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Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia, Canada

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Abstract

Tree seedling recruitment was monitored after various types of logging in mixed conifer and deciduous forests of northern British Columbia, Canada. Predicting tree seedling recruitment after disturbance is fundamental to understanding forest dynamics and succession and is vital for forest management purposes. Seedling recruitment success in multi-species northern latitude forests varied as a function of mature tree canopy cover, gap size and position in a gap. Recruitment was abundant within canopy gaps across a wide range of gap sizes (20–5000 m²), but recruit numbers dropped off rapidly under the closed forest canopy and in the open conditions of clearcuts. Inside canopy gaps, recruitment was similar by gap position in small gaps (<300 m²) but, in these northern latitude forests, exhibited a trend of increasing density from the sunny north to shady south end of larger gaps. This was true for all tree species regardless of their shade tolerance ranking. There was no evidence of gap partitioning by any of the tree species during the regeneration phase suggesting that adaptation to the subtleties of gap size during early recruitment are not well developed in these tree species. Favorable locations for emergence and early establishment of germinants were less favorable for growth and survival of established seedlings, i.e. the regeneration niches in these forests were discordant. Tree abundance and species diversity appears to be controlled more by differentiation among growth and survival niches than by the regeneration niches. From the perspective of forest management, abundant natural regeneration of all the dominant tree species of these mixed-species forests can be obtained after partial cutting. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

A major challenge for the disciplines of silviculture and ecology is to understand how community structure in forests develops over time following a disturbance. One of the first critical events after a disturbance is the recruitment of new tree seedlings. The observed patterns of recruitment are a result of a broad suite of factors including yearly variation in seed production,

seed dispersal opportunities (abundance, location and arrangement of parent trees), type and distribution of seedbeds and their favorability, microclimate, potential for vegetative reproduction and the abundance of seed or seedling predators (e.g. Farmer, 1997). A clear understanding of which stages in the recruitment process have the greatest consequences on recruitment of established seedlings (Clark et al., 1999) is required for development of models of forest dynamics, such as the model SORTIE (Pacala et al., 1996). SORTIE is being used to understand successional dynamics and to aid in the development of partial overstory removal

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logging prescriptions for the forests of British Columbia (Kobe and Coates, 1997; Wright et al., 1998a; Canham et al., 1999; LePage et al., 2000; Wright et al., 2000).

Clark et al. (1999) found that tree seedling recruitment studies usually fall into one of two broad categories: (1) those that examine whether tree populations are recruitment limited by low or uncertain seed supply and establishment; or (2) those that determine if recruitment is limited by lack of suitable microsites and factors that affect early seedling growth and mortality. Both categories of recruitment limitation have been observed to occur in the forests of northwestern British Columbia, Canada (Wright et al., 1998b; LePage et al., 2000). Few studies are of long enough duration to critically examine the various stages of recruitment limitation and their interactions (Clark et al., 1999; Turnbull et al., 2000).

The data on tree seedling recruitment in experimental treatments created by logging at the Date Creek silvicultural system study (Coates et al., 1997) is presented here. Tree seedling recruitment was followed over 5 years across a gradient of canopy openness from undisturbed closed forest to gaps of varying size, including different spatial positions within and outside those gaps, to the open conditions of clearcuts. Tree species diversity at Date Creek is among the highest in British Columbia (Meidinger and Pojar, 1991) with species ranging from very shade tolerant to shade intolerant (Kobe and Coates, 1997; Klinka et al., 2000). These tree species are dominant in early to late successional stands in forests throughout British Columbia, making Date Creek an excellent area in which to test the critical stages of recruitment limitation. Companion studies have demonstrated that partial logging creates a gradient of parent tree availability (and thus seed availability) and substrate types that in turn affect early recruitment abundance of the major tree species (Wright et al., 1998b; LePage et al., 2000). The range of gap sizes created at Date Creek (20–5000 m²) provides an environmental gradient that affects tree seedling growth and mortality rates (Coates, 2000).

This study is one in a series (Wright et al., 1998b; LePage et al., 2000) designed to explore recruitment dynamics in the temperate northern forests of British Columbia. The first broad objective of this study was

to provide a better understanding of how small- to intermediate-scale disturbance to the tree canopy affects recruitment of new tree seedlings. A number of hypotheses, not mutually exclusive are possible: (1) density of shade intolerant recruits increase as gap size increases (after Brokaw, 1985, 1987; Whitmore, 1989); (2) density of shade intolerant recruits vary with position inside or outside of the gap, especially at larger gap sizes; (3) the best gap size or gap position for early establishment of recruits might not be the best location for future seedling growth and survival, i.e. the regeneration niche is “discordant” (after Schupp, 1995). A second, more specific objective, was to combine results from this study with the earlier findings of the companion studies (Wright et al., 1998b; LePage et al., 2000) to gain a better understanding of which stages in the recruitment process most limit recruitment of established individuals.

