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# Conifer seedling response to northern temperate forest gaps

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**Abstract**

Studies of gap dynamics have contributed significantly to our understanding of the role of small-scale disturbance in forest ecosystems, but have been little used by foresters for predicting tree responses to partial cutting. Fifth year growth and survival of five commonly planted tree species were contrasted in canopy gaps (single-tree to 5000 $m^2$), in the forest understory and in the open conditions of a clear-cut. There were strong and consistent trends in growth response among the tree species as gap size increased. Growth of all the species increased rapidly from small single-tree gaps to about 1000 $m^2$ gaps, but thereafter, showed little change up to 5000 $m^2$. Tree size and current growth rates for all species were highest in full open conditions. Performance of lodgepole pine (*Pinus contorta*), the most light-demanding species, exceeded that of all other species in large gaps (1001–5000 $m^2$) and clearcuts. In large and medium gaps (301–1000 $m^2$), the largest trees of all species were found in the middle gap position and there was little difference between the sunny north and shady south positions, except for lodgepole pine which clearly grew poorly in the south position. Total size and growth rates of all species were nearly identical in small gaps (20–300 $m^2$) and again in the forest understory. The light advantage expected off the north end of high latitude gaps was not a benefit for tree growth, suggesting that below-ground effects of canopy edge trees have an important influence on seedling growth in these forests. Differences in mortality among the tree species were evident, with the most light demanding species having the greatest early mortality in shaded areas of medium gaps, in small gaps and in the forest understory. Careful matching of tree species to gap size and gap position can minimize early mortality and maximize growth rates. Opening sizes need not be very large (0.1–0.2 ha or larger) in order for most tree species to achieve growth rates similar to those found in the open conditions of clearcuts. © 2000 Elsevier Science B.V. All rights reserved.

*Keywords:* Gap size; Growth; Position in gap; Planting; Regeneration; Small-scale disturbance; Silvicultural system

## 1. Introduction

During the 1970s and 1980s the majority of forest regeneration practices in British Columbia followed an agricultural model. Forest researchers examined techniques for establishing and promoting early growth of planted seedlings after clearcutting (Walstad and Kuch, 1987; Lavender et al., 1990), followed by growth and yield studies that emphasized single-aged and single-species growth with no overstory canopy influences (e.g. Ek et al., 1988). In recent years this agricultural forestry model has been questioned. The emphasis has shifted to a more ecologically and socially-based approach to forest management that requires greater structural diversity be maintained in managed stands in order to meet a broader range of ecological and social values (e.g. Gilmore, 1997;

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Kohm and Franklin, 1997). As managed forest stands become more complex, foresters will require more complex predictive models of forest regeneration and growth that are capable of accommodating variable levels of canopy retention.

Tree regeneration occurring inside canopy gaps after a disturbance has been studied worldwide (see reviews by Bazzaz and Pickett, 1980; Denslow, 1987; Platt and Strong, 1989). Population- or community-level responses within gaps of varying size are often used to explain how tree species diversity is maintained in forests subject to small-scale disturbance, a process referred to as 'gap partitioning' (e.g. Ricklefs, 1977; Denslow, 1980). While gap dynamics studies have contributed significantly to our understanding of the role of small-scale disturbance in forest ecosystems, they have been little used by foresters to predict tree responses following partial cutting (Coates and Burton, 1997).

In high latitude northern forests, position inside a gap can have considerable effect on resource levels (such as light availability; see Canham et al., 1990) and microclimate conditions (e.g. soil temperature), especially along the north-south axis. Such environmental heterogeneity should result in differential success of seedling establishment and subsequent growth (Bazzaz, 1984). Gap size and gap position effects on early tree growth have rarely been experimentally tested in high latitude forests (but see Kuuluvainen, 1994).

Relying solely on natural regeneration to separate the effects of gap size and position is problematic. Many factors influence seedling establishment following canopy disturbance. Parent tree proximity and abundance (Ribbens et al., 1994), seedbed substrate (Garman and Orr-Ewing, 1949; Prochnau, 1963; Day, 1964; Putz, 1983; Lawton and Putz, 1988; Stewart et al., 1991; Wright et al., 1998a), presence of seed consumers and dispersers (Schupp, 1988; Schupp et al., 1989) and climatic and microclimatic variability (Waldron, 1966; Hennessey, 1968; Noble and Alexander, 1977, 1984) all cause dramatic spatial and temporal variation in seedling recruitment. Planted trees can be used to avoid many of the stochastic events surrounding natural seedling establishment.

Partial cutting creates gradients of canopy influence that can affect seedling growth in many ways. Studies that examine tree growth responses within gaps (of varying size and configuration) and within the adjacent forest matrix can form one basis for tree species selection following partial cutting. This study was specifically designed to address four questions. (1) How does gap size affect the growth of tree seedlings in high latitude forests? (2) Are gap size and gap position good predictors of tree growth? (3) How is growth of planted trees affected by position inside and outside of gaps in high latitude forests? (4) Do these responses vary with the shade tolerance rankings of tree species?

## 2. Methods

This study is a component of the Date Creek silvicultural systems study (Coates et al., 1997), established in 1992, in northwestern British Columbia, Canada, approximately 21 km north of Hazelton, west of the Kispiox River (55°22′N, 127°50′W; 370–665 m elevation). Date Creek 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 detailed description of the ICHmc subzone. Mature forests (140 years since wildfire) in the area are dominated by a mixture of conifer and deciduous tree species. Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) dominates, in mixture with western redcedar (*Thuja plicata* Donn. ex D. Don), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), lodgepole pine (*Pinus contorta* var *latifolia* Engelm.), hybrid spruce [the complex of white spruce (*Picea glauca* (Moench) Voss), Sitka spruce (*P. sitchensis* (Bong.) Carr.) and occasionally Engelmann spruce (*P. engelmannii* Parry ex Engelm.)], paper birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), and black cottonwood (*Populus balsamifera* ssp. *trichocarpa* Torr. and Gray). Amabilis fir (*Abies amabilis* Dougl. ex Forbes) is found at higher elevations in the study area. In the old-growth stands (300 years+ since fire), 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 LePage (1995) and Coates et al. (1997). Canopy trees averaged about 30 m tall, but there were abundant intermediate and understory trees, resulting in full canopies to near ground level.

Three harvesting treatments and a control (in approximately 20 ha treatment units) were replicated four times (16 units in total), applied in a randomized block design, with blocking factor being ecological site type and age of forest (mesic 140 years; mesic-submesic 140 years; mesic-subhygric 140 year; mesic 350 year). The treatments included a control (undisturbed forest), light and heavy partial cutting and clearcuts. In the light partial cutting treatment, approximately 30% of the stand volume was removed by cutting either single stems or small groups (3–10 trees). In the heavy partial cutting treatment, approximately 60% of stand volume was removed. The cutting pattern utilized both large gaps (0.1–0.5 ha in size), evenly distributed across the treatment units and either single tree or small gaps in the forest matrix between the large gaps. In the clearcut treatment units all stems were removed except for scattered residual deciduous trees, mostly trembling aspen and paper birch. Cutting treatments and the pre- and post-treatment stand attributes are fully described in Coates et al. (1997).

### 2.1. Gap selection

In spring 1993, logging-created canopy gaps were enumerated at approximately 63 evenly spaced grid points (50 by 50 m) within each light and heavy partial cutting treatment unit. Gaps were enumerated if they could be seen from the grid point, if they had an evenly distributed canopy around their perimeter and if they were dominated by the mesic site series (Banner et al., 1993). From this population of openings, individual gaps were randomly selected in roughly equal numbers from each treatment unit. A total of 109 gaps were selected: 76 less than 1000 $m^2$ in size, 33 between 1000 and 5000 $m^2$, including all 5 suitable gaps greater than 3000 $m^2$. The size of each gap (canopy gap) was determined using methods described by Runkle (1992). Briefly, canopy gap size was calculated as the area of an ellipse. The major axis of the ellipse was the longest line that could be run from canopy edge to canopy edge inside the gap. The minor axis line of the ellipse was the longest line that could be run from canopy edge to canopy edge perpendicular to the long line.

Each canopy gap was divided into four sections or positions along the north-south axis. There were three positions inside the gap (northern, middle and southern thirds) and one gap edge position — the immediate understory area off the edge of the canopy gap. Thus the term 'gap position' refers to areas both inside and outside of a distinct canopy gap.

