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VEGETATION RESPONSES TO EDGE ENVIRONMENTS IN OLD-GROWTH DOUGLAS-FIR FORESTS[1]

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Abstract. Forest edges created by dispersed-patch clear-cutting have become a conspicuous landscape feature in western North America, but the effects of edge on forest structure and function are still poorly understood. In this paper we describe responses of stocking density, growth, mortality, and regeneration for three conifer species from the clear-cut edge into the interior of old-growth forest patches adjacent to 10–15 yr old clearcuts in southern Washington and central Oregon. The significance of edge effects for each variable was tested through a single-factor (distance) analysis of variance (*F* test). Relationships between these variables and depth-of-edge influence (i.e., edge width) on old-growth forest were characterized by nonlinear regression models. Near the edge (forest–clearcut boundary line), the old-growth forest has (1) reduced stocking density, as measured by canopy cover, number of stems per hectare, and basal area; (2) increased growth rates of dominant Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*), as calculated by an index of relative growth rate; (3) elevated rates of tree mortality, as measured by standing dead and down trees (snags and logs); and (4) greater numbers of Douglas-fir and western hemlock seedlings ($\leq$100 cm tall) and saplings (101–200 cm) but fewer of Pacific silver fir (*Abies amabilis*). The depth-of-edge influence, when calculated as the point along the clearcut–forest gradient at which a given variable has returned to a condition representing ⅔ of the interior forest environment, ranged from 16 to 137 m for variables related to distance from the edge. The amount of a square forest patch affected by edge decreased as patch size increased and varied greatly with the depth-of-edge influence. With increasing concerns about organisms and processes that require interior forest habitat, determining the area of residual forest influenced by adjacent clearcut is critical to current and future resource management. Responses of additional biological variables must be explored and information on edge phenomena should be extended to the scale of landscapes.

Key words: biological features; Douglas-fir; edge effects; edges; fragmentation; growth; landscape; mortality; old-growth; regeneration; stand density; structure.

INTRODUCTION

Old-growth forests of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and associated coniferous species have high ecologic and economic values in North America (Waring and Franklin 1979, Franklin et al. 1981), but in the last few decades, human activities, primarily clear-cutting, have greatly reduced the area of these forests. Furthermore, much of the remaining old-growth forest has been converted from large contiguous stands to small isolated patches (Franklin and Forman 1987, Spies and Franklin 1988, Morrison 1990, Ripple et al. 1991) (Fig. 1), creating a considerable amount of edge between residual forest and clearcuts. Indeed, many of the remaining old-growth patches probably are too small to preserve an interior forest environment (Chen 1991).

Edge—an important landscape element—has been described as a boundary line (Clements 1907, Thomas et al. 1979) or a narrow transition zone between communities (Leopold 1933, Wales 1972, Lovejoy et al. 1986). It is usually characterized by edge length, width, and height, and their spatial and temporal patterns. Edge length and height can be measured precisely, while width is always arbitrary depending on the variable of interest, timing of measurement, and the approach used for calculation (Chen 1991). In this paper, we define "edge" as a boundary line between the clearcut and adjacent old-growth forest, and we define "depth-of-edge influence" (or edge width) as a transition zone in which the adjacent contrasting ecosystems of clearcut and old-growth interact. Differing ecological phenomena associated with the zone's physical nature are called "edge effects." In the landscape, depth-of-edge influence may provide a refuge and (or) buffer zone for plants and animals, and it may strongly influence the movement of materials and energy (Forman and Godron 1986). Varying over time and space, as determined with different physical and biological measures, the depth-of-edge influence may affect the regional envi-

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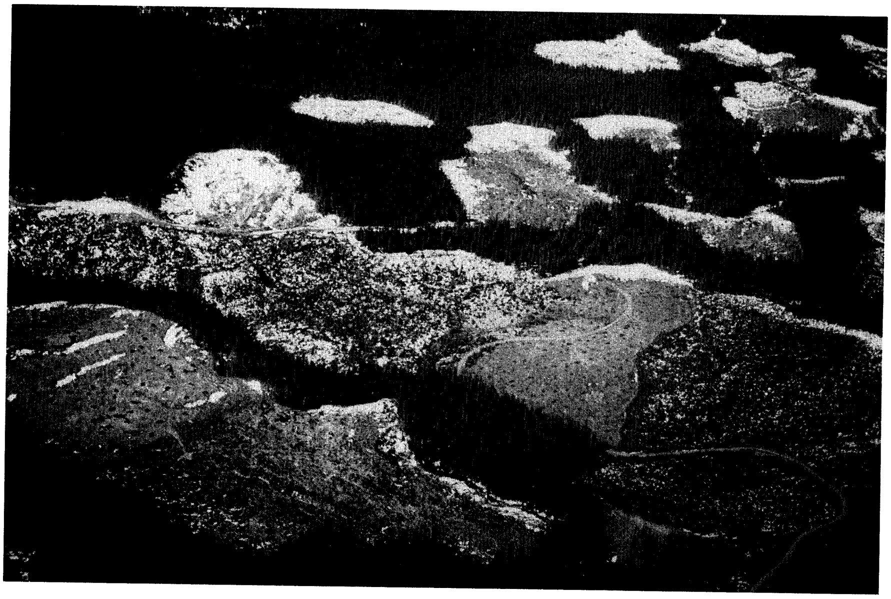

FIG. 1. A Pacific Northwest forest landscape fragmented by clear-cutting.

ronment, aesthetics, recreation, wildlife conservation, disturbance regimes, and management of other resource elements (Franklin and Forman 1987, Franklin 1989, Chen et al. 1990, Lehmkuhl and Ruggiero 1991, Ripple et al. 1991).