2. Methods

2.1. Study site

This study is a component of the Date Creek silvicultural systems study (Coates et al., 1997), established in 1992, in northwestern British Columbia. The study is located approximately 21 km north of Hazelton and west of the Kispiox River within the 4000 ha Date Creek Research Forest (55°22' N, 127°50' W; 370–665 m elevation) operated by the British Columbia Forest Service. The study area is within the moist cold subzone of the Interior Cedar-Hemlock zone (ICHmc), a transitional zone between the interior and coastal areas of northwestern British Columbia. See Pojar et al. (1987) or Meidinger and Pojar (1991) for a description of this system of vegetation classification and Banner et al. (1993) for a detailed description of the ICHmc subzone.

Research sites were located in mature stands that originated from a fire in 1855 and in old-growth stands (300 years + since fire). Understories in these forests are typified by sparse shrub and herb development with a continuous layer of moss, dominated by red-stemmed feather moss (*Pleurozium schreberi* [Bird.] Mitt.), step moss (*Hylocomium splendens* [Hedw.] B.S.G.), knight's plume (*Ptilium crista-castrensis*

[Hedw.] and electrified cat's tail moss (*Rhytidiadelphus triquetrus* [Hedw.] Warnst.) (Banner et al., 1993). Soils on mesic sites are typically eluviated or Orthic Dystric Brunisols (Agriculture Canada Expert Committee on Soil Survey, 1987) developed on morainal parent materials, ranging in texture from loamy sand to clay loam with 5–10 cm thick Hemimor or Mormoder forest floors (Coates et al., 1997).

Hybridization of spruce in the study area is complex with individual trees rarely identified to species (Coates et al., 1994). Spruce trees in the study area are collectively called "hybrid spruce" and can be crosses of white spruce (*Picea glauca* [Moench] Voss), Sitka spruce (*P. sitchensis* [Bong.] Carr.) and occasionally, at higher elevations, Engelmann spruce (*P. engelmannii* Parry ex Engelm.).

Mature stands in the study area are a stratified mixture of coniferous and deciduous tree species. Western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) dominates with western redcedar (*Thuja plicata* Donn. ex D. Don), hybrid spruce, subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), amabilis fir (*Abies amabilis* Dougl. ex Forbes), lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), paper birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), and black cottonwood (*Populus balsamifera* ssp. *trichocarpa* Torr. & Gray). In the old-growth stands western hemlock dominates with minor components of western redcedar, subalpine fir and amabilis fir. Descriptions of these mature and old-growth stages can be found in Coates et al. (1997). Canopy trees average about 30 m tall, but there are abundant intermediate and understory trees, resulting in full canopies to near ground level.

The dominant tree species of these forests are good seed producers with seed crops every year and mast crops at 2–6 year intervals (Burns and Honkala, 1990; Klinka et al., 2000). Subalpine fir has the heaviest seed (76 seeds/gm) and paper birch the lightest (3040 seeds/gm). Seed weights of the other species range from 200 to 570 seeds/gm. Seeds of these species are primarily wind-dispersed. Seed dispersal distances can be a kilometre or more (paper birch), but most seed from trees on clearcut edges falls within 100–400 m of the parent trees (Klinka et al., 2000). Dispersal distances of seedlings around parents was much smaller in partially cut forests of the study area (LePage et al., 2000) suggesting shorter seed dispersal

distances in partially cut forests than at clearcut edges. Most of the species can regenerate on a wide range of seedbeds but tend to do best on mineral soil, decaying wood and other organic substrates. Some species also have vegetative reproduction: aspen from root suckers and stump sprouts, cottonwood from branch fragments and stump sprouts, and birch from resprouting stumps. Virtually all aspen reproduction in the study area is from root suckers (Haeussler et al., 1990). Lodgepole pine in the study area has serotinous cones that require high temperatures (usually fire) to open and release seed. After logging, pine cones on the ground can slowly open over time and release viable seed.

The Date Creek silvicultural systems study has four tree removal treatments, each replicated four times, in a randomized block design. Each of the 16 treatment units was about 20 ha in size. The blocking factor was a combination of stand age and ecological site type: 1) mature stands, mesic site type; 2) mature stands, mesic–submesic site types; 3) mature stands, mesic–subhygric site types and; 4) old-growth stands, mesic site types.

The four treatments were no removal (the undisturbed forest), light and heavy partial cutting and clearcutting. In the light partial cutting, about 30% of the stand volume was removed by cutting either single stems or small gaps (3–10 trees). In the heavy partial cutting, about 60% of stand volume was removed. Here, the cutting pattern used both large gaps (500–5000 m² in size), evenly distributed across the treatment units, and either single tree or small gaps (<300 m²) in the forest matrix between the larger gaps. The distribution of gap sizes created by each partial cutting treatment and the gap size distribution within the undisturbed forest is presented in Coates and Burton (1997). In the clearcut treatment all stems were removed except for scattered residual deciduous trees, mostly trembling aspen and paper birch.

