Potentials of Natural Tree Regeneration after Clearcutting in Subalpine Forests

Juergen Kreyling, Andreas Schmiedinger, Ellen Macdonald, and Carl Beiekuhnlein

ABSTRACT

Regeneration of interior mountain forests still is not adequately understood, although these forests are subject to intensified use over the last decades. We examined factors influencing the success of natural tree regeneration after harvesting in the Engelmann spruce–subalpine fir zone of the Monashee Mountains, British Columbia, Canada. Distance from the forest edge was an important factor for regeneration; at distances exceeding 70 m from the forest edge only 50% of plots showed sufficient natural regeneration to meet stocking targets compared with 90% of plots closer to forest edges. Seedling density and growth were superior in the more protected southern portions of clearcuts. Seedling growth was less in plots containing high cover of downed woody debris. There was no relationship between understory plant diversity or composition and tree seedling regeneration. However, cover of fireweed (*Epilobium angustifolium*) had a significant negative relationship with density but not growth of tree seedlings, particularly for lodgepole pine (*Pinus contorta* var. latifolia). Cover of fireweed declined substantially within the first 10 years after clearcutting. We conclude that natural regeneration of trees has potential to help achieve stocking targets and also to maintain natural diversity of tree species if spatial constraints, especially thresholds in clearcut size, are considered.

Keywords: dispersal, clearcut size, edge effect, fireweed, woody debris

Sustainable management of forest ecosystems is set as a goal by most nations (Norton 1996), and maintaining biological diversity is one important component of this (Hansen et al. 1991, British Columbia [BC] Forest Service 1995). Biodiversity conservation strategies that include a variety of individual management strategies for specific species are neither feasible nor effective (e.g., Hunter [1993] and Attiwill [1994]). As an alternative, "coarse-filter" management strategies focus on maintenance of broad patterns of forest age and composition, under the assumption that this will provide the necessary habitat to support a wide variety of native species (Franklin and Forman 1987, Franklin 1993, Larsen et al. 1997, BC Forest Service 1995). Native species are assumed to be adapted to the natural disturbance regime of their environment; thus, management that simulates the natural disturbance regime has become a popular approach to maintaining species diversity as well as ecological integrity (Hunter 1993, Bergeron et al. 2002). With this approach, natural processes are to be protected, which include forest regeneration after disturbances such as fire or logging.

A central component of biodiversity conservation in managed forest landscapes is successful regeneration of natural tree species mixes after logging (Burton et al. 1992, Bergeron and Harvey 1997). This often proves to be a substantial challenge. Site preparation and planting of tree seedlings have been widely adopted as strategies to ensure rapid and successful postharvest regeneration. These require a substantial silvicultural and financial investment, however, and are not always successful in meeting legal regeneration standards, let alone achieving a natural species mix. Although natural regeneration can be much less expensive and lead to more natural species mixes, its success depends on availability of seed sources, regeneration microsites, and microenvironmental and biotic conditions favoring establishment and early survival of tree seedlings (Feller 1998, Greene et al. 1999, Nguyen-Xuan et al. 2000).

Compared with other conifer forests, e.g., those in central Europe or in the true circumboreal regions, forests in the mountainous regions of western North America often have high diversity of tree species. For example, 12 conifer species are commonly found in the subalpine region of southern British Columbia, Canada (the investigated forest zone; Coupé et al. [1991]). High demands for timber and increasing accessibility are leading to increased exploitation of these high-elevation forests. They are characterized by slow growth rates of postdisturbance regeneration and established trees; thus, meeting objectives for regeneration of natural species mixes and sustainability of fiber and other ecosystem components can prove challenging (Selmants and Knight 2003). To facilitate natural regeneration, and where water production and wildlife habitat are important considerations, Alexander (1987) recommends that clearcuts in the Engelmann spruce (*Picea engelmannii*)–subalpine fir (*Abies lasiocarpa*) (ESSF) forest type in the central and southern Rocky Mountains should be irregular in shape with a maximum width of four to eight times the tree height. The scientific or ecological basis for this recommendation, which would result in clearcuts less than 200 m in diameter, is unclear. There are no other published studies about clearcut size and its effect on natural forest regeneration in this region.

We examined the impact of ecological factors (e.g., richness, cover, and composition of understory plants) and spatial constraints

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Table 1. Properties of investigated clearcuts.

