

Regeneration from seed of six tree species in the interior cedar–hemlock forests of British Columbia as affected by substrate and canopy gap position

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Abstract: Canopy gap size can play a major role in determining composition of tree regeneration after disturbance. The effect of different positions within gaps and within the intact forest has received less study. We seeded six tree species onto two substrates (organic and undisturbed moss) in three positions along a north–south gradient within eight replicate 600-m² canopy gaps and in the intact forest south of each gap (the gap positions), in 1995 and 1996. Emergence of all species was strongly affected by gap position, seedbed substrate, and year, but there was little evidence of partitioning by gap position among the species. Average emergence was higher in the shady southern position in gaps and within the intact forest and significantly higher on organic than undisturbed moss substrates (with the exception of *Abies lasiocarpa* (Hook.) Nutt., which showed no preference for seedbed). Seedling survival was greatest for all species in the south end of the gap, where soil moisture remained highest and light levels of approximately 20% full sun were adequate for survival. A species trade-off was observed in the understory of the intact forest, where differential survival based on shade-tolerance ranking occurred. To predict regeneration success in these forests, for either silvicultural purposes or to permit a better understanding of community dynamics and succession, it is important to consider the influence of position inside and outside of gaps and the nature of the seedbed substrate.

Résumé : La taille des trouées dans le couvert peut jouer un rôle prépondérant dans la composition de la régénération arbustive après une perturbation. L'effet de la position dans les trouées et dans la forêt intacte a été peu étudié. Nous avons semencé six espèces d'arbres sur deux substrats (organique et mousse non perturbée) et dans trois positions le long d'un gradient nord–sud à l'intérieur de huit trouées de 600 m² et dans la forêt intacte au sud de chaque trouée (les positions des trouées), en 1995 et 1996. L'émergence de toutes les espèces a été fortement affectée par la position dans les trouées, par le substrat et par l'année, mais il y avait peu d'indices d'une distribution des espèces en fonction de leur position dans les trouées. En moyenne, l'émergence était meilleure au sud des trouées, dans la zone ombragée, et dans la forêt intacte et significativement meilleure sur le substrat organique que sur la mousse non perturbée, excepté dans le cas de l'*Abies lasiocarpa* (Hook.) Nutt. qui ne montrait aucune préférence pour un lit de germination. La survie des semis était la plus élevée chez toutes les espèces à l'extrémité sud des trouées où l'humidité du sol demeurait la plus élevée et où la luminosité, qui atteignait environ 20% du plein ensoleillement, était adéquate pour la survie des semis. Un ajustement entre les espèces a été observé en sous-étage dans la forêt intacte où le taux de survie des différentes espèces variait en fonction de leur degré de tolérance à l'ombre. Il est important de considérer l'influence de la position à l'intérieur ou à l'extérieur des trouées ainsi que la nature du lit de germination pour prédire le succès de la régénération dans ces forêts, que ce soit pour des fins sylvicoles ou pour permettre une meilleure compréhension de la succession et de la dynamique des communautés.

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Introduction

Tree regeneration has often been studied after disturbance has formed a canopy gap (e.g., Runkle 1982; Brokaw 1985, 1987; Lawton and Putz 1988; Spies et al. 1990). These studies have generally concentrated on population or community-

level responses within gaps of varying size; often with an objective of explaining processes that affect tree species diversity in forests subject to small-scale disturbance (e.g., Ricklefs 1977; Denslow 1980). The role of different positions within and outside gap areas has received less study in terms of assessing their effects on tree seed germination,

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establishment, and subsequent growth. For example, Coates and Burton (1997) found that of 19 studies examining tree establishment, density, or composition in gaps, 15 tested for gap size effects but only 4 considered position within gaps. In part, this may be due to the majority of gap studies being from southern latitudes where gap size is likely to affect biotic and abiotic conditions more than position in a gap.

In northern latitude forests, position within a gap can have considerable effect on microclimate conditions (e.g., light availability and soil temperature; Canham et al. 1990) and biological processes (e.g., photosynthesis; Sipe and Bazzaz 1995), especially along the north–south axis of a gap. It has been well established that, in more southern temperate and tropical forests, gap size can play a major role in determining tree species composition after disturbance (Denslow 1980, 1987; Brokaw 1985, 1987; Whitmore 1989; Stewart et al. 1991). While there is similar evidence of gap size effects on tree species presence and abundance for northern British Columbia forests (Coates and Burton 1997), the role that gap position exerts on tree species establishment and composition following either natural or partial logging disturbance is largely unknown.

Seedling emergence and survival following canopy disturbance is influenced by many factors including parent tree proximity and abundance (Ribbens et al. 1994), type of seedbed substrate (Garman and Orr-Ewing 1949; Prochnau 1963; Day 1964; Eis 1965, 1967; Waldron 1966; Putz 1983; Lawton and Putz 1988; Stewart et al. 1991; Hofgaard 1993), presence of seed consumers and dispersers (Schupp 1988, Schupp et al. 1989), and variation in climatic and microclimatic conditions (Waldron 1966; Hennessey 1968; Noble and Alexander 1977; Alexander 1984). All these factors can cause dramatic spatial and temporal variation in natural seedling recruitment, making it difficult to separate out the effects of gap position.

More refined studies of how gradients of canopy influence affect the regeneration of different tree species, and better estimates of the spatiotemporal extent of canopy influence in forest stands, hold the most promise for better predicting tree regeneration and successional dynamics following natural or logging disturbance in northern forests. To more closely examine the effects of variation in canopy influence on tree regeneration, we examined tree seedling emergence and early survival on two seedbed substrates along a north–south gradient within and outside canopy gaps. Specifically, the study was designed to address four main questions:

- (1) What effect does position inside and outside canopy gaps have on total emergence of six of the major species in northern temperate forests of British Columbia?
- (2) How is subsequent survival of the emergents affected by position inside and outside gaps?
- (3) Are these relationships affected by seedbed substrate type?
- (4) Are the relationships best correlated with resource availability (light and soil moisture) or abiotic conditions (soil temperature)?

Methods

Study area

This study is a component of the Date Creek silvicultural systems study (Coates et al. 1997), located near Hazelton, B.C., Can-

ada (55°22'N, 127°50'W; 370–665 m elevation). The study area lies within the Moist Cold subzone of the Interior Cedar–Hemlock biogeoclimatic zone (ICHmc) (Pojar et al. 1987; Banner et al. 1993), a transitional area between the coastal and interior forests of northwestern British Columbia. All study sites were located on mesic, hemlock – step moss ecosystems (ICHmc2, site series 01) at 450 m elevation. The soils of the study sites, typically Eluviated or Orthic Dystric Brunisols (Agriculture Canada Expert Committee on Soil Survey 1987) are developed on morainal parent materials, ranging in texture from loamy sand to clay loam.

Mature forests in the study area (spanning hundreds of hectares) originated from a fire in 1855 and are a stratified mixture of coniferous and deciduous tree species. Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) dominates; other species include 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 (*Picea sitchensis* (Bong.) Carr.), and on occasion Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)), paper birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), and black cottonwood (*Populus balsamifera* ssp. *trichocarpa* Torr. & Gray).

The understory of these forests are typified by sparse shrub and herb development with a thick 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).

