Journal of Vegetation Science 13: 685-696, 2002
© IAVS; Opulus Press Uppsala. Printed in Sweden

Gap disturbances in northern old-growth forests of British Columbia, Canada

Bartemucci, Paula[1,2]; Coates, K. Dave[1*]; Harper, Karen A.[2] & Wright, Elaine F.[1,3]

[1]*British Columbia Forest Service, Research Section, Bag 5000, Smithers, British Columbia, V0J 2N0, Canada;* [2]*Groupe de recherche en écologie forestière, Université du Québec à Montréal, CP 8888 Succ. A, Montréal, Québec, H3C 3P8, Canada;* [3]*Department of Conservation, Southern Regional Office, P.O. Box 13-049, 3/137 Kilmore St., Christchurch, New Zealand;* [*]*Corresponding author; Fax +12508477217; E-mail dave.coates@gems7.gov.bc.ca*

Abstract. We characterized the abundance, size and spatial patterning of canopy gaps, as well as gap-forming processes and light availability in boreal, sub-boreal, northern temperate and subalpine old-growth forests of northwestern British Columbia. The proportion of area in canopy gaps ranged from 32% in northern temperate forests to 73% in subalpine forests. Evenly distributed developmental gaps were dominant but permanent openings created by edaphic components and by shrub communities were also common, particularly in sub-boreal forests. Abundant gaps, large gap sizes, high numbers of gap makers per gap and frequent gap expansion events suggest that gaps have long tenure in these forests. Snapped stems and standing dead mortality were the most common modes of mortality in all forest types resulting in little forest floor disturbance, creating few germination sites for seedling establishment. We found high mean light levels (16-27% full sun) and little difference between non-gap and gap light environments. Our results suggest that gap dynamics in these forests differ fundamentally from those in temperate and tropical forest ecosystems.

Keywords: Developmental gap; Edaphic gap; Gap dynamics; Gap maker; Gap size distribution; Small-scale disturbance; Spatial pattern; Three-term local quadrat variance; Tree mortality.

Nomenclature: Hitchcock & Cronquist (1994).

Introduction

The importance of small-scale gap disturbances in forest dynamics has been well-established in tropical and temperate hardwood forests (Pickett & White 1985; Platt & Strong 1989) and, to a lesser extent, in the conifer dominated coastal forests of western North America (Spies et al. 1990; Lertzman et al. 1996; Ott & Juday 2002) where large-scale disturbances are rare. Despite Sernander's (1936) early recognition of the importance of gap disturbances in boreal forests of Sweden, gap disturbances have been largely ignored in northern latitude forests, especially those with frequent large stand-destroying fires (Leemans 1991). This historical view of northern forests is undergoing a transition as new studies identify the extent and function of small-scale disturbances in northern latitude forests (Hytteborn et al. 1991; Hofgaard 1993; Kuulavainen 1994; Kneeshaw & Bergeron 1998; Cumming et al. 2000; Kubota 2000; McCarthy 2001).

Small-scale disturbance in forests has generally been characterized in older forests by the presence of canopy gaps, their frequency, age, origin and size distribution. The spatial patterning of gaps within a forest has received less study. Gaps showed either aggregated (Lawton & Putz 1988; Battles et al. 1995; Chen & Bradshaw 1999) or random (Ward & Parker 1989; Liu & Hytteborn 1991) spatial patterns in other forested systems. Very few studies have quantified the extent of old forest or any of these basic descriptors of small-scale disturbances in the forests of northern British Columbia (Coates & Burton 1997). We sampled in four major forest types with varying fire return intervals, stand composition and climate. We propose that patterns and processes of gap disturbances, and the extent of these disturbances differ among these major forest types. For example, Lertzman et al. (1996) found that the prevalence and characteristics of gaps in coastal temperate rainforests varied according to altitude, site factors and stand age.

Many studies have examined the functional role of small-scale disturbances on resource availability (Platt & Strong 1989). Light is the principal resource affected in tropical and temperate forests (Denslow & Hartshorn 1994; Pacala et al. 1996) although below-ground resources are also affected. In our study, we chose to focus on light availability since it plays a crucial role in tree dynamics in high-latitude forests (Lieffers et al. 1999). High latitude forests with their lower sun angles and frequent openings between tall, narrow, conical crowns of conifers allow greater penetration of light into the understorey than that observed in tropical and southern temperate forests (Terborgh 1985; Canham et al. 1990, 1999). In tropical and southern temperate forests, gap disturbances create patches of increased light availability in an otherwise uniform low-light environment (Chazdon & Fetcher 1984). We hypothesized that differences in light availability between gap and non-gap environments will be minimal in high-latitude forests.

Specifically, our study objectives were: (1) to assess the extent of old forest and the amount of gap disturbance in forests of northern British Columbia, (2) to identify the gap-forming processes, (3) to determine the spatial patterning of gaps and (4) to characterize understorey light regimes.

Study area and forest types

Our study area spans a large portion of northwestern British Columbia, Canada (Table 1). The landscape varies from gently rolling plateaus to mountainous areas. Soils on upland forest types developed mainly from morainal parent materials and are generally Luvisols, Podzols or Brunisols (Anon. 1987). The dominant humus forms are Hemimors (5-15 cm thick, Green et al. 1993). Forests were dominated by conifers at a canopy height of 15-30 m. Understories had well-developed moss layers and poor to moderately developed shrub and herb layers.

We stratified the study area into four broad areas of similar climate and vegetation (‘forest types’) using British Columbia’s ecosystem classification system: ‘boreal’, ‘sub-boreal’, ‘subalpine’ and ‘northern temperate’ forests (Table 1). Boreal forests have a northern continental climate with frequent outbreaks of arctic air masses, very cold long winters and short growing seasons (Banner et al. 1993). Older stands are dominated by *Picea glauca* and *P. mariana* with *Pinus contorta* var. *latifolia* and *Abies lasiocarpa* as co-dominant species (Table 1). Sub-boreal forests occur further south on gently rolling plateaus and have a milder, boreal continental climate. Forests are dominated by *A. lasiocarpa*, *P. glauca* × *engelmannii* and *P. contorta* var. *latifolia.* Subalpine forests, comprised of the same tree species, are found at higher altitudes above the sub-boreal forests. Winters are colder, snow packs persist longer and

Table 1. Ecosystem classification and climate data of forest types; locations, general characteristics and sampling information for sampled forest stands.

