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Kenneth P. Lertzman; Glenn D. Sutherland; Alex Inselberg; Sari C. Saunders

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## CANOPY GAPS AND THE LANDSCAPE MOSAIC IN A COASTAL TEMPERATE RAIN FOREST<sup>1</sup>

KENNETH P. LERTZMAN

*School of Resource and Environmental Management, Simon Fraser University,  
Burnaby, British Columbia, Canada V5A 1S6*

GLENN D. SUTHERLAND

*Centre for Applied Conservation Biology, Faculty of Forestry, University of British Columbia,  
Vancouver, British Columbia, Canada V6T 1Z4*

ALEX INSELBERG

*Consulting Forest Ecologist, RRI S14-C1, Enderby, British Columbia, Canada V0E 1V0*

SARI C. SAUNDERS

*School of Resource and Environmental Management, Simon Fraser University,  
Burnaby, British Columbia, Canada V5A 1S6*

**Abstract.** We studied canopy gaps over a range of stand ages and site moisture classes in the temperate rain forest of Clayoquot Sound, southwestern British Columbia, Canada. We tested predictions about the landscape mosaic at three levels of resolution: the forest as a whole, gaps, and gapmakers. In addition to canopy gaps arising from the patchy mortality of dominant trees (developmental gaps), we described the prevalence and characteristics of gaps arising from edaphic and topographic features. Roughly 56% of the forest area is influenced to some degree by canopy openings (canopy gap + expanded gap), with 30% of forest area in canopy gaps averaged over all sites (14% developmental canopy gaps and 16% in edaphic canopy gaps). Within the most intensively sampled biogeoclimatic subzone, 73% of gaps were developmental in origin. The majority of edaphic gaps result from streamcourses. Though percent area in developmental canopy gaps was similar across stand age classes, gaps and gapmakers were more common in old growth than in mature stands.

Most developmental gaps resulted from the mortality of more than one tree: 96% of the developmental gaps had more than one gapmaker, and 50% had three or more. Mature stands had a significantly higher number of gapmakers per gap than old-growth stands. Old-growth forests were thus dominated by many small gaps and mature forests by fewer larger gaps. Drier and wetter sites had more gapmakers per gap than did stands on mesic sites. The number of decay classes of gapmakers in developmental gaps increases with number of gapmakers per gap, indicating that larger gaps represent the combined effects of distinct mortality events separated in time, rather than single large events. Gapmakers in developmental gaps were distributed broadly and evenly over the range of decay classes, suggesting a continuous pattern of recruitment of gapmakers rather than larger episodic mortality events. The snapping of boles and standing death were the most common modes of gapmaker mortality, together accounting for 76% of the mortality of all gapmakers. Uprooting was the least common mode of gapmaker mortality in both mature and old-growth forests (23.6% and 15.6%, respectively; 20.6% of all gapmakers) and uprooting was more common in drier and wetter sites than in mesic sites.

These general trends in gap-phase structure and gap formation processes are consistent with data on gaps and forest age structure collected elsewhere on the British Columbia coast, suggesting that a regime of small-scale, low-intensity disturbance is common in the old-growth forests of coastal British Columbia. We estimate that, in the absence of large-scale disturbances, turnover time for this forest is between 350 and 950 yr, resulting in ubiquitous late successional character throughout the landscape mosaic. Silvicultural practices intended to emulate the natural disturbance regime of these forests should create small gaps of 3–10 trees in an otherwise continuous forest matrix and should retain substantial late-successional characteristics within managed forests.

*Key words:* canopy gaps, developmental and edaphic; edaphic mosaic; natural disturbance; temperate rain forest; tree mortality.

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## INTRODUCTION

Forested landscapes at the scale of  $10^1$ – $10^5$  ha are mosaics whose structure is largely determined by the combined effects of a disturbance regime and the underlying patterns of soils and topography. This site-by-site variation in successional and edaphic status exerts strong influences on various aspects of species composition (Romme and Knight 1981, Pastor and Broschart 1990, Spies 1991, Arsenault and Bradfield 1995), forest structure (Grier and Running 1977, Veblen and Lorenz 1987, Spies et al. 1988, Spies and Franklin 1991, Hunter and Parker 1993, Arsenault and Bradfield 1995), and ecosystem function (Van Cleve and Viereck 1981, Matson and Boone 1984, Entry and Emmingham 1995). These factors are not independent. Both the types of mortality experienced by trees and the rates at which mortality events occur vary with edaphic characteristics and topographic position (Hartshorne 1978, Hemstrom and Franklin 1981, Romme and Knight 1981, Pastor and Broschart 1990, Hunter and Parker 1993, Boose et al. 1994, Turner and Romme 1994).

The importance of small, gap-forming disturbances has emerged as a common theme in research on forest dynamics from a variety of forests worldwide (see, for example, the Special Feature in *Ecology* 70(3), 1989). In forests where stand-destroying disturbances are rare, small-scale disturbances that create gaps by killing one to a few canopy trees play key roles in the development and maintenance of forest structure. For instance, many of the structural characteristics that distinguish older stands from younger ones in the conifer forests of northwestern North America are a consequence of gap-making individual tree-by-tree mortality events (Spies et al. 1988, Franklin and Spies 1991, Marcot et al. 1991). The canopy gaps, snags, and logs that result from small-scale mortality events have a pervasive influence on various aspects of the ecology of these forests, including patterns of tree recruitment and understory vegetation dynamics (Alaback 1982, Stewart 1986, 1988, Tappeiner and Alaback 1989, Spies et al. 1990, Lertzman 1992), wildlife habitat (Ralph et al. 1991, Welsh and Lind 1991), stream ecosystem structure and dynamics (Harmon et al. 1986, Maser and Sedell 1994), and biomass dynamics and carbon budgets (Grier and Logan 1977, Harmon et al. 1986, 1990, Spies et al. 1988). These structural elements are also the focus of substantial recent research on forest management practices (Bunnell and Kremsater 1990, Hansen et al. 1991, Swanson and Franklin 1992).

Although the importance of gap-forming mortality and its structural consequences have been recognized for some time, the ways in which they vary over the landscape mosaic have rarely been examined and are poorly understood. In fact, much of the potential variation in gap characteristics induced by site-to-site vari-

ability has been excluded from consideration in many gap studies by an explicit focus on single tree disturbances, circum-mesic sites, a single slope position or aspect, or single age classes of forest (e.g., Barden 1979, 1980, Runkle 1981, Naka 1982, Lang and Knight 1983, Mladenoff 1987, Armesto and Fuentes 1988, Lawton and Putz 1988, Lertzman and Krebs 1991, Rebertus and Veblen 1993). The few studies that allow examination of spatial variation in gap parameters indicate that generalizations over the landscape mosaic should be treated with caution (e.g. Hartshorne 1978, Spies et al. 1990, Hunter and Parker 1993). Temporal variation in gap-forming processes is also of significance in interpreting forest structure in terms of forest dynamics (Lertzman 1995), but has received little attention because of the difficulty in obtaining empirical time series of disturbance frequency.

Forest mosaics can be described by the attributes characterizing different mosaic elements, by the spatial relations among those elements, and by the dynamics of both of these features. In this paper, we examine variation in gap-related forest structure in mature and old-growth stands on sites of different relative moisture status. We focus on mature and older forests because mortality in young stands is primarily through self-thinning, and is not gap creating. Gap formation and its structural and compositional consequences become significant factors in stand development during the transition from mature stands to old growth. As the canopy becomes increasingly heterogeneous through the mortality of canopy dominants, there follows a characteristic sequence of gap-related changes in forest structure, composition, and function, notably the reinitiation of understory development and increases in understory diversity and productivity (Oliver 1981, Alaback 1982, Tappeiner and Alaback 1989, Spies 1991, Spies and Franklin 1991). We thus focus on the characteristics of different elements of the landscape mosaic and make inferences about their dynamics, but do not consider explicitly their spatial relationships.

The need to recognize other contributions to the "gapiness" of forests than that from tree mortality is a significant consequence of considering canopy openings under a range of edaphic conditions. In addition to the direct effects of varying soil conditions, various topographic and geomorphic features contribute to canopy openness, and their contribution is likely to increase on sites progressively drier or wetter than mesic. We define canopy openings resulting from tree mortality as *developmental gaps*. Developmental gaps are the classic "canopy gaps" described in the literature. Developmental gaps arise from the mortality of canopy dominants during stand development, generally beginning during the transition from mature to old-growth forests, and are distinguished by the presence of a gapmaker (a gapmaker is a tree whose mortality creates a gap; Runkle 1981, Lertzman and Krebs 1991). We de-

TABLE 1. Predictions of effects of the landscape mosaic on gap variables at three scales of analysis; forest, gap, and gapmaker. Separate predictions are made for the effects of (A) stand age and (B) the edaphic mosaic.

A) Predictions related to stand age	
Forest level	
1.	Higher proportion of area in developmental canopy gap in older forests.
2.	More gapmakers and more developmental gaps in older forest.
3.	Similar proportions of area in edaphic canopy gap in older and in younger forests.
Gap level	
4.	More gapmakers per gap in older forests.
5.	Large gaps have a range of gapmaker decomposition classes.
Gapmaker level	
6.	More gapmakers in later decay classes in older forests.
B) Predictions related to the edaphic mosaic	
Forest level	
7.	More area in developmental canopy gap in dry and wet stands than in mesic stands.
8.	More area in edaphic canopy gap in dry and wet stands than in mesic stands.
Gap level	
9.	Higher ratio of expanded gap to canopy gap in moister sites where we expect trees to be larger. Should be expressed strongest in older forests that have approached maximum tree size.
Gapmaker level	
10.	Variation in modes of mortality across sites: more uprooting in drier and wetter sites than in mesic sites; standing death common in dry sites.

fine *edaphic gaps* broadly as canopy openings which are associated with an identifiable edaphic or topographic condition, such as a streamcourse or thin soils on a rock outcrop. Edaphic gaps need not be associated with a gapmaker. Dead trees may be present on the periphery of edaphic gaps, but the opening in the canopy cannot be explained solely by their presence. The relative contribution of developmental and edaphic processes to the overall openness of a gap-regenerating forest has not been described previously.

We made a number of a priori predictions regarding how gap attributes of developmental or edaphic origins should vary across a mosaic of stand ages and site types (Table 1). These can be considered at three levels of resolution: the forest level, the gap level, and the gapmaker level. Variables that are likely to be influenced by stand age or site type are: percent area in developmental or edaphic canopy gap, the number of gapmakers per gap, the geometry of gaps, and the modes of mortality and degree of decomposition of gapmakers. In general, we expect the abundance or frequency of attributes that are a product of stand developmental processes to increase with stand age. For instance, at the forest level, we predict that older stands will have more developmental gaps and gapmakers than younger stands, and at the gap level, we expect gaps in older stands to have a greater range of decay classes of gap-

makers present in them. Similarly, we expect that, in general, stands that are wetter or drier than mesic will have a greater frequency of attributes resulting from edaphic features. For instance, at the forest level, we expect that dry or wet stands will have a higher percentage of area in edaphic canopy gaps than mesic stands, and at the gapmaker level, we expect different modes of tree mortality to predominate in different sites because of variation in the degree of restriction of rooting depth.