Clearcut	Opening no.[a]	No. of plots	Size (ha)	Logging (yr)	Planted interior spruce (per ha)	Planted lodgepole pine (per ha)	Planted Western White Pine (per ha)	Planted interior Douglas-fir (per ha)
A	185	5	3.3	1996	1,010		580	
B	206	6	3.8	1994	560	878		
C	170	7	4.4	1993	1,004	554		
D	230	12	7.4	1997	253	441	235	444
E	197	22	11.7	1995	542	645	26	536
F	237	23	14.0	1997	1,353			

All clearcuts had been mechanically cleared and pile burned. Sampling was conducted during the summer of 2003.
[a] Forest cover map 82 L 008 (BC Forest Service 2001)

(e.g., clearcut size and distance to the nearest forest edge) on natural regeneration of trees after clearcutting in the ESSF forest type in southern British Columbia, Canada. Our objective was to define limiting conditions for natural regeneration in this forest type and to determine conditions favoring success of natural regeneration.

Materials and Methods

Study Area

The study area was located in the Monashee Mountains of British Columbia, Canada, at 50°2′N and 118°3′W. The elevational range extended from 1,400 to 1,650 m above sea level (asl). The study was conducted in the ESSF zone, which is the uppermost forested zone in southern interior British Columbia (Coupé et al. 1991). This zone is characterized by a mean annual temperature of approximately 0°C (Coupé et al. 1991). Mean annual precipitation is approximately 1,200 mm, 800 mm of it occurring as snow (Lloyd et al. 1990). All investigated clearcuts and most of the surrounding area were situated on morainal deposits (often more than 1 m thick), which overlay plutonic rocks (Lloyd et al. 1990). According to the Canadian System of Soil Classification, the soils are Dystric Brunisols (Dystrocryepts in the US Soil Taxonomy and Dystric Cambisols in the World Reference Base/Food and Agriculture Organization System), accompanied by Humic Gleysols (Humic Cryaquepts or Umbric Gleysols, respectively) in wet depressions. Soils have generally low pH (pH_{KCl} values, mean = 4.4 and SD = 0.5).

Interior spruce (*Picea glauca* × *engelmannii*) and subalpine fir (*A. lasiocarpa*) are the dominant tree species in mature stands in the ESSF zone of the study area. Lodgepole pine (*Pinus contorta* var. *latifolia*) is a widespread early seral (postfire) species. Other tree species that commonly occur in lower-elevation zones, but occasionally in the ESSF zone as well, are interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and western white pine (*Pinus monticola*). Deciduous trees are uncommon in the ESSF zone. The disturbance regime of spruce–fir forests includes fires, blowdowns, and insect outbreaks. Fire usually is considered to be the most important of these factors (e.g., Aplet et al. [1988], Johnson et al. [1990], Bunnell [1995], Antos and Parish [2002], and DeLong et al. [2003]). Charcoal was found in several soil profiles in the study stands, in horizons up to 20 cm below the surface, indicating a long history of fire.

Fires in the subalpine zone are characteristically infrequent but stand replacing (Baker and Veblen 1990, Arno 2000). Reported mean return intervals range from 100 to 1,000 years (Arno [2000], 100–400 years; Veblen et al. [1994], 200 years; Bunnell [1995], 250 years; BC Forest Service [1995], 350 years; Aplet et al. [1988], 500–1,000 years). Fires at these subalpine elevations generally are small (mean size of 275 ha) compared with those in true boreal regions, where thousands of hectares might be affected (Hunter 1993). Nevertheless, fires as large as 10,000 ha may occur in the ESSF zone and large burned areas typically include a considerable amount of surviving trees in a patchy distribution (Bunnell 1995, Turner et al. 1997, Franklin et al. 2002). Current clearcut sizes in the region range between 3 and 25 ha (BC Forest Service 2001).

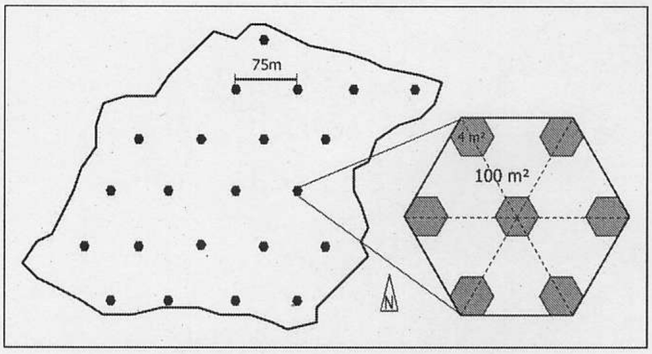

Figure 1. Sampling design in a systematic hexagonal grid (left). Single plots of 100 m² contained seven subplots of 4 m² in which frequency of understory species was obtained (right).