Experimental treatments

A randomized block split-split-plot design was employed to study the influence of four canopy gap positions, two seedbed substrates, and 2 years on emergence and early survival of six tree species (western hemlock, western redcedar, lodgepole pine, subalpine fir, hybrid spruce, and paper birch). The experimental blocks were eight elliptical-shaped canopy gaps aligned north–south (the open area from crown edge to crown edge; see Runkle 1992) approximately 600 m² in size (35 m north–south × 25 m east–west). The opening size was selected to provide a good light gradient along the north–south gap axis.

The eight gaps were located in a 10-ha area of the much larger mature forest stand originating after the 1855 fire. The 10-ha area was very uniform in slope, aspect, and canopy tree species composition and size to minimize microclimatic variation after gap formation. The gaps were flat or southeast facing; slope varied between 0–5% for five gaps and 5–10% for three gaps. Stand density (stems > 7.5 cm diameter at 1.3 m height) was approximately 1764 stems/ha with canopy tree height averaging about 30 m. Stand basal area (61 m²/ha) was dominated by western hemlock (40 m²/ha), with western redcedar next at 8 m²/ha. Hybrid spruce, paper birch, and lodgepole pine varied between 2 and 4 m²/ha. Trembling aspen, subalpine fir, and black cottonwood were minor components of the stand. Diameter of western hemlock averaged 30 cm; western redcedar, 23 cm; and lodgepole pine, 37 cm. Black cottonwood (45 cm) and hybrid spruce (43 cm) had the largest average diameter. Within this stand, gaps were selected so that hemlock dominated the perimeter and deciduous species were minor in abundance.

These gaps were created by horse logging on frozen ground in the late winter of 1994–1995. Logging at this time of year resulted in minimal forest floor disturbance. All logging debris was hand removed from the gaps leaving each gap with a uniform moss-dominated forest floor. Each experimental block (canopy gap) was subdivided into four dominant gap positions along its north–south axis (main plots). The four gap positions include three positions within the gap and one in the intact canopy area surrounding the gap: the northern, middle, and southern thirds of the canopy gap

Table 1. Attributes and source of the seedlots used for each tree species in the experiment.

	Species					
	Subalpine fir	Western redcedar	Lodgepole pine	Hybrid spruce	Paper birch	Western hemlock
Seedlot	35573	35033	13902	27777	2756	35034
Zone ^a	ICH	ICH	ICH	ESSF	ICH	ICH
Stratified	Yes	No	Yes	Yes	No	Yes
Collection year	1992	1990	1985	1986	1975	1990
Germination (%)	79	93	95	75	81	95
Latitude (N)	55°16'	55°27'	55°03'	55°34'	50°41'	55°28'
Longitude (W)	128°24'	127°50'	121°31'	127°10'	119°08'	127°55'
Elevation (m)	1100	370	350	800	824	440
Source	Burdick Creek	Date Creek	Hazelton	Gail Creek	Larch Hills	Date Creek

^aICH, Interior Cedar-Hemlock; ESSF, Engelmann Spruce – Subalpine Fir (Banner et al. 1993; Pojar et al. 1987).

and the forested understory area off the south end of the gap (approximately 15 m into the understory). Thus the term “gap position” refers to areas both inside and outside of a distinct canopy gap. Seedbed substrate (split plot with two levels) was randomly assigned to each gap position. A companion study has shown that following logging in similar stands (using a range of harvesting techniques) mineral soil exposure represents less than 7% of substrate, compared with up to 34% for organic and 45% for moss within gaps, and that an organic substrate is suitable for natural regeneration of our study species (P.T. LePage, C.D. Canham, K.D. Coates, and P. Bartemucci, unpublished data). The most common seedbed substrates were used in this study: (i) undisturbed forest floor, which was a moss layer dominated by red-stemmed feather moss, step moss, knight’s plume, and electrified cat’s tail moss; and (ii) organic layer (primarily a mor humus form varying from 5 to 8 cm in thickness), which was created by careful removal of the live moss layer (2–3 cm). Since the humus layer is the same thickness for each seedbed, substrate removal of the live moss layer resulted in a 2–3 cm difference in depth to mineral soil between treatments. While there was no layer of dead moss present in the undisturbed forest floor seedbed, moss in the middle and northern gap positions receiving direct sunshine became more desiccated. Moss in the shaded south end of gaps was unaffected.

Each substrate plot in each gap position was protected by seed predator exclusion cages. The cages covered a 1 × 1.5 m area, were enclosed by 1 × 1 cm wire screening stapled onto a wooden frame, and backfilled to exclude rodents. Each cage was subdivided into three equal-sized subplots with one of the six tree species randomly assigned to each subplot. Two cages per substrate type were required.

Seed was obtained from seedlots registered with the B.C. Ministry of Forests Seed Centre (Table 1). Seedlots were used from collection sites near the study area if available. Seed of all six species are wind dispersed primarily in the fall. Subalpine fir has the heaviest seed (76 seeds/g) and paper birch the lightest (3040 seeds/g); the other species range from 200 to 570 seeds/g (Burns and Honkala 1990; Young and Young 1992). Seed crops are produced every year with mast crops occurring at 2- to 6-year intervals. Seed dispersal distances can be quite large (paper birch), but most seed falls within 200 m of the parent trees. In a companion study, mean seedling dispersion distances were generally low for the six species (within 11–24 m of parent trees; P.T. LePage, C.D. Canham, K.D. Coates, and P. Bartemucci, unpublished data). All the species regenerate on a wide range of substrates but tend to prefer mineral soil, rotten wood, or disturbed organic substrates (Burns and Honkala 1990). The shade-tolerance ranking of these species from the most to least shade tolerant is western redcedar > western hemlock = subalpine fir > hybrid spruce > lodgepole pine > paper birch (Krajina 1969; Krajina et al. 1982; Kobe and Coates 1997).

In early May 1995, one hundred seeds of each tree species were scattered on the surface of randomly selected subplots (the 1995 cohort). Because of the spring sowing date, stratified seed was used for four of the six species. Sowing was repeated in the same manner in late fall of 1995 (following the first frost, just prior to snowfall) with dry, unstratified seeds to allow them to stratify naturally in the field (the 1996 cohort). The 1996 cohort more closely matched typical dispersal opportunities for these species. The use of stratified versus nonstratified seed to some extent compensates for season of sowing, though there are obvious differences in the length of time exposed to potential seed predators and microorganisms.

In addition to the main experiment described above, three sub-experiments were simultaneously established in spring 1995 within a subset of the gaps. Each subexperiment was randomly assigned to three of the eight experimental blocks (three replicates). The subexperiments were (i) seed and seedling predation, where 100 seeds of all six species were seeded on both substrates in all gap positions without cage protection to examine effect of seed consumers on tree species emergence and early survival; (ii) natural seed rain, where caged plots were established on both substrates in all gap positions without any seeding to monitor ingress of natural regeneration; and (iii) substrate variability, where in the middle position, 100 seeds each of redcedar and birch were seeded on both substrates (with cage protection to assess the range of variability in emergence by substrate type). Sowing was repeated as above in late fall of 1995 in both the predation and substrate variability experiments using dry, unstratified seeds.