#### STUDY AREA

We conducted this research in a temperate rain forest watershed on the west coast of Vancouver Island, British Columbia. Such forests experience a very maritime climate with precipitation throughout the year (Alaback 1991, Meidinger and Pojar 1991, Green and Klinka 1994). Seasonal drought and fire are much less significant factors shaping the ecological history of this area than they are in many other forested regions to the east and south. Natural disturbance regimes are characterized by long periods dominated by small, patchy, low-intensity disturbances, which are punctuated by infrequent stand replacing events in some forest types (e.g., catastrophic windthrow associated with large cyclonic storms).

This research examines the Tofino Creek watershed in Clayoquot Sound (125°40' N, 49°20' W). Tofino Creek drains into the head of Tofino Inlet ≈25 km northeast of the town of Tofino. This 5100-ha watershed contains a mixture of ecosystem types representative of drainages on the west coast of Vancouver Island. Where there is no history of logging, forests in such watersheds are virtually all mature or older. A sample of unlogged watersheds in Clayoquot Sound showed >98% cover in mature and old-growth forests (much of that older than 250 yr; British Columbia Ministry of Forests, *unpublished data*). Most of the Tofino Creek watershed remains unmodified by industrial activities, with the exception of ≈350 ha, which were logged over the last 8 yr. This area includes the majority of the most productive valley floor and lower slope. Because the logged area exceeds 2% of the watershed area, this watershed is classified as a "developed" watershed according to the criteria defined in Moore (1991). Administratively, Tofino Creek is crown land, owned by the Province of British Columbia and is part of MacMillan Bloedel Limited's Tree Farm Licence 44. It is part of the Nuu Chaa Nulth Tribal territory. Tofino Creek has been the subject of an intense resource analysis and forestry planning process (British Columbia Ministry of Forests 1991).

The Tofino Creek watershed ranges in elevation from sea level to ≈1200 m. Mean annual precipitation in the town of Tofino is 3300 mm, with little falling as snow. However, there are strong orographic effects and considerable variability in climate from one part of the watershed to another. Substantial winter snowpack de-

TABLE 2. Biogeoclimatic zones, subzones, and variants in the Tofino Creek watershed. Modified after R. Keenan and A. Inselberg (*unpublished manuscript*). See Pojar et al. (1987) and MacKinnon et al. (1992) for descriptions of the biogeoclimatic classification system. The submontane variant of the Very Wet Maritime subzone of the Coastal Western Hemlock zone (CWHvm1) is the focus of this study and is boldfaced in the table. *n* is the number of plots in each ecosystem association.

Zone	Subzone	Variant	Code	Area (ha)	Elevation (m)	<i>n</i>
Coastal Western Hemlock (CWH)	Very Wet Hypermaritime (vh)	Southern (1)	CWHvh1	150	0–150	...
	<b>Very Wet Maritime (vm)</b>	<b>Submontane (1)</b>	<b>CWHvm1</b>	<b>1810</b>	<b>150–600</b>	<b>43</b>
	Very Wet Maritime (vm)	Montane (2)	CWHvm2	2000	600–950	7
Mountain Hemlock (MH)	Moist Maritime (mm)	Windward (1)	MHmm1	1140	950–1300	3

velops at higher elevations in the watershed. Daily mean temperatures in the town of Tofino vary from 4°C in January to 14°C midsummer, with an annual mean of 9°C (Canadian Climate Program 1991).

Tofino Creek is a glacial valley with a relatively flat floor and steep side walls; slopes in the watershed are commonly greater than 20°. Evidence of glacial scarring can be found through most of the valley. Soils are largely derived from bedrock of volcanic and igneous origins, and morainal or colluvial materials from the westcoast complex, the Karmutzen formation, and the Bonanza group (Muller 1977). Soils on middle to upper slopes are generally shallow, with finer textured and deeper mineral soils on floodplains and lower slopes.

The Coastal Western Hemlock (CWH) zone is the dominant biogeoclimatic zone in the Tofino Creek watershed, with a lesser area at higher elevations in the Mountain Hemlock (MH) zone (Table 2; see Pojar et al. 1987, Meidinger and Pojar 1991, MacKinnon et al. 1992 for description of this system of vegetation classification and details on the CWH zone). Most of the more productive forest is in the Submontane variant of the Very Wet Maritime subzone (CWHvm1). In this paper we focus on sites in the CWHvm1. The CWHvm1 occupies sites representing a range of soil moisture and nutrient regimes between 150 and 600 m elevation and covering over 35% of the watershed. We also collected data from the Montane variant of the Very Wet Maritime subzone of the CWH zone (CWHvm2) and the Windward variant of the Moist Maritime subzone of the MH zone (MHmm1), but sample sizes were insufficient to perform analyses stratified by age or soil moisture class.

Botanical nomenclature follows Hitchcock and Cronquist (1973) for vascular plants, which should be consulted for full nomenclatural references. Lower slopes, stream terraces, and floodplains support productive stands of Pacific silver fir (*Abies amabilis*), western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and Sitka spruce (*Picea sitchensis*). However, because of their accessibility and value, few productive spruce stands remain today. Mid-slope forests are dominated by western hemlock and Pacific silver fir. In upper slope forests and on rocky outcrops at lower elevations western hemlock, western

redcedar, and yellow-cedar (*Chamaecyparis nootkatensis*) are common. Montane ridges and slopes support mixes of Pacific silver fir, western hemlock, western redcedar, and yellow-cedar. Subalpine forest and parkland is composed of mountain hemlock (*Tsuga mertensiana*), Pacific silver fir, and yellow-cedar. Well-developed ericaceous shrub understories are common to most of these forest types. A variety of other tree species are less common or restricted to disturbed or specialized habitats. These include lodgepole pine (*Pinus contorta contorta*) on xeric rocky ridges, and big-leaf maple (*Acer macrophyllum*) and red alder (*Alnus rubra*) in recently disturbed and riparian areas. Inselberg (1993) provides a more complete description of soils and vegetation in the Tofino Creek watershed.

## METHODS

### General sampling design

This research on canopy gaps in the Tofino Creek watershed was part of a broader study of forest structure and species composition (Inselberg 1993, R. Keenan and A. Inselberg, *unpublished manuscript*, British Columbia Ministry of Forests 1991). The gap data were one product of a sampling design intended to provide a description of forest structures relevant to forest management and biodiversity issues.

An initial survey of the watershed allowed the delineation of biogeoclimatic zones, subzones, and variants (Table 2; for methods see Luttmerding et al. 1990). Initially, 5–7 plots were planned for each of three developmental stages (young, mature, and old-growth forest) in each of the three variants of the Coastal Western Hemlock zone and in the Mountain Hemlock zone. However, almost all the forest in the CWHvm2 (montane variant) and in the Mountain Hemlock zone is old growth. Additionally, the Very Wet Hypermaritime subzone of the CWH (CWHvh) occupies only a small area near the mouth of the watershed and is transitional to the Very Wet Maritime Submontane variant (CWHvm1) in character. Ultimately, only the CWHvm1 was sampled with sufficient breadth and intensity for our examination of structural changes over sites of varying relative moisture status and stand age. For the other ecosystem units, we present only summary statistics.

TABLE 3. Number of plots and distance sampled in stands of each stand age and soil moisture class. All are in the CWHvm1 subzone (see Table 2). The total length of transect sampled (in metres) in each category is enclosed in parentheses.

Moisture category	Stand age	
	Mature (100–250 yr)	Old growth (>250 yr)
Drier	2 (340 m)	10 (1520 m)
Mesic	7 (1340 m)	4 (800 m)
Wetter	7 (1400 m)	8 (1400 m)
Total	16 (3080 m)	22 (3720 m)

We identified broad vegetation units throughout the watershed using aerial photographs. Vegetation units representing each site by age category were selected largely based on accessibility and area: they needed to be large enough to encompass a plot. Within each such vegetation unit, a plot corner was selected and then plot boundaries established along predetermined bearings. We established 43 plots in the CWHvm1; 5 in young stands (<100 yr, mostly <30 yr), 16 in mature stands (100–250 yr), and 22 in old growth (>250 yr) (Table 3). In our analysis of canopy gap structure we considered only the data from mature and old-growth forests. Young stands will not have had sufficient time for the ontogeny of developmental gaps, i.e., any gaps present will be of silvicultural origin or a result of patchy infilling of natural conifer regeneration and initial occupancy by shorter lived hardwoods (see R. McGhee and K. P. Lertzman, *unpublished manuscript*).

Plot locations spanned the range in moisture regime from dry rocky outcrops to floodplains. We divided site series into three broad categories of relative soil moisture status; circum-mesic sites (gentle to moderate slopes with well-drained, deep soils), drier sites (rocky ridges and other sites with thin soils and low moisture status), and wetter sites (gentle to flat slopes and floodplains with high moisture status). The drier sites include the HwPI-Cladina, HwCw-Salal, and CwHw-Swordfern site series (Hw = western hemlock; PI = lodgepole pine; Cw = western redcedar). The mesic sites were represented by the HwBa-Blueberry site series (Ba = Pacific silver fir). Wetter sites included the HwBa-Deerfern, BaCw-Salmonberry, and Ss-Salmonberry site series (Ss = Sitka spruce). See Green and Klinka (1994) for a detailed description of these ecosystems.

We thus represented the landscape mosaic within the CWHvm1 as a matrix of two age classes by three relative soil moisture categories. These six cells received an unbalanced sampling effort, with mature stands on drier sites being poorly represented (Table 3). Relative soil moisture classes can be considered a proxy for productivity classes, with increasing productivity in the sequence: drier sites, mesic sites, and wetter sites (e.g., R. Keenan and A. Inselberg *unpublished manuscript*).

In the CWHvm2 (montane variant), we sampled a total of seven plots of predominantly mesic soil moisture status, while three plots were sited in circum-mesic sites of the MHmm1 (windward moist maritime variant). All plots in the CWHvm2 and MHmm1 subzones were old growth.

We adopted relatively large plot dimensions in order to sample within-stand heterogeneity adequately and to minimize the likelihood that all of a plot would fall within one gap or area of closed canopy. Plot dimensions were 50 × 50 m (0.25 ha) plots for stands of lower tree density, and 50 × 20 m (0.1 ha) plots for stands of higher density. Stands with a higher density of trees tended to be associated with areas where the size of units of homogeneous vegetation type was smaller, such as rocky ridgetops. Plot dimensions were not corrected for slope, but percent slope for each sample plot was recorded.

#### *Assessing the distribution of canopy cover classes*

Each gap in the canopy (developmental or edaphic in origin) has a core area termed the canopy gap and periphery termed the expanded gap. The canopy gap is the vertical projection onto the ground of the opening in the forest canopy. The boundary of the expanded gap is defined by the boles of the trees whose canopies define the canopy gap (Runkle 1981, Veblen 1985, Lertzman and Krebs 1991). A point is considered in expanded gap if it is underneath the foliage of these trees. At higher latitudes and on slopes, sun angles are rarely near vertical. In such cases the microclimatic effects of openings in the canopy are frequently larger than and displaced from the direct vertical projection of the opening (Canham 1989, Canham et al. 1990). We measured expanded gap area in addition to the canopy gap area in recognition of this additional area of gap influence. It is likely, however, that expanded gap area still underestimates the total area of gap influence on sites of substantial slope at these higher latitudes.

