

Effects of Clearcut Edges on Trees in the Sub-Boreal Spruce Zone of Northwest-Central British Columbia

Philip J. Burton

Burton, P.J. 2002. Effects of clearcut edges on trees in the sub-boreal spruce zone of Northwest-Central British Columbia. *Silva Fennica* 36(1): 329–352.

Clearcut-forest boundaries were evaluated for their effects on mature and regenerating trees in the northern interior of British Columbia, Canada. Two hundred and eighteen rectangular plots measuring 200 m² each were arrayed in transects across 12 cutblock edges created 9 to 21 years earlier, with the wall of standing timber facing either north or south. The density of canopy trees on the inner edge was found to be reduced by 19% (on north-facing edges) to 46% (on south-facing edges) from average densities found in forest interiors. This reduction was primarily due to windthrow after logging, which was elevated by 27% (over interior background levels) at north-facing edges, and by 216% at south-facing edges. Of the trees situated within 10 m of south-facing cutblock edges, 11% of the *Pinus contorta*, 18% of the *Abies lasiocarpa*, and 42% of the *Picea engelmannii* × *glauca* trees have apparently collapsed, primarily those having height-to-dbh ratios greater than 71:1. As a result, irradiance in the forest understory was elevated (over interior levels) at south-facing edges to distances of approximately 65 to 70 m into the forest. Increased irradiance from adjacent cutblocks enhanced the understory growth of *Picea* for approximately 60 m into the inner edge of forests, 75 m for *Abies*. Mature *Pinus* trees on south-facing edges showed an unexplained 48% decrease in radial growth compared to average growth rates in forest interiors, an effect that was detectable up to 45 m into the forest. Elevated densities of conifer seedlings were evident for up to approximately 70 m into clearcuts from north-facing forest edges. Seedling growth in clearcuts was largely unaffected by shade from stand edges. Though the extent of edge effects varies considerably with the statistical techniques used to detect them, it appears that opening effects on trees can extend between 40 and 120 m into this forest type, while canopy effects reach shorter distances into clearcuts.

Keywords canopy influence, clearcut logging, edge effects, edge orientation, opening influence, tree growth, windthrow

Author's address Symbios Research and Restoration, P.O. Box 3398, 3868 13th Avenue, Smithers, British Columbia, Canada V0J 2N0 **E-mail** symbios@.bulkley.net

Received 14 November 2000 **Accepted** 13 February 2002

1 Introduction

1.1 Background

In recent years, public concern across Canada has been expressed about the extent of clearcut logging and the size of clearcut openings in forests being harvested for timber. This pressure has resulted in some regulatory limits being placed on the size of clearcuts, and a general promotion of harvesting and silvicultural alternatives to clearcuts, namely through the use of partial cutting, patch cuts, and patch retention within larger cutblocks. These efforts to reduce the visual impacts of industrial forestry and to protect non-timber resources are bound to result in fragmented landscapes increasingly dominated by edge effects (Murcia 1995). Smaller cutblocks mean increased ratios of edge to interior conditions in forest openings and in the remaining mature forest; more dispersed cutblocks (instead of larger or contiguous ones) mean more roads that also introduce edge effects along such corridors.

Edge effects can be considered the influence exerted by a stand or forest cover polygon on the ecological processes and attributes of an adjacent stand or polygon. Edge effects usually consist of altered canopy openness, irradiance and wind conditions compared to the interior of the stand, and the resulting alteration of processes ranging from plant water balance and propagule dispersal to animal behaviour. Because edge effects, as a subset of ecotone dynamics (Hansen and di Castri 1992), explicitly deal with the trans-boundary processes of ecosystems in a given spatial arrangement, they represent an interface between ecosystem ecology and landscape ecology.

Biologists and foresters still know little about the influence of edge effects on mature and old-growth northern forests following timber harvest. Work in coastal forests of the U.S.A. has demonstrated significant effects of adjacent clearcuts on microclimate, understory vegetation, forest edge stability with respect to windthrow, and the retention of forest interior habitat attributes important to birds (Chen et al. 1992). Yet those coastal forests are floristically quite different from northern ones, and do not experience wildfire

disturbance as frequently as the 100 to 125 year fire cycle found in boreal and sub-boreal zones (Old-growth forests... 1992). Preliminary observations suggest that edge effects in boreal forests may not be so important to vascular vegetation and vertebrate habitat (Hansson 1994), but may be more important to windthrow in forests dominated by shallow-rooted spruce (*Picea* L.) species. These issues need to be resolved to help forest planners intelligently distribute forest cutting activities, designate forested reserves and corridors, and make other landscape management decisions.

The effects of adjacent openings on old-growth forest are widely appreciated among conservation biologists. But the analogous effects of standing timber on forest regeneration, vegetation development and habitat values in newly created forest openings have rarely been considered. Significant differences in natural regeneration, seedling establishment, and tree growth are now known to be associated with distance from stand edges (Hansen et al. 1993). Clearcuts are presumably dominated by open conditions rather than the influence of standing trees. But preliminary simulations conclude that square cutblocks as large as 15 ha still have half of their area receiving less than 95% full sunlight during the growing season (with a 30 m tall canopy edge, on level ground at 54°N latitude). Total tree growth is a monotonically increasing function of available light for most species (Sipe and Bazzaz 1994, Barker et al. 1997, Coates and Burton 1999), yet managed-stand growth and yield models assume full light availability and no edge effects. Thus second-growth stand production may be significantly over-estimated as smaller cutblocks, patch cuts, and group-selection coupes become more prevalent.

Quantifying both kinds of edge effects (i.e., the effects of openings on forest, and of standing forest on openings) would help provide some answers to the biological and operational questions regarding critical sizes for conservation corridor widths, the utility of residual patches within clearcuts, and critical sizes for patch and strip cuts. The effect of edge-influenced zones in mature and regenerating stands (on regeneration, windthrow, growth and yield and ultimately on timber supply) are unknown sources of variation

which are becoming more important as cutblocks become smaller and as forest-level models for harvest scheduling and timber supply analysis are becoming spatially explicit (Rouck and Nelson 1995). Ideally, researchers would test a full range of cutblock sizes, retention patch sizes, and corridor widths over time, but this would be a large undertaking with results not forthcoming for many years. Retrospective study (i.e., sampling forest edges established in the past) using continuous transects to document edge effects provides a reasonable first step and a practical alternative for predicting the importance and extent of both kinds of edge effects (Bradshaw 1992).

1.2 Theory and Terminology

Two kinds of edge effects can be recognized in forested biomes subject to stand-level disturbance that leaves some locations dominated by mature trees and adjacent areas dominated by much shorter herbs, shrubs or juvenile trees. An "adjacent canopy effect" determines the zone of influence of mature forest in an adjoining plant community, typically one that is open or not forested. Adjacent canopy effects can be envisioned as "the shadow" (in terms of light, litterfall, seeds, etc.) of mature trees on an adjacent open area, and determine the extent of the "outer edge," as the term was coined by Geiger (1965) and subsequently used by Thomas et al. (1979) and others. Bradshaw (1992) suggests a number of mechanisms (seed rain, shading, browsing, damage from windthrow, etc.) by which mature stands can influence the recovery of vegetation in forest openings. This outer edge is of special interest to silviculturists who wish to predict the dispersal of tree seeds from the mature stand, the distance to which adequate stocking of natural regeneration can be counted on, and the growth of young trees and competing vegetation under the influence of partial shading (at the southern edge of a clearcut if in the northern hemisphere). The existence of broad outer edges might compromise the stocking densities, successional dynamics, and rates of tree growth expected for second-growth stands.

Conversely, an "adjacent opening effect" determines the zone of influence of a disturbed or open area on adjoining forest. It can be envisioned

as "the aura" (of irradiance, wind, weeds, etc.) emanating from an open area into adjacent forest, and determines the extent of the "inner edge" (Geiger 1965, Thomas et al. 1979). This inner edge is of interest to both foresters and conservation biologists because of its effect on the stability, productivity, and associated biota in a band of forest newly exposed to open conditions. Many scientists and land managers concerned with the protection of old-growth forests and forest-dependent wildlife are now recognizing that adjacent opening effects can greatly diminish the area of high-quality forest habitat previously considered reserved (Alverson et al. 1994, Murcia 1995). If inner edges are extensive, then land clearings, clearcut harvest blocks, destructive wildfires and other disturbances have a footprint on the landscape that extends beyond the boundaries which their map area alone would indicate.

It is expected that edge effects are directionally asymmetrical at high latitudes, and wherever winds have a predominant direction. In this paper, edge orientation is referred to in terms of the direction one would be facing with standing forest at one's back; hence a "south-facing" edge has the cutblock south of intact forest, while for "north-facing" edges the cutblock is north of the forest.

1.3 Objectives

This research was undertaken to document the effects of forest stand edges on vegetation and stand development in the moist cold subzone of the Sub-Boreal Spruce (SBSmc) biogeoclimatic zone in northwest-central British Columbia. Field sampling consisted of transects across similar, well established forest edges, utilizing identical methods, in order to:

- 1) Quantify the magnitude and distance to which the effects of open conditions reach into the inner edge of uncut mature forest, as measured in terms of the:
 - (a) density and attributes of windthrown trees;
 - (b) recent growth of residual canopy trees;
 - (c) density and composition of tree regeneration; and
 - (d) recent growth of conifer regeneration.

- 2) Quantify the magnitude and distance to which the effects of canopy influences from uncut mature forest extend into the outer edge of clearcuts as measured in terms of the:
- density and composition of tree regeneration; and
 - recent growth of conifer regeneration.

Additional data on the abundance of vascular plant, bryophyte and lichen species were collected simultaneously, but are not reported here.

2 Study Area

The western portion of the Sub-Boreal Spruce region of central British Columbia (B.C.) was chosen for study because of the lack of previous work concerning edge effects in boreal and sub-boreal environments in B.C., and because the terrain is not characterized by abrupt changes in topography and ecology. Candidate edges were restricted to the Babine variant of the SBSmc subzone (Meidinger et al. 1991, MacKinnon et al. 1992), near the towns of Smithers and Houston. Dominating the interior plateaus of central B.C., particularly from 53 to 56°N, these forests can be considered transitional between the true boreal forest (found further north) and neighbouring sub-alpine forests (found at higher elevations, >1025 to 1300 m in this area).

The moist cold subzone of the Sub-Boreal Spruce biogeoclimatic zone has a moderate continental climate characterized by moist, short summers and severe, snowy winters. The mean annual air temperature for this subzone ranges from -0.7 to 3.6°C; monthly mean air temperatures are below freezing for 5 to 6 months of the year, with an average frost-free period of 106 to 125 days. Annual precipitation ranges from 460 to 724 mm, with an average of 41% of precipitation falling as snow. Mean temperatures in July average 12.3°C, while mean temperatures in January average -12.6°C (Meidinger and Spittlehouse 1997). Soils are predominantly gray luvisols, brunisols and humoferric podzols (Meidinger et al. 1991, Banner et al. 1993).