	Boreal	Sub-boreal	Sub-alpine	Northern temperate
Forest type characteristics				
Biogeoclimatic ecosystem classification[1]	BWBSdk	SBSmc2	ESSFmc	ICHmc2
Dominant tree species[2]	Pg, Pm, Pc, Al, Pt	Al, PgxPe, Pc	Al, PgxPe, Pc	Th, Tp, Al, Aa, PgxPs
Fire return interval (years)[3]	75-150	100-150	200-300	150-250
Mean annual precipitation (mm)[4]	355-445	575	441	549
Mean annual temperature (°C)[4]	–2.1 to –1.4	1.5	–0.7	3.8
Mean annual snowfall (cm)[4]	162-204	237	249	207
Frost-free days[3]	51-83	116	no data	117
Characteristics of sampled stands				
Stand age (years)	140-180	150-200	200-375	300-370
Latitude (N°)	57° 50'-59°03'	54° 55'-55° 05'	54° 45'-55° 15'	55° 22'-55° 70'
Longitude (W°)	130° 15'-130° 22'	126° 24'-126° 35'	126° 45'-127° 20'	127° 50'-128° 40'
Altitude (m a.s.l.)	700-950	800-1000	1050-1200	200-600
Total transect length (m)	7207	7300	7378	6350
Transect lengths for spatial analysis (m)	384-500	299-814	450-757	419-750
Number of gaps sampled	120	120	120	156

[1] Biogeoclimatic units (Banner et al. 1993; Pojar et al. 1987): BWBSdk = Boreal White and Black Spruce, dry cool subzone; SBSmc2 = Sub-boreal Spruce, moist cold subzone, Babine variant; ICHmc2 = Interior Cedar-Hemlock, moist cold subzone, Hazelton variant; ESSFmc = Engelmann Spruce-Subalpine Fir, moist cold subzone. [2] Species codes: Pt = *Populus tremuloides*, Aa = *Abies amabilis*, Al = *Abies lasiocarpa*, Tp = *Thuja plicata*, Th = *Tsuga heterophylla*, Pc = *Pinus contorta*, Pm = *Picea mariana*, PgxPe = *Picea glauca* × *engelmannii*, Pg = *Picea glauca*, PgxPs = *Picea glauca* × *sitchensis* or *Picea glauca* × *engelmannii* × *sitchensis*; [3] Parminter (1990); [4] Normalized climatic data from Environment Canada (Anon. 1980).

summers are cooler, shorter and more moist than adjacent low altitude sub-boreal forests. Northern temperate forests occur further west at low to middle altitudes and are transitional between sub-boreal forests and coastal temperate rain forests with warm summers and cool, wet winters. Older stands are dominated by *Tsuga heterophylla* and *Thuja plicata*.

Large-scale fire events are considered the dominant natural disturbance agent, with fire return intervals varying among the forest types (Table 1). Other agents of tree mortality include windthrow and snowloading, as well as bark beetle (*Dendroctonus rufipennis, D. ponderosae, Dryocoetes confusus*) and fungal infestations (e.g. *Inontonus tomentosus*) (Banner et al. 1993).

Methods

Old-growth forests were defined as forests older than 140 yr for sub-alpine, sub-boreal and northern temperate forest types and older than 120 years for the boreal forest type (Wells et al. 1998; MacKinnon & Vold 1998). These quantitative definitions identify ages when structural and biological characteristics typical of old growth forests begin to develop (Spies & Franklin 1991; MacKinnon & Vold 1998). The extent of old-growth was estimated by overlaying inventory and forest cover data on a map of forest types (after MacKinnon & Vold 1998).

We sampled four old-growth stands (5-100 km apart) within each forest type. Stands were relatively uniform in topography and soils, represented average soil moisture, nutrient regimes and had no evidence of human disturbance.

Forest stand sampling

We established three to nine parallel transects at 50 m intervals for a minimum of 1800 m per stand (except 950 m in one stand). We classified each metre of transect as canopy gap or closed canopy (as in Runkle 1982, 1992; Lertzman & Krebs 1991). We distinguished canopy gaps from interstitial spaces between crowns by the presence of canopy tree mortality or edaphic features. Canopy gaps were considered filled, and no longer gaps, when understorey trees which were released or established after gap formation reached two-thirds the height of the dominant tree canopy. We defined four types of canopy gaps: (1) ‘developmental’ (*sensu* Lertzman et al. 1996), the classic canopy gap defined as the vertical projection onto the ground of the opening in the forest canopy (Runkle 1982) resulting from the death of one or more canopy trees; (2) ‘edaphic’, gaps caused by edaphic or topographic features; (3) ‘shrub’, gaps maintained by well-established shrub communities and (4) ‘combination’, shrub gaps with tree mortality on their periphery. The proportion of each type of canopy gap was calculated as a percentage of the total transect distance in each forest stand (Runkle 1992), and combination gaps were broken down by their developmental and shrub components.

To measure light availability, hemispherical photographs were taken every 50 m along each transect for a total of 36-40 photographs per stand. We used a Nikon F2.8 true fish-eye lens at 1.0-1.5 m above the ground. For all forest types except sub-alpine forests, we recorded whether the photograph was taken in a gap or under closed canopy to allow for comparisons between ‘gap’ and ‘non-gap’ light environments.

Gap sampling

We randomly selected 30 canopy gaps per stand (excluding edaphic gaps) to assess gap size, mode of gap formation and gap maker characteristics. Gap borders were carefully delineated from the forest matrix by the presence of dead trees. Gap size was calculated using the formula for an ellipse (Runkle 1982). We did not correct for the sampling bias in line intersect methods, which favours large gaps (Runkle 1982), therefore small gaps may be underestimated. We recorded the number of gap makers present (a tree whose mortality created a gap, Runkle 1992) and the species, mode of mortality (snapped, uprooted or standing dead) and decay class of each gap maker. The decay class of gap makers was estimated qualitatively using physical characters observable in the field (Table 2; modified from Lertzman & Krebs 1991; Liu & Hytteborn 1991). Because decomposition rates differ among forest types and species, we used the number of decay classes of gap makers as a relative measure of the number of disturbance events that created each gap.

We also identified ‘fire survivors’, gap makers that survived the stand initiating wildfire and then persisted for extended periods. We distinguished fire survivors by their larger diameter, the presence of fire scars and the exclusion of regeneration immediately around the survivor (in comparison to the stand matrix).

Statistical analysis

To assess the spatial pattern of gaps in forest types, we introduce a new application for three-term local quadrat variance (3TLQV) which calculates the variance of a given variable, x, at different scales by sliding a window of three adjacent blocks of size b along the transect (Dale 1999):

$$V_3(b) = \sum_{i=1}^{n+1-3b} \left(\sum_{j=i}^{i+b-1} x_j - 2 \sum_{j=i+b}^{i+2b-1} x_j + \sum_{j=i+2b}^{i+3b-1} x_j \right)^2 / 8b(n+1-3b) \quad (1)$$

$V_3(b)$ = three-term variance for block size b
b = block size (m)
n = length of the transect (m).

In our study, x is the presence/absence of gaps with a value of 0 or 1, and V is the variance in the presence of gaps for different block sizes. Larger values of V indicate greater clumping of gaps at the scale given by the block sizes. We calculated the mean 3TLQV for five different block sizes (0-10, 0-20, 0-30, 0-40, 0-50 m) for the longest contiguous transect segment within each forest stand; transect segment lengths ranged from 299 to 814 m (Table 1). We standardized the 3TLQV by dividing it by the total variance along each transect segment (*sensu* Rossi et al. 1992), which allows comparisons of spatial pattern, independent of gap abundance. This analysis provides the scales at which spatial patterning of gaps occur (i.e. it is the scale or level of resolution at which gaps are clustered). The scale of pattern is apparent as a peak in the graph of V vs b, and represents half the distance between the centres of two gaps (or gap clusters). Separate analyses were performed for gap vs non-gap, and for each gap type except edaphic gaps, which were too rare to include in the analysis. Analyses were not performed if there were fewer than three gaps of a given type along a transect segment, resulting in missing values for some sites.

