Factors affecting natural regeneration of *Abies lasiocarpa* and *Picea engelmannii* in a subalpine silvicultural systems trial

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Abstract: An experiment was established in 1991–1992 in northern British Columbia to investigate factors influencing natural regeneration rates of Engelmann spruce (*Picea engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) in three stand structures created by harvesting. Harvest treatments were a 32-ha clearcut, 0.2-ha patch cuts, and single-tree selection. Cone crop periodicity was independent of harvesting system. Natural seedfall was higher in the selection treatment and small patch cut than the clearcut treatment every year. Five years after harvest, the selection and patch cut treatments had 7 times as many spruce germinants and 10 times as many subalpine fir germinants as the clearcut treatment. Seed availability appears to be the primary limiting factor for establishment of both subalpine fir and spruce in the clearcut treatment. For spruce establishment in the selection and small patch cut treatments, availability of both seed and mineral soil seedbeds were limiting factors, while for subalpine fir, germinant establishment appears primarily limited by availability of disturbed forest floor seedbeds. Foresters could increase opportunities for natural regeneration in these subalpine forests by (*i*) modifying harvest patterns to enhance conifer seed distribution over harvested areas and (*ii*) applying seedbed preparation treatments prior to anticipated heavy seedfalls.

Résumé : Une expérience a été conduite dans le nord de la Colombie-Britannique en vue d'étudier les facteurs qui influencent le taux de régénération naturelle de l'épinette d'Engelmann (*Picea engelmannii* Parry) et du sapin subalpin (*Abies lasiocarpa* (Hook.) Nutt.), dans trois types de structure du peuplement créés par la récolte. Les traitements de récolte appliqués étaient une coupe à blanc de 32 ha, des coupes par blocs de 0,2 ha et le jardinage par arbre. La périodicité des années semencières était indépendante du type de récolte. La quantité de semences tombées au sol était, à chaque année, plus élevée dans le cas du jardinage par arbre et de la coupe par blocs que dans le cas de la coupe à blanc. Cinq ans après la récolte, les aires de jardinage par arbre et de coupe par blocs comportaient sept fois plus de semences germées d'épinette et 10 fois plus de semences germées de sapin que la coupe à blanc. Dans le cas de la coupe à blanc, c'est la disponibilité des graines qui semble le facteur limitatif primordial pour l'établissement et de l'épinette et du sapin. Dans les peuplements jardinés par arbre et coupés par blocs, les facteurs limitatifs pour l'établissement de l'épinette sont, à la fois, la disponibilité des graines et des lits de germination sur sol minéral. Par contre, chez le sapin subalpin, l'établissement des semis paraît limité avant tout par la disponibilité des lits de germination sur un parterre perturbé. Les forestiers pourraient augmenter les possibilités de régénération naturelle de ces types de forêt subalpine (*i*) en modifiant les patrons de récolte pour augmenter la répartition des graines dans les aires coupées et (*ii*) en appliquant des traitements de préparation des lits de germination lorsqu'une bonne année semencière est prévue.

[Traduit par la Rédaction]

Introduction

The Engelmann spruce (*Picea engelmannii* Parry) – subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) forest zone (ESSF) of western North America has a severe climate for forest regeneration and growth (Farnden 1994). These forests occupy high-elevation mountain habitats, and the zone extends from northern British Columbia to New Mexico (Henderson 1981). Feller (1997) noted that the ESSF zones of the British Columbia central interior have few ecological similarities with other North American spruce–fir zones and that the degree to which forest regeneration information from elsewhere can be used in British Columbia is unknown.

Slow rates of regeneration and forest regrowth after clearcut harvesting have stirred controversy about the sustainability of harvesting in subalpine forests (Farnden 1994; Vyse 1997). Slow rates of natural regeneration in large clearcuts, combined with legislated reforestation deadlines, have led many silviculturists to dismiss natural regeneration on subalpine sites in favour of artificial regeneration. Improvements in artificial reforestation, including seedling stock types and site preparation, have increased regeneration success rates on clearcut-harvested subalpine sites. Nevertheless, the steady ingress of natural regeneration in harvested areas often contributes significantly to overall restocking, species diversity, and the spatial structure of

Received January 5, 1999. Accepted July 27, 1999.

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Table 1. Summary of growing season climate conditions collected within the clearcut treatment from 1992 to 1996.

Year	Total summer precipitation (mm)	Mean air temp. at 1.3 m (°C)	Mean min. air temp. at 30 cm (°C)	Mean soil temp. (°C)	Date of first killing frost	% of potential solar irradiance
1992	9	10.6	4.0	9.9	Aug. 21	64
1993	188	10.6	5.1	9.9	Sept. 12	61
1994	170	12.6	6.4	10.6	Oct. 2	70
1995	264	10.8	4.9	9.7	Sept. 18	59
1996	208	11.2	4.6	9.7	Sept. 16	62

Note: Growing season frosts are defined as any temperature 0°C or lower.

regenerating stands. Current changes in harvest practices, including reductions in average clearcut size and increasing use of partial-cut silvicultural systems, may increase the use of natural regeneration opportunities on harvested subalpine forest sites.

Natural regeneration success is determined by the availability of viable seed landing on suitable germination sites that subsequently promote seedling growth. Our local knowledge of cone crop periodicity and the quality of seeds for high-elevation subalpine fir and Engelmann spruce comes from the few operational cone collections conducted over the past 30 years. Cone collections have been few, because crops were considered too small to warrant operational collection. Stand structure after harvesting also influences the amount of seed by species, seed dispersal, and the conditions for both germination and seedling growth. A better understanding of the factors affecting natural regeneration in northern British Columbia ESSF sites would allow for more reliable site-specific assessment of its potential and opportunities. This study addressed the limitations in viable seed production, seed dispersal, germination, and seedbed treatments among partial-cut and clearcut harvest treatments.