Sampling Design

Six clearcuts were chosen with the constraints that all were located in a comparable elevational range (1,400–1,650 m asl), on similar bedrock (morainal deposits overlaying granite), and possessed mean slope smaller than 10°. Three small-sized (3–5 ha) clearcuts were chosen as well as three medium-sized (10–15 ha) clearcuts to address effects of clearcut size and distance to the nearest seed source. All clearcuts were 6–10 years old and had been harvested in summer. All had been mechanically cleared after harvest and slash piles were burned. The clearcuts had been planted with interior spruce and lodgepole pine at known densities. Western white pine and interior Douglas-fir were planted in two clearcuts at low densities (see Table 1 for further information about the clearcuts). No extraordinarily shaped clearcuts were sampled; all had irregular boundaries but were more or less rectangular with minor variations due to relief. All six clearcuts were located within a 60-km² area and were surrounded by a more or less uniform matrix of typical mature ESSF stands. Sampling was conducted during 3 weeks in August/September 2003.

A systematic sampling scheme was applied on each clearcut (Figure 1, left). Thus, each sampling plot had six equally spaced neighbors (except for those located at the edges). Distance between plot centers was 75 m; this resulted in five or more plots in every clearcut. We maintained a minimum distance of 10 m from the plot center to the nearest forest edge to prevent sampling the edge itself. Distance from the plot center to the nearest forest edge was measured with a laser-dendrometer (LEDHA-GEO; Jenoptik, Jena, Germany). In total, there were 75 plots in the 6 clearcuts.

Tree regeneration was characterized by determining every individual within the 100-m^2 plot to species and measuring total height and terminal shoot length of each individual. Each plot was subdivided into seven 4-m^2 subplots (Figure 1, right). Understory vegetation, including mosses and all vascular plants except tree species (no lichens were observed on the clearcuts), was recorded as presence–absence by species in these subplots. Relative abundance for each species was calculated as the percentage of subplots occupied. To quantify the effects of fireweed (*Epilobium angustifolium*) more precisely, its cover was estimated (in 10% classes) in the same seven subplots. The nomenclature of plant species follows Douglas et al. (1998–2001). Cover of coarse woody debris was estimated (in 10% classes) within the 100-m^2 plot.

Data Processing and Statistical Analysis

We estimated abundances of naturally regenerated seedlings by taking the total count to species of all seedlings found in each plot and then subtracting the average number per clearcut of seedlings planted per 100 m^2 by species (Table 1). Numbers of planted seedlings were provided by the BC Forest Service. The result is a conservative estimate of densities of natural seedlings because it is unlikely that all planted seedlings survived; indeed, space released by death of planted individuals might have provided spots for germination and growth of natural regeneration.

Growth was quantified for all seedlings and for each species separately as the mean terminal shoot length of the 16 tallest seedlings per 100-m^2 plot in the data set after subtracting the average number of planted seedlings from the tall end (as described previously). We used the 16 tallest seedlings for growth measurements because the silvicultural target at the regeneration stage is 1,600 stems ha^{-1} (which is 16 per 100 m^2; silvicultural prescriptions, Hadrian Merler, BC Forest Service, personal communication, Aug. 15, 2003; Lloyd et al. 1990). Presumably this is our current best estimate of naturally regenerated future crop trees. We noted that sites with higher regeneration densities usually contained high numbers of small seedlings than sites with poorer regeneration.

To determine whether densities or growth rates of naturally regenerated seedlings change between 6 and 10 years (the age of clearcuts we sampled), we used a simple correlation between clearcut age and (1) the calculated density of natural regeneration (for all species combined) and (2) the average terminal shoot length for the subset of the 16 tallest seedlings from each plot. To examine any possible influence of distance from forest edge on natural regeneration density (all species combined), we performed a regression. All regressions were run with several linear and nonlinear functions, and the one that was significant ($P < 0.05$) and resulted in highest coefficient of correlation was kept. Subsequently, we categorized the plots by distance from nearest forest edge in 20-m classes and calculated the proportion of plots in which estimated density of natural regeneration was 1,600 seedlings ha^{-1} or more, which represents the target for sufficient regeneration. We also assessed whether there was any relationship between distance from edge and growth (terminal shoot length for the subset of 16 seedlings per plot) using regression. To examine whether there was an effect of location within the clearcut on regeneration density or growth, we used a Mann-Whitney *U* test to compare plots within 60 m of a forest edge in the north versus the south end of a clearcut with respect to the calculated density of natural regeneration and average terminal shoot length (for the subset of 16 seedlings per plot) for the two most abundant species (interior spruce and subalpine fir).

