbed conditions and light availability. However, expanded direct-seeding experiments into a wider range of sites representing wildfire severities can help produce data to improve regeneration outcomes after harvesting.

5. Conclusions

Both wildfire and harvesting relieved light and moisture limitations to seedling establishment. Seeding into the High Severity Burn led to the greatest improvement in growth relative to the Undisturbed Forest through increased light and nutrient availability. However, direct-seeding in the Screefed Clearcut produced comparable growth performance, suggesting that site preparation may produce similar effects on growth and foliar nutrition to wildfire on regeneration from seed. Addressing the complexity of natural regeneration in a mixed-severity disturbance regime requires a multi-faceted adaptive management and research approach to understanding and managing regeneration. Future studies of using harvesting to mimic aspects of natural disturbance can employ direct-seeding to compare the regeneration potential of wildfire verses harvesting in a rapidly changing environment.

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References

Ballard, T.M., Carter, R.E., 1986. Evaluating forest stand nutrient status. Land Management Report No. 20. Ministry of Forests, Victoria, BC.

Bauer, G.A., Gebauer, G., Harrison, A.F., Hogberg, P., Hogbom, L., Schinkel, H., Taylor, A.F.S., Novak, M., Buzek, F., Harkness, D., 2000. Biotic and abiotic controls over ecosystem cycling of stable natural nitrogen, carbon and sulphur isotopes. In: Carbon and Nitrogen Cycling in European Forest Ecosystems. Springer Verlag, pp. 189–214.

Berry, S.C., Varney, G.T., Flanagan, L.B., 1997. Leaf ^{13}C in Pinus resinosa trees and understory plants: variation associated with light and CO_2 gradients. Oecologia 109, 499–506.

Bremner, J.M., 1996. Nitrogen availability indexes. In: Black, C.A. (Ed.), Methods of Soil Analysis, Part 2, Agronomy 9. American Society of Agronomy, Madison, pp. 1324–1345.