For years, wildlife biologists have promoted forest edge as beneficial to wildlife and other components of biological diversity (Thomas et al. 1979, Lovejoy et al. 1986). Managers were urged to create as much edge as possible because wildlife is a product of the places where two habitats meet. However, with increasing concern about biological conservation of species and about many associated processes and suitable habitat that require interior environment, resource managers must now assess the balance between edge and interior environment (Yahner 1988, Hunter 1990).

Biological investigations of edge effects in the literature have focused on changes in residual forest structure, function, and species composition associated with forest boundaries. Parameters studied include stem density and basal area (Gysel 1951, Wales 1972, Caruso 1973, Ranney et al. 1981, Williams-Linera 1990), tree mortality (Alexander 1964, Wales 1972), tree regeneration (Gysel 1951, Caruso 1973, Wagner 1980, Williams-Linear 1990), and tree growth rate (Wales 1972, Wagner 1980). However, edge effects associated with residual northwestern coniferous forests have received little attention other than a few studies of windthrow associated with clear-cut boundaries (Ruth and Yoder 1953, Gratkowski 1956). After clear-cutting, a microclimatic gradient forms between the more severe conditions of the clearcut and the muted conditions of the interior forest (Geiger 1965, Raynor 1971). Near the edge, the forest floor receives more light but also experiences stronger winds and greater variation in temperature and moisture (Ranney 1977). In this study, we measured the responses of tree stocking density, mortality, growth, and regeneration in residual old-growth Douglas-fir forests in relation to distance from the edge of adjacent clearcuts; and through nonlinear regression, we characterized the relationships between these variables and the depth-of-edge influence. The results provide forest managers a starting point in assessing the potential impacts of edges on some biological phenomena.

METHODS

Study areas and sampling scheme

The two study areas are located on the western slope of the Cascade Range in the western United States. One is on the Wind River Experimental Forest, 45°48′N and 121°55′W, on the Gifford Pinchot National Forest in southern Washington; and the other is on H. J. Andrews Experimental Forest, 44°14′N and 122°11′W, on the Willamette National Forest in central Oregon. Elevation of the study areas ranges from 650 to 1000 m; slopes are gentle (< 10°). The forests are representative of typical old-growth Douglas-fir forest in western Oregon and Washington (Franklin and Dyrness 1973, Franklin et al. 1981) and are characterized by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Pacific silver fir (*Abies amabilis* Dougl. ex Forbes), Pacific yew (*Taxus brevifolia* Nutt.), and western red cedar (*Thuja plicata* Donn ex D. Don) as well as Douglas-fir (Franklin et al. 1981). Dominant trees are typically 50 to 60 m tall.

Sixteen edges (13 at Wind River, 3 at H. J. Andrews) were selected for study along old-growth forest patches. The edges were created by clear-cutting between 1974 and 1979 (i.e., edge age ranges: 10–15 yr). Planted trees on these cutover areas were generally <2.5 m tall. We randomly located a transect that extended perpendicularly 240 m from each edge (0 m) into the old-growth forest ("inner edge"; Thomas et al. 1979) and established sampling stations at 0, 30, 60, 120, 180, and 240 m from the edge. Transect length was determined following a study of microclimatic patterns that suggests the depth-of-edge influence was limited to 240 m into the forest (Chen et al. 1990).

Tree stocking density (canopy cover, number of stems per hectare, basal area, and average tree diameter), growth, mortality, and regeneration along the transects were measured as follows: We computed canopy cover by visually observing canopy conditions (without cover = 0, cover = 1) at 40 points (every meter) along a 40-m line perpendicular to the transect at each sampling station (i.e., percentage of 40 points with overstory cover). To determine basal area, tree mortality, and the number of stems per hectare, we recorded the number of trees >6 cm in diameter at breast height (dbh) by species, dbh class (6–30, 31–100, >100 cm), condition (live or dead), and the number of fallen boles within a 10 × 100 m plot with its long dimension paralleling the edge at each station. Also, within each 10 × 100 m plot we randomly selected three Douglas-firs and three western hemlocks. Each of the six trees was cored and tree growth rates were analyzed by measuring the 10 tree rings (10 yr) before and after clear-cutting on each core. We also computed the 10-yr means, and then calculated an index, the relative growth rate (RGR), for each core:

$$\mathrm{RGR} = \frac{\mathrm{GR}_{10\mathrm{a}} - \mathrm{GR}_{10\mathrm{b}}}{\mathrm{GR}_{10\mathrm{b}}} \times 100,$$

where $\mathrm{GR}_{10\mathrm{a}}$ is the average 10-yr growth rate after clear-cutting, and $\mathrm{GR}_{10\mathrm{b}}$ the average 10-yr growth rate before clear-cutting. We measured every seedling and sapling (<200 cm tall) along a 2 × 20 m plot, its long dimension paralleling the edge, at each station, by recording tree species and the height of each seedling or sapling. The seedlings and saplings were grouped into four height classes (1–10, 11–30, 31–100, and 101–200 cm).

Statistical analysis

The means and standard errors of these variables were computed and plotted against distance from the edge to describe changes in these variables associated with edge. Since there exists a higher variation near the edge than inside the forest (Wales 1972, Ranney 1977, Chen 1991), we will stress the changing pattern in the standard error from the edge into the interior forest. Single-factor analysis of variance (one-way ANOVA) was used to test the null hypothesis that the mean for each variable from the edge into the interior forest remains the same. The F statistic was computed and the test was applied to determine the significance of edge effect on each variable (Neter et al. 1985, SAS 1985).