We calculated richness (*S*, number of understory plant species per plot), diversity (*H*, Shannon index, per plot, using frequency of occurrence of a species in the subplots as the measure of relative abundance), and evenness ($E = H/\ln S$) for the understory vegetation community. We then used simple correlation of these values with the calculated density of natural regeneration and seedling growth (total height and terminal shoot length for the subset of 16 seedlings per plot) to determine whether there was any relationship between understory diversity and tree regeneration. Because of the apparent importance of fireweed in these clearcuts we also explored the relationship between its cover (mean value per 100 m^2 plot calculated from the values in the subplots) and both the calculated density of naturally regenerated seedlings and seedling growth (terminal leader length for the subset of 16 seedlings per plot). The analysis of density was done for all tree species together and then separately for the most abundant tree species (lodgepole pine, subalpine fir, and interior spruce). We also used regression to examine whether the cover of fireweed varies over time (among the range of clearcut ages we had). Finally, we used regression to examine whether there was a relationship between tree seedling growth (mean value based on the 16 seedlings per plot) and cover of downed woody debris in the plots. For these regressions, several different linear and nonlinear relationships were tried and the one significant model best fitting the data was chosen based on coefficient of correlation. All of the foregoing analyses were completed using SigmaPlot 7.1 (Systat Software, Inc., Richmond, California) and SPSS 10 (SPSS, Inc., Chicago, Illinois) programs and an alpha = 0.05.

We used a Mantel test (Mantel 1967) to examine whether there was any relationship between understory composition and tree regeneration (both calculated density of natural regeneration and seedling growth). The Sørensen Index was used as a measure of similarity. Significance testing was performed by Monte Carlo randomization (1,000 permutations; McCune and Grace [2002]). The analysis was conducted by using PC-ORD version 4.17 (MjM Software, Gleneden Beach, OR).

Results and Discussion

General

Densities of total seedlings were substantially greater than planted densities, indicating the importance of natural regeneration (overall mean planting density, 1,514/ha; overall mean density of all seedlings in field plots, 9,360/ha). This is further supported by examining the species composition of the tree seedlings. All tree species that occurred before harvesting (perharvest silvicultural prescriptions, Hadrian Merler, BC Forest Service, personal communication, Aug. 15, 2003) regenerated successfully (Figure 2). Based on the calculated densities of natural regeneration, subalpine fir was the most abundant followed by interior spruce. In general, tree diversity in the clearcuts reflected the natural, preharvest condition. This was encouraging given the fact that only interior spruce and lodgepole pine had been planted in four of the six clearcuts and it was only these two species that were planted at high densities. Western white pine was not present in the mature stands but appeared as a small percentage of the total seedling population; this was caused by the fact that it was planted in low densities on two of the six clearcuts. In the study area, usually, it is restricted to lower elevations.