Forest canopy cover class was measured using the plot perimeter as a basis for line intercept sampling, providing a transect length of 200 m per plot in the 50 × 50 m plots and 140 m in the 20 × 50 m plots. At intervals of 1 m along each transect we classed each point as one of three canopy cover classes: EG—expanded gap, CG—canopy gap, or CC—closed canopy. When a point was near a boundary of canopy cover classes, we used a clinometer to ascertain the canopy status directly overhead. Each gap encountered along the plot perimeter was recorded for more detailed sampling. We defined CG as any area without live trees taller than the suppressed tree layer (Luttmerding et al. 1990). We classed each CG or EG designation as developmental or edaphic in origin. If a gap had a substantial edaphic component, we labelled it as an edaphic gap. Some gaps classed as edaphic in origin had a developmental component around their periphery. If gaps were classed as edaphic, the type of edaphic fea-

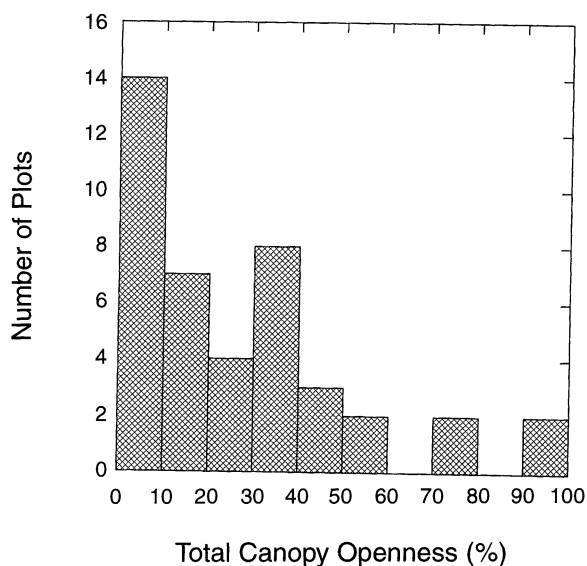


FIG. 1. Frequency distribution of the total canopy openness (percentage of developmental + edaphic gap), for all 34 plots from the CWHvm1 biogeoclimatic subzone. Plots for which the total canopy openness exceeded 60% were either dominated by or contained only edaphic gaps.

ture was noted. Uneven sampling effort (size of plots  $\times$  number of plots) in each combination of age and relative soil moisture class resulted in a range of total transect lengths sampled per age-soil moisture combination ranging from 340 to 1520 m (Table 3).

We used the gaps identified by the above procedure as a basis for sampling gapmakers. In each gap we counted the number of gapmakers and noted for each its mode of mortality (uprooted, snapped, standing dead, or unknown). We also noted the decay class of each gapmaker using the system presented in Table 3 of Lertzman and Krebs (1991) as *young*, *medium*, *old*, or *very old*, based on morphological decay features. We did not measure gap size directly, though the number of gapmakers per developmental gap is well correlated with gap size (K. Lertzman, unpublished data) and may be used as its proxy.

### Statistical analyses

Some plots in the drier site category exhibited  $>60\%$  cover in edaphic canopy gap and the distribution of percent of plot in canopy gap is somewhat disjunct at 60% (Fig. 1). Based on this we decided that vegetation with  $>60\%$  area in canopy gap would not be considered "forest" for our purposes and could be excluded from many of our analyses.

Where possible, we used *t* tests or one- and two-way ANOVAs to assess differences within and among age and moisture classes using forest- and gap-level variables. Before analysis, all data were tested for normality using residual plots; nonnormal data were arcsine transformed or tested using rank values. Where frequency counts were examined, analyses used one-, two-, and three-way log-likelihood tests. All statistical tests were performed using SPSS for Windows Version 6.0 (Norris 1993). Unless otherwise specified, means are presented with  $\pm 1$  SD.

## RESULTS

### Forest-level structure

Overall, of 6800 m sampled over the watershed,  $30.2 \pm 25.0\%$  was in canopy gap,  $25.9 \pm 14.7\%$  was in expanded gap, and  $43.7 \pm 28.7\%$  in closed canopy (Table 4). Of the transect in canopy gap, on average,  $13.9 \pm 12.5\%$  was in gaps of developmental origin and  $16.3 \pm 26.1\%$  was in gaps of edaphic origin. Plots varied substantially both within and between zones in the type and amount of percent gap. The Mountain Hemlock (MH) zone had substantially more edaphic canopy gap and less developmental canopy gap than either of the two Coastal Western Hemlock (CWH) variants. There was little area in the MH zone uninfluenced by adjacent gaps (1.0% closed canopy).

Four of 38 plots in the CWHvm1 (Submontane variant), one of seven plots in CWHvm2 (Montane variant) and two of three plots in MHmm1 had  $>60\%$  of their area in canopy gap. In each case, the gap area was dominated by or was solely edaphic gap. Thus over the watershed as a whole, stands with a very substantial amount of edaphic gap are well represented. For

TABLE 4. Forest-level summary statistics for canopy structure and gapmakers for all subzones. See Table 2 for explanation of subzone code names. Values are presented for the three soil moisture categories and two age categories combined. EG = expanded gap; CG = canopy gap; CC = closed canopy; D = developmental; E = edaphic. Data are means  $\pm 1$  SD.

Attribute	Biogeoclimatic subzone				Overall
	CWHvm1*	CWHvm1†	CWHvm2	MHmm1	
Percent CG-D	14.5 ( $\pm 13.0$ )	14.9 ( $\pm 12.8$ )	16.0 ( $\pm 10.5$ )	5.8 ( $\pm 7.7$ )	13.9 ( $\pm 12.5$ )
Percent CG-E	14.9 ( $\pm 25.0$ )	7.6 ( $\pm 11.4$ )	4.2 ( $\pm 6.5$ )	62.9 ( $\pm 20.3$ )	16.3 ( $\pm 26.1$ )
Percent EG-D	16.7 ( $\pm 13.8$ )	18.4 ( $\pm 13.5$ )	27.5 ( $\pm 11.3$ )	9.2 ( $\pm 12.9$ )	17.8 ( $\pm 13.9$ )
Percent EG-E	7.2 ( $\pm 9.6$ )	7.0 ( $\pm 9.8$ )	7.3 ( $\pm 11.7$ )	21.1 ( $\pm 4.0$ )	8.1 ( $\pm 10.1$ )
Percent CC	47.1 ( $\pm 28.9$ )	52.1 ( $\pm 26.3$ )	43.5 ( $\pm 17.1$ )	1.0 ( $\pm 1.7$ )	43.7 ( $\pm 28.7$ )
No. of plots	38	34	7	3	48

\* All plots for the CWHvm1 subzone.

† CWHvm1 plots excluding those with canopy openness  $>60\%$  (subset used for all statistical analyses).

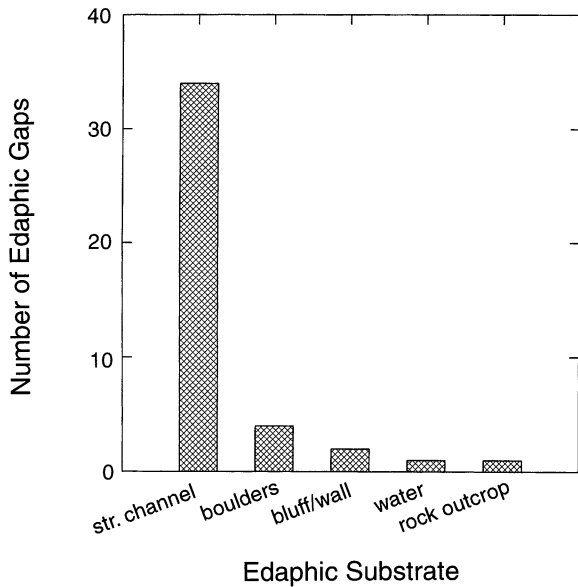


FIG. 2. Frequency distribution of the number of edaphic gaps ( $n = 42$ ) created by each of a number of physiographic causes.

CWHvm1, when the four plots with canopy gap  $>60\%$  are excluded from analysis, on average  $14.9 \pm 12.8\%$  of the forest was in developmental canopy gap and  $7.6 \pm 11.4\%$  was in edaphic canopy gap (Table 4). Even with the extreme values removed, plots varied substantially in gapiness. This subset of 34 plots in CWHvm1 with  $<60\%$  canopy gaps is the subject of all subsequent analyses unless stated otherwise.

In the CWHvm1, developmental gaps were the most common type of gap. Of the 157 gaps sampled there, 114 (73%) were created by developmental processes, while the remaining 43 (27%) were edaphic gaps. Most (74%) of the edaphic gaps resulted from streamcourses (Fig. 2). Other sources of open space in the canopy (e.g., boulders, rock outcrops, etc.) each contributed a smaller proportion of the edaphic gaps.

Does the source of canopy openness vary with the total amount of openness per plot? All plots in CWHvm1 with  $>60\%$  total openness (CG-D + CG-E) are either dominated by (one plot) or are exclusively (three plots) edaphic canopy gaps (Fig. 3). All plots that contained exclusively gaps of developmental origin had  $<60\%$  total openness. Between these extremes, plots over a wide range of total openness (3.5–58.5%) exhibited little pattern in the relative importance of developmental and edaphic sources of canopy openness.

We predicted that older forests should have a greater proportion of their area in developmental canopy gap than edaphic canopy gap because developmental gaps should increase in their abundance with forest age (to some maximum), while the area represented by edaphic features should remain independent of forest age (Table

1; Predictions 1 and 3). Similarly, we predicted a higher percentage of area in edaphic gap in either drier or wetter sites than in mesic sites (Table 1: Prediction 8). We expected higher rates of disturbance, in general, in drier and wetter sites than in mesic sites (Prediction 7).

Although mean percent area in developmental canopy gap was slightly higher in old stands ( $15.88 \pm 11.89\%$ ) than in mature stands ( $13.83 \pm 14.06\%$ ; Prediction 1), and the mean for mesic sites ( $9.64 \pm 10.57\%$ ) was lower than drier ( $17.45 \pm 15.08\%$ ) or wetter ( $13.79 \pm 12.95\%$ ; Prediction 7), the comparisons were not significant (two-way nonparametric analysis of variance;  $df = 5, 33$ ;  $P > 0.58$ ; power = 0.114). The mean percent of plot area in edaphic canopy gap was similar between mature ( $8.35 \pm 12.3\%$ ) and old stands ( $6.94 \pm 10.92\%$ ; Prediction 3), and mesic sites do have a lower mean area in edaphic canopy gap ( $1.91 \pm 3.28\%$ ) than do either drier ( $7.24 \pm 13.07\%$ ) or wetter ( $10.26 \pm 12.05\%$ ; Prediction 8). However, neither comparison is statistically significant and low power precludes making an inference in support of Prediction 3 from the lack of significance (two-way nonparametric analysis of variance;  $df = 5, 33$ ;  $F = 1.18$ ;  $P = 0.344$ ; power = 0.105).