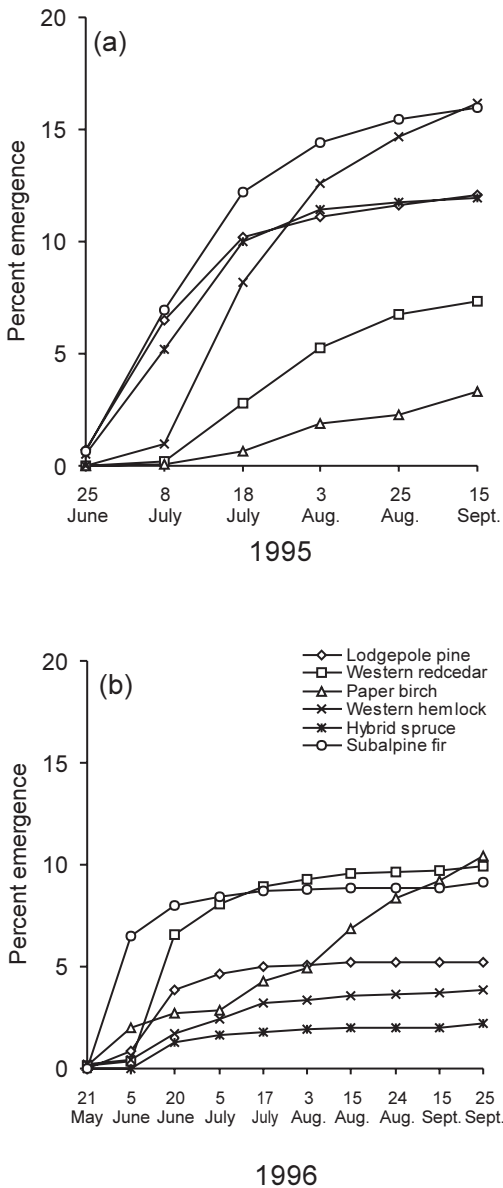
Seedling monitoring

Emergence of the 1995 cohort was monitored every 2 weeks from June 25 to September 15 by placing coloured toothpicks adjacent to each new germinant. Recruitment and mortality were determined at each measurement interval for each emergent. Seedling emergence of tree species (extra species) other than the species sown in each subplot were recorded to allow for a plot adjustment factor due to natural seed rain. Overwinter mortality of the 1995 cohort was enumerated in May 1996, following snowmelt. Recruitment and mortality of the 1996 cohort (seeded fall 1995) and survival of the 1995 cohort was followed throughout the 1996 growing season at 2-week intervals (May 7 to September 19).

Environmental data

We used hemispherical canopy photographs, taken above the cages, to estimate light levels in each of the four gap positions. The photographs were digitally scanned using a Polaroid SprintScan 35 slide scanner. An index of growing season light availability (GLI) was computed from each photograph (using GLI 2.0 software), following Canham (1988). This index combines the

Fig. 1. Mean percent emergence of the 1995 (a) and 1996 (b) cohorts across all gap positions and substrates by tree species.



seasonal and diurnal distribution of solar radiation transmitted through the canopy into a single index of available light in units of percent full sun for a specified growing season (in our case, mid-April through mid-September) (Canham et al. 1990).

Soil temperature and soil moisture were recorded at 2-week intervals in each gap position and seedbed combination in all gaps during May–September 1996. Soil temperature was recorded in each substrate plot at 5 and 10 cm depths using a digital soil temperature probe (Atkins Technical Inc., Series 396; 0.1°C resolution). Soil moisture was determined gravimetrically on 25–50 g samples taken at 0–5 cm depth adjacent to the substrate plots in each gap position (measurements were not done if it rained the previous night or on the measurement day).

Data analysis

Each tree species was analyzed separately. New emergents recorded during each monitoring interval were summed to derive a total cumulative emergence for the season. The number of living

seedlings recorded at each measurement date was subtracted from total number of emergents to date and divided by the total emerged, providing percentage of seedlings present on each date. Survival was the percentage of the total seedlings that emerged. Data from each caged plot were adjusted to account for natural seed rain. The adjustments for natural seed rain were plot specific using the “extra species” data collected at each monitoring interval. All plots had the potential to be modified if needed. Since the extra species counts were made on the whole caged area, but each direct-seeded species occupied only one third of the plot, total natural ingress was adjusted for subplot size.

All percent emergence data were arcsine square-root transformed (to correct for skewed distributions) and subjected to an analysis of variance (SYSTAT, Inc. 1996) using a split-split-plot design to evaluate the effect of gap position, substrate, year, and their interactions. Single degree of freedom contrasts were used to partition the treatment sums of squares for gap position and gap position × substrate to test for differences between the (i) combined north and middle gap positions versus the combined south gap and understory positions, (ii) north versus middle, and (iii) south versus understory.

Linear and nonlinear regression was used to examine the relationship between total emergence, light level, soil temperature, and soil moisture (temperatures expressed as monthly or seasonal means) for the 1996 cohort only.

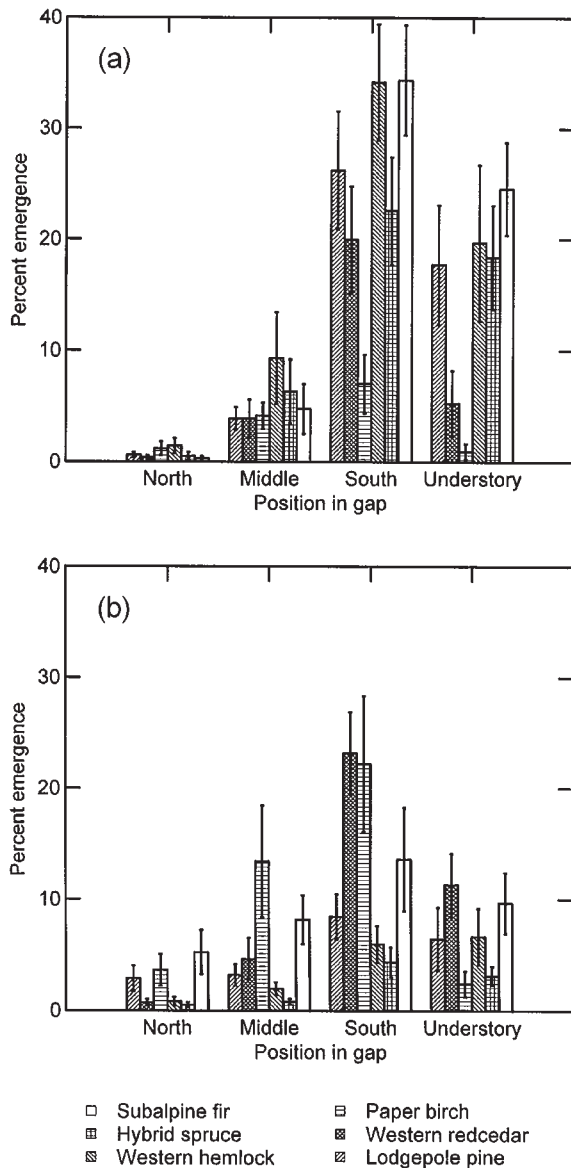
Results

Seedling emergence

Seedling emergence of lodgepole pine, hybrid spruce, and subalpine fir from the 1995 cohort began in late June 1995. Western redcedar, paper birch, and western hemlock emergence began approximately 3 weeks later. Emergence of all species was largely completed by mid-September (Fig. 1a). Overall, subalpine fir and western hemlock had the highest number of emergents (16%), and paper birch had the least (3%). In contrast to the 1995 cohort, the fall-seeded subalpine fir and western redcedar (1996 cohort) emerged following snowmelt in spring 1996; emergence proceeded rapidly and was generally complete by early July (Fig. 1b). A similar response was seen for lodgepole pine, western hemlock, and hybrid spruce, but fewer seedlings emerged. New emergents of paper birch were observed through to mid-September. Overall, the highest number of seedling emergents in 1996 was recorded for paper birch (11%) and the least in hybrid spruce (2%).

