# Canopy gaps in Douglas-fir forests of the Cascade Mountains

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

Types and rates of mortality were measured and canopy gap formation rates were estimated from 5- to 15-year records of mortality in 34 permanent plots in mature (100- to 150-year-old) and old-growth (>200-year-old) Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)/western hemlock (*Tsuga canadensis* (Raf.) Sarg.) forests in western Oregon and Washington. Gap surveys were conducted in a mature and an old-growth stand, and characteristics of 40 gaps and regeneration were measured. Most canopy trees died without disrupting the forest in both mature (87.6%) and old-growth stands (73.3%). The amount of forest area per year representing new gaps was 0.7% in mature stands and 0.2% in old-growth stands. The gap survey found a higher proportion of gaps in the mature stand than in the old-growth stand. Most regeneration (>1 m tall) in gaps was western hemlock; Douglas-fir regeneration did not occur. The ratio of seedling density in gaps to density under canopies was about 3 for the mature stand and about 9 for the old-growth stand. Seedling density was correlated with measures of gap age but not gap size. The study suggests that gap disturbances and vegetative responses are important processes in the dynamics of these forests. However, gap formation rates and vegetative responses appear to be slow relative to other forest types. In addition to gap size, canopy structure and disturbance severity are important determinants of gap response.

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

Les causes et les taux de mortalité furent mesurés et le taux de formation des trouées dans le couvert forestier fut estimé à partir de données de mortalité datant de 5 à 10 ans et provenant de 34 placettes permanentes établies dans une forêt mature (100-150 ans) et une vieille forêt (>200 ans) de Sapin de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco)/Pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) de l'ouest des états de Washington et de l'Orégon. Les trouées furent inventoriées dans une forêt mature et une vieille forêt et les caractéristiques de 40 trouées et de la régénération furent mesurées. La plupart des arbres dominants sont morts sans perturber la forêt mature (87,6%) ou vieille (73,3%). Les nouvelles trouées représentaient 0,7% de la superficie par année dans les peuplements matures et 0,2% dans les vieux peuplements. L'inventaire a révélé une plus forte proportion de trouées dans la forêt mature que dans la vieille forêt. Dans les trouées, la régénération (>1 m de haut) était surtout composée de Pruche de l'Ouest; il n'y avait pas de régénération de Sapin de Douglas. La densité des semis dans les trouées était environ 3 fois plus forte que sous couvert dans la forêt mature et 9 fois plus forte dans la vieille forêt. La densité des semis était corrélée avec l'âge des trouées mais pas avec leur dimension. L'étude suggère que les perturbations à l'origine des trouées et les réactions de la végétation sont des processus importants dans la dynamique de ces forêts. Cependant, le taux de formation des trouées et les réactions de la végétation semblent lents comparativement à d'autres types de forêts. Outre la dimension de la trouée, la structure du couvert et la sévérité de la perturbation sont déterminantes dans l'évolution d'une trouée.

[Traduit par la revue]

## Introduction

The death of canopy trees is a major determinant of the structure and dynamics of forest ecosystems. The type, size, and frequency of canopy disturbance events can control species composition, successional change, nutrient cycles, and habitat structure. Although large disturbance events are most dramatic, smaller events may be more frequent, affecting a larger area over time. The role and importance of small canopy gap disturbances have been documented in numerous studies in deciduous forests in eastern North American and tropical forests (Runkle 1982; Brokaw 1985a, 1985b; Uhl et al. 1988). The characteristics and importance of small canopy gaps in coniferous forests have received far less attention, where research on forest dynamics has typically focused on large patches created by fire.

Coniferous forests of the Pacific Northwest offer many opportunities to understand the role and dynamics of canopy gaps in coniferous ecosystems. Fires occur at relatively long intervals, allowing canopy gap dynamics to operate for 1 to

many centuries between intense fire; and extensive areas of varied, unmanaged old and young forests can be found. As in other coniferous forests, research has concentrated on large gaps created by wildfire or clear-cutting (Dyrness 1973; Agee and Huff 1981; Hemstrom and Franklin 1982; Halpern 1987), whereas relatively little information is available on the ecology of small canopy gaps (Means 1982; Stewart 1986; Spies and Franklin 1989). Large fires are clearly an important regulator of patch patterns and dynamics in these landscapes; however, the importance of smaller canopy disturbances at stand and landscape scales is much less clear. Information about the sizes, rates, and types of smaller canopy disturbances in these forests is needed to assess the relative importance of fine- and coarse-scale disturbances in these ecosystems. Our objectives are to characterize the following: (*i*) rates and types of fine-scale canopy tree mortality and gap formation; (*ii*) area, size, and age of gaps; and (*iii*) density and composition of regeneration with respect to gaps and canopies. Our scope is mature (80- to

200-year-old) and old-growth ( >200-year-old) Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)/western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forests in western Oregon and Washington.