Although old-growth plots did not have significantly more area in gaps than mature plots, old growth had a higher density of gapmakers than did mature forest (Table 1: Prediction 2). Over the total length of transect sampled, gaps were encountered at a rate of 0.019 gaps/m sampled in old growth and 0.014 gaps/m in mature forest. Gapmakers were encountered at roughly twice

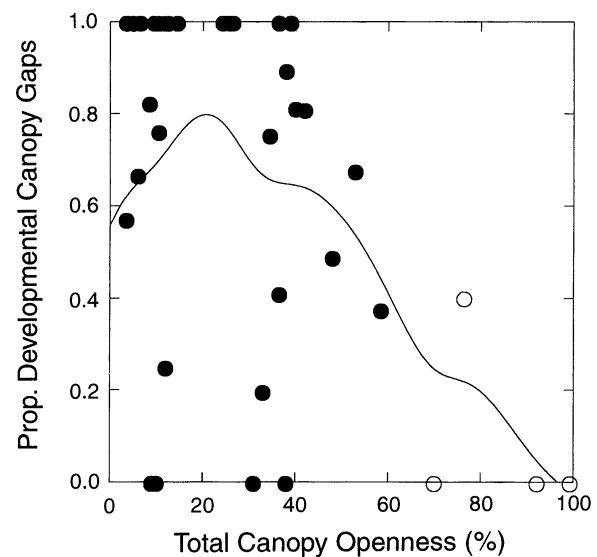


FIG. 3. Relationship between the proportion of developmental canopy gap and the total canopy openness in each plot. ● represent plots with gap area dominated by developmental gaps; ○ are plots with gap area dominated by edaphic gaps. The line is a distance-weighted least squares smoothing of the data (Wilkinson et al. 1992).



TABLE 5. Forest-level summary statistics for gapmakers for all subzones. See Table 2 for explanation of subzone code names. Values are presented for the three soil moisture categories and two age categories combined. Only data from developmental gaps are included. Data are means  $\pm$  1 SD.

Attribute	Biogeoclimatic subzone			Overall
	CWHvm1	CWHvm2	MHmm1	
No. gapmakers/gap	5.0 ( $\pm$ 2.9)	3.7 ( $\pm$ 2.2)	3.7 ( $\pm$ 2.4)	4.7 ( $\pm$ 2.8)
Decay class				
Young (%)	25.3 ( $\pm$ 18.5)	21.6 ( $\pm$ 16.5)	25.0 ( $\pm$ 35.4)	24.6 ( $\pm$ 18.4)
Medium (%)	26.5 ( $\pm$ 15.2)	18.1 ( $\pm$ 17.0)	5.0 ( $\pm$ 7.1)	23.9 ( $\pm$ 15.9)
Old (%)	29.5 ( $\pm$ 17.3)	39.8 ( $\pm$ 23.7)	0	29.9 ( $\pm$ 19.5)
Very old (%)	18.1 ( $\pm$ 17.7)	17.8 ( $\pm$ 10.8)	70.0 ( $\pm$ 35.4)	20.7 ( $\pm$ 20.9)
Mode of mortality				
Uprooted (%)	19.0 ( $\pm$ 18.6)	30.5 ( $\pm$ 16.2)	10.0 ( $\pm$ 14.1)	20.6 ( $\pm$ 18.4)
Snapped off (%)	41.8 ( $\pm$ 28.5)	28.7 ( $\pm$ 17.7)	5.0 ( $\pm$ 7.1)	37.7 ( $\pm$ 27.5)
Standing dead (%)	26.6 ( $\pm$ 22.9)	33.2 ( $\pm$ 21.0)	15.0 ( $\pm$ 21.2)	27.2 ( $\pm$ 22.3)
Unknown (%)	12.6 ( $\pm$ 17.1)	7.6 ( $\pm$ 8.3)	70.0 ( $\pm$ 42.2)	14.6 ( $\pm$ 21.2)
No. of gaps*	114	42	2	155

\* The number of gaps (developmental only) for all gapmaker attributes.

the rate in old-growth than in mature forest: 0.07 gapmakers/m in old-growth and 0.034 gapmakers/m in mature forest. Sixty-two percent of the gaps (71 of 114;  $\chi^2 = 2.64$ ;  $df = 1$ ;  $P > 0.05$ ) and 68% of the gapmakers (260 of 381;  $\chi^2 = 28.17$ ;  $df = 1$ ;  $P < 0.001$ ) were in old-growth plots. The higher relative density of gapmakers in older forest is likely due to the slow decay of large trees leading to the continuing growth of the gapmaker population well into the old-growth stage.

#### Gap-level structure

Summing over all zones and subzones, most of the 155 developmental gaps sampled in mature and old-growth stands resulted from the mortality of more than one tree (Table 5). Overall, 80.1% of the developmental gaps sampled had  $>1$  gapmaker, and 62.0% of these gaps had  $\geq 3$  gapmakers, up to a maximum of 19 gapmakers. For the CWHvm1, 96.4% of the 114 developmental gaps had more than one gapmaker, and 50% of these gaps had three or more gapmakers.

We predicted that older stands would have more gapmakers per developmental gap than would mature stands (Table 1: Prediction 4). Contrary to this, mature stands had a significantly higher number of gapmakers per gap (Fig. 4; mature: mean  $\pm$  1 SD =  $4.84 \pm 4.32$  gapmakers/gap; median = 3.00 gapmakers/gap; maximum = 19 gapmakers/gap; old-growth: mean  $\pm$  1 SD =  $3.93 \pm 2.48$  gapmakers/gap; median = 4.00 gapmakers/gap; maximum = 12 gapmakers/gap; two-way analysis of variance on square-root transformed data;  $df = 1, 119$ ;  $F = 4.32$ ;  $P = 0.04$ ). While we did not have an a priori expectation of the influence of moisture type on number of gapmakers per developmental gap, the number of gapmakers per gap differed significantly among moisture categories ( $df = 2, 119$ ;  $F = 9.4$ ;  $P < 0.001$ ) with both drier and wetter sites having more gapmakers per gap than did mesic sites [ $5.17 \pm 3.07$  gapmakers/gap (drier sites),  $3.09 \pm 2.39$  gapmakers/gap (mesic sites),

$4.84 \pm 3.70$  gapmakers/gap (wetter sites); Bonferroni LSD comparisons;  $\alpha = 0.05$ ].

Large gaps with multiple gapmakers could result from either a single mortality event in which a number of trees were killed or from the combined effects of distinct mortality events separated in time. Based on Lertzman and Krebs (1991), we predicted that larger gaps would result from the latter process and would therefore have a wider range of gapmaker decay classes than smaller gaps (Table 1; Prediction 5). We used the number of gapmakers per gap as a proxy for gap size. The number of decay classes of gapmaker per developmental gap does increase significantly with number of gapmakers per gap (Fig. 5; one-way analysis of variance;  $df = 3$ ;  $F = 39.2$ ;  $P < 0.001$ ). Thus, although gaps characteristically have several to many gapmakers, they do not generally result from the simultaneous mortality of all those trees, but rather from smaller mortality events dispersed in time.

If our sequence of relative soil moisture status represents a gradient of productivity, there should be an increasing ratio of expanded gap to canopy gap from drier to mesic to wetter sites as trees become larger (Table 1: Prediction 9). However, mesic sites had a significantly higher mean ratio of expanded gap to canopy gap ( $2.38 \pm 1.32$ ; Fig. 6) than did either drier ( $0.98 \pm 0.78$ ) or wetter sites ( $1.27 \pm 1.02$ ; one-way analysis of variance;  $df = 2$ ;  $F = 4.93$ ;  $P = 0.014$ ). This suggests that either trees in the wetter sites are not larger than those in the mesic sites, or that an increased amount of open space in wetter sites swamped the effects of canopy geometry. Though wetter sites did tend to have more open space than mesic sites, the differences were not significant (Predictions 7 and 8 not supported). Trees on mesic sites were quite large and had canopy radii comparable to those of the taller trees on wetter sites. In these maritime ecosystems, mesic

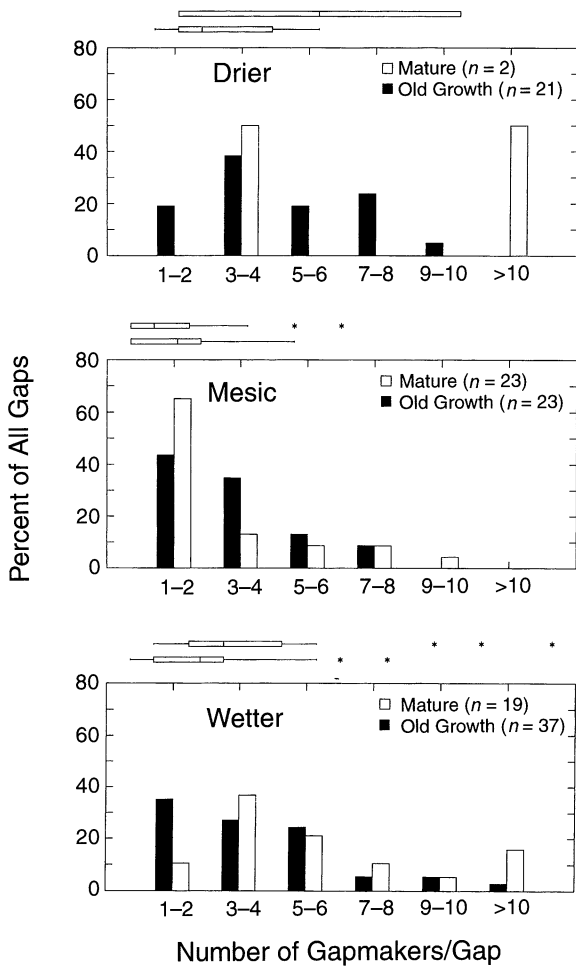


FIG. 4. Frequency distributions of the number of gapmakers per developmental gap for mature and old-growth stand age categories sampled within moisture categories (see *Methods: General sampling design* for definition of the moisture categories) in subzone CWHv1. Marginal box plots, calculated from the ungrouped data, indicate median (central vertical line), quartiles of the distribution, and outlying values. Outlying values shown by asterisks represent values that fall farther than 1.5 times the interquartile range from the ends of the box (Wilkinson et al. 1992). For each graph, the box plots are arranged as Mature (top) and Old-Growth (bottom).

sites are moist year-round and trees experience little summer moisture deficit in typical years.

*Gapmaker-level structure*

Over all zones and subzones, the 665 gapmakers in developmental gaps were distributed broadly and evenly over the range of decay classes (Table 5). This broad distribution of decay classes indicates a more-or-less continuous pattern of recruitment of gapmakers, as would result from a constant, low-level pattern of disturbances, rather than from more pulsed mortality events. This is corroborated by the increasing variation

in decay classes per gap with increasing numbers of gapmakers per gap (Fig. 5).