Total emergence for all six species was strongly influenced by gap position (Figs. 2a and 2b), seedbed substrate (Figs. 3a and 3b), and year (Tables 2 and 3). In both years, for all six species, there was a clear trend of total emergence increasing from the sunny north to shaded south end of gaps, with the understory environment off the south end of gaps being somewhat intermediate (Figs. 2a and 2b). For all species except paper birch, average emergence was significantly greater in the south and understory positions than the north and middle positions (Table 3). Further partitioning of the data found significant differences in emergence of western redcedar, paper birch, and subalpine fir between the north and middle positions (Table 3), but total emergence was higher in the middle than the south position in both years for all species (Figs. 2a and 2b). Total emergence of lodgepole pine, western redcedar, and paper birch was significantly

Fig. 2. Mean percent emergence of the 1995 (a) and 1996 (b) cohorts by tree species and gap position. Error bars are 1SE.

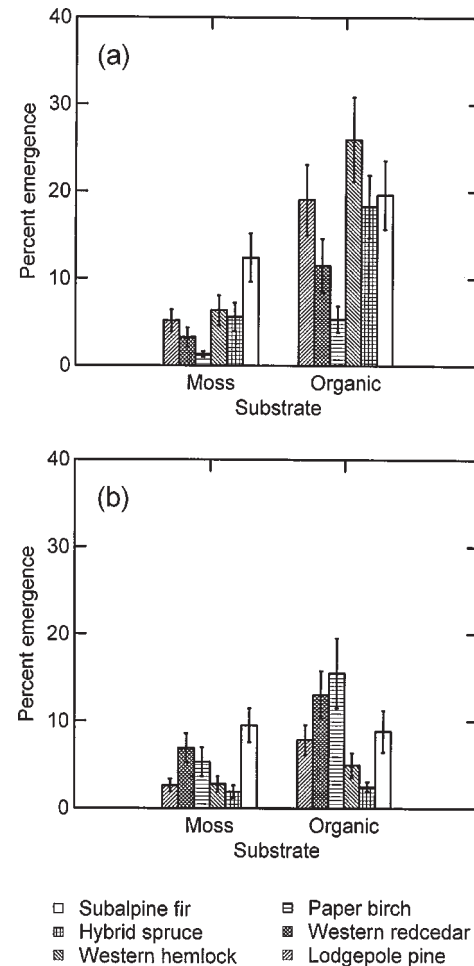


higher in the south versus the understory position off the south end of the gap (Table 3).

In general, total emergence was highest on the organic substrate (Figs. 3a and 3b, Table 3). Overall, emergence of paper birch on organic substrate compared favourably with that of western redcedar and western hemlock, despite reported preferences for mineral seedbeds (Peterson et al. 1997). There were two exceptions to the trend of superior emergence on the organic substrate. There was no evidence for substrate preference by subalpine fir ($p = 0.28$; Table 3), and western redcedar had higher (though not significant) total emergence on the moss substrate at the middle position of the gap (Table 2). Finally, average emergence on the organic substrate was significantly higher in the south and understory positions than the north and middle positions for all species except paper birch (Table 3).

Although there was an indication that differences in emergence between substrates depended to some extent on gap

Fig. 3. Mean percent emergence of the 1995 (a) and 1996 (b) cohorts by tree species and substrate. Error bars are 1SE.



position for two of the species (lodgepole pine, $p = 0.002$; western redcedar, $p = 0.012$), gap position differences and substrate differences (with the exception of subalpine fir) were highly significant for all species (Table 3) suggesting the main effects were most important.

The trend of increasing emergence from north to south and understory was most obvious in 1995 (Figs. 2a and 2b), a year with little rain during all of May and early June (D. Maloney, unpublished data). In 1996, when May and June were wetter, the trend was less obvious. Despite the wetter spring in 1996, total emergence was significantly less than in 1995 for subalpine fir, hybrid spruce, western hemlock, and lodgepole pine; only paper birch and western redcedar showed higher emergence than in 1995 (Tables 2 and 3).

Growing season light in the north, middle, and south positions and the understory off the south end of the gap averaged 34.3 ± 1.2 , 36.8 ± 2.9 , 20.0 ± 1.4 , and $9.7 \pm 0.6\%$ of full sun, respectively (mean \pm SE, $n = 8$). In 1996, average seasonal soil moisture ranged between 52 and 80% of fresh weight, ranking from lowest to highest as follows: north end = understory < middle < south end. In 1996, average soil temperature (May and June) at 5 cm depth on moss seedbeds ranged from a low of 9°C under the canopy at the south end

Table 2. Percentage of applied seed that emerged by gap position, substrate, and year for the six tree species.

Position in gap	Substrate	Pine		Redcedar		Birch		Hemlock		Spruce		Subalpine fir	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
1995 cohort													
North	Moss	0.5	0.33	0.1	0.13	0.8	0.25	0.4	0.26	0.0	0.00	0.1	0.13
	Organic	0.8	0.31	0.6	0.38	1.6	1.22	2.5	1.20	1.0	0.73	0.5	0.38
Middle	Moss	3.0	1.16	4.3	3.13	1.6	0.50	1.3	0.98	2.5	1.41	4.4	3.81
	Organic	4.8	1.72	3.5	1.64	6.6	2.00	17.4	7.31	10.1	5.41	5.1	2.59
South	Moss	14.5	2.89	8.3	2.17	2.8	0.94	19.0	4.19	13.8	4.86	28.6	6.29
	Organic	37.9	8.67	31.6	7.48	11.3	4.83	49.4	5.86	31.4	7.39	40.1	7.56
Understory	Moss	2.6	1.07	0.4	0.26	0.1	0.13	4.8	1.63	6.1	2.49	16.5	3.25
	Organic	32.8	7.65	10.1	5.51	1.8	1.33	34.6	12.09	30.6	6.67	32.6	6.82
Total		12.1	2.28	7.4	1.72	3.3	0.80	16.2	2.83	11.9	2.11	16.0	2.44
1996 cohort													
North	Moss	0.5	0.19	0.1	0.13	2.1	0.88	0.3	0.16	0.0	0.00	5.5	2.10
	Organic	5.3	2.06	1.4	0.50	5.2	2.70	1.4	0.78	1.0	0.38	5.0	3.56
Middle	Moss	2.0	0.87	6.5	3.63	5.6	1.89	2.2	1.09	0.8	0.41	10.5	2.65
	Organic	4.4	1.68	2.8	0.97	21.3	9.31	1.8	0.53	0.9	0.35	5.9	3.45
South	Moss	7.8	1.81	16.7	3.79	13.3	5.45	6.1	2.92	5.0	2.47	11.4	5.93
	Organic	9.1	3.78	29.6	5.74	31.1	10.42	5.8	1.73	3.7	1.29	15.8	7.42
Understory	Moss	0.1	0.13	4.2	1.18	0.4	0.38	2.5	1.14	1.9	0.85	10.7	4.37
	Organic	12.7	4.86	18.4	4.32	4.4	2.07	10.8	4.66	4.4	1.40	8.6	3.54
Total		5.2	0.98	10.0	1.63	10.4	2.23	3.8	0.82	2.2	0.45	9.2	1.54

Table 3. Analysis of variance of total number of emergents at the end of the first growing season by gap position, substrate, year, and their interactions.