### 2.2. Planted seedlings

In spring 1993, seedlings of five species (western redcedar, western hemlock, subalpine fir, hybrid spruce and lodgepole pine) were planted in gaps and in the undisturbed and clearcut treatment units. Due to shortage of stock, no subalpine fir seedlings were planted in the understory of the undisturbed forest treatment units. All planting stock was PSB $1 + 0$ 415 except for subalpine fir seedlings which were PSB $1 + 0$ 313. Stock was grown in peat- and perlite-filled styroblocks in greenhouses and open compounds at Kalamalka Nursery in the summer of 1992 and stored at $-5$°C over winter. Initial sizes were fairly consistent among species except that subalpine fir were shorter and redcedar taller (Table 1). In all the gaps, seedlings were planted in single-species rows oriented north-south; planting rows were spaced 2 m apart and trees within lines spaced 1.5 m apart. In larger gaps, east-west planting lines for each species were also established. In all the cases, tree species were randomly assigned to planting lines. Where conditions allowed, up to 10 seedlings were planted in each cardinal direction from the edge of the gap into the understory of the forest matrix. In clearcuts, seedlings were planted at least three tree heights ($\sim$90 m) from a forested edge to ensure they were in full open conditions.

Measurement trees were selected in the fall of 1993. In gaps larger than 300 $m^2$, trees were selected so that the number of each species was balanced in each gap position. All seedlings were measured in smaller gaps. In the undisturbed forest and clearcut treatment units, 15 of 30 planted seedlings per species were measured. In all, about 1000 trees per species were measured. The current height increment, total height and seedling condition were recorded at the end of the first growing season. Basal diameter, total height, and seedling condition were recorded at the end of the second, third and fifth growing seasons.

Table 1
Provenance descriptions and size characteristics of trees at planting

| | Western redcedar | Western hemlock | Subalpine fir | Hybrid spruce | Lodgepole pine |
|---|---|---|---|---|---|
| *Provenance description* | | | | | |
| Seedlot number | 35033 | 03437 | 35005 | 14577 | 27792 |
| Subzone | ICHmc | ICHmc | ICHvc | ICHmc | ICHmc |
| Location | Date Creek | Suskwa River | Bell II | Calvin Creek | Kitseguecla River |
| Latitude | 55°27′N | 55°17′N | 56°45′N | 55°30′N | 55°06′N |
| Longitude | 127°50′W | 127°17′W | 129°50′W | 128°45′W | 127°50′W |
| Elevation (m) | 370 | 500 | 700 | 610 | 650 |
| *Characteristics at planting*[a] | | | | | |
| Height (cm) | $41.2 \pm 0.81$ | $24.5 \pm 0.82$ | $13.4 \pm 0.36$ | $27.4 \pm 0.56$ | $21.8 \pm 0.81$ |
| Diameter (mm) | $3.3 \pm 0.07$ | $3.3 \pm 0.07$ | $3.9 \pm 0.08$ | $3.7 \pm 0.06$ | $4.2 \pm 0.08$ |

[a] Forty-five trees randomly selected per species; planted spring, 1993; mean ± SE.

### 2.3. Analysis

A randomized block, split-split-plot design was employed to study the influence of three size classes of gaps, four different gap positions and tree species on planted tree growth performance. Main plots were small gaps (20–300 $m^2$), medium gaps (301–1000 $m^2$) and large gaps (1001–5000 $m^2$). The four 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 (five) providing the second split-plot. An individual gap was considered the experimental unit in this design and individual planted seedlings were sub-samples. This mixed effects ANOVA model design with error terms used to calculate the $F$ values for each term is illustrating in Table 2. Analysis was also performed on each tree species separately using a split-plot design. This model design is also illustrated in Table 2.

Pairwise comparisons were used to test for differences among size classes and gap positions. An adjustment was used to control for Type I error inflation: namely the pre-determined $\alpha$-level for differences between pairwise comparisons to be deemed significant (0.05) was divided by the number of comparisons being tested (Milliken and Johnson, 1992). Thus, an observed $p$-value had to be less than this preset level of significance for the comparison to be deemed significantly different. Three pairwise comparisons were selected to examine the influence of gap size class: large versus medium, medium versus small and large versus small. For a response variable to be significant between two size classes, a $p$-value of less than 0.0167 ($\alpha$ level 0.05/3) was needed. The observed $p$-value for a gap position pairwise comparison (gap edge versus south, middle versus north, middle versus south and north versus south) was deemed significant if less than 0.0125 ($\alpha$ level 0.05/4).

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

The clearcut treatment (representing full open conditions) and the undisturbed forest treatment (representing understory conditions) were analyzed separately as a randomized block, split-plot design because they contain no anologous treatments to gap position. In this analysis, open and understory conditions were the main plots and tree species were the split-plots. Values from this analysis and from the two designs above, were used to manually calculate pairwise comparisons between full open conditions and large gaps and between small gaps and the understory of the undisturbed forest for each tree species. $p$-values less than 0.025 ($\alpha$ level 0.05/2) were deemed significant.

Table 2
Mixed effects ANOVA model designs with error terms used to calculate the *F* values for each term

| Source | DF | Error term used to calculate *F*-value |
|---|---|---|
| A[a] | | |
| Block | 3 | – |
| Gap size class | 2 | Block × gap size class |
| Block × gap size class | 6 | – |
| Gap position | 3 | Block × gap position |
| Block × gap position | 9 | – |
| Size class × position | 6 | Block × size class × position |
| Block × size class × position | 15 | – |
| Gap number (block × size class) | 79 | – |
| Tree species | 4 | Block × species |
| Block × species | 12 | – |
| Size class × species | 8 | Block × size class ×species |
| Block × size class × species | 24 | – |
| Position × species | 12 | Block × position × species |
| Block × position × species | 36 | – |
| Size class × position × species | 22 | Block × size class × position × species |
| Block × size class × position × species | 56 | – |
| Gap number × species (block × size class) | 306 | – |
| Overall error | 764 | |
| Total | 1367 | |
| B[b] | | |
| Block | 3 | – |
| Gap size class | 2 | Block × gap size class |
| Block × gap size class | 6 | – |
| Gap number (block × size class) | 79 | – |
| Gap position | 3 | Block × gap position |
| Block × gap position | 9 | – |
| Size class × position | 6 | Block × size class × position |
| Block × size class × position | 14 | – |
| Overall error | 166 | |
| Total | 288 | |

[a] Randomized block split-split-plot mixed effects ANOVA design for the planted seedling study. Gap size is the main plot factor, gap position is the split-plot factor, tree species is the split-split plot factor. This example includes the four gap positions. Some analysis are presented with the gap edge understory position excluded. Results from this analysis are presented in Table 4

[b] Randomized block split-plot mixed effects ANOVA on seedling size where each tree species was analyzed separately. Gap size is the main plot factor and gap position is the split-plot factor. This example includes the four gap positions. Some analysis are presented with the gap edge understory position excluded. Results from this analysis are presented in Tables 5 and 6.

Analyses of variance (ANOVA) used the MIXED Procedure from SAS because the model being tested included both fixed (gap size, gap position and tree species) and random factors (block and its interactions) (Littell et al., 1996). All analyses were performed on least squared means calculated by MIXED Procedure in SAS.

Tree responses to gap size can also be described with non-linear regression models. In earlier companion studies of the same tree species (Wright et al., 1998b; Coates and Burton, 1999) the Michaelis–Menten equation was found to best predict tree growth as a function of ambient light levels. I also used the Michaelis–Menten equation here to develop growth functions for each of the five tree species as a function of gap size. The equation takes the form:

$$Y = \left(\frac{(aG)}{(a/s) + (G)}\right) + \epsilon \qquad (1)$$

where $Y$ is seedling growth response, $a$ is the asymptote of the function, $s$ is the slope of the relationship at small gap sizes, $G$ is the measure of gap size and the error term, $\epsilon$ is assumed to be normally distributed. Model parameters were estimated for each species using the Nonlin procedure in Systat 6.0 with the simplex estimation method to minimize the loss function (Systat, 1996).

## 3. Results

### *3.1. Effects of gap size*

There were strong and consistent trends in growth response among the tree species as gap size increased from single-tree openings to 5000 $m^2$ in size. Fifth-year height and diameter, and height and diameter increments averaged over the last 3 years (recent growth) increased rapidly from small single-tree gaps to about 1000 $m^2$ gaps, but thereafter, showed little change in gaps up to 5000 $m^2$ (Fig. 1). These trends were also present at the end of the third growing season (data not presented). Gap size explained between 40–72% of the variation in 5-year-old seedling size and 58–79% of the variation in height and diameter growth rates over the last 3 years (Table 3). For both total size and growth rates, the gap size curves asymptoted near or just above 1000 $m^2$, indicating little growth advantage as gap size increases above 0.1 ha (Fig. 1).