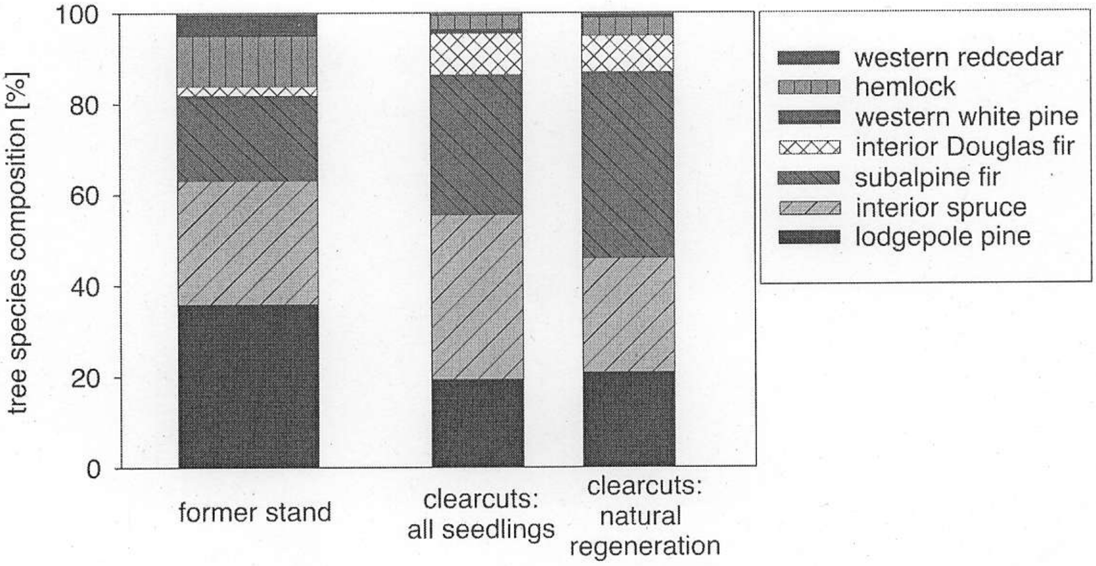

Figure 2. Tree species composition before and after clearcutting expressed as mean percentages by species over all six clearcuts ($n = 75$ plots). For the former stands (90–220 years old) we present percent basal area (Hadrian Merler, BC Forest Service, personal communication, Aug. 15, 2003), for the clearcuts proportions of number of seedlings, are displayed. "Calculated natural regeneration" was calculated by subtracting the average number of planted individuals (by species, see Table 1) from the total number of seedlings observed in the plots.

Lodgepole pine is a shade-intolerant species that often has been considered an early seral species in ESSF forests and, therefore, should thrive stronger than other species in open conditions such as those after clearcutting. Despite the fact that it was planted on four of the six clearcuts, its proportional contribution to total tree composition was considerably lower (20% of all seedlings) than in the mature stands (35% of total basal area). Subalpine fir was the most abundant tree species on the clearcuts (40%), although its regeneration relied completely on natural recruitment (i.e., it was not planted). The other major component of tree regeneration was interior spruce; planting seemed to be important to regeneration densities of this species (35% of all seedlings and 24% of calculated naturally regenerated seedlings). Interior Douglas-fir (8%), hemlock (5%), western redcedar (1%), and western white pine (1% of all seedlings) occurred as minor components.

There was no significant correlation of any type between clearcut age and either total density of natural tree regeneration or growth, for all species combined. This implies that most natural regeneration establishes shortly after harvesting (within 6 years, the age of our youngest clearcuts) and that there are no significant changes in regeneration density or rate of annual growth between 6 to 10 years after harvesting.

Distance to Nearest Forest Edge

Distance to nearest forest edge is known to influence the regeneration of those trees that do not originate from the soil seed bank (e.g., Treter [1992], Greene and Johnson [1996], and Greene et al. [1999]) because dispersal follows a nonlinear decay function with distance. We found a weak but significant ($P = 0.009$) negative (power) relationship between density of natural regeneration and distance to the nearest forest edge (Figure 3). The regression did not explain much of the total variation ($R^2 = 0.12$) because there was high variability in regeneration density among plots. However, no plot with high regeneration densities was found far from an edge and the trend of declining density of natural regeneration with distance from edge was clear for all but the two smallest clearcuts.

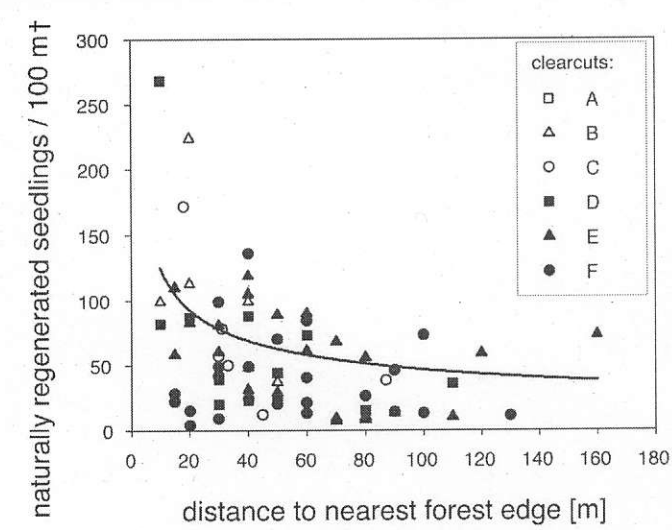

Figure 3. Relationship between density of naturally regenerated seedlings and distance to nearest forest edge for 75- to 100-m² plots in six clearcuts (A–F). Line shows the power trend computed for all plots combined ($y = 326.5x^{-0.53}$; $R^2 = 0.12$; $P = 0.009$).

The percent of plots in which the calculated density of natural regeneration would meet the target for sufficient regeneration varies from 40 to 94%. There was a discontinuity at distances greater than 70 m. Although approximately 90% of plots within 70 m of a forest edge had sufficient natural regeneration to meet the target density only 60–40% of plots farther than 70 m from an edge met the standard (Table 2). This difference was highly significant (Mann-Whitney U test; $P = 0.004$). Only four plots within 50 m of the forest edge had less than 1,600 stems ha^{-1} of natural regeneration. Their failure can be explained by other environmental factors: one had stagnant standing water and more than 90% cover by understory vegetation; in another, cover of fireweed exceeded 50%; the other two plots were covered with more than 50% downed woody debris. The clear evidence of poorer natural regeneration in the

Table 2. The influence of distance from the nearest forest edge on the percentage of plots in which natural regeneration met the target regeneration density (1,600 seedlings ha^{-1}; Lloyd et al. 1990).