We predicted that we would find more gapmakers in older decay classes in the old-growth stands than in mature stands (Table 1: Prediction 6) but had no a priori prediction for the influence of moisture regime on the distribution of decay classes among gapmakers. Fig. 7A shows the percentage of gapmakers in each decay class for mature and old growth stands across moisture classes. Because there were very few gapmakers in the “very old” decay class in some mature sites, we pooled the “old” and “very old” classes before statistical analysis. Consistent with Prediction 6 in Table 1, gapmakers in old-growth stands were, on average, farther along in the decay process than in mature stands (one-way log-likelihood ratio test;  $G = 17.55$ ;  $df = 2$ ;  $P = 0.0001$ ). There was no evidence for an association between gapmaker decay class and moisture regime (two-way log-likelihood ratio test;  $G = 3.53$ ;  $df = 4$ ;  $P = 0.473$ ), or for a more complex interaction between gapmaker decay class, moisture regime or stand age (three-way log-likelihood ratio test;  $G = 5.44$ ;  $df = 4$ ;  $P = 0.271$ ).

The mode of mortality could be determined for 87% of the gapmakers found in all subzones (578/662; Table 5; Fig. 7B). Of these, 42.6% had snapped between 2 and 10 m above the ground, while 33% died standing. The remaining 24.6% were uprooted. An undetermined percentage of the gapmakers classified as snapped probably died intact and snapped later. Although some gapmakers could not have a mode of mortality assigned to them, nearly all of the recent gapmakers had an

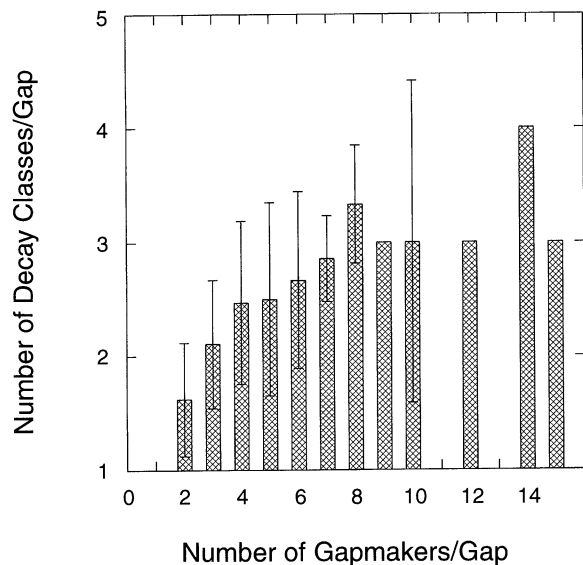


FIG. 5. Relationship between the mean number of decay classes determined for all gapmakers, and the mean number of gapmakers in each developmental gap ( $n = 125$  gaps). Also shown are the 95% confidence intervals about each mean for those categories with more than one gap represented.

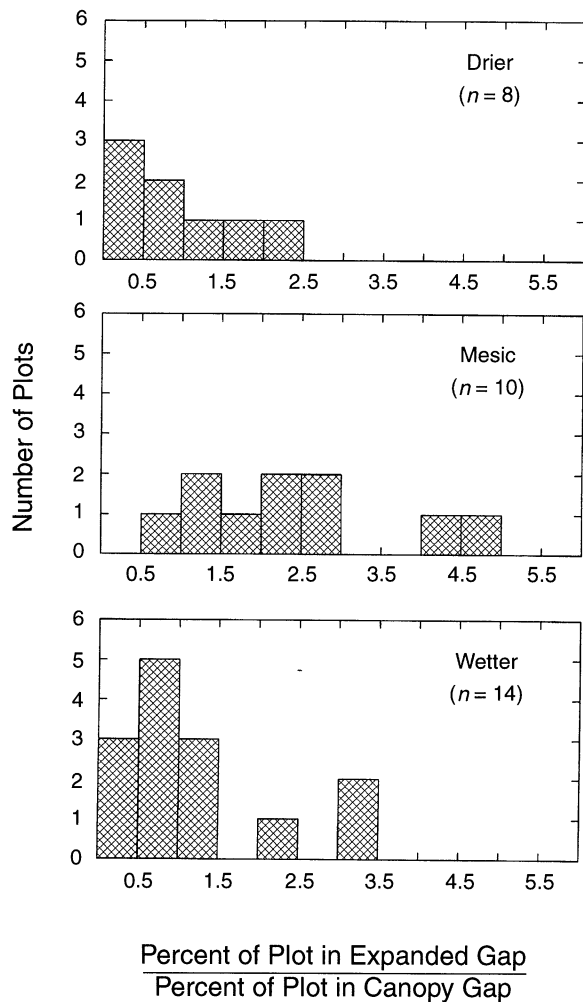


FIG. 6. Frequency distributions of the ratio of expanded gap to canopy gap for stands on drier, mesic, and wetter sites. Sample sizes are shown in parentheses.

identifiable mode of mortality (98.4% of the young and medium decay class gapmakers). When only these more recent gapmakers are considered, the proportion of gapmakers that died standing increases to 45.0%, largely due to a reduction in the proportion of snapped gapmakers. This suggests that an even higher proportion of the gapmakers died standing than is indicated by considering all decay classes of gapmakers, supporting the notion that many of the gapmakers that now appear as snapped-off actually died standing.

We expected that the dominant mode of mortality might vary with stand age, but had no strong expectation for the pattern of variation (therefore no a priori prediction for this in Table 1). In fact, in both mature and old-growth stands, snapping of stems was the most common apparent mode of mortality (37.8% gapmakers in mature plots and 44.6% in old growth; Fig. 7B), but likely represented both true snap-off mortality events and older standing dead trees. Uprooting of trees was

the least common mode of mortality in both age classes, but was more common in mature than in old-growth plots (23.6% in mature forest and 15.6% in old growth). Jointly, snapping and standing death accounted for most of the mortality in the forest, especially in old growth.

We expected that more trees would be uprooted in drier and wetter sites than in mesic sites because of increasing restrictions in the depth of the rooting zone (Table 1: Prediction 10). Combining data across age classes, this prediction was supported: significantly more gapmakers were uprooted in dry and wet sites than in mesic sites (log-likelihood ratio test;  $G = 7.44$ ;  $df = 2$ ;  $P < 0.025$ ; Fig. 7B). However, in no case was uprooting the most common mode of mortality, and it was the least common identified mode of mortality in three of the six site by age categories. Based on casual observations, we expected standing mortality to be common on drier sites. In fact, trees on drier sites were more likely to die standing than in mesic and wetter sites (log-likelihood ratio test;  $G = 34.59$ ;  $df = 2$ ;  $P < 0.001$ ).

#### DISCUSSION

Canopy gaps are a dominant feature of forests in the Tofino Creek landscape. Roughly 56% of the forest area is influenced to some degree by canopy openings (CG-D and -E + EG-D and -E; Table 4). Though less than a third of the gaps were of edaphic origin, both developmental and edaphic processes contribute significantly to the overall openness in the forest (ratio of percent CG-D/percent CG-E over all zones and sub-zones = 0.85; for CWHvm1 = 0.98). The few plots in the Mountain Hemlock zone were largely dominated by edaphic gaps (percent CG-D/percent CG-E = 0.09; CG-E = 63% of plot area overall). Disturbances that create gaps are generally of the least intense modes of gap-forming mortality, standing death and snapping. Uprooting, with its potential as a major agent of disturbance to soils (Beatty and Stone 1986, Schaetzl et al. 1989), was uncommon, especially in old growth.

The general trends in gap-phase structure and gap formation processes observed at Tofino Creek are similar to those described elsewhere on the southern British Columbia coast. In transitional CWH/MH forest on the Lower Mainland of the British Columbia coast, Lertzman and Krebs (1991) found 18% of the forest area in developmental canopy gaps, a predominance of standing mortality, and a majority of gaps with multiple gapmakers dating to gap-making events dispersed in time. Spies et al. (1990) found similar overall patterns in their comparison of mature and old-growth Douglas-fir/western hemlock stands in western Oregon and Washington. In a comparison of old-growth CWH forests in three sites on the Lower Mainland and Vancouver Island, Arsenault (1995) found 38% of the forest area in developmental canopy gap, roughly equal proportions of gapmakers that died standing or were up-

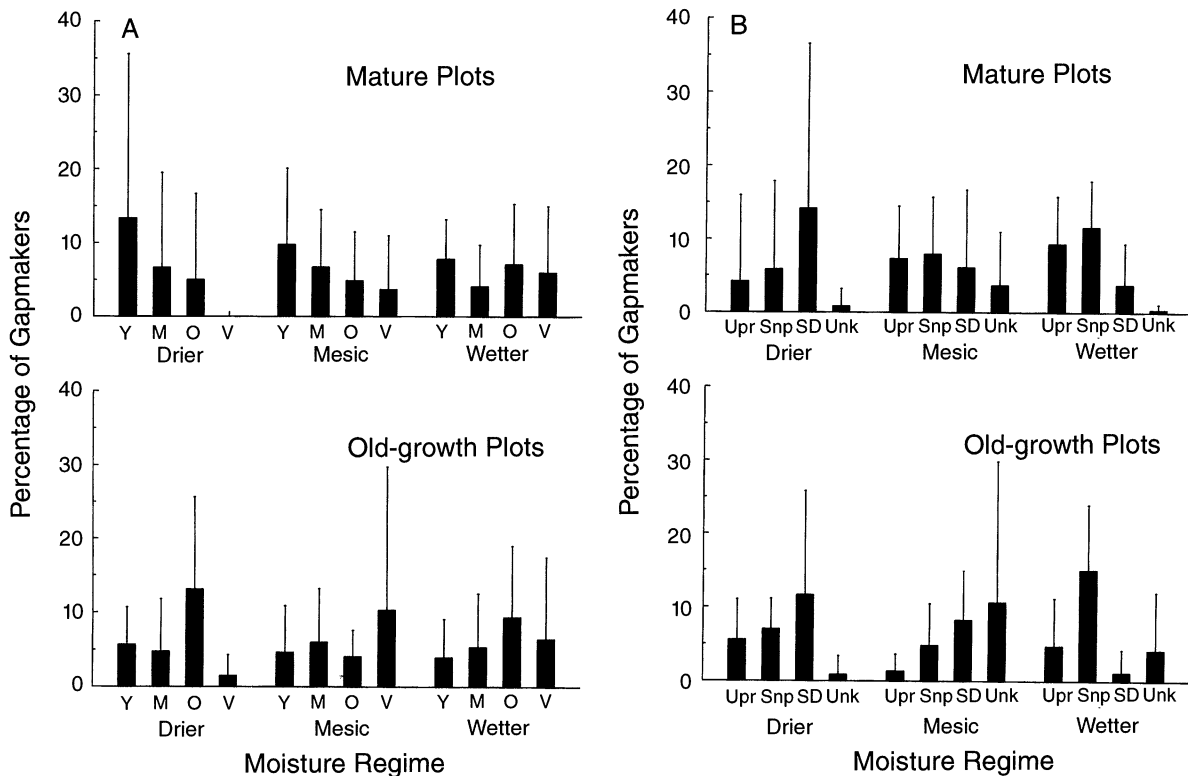


FIG. 7. (A) Mean percentage of all gapmakers in each gapmaker decay class, stratified by moisture regime and stand age class. Also shown are 95% confidence intervals about each mean. Codes for gapmaker decay classes are: Y = young; M = medium; O = old; and V = very old. Criteria for defining the decay classes are as in Lertzman and Krebs (1991). (B) Mean percentage of all gapmakers that died by each mode of mortality, also stratified by moisture regime and stand age class. Also shown are 95% confidence intervals about each mean. Codes for modes of mortality: Upr = uprooted; Snp = snapped off; SD = standing dead; and Unk = unknown.

rooted, and most gaps with multiple gapmakers. The amount of forest area in expanded gap did vary substantially among these studies. Both Lertzman and Krebs (1991) and Arsenault (1995) found substantially more expanded gap than we did at Tofino Creek (52% and 38% of forest area, respectively, compared with 18% overall at Tofino Creek).