The split-split-plot ANOVA demonstrated that gap size, seedling position inside or outside a gap, tree species involved and the interactions among size, position and species, all influence seedling size or current growth rates (Table 4). For all the tree species, mean size after 5 years and recent growth rates (average increment per year for years 3, 4 and 5 after outplanting) was strongly affected by gap size (large,

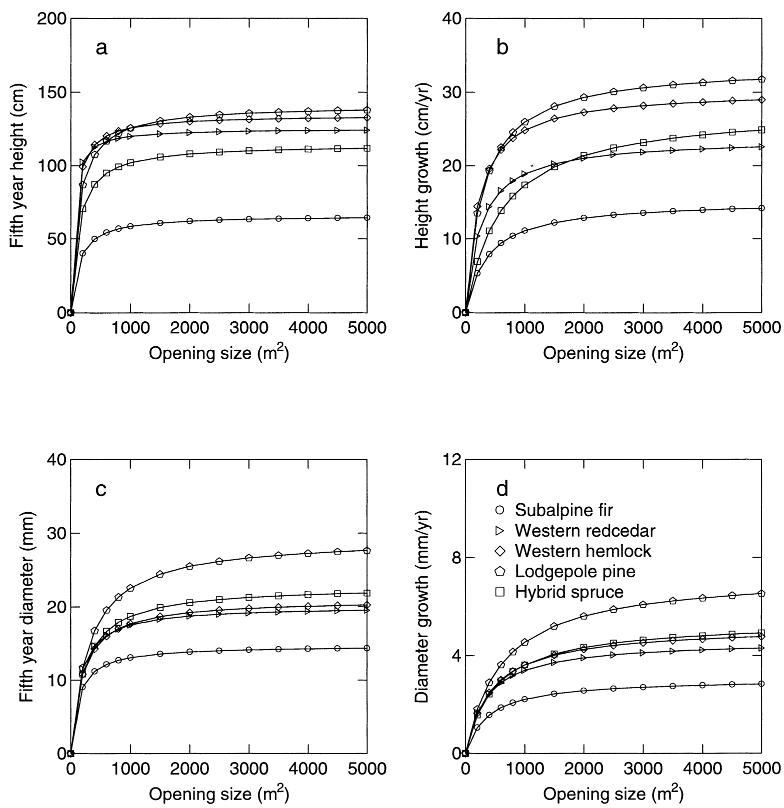


Fig. 1. Predicted 5th year height (a), height growth rate (b), 5th year diameter (c) and diameter growth rate (d) as a function of opening size ($m^2$), using Eq. (1) and parameter values in Table 3.

Table 3
Parameter estimates for predicted 5th year height and diameter and height and diameter growth rates (average increment per year for years 3, 4 and 5 after outplanting) using the equation $Y = ((aG)/((a/s) + G))$ where $G$ is gap size ($m^2$)

| Fifth year height | | | | | | Height growth rate | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | *a* | 95% C.L. | *s* | 95% C.L. | $R^2$ | *a* | 95% C.L. | *s* | 95% C.L. | $R^2$ | *N* |
| Western redcedar | 125.20 | 8.092 | 2.818 | 0.983 | 0.40 | 23.728 | 2.680 | 0.092 | 0.028 | 0.62 | 92 |
| Western hemlock | 134.45 | 9.893 | 1.899 | 0.614 | 0.50 | 30.202 | 3.472 | 0.139 | 0.046 | 0.58 | 90 |
| Subalpine fir | 66.11 | 4.555 | 0.506 | 0.124 | 0.64 | 15.249 | 1.581 | 0.041 | 0.011 | 0.75 | 84 |
| Hybrid spruce | 114.68 | 7.701 | 0.915 | 1.035 | 0.61 | 27.846 | 3.196 | 0.046 | 0.012 | 0.79 | 92 |
| Lodgepole pine | 141.17 | 9.048 | 1.128 | 0.250 | 0.65 | 33.645 | 2.869 | 0.113 | 0.026 | 0.74 | 90 |
| Fifth year diameter | | | | | | Diameter growth rate | | | | | |
| Western redcedar | 20.09 | 1.589 | 0.137 | 0.035 | 0.61 | 4.603 | 0.56 | 0.013 | 0.004 | 0.64 | 92 |
| Western hemlock | 21.01 | 1.954 | 0.112 | 0.032 | 0.60 | 5.175 | 0.74 | 0.012 | 0.005 | 0.62 | 90 |
| Subalpine fir | 14.72 | 0.973 | 0.118 | 0.028 | 0.64 | 3.048 | 0.36 | 0.008 | 0.003 | 0.67 | 84 |
| Hybrid spruce | 22.84 | 1.901 | 0.103 | 0.025 | 0.67 | 5.395 | 0.716 | 0.011 | 0.003 | 0.69 | 92 |
| Lodgepole pine | 29.29 | 2.540 | 0.098 | 0.022 | 0.72 | 7.314 | 1.002 | 0.012 | 0.004 | 0.72 | 90 |

Note: *a* and *s*, parameters of model; 95% C.L., 95% confidence limits.

medium, small) ($p < 0.004$) (Tables 5 and 6). There was a consistent decrease in mean tree size, with diameter responding more dramatically than height, from large to medium to small gap size classes.

Differences among size classes were greater as seedling shade-tolerance decreased (from tolerant western redcedar to intolerant lodgepole pine). With the exception of redcedar, 5th-year size of all the species was significantly greater in large gaps than medium gaps (Table 5). Similar differences existed between medium and small gaps, except that height and diameter of redcedar and hybrid spruce were not

Table 4
Randomized block split-split-plot ANOVA for planted seedling study. Observed *p*-values for gap size class (main plot factor), gap position (split-plot factor), tree species (split-split-plot factor) and their interactions. Analysis is presented twice: first, without gap edge understory trees so only trees inside gaps are being considered; second, with gap edge understory trees included, thus tests include trees both inside and outside the gap

| Source of variation | Gap edge understory position not included | | | |
|---|---|---|---|---|
| | Fifth year height (cm) | Height growth (cm/year, last 3-year) | Fifth year diameter (mm) | Diameter growth (mm/year, last 3-year) |
| Size class | 0.0001 | 0.0001 | 0.0001 | 0.0001 |
| Position | 0.0065 | 0.0146 | 0.0035 | 0.0054 |
| Size class × position | 0.0373 | 0.0183 | 0.0303 | 0.0695 |
| Species | 0.0001 | 0.0001 | 0.0001 | 0.0001 |
| Size class × species | 0.0001 | 0.0001 | 0.0001 | 0.0001 |
| Position × species | 0.0459 | 0.0355 | 0.0258 | 0.0238 |
| Size class × position × species | 0.0855 | 0.0633 | 0.0139 | 0.0079 |
| | Gap edge understory position included | | | |
| Size class | 0.0002 | 0.0002 | 0.0001 | 0.0002 |
| Position | 0.0001 | 0.0001 | 0.0001 | 0.0001 |
| Size class × position | 0.0003 | 0.0002 | 0.0001 | 0.0003 |
| Species | 0.0001 | 0.0001 | 0.0004 | 0.0009 |
| Size class × species | 0.0001 | 0.0001 | 0.0001 | 0.0001 |
| Position × species | 0.0056 | 0.0033 | 0.0067 | 0.0054 |
| Size class × position × species | 0.0557 | 0.0849 | 0.0168 | 0.0140 |