## Methods

### Study sites

Studies were conducted in Douglas-fir dominated forests in two areas in the Cascade Range: the H.J. Andrews Experimental Forest, and vicinity, in western Oregon, and Mount Rainier National Park in western Washington. Both areas are characterized by steep mountainous topography and well-drained soils derived from aeolian volcanic materials, colluvium, and residual materials from Tertiary basalts and andesites. The climate is mild and wet in winter and relatively warm and dry in summer. Annual precipitation ranges from 2000 mm at H. J. Andrews to almost 3000 mm at Mount Rainier.

We sampled Douglas-fir dominated stands primarily in the area where western hemlock is the dominant climax species and in the lower portion of the Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) zone (Franklin and Dyrness 1973). Under natural conditions, Douglas-fir is a seral dominant on these sites and typically develops young, nearly pure, even-aged stands after severe fires. Stands over 200 years old generally exhibit old-growth characteristics (Franklin et al. 1981; Spies and Franklin 1988) such as codominance of western hemlock in the overstory, diverse vertical foliage distribution, and large accumulations of coarse woody debris (Spies et al. 1988).

At H.J. Andrews Experimental Forest two stands were surveyed intensively for gaps and gap characteristics. The Blue River Ridge stand is a 10-ha mature stand of Douglas-fir that originated following a fire around 1845. The Roswell Ridge stand is a 40-ha stand of 400- to 500-year-old Douglas-fir and younger western hemlock. Both stands are bordered by intact forest and occur in upper topographic positions with elevations of about 1000 m, slopes of 30%, and south-easterly aspects. Portions of the Roswell Ridge old-growth stand may have experienced a surface fire 140 to 150 years ago; many hemlocks in this area postdate this time, some old-growth Douglas-firs have charred bark, and relatively even-aged patches of 140-year-old Douglas-fir occur on the margins of this stand. Low intensity fires have burned in many old-growth stands in H. J. Andrews Experimental Forest and vicinity before 1850 (Morrison and Swanson 1990; Teensma 1987).

### General approach

Two different approaches were used. The first consisted of estimating gap dynamics from a long-term record of permanent plots established in the Oregon and Washington Cascade Range. The second approach consisted of a gap survey and measurements of gap characteristics in two stands in the Oregon Cascades.

### Approach 1: tree mortality and gap formation

Type and rates of canopy tree mortality were determined from a set of long-term reference plots, 28 from the vicinity of the H. J. Andrews Experimental Forest and 6 from Mount Rainier National Park. These plots range in size from 0.25 to 6.88 ha, with most plots 1.0 ha in size. Within each plot all trees were tagged and mapped. Tree locations and tree species and sizes were entered into a geographic infor-

mation system. All plots were located within much larger stands, so edge effects were nonexistent or minimal. The length of record is 5 to 15 years, with most stands having an 8- to 10-year record of annual mortality for all trees >5 cm dbh. Rates of gap formation were determined from 17 of the reference stands, which were at least 1 ha in size. A 5 m wide edge around the margin of the plot was deleted from the analyses to restrict the trees to those whose crown fell mostly within the plot boundaries. Rates of mortality were computed based on the number of individuals present at the beginning of each measurement period. Mortality rates were adjusted for variable population sizes during the periods under consideration. Mortality rates were computed separately for understory trees (5–25 cm dbh) and overstory trees ( >25 cm dbh). Diameters were used to separate the trees into canopy classes because information on the relative positions of the crowns was not available and because standard crown classes are not very applicable to uneven-aged or mixed-species stands. Trees less than 25 cm dbh were well below the dominant trees in both mature and old-growth stands. Trees larger than 25 cm dbh included both the tallest trees in the stand and trees beneath the main canopy. Within each age-class and size class, the percentages of trees that died standing, died from breakage, and died from uprooting were calculated for all trees together and for each species separately.