Logging of mature experimental blocks occurred in summer and fall of 1992 and logging of the old-growth experimental block occurred in the winter of 1992/1993 on 1–2 m of snow. Hence, there was generally less disturbance to the forest floor in the old-growth experimental block. The experimental design and the pre- and post-treatment stand attributes are fully described in Coates et al. (1997).

2.2. Gap selection

In spring 1993, logging-created canopy gaps were identified at approximately 63 evenly spaced grid points (50 by 50 m) within each light and heavy partial cutting treatment unit (eight in total). If a gap could be seen from the grid point then it had to meet two criteria to be enumerated: (1) the presence of a uniform closed canopy around its perimeter (only broken by skid trails) and (2) average moisture and nutrient conditions—the mesic site series (see Banner et al., 1993).

The size of each enumerated canopy gap (not extended gap) was calculated as the area of an ellipse described by Runkle (1992). The long line of the ellipse was the longest line that could be run from canopy edge to canopy edge inside the gap. The short line of the ellipse was the longest line that could be run from canopy edge to canopy edge perpendicular to the long line.

From this population, individual gaps were randomly selected in roughly equal numbers from each replicate of the two partial removal treatments. A total of 109 logging created gaps were selected in spring 1993 for this study. Over time some gaps were damaged by windthrow or other events so that by the 5th year assessment only 86 gaps remained: 45 were 20–300 m² in size; 12 were 301–1000 m²; and 29 were 1001–5000 m². The vast majority of natural gaps in these forests are <300 m² in size (Coates and Burton, 1997).

2.3. Recruit sampling

Seedling recruitment was assessed in circular 0.25 m² quadrats. Twenty quadrats were established in each replicate of the clearcut and undisturbed forest treatment units. The number of recruitment quadrats in gaps varied with size and gap position (Fig. 1). Each canopy gap was divided into four sections or positions along the north–south line. There were three positions inside the gap (northern, middle and southern thirds) and a gap edge position—quadrats up to 16 m into the closed forest off the north and south ends of sample canopy gaps. Thus the term “gap position” refers to areas both inside and outside of a distinct canopy gap.

Recruitment quadrats were assessed in the fall of 1994 and early spring of 1996 and 1998, just before

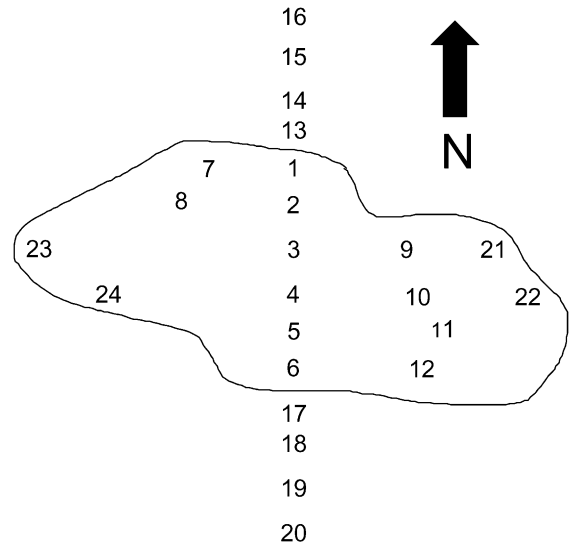


Fig. 1. Experimental layout and number of 0.25 m² recruitment quadrats in all experimental gaps by gap size and gap position. The depicted irregular shaped large gap is an example to convey one possible spatial arrangement of recruitment quadrats. The length of the longest north to south line that could be run from canopy edge to canopy edge was used to spatially orient quadrats within and outside each experimental gap. Quadrats 1–6 were located on the north–south line, with quadrat 1 always to the north. Recruitment quadrats were assigned to the four gap positions as follows: north = 1, 2, 7, 8; middle = 3, 4, 9, 10 (in >1000 m² gaps an additional four quadrats [21–24] were added to the middle position, see below); south = 5, 6, 11, 12; and gap edge understory = 13–20. Gaps <1000 m² have 20 quadrats (1–20). Gaps >1000 m² have 24 quadrats (1–24). In gaps <300 m² quadrats 1 and 6 are 1 m from the canopy edge into the gap. In gaps >300 m² quadrats 1 and 6 are 2 m from the canopy edge into the gap. Quadrats 2–5 are equally spaced along the N–S line (i.e. length of N–S line/5 = distance to quadrat 2 from canopy edge and the distance between quadrats 2, 3, 4, and 5). Quadrats 7–12 are located half-way to the furthestmost canopy edge from quadrats 1–6, respectively (quadrats 7–12 can be either to the east or west of the N–S line depending on the distance to the canopy edge). Quadrats 13–16 and 17–20 are 2, 4, 8, and 16 m into the canopy from the north and south canopy edges, respectively. Quadrats 21–22 and 23–24 (only in gaps >1000 m²) are located 2 m from the canopy gap edge to the far east and west of quadrats 3 and 4, respectively.

onset of current year germination. In each quadrat individual stems by species were counted (except amabilis and subalpine fir which were identified to genus only, hereafter referred to as *Abies*) and origin—new sexual or vegetative stem since logging or advance regeneration from prior to logging. A few birch stump sprouts were recorded but no aspen or

cottonwood stump sprouts were observed. Stems of advance regeneration (of which there were few) and stems from stump sprouts were not included in this analysis.