When the null hypothesis (that there was not an edge effect) was rejected, nonlinear regression techniques were used to fit the changes in these variables to various exponential models for estimating depth-of-edge influence to find the best model for each variable. Data were transformed and weighting factors were used, when needed, to obtain a random distribution of the residuals. All statistical analyses were performed with SAS (SAS 1985). Ultimately, the following three models were selected, based on analysis of residuals and the lowest Furnival's index (Furnival 1961):

$$Y = \beta_0 + \beta_1 e^{-\beta_2 X} + \epsilon \tag{1}$$

$$Y = \beta_0 e^{-\beta_1 X} + \epsilon \tag{2}$$

$$Y = \frac{\beta_0}{1 + \beta_1 e^{-\beta_2 X}} + \epsilon, \tag{3}$$

where Y is the response to the biological variable (dependent variable); X is the distance from edge to interior forest; β_0, β_1, and β_2 are the regression coefficients; and ϵ is the random-error term.

Decisions regarding the limit of the depth-of-edge influence are arbitrary, regardless of the technique applied, simply because changes in any biotic or abiotic variable from the stand edge are gradual. The cutting boundary represents 100% edge, and the condition of a given variable changes depending on its position along the edge–interior forest gradient (i.e., 0–240 m transect). In this study we calculated depth-of-edge influence as the point on the gradient at which a given Y has returned to a condition representing ⅔ of the interior forest environment:

$$Y = Y_0 \pm \frac{2}{3}|Y_0 - Y_{240}|,$$

where Y_0 and Y_{240} are the forest vegetation responses at the edge (0 m) and 240 m into the forest (i.e., beginning and end of the transect). For instance, the depth-of-edge influence (DEI) for a decreasing trend (DEI-1, Fig. 2: case 1) is calculated as $Y_0 - (2/3)(Y_0 - Y_{240})$, that for an increasing trend (DEI-2, Fig. 2: case 2) as $Y_0 + (2/3)(Y_0 - Y_{240})$. The ⅔ criterion can provide a relative value useful for comparing the responses of the variables and helping to assess the relationship of depth-of-edge influence to forest and edge width and forest patch size (Laurance and Yensen 1991).

RESULTS

Stocking density

Canopy cover increased significantly ($P = .0001$) from the edge into the interior forest (Fig. 3a). The increase was rapid, from 35% to 75% within 60 m into the forest. Variation in canopy cover was also higher near the edge.

The number of stems per hectare for trees >6 cm dbh increased significantly ($P < .005$) from the edge for 60–120 m into the forest, averaging 310 near the edge and 480 in the interior (Fig. 3b). However, unlike canopy cover, variation in stem numbers increased with distance from the edge. The number of stems per hectare rose more dramatically for small trees (dbh 6–30 cm) than larger ones and was significant for western hemlock ($P = .009$) but not Douglas-fir or Pacific silver fir (Table 1). Variation in numbers of small stems of western hemlock increased with distance from the edge (Table 1).

Basal area increased slightly (≈20%) from the edge into the interior forest but not significantly ($P > .5$, Fig. 3c). The extent of reduced basal area was from 0 to 120 m from the edge. Variation in basal area did not vary significantly with distance from the edge.

Mean dbh decreased slightly from the edge into the forest interior (Fig. 3d), although the trend was not significant ($P > .6$) and its variation did not vary greatly with distance from the edge.

Growth, mortality, and regeneration

Growth rates of Douglas-fir and western hemlock near the edge increased after clear-cutting (Fig. 4), and their relative growth rates (RGRs) were significantly decreased ($P = .2$ and $.0001$ for Douglas-fir and western hemlock, respectively) with distance from the edge. Some trees did not respond even though they were close to the cutting boundary; hence, variation in growth rates was also higher near the edge.

RGRs for western hemlock were greater than those for Douglas-fir (Fig. 5). Near the edge the average RGR of western hemlock was 150% higher than before clear-cutting and decreased exponentially with distance from the edge (Fig. 5b). The pattern for Douglas-fir is similar, but its magnitude is less: average RGR was at most only 33% higher than before clear-cutting (Fig. 5a). Variation in RGRs was extremely high for both species near the edge and decreased quickly within 60 m into the forest.

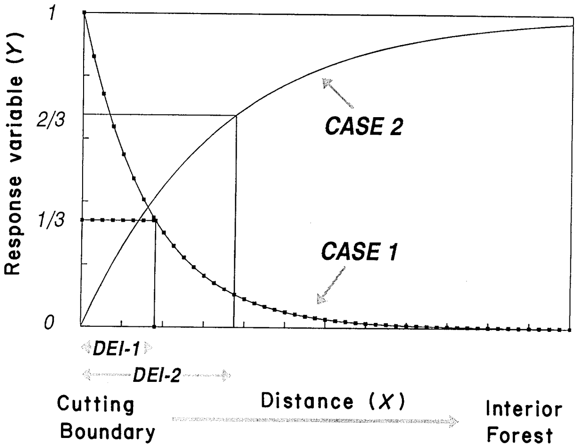

FIG. 2. Depth-of-edge influence (DEI) for two example cases: DEI calculated as $Y = Y_0 + (⅔)(Y_0 - Y_{240})$ and as $Y = Y_0 - (⅔)(Y_0 - Y_{240})$, where Y is the response of a given biological variable from an edge (0 m, Y_0) into the forest (240 m, Y_{240}).