Site description

The study site is located on a northwest-facing slope in the Engelmann Spruce – Subalpine Fir moist, mild subzone (ESSFmm) on Lucille Mountain, approximately 8 km southwest of McBride, B.C. (53°30′N, 120°20′W). The range in elevation for the study area is 1375 to 1600 m, and slopes range from 15 to 45%. The soils are poorly sorted uncompacted glacial tills overlying metamorphic (phyllite and schist) bedrock at depths of about 1 m or more.

The climate is typically moist and cool throughout the growing season, but growing season frosts are not frequent. Snowpacks develop in about mid-October, reach several metres in depth, and last until mid-June. Weather data were collected annually from June to September with a CR10 datalogger (Campbell Scientific, Logan, Utah) housed in a Stevenson screen mounted at 1.3 m. Air temperature (1.3 m, 30 cm, and 5 cm height), soil temperature (10 cm depth), solar radiation, and rainfall were monitored continuously and summarized yearly (Table 1).

Preharvest stand conditions were typical of multiaged and multistoried old-growth spruce and subalpine fir stands including trees up to 250–300 years old. The uncut stands contained a high proportion of snags, and regeneration of subalpine fir and spruce was primarily confined to favourable microsites such as rotting wood. The shrub layer was dominated by white flowered rhododendron (*Rhododendron albiflorum* Hook.), false azalea (*Menziesia ferruginea* Sm.), and huckleberry (*Vaccinium* sp.). The herb layer was typically five-leaved bramble (*Rubus pedatus* Sm.) and twisted-stalk (*Streptopus roseus* Michx.). The moss layer was dominated by red-stemmed feathermoss (*Pleurozium schreberi* (Brid.) Mitt.) and common leafy liverwort (*Barbilophozia lycopoidoides* (Wallr.) Loeske).

Methods

Study design

The three harvest treatments were single-tree selection, 0.2-ha patch cuts, and a 32-ha clearcut opening. A 40-m uncut buffer strip was maintained between the clearcut and the selection treatments. The single-tree selection was randomly assigned to five 1-ha treatment units, and the summer-logged patch cut was randomly assigned to four treatment units. The clearcut treatment was not repeated because of size.

A single 40-m^2 natural regeneration assessment plot consisted of 16 seed traps arranged in four rows of four with approximately 10 m between traps, and nine 2-m^2 germination-assessment plots arranged in three rows of three with approximately 10 m between plots. One 40-m^2 plot was established in each of the nine partial-harvest treatments units the year after logging. Five natural-regeneration assessment plots were randomly located within the clearcut treatment during the summer of 1993. The number of seed traps in each plot was reduced from 16 to 8 after 1993 by using the variability between traps within an assessment plot, a confidence level of 95%, and the formula $n = t^2s^2/d^2$ (Steel and Torrie 1980) where t is the tabulated t value for the desired confidence level and the degrees of freedom of the initial sample, s is the sample variance, and d is the half width of the desired confidence interval.

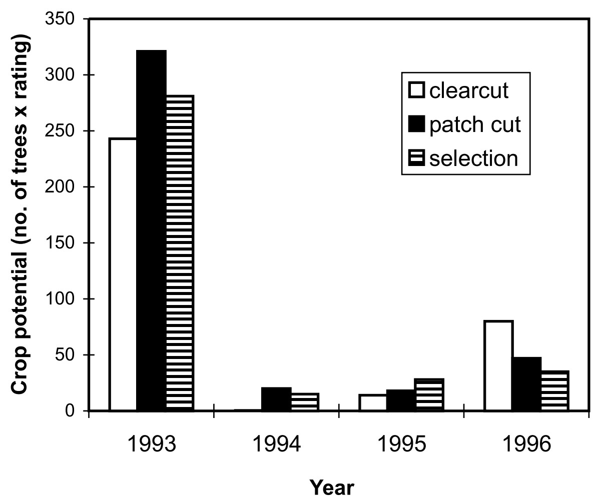
Each of the nine 2-m^2 germination assessment plots (within a 40-m^2 natural regeneration assessment plot) was further divided into four 1-m^2 subplots, and each subplot was randomly assigned one of four seedbed treatments. The four seedbed treatments were (*i*) disturbed and seeded (DS), (*ii*) disturbed and not seeded (DN), (*iii*) undisturbed and seeded (US), and (*iv*) undisturbed and not seeded (UN). One plot in the selection harvest treatment, and two plots in the patch-cut treatment, had fewer than nine germination plots in the 40-m^2 plot because of space limitations.

Harvest treatments and residual stand structures

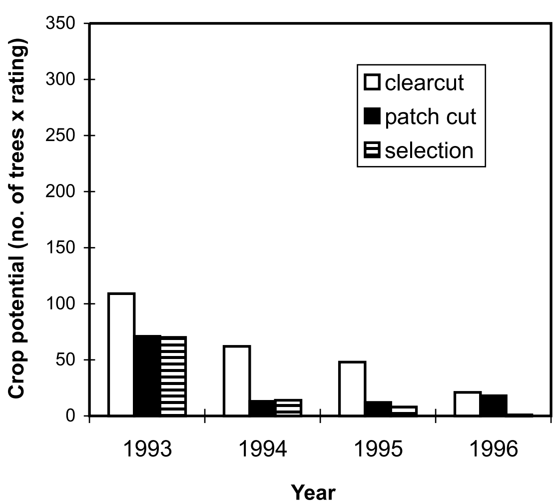
The single-tree selection treatment removed 45% of mean basal area and 44% of mean volume across all diameter classes leaving a mean residual basal area of approximately 15 m^2/ha composed of 90% subalpine fir and 10% spruce. Trees were hand-felled and skidded using small tracked skidders on a 1-m snowpack in the winter of 1991–1992. The small patch-cut treatment removed approximately 50% of the area in 0.2-ha small openings in a “checkerboard” pattern leaving areas of uncut mature forest directly adjacent. The patch cut treatment units were logged in September 1991 on bare ground. The clearcut treatment was hand-felled and ground skidded in the summer of 1991.