Source of variation	df	Lodgepole pine	Western redcedar	Paper birch	Western hemlock	Hybrid spruce	Subalpine fir
Gap position	3	15.291 (<0.001)	21.591 (<0.001)	6.972 (0.002)	13.447 (<0.001)	13.892 (<0.001)	30.918 (<0.001)
North + middle vs. south + understory	1	36.744 (<0.001)	39.428 (<0.001)	0.218 (0.645)	33.631 (<0.001)	37.144 (<0.001)	85.264 (<0.001)
North vs. middle	1	2.189 (0.154)	4.383 (0.049)	4.328 (0.050)	3.157 (0.090)	3.408 (0.079)	4.659 (0.043)
South vs. understory	1	6.940 (0.015)	20.962 (<0.001)	16.370 (0.001)	3.553 (0.073)	1.125 (0.301)	2.832 (0.107)
Substrate	1	32.034 (<0.001)	16.707 (0.001)	28.133 (<0.001)	26.625 (<0.001)	24.233 (<0.001)	1.230 (0.280)
Substrate × gap position	3	6.973 (0.002)	4.668 (0.012)	2.483 (0.089)	1.910 (0.159)	2.066 (0.135)	1.231 (0.323)
Organic substrate:							
North + middle vs. south + understory	1	53.431 (<0.001)	68.468 (<0.001)	1.565 (0.225)	40.845 (<0.001)	57.700 (<0.001)	71.873 (<0.001)
Organic vs. moss							
North + middle	1	2.924 (0.102)	0.121 (0.731)	9.807 (0.005)	5.198 (0.033)	4.607 (0.044)	0.293 (0.594)
South + canopy	1	39.617 (<0.001)	29.510 (<0.001)	19.093 (<0.001)	25.174 (<0.001)	23.188 (<0.001)	4.450 (0.047)
Year	1	26.526 (<0.001)	11.029 (0.003)	49.389 (<0.001)	40.721 (<0.001)	45.309 (<0.001)	5.824 (0.025)
Gap position × year	3	14.400 (<0.001)	2.465 (0.090)	6.209 (0.003)	8.898 (0.001)	7.752 (0.001)	13.520 (<0.001)
Substrate × year	1	3.998 (0.059)	0.565 (0.460)	5.751 (0.026)	16.527 (0.001)	11.715 (0.003)	4.930 (0.038)
Gap position × substrate × year	3	5.395 (0.007)	1.054 (0.390)	0.210 (0.888)	1.289 (0.304)	2.182 (0.120)	0.363 (0.780)

Note: Values are *F* ratios, with *p* values given in parentheses. Data were arcsine transformed prior to analysis.

Table 4. Parameter estimates of the 1996 cohort for predicted total seedling emergence at the end of the first growing season using the equations $y = ae^{(b-c)}$ and $y = ae^b$ (for subalpine fir and paper birch), where a is the intercept, b is the soil moisture parameter, and c is the percentage of full sun parameter.

Species	Substrate	Parameters of nonlinear regression				
		a	b	c	r^2	n
Subalpine fir	Both	0.32	0.05		0.05	62
Western redcedar	Moss	0.01	0.14	0.10	0.79	32
	Organic	0.00	0.22	0.03	0.67	32
Lodgepole pine	Moss	0.00	0.28	0.07	0.62	32
	Organic	1.12	0.04	0.02	0.11	31
Paper birch	Moss	0.00	0.14		0.20	32
	Organic	0.01	0.11		0.24	32
Western hemlock	Moss	0.00	0.14	0.05	0.28	32
	Organic	0.00	0.32	0.49	0.50	32
Hybrid spruce	Moss	0.00	0.30	0.14	0.56	32
	Organic	0.82	0.04	0.06	0.28	32

Note: All models were significant at $p < 0.0005$.

of the gap to a high of 12.6°C in the north position. Soil temperatures on the organic seedbeds were less than 0.5°C lower than the moss, at each gap position. Temperatures were approximately 2°C lower at 10 cm depth, with no differences observed between the two seedbed substrates.

Regression analysis was used to examine the relationship between soil moisture and temperature, and light availability, on seedling emergence of the 1996 cohort. Significant nonlinear relationships ($p < 0.0005$) were found between average soil moisture (May through August), percentage of full sun, and total emergence of western redcedar, lodgepole pine, western hemlock, and hybrid spruce and soil moisture alone for paper birch and subalpine fir (Table 4). Soil temperature did not contribute significantly to the models. Separate models were fit for moss and organic seedbeds for all species except subalpine fir, which exhibited little substrate preference. The regressions accounted for 5 (subalpine fir) to 70% (western redcedar) of the variation in total emergence. These models suggest that seedling emergence has a threshold response to soil moisture, remaining low at low soil moisture levels and increasing exponentially once a critical level has been reached. Increases in light (corresponding to gap position) had a negative effect on emergence (Table 4).

First summer seedling survival

By mid-September, survival of the 1995 cohort (seeded spring 1995) ranged between 45% (paper birch) and 65% (western hemlock) (Fig. 4a). While the cause of individual seedling mortality was not recorded, mortality was attributable to fungal attack, herbivory, desiccation of radicles, and mechanical damage. Herbivory and seed predation were more prevalent near canopy edges and in the understory. Survival of the 1996 cohort (seeded fall 1995) compared favourably with 1995, ranging from 45% (hybrid spruce and lodgepole pine) to 64% (paper birch) by mid-September (Fig. 4b).

First summer survival of all six species was more strongly influenced by position in gap (generally lower p values) than by substrate type and, with the exception of paper birch, did