Stem counts of western hemlock were undertaken in a slightly different way at each assessment period. Hemlock is a prolific seed producer (Klinka et al., 2000) and regenerates well on a variety of seedbed substrates in the study area (LePage et al., 2000) resulting in the continuous recruitment of high numbers of germinants every year. However, in most years mortality rates of hemlock germinants are high as well. At the 1st assessment (taken at the end of the 2nd growing season) all individual hemlock stems were counted—hence the youngest had survived one summer. At the 2nd assessment (3rd year, taken in the spring after three summers and three winters) only established hemlock seedlings (3 cm or taller) were counted. Most hemlock seedlings >3 cm have survived at least two full years since germination and these were considered established (after Zasada et al., 1992; Duchesneau and Morin, 1999). This greatly increased sampling efficiency as there were abundant one year germinants present (<3 cm high) at the 2nd assessment. During the fifth growing season (summer 1997), a summer with plentiful rainfall, high numbers of western hemlock germinants survived to the end of the summer (D. Coates, personal observation) and many were still present at the 3rd assessment in spring 1998. I decided to break this 5th year hemlock recruit data set into two groups: one year olds or small seedlings (<3 cm high), and established seedlings (3 cm or taller) to examine how recruitment results can vary depending on timing of assessment or size of recruits counted.

2.4. Analysis

A randomized block split-split-plot design was employed to study the influence upon recruit density (# per m²) of gap size, gap position and tree species. Main plots in this design were small gaps (20–300 m²), medium gaps (301–1000 m²) and large gaps (1001–5000 m²). The gap positions (north, middle and southern thirds inside gaps and understory off the gap edge) formed the first split-plot, with the different tree species providing the second split-plot. An individual gap was considered the experimental unit in this

design and individual recruitment quadrats were sub-samples.

Analyses of variance was performed on least squared means using the MIXED procedure from SAS (SAS Institute Inc., 1987). The mixed model was used because factors were both fixed (gap size, gap position and tree species) and random (block and its interactions) (Littell et al., 1996). A least significant difference (LSD) comparison method, with a Bonferroni correction to control for Type I error inflation (Milliken and Johnson, 1992) was used to test for differences among size classes and gap positions.

The gap edge position caused problems with analysis of the main effects (the three size classes of gaps), so recruitment quadrats in the edge position were excluded so that response means for individual gaps, and the mean for all gaps within a size class, properly represented average conditions inside the gap. Including the gap edge position data in the analysis of the main effects would have artificially lowered the mean for individual gaps as gap size increased. For statistical tests of gap position effects all recruitment quadrats were retained.

The clearcut treatment (representing full open conditions) and the undisturbed forest treatment (representing closed canopy conditions) were analyzed separately as a randomized block split-plot design because they contain no analogous treatments to gap position. In this analysis, open and closed canopy conditions were the main plots and recruit tree species the split-plots. Values from this analysis and from the split-split-plot design above were used to manually calculate pairwise comparisons between full open conditions and large gaps and between small gaps and the closed canopy of the undisturbed forest for each tree species. *P*-values <0.025 (α level 0.05/2) were deemed significant.

3. Results

Recruitment in the open conditions of large clearcuts was poor compared to gaps for all tree species except trembling aspen and black cottonwood (Fig. 2). Recruitment on the undisturbed forest floor under a closed canopy was poor over the 5-year period of the study and restricted to the most shade tolerant species, even though parent trees of all species were well