Table 5
Observed *p*-values from a randomized block split-plot ANOVA on seedling size. Each tree species was analyzed separately

| | Gap edge understory position not included | | | | |
|---|---|---|---|---|---|
| | Western redcedar | Western hemlock[a] | Subalpine fir[a] | Hybrid spruce | Lodgepole pine |
| *Fifth year height* | | | | | |
| Size class | 0.0036** | 0.0001** | 0.0001** | 0.0001** | 0.0001** |
| Position | 0.0144** | 0.0657 | 0.0415** | 0.0271** | 0.0126** |
| Size class × position | 0.2898 | 0.2483 | 0.1018 | 0.5226 | 0.0066** |
| Large versus medium | 0.1137 | 0.0117** | 0.0055** | 0.0004** | 0.0025** |
| Medium versus small | 0.0237 | 0.0041** | 0.0012** | 0.0168 | 0.0010** |
| Large versus small | 0.0013** | 0.0001** | 0.0001** | 0.0001** | 0.0001** |
| *Fifth year diameter* | | | | | |
| Size class | 0.0011** | 0.0002** | 0.0001** | 0.0001** | 0.0001** |
| Position | 0.0197** | 0.1233 | 0.0800 | 0.0101** | 0.0039** |
| Size class × position | 0.2910 | 0.3360 | 0.4093 | 0.0601 | 0.0037** |
| Large versus medium | 0.0185 | 0.0073** | 0.0016** | 0.0007** | 0.0006** |
| Medium versus small | 0.0233 | 0.0052** | 0.0020** | 0.0477 | 0.0068** |
| Large versus small | 0.0004** | 0.0001** | 0.0001** | 0.0001** | 0.0001** |
| *Fifth year height* | Gap edge understory position included | | | | |
| Position | 0.0051** | 0.0657 | 0.0415** | 0.0016** | 0.0010** |
| Size class × position | 0.0580 | 0.2483 | 0.1018 | 0.0077** | 0.0036** |
| Gap edge versus south | 0.0321 | – | – | 0.0091** | 0.0092** |
| Middle versus north | 0.0027** | 0.0521 | 0.0251 | 0.0258 | 0.2416 |
| Middle versus south | 0.0240 | 0.0388 | 0.0311 | 0.0056** | 0.0022** |
| North versus south | 0.2104 | 0.8487 | 0.8983 | 0.3581 | 0.0149 |
| *5th year diameter* | | | | | |
| Position | 0.0047** | 0.1233 | 0.0800 | 0.0007** | 0.0005** |
| Size class × position | 0.0179** | 0.3360 | 0.4093 | 0.0028** | 0.0007** |
| Gap edge versus south | 0.0243 | – | – | 0.0059 | 0.0098 |
| Middle versus north | 0.0060** | 0.1131 | 0.0549 | 0.0114 | 0.0476 |
| Middle versus south | 0.0114** | 0.0631 | 0.0487 | 0.0021** | 0.0006** |
| North versus south | 0.7082 | 0.7066 | 0.9225 | 0.2907 | 0.0164 |

[a] Due to inadequate sample sizes comparisions of hemlock and subalpine fir in south versus gap edge positions was not possible.
[*] P-values with asterisks are significant at $p < 0.05$. 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 ($\alpha$ level 0.05/number of comparisons).

significantly different between the two size classes. All tree species were larger and growing more rapidly in large than in small gaps (Tables 5 and 6). Recent height and diameter growth of western redcedar varied little between large and medium and between medium and small gaps (Table 6). Hemlock height growth was similar in large and medium gaps.

Seedling height after 5-year was generally greatest in the open conditions of the clearcuts (Fig. 2), however, of the five species only lodgepole pine height was significantly different between large gaps and clearcuts ($p = 0.0012$). Western redcedar grew more slowly than hemlock and spruce in the open and was similar in total height after 5 years in clearcuts primarly because of its 14–17 cm initial height advantage (Table 1). Fifth-year diameter, for all species but subalpine fir ($p = 0.11$), was significantly greater in clearcuts than large gaps ($p < 0.0021$), with lodgepole pine having the greatest differential between open conditions and large gaps (Fig. 3).

Diameter growth rates of all species showed a steady decline from open conditions to large, medium and small gaps and to the forest understory (Fig. 5). This was especially true for the two most light-

Table 6
Observed $p$-values from a randomized block split-plot ANOVA on seedling growth rates. Each tree species was analyzed separately

| | Gap edge understory position not included | | | | |
|---|---|---|---|---|---|
| | Western redcedar | Western hemlock[a] | Subalpine fir[a] | Hybrid spruce | Lodgepole pine |
| *Height growth (cm/year, last 3-year)* | | | | | |
| Size class | 0.0024** | 0.0002** | 0.0001** | 0.0001** | 0.0001** |
| Position | 0.0367** | 0.0513 | 0.0309** | 0.0210** | 0.0271** |
| Size class × position | 0.1808 | 0.3512 | 0.1281 | 0.3662 | 0.0079** |
| Large versus medium | 0.0734 | 0.0250 | 0.0035** | 0.0003** | 0.0019** |
| Medium versus small | 0.0186 | 0.0052** | 0.0007** | 0.0208 | 0.0011** |
| Large versus small | 0.0008** | 0.0001** | 0.0001** | 0.0001** | 0.0001** |
| *Diameter growth (mm/year, last 3-year)* | | | | | |
| Size class | 0.0012** | 0.0003** | 0.0001** | 0.0002** | 0.0001** |
| Position | 0.0300** | 0.1405 | 0.0724 | 0.0115** | 0.0070** |
| Size class × position | 0.3832 | 0.3173 | 0.5884 | 0.1030 | 0.0049** |
| Large versus medium | 0.0177 | 0.0096** | 0.0051** | 0.0008** | 0.0013** |
| Medium versus small | 0.0284 | 0.0085** | 0.0046** | 0.1023 | 0.0145 |
| Large versus small | 0.0004** | 0.0001** | 0.0001** | 0.0001** | 0.0001** |
| *Height growth (cm/year, last 3 year)* | Gap edge understory position included | | | | |
| Position | 0.0078** | 0.0004** | 0.0002** | 0.0008** | 0.0018** |
| Size class × position | 0.0406** | 0.2040 | 0.0179** | 0.0064** | 0.0032** |
| Gap edge versus south | 0.0220 | – | – | 0.0053** | 0.0110** |
| Middle versus north | 0.0060** | 0.1660 | 0.0065** | 0.0182 | 0.1744 |
| Middle versus south | 0.0572 | 0.0295 | 0.0217 | 0.0035** | 0.0045** |
| North versus south | 0.2037 | 0.7396 | 0.5062 | 0.3209 | 0.0466 |
| *Diameter growth (mm/year, last 3 year)* | | | | | |
| Position | 0.0072** | 0.0010** | 0.0003** | 0.0007** | 0.0009** |
| Size class × position | 0.0195** | 0.0980 | 0.2721 | 0.00514** | 0.0018** |
| Gap edge versus south | 0.0313 | – | – | 0.0070** | 0.0119 |
| Middle versus north | 0.0067** | 0.1121 | 0.0357 | 0.0084** | 0.0841 |
| Middle versus south | 0.0198 | 0.0533 | 0.0271 | 0.0019** | 0.0014** |
| North versus south | 0.3323 | 0.6751 | 0.8570 | 0.3375 | 0.0285 |

[a] Due to inadequate sample sizes comparisions of hemlock and subalpine fir in south versus gap edge positions was not possible.
[*] P-values with asterisks are significant at $p < 0.05$. 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 ($\alpha$ level 0.05/number of comparisons).

demanding conifers, lodgepole pine and hybrid spruce. For pine, diameter growth rates in open conditions were more than twice that found in large gaps (Fig. 5), and height growth rates behaved similarly (Figs. 4 and 5). Diameter growth of all species except subalpine fir ($p = 0.2$) was greater in the open condition of the clearcuts compared to large gaps ($p < 0.0025$). Height growth of lodgepole pine and hybrid spruce was significantly greater in clearcuts than large gaps ($p < 0.02$); there was little difference in height growth among the other three species between clearcuts and large gaps ($p > 0.16$).

In the forest understory all species performed poorly and after 2 years all lodgepole pine had died. Fifth-year height and diameter of redcedar and hemlock was significantly greater in small gaps than in the forest understory ($p < 0.015$). In the last 3 years, only average hemlock height increment was significantly greater in small gaps than the forest understory ($p = 0.0127$). Neither total size or recent growth of spruce varied between small gaps and the forest understory ($p > 0.053$).

Subalpine fir was consistently the poorest performer in all opening types. Planting stock conditions were