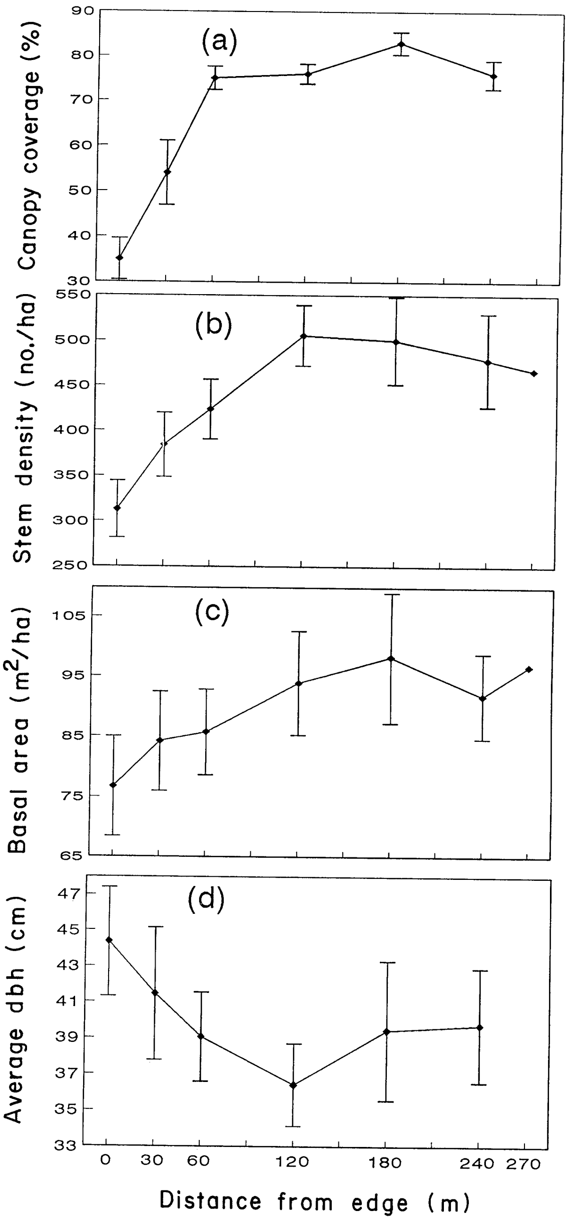

FIG. 3. Changes in (a) canopy cover, (b) number of stems per hectare for trees >6 cm in diameter at breast height (dbh), (c) total basal area, and (d) dbh, with distance from the edge (0 m) into the interior forest. Data are means ± 1 SE. $N = 14$. For (b) and (c), data at 270 m are from Franklin and DeBell (1988) and Franklin et al. (1981).

The number of dead trees was strongly influenced by proximity to the edge (Fig. 6, Table 2). The numbers of standing dead trees (snags) and fallen trees (logs) decreased with distance from edge, apparently at least to 120 m ($P < .0001$). These patterns are due primarily to logs (Table 2), whose number declined from very

TABLE 1. Numbers of trees >6 cm in diameter at breast height (dbh) (per 10 × 100 m plot) with distance from the edge (0 m) into the interior forest ($N = 14$). P values are from F tests in the ANOVA to test significance of edge effects. Data are means ± 1 SE.

Distance from edge	dbh class (cm)			Species*		
(m)	6–30	31–100	>100	WH	DF	PSF
0	167.0 ± 27.1	116.4 ± 13.1	28.6 ± 7.0	179.3 ± 12.6	43.6 ± 8.8	77.1 ± 24.5
30	223.6 ± 30.2	129.3 ± 11.6	31.4 ± 7.7	222.9 ± 32.5	50.0 ± 8.6	87.9 ± 18.3
60	246.4 ± 30.1	145.0 ± 12.5	32.1 ± 6.5	215.7 ± 19.9	54.3 ± 9.5	122.1 ± 29.3
120	319.2 ± 32.6	152.8 ± 12.4	33.6 ± 6.8	243.6 ± 27.4	55.0 ± 13.5	165.7 ± 36.4
180	315.3 ± 46.1	153.6 ± 11.6	31.4 ± 6.7	282.1 ± 22.8	51.4 ± 11.4	130.7 ± 42.0
240	280.4 ± 50.3	142.1 ± 11.5	32.1 ± 5.2	256.4 ± 21.6	51.4 ± 10.7	115.7 ± 51.6
P	.040	.224	.997	.009	.536	.554

* WH = western hemlock, DF = Douglas-fir, PSF = Pacific silver fir.

high levels close to the edge to very low levels beyond 60 m ($P < .0001$). Differences in numbers of snags by species were not significantly ($P > .13$) related to distance from the edge, either collectively or for individual species (Table 2).

The numbers of tree seedlings and saplings of Douglas-fir, western hemlock, and Pacific silver fir differed with distance from the edge into the forest (Fig. 7). The numbers of Douglas-fir and western hemlock seedlings and saplings decreased with distance ($P < .0001$ and .1, respectively), whereas those of Pacific silver fir increased ($P = .02$). Similarly, variation for Douglas-fir and western hemlock also decreased with distance from the edge, while that for Pacific silver fir increased (Fig. 7). Douglas-fir seemed to be affected for <60 m into the forest, but western hemlock and Pacific silver fir for ≈120 and <120 m, respectively.