An index of whole growing season light availability was calculated from hemispherical photographs using GLI/C 2.0 software (Canham 1988). This index integrates the seasonal and diurnal distribution of solar radiation transmitted through the canopy into a single index of available light in units of percent of full sunlight for our growing season (mid-April to mid-September).

To examine differences among forest types (the main factor), stand-level variables (e.g. proportion of area in each gap type, 3TLQV and light availability) were subjected to a one-way ANOVA using a completely randomized design (Wilkinson et al. 1992). Means separation was performed using a Tukey's multiple comparison test. Gap-level variables (e.g. gap maker data, gap size) were subjected to the same one-way ANOVA model but with an extra level of nesting (i.e. sub-sampling). Nested ANOVAs used the MIXED Procedure from SAS to account for both fixed (forest type) and random factors (gap) in the model (Littell et al. 1996).

We used a two-way ANOVA with a completely randomized design to test the effects of forest type and canopy cover class (gap or non-gap) on light availability (Wilkinson et al. 1992). Single degree of freedom contrasts were employed to test differences within a given forest type. We used Kolmogorov-Smirnov two-sample non-parametric tests to compare the distributions of gap sizes and understorey light levels among forest types.

Table 2. Decay classes for gap makers.

Decay class	Canopy branch structure		Foliage	Bark	Wood
	Large branches	Fine branches			
Green	Fully intact	Fully intact	Fully intact, green	Intact	No decomposition
Red	Fully intact	Fully intact	Present, red or brown	Intact	No decomposition
Young	Fully intact	Mostly present	Little or no needles	Intact	No decomposition
Young-Medium	+/- intact	Occasional	Absent	Intact	Little decomposition
Medium	+/- intact	Absent	Absent	Sloughing	Little decomposition
Medium-Old	Occasional	Absent	Absent	Mostly sloughed off	Moderate decomposition
Old	Absent	Absent	Absent	Absent	Advanced decomposition; substantial sound wood present
Old-very old	Absent	Absent	Absent	Absent	Advanced decomposition, some sound wood present; log mostly incorporated into forest floor
Very old	Absent	Absent	Absent	Absent	No sound wood, log incorporated completely into forest floor

Results

Extent of old-growth forest

The major forest types we sampled cover ca. 6.6 million ha of forested land in northern British Columbia, of which nearly 42% was occupied by older age classes. Sub-alpine forests had the greatest proportion of old-growth (79% of forested area), followed by sub-boreal forests (42%), northern temperate forests (33%) and boreal forests (32%).

Forest stand level

Canopy gaps occupied over half of the 28 235 m of transect that we surveyed across 16 old-growth stands. Estimates of the proportion of the area occupied by gaps ranged from one-third in northern temperate forests to three-quarters in sub-alpine forests (Table 3). Developmental gaps were the most common gaps in all forest types, and were more abundant in sub-alpine than in the other forests (Table 3). Edaphic and shrub gaps were rare in northern temperate forests and infrequent in sub-alpine and boreal forests, but shrub gaps were common in sub-boreal forests. Edaphic gaps in our study were caused by stream courses, swamps, other wetlands or rock outcrops.

Alnus sinuata, *Salix* spp. or *Betula glandulosa* shrub communities occupied the shrub gaps. Combination gaps were most abundant in sub-boreal forests where 21% of all developmental gaps also had a shrub component. Within combination gaps, shrubs occupied ca. 48% of the gap area. Combination gaps were less common in sub-alpine and boreal forests and were not found in northern temperate forests.

The strongest trend in the spatial pattern of gaps was differences among gap types (Fig. 1). Compared to other gap types, developmental gaps were more evenly distributed with many smaller-sized gaps clumped at scales of 10-15 m. Secondary peaks at 30-50 m suggest that these smaller gaps were sometimes aggregated at larger scales. Other types of gaps were more spatially clustered with fewer larger gaps; scales of pattern for these gaps were greater than 15 m. Differences in standardized variance among gap types were significant at all scales except 0-20 m however, multiple comparison tests detected no difference among means at 0-50 m (Table 4). Differences among forest types were not as evident; there were significant differences in spatial pattern for shrub gaps at most scales, for combination and developmental gaps at some scales (Table 5), but no differences were observed for all gap types combined (not shown). Developmental gaps in northern temperate forests were more clumped at smaller scales (0-10 m

Table 3. Characteristics of canopy gaps by forest type. Values are means from one-way ANOVA; $n = 4$ stands per forest type. Different letters within a row indicate significant differences among forest types (least square means, $p < 0.05$). Gap maker data and mean gap size (indicated by *) were subjected to a nested one-way ANOVA; $n = 30$ gaps per forest stand.

	Boreal	Sub-boreal	Sub-alpine	Northern temperate	*F*-ratio	*p*-value
Stand level						
% area in canopy gaps	50.4 a	57.4 a	73.2 b	32.2c	26.674	< 0.001
% area in developmental gaps	45.1 a	36.5 a	66.1 b	31.9 a	17.79	< 0.001
% area in combination gaps	11.1 a	34.0 b	9.2 a	0 a	10.808	0.001
% area in shrub gaps	5.2 a	19.4 b	2.8 a	0 a	13.904	< 0.001
% area in edaphic gaps	0.1	1.3	3.1	0.2	3.215	0.062
Frequency of gaps (#/m)	0.070 a	0.056 b	0.056 b	0.036c	34.78	< 0.001
% gaps < 300 m^2	97.5 a	86.7 b	81.7 b	91.0 b	5.21	0.016
% gaps > 600 m^2	0.0	2.5	2.5	2.3	1.05	0.407
Gap level						
Mean gap size (m^2)*	92 a	173 c	196 c	148 b	6.98	0.006
Median gap size (m^2)	70 a	128 a	154 b	99 a	9.771	0.002
Range of gap sizes (m^2)	9-542	19-830	12-1570	9-1253		
Total number of gap makers/gap*	4.6 a	5.9 a	14.5 b	6.1 a	19.31	< 0.001
Maximum number of gap makers/gap*	52	36	78	33		
Number of decay classes/gap*	2.0 a	2.5 a	3.7 b	2.7 a	13.26	0.0004
Understorey light levels						
Mean light levels (% full sunlight)	26.7 a	18.0 b	19.0 b	16.0 c	47.963	< 0.001
Median light levels (% full sunlight)	27.2 a	17.7 b	17.3 b	13.9 b	5.933	0.008
Range of light levels (% full sunlight)	8.7-43.3	3.6-53.0	5.8-82.1	3.4-46.3		
Coefficient of variation of light levels	0.213 a	0.396 ac	0.422 bc	0.370 ac	4.752	0.017
% of light levels < 30% full sunlight	64.7	93.3	93.5	91.2	3.467	0.045
Mean non-gap light levels (% full sunlight)	26.4 a	15.4 b		15.4 b	46.465	< 0.001
Mean gap light levels (% full sunlight)	27.2 a	20.4 b		16.3 c	28.307	< 0.001