The overall similarity in the gap-phase structure of forests on Vancouver Island and British Columbia's lower mainland, despite their geographical and climatic differences, supports the idea that small-scale, low-intensity disturbance and its structural and demographic consequences are of broad significance for wet rain forests in coastal British Columbia. Recent studies of tree age structure sampled over a broad range of sites in southern coastal British Columbia support this conclusion, showing all- or multi-aged stands with pulsed or continuous patterns of recruitment (Beese and Sanford 1992, Stolz and Scheidemann 1992, Inselberg 1993, Daniels et al. 1995).

#### Forest-level dynamics

Turnover time is a summary statistic that describes the overall rate at which space "turns over" in the

forest. It can be interpreted as the average length of time between successive disturbances at each location in the forest; the sum of the time it takes for gaps to fill after a tree dies ( $T_{\text{fill}}$ ) and the time trees are resident in the canopy before the next gap creation event ( $T_{\text{res}}$ ). We estimated turnover time using a proportionality between the amount of forest in gap and canopy phases and the amount of time spent in each phase: turnover time =  $T_{\text{fill}}/CG-D$  (Lertzman and Krebs 1991). Because we have no measures of the rate at which gaps fill in, we calculated turnover time for a range of possible values for  $T_{\text{fill}}$  (Table 6).

Turnover time estimates range for Tofino Creek from just under 350 yr to almost 3500 yr, varying substantially among biogeoclimatic variants and with assumptions regarding the time taken for gaps to fill (Table 6). The estimates for the two subzones of CWH are rather similar, but the estimates for MH are much higher. The MH turnover estimates are also substantially higher than Lertzman and Krebs (1991) found for MH zone forests on the British Columbia lower mainland (they estimated a turnover time of 683 yr for a  $T_{\text{fill}}$  of 150 yr as compared to a turnover time of 2586 yr for the same  $T_{\text{fill}}$  from our data). The turnover time esti-

TABLE 6. Estimates of turnover time for each subzone. See Table 2 for explanation of subzone code names.  $T_{\text{fill}}$  is the time taken for a newly created gap to fill to the point where it is no longer a gap. Turnover times are calculated as  $T_{\text{fill}}/\text{CG-D}$  where CG-D is proportion of forest area in developmental canopy gaps (Lertzman and Krebs 1991).

$T_{\text{fill}}$	Turnover times by subzone (yr)			
	CWHvm1 (CG-D = 0.145)	CWHvm2 (CG-D = 0.160)	MHmml (CG-D = 0.058)	Overall (CG-D = 0.139)
50	345	313	862	360
100	610	625	1724	719
150	1035	937	2586	1079
200	1379	1250	3448	1439

mates for MH in our study are suspect for two reasons: the small overall sample size in MH and the dominance of edaphic gaps in these stands. The developmental canopy gap data used to calculate turnover time are poorly representative of these stands. Lertzman and Krebs (1991) focussed on stands in which edaphic gaps were insignificant contributors to forest structure. Most of the open space in the MH stands we sampled does not "turn over" because it results from stable edaphic features, not tree mortality.

The estimated turnover time is sensitive to assumptions regarding  $T_{\text{fill}}$ , and we expect that  $T_{\text{fill}}$  will vary substantially among sites of varying productivity within a biogeoclimatic variant and among variants (increasing with decreasing site productivity or increasing elevation). We expect, however, that  $T_{\text{fill}}$ s in the range of 50–150 yr reflect the majority of gapfilling processes in most of these stands, leading to turnover times ranging from 350 to 950 yr, similar to the range reported by Lertzman and Krebs (1991). These estimates are consistent with data on tree ages from the Tofino Creek watershed. For example, one plot had tree ages spread between 100 and 1200 yr in age, the majority of plots had many trees over 400 yr in age, and a yellow-cedar in the MH zone was 1380 yr old (Inselberg 1993).

However, even the more productive CWHvm1 stands on which our analyses focussed had a mean of 15% of stand area in edaphic gaps. This suggests that turnover time estimates, in general, must be interpreted in the context of that proportion of the forest area that is actually turning over. An equal proportion of stand area in CWHvm1 was in edaphic gaps, stable open patches that do not "turn over," or do so very slowly (e.g., Wheeler and Fonda 1995). If we are to understand the linkages between forest structure and compositional dynamics, analyses must include estimates of the contributions to forest structure from edaphic features.

The disturbance regime of these forests is thus characterized by small-scale, low-intensity disturbances that are dispersed in time and space and that occur through a diversity of processes that vary in their structural consequences to the forest. We base this conclusion on the combination of long turnover times, the

origins of larger gaps in sequential, small mortality events that result in gapmakers of varying stages of decomposition and modes of mortality, and the infrequency of uprooting as a mode of mortality. Larger windthrow events (e.g., 20–40 ha or more) certainly do occur in forests of the types represented at Tofino Creek. However, they are generally restricted to particular combinations of topographic exposure and stand structure. There was no evidence of such large disturbance events in any of our data. Similarly, in the nearby Clayoquot River watershed, no openings of wind origin >9 ha could be found in any air photos from 1939 to the present (Pearson 1995).

Do our data from Tofino Creek reflect a mosaic whose structure is largely determined by the combined effects of a disturbance regime and the underlying patterns of soils and topography? At the forest-level of analysis, we found few statistically significant differences in the amount of canopy gap between mature and old-growth forest or among sites of varying moisture status (Table 1: Predictions 1, 3, 7, and 8 not supported). This could reflect a similarity of forest structure across the mosaic of stand ages and site types. We suspect, however, that it more likely reflects a lack of statistical power to detect differences that do in fact exist, and substantial variability within and among sites of a given type. Statistical power for the tests of these four predictions was <0.61. In our study, the frequency of statistically significant results increases with sample size; we obtained highly significant results for the related forest-level analyses with much greater sample size (Prediction 2). This suggests that those who desire high power to detect landscape-level trends in forest structure must be prepared for a substantial sampling effort: we did not achieve this with almost 7 km of sampling at 1-m intervals.

#### *Gap-forming processes: developmental gaps*

We expected that both gaps and gapmakers would accumulate in the forest as stands aged from maturity to old growth and that this would be reflected in a higher percentage of area in gaps, more gaps and gapmakers overall, and more gapmakers per gap in old-growth stands (Table 1: Predictions 1, 2, and 4). These trends were found by Spies et al. (1990) in their comparison of mature and old-growth Douglas-fir/western hemlock forests in western Oregon and Washington. However, although old-growth stands had twice the density of gapmakers as mature stands in Tofino Creek, they did not have significantly more area in gap and had smaller gaps (fewer gapmakers per gap). With a similar overall amount of total area in gaps, old-growth stands in Tofino Creek distribute that area among many smaller gaps and mature stands among fewer larger gaps.

We find this difference puzzling. It is hard to imagine how stands characterized by a few large openings develop into stands with many small ones. Two alter-

native hypotheses could account for this difference in gap characteristics between mature and old-growth stands. The first hypothesis is that maturing stands pass through a developmental stage where trees that are not windfirm blow down. If this sometimes occurs in patches much larger than average, it would create the few large observed gaps in mature stands. In this case, the main body of the gap size distribution in mature forests represents similar developmental processes to those seen in the old-growth stands, while the upper tail represents rarer larger disturbance events in stands that will eventually develop into old growth that is similar to that which we sampled. If this is so, we just happened not to sample any residual gaps in old growth comparable to the largest ones in mature forest. This hypothesis is supported by the increased incidence of windthrow in mature relative to old-growth stands, but is not supported by an examination of the modes of mortality in large gaps. The three largest gaps we found were in mature stands (with 15, 16, and 19 gapmakers each). Although the trees in any one of these gaps tended to have died in the same way, there was no consistent pattern in mode of mortality among these three large gaps, and uprooting was the most common mode of mortality in only one of them. However, assuming that snapping and uprooting together represent wind-associated mortality, 65% of the gapmakers in the three large gaps died in ways potentially attributable to wind.

The second hypothesis is that the mature stands exhibiting very large gaps are on a different developmental trajectory than the old-growth stands we describe; they are not part of the same chronosequence and will not develop into old growth similar to that which we described. At Tofino Creek, the distribution of gapmakers per gap in mature stands was influenced by a few large gaps in a subset of the stands—the two gaps with the most gapmakers were in the same sample plot. Under this hypothesis, the stands containing these gaps should be distinct in some way from other mature stands and from the old-growth stands. Research elsewhere on Vancouver Island has examined the hypothesis that two distinct communities exist on similar sites with different disturbance histories; a windfirm cedar-hemlock phase with little history of windthrow, and a windthrow-prone hemlock-amabilis fir phase that experiences frequent larger scale windthrow events (Prescott et al. 1993, Keenan et al. 1994). However, while some of the mature stands in the CWHvml subzone at Tofino Creek may fit this pattern (Inselberg 1993), the two phases are distributed roughly equally among the mature and old-growth stands we sampled. Furthermore, as discussed above, the evidence for wind as a primary mortality agent in the few largest gaps is equivocal at best. Distinguishing between these two hypotheses awaits more focussed study of the developmental processes in old-growth stands and the etiology of gap formation in mature forests.

#### *Edaphic gaps and developmental gaps*

Interest in gap-phase processes arose from concerns about patterns and modes of tree mortality and replacement. Edaphic gaps do not fit well into this framework because they are not loci of tree mortality and replacement, but rather are nodes of persistent open space in the matrix of the forest canopy. They may, in fact, be associated with high rates of tree mortality on their periphery: windthrow of young trees colonizing on the edge of edaphic gaps is common, but such processes probably reflect primarily a locally restricted rooting zone. Edaphic gaps are significant elements of forest structure, but are not significant contributors to forest dynamics.