Fig. 1. Cone crop potential calculated by multiplying the number of trees bearing cones times the mean individual cone crop rating by species and year. Bars show the calculated potential for each of the three harvesting treatments for subalpine fir and Engelmann spruce.

a) Subalpine fir



b) Spruce



Cone crop assessment

Cone crop ratings were conducted by the same observer in early to mid-August from 1993 to 1996. Individual dominant and codominant subalpine fir and spruce trees were rated using a scheme derived from the method used for rating stands (Eremko et al. 1989) as follows: (0) no seed cones; (1) low, less than 25% of cone bearing crown has cones; (2) medium, 25–50% of cone bearing crown has cones; and (3) heavy, greater than 50% of cone bearing crown has cones. The cone-bearing crown of subalpine fir is the top four or five whorls, whereas in spruce, it is the top half of the crown (Eremko et al. 1989). Assessments were conducted from the ground using binoculars. Trees visible to the observer were assessed along the perimeter of the opening in the clearcut treatment. Trees visible from the centre of each 40-m^2 natural regeneration assessment plot were assessed in the selection and patch-cut treatments. The number of trees assessed varied annually because of new trees becoming cone bearing, loss of trees to windthrow, and visibility from the assessment points. Individual tree cone crop ratings were averaged by sample plot, harvest treatment and species, then multiplied by the number of trees producing cones, and the calculated variable equal to crop potential.

Cone collection and seed assessment

Seed cones were collected mid-August in 1993, 1995, and 1996 to determine the potential number of filled seeds per cone and seed condition prior to dispersal. A collection was not done in 1994 because of the low number of cones. The number of cones collected each year varied with the intensity of the crop. Both subalpine fir and spruce trees were accessed by helicopter and cones collected by clipping with minimal damage to the trees. Sampling was limited to those trees that were accessible by helicopter. Cones were transported immediately after collection to a cold-storage facility maintained at 5°C and assessed within 3 weeks of harvest.

Each cone was sliced longitudinally along its axis to determine the number of filled seeds. The number of exposed, filled seeds in one half section were counted, and transformed to whole cone (WC) estimates of number of filled seed per cone using the equations: WC = $8.3S + 11.1$ for subalpine fir, and WC = $6.3S + 6.0$ for spruce, where S is the observed half-cone value (Eremko et al. 1989). Samples of insect-infested cones and seeds were sent to the Ministry of Forests laboratory in Victoria for identification of pests. Statistical analysis was not performed on these data because of the restrictions on collection.

Seed dispersal

Seed traps were installed in the three harvest treatments by the summer of 1993. Seed traps were woven, polyurethane bags with a top area of 0.096 m^2. Collections occurred three times in 1993 (June 7, July 5, and September 23) by removing bags to the laboratory and fastening a new bag in place. No conifer seedfall was detected over winter and up to the end of July, 1994, so in subsequent years, bags were installed mid-August prior to seed shed and collected in late September. Contents of bags were sorted as soon as possible after collection, whole seed extracted, number of seeds by species recorded, and the seeds stored in envelopes for further testing. Seeds in trap bags or envelopes were stored for a maximum of 7 days in a laboratory fridge maintained at 4°C.

Seeds from the traps were pooled by natural regeneration plot, and assessed at the Canadian Forest Service Pacific Forestry Centre, Victoria, B.C., for seed mass, percent filled seed, and percent germination when there was sufficient seed for testing within a sample. Seeds were stratified for 21 days at 0°C. Germination test conditions were 30°C day and 20°C night with an 8-h day length. The test period for both subalpine fir and spruce was 28 days and seeds were considered germinated at the stage where the radicle was four times longer than the length of the seed.

A factorial analysis of variance was used to detect species and treatment differences in mean number of seeds per assessment plot on an annual basis from 1993 to 1996. The square-root transformation of data was used because of the large number of zeros and because it provided homogeneous variances. To further explore the significant treatment differences, a Dunnett's two-sided t test was performed, with the selection treatment as the nominal control used to compare all other treatments. Seed trap data were computed in seeds per hectare for graphical presentation and comparison of treatments.

Seedbed preparation and germination

The four seedbed treatments of DS, DN, US, and UN (as previously described) were randomly applied to each of the 1-m^2 subplots in a germination assessment plot. Disturbance was done in

Table 2. Percent (%) cones damaged by insects or other causes and mean filled seed for spruce and subalpine fir within three silvicultural systems collected 2, 4, and 5 years after harvest.