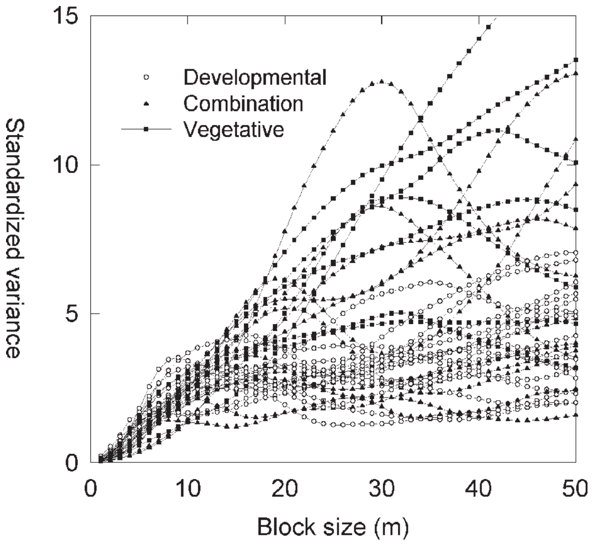

Fig. 1. Three-term local quadrat variance as a function of block size. Values are standardized such that one unit equals the sample variance. Results are subdivided by gap type; each line represents a single forest stand. Peaks on the variance graph indicate half the distance between gap centres or clusters of gaps.

and 0-30 m) compared to other forests (Table 5). Combination gaps were more clumped at larger scales in sub-alpine than in sub-boreal forests and shrub gaps were more evenly distributed in sub-boreal forests compared to other forest types.

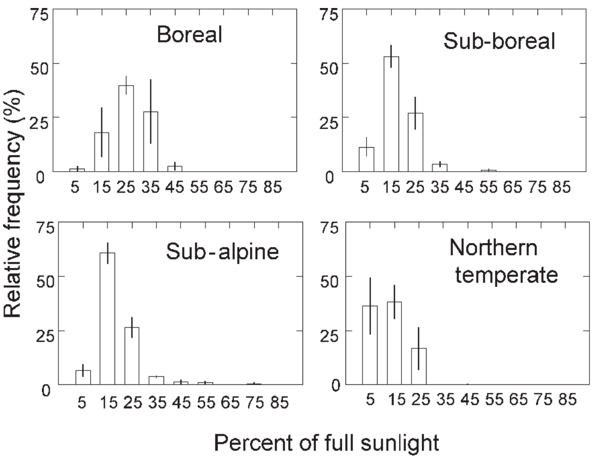

Fig. 2. Frequency distribution histograms of understorey light levels in each forest type. Bars represent means of four forest stands in intervals of 10% full sunlight; error bars are ± 1 s.e.

Mean and median light availability were lowest in northern temperate forests and highest in boreal forests, compared to other forest types (Table 6). Light levels were generally below 30% of full sunlight in all forest types (86% of total observations), and rarely exceeded 50% of full sunlight; the higher light levels were more common in boreal forests (Fig. 2). Distributions of light levels varied among forest types except for sub-alpine and sub-boreal forests, which had very similar distributions of light levels (Fig. 2; Kolmogorov-Smirnov tests, $p \geq 0.05$). The lowest irradiance in each forest type was between 3 and 9% full sunlight (Table 3); light levels were rarely less than 5% full sunlight (only 1% of total observations). Differences in light levels between gaps and non-gaps were only detectable in sub-boreal forests, where light availability was higher in gaps (Table 6, Kolmogorov-Smirnov tests, $p < 0.001$).

Table 4. ANOVA of the effect of gap type on standardized three-term local quadrat variance at five different scales of variation. All forest types were combined. Mean values of three-term local quadrat variance are reported in units of sample variance. Different letters within a row indicate significant differences among gap types ($p < 0.05$; $n = 32$).

Scale of variation (m)	Develop-mental	Combination	Shrub	*F*-ratio	*p*-value
0-10	1.45 a	0.94 b	1.23 a	12.960	< 0.001
0-20	2.16 a	2.32 a	2.43 a	0.769	0.472
0-30	2.42 a	3.39 b	3.28 ab	4.214	0.025
0-40	2.69 a	3.97 b	3.85 ab	4.211	0.025
0-50	2.95 a	4.35 a	4.27 a	4.068	0.028

Gap level

Gap sizes formed negative exponential distributions in all sampled forest types (Fig. 3). Overall, 89% of the gaps were < 300 m^2 and less than 2% were > 600 m^2 (Table 3). Gap size distributions were similar among forest types (Fig. 3); only boreal forests had a significantly different distribution than the other forest types (Kolmogorov-Smirnov tests, $p < 0.05$). Boreal forests had more small gaps (< 300 m^2) than the other forest types, whereas sub-boreal and sub-alpine forests had more large gaps (> 300 m^2; Table 3; Fig. 3). Median gap size was greatest in sub-alpine forests (Table 3).

Developmental gaps comprised of a single dead tree were rare (7%) while gaps with many gap makers were common (70% and 21% with more than 3 and 10 gap makers, respectively). Most gaps had gap makers of at least two or three decay classes (74% and 54% of gaps, respectively). Sub-alpine forests had the highest mean number of gaps makers per gap, the greatest number of decay classes per gap and the record number of gap makers (78) observed in a single gap (Table 3).

For the 3907 gap makers in our sampled gaps, the mode of gap maker mortality was fairly evenly distrib-

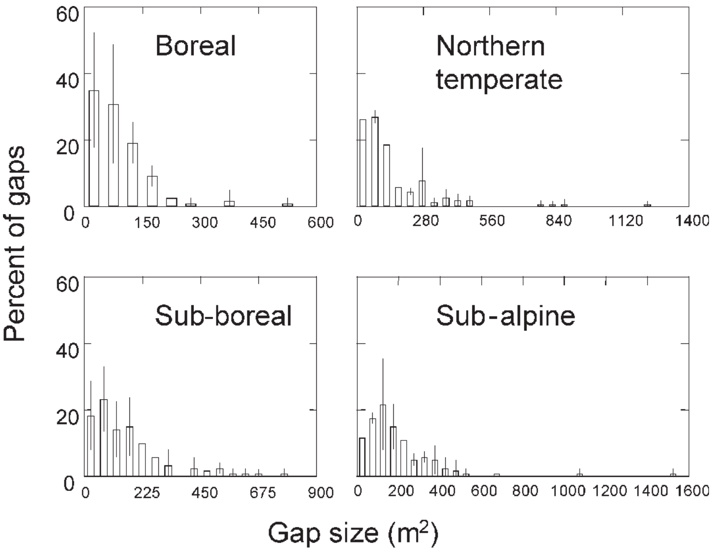

Fig. 3. Frequency distribution histograms of gap sizes in each forest type. Bars represent means of four forest stands in 50-m^2 intervals; error bars are ±1 s.e. Note: *x*-axis differs for each forest type.