Canopy gaps arising from edaphic processes should play related but somewhat distinct roles in the forest community from developmental gaps. Open space in the canopy is itself a resource for some species (e.g., Spotted Owls, Thomas et al. 1990, Carey et al. 1992; bats, Crome and Richards 1988) and we expect little qualitative difference between the open space provided by edaphic and developmental gaps for such species. However, gap formation processes are also the primary mechanism responsible for the production of snags and fallen logs in mature and old-growth forests, and edaphic gaps, by definition, are not necessarily associated with such structures. For the many organisms whose habitat associations with gaps depend on these structural features, rather than the open space in the canopy per se, edaphic gaps should not provide the same suite of resources as developmental gaps. The distinct substrates and moisture status of edaphic gaps means that the understory plant community of edaphic gaps should be distinct from that of nearby developmental gaps (e.g., Wheeler and Fonda 1995). While a variety of understory herbs and shrubs exhibit consistently greater cover in developmental gaps in Tofino Creek than in nearby closed-canopy areas (Inselberg 1993), a comparison of the vegetation in developmental and edaphic canopy gaps has not yet been made.

Considering the total open space in a forest arising from both edaphic and developmental processes should allow the integration of the traditional focus of gap studies on compositional dynamics with the recent emphasis on the dynamics of forest structure and ecological function. The prevalence of streamcourses as a source of edaphic gaps in Tofino Creek is a good example of this and highlights the pervasive interactions between terrestrial and aquatic processes in temperate rain forest ecosystems (e.g., Nakamura and Swanson 1994).

#### *Management implications*

Consideration of natural patterns of forest structure and dynamics are of increasing applied significance. Many scientists and managers advocate the emulation of natural disturbance processes and stand structures

in silvicultural practices as a basis for ensuring that managed forests will continue to provide the range of habitats present historically (Bunnell and Kremsater 1990, Hansen et al. 1991, Swanson and Franklin 1992, Hunter 1993, Scientific Panel for Sustainable Forest Practices in Clayoquot Sound 1994). Yet in many cases, natural disturbance regimes, their consequences for forest structure, and their variability over the landscape mosaic are poorly understood. Forests similar to those we studied at Tofino Creek are widespread on the British Columbia Coast and are the focus of extensive forest management activity. Based on our analyses of gap characteristics in Tofino Creek, we identify four main implications for managing forests such as these.

1) *Silvicultural systems should maintain late-successional character at the stand level by creating gaps in a matrix of continuous forest cover.*—With natural turnover times of 350–950 yr, any traditional even-aged management system is highly unlikely to maintain or recreate the structural characteristics that dominate the forests we examined, even one with rotation lengths much longer than is generally considered economically feasible. In traditional silvicultural terminology, creating small gaps is equivalent to group selection involving the removal of 3–10 stems. Of the traditional uneven-aged silvicultural systems, group selection is probably more appropriate than single-stem selection, which is unlikely to provide substantial regeneration opportunities in these tall canopies (Canham et al. 1990, Spies et al. 1990). Small group selection would provide regeneration opportunities similar to those within the intact forest and maintain an uneven age structure with trees of varying age, height, and diameter distributed patchily in a fine-grained mosaic. To maintain the range of old-growth-like habitats at the stand level, traditional timber-oriented group selection regimes would require some modification to ensure the continuing presence of large-diameter snags and down logs (Scientific Panel for Sustainable Forest Practices in Clayoquot Sound 1995). Prescriptions for silvicultural gap size and frequency should recognize the variation in forest structure and openness among different site types and ecological zones.

2) *Managers should recognize the persistent open space associated with edaphic gaps.*—It is unreasonable to expect full occupancy of a stand following logging if many sites were not forested in the pre-logging state. These more open areas should contribute to the diversity of habitats and species in managed forests. Silvicultural gaps should be treated as developmental gaps that are embedded in a matrix of uncut forest and openings of edaphic origin.

3) *Managers should recognize that windthrow is a natural, but infrequent part of the historical dynamics of these forests.*—Tree uprooting is an important, but low-frequency source of structural diversity in the forests we observed. We hypothesize that endemic windthrow may be a process through which stands develop

a windfirm, old-growth structure. However, the low frequency of windthrow we observed in intact stands contrasts strongly with the large-scale windthrow problems commonly observed in silvicultural settings (Esseen 1994, Stathers et al. 1994). We suggest that these problems are frequently an artifact of the silvicultural regime imposed on the forest.

4) *Maintain late-successional character over the landscape as a whole by adopting a rate of cut that limits the total disturbed area at any given time.*—If too high a rate of cut is adopted at the landscape scale, late-successional character will be lost, irrespective of the silvicultural system employed in individual stands. Consistent with the long turnover times we found, the ages of individual trees (Inselberg 1993), and the distribution of forest age classes over the watershed (British Columbia Ministry of Forests, unpublished data), the prelogging landscape at Tofino Creek was one of largely late-successional character. If managers expect the wetter types of coastal temperate rain forests to continue to provide the range and distribution of the habitats historically present in unmanaged forests, this dominance of the landscape by forests of late-successional character should be maintained.

Clearly, studies such as ours cannot be the sole criteria for defining appropriate silvicultural systems. They do, however, provide a clearer picture of the historical patterns of forest dynamics defining the context in which silviculture takes place.

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#### LITERATURE CITED

- Alaback, P. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. *Ecology* **63**:1932–1948.
- . 1991. Comparative ecology of temperate rainforests of the Americas along analogous climatic gradients. *Revista Chilena de Historia Natural* **64**:399–412.
- Armesto, J. J., and E. R. Fuentes. 1988. Tree species regeneration in a mid-elevation, temperate rain forest in Isla de Chiloe, Chile. *Vegetatio* **74**:151–159.
- Arsenault, A. 1995. Pattern and process in old-growth temperate rainforests of southern British Columbia. Disserta-

- tion. Department of Botany, University of British Columbia, Vancouver, British Columbia, Canada.
- Arsenault, A., and G. E. Bradfield. 1995. Structural-compositional variation in three age-classes of temperate rainforests in southern coastal British Columbia. *Canadian Journal of Botany* **73**:54–64.
- Barden, L. S. 1979. Tree replacement in small canopy gaps of a *Tsuga canadensis* forest in the southern Appalachians, Tennessee. *Oecologia* **44**:141–142.
- . 1980. Tree replacement in a cove hardwood forest of the southern Appalachians. *Oikos* **35**:16–19.
- Beatty, S. W., and E. L. Stone. 1986. The variety of microsites created by tree falls. *Canadian Journal of Forest Research* **16**:539–548.
- Beese, W. J., and J. S. Sanford. 1992. Age of old-growth on Vancouver Island. Contract report to British Columbia Ministry of Forests, MacMillan Bloedel Limited, Woodlands Services Division, Victoria, British Columbia, Canada.
- Boose, E. R., D. R. Foster, and F. Marcheterre Fluet. 1994. Hurricane impacts to tropical and temperate forest landscapes. *Ecological Monographs* **64**:369–400.
- British Columbia Ministry of Forests. 1991. Tofino Creek integrated resource management strategy. Draft Report, August 1991, Victoria, British Columbia, Canada.
- Bunnell, F. L. B., and L. L. Kremsater. 1990. Sustaining wildlife in managed forests. *Northwest Environmental Journal* **6**:243–269.
- Canadian Climate Program. 1991. Canadian climate normals, temperature and precipitation 1961–1990, British Columbia. Environment Canada, Atmospheric Environment Service, Ottawa, Ontario, Canada.
- Canham, C. D. 1989. Different responses to gaps among shade-tolerant tree species. *Ecology* **70**:548–550.
- Canham, C. D., J. S. Denslow, W. J. Platt, J. R. Runkle, T. A. Spies, and P. S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research* **20**:620–631.
- Carey, A. B., S. P. Horton, and B. L. Biswell. 1992. Northern spotted owls: influence of prey base and landscape character. *Ecological Monographs* **62**:223–250.
- Crome, F. H. J., and G. C. Richards. 1988. Bats and gaps: microchiropteran community structure in a Queensland rain forest. *Ecology* **69**:1960–1969.
- Daniels, L. D., P. Marshall, R. E., Carter, and K. Klinka. 1995. Age structure of western redcedar in the tree layer of old-growth stands near Vancouver, British Columbia. *Northwest Science, in press*.
- Entry, J. A., and W. H. Emmingham. 1995. Influence of forest age on nutrient availability and storage in coniferous soils of the Oregon Coast Range. *Canadian Journal of Forest Research* **25**:114–120.
- Esseen, P.-A. 1994. Tree mortality patterns after experimental fragmentation of an old growth conifer forest. *Biological Conservation* **68**:19–28.
- Franklin, J. F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? *Ecological Applications* **3**:202–205.
- Franklin, J. F., and T. A. Spies. 1991. Ecological definitions of old-growth forests. Pages 61–69 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, editors. *Wildlife and vegetation of unmanaged Douglas-fir forests*. United States Department of Agriculture Forest Service, General Technical Report **PNW-GTR-285**.
- Green, R. N., and K. Klinka. 1994. A field guide to site identification and interpretation for the Vancouver Forest Region. British Columbia Ministry of Forests, Victoria, British Columbia, Land Management Handbook **28**.
- Grier, C. C., and R. S. Logan. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. *Ecological Monographs* **47**:373–400.
- Grier, C. C., and S. W. Running. 1977. Leaf area of mature northwestern coniferous forests: relation to site water balance. *Ecology* **58**:893–899.
- Hansen, A. J., T. A. Spies, F. J. Swanson, and J. L. Ohmann. 1991. Conserving biodiversity in managed forests. *BioScience* **41**:382–392.
- Harmon, M. E., W. K. Ferrell, and J. F. Franklin. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. *Science* **247**:699–702.
- Harmon, M. E., J. F. Franklin, T. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Andrews, S. P. Cline, N. C. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, Jr., and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* **15**:133–382.
- Hartshorn, G. S. 1978. Tree falls and tropical forest dynamics. Pages 617–638 in P. B. Tomlinson and M. H. Zimmerman, editors. *Tropical trees as living systems*. Cambridge University Press, Cambridge, England.
- Hemstrom, M. A., and J. F. Franklin. 1981. Fire and other disturbances of the forests in Mount Rainier National Park. *Quaternary Research* **18**:32–51.
- Hitchcock, C. L., and A. Cronquist. 1973. *Flora of the Pacific Northwest*. University of Washington Press, Seattle, Washington, USA.
- Hunter, J. C., and V. T. Parker. 1993. The disturbance regime of an old-growth forest in coastal California. *Journal of Vegetation Science* **4**:19–24.
- Hunter, M. 1993. Natural fire regimes as spatial models for managing boreal forests. *Biological Conservation* **65**:115–120.
- Inselberg, A. E. 1993. A survey of the composition and structure of forest ecosystems in the Tofino Creek watershed on Vancouver Island. Report for the British Columbia Ministry of Forests, Victoria, British Columbia, Canada.
- Keenan, R. J., C. Messier, and J. P. Kimmins. 1994. Effects of clearcutting and soil mixing on soils properties and understorey biomass in western red cedar and western hemlock forests on northern Vancouver Island, Canada. *Forest Ecology and Management* **68**:251–261.
- Lang, G. E., and D. H. Knight. 1983. Tree growth, mortality, recruitment, and canopy gap formation during a 10-year period in a tropical moist forest. *Ecology* **64**:1075–1080.
- Lawton, R. O., and F. E. Putz. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. *Ecology* **69**:764–777.
- Lertzman, K. P. 1992. Patterns of gap-phase replacement in a subalpine, old-growth forest. *Ecology* **73**:657–669.
- . 1995. Forest dynamics, differential mortality and variable recruitment probabilities. *Journal of Vegetation Science* **6**:191–204.
- Lertzman, K. P., and C. J. Krebs. 1991. Gap-phase structure of a subalpine old-growth forest. *Canadian Journal of Forest Research* **21**:1730–1741.
- Luttmerding, H. A., D. A. Demarchi, E. C. Lea, D. V. Meidinger, and T. V. Vold, editors. 1990. *Describing ecosystems in the field*. Ministry of Environment Manual **11**. British Columbia Ministry of Environment in cooperation with British Columbia Ministry of Forests, Victoria, British Columbia, Canada.
- MacKinnon, A., D. Meidinger, and K. Klinka. 1992. Use of the biogeoclimatic ecosystem classification system in British Columbia. *Forestry Chronicle* **68**:100–120.
- Marcot, B. G., R. S. Holthausen, J. Teply, and W. D. Carrier. 1991. Old-growth inventories: status, definitions, and visions for the future. Pages 47–60 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, editors. *Wildlife and vegetation of unmanaged Douglas-fir forests*. United States