	Subalpine fir				Spruce			
	n[a]	Insect	Other	Filled seed/cone	*n*	Insect	Other	Filled seed/cone
1993								
Clearcut	210	27	0	48	168	15	4	32
Patch cut	55	7	0	55	45	20	0	26
Selection	50	18	0	69	50	6	4	39
1995								
Clearcut	10	30	3	14	33	15	36	15
Patch cut	10	10	0	15	0	na[b]	na	na
Selection	0	na	na	na	22	9	59	13
1996								
Clearcut	100	59	3	23	46	72	9	14
Patch cut	57	84	7	22	64	80	2	19
Selection	28	71	29	21	32	91	3	17

[a]*n* = number of cones sampled.
[b]na, none available.

July 1993 using a motorized hand-held scarifier that removed the forest floor down to the mineral soil.

The seed used for direct seeding subalpine fir and spruce was of local origin, obtained from the B.C. Ministry of Forests Tree Seed Centre, Surrey, B.C. Germination test results were 72 and 90% for subalpine fir and spruce, respectively, with 99% filled seeds for both seedlots. Seeds were soaked in water for 24 h and toweled dry prior to seeding. Artificial seeding was completed on October 1, 1993, by hand spreading on bare ground, 100 seeds of each species per 1-m^2 plot.

Subalpine fir and spruce germinants were counted mid-August from 1994 to 1996 using a 50 × 100 cm Daubenmire grid placed level in approximately the middle of each treated plot (Daubenmire 1960). Advanced regeneration seedlings that existed prior to harvesting were excluded from the germination count. The four corners of the grid location on each plot were permanently marked with rebar stakes to ensure assessment of the same area from year to year. A factorial analysis of variance was used to detect differences in mean number of germinants by year, harvest treatment, and seedbed treatment on data transformed to the square root of (X + 0.5) to produce homogeneous variances. Number of germinants per hectare was computed for graphical presentation and general comparison of treatments. All analyses were completed using statistical software from SPSS Inc., Chicago, Ill.

Results

Cone crop assessment

All of the trees assessed had medium to heavy cone crops resulting in high crop potentials in 1993 (Fig. 1). The following year, only 6% of the subalpine fir and 25% of the spruce trees bore cones. Crop potential for subalpine fir generally exceeded that for spruce because of the relatively low spruce composition of the residual stand. Crop potential has been slowly rising for subalpine fir since 1994 as a result of more trees bearing low cone crops. Spruce trees around the perimeter of the clearcut appear to produce low to medium cone crops each year, although 1996 was the lightest.

Seed assessment

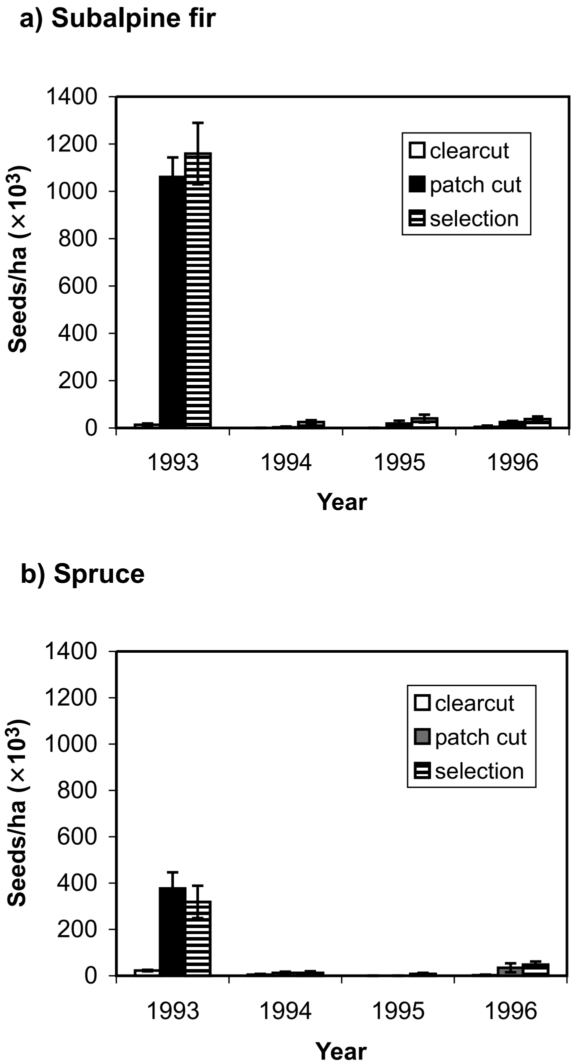
The average number of spruce and subalpine fir seeds per cone was highest in the single tree selection treatment in 1993 (Table 2). The selection treatment had 33% more filled spruce seed per cone compared with the patch-cut treatment and 18% more compared with the clearcut. Similarly for subalpine fir, the selection treatment yielded 20 and 30% more filled seed per cone compared with the patch-cut and clearcut treatments, respectively. Filled seed counts in 1993 may have been high, since the assessments were done at the multiple embryo stage when selection and embryo abortion had not yet occurred. Seed assessments were subsequently done later in August after this critical stage. The variation in filled seeds per cone among silviculture system treatments was not evident in subsequent light cone crop years (Table 2). The average filled seed per cone dropped below 50% of the 1993 seed yields for all silviculture systems, to a low of 27% for subalpine fir in the patch-cut treatment between 1993 and 1995.

Insect infestations have increased over the 4 years (Table 2). The insects identified annually were the cone maggot (*Strobilomyia abietis* (Hackett)) and midge larvae *Dasineura* sp. in the subalpine fir cones. The seed wasp (*Megastigmus atedius* Walker), spruce seed midge (*Mayetiola carpophaga* (Tripp)), axis midges (*Kaltenbachiola rachiphaga* (Felt) and *Kaltenbachiola canadensis* (Felt)), and spruce seedworm (*Cydia strobilella*) were found in the spruce cones. The only disease identified was spruce cone rust, *Chrysomyxa pirolata* Wint., included under “other” for 1993 in Table 2.