uted overall (36% standing dead, 44% snapped, 20% uprooted), but varied significantly among forest types (Fig. 4). Because of the difficulty in determining whether the tree was alive or dead when snapping occurred, it is likely that standing dead gap makers were underestimated (e.g. Lertzman & Krebs 1991). Sub-alpine forests had the greatest proportion of standing dead gap makers (Fig. 4), the majority of which were *Abies lasiocarpa* (98%). Snapped trees were most common in boreal and northern temperate forests. Modes of mortality were more evenly distributed in sub-boreal forests (Fig. 4). Modes of mortality differed by decay class of gap makers: old and medium gap makers were mostly snapped and uprooted in all forest types, whereas most young gap makers were standing dead for sub-boreal, sub-alpine and boreal forests, and uprooted for northern temperate forests. We classified 4.3% of the total gap makers as fire survivors, most of which were observed in sub-boreal forests (83% of all fire survivors) with the remainder in sub-alpine forests. Almost one-fifth of the gap makers in sub-boreal forests were classified as fire survivors and the vast majority (78%) were associated with combination gaps. Gap makers tended to be older in northern temperate forests compared to the other forest types; only this forest type contained gap makers in the two oldest decay classes (Table 7). Gap makers were distributed evenly over the decay classes in all forest types except boreal forests, suggesting a gradual pattern of recruitment. Almost half of the gap makers in boreal forests were in young decay classes, suggesting an episodic mortality event (Table 7).

Table 5. The effect of forest type on the standardized three-term local quadrat variance by gap type at five different scales of variation. Mean values of three-term local quadrat variance are reported in units of sample variance. Different letters within a row indicate significant differences among forest types ($p < 0.05$).

Type of gap	Scale of variation (m)	DF	*n*	Boreal	Sub-boreal	Sub-alpine	Northern temperate	*F*-ratio	*p*-value
Developmental	0-10	3	16	1.45 ab	1.31 a	1.28 a	1.76 b	7.89	0.004
	0-20			2.15 a	2.05 ab	1.89 a	2.54 b	3.464	0.051
	0-30			2.24 a	2.36 ab	2.11 a	2.95 b	6.229	0.009
	0-40			2.36 a	2.76 a	2.46 a	3.16 a	2.418	0.117
	0-50			2.60 a	3.18 a	2.84 a	3.18 a	0.763	0.536
Combination	0-10	2	8	1.08 b	1.05 b	0.55 a		18.115	0.005
	0-20			2.73 a	2.17 a	2.09 a		0.671	0.541
	0-30			4.02 a	2.59 a	3.81 a		2.237	0.177
	0-40			4.80 ab	2.76 a	5.31 b		7.029	0.021
	0-50			5.11 ab	3.20 a	6.54 b		6.509	0.025
Shrub	0-10	2	10	1.16 a	1.14 a	1.63 b		10.361	0.026
	0-20			2.69 ab	1.97 a	2.99 b		5.336	0.039
	0-30			4.54 b	2.33 a	3.80 ab		6.603	0.024
	0-40			5.80 b	2.64 a	4.27 ab		5.861	0.032
	0-50			6.56 a	3.08 a	4.51 a		3.275	0.099

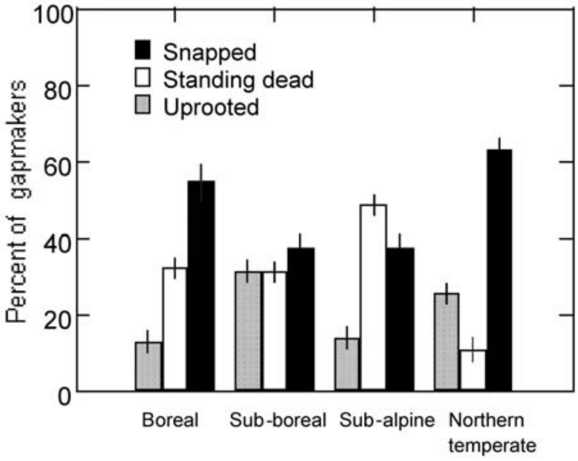

Fig. 4. Modes of gap maker mortality by forest type. Data were subjected to a nested one-way ANOVA to test for differences among forest types (n = 30 gaps within each of four forest stands). Bars represent least squares means ±1 s.e.

Species of gap makers reflected differences in species composition among the forest types. Most gap makers in boreal forests were *Pinus contorta*, *Picea glauca* and *Populus tremuloides*. Gap makers in sub-boreal and sub-alpine forests were primarily *Abies lasiocarpa*, with minor components of *P. contorta* and *P. glauca* × *P. engelmannii*. In northern temperate forests, there were *Tsuga heterophylla* gap makers with small percentages of *Thuja plicata*. We observed differences in mode of mortality among tree species. The majority of *A. lasiocarpa* gap makers were standing dead (55.1%), whereas most *T. heterophylla* gap makers were snapped (57.4%).

Discussion

Extensive old-growth areas exist in northern latitude forests with intermediate to frequent fire return intervals. In these older forests we found 'classical' small-scale gap disturbance to be common. Boreal and sub-alpine forest types had higher proportions of their area in developmental canopy gaps than is commonly reported in the gap dynamics literature (McCarthy 2001); whereas proportions in northern temperate and sub-boreal forest types were within the range of results reported from coastal temperate forests of British Columbia (Lertzman & Krebs 1991; Arsenault 1995; Lertzman et al. 1996), Alaska (Ott & Juday 2002) and the southern boreal forests of Québec (Kneeshaw & Bergeron 1998). The high frequency and skewed size distribution of abundant small developmental gaps that we observed is consistent with other gap studies (McCarthy 2001). Developmental gap sizes in northern British Columbia forests were at the upper end of ranges reported for other high latitude forests and were mostly larger than those in tropical and temperate deciduous forests (Runkle 1982; Brokaw 1985).

The high proportion of area in developmental canopy gaps and the generally larger gap sizes compared to other ecosystems may be a result of three factors particular to northern coniferous forests. First, these conifer stands are more open than the continuous dense canopies of tropical and temperate deciduous forests due to interstitial spaces between the tall, narrow, conical crowns. Although we did not consider these spaces between live conifer crowns as gaps they did add to our measurements of gap size and area. Second, filling of canopy gaps by regenerating trees can be slow at high latitudes. Tree regeneration and replacement in gaps can be delayed due to short growing seasons, slow growth rates and persistent snow packs (Lertzman et al. 1996).

Table 6. ANOVA of understorey light levels by forest type and canopy cover class (gap vs non-gap) and their interaction. Non-gap and gap light levels were contrasted within each forest type using single degree of freedom contrasts.

Source of variation	*df*	*n*	*F*-ratio	*p*-value
Forest type	2	12	24.43	0.039
Forest type × Canopy cover class	2	12	3.153	0.044
Canopy cover class	1	12	3.125	0.219
Northern temperate	1	4	1.44	0.219
Sub-boreal	1	4	15.24	< 0.001
Boreal	1	4	0.197	0.657

Table 7. Percent of gap makers by decay class and forest type. Values are mean ± 1 s.e.; n = 4.