Seedlings and saplings responded differently to edge by their height class (Table 3). Numbers of smaller seedlings (<30 cm) differed significantly with distance from the edge ($P < .16$), whereas those of taller saplings (>30 cm) showed no change with distance ($P > .26$). Moreover, the depth-of-edge influence also varied with seedling height class. The numbers of small seedlings (0–10 cm tall) declined over a greater distance than those of larger seedlings. For example, small western hemlock seedlings were affected for >120 m into the interior forest, but larger hemlock seedlings (10–30, 31–100 cm tall) were affected for only 60 and 30 m, respectively (Fig. 7).

Relationship of vegetational variables to depth-of-edge influence

The depth-of-edge influence varied dramatically—from essentially none (0 m, no edge effect) to substantial—among the variables (Table 4). For example, depth-of-edge influence was 137 m for small (0–10 cm tall) western hemlock seedlings, but only 16 m for taller (31–100 cm) Douglas-fir seedlings. This difference strongly affects the amount of area under the influence

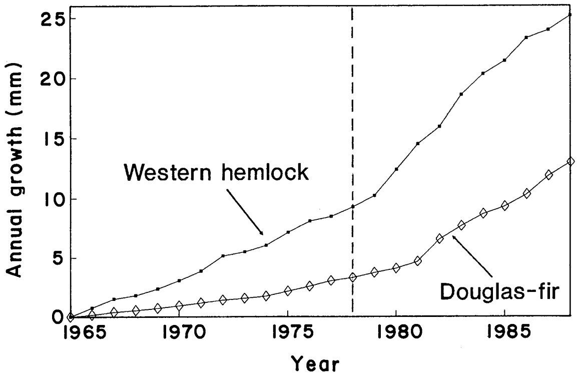

FIG. 4. Influence of clear-cutting (dashed line) on the growth rates of Douglas-fir and western hemlock at the forest edge. The vertical line indicates the year of clear-cutting.

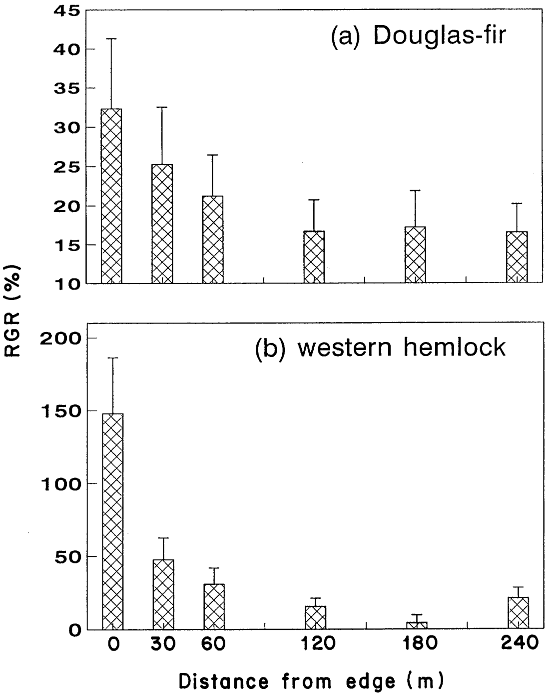

FIG. 5. Changes in relative growth rates (RGRs) of (a) Douglas-fir ($N = 48$) and (b) western hemlock ($N = 51$) with distance from the edge (0 m) into the interior forest. Data are mean and 1 SE.

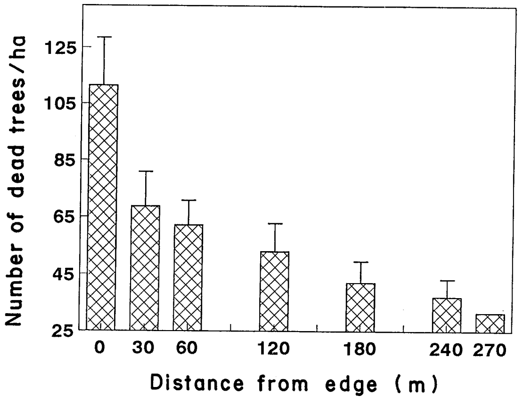

FIG. 6. Changes in numbers of standing dead trees (snags) and fallen boles (logs) with distance from the edge (0 m) into the interior forest. Data are means and 1 SE. $N = 14$. Data at 270 m are from Franklin and DeBell (1988) and Franklin et al. (1981).

of the edge within a remnant forest patch. Using the ⅔ criterion, we noticed that, though the percentage of a square forest patch affected by edge decreased as patch size increased, this percentage still varied greatly with the depth-of-edge influence (Fig. 8). For example, when depth-of-edge influence was 137 m, as for small (0–10 cm tall) western hemlock seedlings (see Table 4), a 10-ha forest patch would be nearly all "edge affected." In contrast, a 100-ha patch would be only ≈55% affected. When depth-of-edge influence is 16 m, as for taller (31–100 cm) Douglas-fir seedlings, only 18% of a 10-ha patch and 5% of a 100-ha patch would be edge affected.