Seed dispersal

The amount of seed in the traps was greatest in 1993 compared with all other years (Fig. 2). In 1993, the selection and patch-cut treatments averaged over 1 × 10^6 subalpine fir seeds/ha and yielded approximately 350 000 spruce seeds/ha. The selection treatment had significantly more (p = 0.015 to p < 0.001) seed in the traps than the clearcut treatment every year of the study (Table 3) but was not significantly different from the patch-cut treatment (p = 0.111 to 0.986). There were more subalpine fir seeds than spruce in all years except in the clearcut in 1994 when no subalpine fir seeds were found. Except for the 1993 heavy cone crop year (Fig. 2), a

Fig. 2. Seeds per hectare by year and harvesting treatment calculated from the mean number of seeds collected in traps within a 40-m^2 natural regeneration assessment plot. Bars show the mean for each harvesting treatment for subalpine fir and Engelmann spruce. Error bars are ±1SE.



mean of less than one seed per trap has been collected from within any of the harvest treatments at the Lucille Mountain site.

Seed viability

Testing was done only in 1993. Subalpine fir percent filled seed ranged from 39 ± 2 (mean ± SE) from the selection treatment to 43 ± 21 from the clearcut. Seed mass averaged 191 ± 5 seeds/g. Percent germination from the selection and patch-cut treatments was 29 ± 2 and 31 ± 3, respectively. Spruce percent filled seed ranged from 44 ± 7 from the patch-cut treatment, to 32 ± 13 from the clearcut. Seed mass ranged from 680 ± 65 to 787 ± 64 seeds/g, and percent germination was similar among the selection and patch-cut treatments at 26 ± 3%.

Seedbed preparation and germination

Silviculture treatment had a significant effect ($p < 0.001$) on germination and seedling survival (Table 4). The clearcut

Table 3. Dunnett's two-sided pairwise multiple comparison *t* test for mean seeds per plot by silviculture treatment with selection treatment as the control (J) and comparing all other treatments (I) against it.

Year	Treatment (I)	Treatment (J)	Mean difference* (I–J)	*P*
1993	Clearcut	Selection	–6.1328	<0.001
	Patch cut	Selection	0.0596	0.986
1994	Clearcut	Selection	–0.8464	0.003
	Patch cut	Selection	–0.4946	0.111
1995	Clearcut	Selection	–0.9336	0.015
	Patch cut	Selection	–0.5068	0.257
1996	Clearcut	Selection	–1.4625	<0.001
	Patch cut	Selection	–0.3366	0.517

Note: A square-root transformation was used on the data for analysis.
*Mean difference is significant at the 0.05 level.

treatment had only 14% of the number of spruce, and 9% of the subalpine fir, compared with the two other harvest treatments, 5 years after harvest. The selection treatment had the greatest number of subalpine fir germinants (Fig. 3) and the same number of spruce germinants as the patch cut treatment (Fig. 4). The exception was for the UN treatment, where the selection treatment had 70% more spruce germinants per hectare.

Seedbed treatment had a significant effect ($p < 0.001$) on the germination and survival of subalpine fir and spruce (Table 4). The number of germinants was increased by direct seeding and not by seedbed disturbance, in the clearcut (Figs. 3 and 4). In the patch cut and selection treatments, disturbing the forest floor resulted in more germinants compared with the undisturbed plots. There were more spruce germinants in the DS treatment compared with the DN treatment (Fig. 4). Seeding did not increase the number of subalpine fir germinants in the patch cut and selection treatments (Fig. 3) suggesting that sufficient natural supply of seeds were present. Seedbed scarification alone increased the number of subalpine fir in the patch cut treatment by 116 400 germinants/ha, and by 140 600 germinants/ha in the selection treatment. The statistically significant effect ($p = 0.001$) of replicate may be due in part to variations in seedbed surface arising from the earlier disturbance during harvest (Table 4). The degree or timing of disturbance was not monitored in this study.

Changes in the number of germinants from year to year are a combination of the death of germinants and replacement by new germinants. The total number of germinants has been decreasing since 1994. Exceptions occurred between 1995 and 1996 with an increase in the number of subalpine fir germinants in the clearcut–UN treatment (Fig. 3) and an increase in the number of spruce germinants in the patch cut – DN treatment (Fig. 4).

In summary, there has been one heavy cone crop followed by three light crops. The number of sound seed was low in light cone crop years. The number of seeds trapped in the clearcut was very low even in a heavy cone crop year because of distance from the seed source. Across all harvesting treatments in 1993 there were more subalpine fir seed in the

Table 4. Separate species factorial analysis of variance for number of subalpine fir and spruce germinants within three silvicultural systems, and four seedbed treatments, monitored annually from 1994 to 1996.