Canopy gap formation rates were estimated by computing the area of canopy opened when a tree died, summing all mortality for the measurement period, and then averaging over the entire measurement period. No overlap among tree crowns within a crown class (dominant, codominant, intermediate) was allowed. If the area of the crown of a dead tree overlapped a live tree crown in another canopy class, the area of overlap was subtracted from the gap area created by the death of the tree. Spaces between tree crowns could not be taken into account; however, these are not used in estimating annual rates of new gap creation based on the area of canopy that opens when tree crowns die.

Projected crown areas (assuming circular crowns) for trees that died were estimated from equations for Douglas-fir, western hemlock, and western red cedar (*Thuja plicata* Donn) that predicted crown diameter (m) as function of dbh (cm). The equations were

Douglas-fir

[1]    ln(crown diameter) = 0.051 40 + 0.476 74 ln(dbh)
$$R^2 = 0.23, \text{ SEE} = 0.29, p < 0.0001, n = 84$$

western hemlock

[2]    ln(crown diameter) = 0.052 873 + 0.591 045 ln(dbh)
$$R^2 = 0.53, \text{ SEE} = 0.31, p < 0.0001, n = 114$$

western red cedar

[3]    ln(crown diameter) = 0.565 69 + 0.371 83 ln(dbh)
$$R^2 + 0.50, \text{ SEE} = 0.35, p < 0.0001, n = 59$$

where SEE is the standard error of the estimate.

The equations are based on unpublished data collected by the senior author (T.A. Spies) and Art Mckee and on Kuiper (1988) for sample trees located in mature and old-growth stands in the two study areas and in other areas in the Cascade range. Tree crowns were measured with a tape along two to four radii extending from the base of the tree to the edge of the canopy at that point. The low $R^2$ for the Douglas-fir crown equation reflects high variability, par-

TABLE 1. Annual percent mortality rate by species and age-class for understory trees (5–25 cm dbh) and overstory trees (>25 cm dbh)

| | Mature | | Old growth | |
| --- | --- | --- | --- | --- |
| | Understory | Overstory | Understory | Overstory |
| *Pseudotsuga menziesii* | 2.54 | 0.78 | 0.69 | 0.28 |
| | (2 051) | (16 328) | (5 936) | (12 007) |
| *Tsuga heterophylla* | 0.28 | 0.23 | 0.42 | 0.38 |
| | (7 248) | (3 883) | (20 037) | (16 382) |
| *Abies amabilis* | 0.25 | 0.49 | 0.50 | 0.62 |
| | (4 384) | (1 442) | (24 805) | (9 742) |
| *Abies procera* | 0.95 | 1.52 | 0.43 | 1.82 |
| | (2 419) | (8 404) | (233) | (1 045) |
| *Thuja plicata* | 0.67 | 0.21 | 0.27 | 0.14 |
| | (745) | (954) | (1 856) | (4 144) |
| All species | 0.72 | 0.88 | 0.50 | 0.41 |
| | (21 297) | (35 093) | (62 329) | (50 370) |

NOTE: Values in parentheses are sample sizes, in tree-years.

ticulary in older and larger trees, whose centuries-old crowns have suffered varying degrees of damage and branch death. Crown equations were not available for Pacific silver fir, a shade-tolerant species, and noble fir (*Abies procera*), a shade-intolerant species, so the equations for western hemlock and Douglas-fir were used as substitutes.

*Approach 2: gap survey and characterization*

Characteristics of gaps and regeneration were determined from transect sampling in the two Douglas-fir/western hemlock stands at H. J. Andrews Experimental Forest. In each stand three line transects, each at least 200 m long were established from random starting points. The three transects were oriented parallel to, perpendicular to, and oblique to the slope contours. Sampling continued until the projected areas of 20 gaps were intersected. All canopy openings at least 5 m² in size were included in the sample, whether or not there was evidence of formation by canopy tree death. Gaps in these forests can be quite irregular in shape, forming complex gaps in which relatively large openings are separated by crowns that are close together but do not touch. The projected edges of the crowns of trees bordering the gaps defined the gap margin. If crowns of the surrounding trees were less than one-half crown diameter, then the boundary was defined by the crowns of those trees. Where the spaces between crowns were greater than one-half tree crown, gap margins were extended until surrounding tree crowns were less than one-half crown apart. The tree size that was considered to be part of the canopy and no longer part of the gap vegetation was somewhat arbitrarily set at 25 cm dbh. This represents a western hemlock or Douglas-fir 15 to 25 m tall within stands whose canopies are 40 to 70 m tall. The diameter limit is the same as that used by Runkle (1982) and is similar to height limits of 15 to 20 m used in other studies (Veblen 1985; Nakashizuka 1984) in forests with shorter canopies.