Forests in the study area are characterized by subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.)

and hybrid white spruce, natural crosses between Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) and white spruce (*P. glauca* (Moench) Voss). Lodgepole pine (*Pinus contorta* Dougl. ex. Loud. var. *latifolia* Engelm.) and trembling aspen (*Populus tremuloides* Michx.) are more abundant in younger stands, and subalpine fir is more abundant in older stands. Mixed stands of old-growth spruce and fir in this area can be self-maintaining through gap dynamics, which typically prevail at stand ages greater than 180 years (Kneeshaw and Burton 1997, 1998). The understory of mature modal ecosystems (Site Series 01, Spruce-Huckleberry; Banner et al. 1993) in this subzone is characterized by black huckleberry (*Vaccinium membranaceum* Dougl.), bunchberry (*Cornus canadensis* L.), and the feather mosses *Pleurozium schreberi* (Brid.) Mitt., *Ptilium crista-castrensis* (Hedw.) and *Hylocomium splendens* (Hedw.) B.S.G.. Early successional stages are first dominated by fireweed (*Epilobium angustifolium* L.), bluejoint (*Calamagrostis canadensis* (Michx.) Beauv.), wild red raspberry (*Rubus strigosus* Michx.), thimbleberry (*R. parviflorus* Nutt.) and willows (*Salix* spp.) until the tree canopy closes.

Fire plays a prevalent role in the composition and dynamics of the forests in this region. Wildfires here tend to be a combination of surface and crown fires which can be as frequent as every 75 to 100 yr, or as infrequent as every 150 to 250 yr. Historically, individual fires have burned areas from 0.1 to 50 000 ha, but the average wildfire area has been 50 to 500 ha during recent times (Old-growth forests... 1992, DeLong and Tanner 1996). Other important stand-level disturbances in this region include spruce beetle (*Dendroctonus rufipennis* (Kirby)) which affects 1 to 6200 ha per infestation with 5 to 90% host mortality at intervals of 100 to 200 years, and root rots (especially *Inonotus tomentosus* (Fr.:Fr.) S.Teng.) which infest patches <1 to 100 ha in size with 0 to 10% tree mortality (Old-growth forests... 1992). The disturbance regime of these forests has been dominated by clearcut logging for the last three or four decades, with cutblocks artificially regenerated to promote second-growth stands of conifer trees. Windthrow often expands the area opened by other disturbances, and also occurs independently. Because of the many overlapping

natural disturbances characteristic of this forest region, a large number of plant species seem to be adapted to the full range of successional environments from open habitats to forest interiors. It is quite possible, therefore, that edge effects noted in more stable forest types may not be so pronounced in the Sub-Boreal Spruce zone.

3 Methods

3.1 Site Selection

In this first investigation of edge effects in sub-boreal forests, we limited our search to those habitats most likely to exhibit strong responses to edge creation: uniform sites disturbed one to two decades in the past, with arbitrary boundaries not defined by topographic or forest cover differences, with inner edges exposed to direct sunlight from the south or outer edges on the north (shaded) side of standing timber. Preliminary observations suggested that edges 10 to 20 years old have existed long enough for vegetation to have responded to the new environment, but not so long that new growth of trees and shrubs has ameliorated the differences between open and forested habitats.

Forest cover maps and ISIS/MLSIS databases maintained by the B.C. Ministry of Forests were searched to evaluate all clearcuts > 10 ha in size logged between 1975 and 1987 in the SBSmc subzone of the Bulkley and Morice Forest Districts. Suitability of the north and south boundaries of these clearcuts was evaluated on the basis of edge orientation, uniformity (of topography and forest cover), and forest composition and maturity. Forest-cutblock boundaries which could reasonably be expected to exhibit edge effects not confounded by other factors were those running more or less east and west (so that sample transects could run north and south, $\pm 30^\circ$ azimuth), on level terrain (<15% slope), with apparently identical ecosystems and forest cover types on either side of the boundary prior to logging. With the aid of aerial photographs and field inspections, we rejected those cutblocks which had recently been managed by brushing or spacing, forest stands less than 80 years or greater

than 250 years of age, and sites for which reasonable access by road and foot was not possible. After eliminating unsuitable boundaries according to the above criteria, 12 accessible edges at elevations from 810 to 1031 m were chosen for sampling from a total of 114 suitably oriented candidates (61 south-facing, 53 north-facing), screened from a pool of 535 boundaries of the desired age class. The site selection process was tabulated to document the degree to which sampled edges represent the overall population of cutblocks harvested in the study area, and the prevalence of other factors that might explain vegetation patterns along cutblock boundaries.

Only 20 to 23% of the 268 cutblocks were characterized by boundaries with vegetation likely to be impacted by the creation of an artificial edge more than by confounding site factors. In order to locate a sufficient number of edges that were suitable and accessible for sampling, we had to relax our original site selection criteria to include stands containing pine as well as spruce and fir (on 84% of all south-facing edges), stand ages 86 to 255 years old (65% of edges) and crown closure >45% cover (26% of edges). Similarly, the interpretation of vegetation differences in clearcuts, particularly the portions immediately north of forested edges, is confounded by a variety of silvicultural treatments. Most cutblocks in this area were bounded by bulldozed fire guards and have been artificially regenerated with planted conifers. During the period from 1975 to 1987, 43% of all cutblocks were slash-burned for site preparation, 54% were mechanically site-prepared, 18% received chemical or manual vegetation control, and 0.8% were spaced. Conversely, only 9.0% of the cutblocks had no silvicultural treatments other than planting, while only 10.5% had no site preparation. We therefore had to broaden acceptability criteria to include blocks which had been slash-burned and those in which non-crop vegetation had been treated, but more than 5 years prior to sampling. Two of the manually brushed clearcuts also appear to have had some tree spacing conducted during brushing (Table 1), though not in the plots we sampled.

Table 1. Forest stand edges sampled in 1996 and 1997, with reference to attributes of the standing forest and silvicultural treatments undertaken in the cutblock on either side of each forest-clearcut boundary.

Latitude N	Longitude W	Elevat., m	No. of transects	Adjacent forest attributes		Adjacent cutblock attributes								
				Dominant species*	Age class** (yrs. max.)	Year(s) logged	Area, ha	Slash- burned	MSP***	Planted	Dominant species	Brushed	Spaced, pruned	
Forest edges facing south:														
55°01'	126°34'	945	3	F,S	5	84	1984	20.0	1984	x	1985	S	1991	x
55°02'	126°35'	922	3	F,S	5	—	1984	75.6	1985	x	1986,90	S	1989	x
54°58'	126°34'	912	3	S,F	5	208	1984–86	68.0	x	1986	1987	P,S	x	x
55°03'	126°41'	810	2	F,S,(P)	8	207	1980	12.0	1980	x	1983	P,(S,A)	x	x
54°58'	126°34'	810	1	P,S,(F)	8	198	1976	63.0	spots,77	x	ca.1982	P,(S,A)	1994	(20 ha)
54°58'	126°34'	878	1	F,S	5	123	1983	116.0	1984	x	1985,89	S,(F)	1990	x
Forest edges facing north:														
55°03'	126°34.5'	858	3	S,F,P,(A)	8,5	148	1978	71.0	x	1979	1980	P,S,(F)	(19 ha)	x
54°55'	126°25'	1031	3	S,(F,P)	7	—	1987	43.9	1988	x	1990	P	x	x
54°51'	126°37'	900	3	P,(S)	8	170	1976	52.0	x	1977	1978,79	P,S	1994	?
55°02'	126°39'	893	1	F,S	5	157	1984	75.6	1985	x	1986,90	S	1989	x
55°05'	126°40'	891	1	P,S	8	75	1988–90	41.5	1989	x	1991	S	x	x
55°02'	126°40'	848	1	S,F	8	82	1987–88	70.9	1988,89	x	1989	P,S	(20 ha)	x

* Co-dominant species listed in approximate order of abundance, with minor species listed in parentheses;

A = trembling aspen; F = subalpine fir; P = lodgepole pine; S = hybrid white spruce.

** Age class 5 was 81 to 100 years old as of 1990; age class 6 was 101 to 120 years old; age class 7 was 121 to 140 years old; and age class 8 was 141 to 250 years old, as recorded on B.C. Ministry of Forests forest cover maps.

*** MSP denotes mechanical site preparation, including shark-fin barrels, disc-trenching, and mounding.

3.2 Transect and Plot Layout

Twelve stand edges (six south-facing and six north facing) were sampled with 25 transects running from the centre of each clearcut, perpendicular to the stand edge, deep into the forest interior (Table 1). Over two years of sampling, a total of 218 plots were sampled for tree and stand attributes. Eighty-six plots sampled various positions along the inner edge of forest stands, with another 25 plots representing interior forest conditions. Eighty-two plots sampled various positions along the outer edge of clearcuts next to uncut forest, plus 25 plots situated near the middle of clearcuts. Some edges were sampled by two or three parallel transects situated approximately 50 m from each other, in order to compare variability within and among edges.

Because this was a retrospective study of the impacts of operational forestry practices, there was no control over cutblock layout and development, only over the choice of sampling locations (as described in Section 3.1). Plots were situated on mesic sites where ecological factors other than edge proximity were not readily apparent. As a result, there were constant trade-offs between a uniform sampling design and the need to avoid inherently unsuitable microsites. Each transect was anchored by a plot in the forest interior located 105 to 290 m from the nearest opening (the "forest anchor"), and by another plot in the centre of the clearcut (the "clearcut anchor"), 85 to 375 m from the nearest mature forest. The length of transects, and hence the distance of anchor plots from the nearest edge, depended on the size of the cutblock or forest cover polygon, and whether the edge faced north or south. The inner edge of south-facing edges was intensively sampled with an array of adjacent plots, and it was more important for the forest anchor to be located deep in the forest (>125 m from the edge). For the sampling of adjacent canopy effects in clearcuts, however, the clearcut anchor need not be so distant (≥ 85 m on south-facing transects to ≥ 115 m on north-facing transects) from the edge. Conversely, the outer edge of north-facing edges was intensively sampled with adjacent plots, with the clearcut anchor usually situated further and the forest anchor plot typically located closer to the cutblock boundary than on south-facing edges.

Rectangular sample plots were 200 m² in area, with their long axes laid out parallel to the stand edge. Plots measured 20 m \times 10 m during the first year of sampling (1996), and 30 m \times 6.67 m in the second year (1997). This longer, narrower plot shape was adopted in order to survey a narrower window of edge distances in each plot than could be sampled by the 20 m \times 10 m plots used at first. The exact position of the forest edge was considered to be the canopy drip line of mature uncut trees, at which sampling typically commenced in both directions. Plots were identified by the distance of the plot centre from the forest edge. Five to nine contiguous plots were located in the first 50 to 90 m north of the edge, though only one transect per edge was sampled this intensively. All transects had a clearcut anchor plot, an outer edge plot centred 3.3 to 15 m from the edge, an inner edge plot centred 3.3 to 5 m from the edge, at least one plot 40 to 70 m north of the edge, and a forest interior plot. Outer edge plot centres were sometimes >5 m (in 1996) or >3.3 m (in 1997) from the drip line if the cutblock perimeter had been disturbed by a bulldozed fire guard, which we usually chose not to sample because of the unrepresentative degree of soil disturbance. Plots were not situated at uniform distances from edges on each transect in order to avoid breaks in micro-topography, obviously different soil conditions, and (in clearcuts) human disturbances such as roads and trails. Furthermore, different transect lengths also offered the opportunity to sample edge gradients over a range of distances and intervals. Edge proximity was treated as a continuous independent variable and data were collected in a manner suitable for regression analysis (Section 3.5).