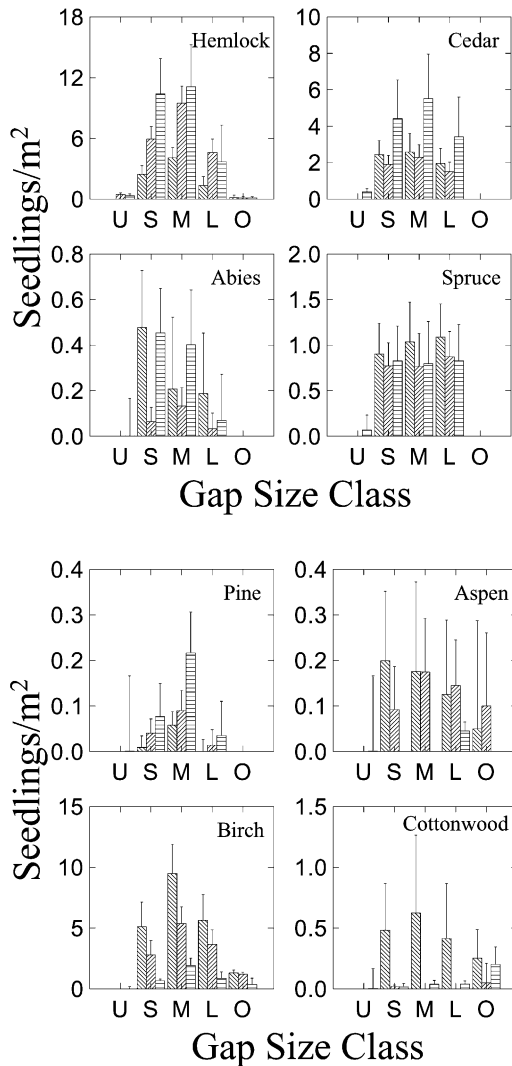


Fig. 2. Average density of recruits by opening type and year of assessment. U = forest understory; S = small gaps (10–300 m²); M = medium gaps (301–1000 m²); L = large gaps (1001–5000 m²); O = full open; ▨ = 2nd year; ▩ = 3rd year; ▪ = 5th year. At the 1st assessment all hemlock seedlings were counted regardless of size. Second and 5th year assessment data for hemlock presents established seedlings only (3 cm or taller). Error bars represent one standard error of the mean.

represented (Coates et al., 1997). Recruitment of most tree species, regardless of their shade tolerance ranking was by far the best in canopy gaps (Fig. 2).

Total recruitment (all tree species combined) inside canopy gaps was little affected by the range of gap

Table 1

Randomized block split-split-plot ANOVA *P*-values from seedling density over all tree species

	Gap edge quadrats removed	Gap edge quadrats present
Size class	0.2313	–
Position	0.0888	0.0009**
Size class × position	0.3276	0.1311
Species	0.0003**	0.0004**
Size class × species	0.2532	0.2780
Position × species	0.0114**	0.0001**
Size class × position × species	0.2235	0.1699

** Significant at *P* < 0.05.

sizes examined in this study (*P* = 0.2313, Tables 1 and 2). There was weak evidence for an effect of gap position on total recruitment within gaps (*P* = 0.0888, Tables 1 and 2—gap edge quadrats removed). There were clearly major differences among the tree species in recruitment density after five growing seasons (*P* < 0.0004, Tables 1 and 2); however, within a species there was little effect of gap size on recruitment density (Tables 1 and 2).

Western hemlock and paper birch were the most abundant species in gaps 5 years after logging (4–12 seedlings/m²), followed by western redcedar (3–6 seedlings/m²). All remaining tree species had similar but much lower densities than the three dominant species (<1 seedlings/m²; Fig. 2). The overall results across all four experimental blocks are presented in Fig. 2. The results were consistent in both the mature and old-growth forest types with a few notable exceptions. First, no birch, pine, aspen and cottonwood recruits were found in the old-growth treatment units reflecting the near absence of parent trees of these species in the old-growth forest (Coates et al., 1997). Second, hemlock recruit density in old-growth medium and large gaps was much higher than in the mature forest. Finally, *Abies* recruitment was much higher in the old-growth than in the mature stands, reflecting the high density of *Abies* parents (especially amabilis fir) in old-growth stands of the study area.

Among individual species, there was little statistical evidence of differences in 5th year recruit density in the north, middle and south ends of gaps (*P* > 0.27, except hemlock, *P* = 0.0949, Tables 1 and 2). The

Table 2

Pairwise contrasts for seedling density in individual tree species or species group analyzed separately^a

	Gap edge understory position not included							
	Redcedar	Hemlock	<i>Abies</i>	Spruce	Pine	Birch	Aspen	Cottonwood
Size class	0.5041	0.3161	0.2687	0.9969	0.2410	0.0950	0.2634	0.7838
Position	0.7169	0.0949	0.5130	0.2668	0.3931	0.3692	0.6257	0.6659
Size class × position	0.5433	0.2840	0.4041	0.3936	0.2656	0.4651	0.6224	0.3919
Large vs. medium	0.2761	0.2019	0.2558	0.9450	0.1095	0.1270	0.2253	0.9485
Medium vs. small	0.5323	0.8923	0.8434	0.9447	0.1885	0.0373	1.0000	0.6429
Large vs. small	0.4514	0.2011	0.1331	0.9981	0.6135	0.3772	0.1393	0.5305
	Gap edge understory position included							
Position	0.0545	0.0050**	0.7923	0.0288	0.2959	0.0856	0.5908	0.5685
Size class × position	0.3475	0.2688	0.7338	0.4581	0.1756	0.2399	0.5253	0.4499
Gap edge vs. south	0.0155	0.0010**	0.9450	0.0139	0.0955	0.0165	0.3422	0.4659
Middle vs. north	0.7201	0.2837	0.3464	0.0934	0.5049	0.7386	0.3414	0.3172
Middle vs. south	0.7941	0.4037	0.7699	0.7683	0.3391	0.4029	0.3414	0.5542
North vs. south	0.5395	0.0749	0.5075	0.1514	0.1232	0.2530	1.0000	0.6674

** Significant at $P < 0.05$.

^a To control alpha inflation, P -values of pairwise comparisons had to be <0.0167 for size class or <0.0125 for gap position to be deemed significant (α level $0.05/\text{number of comparisons}$). Recruitment quadrat sample sizes for contrasts are: large gaps (24); medium and small gaps (20); north, middle and south positions in small and medium gaps (4); middle position in large gaps (8); gap edge position (8).

slight effect of gap position on western hemlock recruitment inside gaps appears to decrease with time (3rd year, $P = 0.0358$). Recruit density was generally lower in the gap edge position under the canopy (Fig. 3).