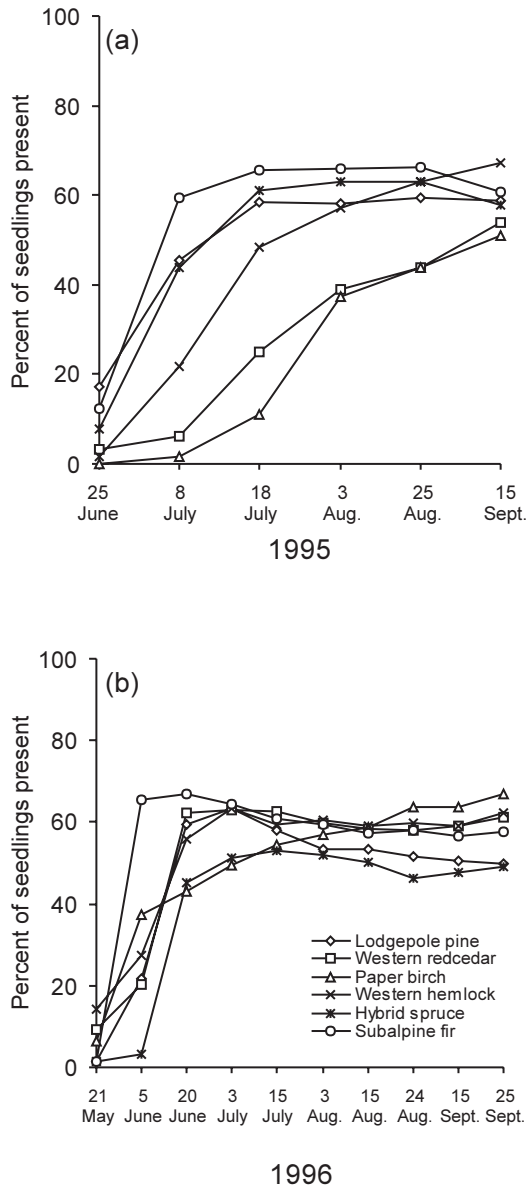
not differ significantly between years (Figs. 5a, 5b, 6a, and 6b; Tables 5 and 6). Summer survival followed patterns similar to that of emergence inside the canopy gap: a trend of greater survival from the sunny north to the shady south position (Figs. 5a and 5b, Table 5). On average, seedling survival was significantly lower in the north and middle positions versus the south and understory positions for western redcedar, western hemlock, hybrid spruce, and subalpine fir (Table 6). Although the north and middle gap positions shared a similar light environment, survival of lodgepole pine, western redcedar, western hemlock, and hybrid spruce were significantly lower in the north end (Table 6). Unlike emergence, seedling survival in the understory off the south end of the gap was not consistently intermediate among the canopy gap positions. Survival of paper birch and lodgepole pine (the two most shade-intolerant species) was poorest in the understory (Figs. 5a and 5b, Table 6). Survival of the remaining species was poorest in the north position.

Averaged across all four gap positions, survival of western redcedar, western hemlock, hybrid spruce, and subalpine fir was best on the organic substrates (Figs. 6a and 6b, Table 6), while lodgepole pine showed a weak preference for organic substrates ($p = 0.053$). When the preferred organic substrate was partitioned by gap position, hybrid spruce and subalpine fir survival were best in the south and understory positions versus the north and middle positions (Table 6). Comparing the north to the middle positions, there was generally a lack of substrate preference for survival (Table 6) with only spruce favouring the organic substrate ($p = 0.048$). In the understory off the south end of the gap, paper birch survival was strongly affected by substrate (Tables 5 and 6) with very poor survival occurring on the moss substrate. The opposite situation occurred at the north position where birch survival was best on the moss substrate, indicated by a significant substrate \times gap position interaction.

Overwinter and second season seedling survival

The mean percentage of 1995 spring-seeded cohorts surviving the winter decreased by 4% (western red cedar) to

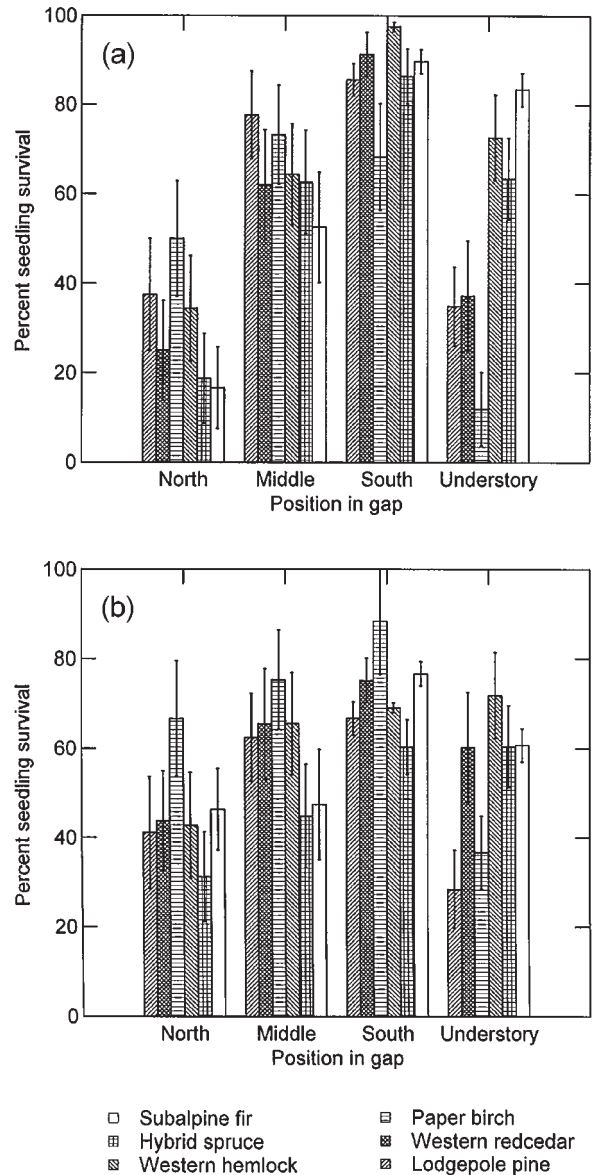
Fig. 4. Percentage of seedlings present during the first summer after emergence for the 1995 (a) and 1996 (b) cohorts.



12% (western hemlock) of prewinter values, with an additional decline over the summer of 1996 by another 6% (subalpine fir) to 11% (western hemlock); tapering off in early August. By the end of the growing season, percentages of total surviving seedlings ranged from 32% (paper birch) to 47% (subalpine fir). During the first winter and early spring, frost heaving, freezing, and herbivory were the primary mortality factors in all gap positions. Herbivory was most noticeable in positions near or under the canopy, whereas frost heaving was a problem on the organic substrate and not the undisturbed forest floor. Microsite flooding, fungal attack, and herbivory continued to cause mortality during the second growing season.

Of the six species examined, only western hemlock showed an indication that overwinter ($p = 0.037$) and second summer ($p = 0.009$) survival differences between substrates depended on gap position. For all species, gap position

Fig. 5. Percentage of seedlings surviving the first summer by tree species and gap position for the 1995 (a) and 1996 (b) cohorts. Error bars are 1SE.

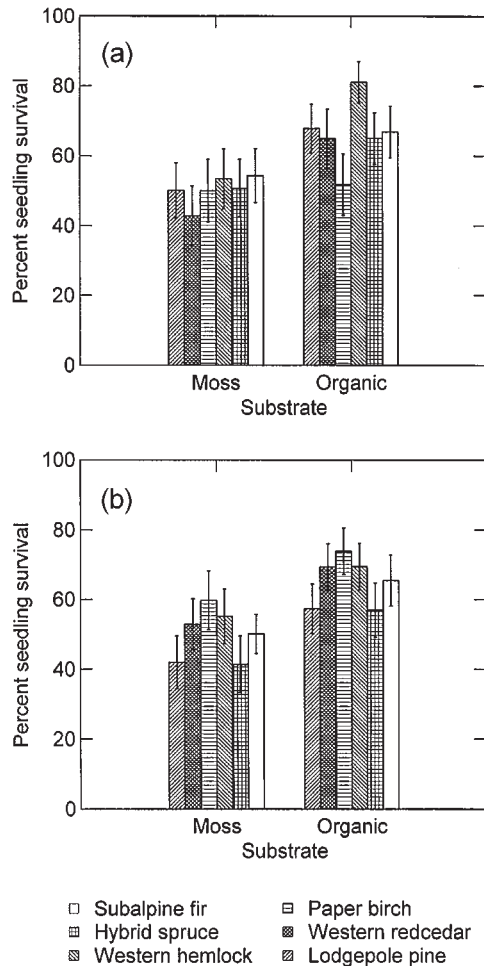


seemed to be the most important determinant of survival with the importance of substrate decreasing over time. The organic substrate was either neutral or the most favourable for survival; there were no situations where survival was significantly better on the moss substrate. The organic substrate was most important for lodgepole pine and western hemlock in the north portion of the gap and for western redcedar in the south and understory. The middle and south positions were generally the best location for survival of all the species. Survival of all species but subalpine fir was much lower in the understory off the south end of the gap.