For each gap intersected, information was collected on the following: size; estimated time since last disturbance; time since earliest observable disturbance; number and species of saplings >1 m tall; number, size and species of gap maker. Area was computed using the methods suggested by Runkle (1985b). Canopy gaps were defined by the projected outline of the tree crowns. Expanded gaps (Runkle 1982), defined by the tree bases surrounding the canopy gap,

TABLE 2. Percent mortality by type of death, species, and age-class for understory trees (5–25 cm dbh) and overstory trees (>25 cm dbh)

| Type of death | Mature | | Old growth | |
| --- | --- | --- | --- | --- |
| | Understory | Overstory | Understory | Overstory |
| **All species** | | | | |
| *n* | 143 | 290 | 312 | 195 |
| Standing | 78.3 | 73.8 | 54.5 | 55.4 |
| Breakage | 4.2 | 13.8 | 12.2 | 17.9 |
| Uproot | 17.5 | 12.4 | 33.3 | 26.7 |
| *Pseudotsuga menziesii* | | | | |
| *n* | 50 | 123 | 42 | 33 |
| Standing | 84.0 | 67.5 | 52.4 | 30.3 |
| Breakage | 4.0 | 14.6 | 19.0 | 30.3 |
| Uproot | 12.0 | 17.9 | 28.6 | 39.4 |
| *Tsuga heterophylla* | | | | |
| *n* | 20 | 9 | 86 | 59 |
| Standing | 80.0 | 66.7 | 54.7 | 45.8 |
| Breakage | 5.0 | 33.3 | 12.8 | 18.6 |
| Uproot | 15.0 | 11.1 | 32.6 | 35.6 |
| *Thuja plicata* | | | | |
| *n* | 5 | 2 | 5 | 6 |
| Standing | 20.0 | 0.0 | 40.0 | 33.3 |
| Breakage | 0.0 | 0.0 | 20.0 | 0.0 |
| Uproot | 80.0 | 100.0 | 40.0 | 66.7 |

were not measured in the field but estimated based on average crown diameters for the stand. The projected area of the gap was assumed to be roughly elliptical, and the length and width were measured with a tape after locating crown margins with a vertical sighting scope. For very irregular shaped gaps, eight or more radii were measured from gap center to gap margin, and the area was computed by summing the areas of the resulting triangles.

Times since the most recent and earliest observable disturbances were estimated from release ages determined from increment cores of saplings of adjacent canopy trees and from decay condition of gap makers (Cline et al. 1980). The species of the tallest and most vigorous tree saplings that

TABLE 3. Weighted mean annual rate of canopy gap creation for mature and old-growth stands in western Oregon

| Stand | Canopy dominants | Years of record | % area per year in new gaps |
|---|---|---|---|
| **Mature stands** | | | |
| HJA 13 | *Abies procera* | 9 | 0.7 |
| HJA 20 | *P. menziesii* | 10 | 0.1 |
| HJA 24 | *P. menziesii* | 9 | 1.6 |
| MR 13 | *P. menziesii/ Tsuga heterophylla* | 7 | 0.2 |
| Mature weighted mean | | | 0.7 |
| **Old-growth stands** | | | |
| HJA 1 | *P. menziesii/ Pinus lambertiana* | 10 | 0.04 |
| HJA 2 | *P. menziesii/ Tsuga heterophylla* | 9 | 0.2 |
| HJA 3 | *P. menziesii/ Thuja plicata – Tsuga heterophylla* | 9 | 0.2 |
| HJA 21 | *P. menziesii/ Tsuga heterophylla* | 10 | 0.3 |
| HJA 22 | *Abies procera/ P. menziesii* | 9 | 0.5 |
| HJA 23 | *Tsuga heterophylla/ P. menziesii* | 10 | 0.04 |
| HJA 26 | *P. menziesii/ Tsuga heterophylla* | 10 | 0.2 |
| HJA 27 | *P. menziesii/ Tsuga heterophylla* | 8 | 0.5 |
| HJA 28 | *P. menziesii/ Tsuga heterophylla* | 9 | 0.2 |
| HJA 31 | *P. menziesii/ Tsuga heterophylla* | 8 | 0.2 |
| MR 1 | *Tsuga heterophylla/ P. menziesii* | 10 | 0.2 |
| MR 4 | *Tsuga heterophylla/ Abies amabilis* | 7 | 0.8 |
| MR 8 | *Tsuga heterophylla/ P. menziesii* | 9 | 0.07 |
| Old-growth weighted mean | | | 0.2 |
| Overall weighted mean | | | 0.3 |