3.3 Canopy Openness and Light Availability

Ideally, a full range of biometeorological measurements would have been taken in all plots in order to establish the gradient of environmental conditions prevailing across stand edges. Such instrumentation would be prohibitively expensive, however, and such measurements in forest understories are known to exhibit a strong correlation with canopy openness and direct beam radiation (Geiger 1965, Stoutjeskijk and Bark-

man 1992). Hemispherical photographs of the canopy were taken in order to precisely measure canopy cover and light availability at selected points along the edge transects. Photographs of the canopy were taken at plot centres from a 1 m height, using a tripod-mounted Minolta model X-700 35 mm camera and a 7.5 mm f4 "fisheye" lens. The camera was levelled and its body was oriented in an east-west direction; photographs were taken with Fujichrome Sensia 400 ASA colour slide film. Slides were scanned using a Microtek ScanMaker 35t-plus scanner, and analyzed using GLI/C Version 2.0 software (Canham 1988, Canham et al. 1990) to determine percent canopy cover and growing season inputs (May through September) of direct (beam), diffuse, and global radiation for each spot. The use of hemispherical photograph analysis is an ideal method for estimating subcanopy irradiance under conditions of heterogenous canopies and strongly directional light inputs (Canham 1988, Fraser et al. 1997).

3.4 Trees and Windthrow

All trees >7.5 cm DBH (diameter at breast height, 1.3 m) were recorded by species and DBH in each 200 m² plot. Tree height and height to the base of the live crown were determined (using a clinometer) for three trees (one fir, one spruce, and one pine, if present) representative of the main canopy layer in each plot. Unhealthy trees suffering from chlorosis, necrosis or defoliation were also noted as "sick." Dead trees were recorded in a similar manner, as were any recent treefalls (windthrow) originating within the sample plot. The directional orientation and mode of falling (uprooting or "tip-up", butt rot, and stem breakage or "snap") were also recorded for recently fallen trees. "Recent" treefalls were those estimated to have fallen since logging occurred nearby, not those incorporated into the forest floor, rotting or covered with moss. Increment cores were taken from the south side of boles at breast height from three living, dominant trees of each species. These cores were mounted and sanded in the lab, viewed under a dissecting microscope fitted with a video monitor and micrometer, and measured to the nearest 0.01

mm increment for each of the previous 15 years. Ages were also determined for the largest pine or spruce in each plot to confirm stand age.

In calculating the wood volume (m³) of live trees, standing snags, or fallen logs, the following allometric equations derived by the B.C. Forest Service (Whole stem cubic... 1976) were employed, using tree height, ht (m) and DBH (cm). The equations for this region are:

$$\text{vol} = 10^{-4.291919} \cdot \text{DBH}^{1.87293} \cdot \text{ht}^{0.998274} \quad [1]$$

for subalpine fir

$$\text{vol} = 10^{-4.349504} \cdot \text{DBH}^{1.82276} \cdot \text{ht}^{1.0812} \quad [2]$$

for lodgepole pine

$$\text{vol} = 10^{-4.294193} \cdot \text{DBH}^{1.85859} \cdot \text{ht}^{1.00779} \quad [3]$$

for hybrid white spruce

$$\text{vol} = 10^{-4.419728} \cdot \text{DBH}^{1.89476} \cdot \text{ht}^{1.05373} \quad [4]$$

for trembling aspen

$$\text{vol} = 10^{-4.400755} \cdot \text{DBH}^{1.836844} \cdot \text{ht}^{1.0994008} \quad [5]$$

for other incidental tree species.

For trees without individual height measurements, heights (m) were estimated from DBH (cm) on the basis of relationships derived from those trees having both DBH and height measurements, pooled with the extensive database compiled for trees growing in the same biogeoclimatic subzone by Kneeshaw and Burton (1997):

$$\text{ht} = 27.63467658 \cdot (1 - e^{-0.07265071 \cdot \text{DBH}})^{2.13593030} \quad [6]$$

for subalpine fir

$$\text{ht} = 48.45478102 \cdot (1 - e^{-0.00532149 \cdot \text{DBH}})^{0.37466566} \quad [7]$$

for lodgepole pine

$$\text{ht} = 34.66283839 \cdot (1 - e^{-0.04372656 \cdot \text{DBH}})^{1.32841495} \quad [8]$$

for hybrid white spruce

$$\text{ht} = 30.71844690 \cdot (1 - e^{-0.06068900 \cdot \text{DBH}})^{1.90749953} \quad [9]$$

for trembling aspen

$$\text{ht} = 30.76481434 \cdot (1 - e^{-0.06296844 \cdot \text{DBH}})^{1.89685241} \quad [10]$$

for all other tree species

where e is the base of natural logarithms. Tree heights estimated only from DBH were not used

for calculating live crown ratio or height-to-dbh ratio.

The number of all seedlings (<1.5 m tall) and saplings (1.5 to 5.0 m tall) was counted by species in each 200 m² plot (or per quarter-plot or half-plot if uniformly distributed and so dense that >60 stems were already counted). Three of the most vigorous individuals of each species were measured for total height, current leader length, and diameter at the base of the leader. The best growing seedling of each conifer species in each plot was sawed off at the base, sanded, and measured (by micrometer under a dissecting microscope as described above) for the last 6 years of annual radial increment.

3.5 Statistical Analysis for Detection of Edge Effects

A wide range of tree-related response variables were tested for measurable edge effects: canopy cover and subcanopy irradiance, total density and the proportional abundance of each tree species, the amount of windthrow and the attributes of fallen trees, the density and composition of regeneration, and the radial growth of mature and juvenile trees. Following Chen et al. (1995), analysis was designed to both measure the significance of edge effect (SEE) and the distance of edge effect (DEE). Analysis of variance using SAS procedure GLM (SAS Institute 1988), with transects nested within edges as a blocking factor, was first used to determine if a response value in plots immediately adjacent to the forest-clearcut boundary (<10 m from the edge) was significantly different from its value in the forest interior (i.e., at forest anchor plots ≥ 105 m from the cutblock) or the clearcut anchor (≥ 85 m from the forest). The contrast between edge and anchor conditions is described in terms of the magnitude of edge effect (MEE), which is defined here to be the ratio of the larger (edge or anchor) mean value to the smaller mean value. In all cases, separate analyses were conducted for south-facing and north-facing edges.

The estimation of DEE is highly sensitive to the regression model (or other technique) selected to portray the attenuation of edge effects with distance. Many researchers have fitted exponen-

tial functions (e.g., Laurance et al. 1997, Hughes and Bechtel 1997) or selected from among a set of non-linear functions according to goodness of fit (e.g., Chen et al. 1992). Others have used a combination of graphical methods, visual inspection and pairwise comparisons among uniformly spaced plots to identify the distance at which edge-associated changes are no longer detectable (e.g., Palik and Murphy 1990, Fraver 1994, Cadenasso et al. 1997, Burke and Nol 1998).

In this study, DEE was estimated as the intersection of a linear regression line with the mean of background (clearcut anchor or forest anchor) levels. Where analysis of variance for edge-anchor contrasts (SEE) was significant at $p = 0.10$, regression analysis was used to infer the distance at which response attributes could not be distinguished from background or anchor levels. Because edge effects are continuous and a uniform set of distances was not sampled in all transects, some sort of continuous analysis (rather than categorical pairwise plot comparisons or a "moving window" approach) was considered the most appropriate method for determining DEE. As a first approximation of the edge response function for these attributes in these forests, linear regression was used to describe the relationship between each attribute and distance north of the edge, excluding any anchor plots from the analysis. To solve for DEE, the mean attribute level at all appropriate (forest or clearcut) anchor plots on the same transects was first calculated. Then y in the equation for a straight line, $y = a + bx$, was set to that mean anchor level (considered a "background" level), and the equation was solved for x . Values for DEE are rounded to the nearest 5 m for purposes of discussion, reflecting the inherent uncertainty regarding these calculations.

Ideally, these background levels might be better defined by a confidence interval rather than a simple mean (e.g., Laurance et al. 1997), because forest or clearcut attributes beyond the influence of an edge can exhibit a wide range of variability (especially if the stand is naturally patchy). The regression model likewise is fit with varying degrees of certainty, so it too is better denoted by a band rather than a line. Conceptually, the distance at which the 95% confidence interval for the regression intersects the 95% confidence interval for background conditions should desig-

nate the DEE. However, both confidence intervals are highly dependent on sample size (which varied from attribute to attribute), and DEE values predicted in this manner were so conservative that they did not agree with visual observations. So it was decided that the most appropriate definition of DEE was that distance at which expected values from any significant and monotonically changing edge influence are no longer distinguishable from average background levels beyond the influence of any edge. Furthermore, the anchor values used to derive those background levels were excluded from regression analysis, as their great distance from the edge (often more than 200 m) unnecessarily dampened the slope of most edge response functions. Methodological differences such as these are common in the literature, making simple comparisons of reported depths of edge effect difficult and often inappropriate. The significance and magnitude of edge-interior contrasts are much more robust and are generally more comparable among different investigations.

4 Results

4.1 Canopy Openness and Light Availability

There were strong differences in all canopy and light measurements between interior forest conditions and those sampled within 10 m of south-facing forest edges (Table 2). Though canopy cover averaged only 1.25 times greater at forest anchor positions, subcanopy global irradiance averaged 2.5 times higher in the south-facing inner edge. On north-facing inner edges, however, beam irradiance and global irradiance did not differ significantly between edge and interior positions. Light conditions in clearcuts were less variable, with an average of 23 to 29% tree cover (from well established trees 7 to 19 years old) even in the middle of these cutblocks (Table 2). As a result, global irradiance measurements at clearcut anchor positions averaged 85% of "full sunlight" rather than being a uniform 100% as otherwise might be expected. Global irradiance

Table 2. Mean (\pm S.E.M.) for canopy cover (%), its converse (open sky, %), and irradiance data (% of full sunlight) at anchor and edge (<10 m from boundary) positions. Significance of edge effect (SEE) is indicated by Prob.>F values*; magnitude of edge effect (MEE) is indicated by ratio values**.

Habitat and attribute	North-facing edges				South-facing edges			
	Anchor	Edge	SEE	MEE	Anchor	Edge	SEE	MEE
n:	12	12	(Prob.>F*)	(Ratio**)	12	14	(Prob.>F*)	(Ratio**)
Adjacent opening effects (into south-facing forest edges):								
Forest								
Canopy cover	88.3 \pm 1.3	77.3 \pm 2.1	0.002	1.14	87.7 \pm 2.4	64.8 \pm 5.7	0.006	1.35
Open sky	11.7 \pm 1.3	22.7 \pm 2.1	0.002	1.93	12.3 \pm 2.4	35.2 \pm 5.7	0.006	2.86
Beam irradiance	18.9 \pm 2.4	17.9 \pm 3.1	0.797	1.06	17.8 \pm 3.2	48.3 \pm 7.8	0.010	2.71
Diffuse irradiance	17.2 \pm 2.0	27.0 \pm 2.6	0.018	1.57	18.1 \pm 3.5	40.5 \pm 6.4	0.027	2.24
Global irradiance	18.1 \pm 2.1	22.6 \pm 2.6	0.244	1.25	17.9 \pm 3.3	44.4 \pm 7.0	0.014	2.48
Mean:				1.39				2.33
n:	12	6			12	5		
Adjacent canopy effects (into clearcuts adjacent to north-facing forest edges):								
Clearcut								
Canopy cover	28.9 \pm 5.5	44.0 \pm 1.9	0.215	1.52	23.1 \pm 6.0	44.1 \pm 7.6	0.092	1.91
Open sky	71.1 \pm 5.5	56.0 \pm 1.9	0.215	1.27	76.9 \pm 6.0	55.9 \pm 7.6	0.092	1.38
Beam irradiance	84.8 \pm 4.3	53.2 \pm 12.4	0.167	1.59	86.9 \pm 5.7	80.9 \pm 4.1	0.638	1.07
Diffuse irradiance	81.8 \pm 5.0	68.9 \pm 3.3	0.272	1.19	85.8 \pm 5.3	69.0 \pm 8.1	0.127	1.24
Global irradiance	83.3 \pm 4.6	61.0 \pm 7.7	0.188	1.37	86.4 \pm 5.5	75.0 \pm 5.7	0.272	1.15
Mean:				1.39				1.35

* Results of analysis of variance on arcsine square-root transformed data using SAS proc GLM (SAS Institute 1988).
 If Prob.>F is less than 0.05, then the difference between anchor and edge plots is considered significant at the 95% confidence level.
 ** MEE is a ratio of the higher mean anchor or edge value to the lower mean anchor or edge value.