Distance from edge (m)	Sufficiently regenerated plots (%)	n
10–29	87	15
30–49	92	25
50–69	94	16
70–89	44	9
90–109	40	5
>110	60	5

Based on a total of 75 plots (100 m^2) in six clearcuts; n = number of plots in a given distance class.

centers of the larger clearcuts suggests that the seed bank is much less important for natural regeneration than is dispersal. Thus, meeting legal reforestation requirements by natural regeneration would be reliable with a clearcut design in which no sites were farther than 70 m from the nearest forest edge or another sufficient seed source. Remnant tree patches could potentially function efficiently as seed sources, enhancing natural regeneration within larger clearcuts; this should be examined further.

The microclimate at clearcut edges varies with the cardinal direction of clearcut edge in relation to sun angle and its effects on light, temperature, and moisture (Palik and Murphy 1990, Chen et al. 1995; Burton 2002). At northern latitudes, northern portions of clearcuts will receive higher amounts of solar radiation and therefore are lighter, warmer, and drier than the more shaded southern portions of the clearcut. Our results suggest that this has a significant impact on success of natural tree regeneration. Areas within 60 m of a forest edge in the southern portions of the clearcuts had higher densities of naturally regenerated interior spruce (Mann-Whitney U test; $P = 0.026$) and subalpine fir ($P = 0.029$) seedlings than did areas within 60 m of a forest edge that were in the northern portion of the clearcuts. In addition to higher densities, interior spruce showed higher terminal growth rates in the southern versus the northern part of the clearcuts ($P = 0.027$). This concurs with the results of Coates (2002) and could be caused by more favorable moisture conditions as a result of shading from the nearby edge. Recruitment and growth of the two major species (interior spruce and subalpine fir) might be enhanced, therefore, if groups of remnant trees were left on clearcuts to provide shade and shelter as well as a seed source. There was no relationship between distance to edge and seedling growth for other species except interior spruce.

Understory Vegetation

In total, 131 plant species including mosses were identified on the clearcuts. Many (64%) of these species commonly occur in mature forests of the ESSF zone and were considered residuals from the former stands. This finding corresponds well with results from forests in the Pacific Northwest where a majority of forest understory species (over 70%) persisted after logging and slash burning (Halpern 1989). Five nonnative species were found (bull thistle [*Cirsium vulgare*], orange hawkweed [*Hieracium aurantiacum*], Timothy grass [*Phleum pratense*], common dandelion [*Taraxacum officinale*], and alsike clover [*Trifolium hybridum*]); however, all had very low abundance. All other species were natives to the region but were species that typically do not occur in closed forests; we term these "native invaders."

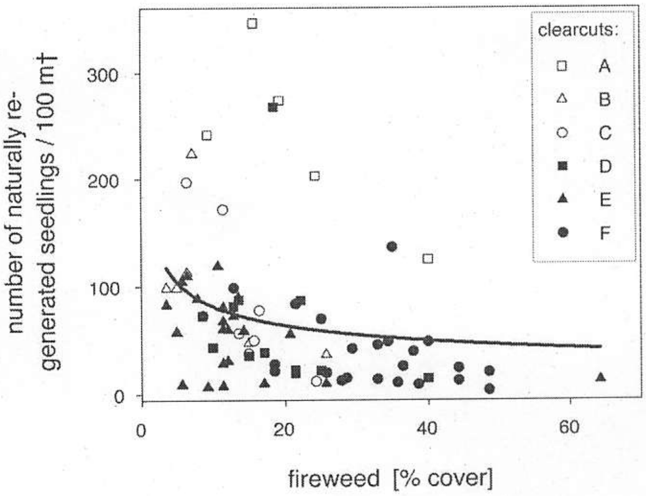

Figure 4. Relationship between cover of fireweed (*E. angustifolium*) and density of naturally regenerated seedlings of all tree species for 75- to 100-m^2 plots in six clearcuts (A–F). Each point represents total number of naturally regenerated seedlings in a 100-m^2 plot and mean cover of fireweed (average of estimations in seven 4-m^2 subplots). The line shows the power trend computed for all plots combined ($y = 268.1x^{-0.63}$; $R^2 = 0.18$; $P = 0.020$).