Even though there were few differences from a statistical perspective by position inside a canopy gap, there do appear to be clear trends in the data. First, in medium and large gaps (those $>300 \text{ m}^2$) there is a consistent trend of decreasing seedling density from the shady south side to the sunny north side of gaps (Fig. 3). This trend is clear for all tree species regardless of their shade tolerance ranking with the exception of *Abies*. Second, the effect of gap position was least consistent for trembling aspen. Third, the density of the most shade intolerant deciduous trees (aspen, birch and cottonwood) steadily decreases with time in gaps (Fig. 2). However, lodgepole pine, a shade intolerant conifer, is slowly increasing, likely as a result of serotinous cones slowly opening over time and releasing viable seeds. The more shade tolerant conifers, especially hemlock and cedar, increase in density with time. Fourth, gap position was least important in small gaps (up to 300 m^2), however, there is clearly

increased recruitment when a small opening is created in a forest stand compared to the undisturbed forest (Figs. 2 and 3).

Western hemlock was by far the most abundant tree species present among the canopy trees, or parent trees, (Coates et al., 1997), and this was reflected in hemlock being the most abundant tree species among the new recruits (Fig. 2). Hemlock had continuous recruitment of high numbers of germinants every year. This phenomenon makes interpretation of hemlock recruitment success across the gradient from closed forest, to varying sized gaps, to full open conditions of clearcuts difficult if recruit size (or age) is not considered (Table 3; Figs. 4 and 5).

Density of small western hemlock recruits ($<3 \text{ cm}$ tall) was high at the 5th year assessment except in the open conditions of clearcuts (Fig. 4). Density was greatest under the closed canopy (63 stems/m^2), decreasing steadily with increasing gap size (21 stems/m^2 in large gaps) (Fig. 4). The most shaded positions (gap edge understory and the south end of gap positions) were the best locations for small hemlock recruits (Fig. 5).

Established hemlock (3 cm or taller) have a much different recruitment pattern than small hemlock

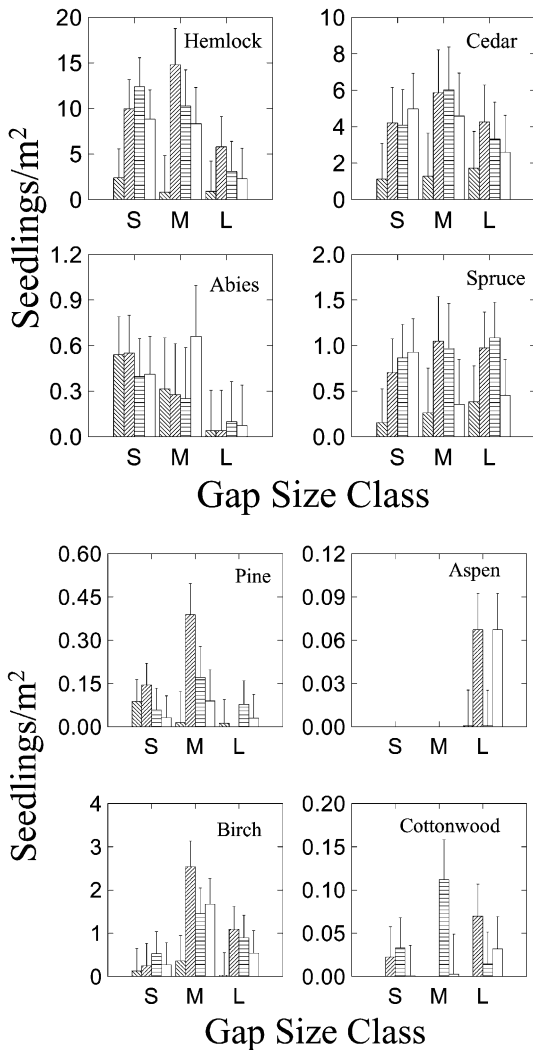


Fig. 3. Fifth year density of recruits by gap size class. S = small gaps (10–300 m²); M = medium gaps (301–1000 m²); L = large gaps (1001–5000 m²) and gap position (from left to right, Gap edge = ▨, South = ▩, Middle = ▧, North = □). Hemlock data is for established seedlings only (3 cm or taller). Error bars represent one standard error of the mean.