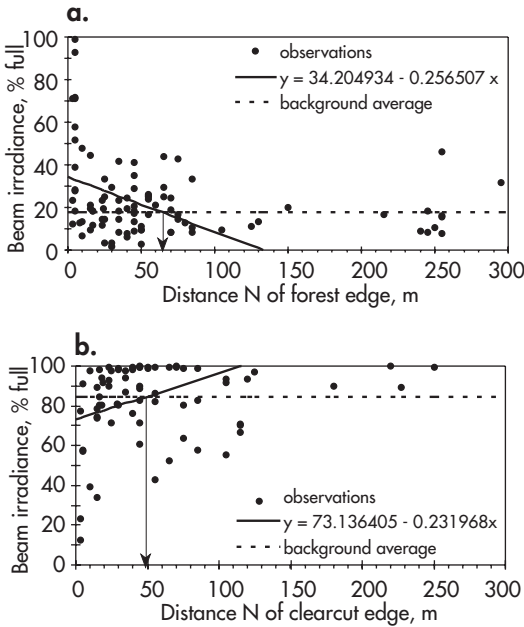


Fig. 1. Measurements of beam irradiance in (a) the forest understory at south-facing edges, and (b) clearcuts at north-facing edges. Arrows show how the distance of edge effect (DEE) is determined, being that distance at which the regression intersects the average background level observed in anchor plots.

determinations within 10 m of cutblock edges averaged 61% of full sunlight on north-facing edges, but variability was so great that irradiance was not significantly lower than in the middle of clearcuts.

The attenuation of beam irradiance in the forest at south-facing edges (Fig. 1a) serves to illustrate how DEE was calculated for all attributes. The equation,

$$\text{beam irradiance} = 34.204934 - 0.256507 * \text{distance} \quad [11]$$

was fit with $r^2 = 0.13$, $p = 0.001$. Since interior forest levels of beam irradiance averaged 17.795% (Table 2), substituting into the above equation and solving for distance yields 64 m as DEE. In contrast, the equation for beam irradiance values in clear-cuts at north-facing edges is:

$$\text{beam irradiance} = 73.136405 - 0.231968 * \text{distance} \quad [12]$$

with $r^2 = 0.07$ and $p = 0.048$ (Fig. 1b). Substituting the anchor value of 84.752% then gives us -50 m for the DEE (where negative values denote distances into clearcuts). Whereas light penetration of south-facing forest edges is significant and detectable for 64 to 69 m into the forest, the shading effects of north-facing edges are detectable only for direct (beam) irradiance and for only 50 m into a clearcut. Regression results and DEE values estimated for all canopy and irradiance attributes are summarized in Table 3.

Light availability decreased sharply and almost linearly on either side of cutblock boundaries, whether the edge faced north or south. Visual inspection and iterative regression analysis over transect segments defined by different distances into the clearcut or into the forest revealed the following highly significant ($p < 0.001$) relationships for global irradiance as a function of distance from the edge:

$$\text{N-facing edges: } Y = 38.518749 - 2.581198 X, \quad [13] \text{ for } X = -25 \text{ m to } +10 \text{ m; } r^2 = 0.78, n = 34$$

$$\text{S-facing edges: } Y = 58.344465 - 1.951731 X, \quad [14] \text{ for } X = -25 \text{ m to } +35 \text{ m; } r^2 = 0.72, n = 51$$

where Y is global irradiance as a percentage of full sunlight, and X is distance from the edge in m, where negative values denote distance into a clearcut. Similar relationships were derived for the other elements of canopy cover and light regime as well.

4.2 Response of Mature Trees

The response of mature trees is limited to the effects of adjacent openings, because (by definition) there were no mature trees growing in clearcuts to respond to the influence of adjacent forest stands. Sampling of interior forest plots revealed mean densities of 1190 canopy stems per ha (sph), with trees averaging 21.3 cm dbh and 24.0 m in height (Table 4). These dimensions result in a mean basal area of 52.2 m²/ha, and total stem volumes of 470 m³/ha. Interior trees

Table 3. Results of linear regression analysis relating canopy cover (%), openness (%) and irradiance (% of full sunlight) to distance from the clearcut-forest boundary (m), in which negative distances denote positions within clearcuts. Distance of edge effect (DEE) is calculated from significant regressions.

Habitat and attribute	Anchor mean (% full)	Regression results					DEE* (m)
		Intercept	Slope	p	r ²	n	
Adjacent opening effects (into south-facing forest edges):							
Forest							
Canopy cover	87.693	75.348042	0.184025	0.001	0.137	78	67
Open sky	12.307	24.651958	-0.184025	0.001	0.137	78	67
Beam irradiance	17.795	34.204934	-0.256507	0.001	0.129	78	64
Diffuse irradiance	18.072	29.100438	-0.160379	0.011	0.082	78	69
Global irradiance	17.933	31.620661	-0.208562	0.003	0.112	78	66
Adjacent canopy effects (into clearcuts adjacent to north-facing forest edges):							
Clearcut							
Canopy cover	28.948			0.168		58	-
Open sky	71.052			0.168		58	-
Beam irradiance	84.752	73.136405	-0.231968	0.048	0.068	58	-50
Diffuse irradiance	81.768			0.366		58	-
Global irradiance	83.263			0.109		58	-

* DEE (m) is derived by substituting anchor values (from Table 2) into each significant (p<0.10) regression equation and solving for distance; i.e., DEE = (Anchor mean - Intercept) / Slope.

had an average height-to-dbh ratio of 68:1, with mean live crown ratios of 61%. Stand interiors were dominated by subalpine fir (averaging 68% of the stems), with lower densities of hybrid white spruce (22%) and lodgepole pine (10%). Background levels of recently fallen trees averaged 7.7% of all stems, while dead and dying trees constituted an average of 12.0% of all upright stems. In forest interiors, 9.1% of all fir stems are likely to have fallen recently, as are 2.2% of pine and 11.7% of spruce stems. Approximately equal numbers of recently fallen trees had been snapped off above the ground (49%) or had been uprooted with a full root plate (45%), while relatively few (6%) originated from butt rot. The height-to-dbh ratio of those fallen trees average 76:1, higher than that of standing trees.

Many of these stand attributes were altered in edge plots, though not significantly so at north-facing edges. In general, fewer stems (and consequently lower basal areas and wood volumes) were left in the canopy at edge plots, primarily because of increased numbers of recently fallen trees. Fallen trees typically had height-to-DBH ratios greater than 71:1 (Fig. 2), while most standing trees (except pine) had height-to-DBH ratios

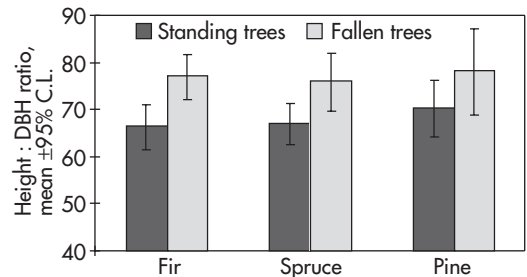


Fig. 2. Comparison of the height-to-DBH ratio in all standing and recently fallen trees >7.5 cm dbh, all edge positions combined.

of less than 71:1, though fallen trees in edge plots included more individuals with lower ratios. More fallen trees in edge plots originated by uprooting rather than stem breakage, while the reverse was true in the forest interior. Larger numbers of standing dead trees were typically observed in edge plots, though the live crown ratios of living trees were often greater than in the forest interior. These trends resulted in statistically detectable (at p = 0.05) edge effects only for the direct windthrow and canopy stem attributes

Table 4. Mean (\pm S.E.M.) attributes of mature trees in forest anchor and edge (<10 m from clearcut boundary) positions, and resulting determinations of SEE, and MEE.

Attribute	North-facing edges				South-facing edges			
	Anchor	Edge	SEE (Prob.>F*)	MEE (Ratio**)	Anchor	Edge	SEE (Prob.>F*)	MEE (Ratio**)
Live canopy trees								
Mean DBH, cm	20.4 \pm 1.4	20.9 \pm 1.5	0.842	1.03	22.1 \pm 0.8	20.4 \pm 0.8	0.192	1.08
Live stem density, stems/ha	1225 \pm 103	983 \pm 106	0.200	1.25	1158 \pm 120	765 \pm 98	0.022	1.51
Basal area, m ² /ha	52.0 \pm 6.1	42.0 \pm 4.8	0.257	1.24	52.4 \pm 4.1	28.1 \pm 3.2	0.001	1.86
Wood volume, m ³ /ha	484 \pm 70	375 \pm 55	0.302	1.29	458 \pm 38	231 \pm 30	0.001	1.98
Mean height, m	24.4 \pm 1.8	24.1 \pm 1.5	0.886	1.01	23.5 \pm 1.0	21.3 \pm 1.0	0.098	1.10
Mean height to DBH ratio	67.5 \pm 4.9	65.5 \pm 3.2	0.611	1.03	68.1 \pm 2.5	71.2 \pm 1.9	0.514	1.05
Mean live crown ratio	64.8 \pm 2.7	65.8 \pm 4.0	0.918	1.02	57.5 \pm 4.1	61.9 \pm 5.9	0.926	1.08
Dead trees, % of upright stems	7.0 \pm 2.0	12.3 \pm 2.9	0.202	1.74	15.0 \pm 3.3	24.1 \pm 5.3	0.242	1.60
Sick & dying, % of upright stems	1.28 \pm 1.28	0 \pm 0	0.339	–	0.43 \pm 0.43	2.61 \pm 1.60	0.143	6.11
Leaning trees, % of upright stems	0.46 \pm 0.46	0.93 \pm 0.64	0.587	2.02	2.6 \pm 1.3	3.9 \pm 2.1	0.843	1.50
Radial increment*** in fir	1.06 \pm 0.11	1.04 \pm 0.12	0.743	1.02	1.04 \pm 0.10	1.06 \pm 0.08	0.643	1.02
Radial incr.*** in spruce	1.12 \pm 0.10	0.96 \pm 0.08	0.096	1.17	0.98 \pm 0.05	0.93 \pm 0.07	0.774	1.06
Radial incr.*** in pine	1.05 \pm 0.19	0.97 \pm 0.16	0.668	1.08	1.11 \pm 0.13	0.58 \pm 0.05	0.013	1.92
Windthrow								
Recently fallen trees, stems/ha	121 \pm 29	154 \pm 27	0.913	1.28	112 \pm 21	354 \pm 61	0.002	3.17
Recently fallen trees, % of stems	8.0 \pm 1.8	12.4 \pm 2.3	0.373	1.55	7.4 \pm 1.0	26.2 \pm 4.5	0.001	3.56
Height to DBH ratio of deadfall	70.9 \pm 5.5	65.5 \pm 4.5	0.247	1.08	80.8 \pm 6.2	75.5 \pm 3.2	0.422	1.07
Snap-off, % of all windthrow	55.8 \pm 12.3	43.8 \pm 11.2	0.720	1.27	44.2 \pm 10.1	17.1 \pm 7.5	0.139	3.52
Uprooted, % of all windthrow	40.8 \pm 12.1	54.6 \pm 11.5	0.613	1.34	48.1 \pm 10.3	80.7 \pm 7.6	0.058	1.68
Fallen fir, % of all fir stems	8.4 \pm 2.8	13.2 \pm 1.8	0.678****	1.58	9.7 \pm 3.6	18.3 \pm 4.9	0.125****	1.89
Fallen spruce, % of all spruce stems	14.7 \pm 8.8	14.8 \pm 8.9	0.984****	1.01	9.0 \pm 4.6	41.5 \pm 10.0	0.096****	4.61
Fallen pine, % of all pine stems	3.7 \pm 2.0	3.6 \pm 2.4	0.348****	1.03	0.0 \pm 0.0	11.4 \pm 5.5	–****	–

* If Prov.>F is less than 0.05 (shown in bold), then edge plots and anchor plots are significantly different from each other at the 95% confidence level.