Available studies do not provide a clear picture about the relationship between understory vegetation and tree regeneration. Understory vegetation could have a positive impact on tree germination, survival, and growth by providing protection against frost heaving in saturated soils and from summer drought due to shading (Alexander 1987, Feller 1998). Alternatively, competition by herbaceous vegetation for nutrients often is considered to affect tree seedlings negatively; e.g., seedlings have been shown to have lower nitrogen uptake when grown in competition (Hangs et al. 2002). However, for the wet and cold ESSF zone, germination as well as initial growth of tree seedlings was not found to differ significantly between plots containing natural abundances of competing vegetation and plots in which competing vegetation was removed completely (Feller 1998).

There were no significant correlations between tree regeneration (density and growth) and measures of understory diversity (species richness, Shannon Index, and evenness). Thus, understory diversity itself does not affect tree regeneration. In addition, no significant relationship was detected between understory composition and density or growth of naturally regenerated seedlings when all tree species were pooled together (results of Mantel test for density, $P = 0.12$; for growth, $P = 0.30$). The same analysis broken down to each tree species separately revealed no significant relations to understory composition except for lodgepole pine. For this species, density ($P = 0.000$; $R = 0.16$) and growth of natural regeneration ($P = 0.000$; $R = 0.23$) were significantly correlated with understory composition. As shown before, this is no effect of diversity itself and therefore may be caused by single understory species.

With a mean frequency of 97% over all 75 plots, fireweed was by far the most abundant understory species on the investigated clearcuts. Its cover ranged from 4 to 64% with a mean of 20%. The relationship between fireweed cover and calculated density of naturally regenerated seedlings followed a negative power function with an $R^2 = 0.18$ (Figure 4). When tree regeneration was separated by species, this pattern was particularly clear for lodgepole pine ($R^2 = 0.25$) but was not significant for subalpine fire or interior spruce.

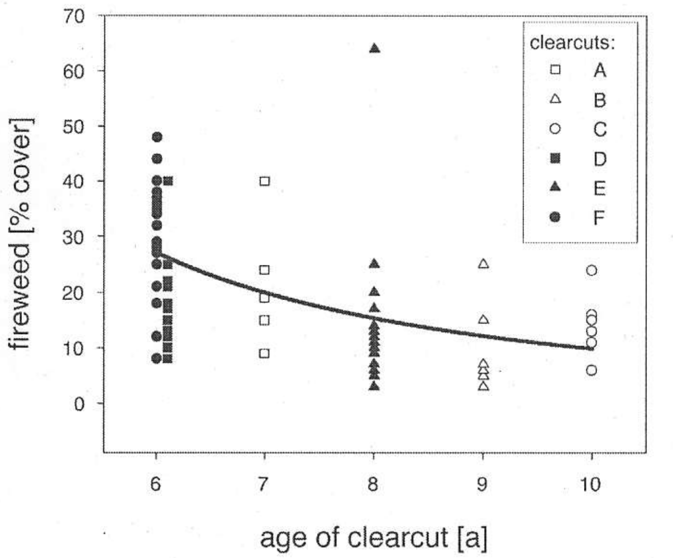

Figure 5. Relationship between cover of fireweed (*E. angustifolium*) and clearcut age. Each point is the mean cover for a 100-m^2 plot (average of estimations in seven 4-m^2 subplots); $n = 75$ plots on six clearcuts (A–F). Line shows the power trend computed for all plots combined ($y = 759.3x^{-1.97}$; $R^2 = 0.34$; $P < 0.0001$).

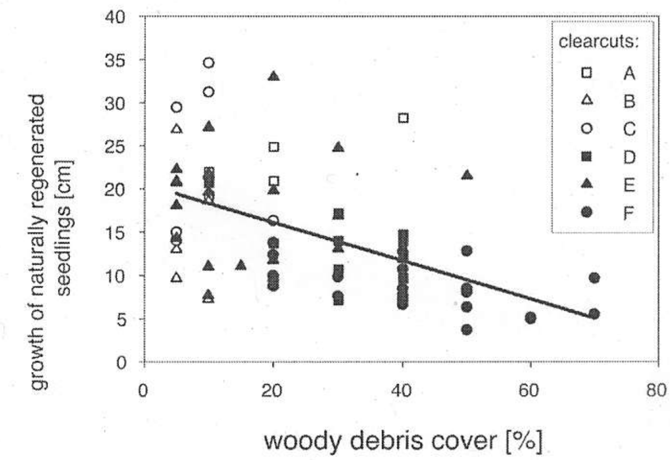

Figure 6. Relationship between growth of naturally regenerated tree seedlings and cover of downed woody debris for 75 plots on six clearcuts (A–F). Nearly all woody debris was laying flat on the ground. Each point represents mean growth (mean terminal shoot length for the 16 largest naturally regenerated individuals) and cover of downed wood in the plot. Line shows the linear relationship computed for all plots combined ($y = 20.5 - 0.22x$; $R^2 = 0.28$; $P < 0.0001$).