(Table 3, Figs. 4 and 5). Medium sized gaps had the highest recruitment of established hemlock and the most shaded locations, favored by small hemlock recruits, were no longer the most favored positions for established hemlock seedlings. Many small germinants of hemlock can be found yearly in the shaded forest understory, however, their chance of longer-

Table 3
Fifth year western hemlock recruitment by seedling type^a

	Hemlock small	Hemlock established	Hemlock all
Gap edge quadrats removed ^b			
Size class	0.0071**	0.3161	0.0066**
Position	0.0197**	0.0949	0.0163**
Size class × position	0.4476	0.2840	0.3219
Large vs. medium	0.2455	0.2019	0.1298
Medium vs. small	0.0589	0.8923	0.1021
Large vs. small	0.0026**	0.2011	0.0023**
Gap edge quadrats present ^b			
Position	0.0032**	0.0050**	0.0009**
Size class × position	0.0297**	0.2688	0.0171**
Gap edge vs. south	0.0005**	0.0010**	0.0001**
Middle vs. north	0.8572	0.2837	0.8485
Middle vs. south	0.0046**	0.4037	0.0045**
North vs. south	0.0062**	0.0749	0.0034**

** Significant at $P < 0.05$.

^a Hemlock seedlings are designated as small (<3 cm tall); established (3 cm or taller) and “all” with all representing small and established seedlings combined. To control alpha inflation, P -values of pairwise comparisons had to be <0.0167 for size class or <0.0125 for gap position to be deemed significant (α level 0.05/ number of comparisons).

^b Recruitment quadrat sample sizes for contrasts are: large gaps (24); medium and small gaps (20); north, middle and south positions in small and medium gaps (4); middle position in large gaps (8); gap edge position (8).

term survival appears to be low based on the low numbers of established hemlock over time recorded in the forest understory (see 3rd and 5th year assessments for hemlock in Fig. 2).

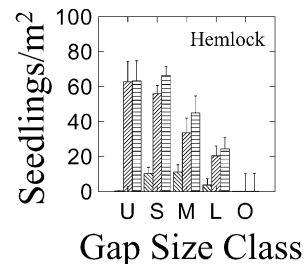


Fig. 4. Fifth year density of western hemlock recruits by seedling class (established ▨; small ▩ and total ▧) and opening type. U = forest understory; S = small gaps (10–300 m²); M = medium gaps (301–1000 m²); L = large gaps (1001–5000 m²); O = full open. Error bars represent one standard error of the mean.

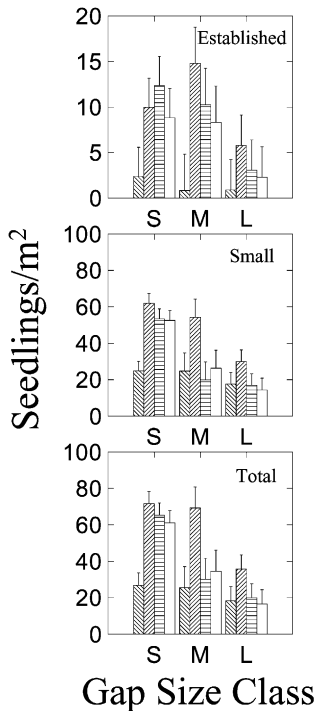


Fig. 5. Fifth year density of western hemlock recruits by seedling class (established, small and total) and gap position. Gap positions from left to right are: Gap edge = ▨, South = ▩, Middle = ▤, North = □. Error bars represent one standard error of the mean.

4. Discussion

Five years after logging tree seedling recruitment was abundant in canopy gaps of the interior cedar-hemlock forest, less abundant under the canopy adjacent to gaps and far less abundant in the understory of the undisturbed forest, except for the continuous turnover of western hemlock germinants. Few of these small hemlock germinants survive under the closed forest canopy to become established seedlings. Recruitment was also poor in the full open conditions of large clearcuts compared to gaps. Only the shade intolerant deciduous tree species were common at the center of clearcuts. Farmer (1997) in a review of seedling recruitment in temperate and boreal forests indicates natural regeneration is often low in large clearcuts due to a combination of unfavorable microclimate and lack of seed source.

Recruit density of individual tree species varied widely in gaps. This was most likely a reflection of

differences in parent tree abundance (Coates et al., 1997; LePage et al., 2000) but could also have been influenced by tree seed production during the study period and the different modes of regeneration among the species. There was, however, little evidence of species partitioning across the range of gap sizes examined (20–5000 m²) during the early regeneration phase (see Ricklefs, 1977; Leibold, 1995), despite the wide range of shade tolerances among the studied tree species (Kobe and Coates, 1997; Klinka et al., 2000). All tree species responded to the range of gap sizes and gap positions (and thus environmental gradients) in a similar manner with no one species showing a clear preference (or lack of preference) for a given gap condition. This finding is consistent with results obtained by Gray and Spies (1996) in Pacific Northwest US forests suggesting that regeneration adaptations to the subtleties of gap size are not well developed in the tree species of temperate western forests. In contrast to early regeneration success, there does appear to be evidence of gap partitioning based on gap size due to mortality of new recruits. This was most evident for trembling aspen where after 5 years no recruits remained in small and medium gaps.