** MEE is a ratio of the higher mean anchor or edge value to the lower mean anchor or edge value.

*** Mean annual radial increment over the period 1982–1996, relativized to the overall average observed in 312 fir, 282 spruce, and 122 pine.

**** Results of one-way ANOVA because of insufficient degrees of freedom to partition out opening effects in a two-way ANOVA.

on south-facing edges (Table 4). The magnitude of edge effect (MEE) was over 3.0 for the amount of windthrow, and over 1.5 for the stand attributes of density, basal area and wood volume. Very high (>3.0) MEE values were also noted for increased proportions of sick and dying trees, decreased proportions of windthrow originating as snapped boles, and higher proportions of spruce trees having fallen on south-facing edges. Variability among transects and openings was so great that

none of these latter contrasts proved significant at the $p = 0.05$ level in a two-way (position \times transect) analysis of variance. Significant linear regressions, and subsequent estimates of the distance of edge effect (DEE), were obtained for stand basal area ($r^2 = 0.07$, DEE = 115 m), stand volume ($r^2 = 0.09$, DEE = 111 m), the density of windthrow ($r^2 = 0.14$, DEE = 54 m), the overall percentage of trees to have fallen ($r^2 = 0.13$, DEE = 62 m), and the percentage of spruce to have

Table 5. Results of linear regression analysis relating attributes of live canopy trees and recent windthrow to the distance north of south-facing forest edges (m). Distance of edge effect (DEE) is calculated from significant regressions.

Attribute	Anchor mean	Regression results					DEE* (m)
		Intercept	Slope	p	r ²	n	
Adjacent opening effects (into south-facing forest edges) on:							
Live canopy trees							
Live stem density, stems/ha	1157.7			0.305		76	
Basal area, m ² /ha	52.44	35.153109	0.150322	0.019	0.072	76	115
Wood volume, m ³ /ha	457.7	291.918682	1.493042	0.011	0.085	76	111
Mean height, m	23.52			0.161		64	
Radial increment** in fir	1.044	1.074646	-0.002298	0.072	0.015	217	13
Radial increment** in spruce	0.982			0.105		187	
Radial increment** in pine	1.106	0.505056	0.013221	<0.001	0.271	68	45
Windthrow							
Recently fallen trees, stems/ha	111.5	217.561166	-1.971567	0.001	0.140	76	54
Recently fallen trees, % of stems	7.36	16.046009	-0.139502	0.002	0.128	76	62
Uprooted, % of all windthrow	48.08			0.298		63	
Fallen spruce, % of all spruce stems	9.03	27.645179	-0.296821	0.005	0.112	69	63

* DEE (m) is derived by substituting anchor values (from Table 4) into each significant (p<0.10) regression equation and solving for distance: DEE = (Anchor mean - Intercept) / Slope.
 ** Mean annual radial increment over the period 1982–1996, relativized to the overall average observed in 312 fir, 282 spruce, 122 pine.

fallen (r² = 0.11, DEE = 63 m) on south-facing forest edges (Table 5).

Measurement of 716 tree cores showed some significant growth responses of residual canopy trees in relationship to edge proximity. Over the period from 1982 to 1996, radial growth of canopy fir trees averaged 13.9 mm (n = 312), that of spruce averaged 12.1 mm (n = 282), and pine averaged 9.9 mm (n = 122). There was no significant difference in fir growth between edge and interior locations for any of the three five-year intervals tested. Based on Type III sums of squares, it was found that edge position explained only 0.1 to 0.2% of the variation in fir growth, while 36 to 38% of the variation was associated with transect (nested within opening) differences. Radial increment of pine, on the other hand, was significantly lower in edge plots than in the forest interior (Table 4, Fig. 3), by 43 to 51% in each of the three most recent five-year periods. Linearly extrapolated, this trend apparently extends 45 m into the forest on south-facing edges (Table 5). There was a marginally significant (14%) growth reduction in canopy spruce trees on north-facing edges, especially in the first 10 years after logging, but

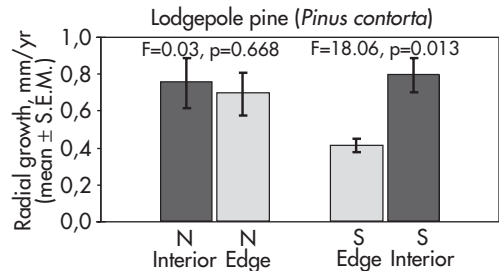


Fig. 3. Radial stem growth of mature *Pinus contorta* trees in edge and interior plots.

any reduced radial growth of spruce on south-facing edges was not significant (Table 4).

4.3 Tree Regeneration

The density of seedlings (<1.5 m tall) and saplings (1.5 to 5.0 m tall) varied considerably across the gradient of edge positions sampled, on both sides of the forest-clearcut boundary (Fig. 4). The outer edge of north-facing forest boundaries supported the highest densities of conifer seedlings (Fig. 4),

Table 6. Regeneration of conifers (mean ±S.E.M.) at anchor and edge locations in forest and clearcut habitats, and resulting determinations of SEE and MEE.

Habitat and attribute	North-facing edges				South-facing edges			
	Anchor	Edge	SEE (Prob.>F*)	MEE (Ratio**)	Anchor	Edge	SEE (Prob.>F*)	MEE (Ratio**)
n:	12	12			13	13		
Forest								
Fir density, stems/ha	5990 ± 1584	6090 ± 920	0.939	1.02	11859 ± 3733	4709 ± 616	0.085	2.52
Spruce density, stems/ha	750 ± 225	2786 ± 1767	0.266	3.71	1135 ± 605	1200 ± 214	0.910	1.06
Pine density, stems/ha	0 ± 0	225 ± 161	0.191	–	15 ± 15	123 ± 59	0.116	8.20
All species, stems/ha	6739 ± 1666	9102 ± 2579	0.105	1.35	13136 ± 4263	6108 ± 668	0.129	2.15
Fir, % of stems	88.1 ± 2.9	79.0 ± 5.1	0.154	1.12	91.5 ± 1.8	76.0 ± 3.4	<0.001	1.20
Spruce, % of stems	11.9 ± 2.9	20.0 ± 4.7	0.165	1.68	6.9 ± 1.7	20.8 ± 3.3	<0.001	3.01
Pine, % of stems	0 ± 0	1.0 ± 0.7	0.167	–	0 ± 0	2.4 ± 1.0	0.062	–
Dead seedlings, stems/ha	978 ± 405	149 ± 65	0.108	6.56	387 ± 89	149 ± 58	0.056	2.60
Dead saplings, stems/ha	403 ± 169	83 ± 53	0.048	4.86	621 ± 238	84 ± 53	0.059	7.39
n:	11	16			12	5		
Clearcut								
Fir density, stems/ha	100 ± 40	8545 ± 6492	0.280	85.45	141 ± 112	1487 ± 322	0.002	10.55
Spruce density, stems/ha	945 ± 166	11926 ± 3881	0.025	12.62	651 ± 135	1853 ± 428	0.025	2.85
Pine density, stems/ha	455 ± 151	1935 ± 603	0.067	4.25	957 ± 413	1130 ± 327	0.871	1.18
All species, stems/ha	1595 ± 174	22415 ± 9612	0.084	14.05	1755 ± 338	4473 ± 778	0.014	2.55
Fir, % of stems	5.8 ± 2.1	24.8 ± 6.1	0.010	4.28	6.2 ± 5.1	34.1 ± 4.4	<0.001	5.50
Spruce, % of stems	61.0 ± 11.3	61.4 ± 5.6	0.210	1.01	57.0 ± 12.7	46.6 ± 5.4	0.375	1.22
Pine, % of stems	29.7 ± 11.3	13.7 ± 3.5	0.745	2.17	36.7 ± 12.0	19.1 ± 4.7	0.050	1.92
Dead seedlings, stems/ha	0 ± 0	99.4 ± 74.7	–	–	65.4 ± 61.3	26.4 ± 18.9	0.901	2.48
Dead saplings, stems/ha	0 ± 0	0 ± 0	0.260	–	30.8 ± 30.8	27.1 ± 14.1	0.449	1.14

* Results of analysis of variance using SAS proc GLM (SAS Institute 1988). If Prob.>F is less than 0.05, then the difference between anchor and edge plots is considered significant at the 95% confidence level.
 ** MEE is a ratio of the higher mean anchor or edge value to the lower mean anchor or edge value.

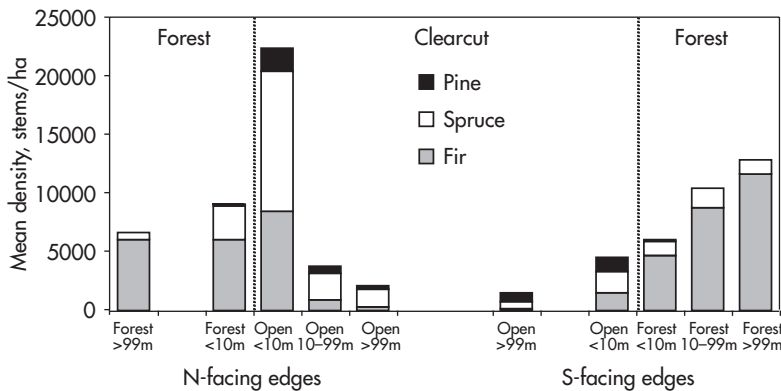


Fig. 4. Conifer regeneration density and composition along forest-cutblock edge gradients at north- and south-facing edges.

with MEE>12 for spruce regeneration at cutblock edges compared to cutblock centres (Table 6). Fir was most abundant in the forest understory, while spruce and pine dominated the clearcuts. Despite

the fact that all cutblocks were planted to spruce or pine seedlings, plot distance from the forest edge seems to be limiting the natural invasion of all conifer species at great distances into these

Table 7. Results of linear regression analysis relating densities (stems/ha) and proportions (%) of conifer regeneration to the distance north of forest-clearcut boundaries (m), in which negative distances denote positions within clearcuts. Distance of edge effect (DEE) is calculated from significant regressions.