Decay class	Boreal	Sub-boreal	Sub-alpine	Northern temperate
Green	1.0 ± 0.6	5.5 ± 1.4	0.1 ± 0.1	1.7 ± 0.5
Red	2.6 ± 0.7	4.2 ± 1.1	12.2 ± 1.6	0.2 ± 0.1
Young	46.7 ± 3.5	29.0 ± 2.8	26.0 ± 1.9	14.2 ± 1.5
Medium-Young	14.0 ± 2.1	4.2 ± 1.2	1.5 ± 0.4	1.1 ± 0.5
Medium	31.3 ± 3.2	35.9 ± 3.1	39.3 ± 2.0	22.5 ± 1.9
Medium-Old	3.3 ± 1.0	0.4 ± 0.3	11.4 ± 1.2	7.1 ± 1.2
Old	1.1 ± 0.8	20.7 ± 2.4	9.4 ± 1.0	44.7 ± 2.4
Old-Very old	0	0	0	1.1 ± 0.4
Very old	0	0	0	7.5 ± 1.3

Snow accumulation and retention in large gaps (e.g. Berry & Rothwell 1992) may restrict tree regeneration to positions within gaps that melt early in the growing season (i.e. raised substrates or sites near other trees; the 'tree island' model of regeneration; Brett & Klinka 1998) and thereby, maintaining open canopies. Lastly, there is little gap filling by gap edge canopy trees. The monopodial growth form of conifers restricts their ability to 'light forage' and grow into openings compared to temperate and tropical ecosystems with more deciduous species (Lertzman & Krebs 1991; Kuulavainen 1994). This is especially the case for *Pinus*, *Picea* and *Abies*, the genera that dominate in the sub-boreal, boreal and sub-alpine forests of northern British Columbia.

Differences in disturbance history, species composition and climate among our forest types resulted in differences in the size and abundance of developmental gaps. Repeated small-scale bark beetle infestations of *Abies lasiocarpa* (Banner et al. 1993) contributed to high levels of gap makers and consequent large gap sizes in sub-alpine forests and, to a lesser extent, sub-boreal forests. The high number of gap makers we observed in some gaps was similar to those found in spruce budworm gaps of eastern Canadian boreal forests (Kneeshaw & Bergeron 1998), but higher than most other studies where gap makers rarely exceed 20 (Spies et al. 1990; Lertzman & Krebs 1991, Liu & Hytteborn 1991). The high incidence of large multiple tree gaps of several decay classes suggested that gap expansion and convergence of small gaps is an ongoing process in these forests. This was not observed in boreal forests where fire return intervals are much shorter. Boreal forests have had less time for gap expansion events to occur and abundant numbers of small gaps with young gap makers were observed. Since almost half of the gap makers were early successional species (*Pinus contorta* and *Populus tremuloides*), our results support those of Kneeshaw & Bergeron (1998) who attributed the abundant small gaps they observed in southern boreal forests to the random senescence and death of early successional tree species. Although fire return intervals are again fairly long in northern temperate forests, the small gap sizes and lower proportion of area in gaps were likely due to a combination of rapid growth rates of regenerating trees (Wright et al. 1998a); less insect-mediated mortality and the less monopodial crown shape and the smaller interstitial spaces between crowns of the dominant canopy tree (*Tsuga heterophylla*).

Developmental gaps can be created suddenly or gradually and their mode of creation has important implications for tree community dynamics and ecosystem processes (Krasny & Whitemore 1991). For example, disturbance to the moss community that dominates forest floors in northern latitude forests is critical for tree seedling establishment (Wright et al. 1998b; Greene et al. 1999; LePage et al. 2000). Tree uprooting creates forest floor disturbance (Schaetzl et al. 1989); however uprooting only played a minor role in gap formation in our forests. The prevalence of standing dead and snapped gap makers will profoundly impact tree regeneration and replacement in these forests because of little forest floor disturbance combined with the gradual relinquishment of space and resources.

Although all canopy gap types contribute to the structural heterogeneity, available open space and dynamics of forests, developmental gaps are considered to be most important in shaping forest dynamics and succession (e.g. Runkle 1992; Lertzman et al. 1996). Edaphic gaps are generally not open to tree establishment and canopy recruitment, nor do they create snags and downed wood, whose importance in ecological processes is widely recognized (Harmon et al. 1986). Shrub and combination gaps fit somewhere in between developmental and edaphic gaps. They have been observed in other studies (e.g. Spies et al. 1990; Lertzman et al. 1996; Kneeshaw & Bergeron 1998), but our study is the first one to characterize their extent in different high latitude forested ecosystems. Shrub gaps were more prevalent and evenly distributed in sub-boreal forests, likely due to the common occurrence of *Alnus sinuata*. It is unclear how long shrub gaps can persist before being filled by conifer regeneration. In sub-boreal forests, many of the shrub gaps we examined may have been present since the last major fire event or even earlier (evidence of large, old, repeatedly re-sprouting *Alnus* main stems).

We found that fire survivors were commonly associated with shrub gaps in wet depressions. Other studies have shown that individual trees or groups of trees can survive stand-destroying fires in sub-boreal and northern temperate forests (Clark 1994; LePage 1995). The presence of shrub gaps may play an important role in maintaining structural complexity in these forests by providing an opportunity for canopy trees to survive fire. Directly after the fire, fire survivors create higher structural diversity by retaining individual or multiple canopy trees within the developing new forest. With time, fire survivors age and die, contributing to the creation of new developmental gaps or when adjacent to shrub gaps as they often are, the creation of combination gaps.

Combination gaps may result from tree mortality events that expand shrub gaps. The presence of shrub gaps can increase the risk of certain types of tree mortality (e.g. uprooting due to crown asymmetry; Young & Hubbell 1991). Both shrub and combination gaps were aggregated as a few larger gaps with larger scales of pattern. This would be expected for combination gaps that have expanded and coalesced, but it also indicates that the initial establishment of shrubs that create shrub gaps occurs at a larger scale than the mortality processes that create developmental gaps. The scales of clumping we detected for developmental gaps (10-20 m with second peaks around 30 m) were similar to those found in other forests (17-20 m, Lawton & Putz 1988; 5-30 m, Bradshaw & Spies 1992).

Gap disturbances also influence understorey light availability, which plays an important role in tree survival and growth in these forests (Kobe & Coates 1997; Wright et al. 1998a). We found strikingly similar light distributions between gap and non-gap areas in northern latitude forests. This contrasts with the dramatic differences in light levels observed between gaps and the forest matrix in tropical and temperate ecosystems (Brokaw 1985). In boreal and northern temperate forests, we believe the narrow conifer crowns combined with the frequent, evenly dispersed small gaps created similar light levels in gaps and non-gaps. In sub-boreal forests, where large combination gaps were present, there were still only small differences in light environments between gap and non-gap conditions. We observed great variability among light levels in both gaps and non-gaps, which suggests these northern latitude forests are better viewed as a continuum of light levels rather than a dichotomy of closed canopy and gap (Lieberman et al. 1989).