NOTE: Means are weighted by years of record. HJA, H.J. Andrews Experimental Forest; MR, Mount Rainier National Park.

appeared to have the best chance of filling the gap was recorded. Mean annual gap formation rates were estimated for each survey stand by summing the transect lengths of gaps in which gap events occurred within the last 25 years and dividing by the total length of the transect multiplied by 25 years.

In addition to measurements under gaps, 10 circular 50-m$^2$ plots were established under canopies in each stand. Information was collected on the dbh and species of all overstory trees and height and species of all understory trees >1 m tall.

## Results

### Permanent plots

#### Rates of mortality

Annual mortality for all overstory and understory trees was higher in mature stands than in old-growth stands (Table 1). Douglas-fir, a shade-intolerant species, had higher annual mortality in mature stands than in old-growth stands for both the upper canopy trees (>25 cm dbh) and the lower canopy and understory trees (5–25 cm dbh). The pattern for the shade-tolerant western hemlock and Pacific silver fir was reversed: higher in the old-growth stand than in mature stands. Western red cedar, which is also a shade-tolerant species, followed the pattern of Douglas-fir, although the sample size is small. The high mortality rates for noble fir are due to a disease epidemic.

### Types of mortality

Most canopy trees died without disrupting the forest floor in both mature (87.6%) and old-growth stands (73.3%) (Table 2). Uprooting was more than twice as common in old-growth as in mature stands. Douglas-fir and western hemlock both follow this general pattern, although Douglas-fir appears to die from bole breakage more frequently than does western hemlock. The small number of western red cedar died primarily from uprooting.
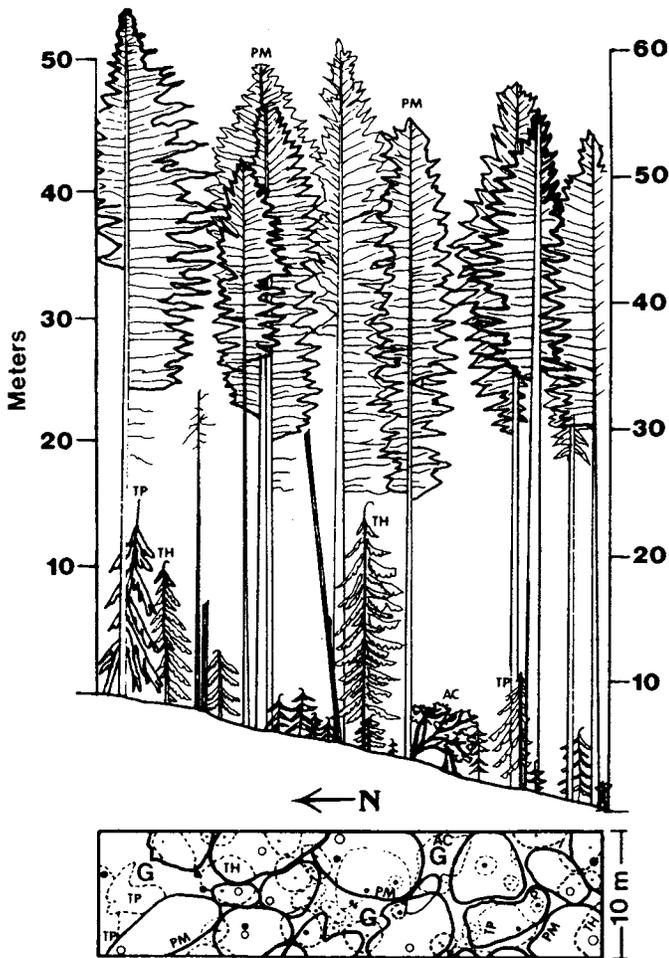
FIG. 1. Vertical and horizontal profile through a 140-year-old Douglas-fir stand. PM, *Pseudotsuga menziesii*; TH, *Tsuga heterophylla*; TP, *Thuja plicata*; AC, *Acer circinatum*; G, canopy gap.