Caccia, F.D., Ballare, C.L., 1998. Effects of tree cover, understory vegetation, and litter on regeneration of Douglas-fir (*Pseudotsuga menziesii*) in southwestern Argentina. Can. J. Forest Res.-Revue Can. Rech. Forest. 28, 683–692.
Carter, R.E., Klinka, K., 1992. Variations in shade tolerance of Douglas-fir, western hemlock and western red cedar in coastal British Columbia. Forest Ecol. Manage. 55, 87–105.
Chapman, L., McNulty, S., Sun, G., Zhang, Y., 2013. Net nitrogen mineralization in natural ecosystems across the conterminous US. Int. J. GeoSci. 4 (9), 1300–1312.
Cregg, B.M., Olivas-Garcia, J.M., Hennessey, T.C., 2000. Provenance variation in carbon isotope discrimination of mature ponderosa pine trees at two locations in the Great Plains. Can. J. Forest Res.-Revue Can. Rech. Forest. 30, 428–439.
Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B., Law, B.E., 2009. Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the klamath-siskiyou mountains. Can. J. Forest Res.-Revue Can. Rech. Forest. 39, 823–838.
Farquhar, G.D., Richards, R.A., 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. Aust. J. Plant Physiol. 11 (6), 539–552.
Flannigan, M.D., Stocks, B.J., Wotton, B.M., 2000. Climate change and forest fires. Sci. Total Environ. 262, 221–229.
Frazer, G.W., Canham, C.D., Lertzman, K.P., 2000. Gap light analyzer. Version 2.0. Bull. Ecol. Soc. Am. 81, 191–197.
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. Forest Res.-Revue Can. Rech. Forest. 29, 824–839.
Guy, R.D., Holowachuk, D.L., 2001. Population differences in stable carbon isotope ratio of Pinus contorta Dougl. ex Loud.: relationship to environment, climate of origin, and growth potential. Can. J. Bot.-Revue Can. Bot. 79, 274–283.
Haeussler, S., Kneeshaw, D., 2003. Comparing forest management to natural processes. In: Burton, P.J., Messier, C., Smith, D.W., Adamowicz, W.L. (Eds.), Towards Sustainable Management of the Boreal Forest. Nat. Res. Council Res. Press, Ottawa, Ont., pp. 307–368.
Haeussler, S., Bedford, L., Boateng, J., MacKinnon, A., 1999. Plant community responses to mechanical site preparation in northern interior British Columbia. Can. J. Forest Res.-Revue Can. Rech. Forest. 29, 1084–1100.
Heyerdahl, E.K., Miller, R.F., Parsons, R.A., 2006. History of fire and Douglas-fir establishment in a savanna and sagebrush-grassland mosaic, southwestern Montana, USA. For. Ecol. Manage. 230, 107–118.
Hope, G.D., Prescott, C.E., Blevins, L.L., 2003. Responses of available soil nitrogen and litter decomposition to openings of different sizes in dry interior Douglas-fir forests in British Columbia. For. Ecol. Manage. 186, 33–46.
Johnstone, J., Chapin, F., 2006. Effects of soil burn severity on post-fire tree recruitment in boreal forest. Ecosystems 9, 14–31.
Kalra, Y., Maynard, D., 1991. Methods manual for forest soil and plant analysis. Forestry Canada information report NOR-X-319 Edmonton.
Keenan, R.J., Kimmins, J.P., 1993. The ecological effects of clear-cutting. Environ. Rev. 1, 121–144.
Kimmins, J.P., 2004. Emulating natural forest disturbance: what does this mean? In: Perera, A.H., Buse, L.J., Weber, M.G. (Eds.), Emulating Natural Forest Landscape Disturbances: Concepts and Applications. Columbia University Press, New York, pp. 8–28.
Klenner, W., Walton, R., Arsenault, A., Kremsater, L., 2008. Dry forests in the Southern Interior of British Columbia: historic disturbances and implications for restoration and management. For. Ecol. Manage. 256, 1711–1722.
Klinka, K., Worrall, J., Skoda, L., Varga, P., 2000. The distribution and synopsis of ecological and silvical characteristics of tree species of British Columbia's forests. Canadian Cartographics Ltd., Coquitlam, B.C.
Kopra, K., Feller, M.C., 2007. Forest fires and old-growth forest abundance in wet, cold, Engelmann Spruce-Subalpine Fir forests of British Columbia, Canada. Nat. Areas J. 27, 345–353.
Larcher, W., 2001. Physiological Plant Ecology: Ecophysiology and Stress Physiology of Functional Groups, fourth ed. Springer, New York, NY.
Lloyd, D., Angove, K., Hope, G., Thompson, C., 1990. A Guide to Site Identification and Interpretation for the Kamloops Forest Region. Ministry of Forests, Victoria, B.C.
Lochhead, K.D., Comeau, P.G., 2012. Relationships between forest structure, understorey light and regeneration in complex Douglas-fir dominated stands in south-eastern British Columbia. Forest Ecol. Manage. 284, 12–22.
Long, J.N., 2009. Emulating natural disturbance regimes as a basis for forest management: a North American view. For. Ecol. Manage. 257, 1868–1873.
Mailly, D., Kimmins, J.P., 1997. Growth of *Pseudotsuga menziesii* and *Tsuga heterophylla* seeds along a light gradient: resource allocation and morphological acclimation. Can. J. Bot. 75, 1424–1435.