There was also little evidence to support the hypothesis that the regeneration of shade intolerant species continuously increases as gap size increases (after Brokaw, 1985, 1987; Whitmore, 1989). Paper birch, one of the least shade tolerant species in these forests (Kobe and Coates, 1997) had greatest densities in medium sized gaps (300–1000 m²) and lower densities in large and small gaps. Recruitment of hybrid spruce was completely unaffected across the range of gap sizes examined ($P = 0.9969$), demonstrating a wide amplitude in habitat for regeneration of this tree of intermediate shade tolerance. It is difficult to draw conclusions about the remaining shade intolerant tree species—pine, aspen and black cottonwood—because of low numbers and disparate regeneration characteristics. Aspen regeneration is mainly of root sucker origin while much of the cottonwood regeneration was from stem and branch fragments (Haeussler et al., 1990; P. Bartemucci, personal observation), hence initial distribution of these species is more strongly tied to parent tree location and soil surface disturbance levels than to gap size. Lodgepole pine has serotinous cones, thus regeneration of pine is not favored by partial cutting, however, densities have

increased over time in all gap sizes, presumably as cones open on the ground. Nevertheless, I could find no evidence that regeneration of any of these tree species increased with gap size.

Recruit density varied in a consistent manner across the environmental gradients created by canopy gaps suggesting intraspecific species partitioning by gap position (for all species except the two *Abies* and aspen). Germination and early survival rates were lowest in the exposed north end of gaps and increased steadily towards the shaded end of gaps. My results show a clear trend among the tree species that is little affected by their shade tolerance ranking—increasing density from the north to south ends of gaps, especially in medium and large gaps receiving direct radiation at the north end. These spatial trends in seedling establishment were less apparent in small gaps (<300 m²) where light levels were more uniform across the entire gap area. Higher rates of germination in shaded microsites have been reported for many western conifer species (Garman and Orr-Ewing, 1949; Day, 1964; Alexander, 1984; Burton, 1997; Farmer, 1997). The early recruitment pattern was still evident 5 years after logging.

Results from this and a companion study (Wright et al., 1998b) support the hypothesis that successful regeneration of shade intolerant species varies with gap position, especially in larger gaps. However, the same was also true for two of the most shade tolerant tree species—western hemlock and western redcedar, a result that conflicts with the hypothesis that density of shade tolerant trees will not vary with gap size or gap position. The two shade tolerant *Abies* species appeared to regenerate equally well at all gap positions but showed a clear preference for shadier small and medium sized gap. The effect of gap position was not consistent for light-demanding trembling aspen, perhaps because recruits were mostly from root suckering and their production was less influenced by the environmental gradients created by gap position.

The similar gap position partitioning by most tree species can result in an interesting trade-off in the regeneration pattern of these tree species over time: the best place for germination and early establishment is not necessarily the best place for survival and growth. Even though most light-demanding species regenerated well in the shaded south position of gaps

and in small gaps, their probability of mortality is high based on their low growth rates in these shaded low light environments (i.e. Kobe and Coates, 1997; Coates and Burton, 1999). The regeneration niches in these interior cedar-hemlock forests are discordant, in the sense of Schupp (1995). Favorable locations for emergence and early establishment are less favorable for growth and survival of established seedlings. Tree abundance and species composition appears to be controlled more by differentiation among growth and survival niches than by the regeneration niches.

Microclimate conditions appear to strongly influence regeneration success in clearcuts. Recruitment was poor in clearcuts despite the presence of a diverse mix of favorable seedbeds (similar to gaps, LePage et al., 2000) and the close proximity to a seed source (100–200 m). The low seedling densities observed after 5 years in the clearcut were likely because of high mortality of germinants due to lack of protection from heat and drought. Similar microclimate effects were also observed in exposed positions of gaps >300 m².

5. Conclusions

My study has clearly shown that recruitment patterns of established seedlings can vary considerably from that of new germinants (hemlock data). This suggests timing of recruitment assessments can play a major role in interpretation of recruitment patterns in mixed forests. In many ways, the number and spatial distribution of established seedlings is a required input for modeling stand dynamics over time in mixed-species forests. Short term recruitment studies (<2 years) might provide misleading data for spatially explicit small-scale disturbance succession models.

Seedling recruitment over time in forests is a reflection of the interaction between seed source availability or fecundity, conditions for early seedling establishment, type and distribution of seedbeds—and their favorability—and factors that affect early seedling growth and survival. Recruitment of all tree species in the temperate interior cedar-hemlock forests was abundant over a wide range of gap sizes. Even lodgepole pine, a species with relatively low numbers of parent trees and whose cones open slowly over time on the ground, had densities of 300–1000 stems/ha in

gaps. Stocking of gaps by all tree species was adequate for forest management purposes. From the perspective of forest management these northern forests are not recruitment limited following partial cutting (this study and LePage et al., 2000). Suitable seedbed substrates and the required conditions for subsequent growth and survival are required for the recruitment of established seedlings. The importance of these two factors in recruitment success can vary as a result of management practices.

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