FIG. 2. Vertical and horizontal profile through a 450-year-old Douglas-fir/western hemlock stand. Abbreviations are the same as in Fig. 1.

Understory trees had roughly the same proportion of uprooting as did canopy trees, but died less frequently from breakage (Table 2). Uprooting also was more frequent in old-growth than in mature forests. Uprooting in the understory was most often the result of falling overstory trees and masses of snow falling from the overstory.

*Gap formation rates*

The overall mean annual percent of area in new canopy gaps was 0.3% (Table 3). The mean for mature stands was higher than for old-growth stands, and individual stands ranged from 0.1 to 1.6%. Most old-growth stands had gap creation rates below 0.5%. Gap creation rates were lower than mortality rates for large canopy trees (>25 cm dbh), although the two estimates were not strictly comparable, since the gap formation rates were based on a smaller sample of plots.

*Gap survey*

*Stand and gap profiles*

The stand profile and canopy map for a small portion of the Blue River Ridge stand (Fig. 1) show that tree heights ranged from 45 to 55 m and crowns were 20 to 30 m long and often asymmetrical. Horizontal overlap among overstory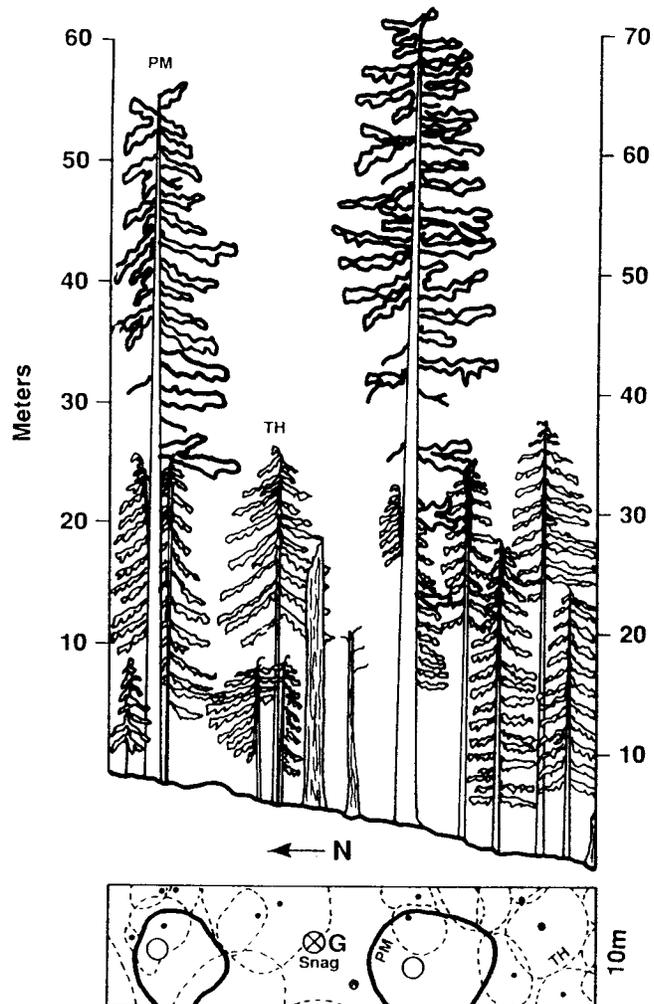 crowns was small. The profile is typical of mature stands of Douglas-fir that have a single canopy layer with or without a developing understory of western hemlock.

Three small canopy gaps are evident in the profile (Fig. 1). At the center of the profile, a gap developed about 10 years ago from the death and subsequent breakage of two adjacent Douglas-firs. A second gap, on the north end of the transect, also developed about this time when three adjacent Douglas-firs died within in the profile area along with other Douglas-firs outside the profile. These first two gaps may have been caused by laminated root rot (*Phellinus weirii*), which is relatively common in Douglas-fir forests (Gedney 1981). A third small gap, just southeast of the center gap, had no obvious gap maker and is occupied by a tall clump of vine maple (*Acer circinatum* Pursh), an understory shrub or small tree. It may have been a gap since the origin of the stand.