Marshall, P.L., Wang, Y., 1996. Growth of Uneven-aged Interior Douglas-fir Stands as Influenced by Different Stand Structures, Can. BC Joint Pub. FRDA II Rpt. 267.
McRae, D.J., Duchesne, L.C., Freedman, B., Lynham, T.J., Woodley, S., 2001. Comparisons between wildfire and forest harvesting and their implications in forest management. Environ. Rev. 9, 223–260.
Moore, J.A., Mika, P.G., Shaw, T.M., Garrison-Johnston, M.I., 2004. Foliar nutrient characteristics of four conifer species in the interior Northwest United States. Western J. Appl. Forest. 19, 13–24.
Newsome, T.A., 1998. Site preparation on dry grassy sites in the Cariboo Forest Region. In: Vyse, A. et al. (Eds.), Managing the Dry Douglas-fir Forests of the Southern Interior, Work paper 34, Ministry of Forests, Victoria B.C., Kamloops B.C., pp. 53–61.
Newton, M., Fitzgerald, S., Rose, R.R., Adams, P.W., Tesch, S.D., Sessions, J., Skinner, C., 2006. Comment on "Post-wildfire logging hinders regeneration and increases fire risk". Science 313 (5787), 615.
Nitschke, C.R., 2005. Does forest harvesting emulate fire disturbance? A comparison of effects on selected attributes in coniferous-dominated headwater systems. For. Ecol. Manage. 214 (1–3), 305–319.
Oswald, B.P., Wellner, K., Boyce, R., Neuenschwander, L.F., 1998. Germination and initial growth of four coniferous species on varied duff depths in northern Idaho. J. Sustain. Forest. 8 (1), 11–21.
Ripullone, F., Lauteri, M., Grassi, G., Amato, M., Borghetti, M., 2004. Variation in nitrogen supply changes water-use efficiency of *Pseudotsuga menziesii* and *Populus* x euroamericana; a comparison of three approaches to determine water-use efficiency. Tree Physiol. 24, 671–679.
Romme, W.H., Tinker, D.B., Stakes, G.K., Turner, M.G., 2009. Does inorganic nitrogen limit plant growth 3–5 years after fire in a Wyoming, USA, lodgepole pine forest? For. Ecol. Manage. 257, 829–835.
Ryker, R.A., 1975. A survey of factors affecting regeneration of Rocky Mountain Douglas-fir. USDA For. Serv. Res. Pap. INT-174. 19 pp.
Shatford, J.P.A., Hibbs, D.E., Puettmann, K.J., 2007. Conifer regeneration after forest fire in the Klamath-Siskiyous: how much, how soon? J. Forest. 105, 139–146.
Shepperd, W.D., Edminster, C.B., Mata, S.A., 2006. Long-term seedfall, establishment, survival, and growth of natural and planted ponderosa pine in the Colorado Front Range. Western J. Appl. Forest. 21, 19–26.
Simard, S.W., Jones, M.D., Durall, D.M., Hope, G.D., Stathers, R.J., Sorensen, N.S., Zimonick, B.J., 2003. Chemical and mechanical site preparation: effects on Pinus contorta growth, physiology, and microsite quality on grassy, steep forest sites in British Columbia. Can. J. Forest Res.-Revue Can. Rech. Forest. 33, 1495–1515.
Soil Classification Working Group, 1998. The Canadian system of soil classification, third ed., Research Branch, Agriculture and Agri-Food Canada, Ottawa, (187pp.), Publication 1646.
Stark, K.E., Arsenault, A., Bradfield, G.E., 2006. Soil seed banks and plant community assembly following disturbance by fire and logging in interior Douglas-fir forests of south-central British Columbia. Can. J. Bot.-Revue Can. Bot. 84, 1548–1560.
Sullivan, T.P., Sullivan, D.S., 1982. The use of alternative foods to reduce lodgepole pine seed predation by small mammals. J. Appl. Ecol. 19 (1), 33–45.
Sutherland, B., Foreman, F.F., 2000. Black spruce and vegetation response to chemical and mechanical site preparation on a boreal mixedwood site. Can. J. Forest Res.-Revue Can. Rech. Forest. 30, 1561–1570.
Turner, M.G., Smithwick, E.A.H., Tinker, D.B., Romme, W.H., 2009. Variation in foliar nitrogen and aboveground net primary production in young postfire lodgepole pine. Can. J. Forest Res.-Revue Can. Rech. Forest. 39, 1024–1035.
Vyse, A., Ferguson, C., Simard, S.W., Kano, T., Puttonen, P., 2006. Growth of Douglas-fir, lodgepole pine, and ponderosa pine seedlings underplanted in a partially-cut, dry Douglas-fir stand in south-central British Columbia. Forest. Chron. 82, 723–732.
Wan, S.Q., Hui, D.F., Luo, Y.Q., 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. Ecol. Appl. 11, 1349–1365.
Wang, T., Hamann, A., Spittlehouse, D.L., Murdock, T.Q., 2012. ClimateWNA-High-resolution spatial climate data for western North America. J. Appl. Meteorol. Climatol. 51 (1), 16–29.
Williams, H., Messier, C., Kneeshaw, D.D., 1999. Effects of light availability and sapling size on the growth and crown morphology of understorey Douglas-fir and lodgepole pine. Can. J. Forest Res.-Revue Can. Rech. Forest. 29, 222–231.
Zwolak, R., Pearson, D.E., Ortega, Y.K., Crone, E.E., 2010. Fire and mice: seed predation moderates fire's influence on conifer recruitment. Ecology 91, 1124–1131.