		Subalpine fir		Spruce	
Source	df	MS	*P*	MS	*P*
Model	167	8.212	<0.001	5.137	<0.001
Year (Y)	2	28.516	<0.001	11.186	<0.001
Silvicultural treatment (S)	2	147.407	<0.001	45.097	<0.001
Seedbed treatment (B)	3	151.904	<0.001	154.306	<0.001
Replicate (R)	4	5.312	0.001	4.803	<0.001
Y × S	4	7.012	<0.001	2.402	0.004
Y × B	6	0.647	0.732	2.863	<0.001
Y × R	8	0.212	0.991	0.163	0.979
S × B	6	31.311	<0.001	16.101	<0.001
S × R	7	18.418	<0.001	5.550	<0.001
B × R	12	3.209	<0.001	3.439	<0.001
Y × S × B	12	0.459	0.954	1.001	0.089
Y × S × R	14	0.290	0.997	0.107	1.000
Y × B × R	24	0.247	1.000	0.365	0.948
S × B × R	21	5.714	<0.001	2.375	<0.001
Y × S × B × R	42	0.360	1.000	0.420	0.951
Error	1222	1.081		0.631	

Note: Data were transformed using the square root plus 0.5.

traps compared with spruce, which is consistent with the greater number of seeds per cone and the greater number of cone bearing trees for this species. There were more spruce and fir germinants in the patch cut and single tree selection harvest treatments compared with the clearcut. Direct seeding increased the number of germinants in the clearcut for both fir and spruce. Direct seeding in the patch cut and single tree selection harvest treatments increased the number of germinants for spruce only. Exposed mineral soil increased the number of fir and spruce germinants in the patch cut and single tree selection harvest treatments.

Discussion

This study has demonstrated that abundant conifer seed can be produced on high-elevation ESSF sites in northern British Columbia. However, there appear to be some inherent limitations in the periodicity of heavy cone crops and the quality of seed produced on an annual basis. Cone crops within the study area appeared to be influenced by climate patterns rather than harvest treatment. This observation has been noted over longer periods of cone crop assessment by others (McDonald 1992). The heavy cone crop in 1993 was preceded by a hot and dry summer the year before, conditions known to induce reproductive bud production in conifers (Daubenmire 1960; Ross and Pharis 1985). Although 1994 was also hot, moisture was not limiting, plus few reproductive buds would have been able to differentiate and develop because of the heavy crop in the year before (Owens and Molder 1985). Reported cone crop periodicity of collectable cone crops for subalpine fir is 2–4 years and 6 years for interior spruce within British Columbia at lower elevations (Eremko et al. 1989). However, a summary from the B.C. Ministry of Forests Tree Seed Centre indicates that collectable cone crops for these species at elevations above 900 m occur less frequently (H. Rooke, B.C. Ministry of Forests Tree Seed Centre, Surrey, unpublished data).

Seed quality appears to be poor in this stand compared with data collected for these species at lower elevations. Subalpine fir seed from collections above 900 m stored in the B.C. Ministry of Forests Tree Seed Centre averaged a mass of 83 seeds/g with a 72% germination rate (D. Koletelo, unpublished data). The subalpine fir seeds collected in our study averaged less than half this mass and germination rate. Similarly for interior spruce, the Tree Seed Centre reported an average of 479 seeds/g and 92% germination compared with an average of 734 seeds/g and 26% germination for spruce seed collected from our site. The smaller size seed from higher elevations may be due to the shorter growing season and cooler temperatures experienced during seed development.

The higher percentage of insect infested cones in the light crop years suggests that, when seed supply is low due to low numbers of cones, predation by insects consume a higher percentage of maturing seeds. Spruce cones that were dry and brown may have been damaged by insects at an early stage of cone development or from low fertilization success followed by a late cone abortion. Normal-looking but empty seeds often result from lack of pollination (Owens and Morris 1998). The 3 months of cone and seed development required to produce mature seeds provides an opportunity for abortion at any stage of development (Owens and Morris 1998). The preliminary results from our study indicate that sound seed is produced in large quantities only when the cone crop is heavy. McDonald (1992) found the same to be true in a 24-year study of several native Californian tree species where the percent sound seed was low when the number of cones produced was low.

Although the periodicity of cone crops and seed quality appear unrelated to harvest treatments, the availability of

Fig. 3. Mean number of subalpine fir germinants expressed on a per hectare basis by year within the three harvesting treatments (clearcut, patch cut, and single tree selection) and four seedbed treatments (DS, disturbed and seeded; DN, disturbed and not seeded; US, undisturbed and seeded; UN, undisturbed and not seeded). Bars show treatment means (n = 5 in the clearcut and single tree selection treatments, and n = 4 in the patch-cut treatment). Error bars are ±1SE.