Predation study

Variability in predation response among experimental blocks, among gap positions, and between years was high. In general, we found that predation of seeds of all species

Fig. 6. Percentage of seedlings surviving the first summer by tree species and substrate for the 1995 (a) and 1996 (b) cohorts. Error bars are 1SE.



was highest in the understory off the south end of the gap. The most favoured seed for predation seemed to be western hemlock, hybrid spruce, and subalpine fir. These species had significantly ($p < 0.05$) lower emergence in uncaged plots. We found no evidence that caging increased emergence of lodgepole pine, western redcedar, and paper birch. The use of cages was not completely successful in excluding entry of seed predators and, in some cases, may have served to provide shelter for seed predators during the winter of 1995–1996. Rodent populations were on the upswing in 1996 (D. Steventon, personal communication), and we found evidence of seed predators (droppings and seed husks) inside some of the cages. However, overall we believe caging reduced variation due to predation in the experiment.

Natural seed rain study

Trends observed for ingress of naturally seeded emergents were similar to those for the main experiment. No natural regeneration of hybrid spruce, subalpine fir, or lodgepole pine was observed in either year. No western redcedar emergents were observed in 1995. All western redcedar emergents recorded in 1996 were found on organic substrates in either the south position of the gap or under the canopy off the

south end. There were significantly ($p < 0.05$) more hemlock and birch emergents in 1996 than 1995. Most hemlock and birch emergents were on organic substrate in the south and understory positions, but emergents of both species were found on all substrates and gap positions. Paper birch emergents comprised the largest component of natural seed rain recorded.

Substrate variability study

To test whether variation in germination within a given seedbed substrate could be greater than variation between positions in the gap, we closely examined germination of western redcedar and paper birch on replicated substrates in the middle position. We found no significant differences in emergence of either species within a given seedbed substrate (moss or organic). This indicated that observed differences in the main experiment on a given substrate are due to gap position effects, not random variability within the substrate.

Discussion

Our study clearly demonstrated that the position a seed falls inside or outside a canopy gap and the substrate on which it lands can profoundly influence emergence success, subsequent establishment, and early survival of the major tree species in northwestern British Columbia. Even though the six species we studied span a wide range of shade tolerances we found little evidence of within-gap partitioning (e.g., Denslow 1980) among these tree species. Our results were similar to those of Sipe and Bazzaz (1995) and Gray and Spies (1996) in northeastern and Pacific Northwest U.S. forests, respectively. We observed a strong gradient in total emergence and early survival for all species within the gaps with the poorest performance in the sunny north end to the best in the shaded south end of the gaps. Emergence in the intact forest off the south end of the canopy gap was excellent, but survival rapidly decreased with time, especially for the more shade-intolerant species. This differential survival or species trade-off based on shade-tolerance ranking (Kobe and Coates 1997) could result in gap partitioning. The relatively poorer emergence of paper birch in the forest understory may be related to insufficient seed reserves (smallest seed size of the six species) precluding adequate root and shoot growth under these low light conditions (Salisbury 1942).

Successful regeneration from seed increased with forest floor disturbance (organic seedbed) and soil moisture and decreased as a function of increasing light availability. The only exception to these trends was subalpine fir, which showed little preference for seedbed substrate, although germination was enhanced by increased shade. The response of subalpine fir was consistent with studies by Day (1964), Cui (1991), and Burton (1997) that report germination on all substrates with little preference for any one, possibly because of the species access to seed reserves (largest seed size) and rapid root growth (Day 1964; Knapp and Smith 1982). We observed successful emergence of birch on both undisturbed forest floor and organic substrates, whereas most other studies have reported that a mineral soil seedbed is required for good regeneration of birch (see review by Peterson et al. 1997; but see Zasada et al. 1983, 1992).

Table 5. Percent of emergents surviving by gap position, substrate, and year for the six tree species.

Position in gap	Substrate	Pine		Redcedar		Birch		Hemlock		Spruce		Subalpine fir	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
1995 cohort													
North	Moss	25	16.4	13	12.5	63	18.3	25	16.4	0	0.0	13	12.5
	Organic	50	18.9	38	18.3	38	18.3	44	17.5	38	18.3	21	14.0
Middle	Moss	69	15.6	63	18.3	75	16.4	36	17.6	63	18.3	36	17.7
	Organic	87	12.4	62	18.0	72	16.0	93	4.6	63	15.4	69	16.2
South	Moss	86	6.6	84	9.4	63	18.3	97	1.9	76	11.4	86	4.1
	Organic	85	3.9	99	0.8	74	16.2	98	0.9	97	1.0	93	3.4
Understory	Moss	20	10.3	13	12.5	0	0.0	56	16.8	64	15.2	82	2.7
	Organic	49	12.8	62	18.1	24	15.6	90	5.0	63	11.3	85	7.2
Total		59	5.4	54	6.1	51	6.2	67	5.4	58	5.5	61	5.4
1996 cohort													
North	Moss	38	18.3	25	16.4	75	16.4	38	18.3	13	12.5	43	11.1
	Organic	45	14.0	63	18.3	58	13.8	48	18.2	50	18.9	49	18.6
Middle	Moss	50	15.6	67	16.4	68	15.3	65	15.2	44	17.5	45	11.5
	Organic	75	12.7	64	14.8	82	11.9	66	14.9	46	17.7	50	15.7
South	Moss	68	6.2	64	6.7	83	12.3	52	16.5	52	15.4	60	12.3
	Organic	65	14.8	86	4.1	94	3.5	86	6.4	69	14.0	94	4.1
Understory	Moss	13	12.5	56	13.7	13	12.5	66	12.3	58	17.1	53	11.3
	Organic	44	14.6	64	12.1	61	17.9	78	8.9	63	11.6	69	12.3
Total		50	5.2	61	5.0	67	5.4	62	5.2	49	5.6	58	4.7

Increased emergence in more shaded sites and on disturbed substrates has been previously reported for several conifer species (Garman and Orr-Ewing 1949; Alexander 1984; Cui and Smith 1991; Little et al. 1994; Burton 1997). Our regression analyses suggest that differences in emergence response by gap position was related to a gradient in soil moisture across the gap. Except for the middle of the summer when the sun was high, the shaded south end of the gap received little direct sunshine, and soil moisture was higher relative to the north and middle gap positions. Soil moisture was again low (canopy interception) in the understory off the south end of the gaps, but emergence was high. With less light under the canopy, there was, however, less rapid drying out of the seedbed substrates than in the exposed northern end of the gap. This suggests that surface substrate drying was the major limitation to successful emergence, and the organic substrate generally retained moisture better than the moss substrate providing the conditions needed for higher rates of emergence in all six species. The strong response in emergence by gap position and seedbed substrate was consistent for both years.