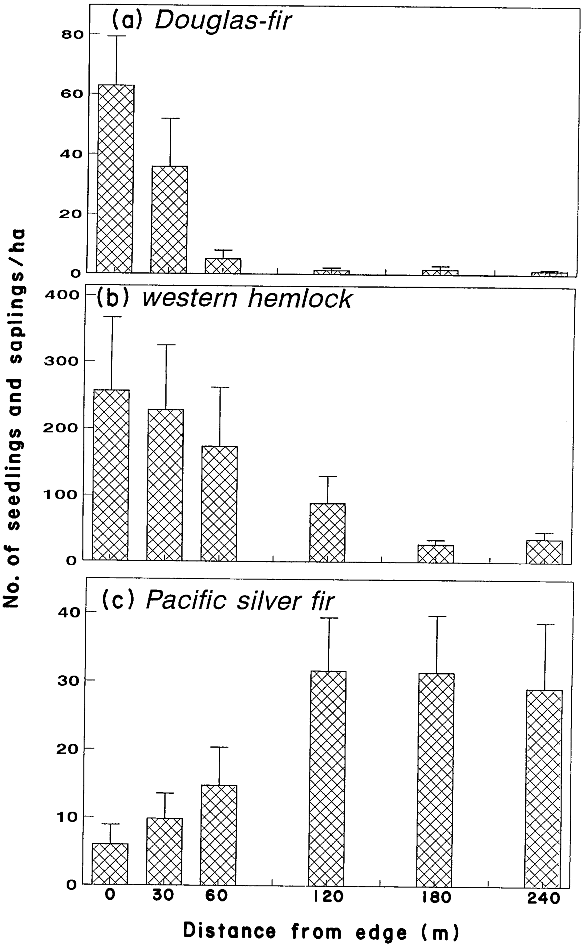

FIG. 7. Numbers of (a) Douglas-fir, (b) western hemlock, and (c) Pacific silver fir seedlings (≤100 cm) and saplings (10–200 cm), with distance from the edge (0 m) into the interior forest. Data are means and 1 SE. $N = 15$.

DISCUSSION

With increasing distance from the edge, the forest interior environment increasingly dominates. Forest species composition, structure, and function respond gradually to these environmental changes. Our data on stocking density, as measured by number of stems per hectare and basal area (Fig. 3), and on tree mortality (Fig. 6), are consistent with the findings of a 1987 pilot study of microclimatic patterns, which indicated that the maximum depth-of-edge influence is 240 m from the edge (Chen et al. 1990). Moreover, our values at 240 m are comparable to those reported by Franklin and DeBell (1988) and Franklin et al. (1981) in studies of intact old-growth Douglas-fir forests in the Pacific

TABLE 2. Mortality, as indicated by numbers of standing dead trees (snags) and fallen boles (logs) (per 10 × 100 m plot) with distance from the edge (0 m) into the interior forest ($N = 14$). P values are from F tests in the ANOVA to test the significance of edge effects. Data are means ± 1 SE.

Distance from edge (m)	Snags, by tree species*					Logs
	DF	WH	PSF	YEW	RC	
0	10.0 ± 2.7	16.4 ± 4.1	10.7 ± 4.6	2.1 ± 2.6	0.0	72.1 ± 14.2
30	4.3 ± 2.0	12.1 ± 4.2	4.3 ± 1.7	2.9 ± 2.9	0.7 ± 0.7	44.3 ± 11.4
60	14.3 ± 3.6	17.9 ± 5.7	15.0 ± 4.7	1.4 ± 1.4	0.0	13.6 ± 6.6
120	16.4 ± 5.7	13.6 ± 2.3	17.9 ± 4.8	4.3 ± 3.1	0.0	0.7 ± 0.7
180	12.1 ± 2.6	9.3 ± 2.7	17.9 ± 5.4	2.9 ± 2.2	0.0	0.0
240	7.9 ± 1.9	11.4 ± 3.8	15.7 ± 6.0	1.4 ± 0.9	0.7 ± 0.7	0.0
P	.137	.654	.302	.938	.553	.0001

* DF = Douglas-fir, WH = western hemlock, PSF = Pacific silver fir, YEW = Pacific yew, RC = western redcedar.

TABLE 3. Numbers of seedlings and saplings per 2 × 20 m plot with distance from the edge into the interior forest ($N = 15$). P values are from F tests in the ANOVA to test the significance of edge effects. Data are means ± 1 SE.

Tree species*	Height class (cm)	Distance from edge (m)						
		0	30	60	120	180	240	P
DF	0–10	23.53 ± 11.29	18.93 ± 6.64	2.27 ± 1.07	0.87 ± 0.41	1.60 ± 1.21	0.93 ± 0.40	
	11–30	26.67 ± 9.15	15.73 ± 10.08	1.07 ± 0.73	0.47 ± 0.47	0.07 ± 0.07	0.13 ± 0.13	.005
	31–100	12.13 ± 3.47	1.20 ± 0.69	1.53 ± 1.53	0.00	0.00	0.20 ± 0.20	.002
	101–200	0.47 ± 0.19	0.00	0.20 ± 0.20	0.00	0.00	0.00	.000
WH	0–10	166.33 ± 69.15	164.80 ± 66.88	159.93 ± 83.03	74.93 ± 35.57	21.40 ± 6.77	29.00 ± 9.07	.016
	11–30	77.20 ± 44.43	56.80 ± 40.41	10.67 ± 9.33	8.93 ± 4.83	3.20 ± 1.09	4.67 ± 2.22	.160
	31–100	11.87 ± 7.00	5.87 ± 2.66	2.80 ± 1.83	4.80 ± 2.88	1.80 ± 0.87	1.27 ± 0.92	.262
	101–200	1.07 ± 0.56	0.13 ± 0.09	0.47 ± 0.34	0.47 ± 0.24	0.40 ± 0.16	0.40 ± 0.16	.388
PSF	0–10	0.20 ± 0.15	1.40 ± 0.65	6.20 ± 3.44	10.87 ± 3.69	9.93 ± 3.01	8.93 ± 4.05	.045
	11–30	1.60 ± 1.07	3.47 ± 1.35	4.67 ± 1.91	11.40 ± 3.10	12.67 ± 4.43	12.20 ± 4.07	.021
	31–100	3.33 ± 1.74	3.73 ± 1.48	3.13 ± 0.95	8.53 ± 2.85	7.60 ± 2.38	7.07 ± 2.72	.274
	101–200	0.87 ± 0.34	1.20 ± 0.51	0.73 ± 0.30	0.80 ± 0.20	1.20 ± 0.51	0.93 ± 0.28	.919

* DF = Douglas-fir, WH = western hemlock, PSF = Pacific silver fir.