Understorey light levels measured in our study were substantially higher than light levels found in hardwood forests of eastern North America or the tropics (1-2% full sun, Canham et al. 1990; Fetcher et al. 1994; Clark et al. 1996). Our values were more similar but generally higher than boreal forests of western Alberta (10-60%, Ross et al. 1986; 6-10%, Lieffers & Stadt 1994; 14 - 32%, Constabel & Lieffers 1996) and Quebec (6-15%, Messier et al. 1998). Smaller interstitial spaces between crowns and more light foraging by *Tsuga heterophylla* branches may have caused lower light levels in northern temperate forests than in the other three forest types.

In summary, old-growth forests and small-scale disturbances were prevalent in the high-latitude forests of British Columbia, which were traditionally considered fire-driven, large-scale disturbance systems. However, important ecological processes associated with gap disturbances in these forests may differ from southern temperate and tropical forests, as suggested by the dominance of snapped and standing dead gap makers, the presence of shrub gaps, open canopies of narrow conical crowns and similar light levels between gaps and non-gaps.

Acknowledgements. We thank Ronnie Drever, Tara Wylie, and Stefan Quaglia for their assistance with field data collection; R. Drever and S. Quaglia for GLI/C 2.0 photo analysis and Russell Klassen for data entry. We also thank Andy McKinnon and Marvin Eng for calculating the extent of old-growth forests in our study area. Peter Ott, Phil LePage and Phil Burton provided helpful advice. Partial funding for this research project was provided by Forest Renewal British Columbia (Harsh Environment Study SB96028-RE). This manuscript benefited greatly from the advice of three anonymous reviewers and thoughtful suggestions by editor Peter White.

References

Anon. 1980. *Canadian climate normals, 1951-1980. Temperature and precipitation, British Columbia*. Atmospheric Environment Services, Downsview, ON, CA.

Anon. 1987. *The Canadian system of soil classification*. Agriculture Canada Expert Committee on Soil Survey. Agric. Can. Publ. 1646, Ottawa, ON, CA.

Arsenault, A. 1995. *Pattern and processes in old-growth temperate rainforests of southern British Columbia*. Ph.D. Thesis, University of British Columbia, CA.

Banner, A., MacKenzie, W., Haeussler, S., Thomson, S., Pojar, J. & Trowbridge, R. 1993. *A field guide to site identification and interpretation for the Prince Rupert Forest Region*. Land Management Handbook 26, British Columbia Ministry of Forests, Victoria, BC, CA.

Battles, J.J., Fahey, T.J. & Harney, E.M.B. 1995. Spatial patterning in the canopy gap regime of a subalpine *Abies-Picea* forest in the northeastern United States. *J. Veg. Sci.* 6: 807-814.

Berry, G.L. & Rothwell, R.L. 1992. Snow ablation in small forest openings in southwest Alberta. *Can. J. For. Res.* 22: 1326-1331.

Bradshaw, G.A. & Spies, T.A. 1992. Characterizing canopy gap structure in forests using wavelet analysis. *J. Ecol.* 80: 205-215.

Brett, R.B. & Klinka, K. 1998. A transition from gap to tree-island regeneration patterns in the subalpine forest of south-coastal British Columbia. *Can. J. For. Res.* 28: 1825-1831.

Brokaw, N.V.L. 1985. Treefalls, regrowth, and community structure in tropical forests. In: Pickett, S.T.A. & White, P.S. (eds.) *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, NY.

Canham, C.D. 1988. An index for understory light levels in and around canopy gaps. *Ecology* 69: 1634-1638.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A. & White, P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.* 20: 620-631.

Canham, C.D., Coates, K.D., Bartemucci, P. & Quaglia, S. 1999. Measurement and modeling of spatially-explicit variation in light transmission through northern temperate forests of British Columbia. *Can. J. For. Res.* 29: 1775-1783.

Chazdon, R.L. & Fetcher, N. 1984. Photosynthetic light environments in a lowland tropical rainforest in Costa Rica. *J. Ecol.* 72: 553-564.

Chen, J. & Bradshaw, G.A. 1999. Forest structure in space: a case study of an old-growth spruce-fir forest in Changbaishan Nature Reserve, PR China. *For. Ecol. Manage.* 120: 219-233.

Clark, D.B., Clark, D.A., Rich, P.M., Weiss, S. & Oberbauer, S.F. 1996. Landscape-scale evaluation of understory light and canopy structure: methods and application in a neotropical lowland rain forest. *Can. J. For. Res.* 26: 747-757.

Clark, D.F. 1994. *Post-fire succession in the sub-boreal spruce forests of Nechako Plateau, central British Columbia.* M.Sc. Thesis, University of Victoria, BC, CA.

Coates, K.D. & Burton, P.J. 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. *For. Ecol. Manage.* 99: 337-354.

Constabel, A.J. & Lieffers, V.J. 1996. Seasonal patterns of light transmission through boreal mixed wood canopies. *Can. J. For. Res.* 26: 1008-1014.

Cumming, S.G., Schmiegelow, F.K.A. & Burton, P.J. 2000. Gap dynamics in boreal aspen stands: is the forest older than we think? *Ecol. Appl.* 10: 744-759.

Dale, M.R.T. 1999. *Spatial pattern analysis in plant ecology*. Cambridge University Press, Cambridge, UK.

Denslow, J.S. & Hartshorn, G.S. 1994. Tree-fall gap environments and forest dynamic processes. In: McDade, L.A., Bawa, K.S., Hespenheide, H.A. & Hartshorn, G.S. (eds.) *La Selva: ecology and natural history of a neotropical rain forest*, pp. 120-127. University of Chicago Press, Chicago, IL.

Fetcher, N., Oberbaer, S.F. & Chazdon, R.L. 1994. Physiological ecology of plants. In: McDade, L.C., Bawa, K.S., Hespenheide, H.A. & Hartshorn, G.S. (eds.*) La Selva: ecology and natural history of a neotropical rain forest,* pp 128-141. University of Chicago Press, Chicago, IL.

Green, R.N., Trowbridge, R.L. & Klinka, K. 1993. Towards a taxonomic classification of humus forms. *For. Sci. Monogr.* 29.

Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I. & Simard, M.-J. 1999. A review of the regeneration of boreal forest trees. *Can. J. For. Res.* 29: 824-839.

Harmon, M.E., Franklin, J.F., Swanson, T.J., Sollins, P., Gregory, S.V., Lattin, J.D., Andrews, N.H., Cline, S.P., Aumen, N.C., Sedell, J.R., Lienkaemper, G.W., Cromack, Jr., K. & Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15: 133-382.

Hitchcock, C.L. & Cronquist, A. 1994. *Flora of the Pacific Northwest*. University of Washington Press, Seattle, WA.

Hofgaard, A. 1993. 50 years of change in a Swedish boreal old-growth *Picea abies* forest. *J. Veg. Sci.* 4: 773-782.

Hytteborn, H., Liu, Q. & Verwijst, T. 1991. Natural disturbance and gap dynamics in a Swedish boreal spruce forest. In: Nakagoshi, N. & Golley, F.B. (eds.) *Coniferous forest ecology from an international perspective,* pp. 93-108. SPB, The Hague, NL.