Habitat and attribute	Anchor mean	Regression results				n	DEE* (m)
		Intercept	Slope	p	r ²		
Adjacent opening effects (into south-facing forest edges):							
Forest							
Fir density, stems/ha	11859.1	4147.760935	100.237303	<0.001	0.178	76	779
Spruce density, stems/ha	1134.7	921.859645	14.423712	0.097	0.037	76	14
Pine density, stems/ha	15.4			0.572		76	
All species, stems/ha	13136.1	5182.425200	113.965795	<0.001	0.163	76	70
Fir, % of stems	91.55	77.863405	0.130729	0.015	0.078	76	105
Spruce, % of stems	6.95	19.949412	-0.109145	0.039	0.056	76	119
Pine, % of stems	0.05	1.235164	-0.016182	0.023	0.068	76	74
Dead seedlings, stems/ha	620.5	-6.606245	8.427246	<0.001	0.198	76	74
Dead saplings, stems/ha	386.6	154.649954	4.964403	0.009	0.089	76	47
Adjacent canopy effects (into clearcuts adjacent to north-facing forest edges):							
Clearcut							
Fir density, stems/ha	100.0			0.109		65	
Spruce density, stems/ha	945.5	8642.019283	115.710058	0.005	0.118	65	-67
Pine density, stems/ha	455.5	1407.342174	13.891627	0.036	0.068	65	-69
All species, stems/ha	1595.5	16661.000000	229.068891	0.018	0.086	65	-66
Fir, % of stems	5.75			0.321		65	
Spruce, % of stems	61.00			0.412		65	
Pine, % of stems	29.72			0.161		65	
Dead seedlings, stems/ha	0.0			0.307		65	
Dead saplings, stems/ha	0.0			0.239		65	

* DEE (m) is derived by substituting anchor values (from Table 6) into each significant (p<0.10) regression equation and solving for distance: DEE = (anchor mean – intercept)/slope.

cutblocks. Edge-anchor contrasts in regeneration density were greatest for fir (MEE = 11 at the north end of cutblocks, MEE = 85 at the south end of cutblocks; Table 6). Consequently, the proportional abundance of fir was greater at all cutblock edges, whether facing north or south (Table 6). The pattern of linearly decreasing regeneration density with greater distance from standing forest was most pronounced for spruce (p = 0.005), extending 67 m into the south end of cutblocks; a similar pattern was observed for pine density (DEE = -69 m; Table 7).

Conifer regeneration in the forest understory also varied in numbers and composition according to edge position. Edge and anchor plot differences in several variables were pronounced at south-facing edges, but only the proportion of saplings which had died was significantly different (less) on north-facing inner edges (Table

6). At south-facing edges, fir constituted a lower proportion of the regeneration (76.0%, compared to 91.5% in the forest interior), while spruce were proportionately more abundant in edge plots (20.8%) than in the interior (6.9%). Differences in the density of dead seedlings and saplings were marginally significant, being consistently lower in south-facing edge plots. Linear regression analysis further revealed some significant trends, with fir and overall density increasing, the proportion of fir increasing and the proportion of spruce and pine decreasing, and the abundance of dead seedlings and saplings increasing at greater distances north of south-facing edges (Table 7). The DEE associated with significant (p<0.05) trends ranged from 47 m for the density of dead saplings, to 119 m for the proportional abundance of spruce, though the absolute density of spruce regeneration may be greater than background

Table 8. Leader growth (mean cm/yr, ± S.E.M.), SEE, and MEE for conifer regeneration growing at forest and clearcut anchors, and at forest-clearcut edges.

Habitat and species	North-facing edges				South-facing edges			
	Anchor	Edge	SEE (Prob.>F*)	MEE (Ratio**)	Anchor	Edge	SEE (Prob.>F*)	MEE (Ratio**)
Adjacent opening effects (into south-facing forest edges):								
Forest								
Subalpine fir	4.0 ± 0.4 n=50	9.8 ± 0.8 n=59	0.002	2.44	3.4 ± 0.3 n=68	13.9 ± 0.8 n=75	<0.001	4.13
Lodgepole pine	38.5 ± 4.8 n=7	17.2 ± 3.3 n=9	i.d.f.***	2.24	—	22.2 ± 3.0 n=15	—	—
Hybrid white spruce	3.3 ± 0.3 n=31	8.7 ± 1.0 n=37	0.062	2.65	2.8 ± 0.2 n=32	15.3 ± 1.7 n=35	0.002	5.55
Adjacent canopy effects (into clearcuts adjacent to north-facing forest edges):								
Clearcut								
Subalpine fir	17.3 ± 1.6 n=27	15.6 ± 1.1 n=64	0.793	1.11	22.9 ± 2.7 n=30	20.7 ± 1.0 n=103	0.529	1.11
Lodgepole pine	34.0 ± 2.6 n=28	25.9 ± 1.8 n=52	0.543	2.24	36.9 ± 2.6 n=25	31.1 ± 1.6 n=47	0.487	1.18
Hybrid white spruce	21.3 ± 2.2 n=23	14.5 ± 0.9 n=60	0.081	1.37	20.2 ± 1.7 n=42	22.0 ± 1.4 n=63	0.162	1.09

* Results of analysis of variance using SAS proc GLM (SAS Institute 1988). If Prob.>F is less than 0.05, then the difference between anchor and edge plots is considered significant at the 95% confidence level.
 ** MEE is a ratio of the higher mean anchor or edge value to the lower mean anchor or edge value.
 *** i.d.f. = insufficient degrees of freedom to test with position * transect (edge) as the error term.

(forest interior) levels for only 15 m into south-facing edges (Table 7).

Growth rates in conifer seedlings, indicated by the length of the current leader, also responded to edge proximity, especially in the forest understory (Table 8). Fir growth showed significant edge effects on both north- and south-facing inner edges, where growth was 2.4 times higher at the north-facing edge and 4.1 times higher on the south-facing edge. Similar trends were observed for pine and spruce on north-facing edges, but the most pronounced effect was illustrated by spruce growth on south-facing edges, where MEE was 5.6. These adjacent opening effects extended to 75 m for fir and 62 m for spruce (Table 9). Figure 5 illustrates average background growth rates for spruce in clearcuts and in the forest interior, and the regression describing the decreasing growth rate with increased distance from the edge. Surprisingly, no significant edge effect was detected for conifer seedling growth on the outer edge of cutblocks (Table 8). Though growth was frequently higher for individual spruce trees growing in the open adjacent to north-facing edges, all other species exhibited some degree of

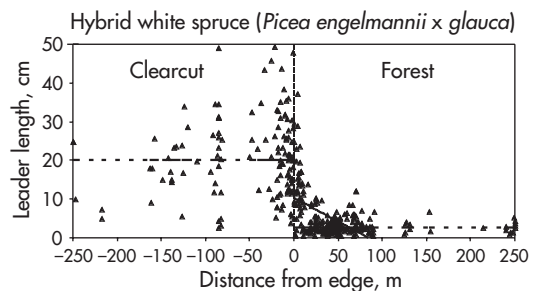


Fig 5. Current leader growth of *Picea engelmannii* × *glauca* seedlings growing at various positions on south-facing edges. Dashed lines represent average growth rates at clearcut anchor and forest anchor locations, and the solid line is the regression derived for seedlings in the understory at south-facing edges, $y = 10.338822 - 0.122287 x$, $p < 0.001$, $r^2 = 0.23$, $n = 213$.

depressed growth at outer edges. Many spruce seedlings growing within approximately 40 m of south-facing forest edges exhibited some of the most superlative growth rates (Fig. 5).

Similar results (data not presented here) were

Table 9. Results of linear regression analysis relating conifer seedling leader growth (cm/yr) to distance from the clearcut-forest boundary (m), in which negative distances denote positions within clearcuts. Distance of edge effect (DEE) is calculated from significant regressions.

Habitat and species	Anchor mean (cm/yr)	Regression results					DEE* (m)
		Intercept	Slope	p	r ²	n	
Adjacent opening effects (into south-facing forest edges):							
Forest							
Subalpine fir	3.35	10.009385	-0.089163	<0.001	0.248	378	75
Lodgepole pine	—**	21.827280	-0.218516	0.036	0.222	20	—**
Hybrid white spruce	2.76	10.338822	-0.122287	<0.001	0.227	213	62
Adjacent canopy effects (into clearcuts adjacent to north-facing forest edges):							
Clearcut							
Subalpine fir	17.27			0.319		201	—
Lodgepole pine	34.01			0.219		186	—
Hybrid white spruce	21.28			0.652		196	—

* DEE (m) is derived by substituting anchor values (from Table 8) into each significant (p<0.10) regression equation and solving for distance.
 ** No lodgepole pine regeneration was found in forest anchor plots, making the calculation of DEE impossible.

obtained for basal ring width in harvested seedlings as related to edge position. Both leader length and average ring width for the past five years were also strongly correlated (p<0.001) with beam irradiance (r = 0.49 and r = 0.56 for fir leader and ring growth, respectively; r = 0.73 and r = 0.81 for spruce leader and ring growth, respectively).

5 Discussion

5.1 Landscape Considerations

By tabulating our site selection process, we arrived at the unexpected conclusion that straight, arbitrary cutblock boundaries are relatively uncommon in this sub-boreal landscape. Despite a forest development policy of "dispersed cutblocks" and satellite images portraying a "checkerboard" pattern to the legacy of industrial forestry (Franklin and Forman 1987), only 43% of cutblock boundaries were laid out without some consideration to topography or forest cover type shifts. Foresters apparently have utilized natural boundaries in laying out more than half of all sub-boreal spruce cutting permits logged between 1975 and 1987, with "squared off" cutblocks being even less common in recent years.

At the landscape level, differences in the underlying terrain and disturbance history are likely to be responsible for more of the variation in forest composition and structure than proximity to edges in and around those cutblocks. Yet edge effects (whether suitable for sampling or not) are certainly increasing as forests of the region become further fragmented, not only because of continued edge generation but also due to increased wind fetch (and the resulting impacts of elevated levels of windthrow) associated with the harvesting of contiguous forest stands.

5.2 Canopy Openness and Light Regime

Soon after logging, fast-growing shrubs (primarily *Alnus* spp., *Rubus* spp. and *Salix* spp. in this region) may invade the clearcut and the inner edge of adjacent forest, taking advantage of increased light availability and rapidly "sealing" newly formed edges. This flush of shrubs was more prevalent on moister sites and microsites, which were avoided during the layout of transects and plots. So the tree growth and regeneration responses reported here can be considered a function of canopy openness induced by edge proximity and subsequent windthrow, independent of understory vegetation (which will be described in a separate paper). The results of hemispheri-

cal photograph analysis quantify the prevailing light regime experienced in both the forest understory and in clearcuts. It is well documented that higher levels of irradiance along edge gradients are strongly correlated with reduced humidity and greater extremes of air and soil temperature (Matlack 1993, Chen et al. 1995).