Although substrate conditions played an important role in emergence success for all species, establishment and subsequent survival was largely controlled by gap position (a surrogate for a resource availability and a gradient in abiotic conditions, particularly in northern latitudes), and responses were more species specific. Seedling survival was greatest for each species in the south end of the gaps where soil moisture remained highest and light levels of approximately 20% full sun were adequate to maintain whole-seedling carbon balance. The two most shade-intolerant species (lodgepole pine and paper birch) had the lowest survival in the understory off the south end of the gap where light levels of approximately 10% full sun were too low for survival. The generally poor survival of all species in the exposed north

position was likely due to lack of protection from heat and drought, two often cited reasons for early mortality of these species (Garman and Orr-Ewing 1949; Day 1964; Eis 1965, 1967; Waldron 1966; Putman and Zasada 1986; Cui and Smith 1991). The strong response in emergence by gap position and seedbed substrate was consistent for both years.

The requirements for emergence and then subsequent survival of these species appear to be "discordant" in the sense of Schupp (1995). Substrate type was most important for emergence, but less so for survival and the best location for emergence was not always the best location for survival of seedlings. Emergence was clearly highest in the understory and shaded south position of the gap. Survival was highest in the south position, but poor in the forest understory, particularly for the shade-intolerant species. Conflicts in seed-seedling requirements for paper birch have been previously described by Peterson et al. (1997). This discordance appears to be a widespread phenomenon among western North American forest species (e.g., Day 1964; Tappeiner et al. 1997) and may become even more apparent over time, especially at low light and hence low growth where differential survival among these species occurs (Kobe and Coates 1997).

Predation of seeds is commonly reported to cause high seed loss (Garman and Orr-Ewing 1949; Johnson and Fryer 1996) and was the cautionary reason for our using caged plots in the study. Our predation subexperiment showed that seed consumers were really only a problem in the intact forest, presumably because it provided some cover from predators, and only for subalpine fir, western redcedar, and western hemlock. Year to year variation in total emergence of a fixed seed supply might be explained by climatic variation or the activity of seed consumers. The 1996 growing season was wetter than in 1995, which should have enhanced total emergence; however, there was a general

Table 6. Analysis of variance for percent of seedlings surviving to the end of the first summer by gap position, substrate, year, and their interactions.

Source of variation	df	Lodgepole pine	Western redcedar	Paper birch	Western hemlock	Hybrid spruce	Subalpine fir
Gap position	3	8.123 (0.001)	8.364 (0.001)	7.543 (0.001)	6.689 (0.002)	6.887 (0.002)	8.815 (0.001)
North + middle vs. south + understory	1	0.068 (0.797)	4.807 (0.040)	2.857 (0.106)	12.283 (0.002)	12.075 (0.002)	21.812 (<0.001)
North vs. middle	1	8.813 (0.007)	8.905 (0.007)	1.329 (0.262)	6.587 (0.018)	7.414 (0.013)	3.184 (0.089)
South vs. understory	1	15.488 (0.001)	11.380 (0.003)	18.444 (0.000)	1.197 (0.286)	1.171 (0.291)	1.449 (0.242)
Substrate	1	4.214 (0.053)	5.299 (0.032)	1.190 (0.288)	5.809 (0.025)	5.218 (0.033)	7.085 (0.015)
Substrate \times gap position	3	0.975 (0.423)	0.988 (0.418)	3.981 (0.022)	0.183 (0.907)	1.988 (0.147)	0.463 (0.711)
Organic substrate:							
North + middle vs. south + understory	1	0.154 (0.699)	2.884 (0.104)	0.015 (0.903)	3.648 (0.070)	5.551 (0.028)	20.991 (<0.001)
Organic vs. moss							
North + middle	1	2.814 (0.108)	1.535 (0.229)	1.254 (0.276)	3.443 (0.078)	4.405 (0.048)	3.063 (0.095)
South + understory	1	1.502 (0.234)	4.067 (0.057)	7.089 (0.015)	2.412 (0.135)	1.281 (0.271)	4.057 (0.057)
Year	1	3.142 (0.091)	1.010 (0.326)	5.477 (0.029)	0.472 (0.500)	0.903 (0.353)	0.067 (0.799)
Gap position \times year	3	0.814 (0.500)	2.995 (0.054)	0.929 (0.444)	1.767 (0.184)	1.132 (0.359)	6.444 (0.003)
Substrate \times year	1	0.035 (0.835)	0.354 (0.558)	0.872 (0.361)	1.158 (0.294)	0.029 (0.865)	0.000 (0.990)
Gap position \times substrate \times year	3	0.364 (0.779)	1.083 (0.378)	0.245 (0.864)	2.102 (0.131)	0.035 (0.991)	1.792 (0.180)

Note: Values are *F* ratios, with *p* values given in parentheses. Data were arcsine transformed prior to analysis.

decline in total emergence of the 1996 cohort compared with the 1995 cohort (Fig. 2). Seeds of the 1996 cohort were available for consumption for a much longer time period than seeds of the 1995 cohort. Increased overwinter and spring predation within cages may have contributed to the decline in total emergence of subalpine fir, western hemlock, hybrid spruce, and lodgepole pine in 1996 compared with the 1995 cohort.

Our natural regeneration subexperiment confirmed that the use of natural seed sources can be problematic when comparing species success across the environmental gradients created in gaps and the forest understory. No naturally regenerated hybrid spruce, subalpine fir, or lodgepole pine were observed over the 2 years of the study even though parents were present and we had provided suitable seedbed substrates. Seed source limitation in partially logged forests was also demonstrated in a companion study (P.T. Lepage, C.D. Canham, K.D. Coates, and P. Bartemucci, unpublished data) where presence of canopy trees reduced effective dispersal distances of the species in our study. The higher number of natural western hemlock and paper birch germinants on the organic substrate at the south end of the gap and under the canopy was consistent with findings in our direct seeding experiment.

In situations where natural regeneration is the preferred regeneration practice, a moderate level of ground cover disturbance will result in a vast improvement in emergence of these six tree species. Exposed mineral soil is not required to achieve good regeneration of these species. Despite the differences among the species in shade tolerance, seed size, and successional status, differences in seedling density were small during emergence and species partitioning along the environmental gradient of these gaps was becoming apparent through differential survival. Although this study was confined to investigations on seedling emergence and early survival, mixed forest management strategies must consider the range in shade tolerance of these species and consequent effects of gap size and gap position on future growth rates and canopy recruitment. High tree species diversity will be facilitated by distributing gaps in locations with a mix of seed trees. Because of the range of shade tolerances in the ICH tree species, successful recruitment into the canopy will depend on a wide range of gap sizes and hence light environments than the single gap size used in this study.

In conclusion, the strong north-south environmental gradient in gaps of northern latitude forests offer diverse habitat conditions for the regeneration of trees, with shaded south gap positions being most favourable for emergence of all the

tree species studied. Forest floor disturbance had direct effects on seedbed quality with successful germination of all species best on organic substrates, with the exception of subalpine fir. Subsequent survival, however, was affected more by gap position than substrate type. Position inside or outside of a gap directly affects early mortality by its influence on microclimate and resource availability. Early mortality, in turn, resulted in species partitioning in the understory of the intact forest, but has yet to clearly do so within the gaps. To predict regeneration success in these forests, for either silvicultural purposes or to permit a better understanding of community dynamics and succession, it is important to consider the influence of position inside and outside of gaps and the nature of the seedbed substrate.

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