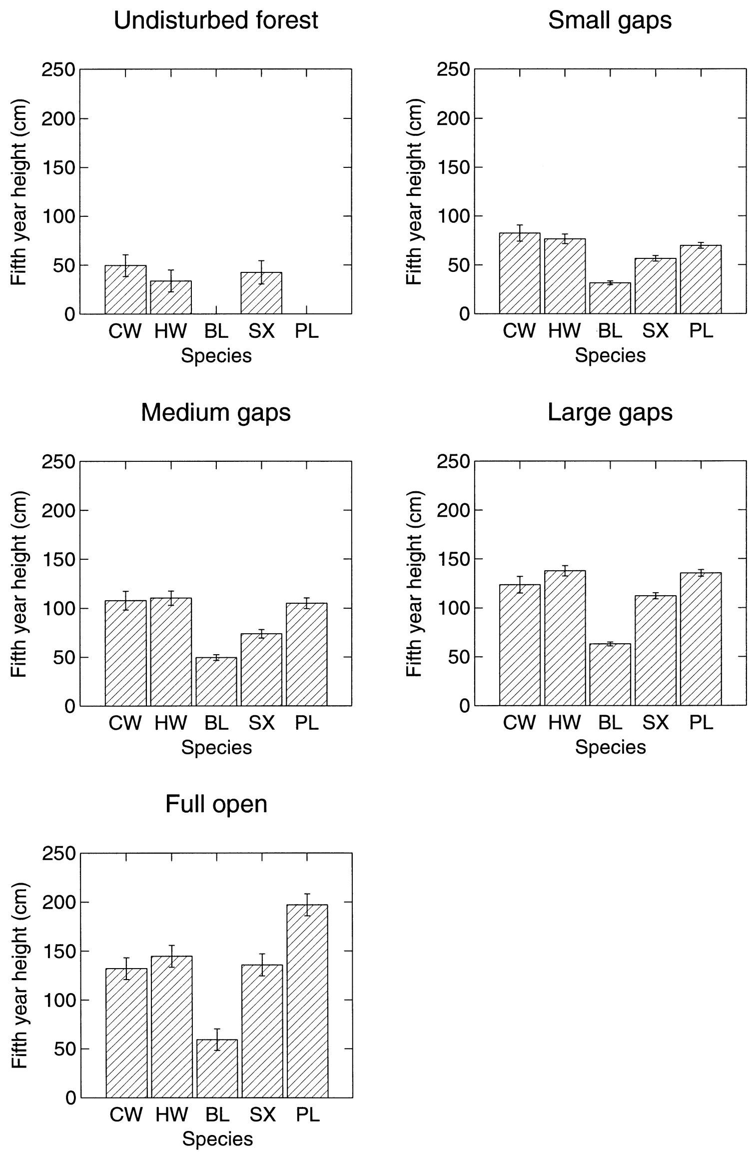


Fig. 2. Mean seedling height (cm) 5 years after planting by species and opening type (undisturbed forest (forest understory); small gaps, 10–300 $m^2$; medium gaps, 301–1000 $m^2$; large gaps, 1001–5000 $m^2$; full open (clearcut)). Subalpine fir were not planted in the forest understory. Error bars, $\pm 1$ SE of the mean. Species codes are: CW = western redcedar; HW = western hemlock; BL = subalpine fir; SX = hybrid spruce; PL = lodgepole pine.

partially responsible. At planting, subalpine fir was the smallest of the five species (see Table 1). This species has a history of poor outplanting performance. After planting, terminal buds often do not flush, resulting in poor apical dominance for the first few years (Pinkerton, 1994), a phenomenon observed in this experiment. Many of the stock problems with subalpine fir have recently been resolved (Pinkerton 1998, pers. commun.) For these reasons, the results presented here should not be considered indicative of current subalpine fir stock performance during the first few years after partial cutting. Western hemlock planting stock was also pro-

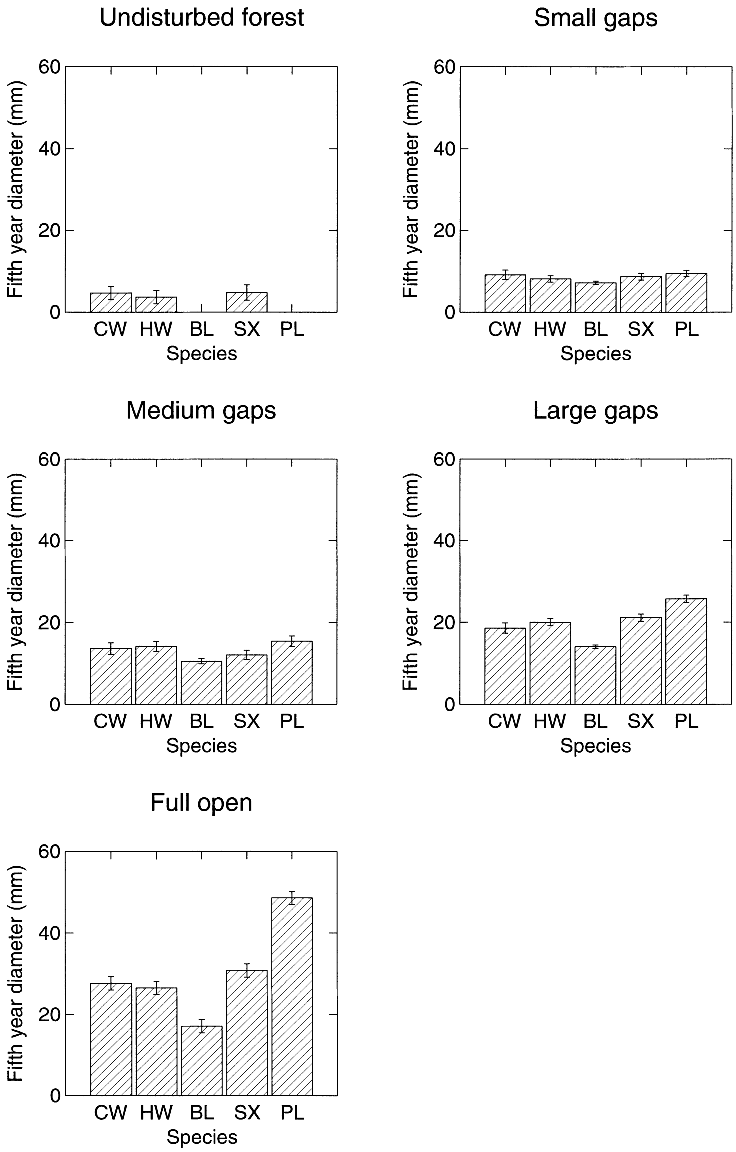


Fig. 3. Mean seedling diameter (mm) 5 years after planting by species and opening type (undisturbed forest (forest understory); small gaps, 10–300 $m^2$; medium gaps, 301–1000 $m^2$; large gaps, 1001–5000 $m^2$; full open (clearcut)). Subalpine fir were not planted in the forest understory. Error bars, $\pm 1$ SE of the mean. Species codes are: CW = western redcedar; HW = western hemlock; BL = subalpine fir; SX = hybrid spruce; PL = lodgepole pine.

blematic. Many seedlings died during the first summer for no apparent reason and this trend continued for several years. Mortality of the three species that exibited no planting stock problems (redcedar, spruce and pine) increased as gap size decreased, with the exception of high mortality of redcedar in open conditions (Table 7).

### 3.2. Effects of gap position

Growth of the three most shade tolerant species (western redcedar, western hemlock and subalpine fir) was consistent by gap position in large, medium and small gaps (Table 5). Hybrid spruce height and

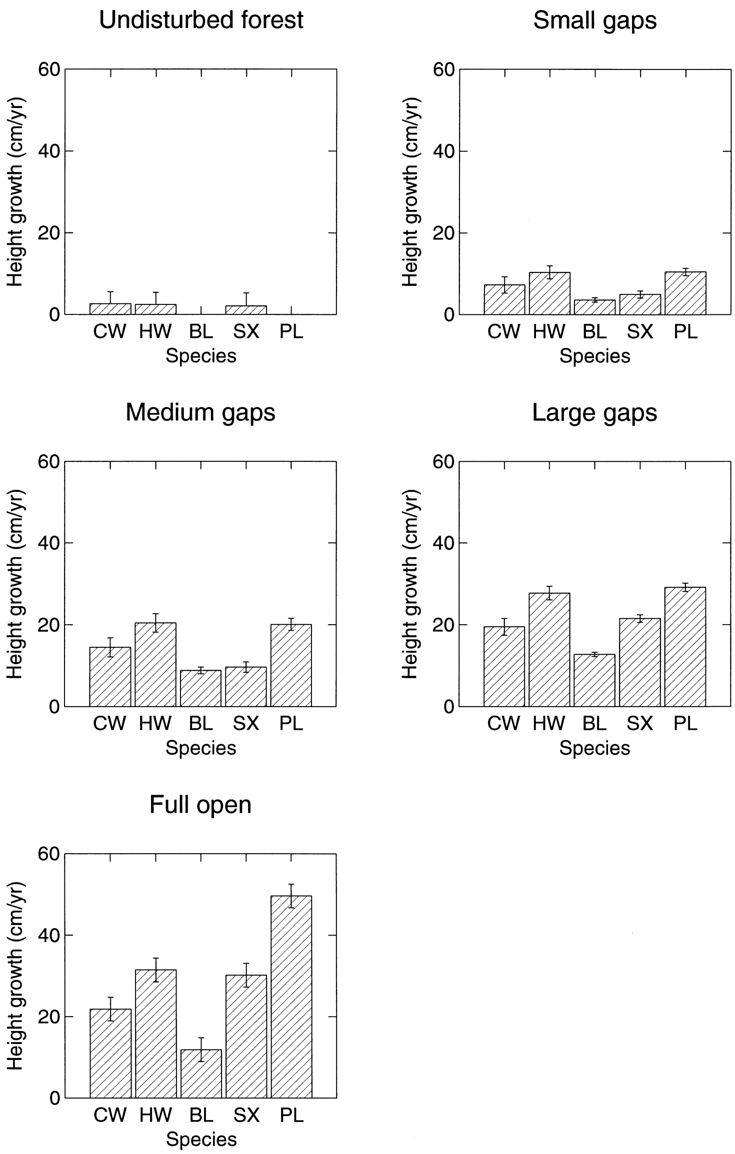


Fig. 4. Mean seedling height growth (cm, average increment per year for years 3, 4 and 5 after outplanting) by species and opening type (undisturbed forest (forest understory); small gaps, 10–300 $m^2$; medium gaps, 301–1000 $m^2$; large gaps, 1001–5000 $m^2$; full open (clearcut)). Subalpine fir were not planted in the forest understory. Error bars, $\pm 1$ SE of the mean. Species codes are: CW = western redcedar; HW = western hemlock; BL = subalpine fir; SX = hybrid spruce; PL = lodgepole pine.