Northwest. Despite this overall trend, however, the variables we studied showed differing and independent responses to distance from forest edge.

Biological responses to clear-cut edges additionally depend on the type of forest ecosystem. In some types (e.g., an edge with forest adjacent to an old field), a dense growth of herbaceous and woody vegetation develops very quickly at the forest boundary, which helps reduce edge effects within the forest (Wales 1972, Ranney et al. 1981, Forman and Godron 1986). However,

TABLE 4. Final models from nonlinear regression analysis for estimating the depth-of-edge influence in forests for the biological variables studied. Depth-of-edge influence was calculated as the point on a gradient, from an edge to the forest interior, at which a vegetation response (such as relative growth rate) reaches ⅔ of the response in the forest interior (see also *Methods: Statistical analysis* and Fig. 2).

Biological variable*	Model type†	Model regression coefficients			Depth-of-edge influence (m)	MSE
		β_0	β_1	β_2		
Canopy cover	1	80.027	−45.744	0.02478	44	171.9
No. stems/ha						
Overall	2	50.065	−19.204	0.01821	59	215.2
6–30 cm dbh	1	30.744	−14.314	0.01895	57	188.6
31–100 cm dbh	1	15.002	−3.488	0.02539	43	20.1
WH	1	27.306	−9.024	0.01158	85	76.5
Growth						
DF	1	16.316	16.124	−0.02057	53	1641.0
WH	1	14.286	133.243	−0.0428	26	16 304.6
Dead tree						
Overall	2	9.593	0.00495		125	16.8
Logs	2	7.355	0.01928		56	4.5
Regeneration						
DF Overall	2	64.420	0.02694		41	1303.0
0–10 cm	2	25.050	0.02093		52	426.5
11–30 cm	2	27.509	0.02776		39	449.5
31–100 cm	2	12.112	0.06874		16	35.9
WH Overall	3	−318 503	1164.3	0.0091	92	74 634.5
0–10 cm	3	177.920	0.031	−0.03013	137	2486.5
11–30 cm	3	87 001.0	1081.2	−0.0201	54	8948.8
31–100 cm	3	13 171.6	1241.1	−0.01279	79	168.2
PSF Overall	3	31.464	6.719	0.03465	81	669.3
0–10 cm	3	9.917	70.925	0.07997	62	124.3
11–30 cm	3	12.760	9.240	0.03273	95	126.7
31–100 cm	3	7.932	2.212	0.02127	92	67.3

* dbh = diameter at breast height, WH = western hemlock, DF = Douglas-fir, PSF = Pacific silver fir, MSE = mean square of error.

† Models selected were based on analysis of residuals and the lowest Furnival's index (Furnival 1961): (1) $Y = \beta_0 + \beta_1 e^{-\beta_2 X}$; (2) $Y = \beta_0 e^{-\beta,1}$; (3) $Y = [\beta_0/(1 + \beta_1{}^{-\beta_2 X})]$; where Y is the response to the biological variable (dependent variable), X is the distance from edge to interior forest, and β_0, β_1, and β_2 are the regression coefficients.

this phenomenon is generally not found at edges of old-growth Douglas-fir forest adjacent to recent clearcuts. In a study of edge effects on vegetation structure in Panama, Williams-Linear (1990) observed that canopy cover, density, and basal area of trees were much higher near the edge than in the interior forest. Similar results have been documented elsewhere (Wales 1972, Ranney et al. 1981). However, we found the reverse. Our measures of stocking density are lower near the edge (Fig. 3), probably because of greater tree mortality caused primarily by windthrow, combined with a slow recovery process near the edge.

Literature concerning edge effects on tree growth does not exist. Clear-cutting appears to have less influence on growth of dominant Douglas-firs than on that of associated species, such as western hemlock. However, the extreme variability we noted, from a negative relative growth rate (RGR; no edge effects if RGR ≤ 0) to 400% (Fig. 5), suggests that tree growth rate is related not only to the levels of light and other resources, but also to other biotic and abiotic factors—such as individual tree position in the stand and current physiological status.

We observed large numbers of snags and fallen trees near the edges (Fig. 6), a pattern that is common (Ruth and Yoder 1953, Gratkowski 1956, Alexander 1964, Ranney 1977, Williams-Linera 1990). Many of the fallen logs were from trees that had been uprooted or broken off by wind. Although 65% of the dead trees was recorded as "logs," some of these were probably snags at the time of clear-cutting; traditionally, all snags within 60 m of an edge were cut during logging for reasons of fire and safety. Hence, the results presented here (Fig. 6) are conservative.

Much of this mortality has been related to high wind velocities, especially where forest edges have been freshly exposed, and to higher probabilities of insect infestations and disease outbreaks in the stressed trees found adjacent to clearcuts (Geiger 1965, Ranney 1977). In the Pacific Northwest, damage caused by log yarding or hauling around the forest edge, from constructing fire lines, and from hot or escaped slash fires can also contribute to the higher tree mortalities near the edge. Regardless of the reason, the higher mortality at the edges of old-growth douglas-fir forests appears to extend deep into the forest, as evidenced by the gradients of stocking density in our study areas (Fig. 3).