- Department of Agriculture Forest Service, General Technical Report **PNW-GTR-285**.
- Maser, C., and J. R. Sedell. 1994. From the forest to the sea. St. Lucie Press, Delray Beach, Florida, USA.
- Matson, P. A., and R. D. Boone. 1984. Natural disturbance and nitrogen mineralization: wave-form dieback of mountain hemlock in the Oregon Cascades. *Ecology* **65**:1511–1516.
- Meidinger, D. V., and J. Pojar. 1991. Ecosystems of British Columbia. Research Branch, British Columbia Ministry of Forests Special Report Series Number 6, Victoria, British Columbia, Canada.
- Mladenoff, D. J. 1987. Dynamics of nitrogen mineralization and nitrification in hemlock and hardwood treefall gaps. *Ecology* **68**:1171–1180.
- Moore, K. 1991. Coastal watersheds: an inventory of watersheds in the coastal temperate forests of British Columbia. Earthlife Canada Foundation and Ecotrust Conservation International, Vancouver, British Columbia, Canada.
- Muller, J. E. 1977. Geology of Vancouver Island. Open File Number 463. Geological Survey of Canada, Vancouver, British Columbia, Canada.
- Naka, K. 1982. Community dynamics of evergreen broadleaf forests in southwestern Japan. I. Wind damaged trees and canopy gaps in an evergreen oak forest. *Botanical Magazine, Tokyo* **95**:385–399.
- Nakamura, F., and F. J. Swanson. 1994. Distribution of coarse woody debris in a mountain stream, western Cascade Range, Oregon. *Canadian Journal of Forest Research* **24**: 2395–2403.
- Norusis, M. J. 1993. SPSS for Windows: base system user's guide. Release 6.0. SPSS, Chicago, Illinois, USA.
- Oliver, C. D. 1981. Forest development in North America following major disturbances. *Forest Ecology and Management* **3**:153–168.
- Pastor, J., and M. Broschart. 1990. The spatial pattern of a northern conifer-hardwood landscape. *Landscape Ecology* **4**:55–68.
- Pearson, A. F. 1995. Disturbance regimes in Clayoquot Valley: a first approximation. Progress report to the British Columbia Forest Service, Victoria, British Columbia, Canada.
- Pojar, J., K. Linka, and D. V. Meidinger. 1987. Biogeoclimatic ecosystem classification in British Columbia. *Forest Ecology and Management* **22**:119–154.
- Prescott, C. E., M. A. McDonald, and G. F. Weetman. 1993. Differences in availability of N and P in the forest floors of adjacent stands of western red cedar–western hemlock and western hemlock–amabilis fir on northern Vancouver Island. *Canada Journal of Forest Research* **23**:605–610.
- Ralph, C. J., P. W. C. Paton, and C. A. Taylor. 1991. Habitat association patterns of breeding birds and small mammals in Douglas-fir/hardwood stands in northwestern California and southwestern Oregon. Pages 379–394 in L. F. Ruggerio, K. B. Aubry, A. B. Carey, and M. H. Huff, editors. *Wildlife and vegetation of unmanaged Douglas-fir forests*. United States Department of Agriculture Forest Service, General Technical Report **PNW-GTR-285**.
- Rebertus, A. J., and T. T. Veblen. 1993. Structure and tree-fall gap dynamics of old-growth *Nothofagus* forests in Tierra del Fuego, Argentina. *Journal of Vegetation Science* **4**:641–654.
- Romme, W. H., and D. H. Knight. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. *Ecology* **62**:319–326.
- Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* **62**:1041–1051.
- Schaetzl, R. J., S. F. Burns, D. L. Johnson, and T. W. Small. 1989. Tree uprooting: review of impacts on forest ecology. *Vegetatio* **79**:165–176.
- Scientific Panel for Sustainable Forest Practices in Clayoquot Sound. 1994. Review of current forest practice standards in Clayoquot Sound. Progress Report 2. Cortex Consultants, Halfmoon Bay, British Columbia, Canada.
- . 1995. Sustainable ecosystem management in Clayoquot Sound: planning and practices. Scientific Panel for Sustainable Forest Practices in Clayoquot Sound, Victoria, British Columbia, Canada.
- Spies, T. A. 1991. Plant species diversity and occurrence in young, mature, and old-growth Douglas-fir stands in Western Oregon and Washington. Pages 111–121 in L. F. Ruggerio, K. B. Aubry, A. B. Carey, and M. H. Huff, editors. *Wildlife and vegetation of unmanaged Douglas-fir forests*. United States Department of Agriculture Forest Service, General Technical Report **PNW-GTR-285**.
- Spies, T. A., and J. F. Franklin. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. Pages 91–109 in L. F. Ruggerio, K. B. Aubry, A. B. Carey, and M. H. Huff, editors. *Wildlife and vegetation of unmanaged Douglas-fir forests*. United States Department of Agriculture Forest Service, General Technical Report **PNW-GTR-285**.
- Spies, T. A., J. F. Franklin, and M. Klopsch. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Canadian Journal of Forest Research* **20**:649–658.
- Spies, T. A., J. F. Franklin, and T. B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology* **69**:1689–1702.
- Stathers, R. J., T. P. Rollerson, and S. J. Mitchell. 1994. Windthrow handbook for British Columbia. British Columbia Ministry of Forests Research Branch, Victoria, British Columbia, Canada.
- Stewart, G. H. 1986. Forest development in canopy openings in old-growth *Pseudotsuga* forests of the western Cascade Range, Oregon. *Canadian Journal of Forest Research* **16**: 558–568.
- . 1988. The influence of canopy cover on understory development in forests of the western Cascade Range, Oregon, USA. *Vegetatio* **67**:534–544.
- Stolz, R., and D. Scheidemann. 1992. Studies of the age structure in virgin forests on Vancouver Island, British Columbia, Canada. Degree dissertation. Technical College Weihenstephan, Germany.
- Swanson, F. J., and J. F. Franklin. 1992. New forestry principles from ecosystem analysis of Pacific Northwest forests. *Ecological Applications* **2**:262–274.
- Tappeiner, J. C., II, and P. B. Alaback. 1989. Early establishment and vegetative growth of understory species in the western hemlock-Sitka spruce forests of southeast Alaska. *Canadian Journal of Botany* **67**:318–326.
- Thomas, J. W., E. D. Foresman, J. B. Lint, E. C. Meslow, B. R. Noon, and J. Verner. 1990. A conservation strategy for the northern spotted owl. Interagency Scientific Committee to Address the Conservation of the Northern Spotted Owl, Portland, Oregon, USA.
- Turner, M. J., and W. H. Romme. 1994. Landscape dynamics in crown-fire ecosystems. *Landscape Ecology* **9**:59–77.
- Van Cleve, K., and L. A. Viereck. 1981. Forest succession in relation to nutrient cycling in the Boreal forest of Alaska. Pages 185–211 in D. C. West, H. H. Shugart, and D. B. Botkin, editors. *Forest succession: concepts and application*. Springer Verlag, New York, New York, USA.
- Veblen, T. T. 1985. Forest development in tree-fall gaps in the temperate rain forests of Chile. *National Geographic Research* **1**:162–183.
- Veblen, T. T., and D. C. Lorenz. 1987. Post-fire stand development of *Austrocedrus-Nothofagus* forests in northern Patagonia. *Vegetatio* **71**:113–126.

Welsh, H. H., Jr., and A. J. Lind. 1991. The structure of the herpetofaunal assemblage in the Douglas-fir/hardwood forests of northwestern California and southwestern Oregon. Pages 395–414 in L. F. Ruggerio, K. B. Aubry, A. B. Carey, and M. H. Huff, editors. *Wildlife and vegetation of unmanaged Douglas-fir forests*. United States Department of Agriculture Forest Service, General Technical Report PNW-GTR-285.

Wheeler, L., and R. Fonda. 1995. A wetland as a forest gap: gradient relationships and canopy return intervals. *Bulletin of the Ecological Society of America* 76: 282.

Wilkinson, L., M. Hill, S. Miceli, G. Birkenbeuel, and E. Vang. 1992. *SYSTAT for Windows: graphics*. Version 5 edition. SYSTAT, Evanston, Illinois, USA.

## ERRATUM

In the article by William H. Schlesinger, Jane A. Raikes, Anne E. Hartley, and Anne F. Cross, entitled, "On the spatial pattern of soil nutrients in desert ecosystems," published in *Ecology* 77(2):364–374, Fig. 3 was printed incorrectly. Due to an unfortunate error in the production process, the internal label for the lower graph was labeled "Grassland" where it should have read "Shrubland." The figure with its legend is reprinted here in its correct form. We apologize to the authors and to our readers.

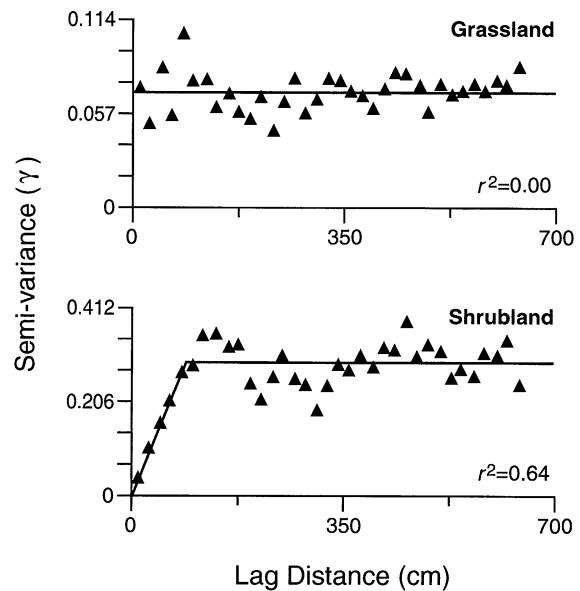


FIG. 3. Spherical model semi-variograms for the distribution of soil phosphate in grassland and shrubland soils at the Sevilleta National Wildlife Refuge, New Mexico.