Kneeshaw, D.D. & Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. *Ecology* 79: 783-794.

Kobe, R.K. & Coates, K.D. 1997. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. *Can. J. For. Res.* 27: 227-236.

Krasny, M.E. & Whitmore, M.C. 1991. Gradual and sudden forest canopy gaps in Allegheny northern hardwood forests. *Can. J. For. Res.* 22: 139-143.

Kubota, Y. 2000. Spatial dynamics of regeneration in a conifer/broad-leaved forest in northern Japan. *J. Veg. Sci.* 11: 633-640.

Kuuluvainen, T. 1994. Gap disturbance, ground microtopography, and the regeneration dynamics of boreal conifer forests in Finland: a review. *Ann. Zool. Fenn.* 31: 35-52.

Lawton, R.O. & Putz, F.E. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. *Ecology* 69: 764-777.

Leemans, R. 1991. Canopy gaps and establishment patterns of spruce (*Picea abies* [L.] Karst.) in two old-growth coniferous forests in central Sweden. *Vegetatio* 93: 157-165.

LePage, P. 1995. *The structure and development pattern of mixed-species forest stands in the Northern temperate zone: Moist Cold subzone of northwestern British Columbia.* M.Sc. Thesis, Oregon State University, OR.

LePage, P., Canham, C.D., Coates, K.D. & Bartemucci, P. 2000. Seed source versus substrate limitation of seedling recruitment in Northern temperate forests of British Columbia. *Can. J. For. Res.* 30: 415-427.

Lertzman, K. P. & Krebs, C.J. 1991. Gap-phase structure of subalpine old-growth forest. *Can. J. For. Res.* 21: 1730-1741.

Lertzman, K.P., Sutherland, G.D., Inselberg, A. & Saunders, S. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rainforest. *Ecology* 77: 1254-1270.

Lieberman, M., Lieberman, D. & Peralta, R. 1989. Forests are not just Swiss cheese: canopy stereogeometry of non-gaps in tropical forests. *Ecology* 70: 550-552.

Lieffers, V.J. & Stadt, K.J. 1994. Growth of understory *Picea glauca*, *Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstory light. *Can. J. For. Res.* 24: 1193-1198.

Lieffers, V.J., Messier, C., Gendron, F., Stadt, K.J. & Comeau, P. 1999. Predicting and managing light in the understory of boreal forests. *Can. J. For. Res.* 29: 796-811.

Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. 1996. *SAS System for Mixed Models.* SAS Institute Inc., Cary, NC.

Liu, Q-H. & Hytteborn, H. 1991. Gap structure, disturbance and regeneration in a primeval *Picea abies* forest. *J. Veg. Sci.* 2: 391-402.

MacKinnon, A. & Vold, T. 1998. Old-growth forests inventory of British Columbia, Canada. *Nat. Areas J.* 18: 293-308.

McCarthy, J. 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. *Environ. Rev.* 9: 1-59.

Messier, C., Parent, S. & Bergeron, Y. 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forest. *J. Veg. Sci.* 9: 511-520.

Ott, R.A. & Juday, G.P. 2002.Canopy gap characteristics and their implications for management in the temperate rainforests of southeast Alaska. *For. Ecol. Manage.* 159: 271-291.

Pacala, S.W., Canham, C.D., Sapanora, J., Silander, Jr., J.A., Kobe, R.K. & Ribbens, E. 1996. Forest models defined by field measurements: estimation, error analysis, and dynamics. *Ecol Monogr.* 66: 1-43.

Parminter, J. 1990. Typical historic patterns of wildfire disturbance by biogeoclimatic zone. In: *Old-growth forests: problem analysis*. British Columbia Ministry of Forest Research, Victoria, BC, CA.

Pickett, S.T.A. & White, P.S. (eds.) *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, NY.

Platt, W.J. & Strong, D.R. 1989. Special feature: gaps in forest ecology. *Ecology* 70: 535-576.

Pojar, J., Klinka, K. & Meidinger, D.V. 1987. Biogeoclimatic ecosystem classification in British Columbia. *For. Ecol. Manage.* 22: 119-154.

Ross, M.S., Flanagan, L.B. & La Roi, G.H. 1986. Seasonal and successional changes in light quality in the understory of boreal forest ecosystems. *Can. J. Bot.* 64: 2792-2799.

Rossi, R.E., Mulla, D.J., Journel, A.G. & Franz, E.H. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecol. Monogr.* 62: 277-314.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63: 1533-1546.

Runkle, J.R. 1992. *Guidelines and sample protocol for sampling forest gaps*. Gen. Tech. Rep. PNW-GTR-283, USDA, Forest Serv. Pac. Northwest Res. Station, Portland, OR.

Schaetzl, R.J., Burns, S.F., Johnson, D.L. & Small, T.W. 1989. Tree uprooting: review of impacts on forest ecology. *Vegetatio* 79: 165-176.

Sernander, R. 1936. The primitive forests of Granskär and Fiby. A study of the part played by storm-gaps and dwarf trees in the regeneration of the Swedish spruce forest. *Acta Phytogeogr. Suec.* 8: 1-232. (In Swedish with English summary.)

Spies, T.A. & Franklin, J.F. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. In: Ruggerio, L.F., Aubrey, K.B., Carey, A.B. & Huff, M.H. (eds.) *Wildlife and vegetation of unmanaged Douglas-fir forests,* pp. 91-109. USDA For. Ser. Gen. Tech. Rep. PNW-GTR-285. Portland, OR.

Spies, T.A., Franklin, J.F. & Klopsch, M. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Can. J. For. Res.* 20: 649-658.

Terborgh, J. 1985. The vertical component of plant species diversity in temperate and tropical forests. *Am. Nat.* 126: 760-778.

Ward, J.S. & Parker, G.R. 1989. Spatial dispersion of woody regeneration in an old-growth forest. *Ecology* 70: 1279-1285.

Wells, R.W., Lertzman, K.P. & Saunders, S. 1998. Old-growth definitions for the forests of British Columbia, Canada. *Nat. Areas. J.* 18: 279-292.

Wilkinson, L., Hill, M., Miceli, S., Birkenbeuel, G. & Vang, E. 1992. *SYSTAT for Windows*. SYSTAT Inc., Evanston, IL.

Wright, E.F., Coates, K.D., Canham C.D. & Bartemucci, P. 1998a. Species variability in growth response to light across climatic regions in northwestern British Columbia. *Can. J. For. Res.* 28: 871-886.

Wright, E.F., Coates, K.D. & Bartemucci, P. 1998b. Regeneration from seed of six tree species in the northern temperate forests of British Columbia as affected by substrate and canopy gap position. *Can. J. For. Res.* 28: 1352-1364.

Young, T.P. & Hubbell, S.P. 1991. Crown asymmetry, treefalls, and repeat disturbance of broad-leaved forest gaps. *Ecology* 72: 1464-1471.

Received 11 September 2001;
Revision received 5 July 2002;
Accepted 10 July 2002.
Coordinating Editor: P.S. White.