diameter showed no interaction between gap size and gap position inside gaps, but a weak interaction was evident when gap edge seedlings were included. Lodgepole pine exhibited a strong gap size by gap position interaction both with and without gap edge seedlings ($p < 0.007$; Table 6), because of poor performance in the south position of large gaps.

The poorest seedling performance was usually in gap edge positions, although in small gaps (and for some species in medium gaps) the edge positions differed little from other positions (Figs. 6 and 7).

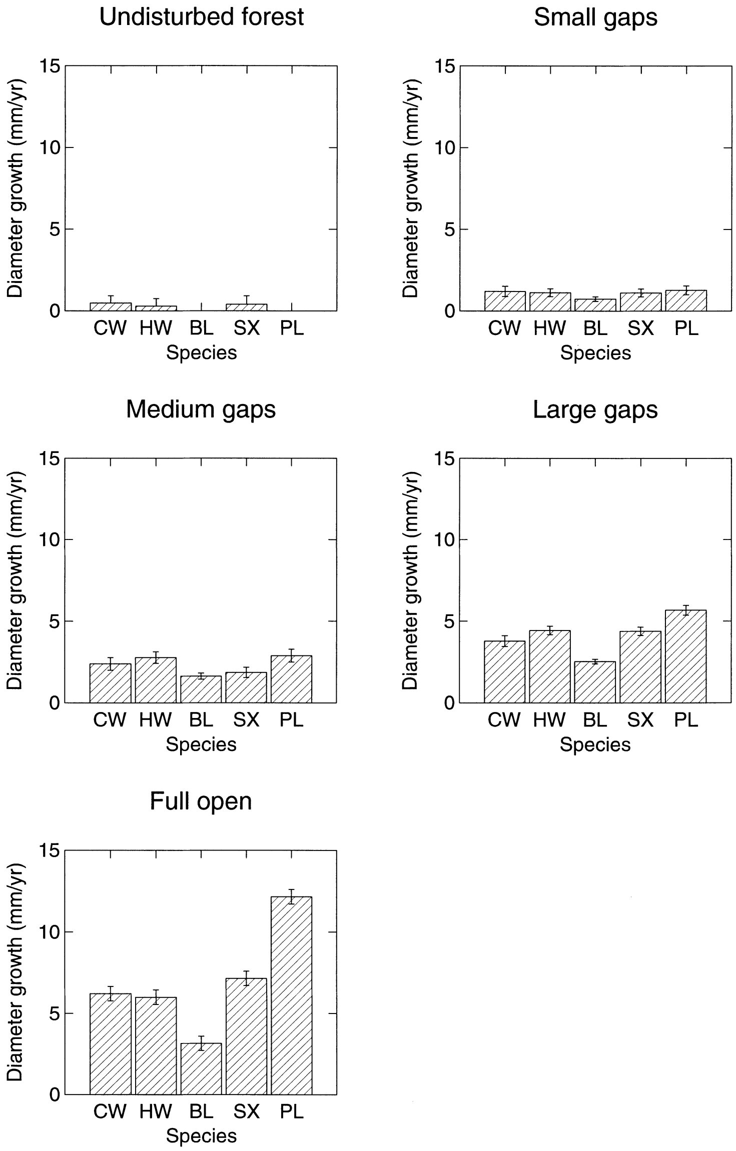


Fig. 5. Mean seedling diameter growth (mm, average increment per year for years 3, 4 and 5 after outplanting) by species and opening type (undisturbed forest (forest understory); small gaps, 10–300 $m^2$; medium gaps, 301–1000 $m^2$; large gaps, 1001–5000 $m^2$; full open (clearcut)). Subalpine fir were not planted in the forest understory. Error bars, $\pm 1$ SE of the mean. Species codes are: CW = western redcedar; HW = western hemlock; BL = subalpine fir; SX = hybrid spruce; PL = lodgepole pine.

Medium gaps had the greatest variability in growth with gap position. Somewhat surprising were the poor performances of all species (except pine height) at the north end of medium gaps and the clear superiority of the middle position in the medium gaps, suggesting strong interference from edge canopy trees, even those to the north of the gap.

Gap position had little influence on western hemlock and subalpine fir but was important for the three other species, which performed well at the middle position, but poorly at the north and south ends. Fifth year height and diameter of all the species varied little between north and south positions. Even though the 5th-year height of all the species was best in the

Table 7
Percent of seedlings that have died (mortality) in the forest understory, in small, medium and large gaps, and in the open condition of clearcuts. Subalpine fir was not planted in the forest understory due to sortage of stock

| | Opening type[a] Forest | Small gaps | Medium gaps | Large gaps | Clearcut |
|---|---|---|---|---|---|
| *Second year mortality (%)*[b] | | | | | |
| Western redcedar | 3.2 | 0.0 | 0.0 | 0.9 | 13.3 |
| Western hemlock | 25.0 | 19.3 | 10.3 | 11.3 | 10.9 |
| Subalpine fir | | 5.3 | 2.7 | 1.5 | 0.0 |
| Hybrid spruce | 48.4 | 2.0 | 0.0 | 0.0 | 0.0 |
| Lodgepole pine | 100.0 | 6.1 | 2.3 | 0.7 | 0.0 |
| *Five year mortality (%)*[c] | | | | | |
| Western redcedar | 17.5 | 1.2 | 1.0 | 2.8 | 35.6 |
| Western hemlock | 48.4 | 26.2 | 16.8 | 20.6 | 20.0 |
| Subalpine fir | | 13.3 | 9.2 | 5.7 | 0.0 |
| Hybrid spruce | 65.6 | 6.9 | 2.8 | 2.7 | 0.0 |
| Lodgepole pine | 100.0 | 13.3 | 3.5 | 4.6 | 1.7 |

[a] Forest is the understory of the undisturbed forest; small gaps are 10–300 $m^2$; medium gaps are 301–1000 $m^2$; large gaps are 1001–5000 $m^2$.
[b] Reflects mortality from fall 1993 to fall 1994; seedlings planted in spring 1993, measurement trees selected in fall 1993. There are no data available on first growing season mortality.
[c] Reflects mortality from fall 1993 to fall 1997.

middle position, only western redcedar height was significantly better in the middle than north position (Table 5). Height of hybrid spruce and lodgepole pine in the middle position was superior to that in the south position. Seedling diameter was more sensitive than height to gap position. Both redcedar and hybrid spruce had larger 5-year diameters in the middle versus north or south positions (Table 5). Lodgepole pine diameter was similar in middle and north gap positions, but 31% greater in middle than south position.

Height and diameter growth rate responses were similar to those observed for total size (Figs. 8 and 9). Again, there was a tendency for the best growth to be in the middle gap position compared to north and south positions, but in many cases the differences were not great enough to be significant (Table 6).

## 4. Discussion

Studies of natural or human-caused disturbances that provide insight on forest dynamics and succession are being used to develop silvicultural systems in Canada that are capable of meeting broad forest management objectives such as cost-effective wood production combined with maintenance or protection of ecosystem attributes and functions (Bergeron and Harvey, 1997; Coates and Burton, 1997; Gilmore, 1997). One of the unique challenges to developing logging strategies is the management of patchiness in the distribution of both harvested and residual trees and how that patchiness affects choice of tree species to regenerate and future growth rates. My study at Date Creek has shown that a gap-based approach can be used to address these issues and that growth of the major tree species in the interior cedar-hemlock forest of northwestern British Coloumbia respond in a similar and consistent manner to increasing opening size.