In the profile of a small portion of the Roswell Ridge stand (Fig. 2), tree heights ranged from 10 to 70 m, with western hemlock occurring below 35 m in height. Crown lengths in the Douglas-fir were over 30 m. The profile is typical of old-growth Douglas-fir/western hemlock stands in the region, which have an emergent layer of Douglas-fir and dense lower layers of western hemlock. A small gap at
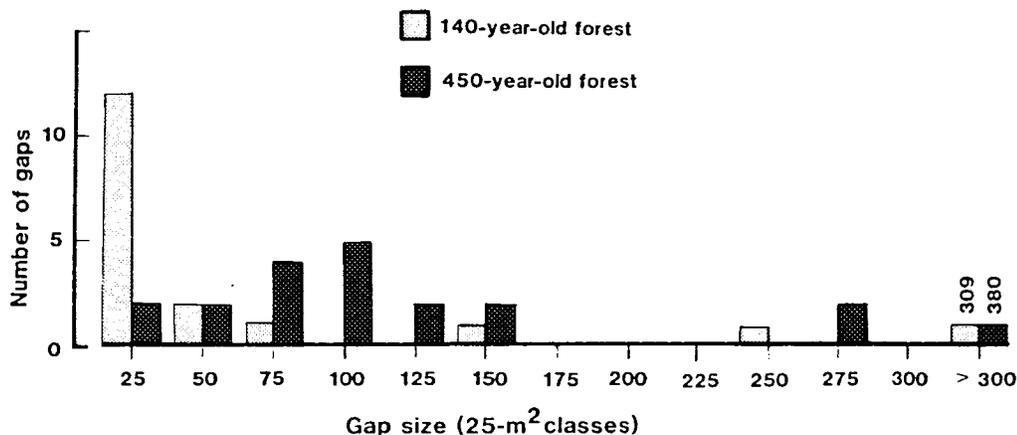
FIG. 3. Gap size distribution in two Douglas-fir stands on the H. J. Andrews Experimental Forest. Distributions were significantly different ($p < 0.01$) in a Kolmogorov–Smirnov test using the square roots of the gap areas for an unbiased size distribution.
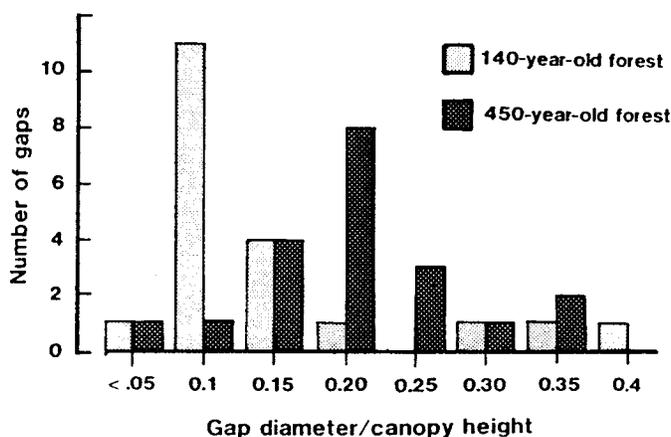


FIG. 4. Distribution of the ratio of gap diameter to canopy height in two Douglas-fir stands.

the center of the transect was created about 8 to 10 years ago when a large Douglas-fir snapped off at about 20 m height and apparently fell on a smaller hemlock, breaking its crown. Tree regeneration consists entirely of western hemlock seedlings less than 0.5 m tall.

*Area and size distribution*

The percentages of area occupied by canopy gaps was 18.2% in the mature stand and 13.1% in the old-growth stand. The two stands differed to a larger degree in the percentage of area in expanded gap, with the mature stand having 41.7% in expanded gap and the old-growth stand having 25.5% in expanded gap.

Gap size distributions were significantly different in the two stands (Fig. 3). The median gap sizes in the old-growth and mature stands were 85 and 19 m². The gap size distribution in the old-growth stand was approximately log normal, whereas in the mature stand it was approximately a negative log with many gaps less than 50 m². The differences in gap size distributions help explain why mature stands have a proportionally greater area in expanded gaps than in the old-growth stand. Because the edge to area ratio is high for small gaps, stands with numerous small canopy gaps will have a larger percentage of the area in expanded gaps than stands in which the same total gap area is distributed in larger gaps.