As expected from the geometry of solar radiation, measurements of tree cover and diffuse irradiance were significantly altered at north-facing inner edges while beam and global irradiance were not (Table 2). Likewise, south-facing inner edges experienced elevated irradiance of all sorts, where an average 26% reduction in tree cover was associated with more than a doubling of global irradiance because of the strong directional effect of beam irradiance at this latitude. This effect extended less than 70 m into south-facing forest edges, which agrees well with observations that one can visually detect a nearby cutblock in this type of forest within 50 to 60 m of the edge. These values are also similar to the DEE of 60 m measured for short-wave radiation in south-facing edges measured by Chen et al. (1995) in coastal conifer forests, though their study area is 9° further south in latitude. In contrast, Matlack (1993) reports DEE values of only 13 to 22 m for photosynthetically active radiation (PAR) measurements in recent south-facing edges in deciduous forests of the eastern United States (39° N). Burke and Nol (1998) detected elevated light levels only within 5 m of the closed edges of long-isolated deciduous woodlots in southern Ontario (44° N). Canham et al. (1990) similarly report that the irradiance footprint of gaps in a spruce-fir forest in the Appalachian Mountains (36° N) extends only 12 to 15 m north of the gap edge. It is clear from these comparisons that the significance, magnitude and depth of irradiance differences within forest edges is not only dependent on latitude and edge orientation (as the geometry of radiation balance would predict), but also on the stem and foliage density of trees (which varies with species composition and time since edge creation) and the variability of light levels within forest interiors.

The adjacent canopy effects of shade from north-facing edges into clearcuts resulted in surprisingly marginal or non-significant differences in the light regime of outer edges compared to

clearcut anchor plots (Table 2). This lack of contrast (only 15 to 37% more global irradiance in clearcut anchor plots than in outer edge plots) may be due to measured light levels in clearcuts being reduced by crowns of 8 to 20 year old conifers, and somewhat irregular canopies in the standing forest. Nevertheless, trends in beam irradiance suggest that detectable shading extends up to 50 m north of forest edges. This extrapolation agrees with the results of geometric solar radiation models (e.g., Chen et al. 1993) predicting that forest openings at least 50 m in diameter are needed (in 30 m tall forests at 55° N) in order to achieve levels approaching full sunlight on the ground (Coates and Burton 1997). It should be noted that shading in small gaps is greater than that experienced at comparable distances from long straight edges because of less side light in the morning and evening.

5.3 Mortality and Growth of Canopy Trees

Since the forest-cutblock edges were 9 to 21 years old at the time of sampling, these edges can be considered stabilized, and the vegetation has had sufficient time to respond to new environmental conditions. The edge stabilization process follows a period of elevated rates of windthrow, in which trees with large height-to-dbh ratios and shallow root systems are soon blown over when protection from prevailing winds is removed. Prevailing winds are from the southwest in this region, so no significant differences in residual tree density, basal area or fallen trees were detected in the inner edge of north-facing forest stands (Table 4). In contrast, highly significant canopy differences were detected at south-facing edges, ranging in magnitude from 1.5 to 3.6 times the background levels prevailing in forest interiors. Though increased densities of recently fallen trees were found approximately 55 m into south-facing edges, the net effect on the remaining basal area of standing trees was evident up to 115 m north of cutblock boundaries. Because 42% of spruce trees had fallen in south-facing inner edge plots (compared to 18% of fir trees and 11% of pine trees), elevated windthrow has acted selectively to alter forest canopy composition up to approximately 65 m from the edge. This mechanism of

selective mortality contrasts with one of selective recruitment (denoted by high densities of younger, shade-intolerant trees) at the edges of species-rich deciduous forest fragments sampled in eastern North America (Ranney et al. 1981, Palik and Murphy 1990, Burke and Nol 1998).

Another aspect of the selective effects of wind is expressed in the height-to-dbh ratio of trees which have fallen compared to those which remained standing (Fig. 2). Trees which had ratios greater than approximately 71:1 were likely to have been blown over in the first few years after logging, while those with stouter proportions were likely to remain standing. It is well accepted that taller trees, in general, are more susceptible to windthrow (Quine 1995, Mitchell 1995). Given the incentive in British Columbia to prevent windthrow of commercially valuable timber and the salvage of windthrown boles after normal clearcut logging is completed (Mitchell 1995), it might be worthwhile to selectively remove susceptible trees at south-facing edges when the cutblock is logged, so long as residual trees are not damaged in the process. If one harvested edge trees with height-to-dbh thresholds midway between those of standing and fallen trees (71.7 for fir, 71.5 for spruce, and 74.2 for pine, as per Fig. 2), one could effectively utilize the wood from more than half of the trees that would eventually fall (60% of the fir, 57% of the spruce, and 58% of the pine) while unnecessarily taking less than 22% of the trees that would likely remain standing (fir 19%, spruce 22%, and pine 13%).

Overall changes in live tree density, primarily attributable to windthrow, are two to five times greater than reported for edges in similar forests in northwestern Sweden (Esseen and Renborn 1998). But when expressed relative to background levels of 7.4 or 8.0% windthrow in this study compared to 0.4% background windthrow in Sweden, MEE is much higher in the Swedish forests. Windthrow is one of the primary mechanisms responsible for "biomass collapse" reported to extend more than 500 m into tropical forest fragments (Laurence et al. 1997). Chen et al. (1992) detected elevated densities of fallen logs up to 56 m, and reduced densities of standing trees up to 59 m, into stand edges in southern Washington and central Oregon. The results of this study (windthrow DEE extending somewhere

between 45 and 115 m) are more similar to those reported for coastal conifer forests, even though the coastal and tropical trees are more similar in stature (>50 m tall). It is likely that differences in the depth of windthrow effects are more related to growth form, wind climate, the size of adjacent openings, or (unmeasured) factors other than tree height, making comparisons among studies difficult. In this study, the density of fallen subalpine fir trees in south-facing inner edge plots was significantly related to the open fetch of adjacent cutblocks ($r = 0.57$, $p = 0.041$, $n = 13$), but no such correlation was detected for other species or the rate of windthrow as a whole. Interestingly, larger cutblocks were associated with proportionately more trees falling through uprooting ($r = 0.42$, $p = 0.018$, $n = 32$) and fewer as a result of stem breakage ($r = -0.39$, $p = 0.027$, $n = 32$) within 55 m of south-facing edges.

It was expected that increased growth rates in canopy trees would be detected where shading and competition from the south had been removed, at least in those trees (such as most fir and many spruce) with vigorous crowns. While the absence of SEE in the growth of old trees is perhaps not surprising, the 48% reduction in the radial increment observed for lodgepole pine (the most light-demanding and drought-tolerant species) growing in south-facing inner edges (Fig. 3) was totally unexpected. Chen et al. (1992) measured immediately elevated radial growth rates in edge trees of *Tsuga heterophylla* (Raf.) Sarg., a shade-tolerant species, and (after a lag of 3 years) in *Pseudotsuga menziesii* (Mirb.) Franco, a shade-intolerant species. Tryon et al. (1992) likewise measured elevated radial growth rates in *Acer saccharum* Marsh., one of the dominant shade-tolerant species of eastern deciduous forests, in the vicinity of forest openings. Because lodgepole pine has very large height-to-DBH ratios and the DEE of reduced tree growth extends to approximately the same distance as the DEE of elevated windthrow density, it is possible that dominant pine trees on south-facing edges were subject to greater wind loading, wind-induced tree sway, and root wrenching. In addition, elevated light levels and wind in the forest understory undoubtedly result in vapour pressure deficits which dehydrate the forest floor and upper soil layers. Though this drying effect may not

harm mature pine trees directly, it may be having a negative effect on mycorrhizae and rhizosphere bacteria important to the growth of lodgepole pine on such sites (Perry et al. 1989, Amaranthus et al. 1993).

5.4 Regeneration Density and Growth

The density of living conifer seedlings and saplings encountered across edge gradients is the net result of two factors: the availability of propagules, and microsite suitability for growth and survival. Regeneration was generally more abundant under or in the proximity of intact forest canopies, where large numbers of seeds are regularly produced by mature trees. But the dense shade of a closed forest canopy in the forest interior means that many seedlings and saplings die (2.6 to 7.4 times more than in south-facing edge plots; Table 6). As a result, only the most shade-tolerant species survive, leaving 90% subalpine fir in the understory. Following cutblock creation, a period of stabilization consisted of windthrow (in which the basal area of standing trees was reduced by 19% on north-facing edges and by 46% on south-facing edges) and rapid shrub growth (in which shrub cover increased from an average of 53% to an average of 90% cover; *unpublished data*). Regeneration has subsequently increased in density by 35% on north-facing edges (as expected), but has apparently decreased in density by 54% on south-facing edges, presumably due to competitive inhibition by vigorous shrub growth but also because the density of fir seedlings in the forest anchor plots of south-facing transects seems anomalously high (twice that found in the forest anchor plots of north-facing transects; Table 6).

Any increase in conifer densities found in the inner edge of forests was primarily due to spruce and pine regeneration. Fir regeneration densities remained constant (north-facing edges) or dropped (south-facing edges) relative to interior values, and fir proportions dropped from 88–92% to 76–79% of all seedlings and saplings. These effects on regeneration density and composition extended 70 to 120 m into south-facing forest edges, much further than that reported for elevated densities of saplings (ca. 15 to 50 m) on

closed edges in eastern deciduous forests (Ranney et al. 1981, Fraver 1994). The DEE for increasing fir regeneration density (77 m) is very similar to that reported for the related *Abies amabilis* Dougl. ex Forbes in coastal conifer forests in the northwest U.S.A (81 m; Chen et al 1992). Abundance of spruce and pine showed no significant DEE in this study (Table 7), but their proportions decreased to background levels at 119 m and 74 m, respectively, analogous to the 92 m determined for *Pseudotsuga* seedlings and 41 m for *Tsuga* seedlings (Chen et al. 1992). From the consistent species differences in DEE observed in these two studies, one could generalize that the contribution of very shade-tolerant species increases with distance from edge, the proportion of species with intermediate shade tolerance decreases with distance (though not as sharply as shade-tolerant species increase), and the percentage of those seedlings with low shade tolerance decreases steeply.

Conifer regeneration exhibited significant increases in density at the outer edges of cutblocks adjacent to both north- and south-facing edges (Table 6). Seedling densities are especially higher on north-facing outer edges (Fig. 4), consistent with the effects of prevailing southwesterly winds. Combined with the fact that light levels were not significantly different from clearcut centres, this pattern suggests that regeneration reflects the conifer seed rain more than enhanced conditions for tree growth. With elevated densities of seedlings declining to background levels approximately 65 to 70 m (2 to 3 tree heights) from north-facing edges, the density of tree seedlings in clearcuts agrees well with predictions and observations of spruce seed rain density in clearings (Greene and Johnson 1996). Nevertheless, observations of greater and more diverse plant cover in the outer edge (*unpublished data*) indicates the prevalence of more humid conditions in that shadow zone, so that more tree seeds probably germinate and tree seedlings establish there, even if their growth and survival is not enhanced.

The growth of conifer seedlings was strongly related to light availability, being more than twice as great in the understory of north-facing edges and more than four times as great in the understory of south-facing edges than in the interior

forest (Table 8). This effect extended approximately 60 m into south-facing forest edges for spruce and 75 m for fir. Leader growth in clearcuts was, on average, 11 to 37% higher in the middle of clearcuts than at outer edges, though variability was so great that no significant differences in tree growth within clearcuts could be ascertained. In contrast, Hansen et al. (1993) found significantly reduced growth rates in planted *Pseudotsuga* tree seedlings 20 m north of a mature stand approximately 45 m in height. Baker and Langdon (1990) report that the growth of *Pinus taeda* L. seedlings is affected up to 9 m from opening edges. Though a band of enhanced conifer regeneration density and growth can be demonstrated (at least at south-facing edges) in the "shelterwood" of inner edges adjacent to clearcuts, the current study found no convincing evidence that growth and yield within cutblocks is compromised by edge effects.