One of the most striking results of this study was the similar growth responses among the five tree species over the range of gap sizes examined (20–5000 $m^2$). All the species showed asymptotic growth as gap size increased. Growth of all the species increased rapidly from single-tree gaps up to 1000–2000 $m^2$ gaps, after which there was little further improvement in average growth rates by gap size. The growth equality among the tree species was most striking in the small (20–300 $m^2$) and medium (301–1000 $m^2$) sized gaps. This gap size range encompasses the size frequency dis-

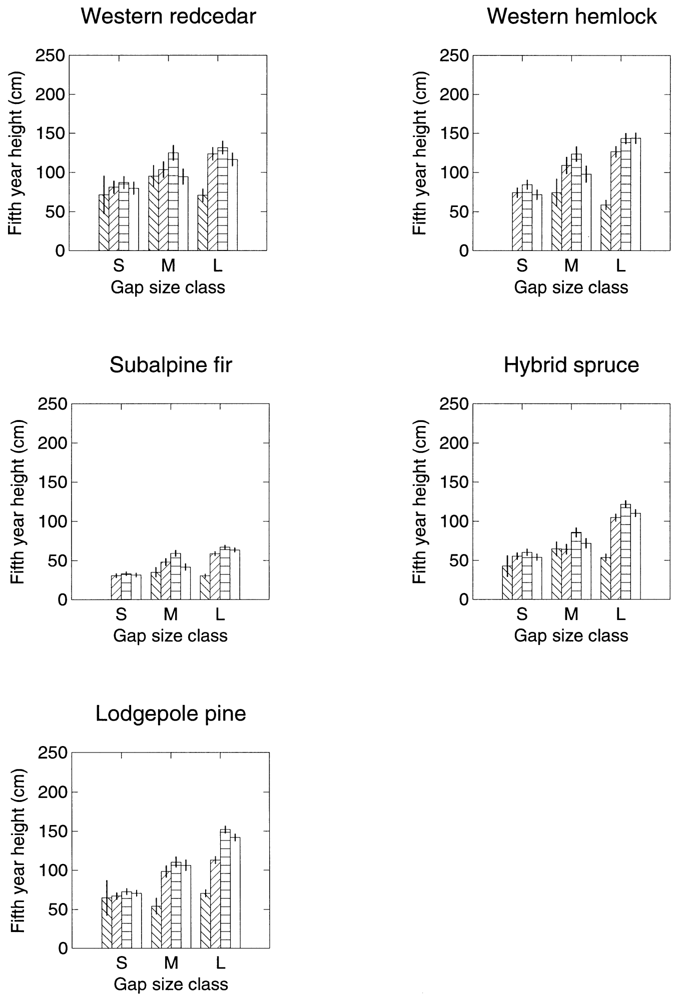


Fig. 6. Mean seedling height 5 years after planting by gap size class (S = small gaps, 10–300 $m^2$; M = medium gaps, 301–1000 $m^2$; L = large gaps, 1001–5000 $m^2$) and gap position (from left to right, Gap edge = ▧, South = ▨, Middle = ▤, North = □). Error bars, ±1 SE of the mean.

tribution of gaps commonly reported for forests where small-scale disturbance events occur (e.g. Lawton and Putz, 1988; Spies et al., 1990; Hytteborn et al., 1991; Lertzman and Krebs, 1991; Rebertus and Veblen, 1993; Coates and Burton, 1997)

Species-specific differences in ranking of height and diameter growth response to gap size and gap position in these high latitude forests were not sufficient to support a species-partitioning model along the lines proposed by Ricklefs (1977) and Denslow (1980) and still actively debated for lower latitude and tropical forests (e.g. Lieberman et al., 1995; Barker et al., 1997). A recent tropical study, in the forests of Borneo, also found no evidence of gap partitioning based on the height ranking among three species of dipterocarp across a gap gradient (Brown, 1996). Studies in US northeastern (Sipe and Bazzaz, 1995) and Pacific Northwest (Gray and Spies, 1996) forests were also unable to show evidence of gap partitioning. The tree species in the northern temperate forests of British Coloubia were generalists across the wide range of gap sizes studied.

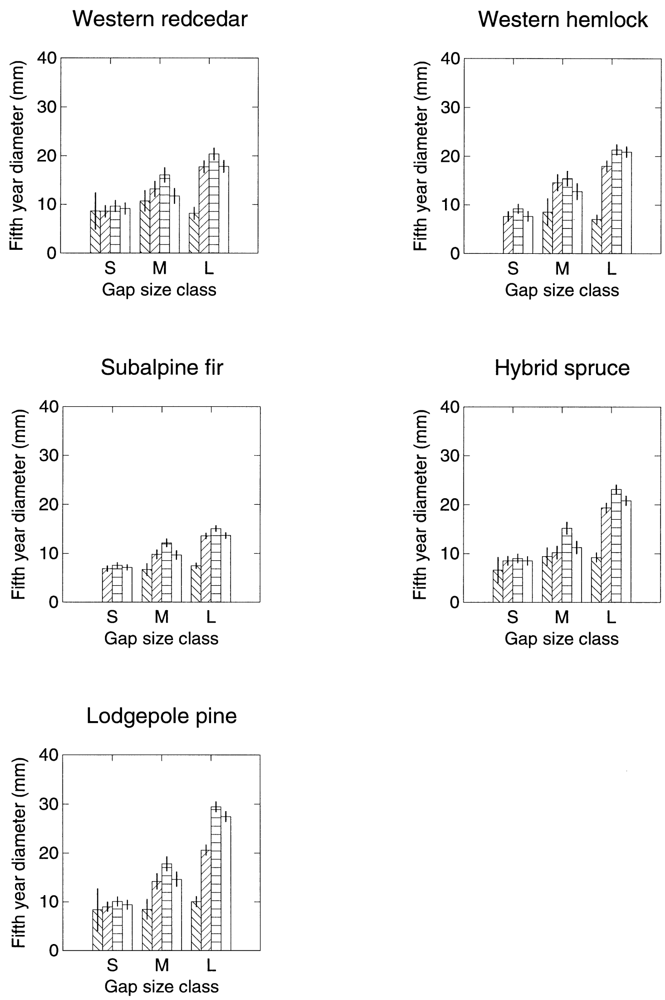


Fig. 7. Mean seedling diameter 5 years after planting by gap size class (S = small gaps, 10–300 $m^2$; M = medium gaps, 301–1000 $m^2$; L = large gaps, 1001–5000 $m^2$) and gap position (from left to right, Gap edge = ▧, South = ▨, Middle = ⊟, North = □). Error bars, ±1 SE of the mean.

Marked species differences in growth rates were only observed in the full open conditions of the clearcut (well away from the forest edge). In open conditions, the performance of lodgepole pine excelled over the other species. Hybrid spruce also performed better in the open than in gaps. Lodgepole pine is considered the most shade intolerant of these conifer species followed next by hybrid spruce (Krajina, 1969; Krajina et al., 1982; Kobe and Coates, 1997).

Because of the north-south light gradient in high latitude gaps (Canham et al., 1990), I expected tree growth rates to be best in the north and middle positions of large gaps and show a strong north to south decline in growth as gap size decreased. Instead, the largest trees of all species were found in the middle gap position of large gaps and there was often little difference between the north and south positions, except for lodgepole pine which clearly grows poorly in the shady parts of gaps. Seedlings of all species planted just off the gap edge under canopy trees performed poorly regardless of the cardinal direction into the understory or the size of the gap. The light advantage experienced off the north end of high