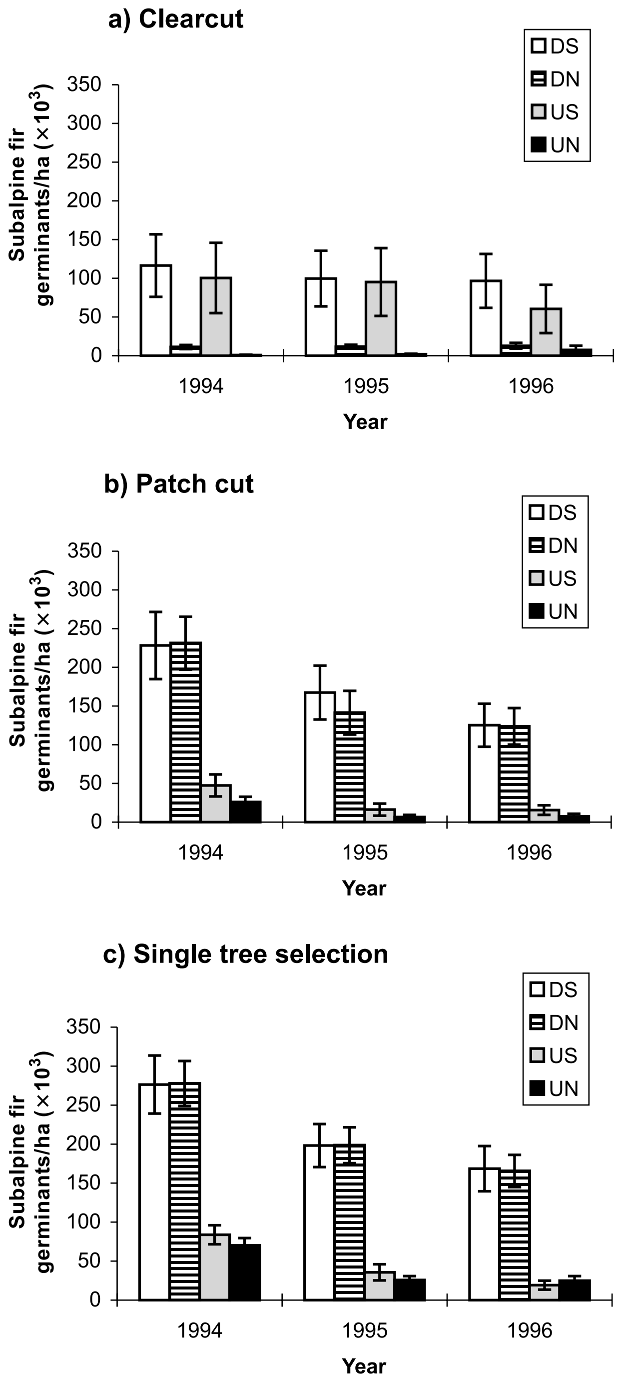
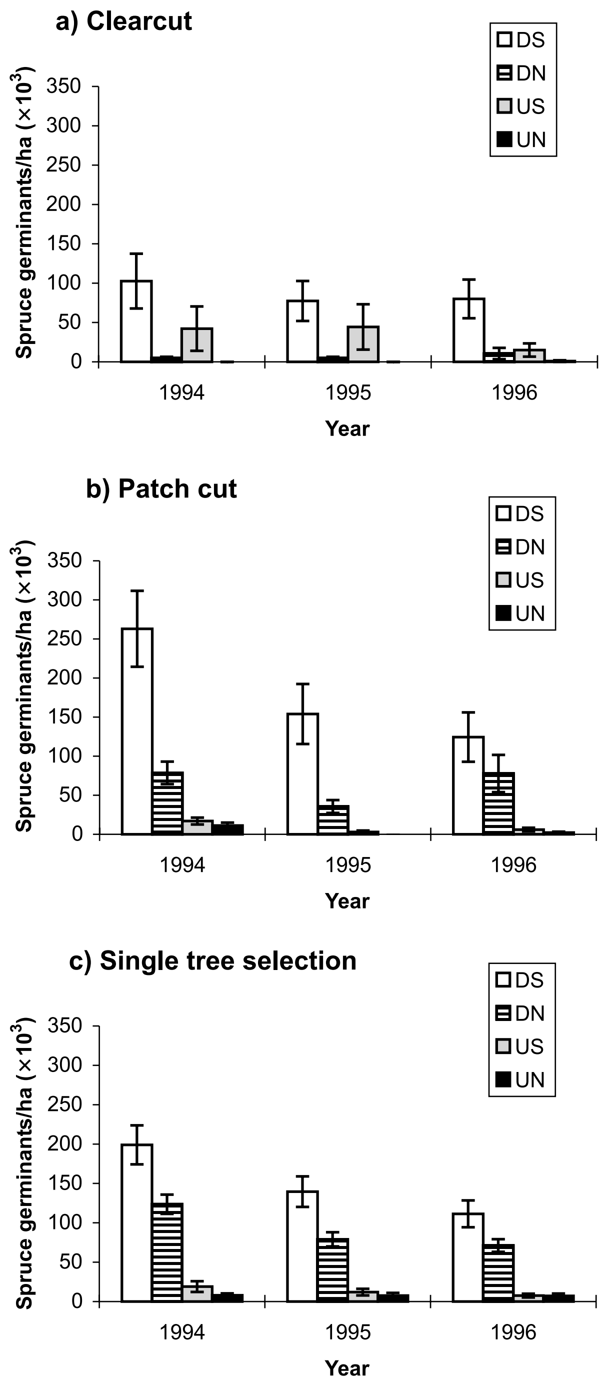


Fig. 4. Mean number of Engelmann spruce germinants expressed on a per hectare basis by year within the three harvesting treatments (clearcut, patch cut, and single tree selection) and four seedbed treatments (DS, disturbed and seeded; DN, disturbed and not seeded; US, undisturbed and seeded; UN, undisturbed and not seeded). Bars show treatment means (n = 5 in the clearcut and single tree selection treatments, and n = 4 in the patch-cut treatment). Error bars are ±1SE.



seed for natural regeneration differed among the three harvesting methods. There were more subalpine fir seed in the single tree selection treatment compared with the patch cut and more spruce seed in the patch cut treatment compared with the single-tree selection. This a function of the postharvest stand composition and, possibly, the greater distance the smaller size spruce seed may travel in the small openings created by the patch cut treatment. In a study using confetti to mimic spruce seed, Stewart et al. (1998) measured greater dispersal distances with an increase in the height of release. The cone-bearing spruce trees at the Lucille study site are generally taller than the dominant subalpine fir perhaps allowing for greater dispersal of the spruce seeds. When they released the confetti within the spruce–aspen stands, most landed within 15 m of the tower. Likely, the majority of seeds in the single tree selection treatment that maintains a closed stand structure, behave like the confetti and fall close to the parent tree. Less than 5% of the Engelmann spruce seed falling under uncut stands dispersed as far as 200 m in a high-elevation study in Colorado (Alexander and Edminster 1983).