This likely reflects the fact that the latter two species are more shade tolerant than pine.

Growth rate of naturally regenerated seedlings was not adversely affected by competing fireweed (no significant regression), a result that is in accord with Feller (1998) and Bell et al. (2000). This suggests that tree regeneration is capable of escaping from the direct effects of aboveground competition without release treatments. Fireweed responds vigorously to high levels of resources (light and nutrients) immediately after clearcutting, but this represents only a transitional phase; we saw a significant decline in its abundance over the 6- to 10-year age range of clearcuts we studied (Figure 5). Thus, it appears that the competitive influence of fireweed might be relatively short-lived and that it is seedling establishment, rather than growth, that is reduced. However, if the time period for natural regeneration of tree seedlings on clearcuts also is short-lived, e.g., because of deteriorating seedbeds (e.g., Peters et al. [2005]), then the short-term impact of fireweed on regeneration density could have long-term consequences.

On the other hand, rapid reestablishment of herbaceous vegetation, such as fireweed, could help maintain site productivity by preventing nutrient loss during the time period after harvesting when decomposition is enhanced, soil moisture levels are elevated, and vegetative cover is relatively sparse. If opportunistic herbaceous species, such as fireweed, can rapidly take up available nutrients, they might act as a reservoir or buffer, subsequently releasing these resources for use by other species, as their cover declines. This corresponds to Vitousek's (1984) general theory of forest nutrient dynamics, which suggests that early successional species immobilize limiting nutrients quickly after a disturbance event, thus preventing them from export into groundwater and streams.

Woody Debris

Coarse woody debris is known to serve many important ecological roles in forest ecosystems (Harmon et al. 1986). Thus, there has been considerable concern that long-term reductions in coarse woody debris, which inevitably arises from forest harvesting, will have serious consequences for species diversity during all stages of forest development (e.g., Halpern and Spies [1995] and McComb and Lindenmayer [1999]). We found a negative linear relationship between cover of downed woody debris and seedling growth ($R^2 = 0.28$; Figure 6). Thus, woody debris presence is not intrinsically beneficial to natural tree regeneration; we believe that this is related to the quality and characteristics of downed wood found in clearcuts. Most woody debris observed in our study was lying flat on the floor, pressed down by heavy machinery. In this form, it does not offer protection against solar insolation, excessive transpiration, trampling, or browsing; rather, it actually limits spots for germination by its own coverage. Personal observations revealed almost no seedlings on top of woody debris. Germination on logs probably does not occur on the clearcuts, because the logs are exposed to full sunlight and therefore are highly desiccated. In addition, woody debris on the clearcuts consists mainly of small-diameter logs (mean diameter over all plots was 15 cm). The negative effect of woody debris on seedling growth also may be related to soil compaction below the woody debris. Thus, the potential benefits of woody debris are reduced by silvicultural practices; in turn, the lack of an appropriate size and condition of downed wood could negatively affect tree regeneration, and a variety of other biota, in the long term. This calls for improved management of downed wood on clearcuts.

Conclusions

Overall, we can conclude that natural regeneration in the studied harvested forests was quite successful, supplementing the planting densities of seedlings and increasing tree diversity. The success of natural regeneration varied spatially within the clearcuts. Density of natural regeneration declined (power trend) with increasing distance to the nearest forest edge while both density (subalpine fir and interior spruce) and growth (interior spruce) were superior in the southern portion of clearcuts. The ability to achieve stocking targets by means of natural regeneration was greatly reduced at distances greater than 70 m from a forest edge. Thus, natural regeneration can be relied on only if distance to seed source is kept short. However, small clearcuts lead to landscape fragmentation, which can have other negative effects on natural biodiversity of previously continuous forests. Hence, aggregating small openings or leaving patches of live trees as seed sources within larger clearcuts are promising management options.

The main effect of understory vegetation on tree regeneration was the negative effect of fireweed on density of tree seedlings, particularly the shade-intolerant lodgepole pine. However, growth of established seedlings was not hampered by competition from herbaceous vegetation. Downed wood left on clearcuts negatively impacted growth of seedlings. There can be little doubt, however, that maintenance of woody debris in forests can have important long-term benefits for biodiversity and maintenance of ecological processes.

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