6. Conclusions

Adjacent opening effects were generally much more important than adjacent canopy effects in and around cutblocks in the sub-boreal spruce zone of northwest-central British Columbia. Clearcuts had a much more pronounced effect on south-facing forest edges than on north-facing edges. This strong orientation effect was due to a combination of irradiance and wind, which blows predominantly from the southwest in the study area. Several years of windthrow after edge creation typically acted to further open the canopy on south-facing edges. The amount of windthrow can be predicted on the basis of edge orientation and the height-to-dbh ratio of trees standing within two tree heights of the edge. Elevated windthrow densities extended approximately 55 m into adjacent stands, though attributes such as basal area and wood volume appear to have been altered to more than 110 m. The net result of low sun angles at this latitude and the thinning of the canopy through windthrow was that elevated understory irradiance levels were detectable for approximately 65 to 70 m into the forest. There may also have been some damage to trees that did not blow over, as mature lodgepole pine trees

growing less than 45 m from south-facing edges exhibited up to a 48% reduction in radial growth rates. Elevated light levels in that inner edge have allowed more conifer seedlings (especially spruce and pine) to survive, even though total conifer regeneration densities are not significantly different from those in the forest interior. Seedlings growing under the partial protection of the remaining canopy in the inner edge benefit significantly from the more open environment immediately adjacent to clearcuts.

North-facing forest edges had little effect on the adjacent clearcut, limited primarily to a zone (reaching approximately 65 to 70 m into cutblocks) of increased conifer regeneration densities. This pronounced zone of enhanced conifer regeneration is probably a result of elevated seed rain, and perhaps an amelioration of microsite conditions suitable for seedling establishment up to 50 m from the edge. Tree seedlings growing at the periphery of cutblocks showed no decrease in growth compared to those growing in fully open conditions.

Foresters, forest planners and biologists can use information on the significance, magnitude and distance of edge effects to determine how much one forest stand can affect the development or habitat values of another. Along with regional site factors such as prevailing winds, the consideration of edge effects allows one to better design appropriate sizes, orientations and configurations for stable cutblock boundaries, retention patches and forested ecosystem networks to maximize the protection of biodiversity and the ecosystem processes of mature forests. Factors associated with elevated densities of natural regeneration and enhanced conifer growth can be employed in the design of novel silvicultural systems appropriate to these forests.

Acknowledgements

This research was funded as project SB96029-RE by the Research Program of Forest Renewal B.C., and was administered by the Science Council of British Columbia. Russ Brewer, Leslie Bush, Mike Dunbar and Garth Ehalt helped with site selection. The bulk of the field work was con-

ducted by Rick Pelletier, Doug Ferris, Carla Burton, Shawn Reed, Carmel Jorgenson, Sam Skinner and Ross Priddle. Tree ring measurements were made by James Hay and Russell Klassen, while Gabe Newman and Tashi Newman helped with data entry. I thank Carla Burton, Dave Coates, Eeva Korpilahti, Marty Kranabetter, Vic Lieffers, Chris Quine, and two anonymous reviewers for their suggestions regarding interpretation of results, and for comments on the manuscript.

References

- Alverson, W.S., Kuhlmann, W. & Waller, D.M. 1994. Wild forests: conservation biology and public policy. Island Press, Covelo, California. Ch. 5. p. 64–75.
- Amaranthus, M.P., Trappe, J.M. & Perry, D.A. 1993. Soil moisture, native revegetation, and *Pinus lambertiana* seedling survival, growth, and mycorrhiza formation following wildfire and grass seeding. *Restoration Ecology* 1: 188–195.
- Baker, J.B. & Langdon, O.G. 1990. *Pinus taeda* L. Loblolly pine. In: Burns, R.M. & Honkala, B.H. (tech. coords.). *Silvics of North America*, volume 1, conifers. Agriculture Handbook 654. USDA Forest Service, Washington, D.C. p. 497–512.
- 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, British Columbia.
- Barker, M.G., Press, M.C. & Brown, N.D. 1997. Photosynthetic characteristics of dipterocarp seedlings in three tropical rain forest light environments: a basis for gap partitioning? *Oecologia* 112: 453–463.
- Bradshaw, F.J. 1992. Quantifying edge effect and patch size for multiple-use silviculture – a discussion paper. *Forest Ecology and Management* 48: 249–264.
- Burke, D.M. & Nol, E. 1998. Edge and fragment size effects on the vegetation of deciduous forests in Ontario, Canada. *Natural Areas Journal* 18: 45–53.
- Canham, C.D. 1988. An index for understory light levels in and around canopy gaps. *Ecology* 69: 786–795.
- , Denslow, J.S., Platt, J.S., Runckle, W.J., Spies, J.R. & White, P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research* 20: 620–631.
- Chen, J., Franklin, J.F. & Spies, T.A. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecological Applications* 2: 387–396.
- , Franklin, J.F. & Spies, T.A. 1995. Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecological Applications* 5: 74–86.
- Chen, J.M., Black, T.A., Price, D.T. & Carter, R.E. 1993. Model for calculating photosynthetic photon flux densities in forest openings on slopes. *Journal of Applied Meteorology* 32: 1656–1665.
- Coates, K.D. & Burton, P.J. 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. *Forest Ecology and Management* 99: 337–354.
- & Burton, P.J. 1999. Growth of planted tree seedlings in response to ambient light levels in northwestern interior cedar-hemlock forests of British Columbia. *Canadian Journal of Forest Research* 29: 1374–1382.
- DeLong, S.C. & Tanner, D. 1996. Managing the pattern of forest harvest: lessons from wildfire. *Biodiversity Conservation* 5: 1191–1205.
- Esseen, P.A. & Renhorn, K.E. 1998. Edge effects on an epiphytic lichen in fragmented forests. *Conservation Biology* 12: 1307–1317.
- Franklin, J.F. & Forman, R.T.T. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. *Landscape Ecology* 1: 5–18.
- Fraver, S. 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River basin, North Carolina. *Conservation Biology* 8: 822–832.
- Frazer, G.W., Lertzman, K.P. & Trofymow, J.A. 1997. A method for estimating canopy cover, leaf area index and photosynthetically active photon flux density using hemispherical photography and computerized image analysis techniques. Canadian Forest Service, Pacific Forest Centre, Information Report BC-X-373. Victoria, B.C.
- Geiger, R. 1965. The climate near the ground. Translation of the 4th German edition. Harvard University Press, Cambridge, Massachusetts. 611 p.

- Greene, D.F. & Johnson, E.A. 1996. Wind dispersal of seeds from a forest into a clearing. *Ecology* 77: 595–609.
- Hansen, A.J. & di Castri, F. (Eds.) 1992. Landscape boundaries: consequences for biotic diversity and ecological flows. *Ecological Studies* 92. Springer-Verlag, New York. 452 p.
- , Garman, S.L., Lee, P. & Horvath, E. 1993. Do edge effects influence tree growth rates in Douglas-fir plantations? *Northwest Science* 67: 112–116.
- Hansson, L. 1994. Vertebrate distributions relative to clear-cut edges in a boreal forest landscape. *Landscape Ecology* 9: 105–115.
- Hughes, J.W. & Bechtel, D.A. 1997. Effects of distance from forest edge on regeneration of red spruce and balsam fir in clearcuts. *Canadian Journal of Forest Research* 27: 2088–2096.
- Kneeshaw, D.D. & Burton, P.J. 1997. Canopy and age structures of some old sub-boreal *Picea* stands in British Columbia. *Journal of Vegetation Science* 8: 615–626.
- & Burton, P.J. 1998. Assessment of functional old-growth status: a case study in the Sub-Boreal Spruce Zone of British Columbia, Canada. *Natural Areas Journal* 18: 293–308.
- Laurance, W.F., Laurance, S.G., Ferreira, L.V., Rankin-de Merona, J.M., Gascon, C. & Lovejoy, T.E. 1997. Biomass collapse in Amazonian forest fragments. *Science* 278: 1117–1118.
- MacKinnon, A., Meidinger, D. & Klinka, K. 1992. Use of the biogeoclimatic ecosystem classification in British Columbia. *The Forestry Chronicle* 68: 100–120.
- Meidinger, D., Pojar, J. & Harper, W.L. 1991. Sub-boreal spruce zone. In: Meidinger, D. & Pojar, J. (eds.). *Ecosystems of British Columbia*. Special Report Series 6, British Columbia Ministry of Forests, Victoria, British Columbia. p. 209–221.
- & Spittlehouse, D. 1997. Climatic data summaries for the biogeoclimatic zones of British Columbia, version 4. Unpublished Report, British Columbia Ministry of Forests Research Branch, Victoria, British Columbia.
- Mitchell, S.J. 1995. A synopsis of windthrow in British Columbia: occurrence, implications, assessment and management. In: Coutts, M.P. & Grace, J. (eds.). *Winds and trees*. Cambridge University Press, Cambridge, U.K. p. 448–459.
- Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* 10(2): 58–62.
- Old-growth forests: problem analysis. 1992. British Columbia Ministry of Forests, Research Branch, Victoria, British Columbia.
- Palik, B.J. & Murphy, P.G. 1990. Disturbance versus edge effects in sugar-maple/beech forest fragments. *Forest Ecology and Management* 32: 187–202.
- Perry, D.A., Amaranthus, M.P., Borchers, J.G., Borchers, S.L. & Brainerd, R.E. 1989. Bootstrapping in ecosystems. *BioScience* 39: 230–237.
- Quine, C.P. 1995. Assessing the risk of wind damage to forests: practice and pitfalls. In: Coutts, M.P. & Grace, J. (eds.). *Winds and trees*. Cambridge University Press, Cambridge, U.K. p. 379–403.
- Ranney, J.W., Bruner, M.C. & Levenson, J.B. 1981. The importance of edge in the structure and dynamics of forest islands. In: Burgess, R.L. & Sharpe, D.M. (eds.). *Forest Island Dynamics in Man-Dominated Landscapes*. Springer-Verlag, New York. p. 67–95.
- Rouck, K. & Nelson, J. 1995. Timber supply and economic impacts associated with sustained yield unit size. *Forestry Chronicle* 71: 647–656.
- SAS Institute. 1988. *SAS/STAT User's Guide*. Release 6.03 Edition. SAS Institute, Inc., Cary, North Carolina, U.S.A. 1028 p.
- Sipe, T.W. & Bazzaz, F.A. 1994. Gap partitioning among maples (*Acer*) in central New England: shoot architecture and photosynthesis. *Ecology* 75: 2318–2332.
- Soutjesdijk, P. & Barkman, J.J. 1992. *Microclimate, vegetation and fauna*. Translated from the 1987 Dutch edition. Opulus Press, Uppsala, Sweden. 216 p.
- Thomas, J.W., Maser, C. & Rodiek, J.E. 1979. Edges. In: Thomas, J.W. (ed.). *Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington*. Agriculture Handbook 553, USDA Forest Service, Washington, D.C. p. 48–59.
- Tyron, E.H., Lanasa, M. & Townsend, E.C. 1992. Radial growth response of understory sugar maple (*Acer saccharum* Marsh.) surrounding openings. *Forest Ecology and Management* 55: 249–257.
- Whole stem cubic metre volume equations and tables. 1976. British Columbia Forest Service, Forest Inventory Division, Victoria, British Columbia.

Total of 45 references