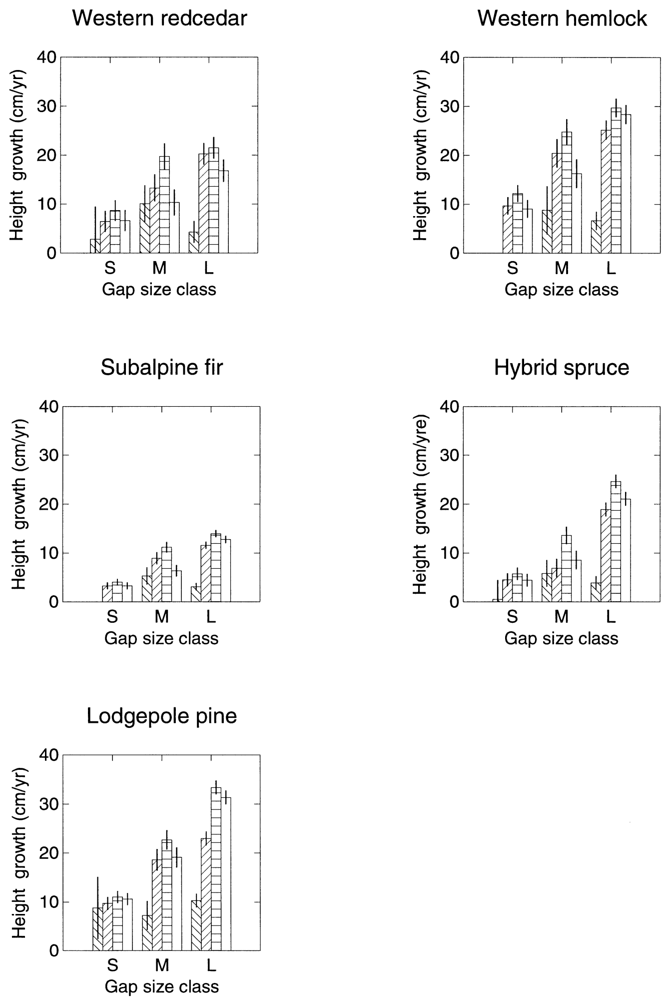


Fig. 8. Height growth rate (cm, average increment per year for years 3, 4 and 5 after outplanting) by gap size class (S = small gaps, 10–300 m$^2$; M = medium gaps, 301–1000 m$^2$; L = large gaps, 1001–5000 m$^2$) and gap position (from left to right, Gap edge = , South = , Middle = , North = ). Error bars, ±1 SE of the mean.

latitude gaps (Canham et al., 1990), compared to other cardinal directions, was not a benefit for tree growth at Date Creek. Overall, these results suggest that below-ground effects of canopy edge trees have an important influence on seedling growth in these forests. Lower water and to a lesser extent lower nitrogen availability has been demonstrated for up to 10 m from the canopy drip line into gaps at Date Creek (Walters, Lajzerowicz, Fredeen and Coates, unpubl. data).

In contrast to growth, early mortality rates varied considerably among the species. There was a trend of increased mortality with decreasing shade tolerance, especially in the low light of the forest understory where average radial growth rates ranged from 0.3–0.5 mm/year for all tree species. Kobe and Coates (1997) also documented wide variation among interior cedar -hemlock tree species in sapling mortality rates as a function of recent radial growth. At a radial growth rate of 0.4 mm/year, Kobe and Coates (1997); equation in Table 1), predict a 3 year mortality rate for western redcedar (1%), western hemlock (4%), subalpine fir (4%), hybrid spruce

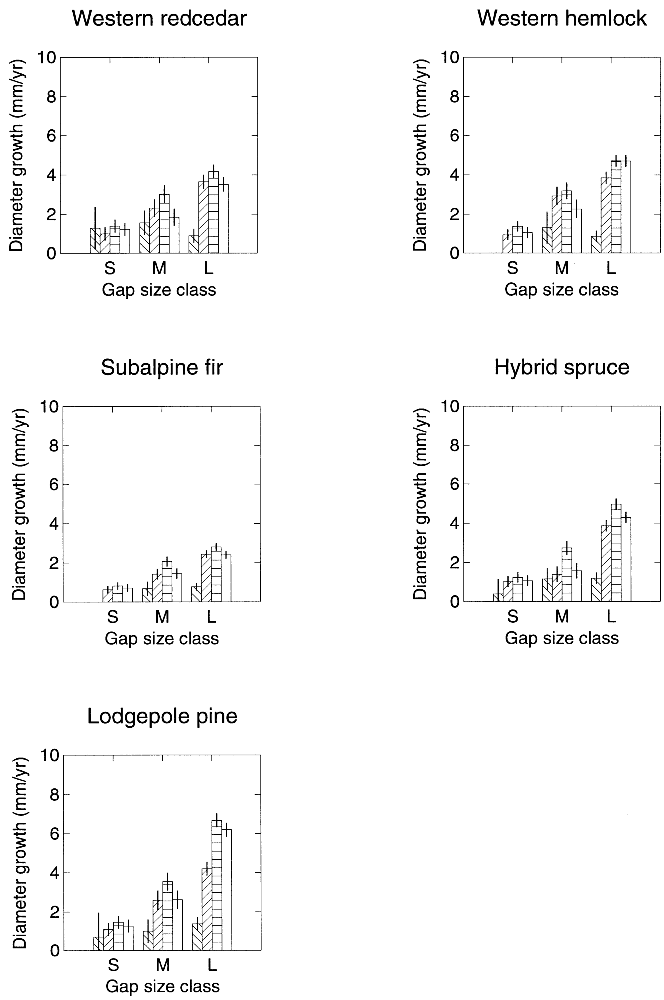


Fig. 9. Diameter growth rate (mm, average increment per year for years 3, 4 and 5 after outplanting) by gap size class (S = small gaps, 10–300 $m^2$; M = medium gaps, 301–1000 $m^2$; L = large gaps, 1001–5000 $m^2$) and gap position (from left to right, Gap edge = ▧, South = ▨, Middle = ⊟, North = □). Error bars, ±1 SE of the mean.

(27%) and lodgepole pine (51%) that are similar to those observed in this study.

In the interior cedar–hemlock forests, gap partitioning may take place gradually in response to differential survivorship among the tree species associated with the different growing conditions found across the gap sizes and among the gap positions examined. Differential suvivorship among the species was observed in the shadiest portions of medium gaps, in small gaps and in the forest understory. Once seedlings are established, gap partitioning appears to be a function of survivorship at low light and hence low growth. Gap partitioning resulting from seedling mortality rather than a shift in height growth hierarchy has also been observed in tropical forests (Brown, 1996).

This study reports 5 year results. Silvicultural research must look beyond the establishment and early growth phase to time periods of decades and centuries to assess effects of stand management activities on forest community dynamics, succession and long-term tree growth rates. In order to practically address these long-term effects, empirical studies must be linked with simulation models of future forest development. My gap-based studies at Date Creek, combined with the work of Kobe and Coates (1997) and Wright et al. (1998b), are being used to calibrate SORTIE (Pacala et al., 1996), a spatially-explicit model designed to examine the effects of small-scale disturbance in mixed-species forests. As a spatially-explicit model, SORTIE can be used to examine the consequences of a wide range of partial cutting strategies, at different spatial scales and over different time periods, an impossible undertaking for field-based research. This will assist forest managers in selecting the spatial pattern of partial cutting (including the optimal mix of sizes and spatial distribution of discrete canopy gaps) in order to meet ecosystem management objectives.

### *4.1. Conclusions and management implications*

Overall, the tree species of the high latitude Date Creek forest are generalists across a wide range of gap sizes, with no one species appearing to perform best in a given gap size or gap position. To some extent, this changes at the two extremes for seedling growing conditions. In large clearcuts, growth of shade intolerant species, like lodgepole pine, is clearly superior compared to the more tolerant species. The low but similar growth rates observed in the understory result in widely differing mortality rates among the species.

The distribution of canopy trees after harvest should be a major consideration in harvest planning because of the strong negative influence of canopy trees on the growth rates of seedlings. Uniform applications where canopy trees are evenly distributed after harvest (uniform shelterwood, seedtree, single-tree selection) should be avoided in favour of patch applications where defined openings are created in the tree canopy (group, irregular, strip or wedge shelterwoods and group-selection) in order to optimize growth rates of regenerating trees.

Careful matching of species to position in gaps, keeping the most light demanding species away from the shadier positions, will reduce the risk of early mortality and maximize growth rates in partially cut forests. Opening sizes need not be very large (0.1–0.2 ha or larger) in order for most tree species to achieve growth rates similar to those found in the open conditions of clearcuts.

Absolute growth rates of lodgepole pine were as good or better than all the other species across the range of conditions studied, suggesting it might be the most preferred species for timber management even in medium and small size class gaps. However, pine seedlings may be quite stressed at low light levels by trying to maintain high rates of growth. Coopersmith, 1998 pers. commun.) believes that height : diameter ratios of greater than 55, lodgepole pine seedlings are exhibiting signs of light stress indicative of poorly balanced seedlings. In small gaps the height : diameter ratio of lodgepole pine averaged 80. Until longer-term results are available, lodgepole pine should only be prescribed for management in small gaps if other species choices are not available.

The important criterion upon which to base tree species selection in partially cut forests is the ability to survive until growing conditions improve, especially under low light conditions. At radial growth rates above 2–2.5 mm per year the mortality risk for all interior cedar–hemlock forest tree species is quite low (Kobe and Coates, 1997). All five of the planted tree species averaged these minimum radial growth rates for good survival in medium sized gaps (301–1000 $m^2$) and these growth rates are achieved by all interior cedar–hemlock tree species at ambient light levels of 20–40% full sun (Coates and Burton, 1999; Wright et al., 1998b).

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