The distance of seed dispersal is the limiting factor for natural regeneration in clearcuts and dispersal patterns are strongly influenced by the direction of the prevailing winds (Alexander and Edminster 1983). Few spruce seeds, and even fewer subalpine fir seeds, have been found in the traps within the clearcut at the Lucille Mountain site. Heavier seeds do not travel by wind as far as lighter seeds, and this could explain the lower numbers of subalpine fir seed compared with the lighter spruce seed. Dispersal of sound seed is less than for empty seed for the same reason (Dobbs 1976). Dobbs measured the dispersal of white spruce (*Picea glauca* (Moench) Voss) seed along a transect across a 400-ha clearcut in the Prince George Region and found that seedfall declined sharply from the clearcut edge to 100 m, but some seed travelled as far as 300 m. In our study, none of the seedtraps were located closer than 100 m from the clearcut edge.

Scarifying seedbeds to expose mineral soil increased the number of germinants in the single tree selection and patch cut harvest treatments, possibly because of a number of factors such as soil warming and reduction of competing vegetation. These results are similar to those of Feller (1997) from a comparable study in the southern interior of British Columbia where the undisturbed seedbeds had the lowest number of subalpine fir and spruce germinants compared with mineral soil or burning. Feller found that competing vegetation decreased the number of subalpine fir but not spruce germinants. However, in our study, more subalpine fir seeds than spruce seeds germinated on the undisturbed seedbeds, particularly in the single tree selection treatment. The specific species of vegetation on undisturbed seedbeds affected the germination of Scots pine (*Pinus sylvestris* L.) in a Swedish forest (Steijlen et al. 1995). *Pleurozium schreberi* decreased the germination of Scots pine through a combination of lack of moisture, chemical interference with germination, and by decreasing nutrient availability to germinants. Not all moss species appear to have the same effect; McLaren and Janke (1996) reported the highest level of germination of balsam fir (*Abies balsamea* (L.) Mill.) on hypnaceous moss compared with four other natural media. Short-term results may differ from long-term results as demonstrated for white ash where beds that were seeded and then scarified initially had four to five times as many seedlings compared with other treatments (Leak 1993). However, at the 34-year assessment, small differences existed among any of the treatments, including undisturbed.

Harvesting treatments have an effect on the number of germinants not only as a result of seed supply as already discussed, but perhaps also because of the moderating effect on the seedbed environment or on level of predation. In our study, gains and losses in the number of germinants were not quantified separately. The higher number of germinants in the clearcut–US treatment compared with the partial harvest – US treatments suggests that the microclimate was suitable for germination in the clearcut, or mortality and predation were less. A lack of seed appears to be the major limiting factor for natural regeneration in the clearcut. Results from a high-elevation natural seed regeneration ingress study in the southern interior of British Columbia have been similar in that scarification had little effect on the number of germinants if a seed source was lacking, and artificial seeding had little effect if a source was available (O. Steen, personal communication). Johnson and Fryer (1996) established that spruce does not exist in seed banks because of predation, germination, and seed mortality during the first year. Therefore, the only seeds available for germination annually in clearcuts are those from direct seeding or the limited dispersal from the surrounding stand.

A greater understanding of the biological factors involved in natural regeneration and the effects of our forest-management practices on its level of success should form the basis for developing site specific prescriptions. The results from this study indicate a positive relationship between number of sound seed and crop rating. McDonald and Abbott (1994) have also demonstrated a strong linear relationship between number of sound seed and crop rating for several tree species. Foresters could benefit from rating the cone crop in stands planned to be harvested the following winter to predict the amount of seed to expect in the first season for natural regeneration (Alexander and Edminster 1983). Green and Johnson (1994) used tree and seed data from nine studies (15 species), and studied 15 other species, to develop a predictive model that estimated the expected number of seeds produced by a stand. They suggested using individual tree measurements in the planning for the layout of partial-harvest systems to determine the optimal size and shape of openings (and which trees to leave) to maximize natural regeneration. Seedbed preparation needs could be determined and the treatments applied prior to an anticipated heavy seedfall and winter logging. If the gradual natural restocking of high-elevation sites is not compatible with the management objectives for a site, planting could be used to augment seedling numbers (McCaughey et al. 1991) and adjust species composition in the future stand.

The results from Lucille Mountain study are preliminary and the future stocking levels and growth performance remain unknown. McCaughey et al. (1991) have found that stocking of subalpine fir and Engelmann spruce on high-elevation sites in Colorado is a gradual accumulative process. Twenty-years after harvest, partial cuts had greater densities of 2- to 4-year-old seedlings compared with clearcuts, demonstrating the long-term receptiveness to natural regeneration to a continuous seed source and moderating climate.

Acknowledgements

Funding for the Lucille Mountain Project was initially through the B.C. Ministry of Forests Sustainable Environment Fund (SEP), and then the Canada – British Columbia Partnership Agreement on Forest Resource Development

(FRDA II) from 1991 to 1995. Forest Renewal BC research funds continue to support this project. We thank the contributors to the original working plan: C. Delong, M. Osberg, D. Coopersmith, and W. Hays of the B.C. Ministry of Forests, Prince George Region. Our thanks are extended to Dr. Bob Sagar for providing the annual climate summaries; Dr. Robb Bennett, B.C. Ministry of Forests, Victoria, for the identification of cone and seed insects; and Frank Portlock for conducting all laboratory seed tests. We are grateful to the Canadian Forest Service for support in completing the fieldwork. Thanks also to Carole Fleetham, B.C. Ministry of Forests, for her volunteer field assistance. Special thanks go to Anne Jankowski for the aerial cone collections and teaching me how to fly.

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