Edge effects on tree seedlings and saplings varied by species. We saw varying patterns at the edge for Douglas-fir, western hemlock, and Pacific silver fir—results that differ from, but do not conflict with, those of other studies (Gysel 1951, Wales 1972, Caruso 1973, Wagner 1980, Williams-Linera 1990) in which many seedlings and saplings have been observed near the edge. The positive response of seedling and sapling numbers seems reasonable because, as previously noted, the edge environment has more favorable radiation, moisture, and temperature conditions for seedling establishment and survival (Chen et al. 1990). Edge conditions are especially favorable for shade-intolerant species, such as Douglas-fir. Two shade-tolerant species showed contrasting responses: suppressed western hemlock seedlings responded well to the edge environment but Pacific silver fir did not. Edge effects were observed to be greater for seedling than sapling density, regardless of species (Table 3), suggesting that the clear-cutting 10 to 15 yr ago has strongly influenced the establishment, growth, and survival of seedlings but that they have not yet had time to grow into the larger size classes.

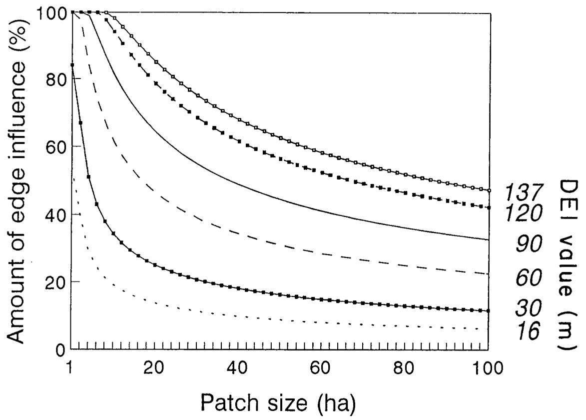

FIG. 8. Depth-of-edge influence (DEI) for variously sized square forest patches, based on a simple calculation. Note: there is no "interior forest" for a patch <10 ha if depth-of-edge influence is 137 m.

Depth-of-edge influence is an important issue in the theory and practice of forestry for multiple values. Historically, the rule-of-thumb has been that edge influences extend for the equivalent of two to three tree heights from a cutting boundary into the forest (FAO 1962, Fritschen et al. 1970). In most cases, depth-of-edge influence was determined by first plotting the objective variable (e.g., population size, number of species) against distance from the edge into the interior forest and then visually judging the trend. More recently, the concepts of a continuum index and edge-to-interior ratios were applied by Ranney et al. (1981) and Williams-Linera (1990). However, they appear to be imprecise and arbitrary. Gates and Mosher (1981) tried to use the analysis of variance in investigating the distribution of birds nests on both sides of an edge. They calculated the mean (and median) and standard deviation distance of avian nests from the edge and used these two values as so-called "structure and function" edge widths. The depth-of-edge influence determined from this approach, however, was also arbitrary because the selection of confidence level is subjective. Since the changes of forest vegetation variables from the edge into the forest are gradual, we believe that regression techniques combined with some arbitrary but quantitative criterion (such as our ⅔ rule) is very straightforward and should satisfactorily quantify depth-of-edge influence. However, goodness-of-fit with other proportions (e.g., ⅓, ⅘) needs to be tested.

Depth-of-edge influence obviously depends strongly on the parameter of interest and the forest type. In our old-growth Douglas-fir forests, we found depth-of-edge influence to range from 0 to 137 m. In hardwood forests in the eastern United States, Ranney et al. (1981) and Wales (1972) suggested that depth-of-edge influence was ≈10–20 m. Williams-Linera (1990) concluded that a distance 15–25 m wide was appropriate for tropical rain forests in Panama. In the Pacific Northwest, Caruso (1973) and Wagner (1980) found that stem density and regeneration pattern differed significantly within 50–70 m of the edge. Values resulting from wildlife studies may be much higher. For example, Wilcove (1985) studied population declines of songbirds in relation to forest fragmentation, and concluded that the edge-related increase in predation may extend 300–600 m inside the forest.

Calculating the amount or percentage of residual forest influenced by clear-cutting is critical for old-growth forests in the Pacific Northwest because much of the old growth is now dispersed in small patches (Harris 1984, Morrison 1990) that have large amounts of edge (Chen et al. 1990, Laurance and Yensen 1991). Our findings show that, for variables with depth-of-edge influences of only 10–20 m, a 10-ha forest patch is minimally affected by edge; but for variables with a large percentage of edge influence (e.g., 137 m), a 10-ha forest patch is too small to contain any true interior forest.

Biological responses at forest edges are influenced not only by distance from the edge, but also by forest type, edge age, orientation, and formation (i.e., clearcut vs. natural bog), patch shape and size, and topographic features (Wales 1972, Ranney 1977, Williams-Linera 1990). For example, large differences in the effects on species composition have been found between edges with northerly and southerly orientations (Wales 1972). Biotic factors other than those studied herein or elsewhere, as well as abiotic factors such as microclimate, need to be explored to completely characterize ecosystem behavior at forest edges. Furthermore, knowledge of edge phenomena must be extended to the landscape level, incorporating landscape features such as residual forest-patch size and shape, and their spatial configuration, to meet the needs of both current and future forest management. The traditional notion of creating as much edge as possible should be re-evaluated, especially for management of biological species that require old-growth interior environments.

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