Gap diameter to canopy height ratios varied between 0.05 and 0.4 (Fig. 4). The old-growth stand had higher ratios than the mature stand, despite the fact that the canopies were shorter in the mature stand. However, as Fig. 2 indicates, the irregularity in canopy heights in the old-growth stand results in considerable within-stand variability in gap diameter to height ratios.

*Number of gap makers and age of gaps*

Most gaps in the old-growth stand were formed by the death of two or more trees (Fig. 5). In the mature stand, most gaps were formed by one tree, and in many gaps no evidence of origin from tree mortality could be found. The single-tree nature of the gaps in the mature stand explains their small size. Gaps without obvious gap makers may have been old gaps in which the small canopy tree decomposed, leaving no evidence, or may have been gaps resulting from initially sparse stand establishment 140 years ago. Branch falls or crown breakage are not a likely origin for most of these gaps.

Many gaps were the consequence of multiple events that occurred at least 25 years ago (Fig. 6). In the old-growth stand most gaps began at least 50 years ago, with the most recent events at least 10 years ago; no gaps were encountered that had canopy trees that died more recently than 10 years ago. In the mature stand, gaps were younger and mortality events were apparently less separated in time. Gaps in the mature stand apparently did not reach the age of those in the old-growth stand.

*Gap formation rates*

Gap formation rates for gap events in the last 25 years were 0.2 and 0.3% in the old-growth and the mature stand. In the case of the old-growth stand this rate is identical with the rate independently calculated for 9 years of mortality record from plot HJA 28 (Table 3), which is located within a portion of the Roswell Ridge old-growth stand. No plot data were available for the Blue River Ridge mature stand, although the value lies within the range of the estimates from the four mature reference stands (Table 3).

*Density and composition of regeneration*

Seedlings were more common in gaps than under canopies in both stands (Table 4). Regeneration in the old-growth stand was about nine times more common under gaps than
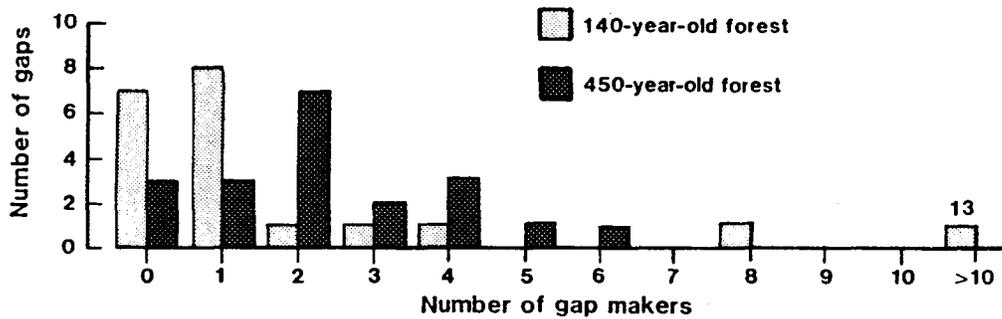
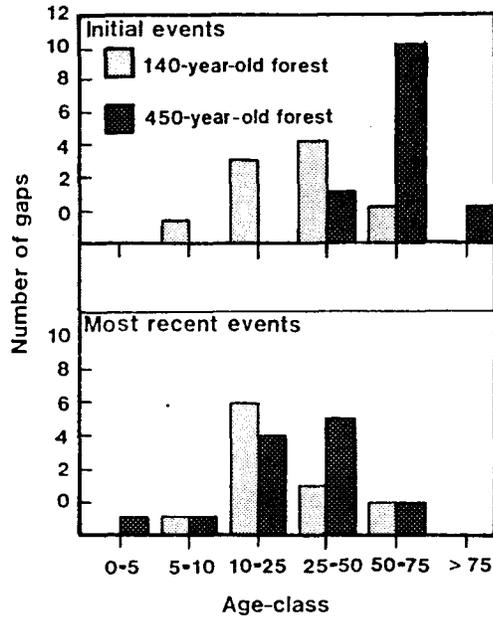FIG. 5. Distribution of number of gap makers in two Douglas-fir stands.



FIG. 6. Distribution of age-classes of initial gap-forming events and most recent gap-forming events in two Douglas-fir stands.

TABLE 4. Mean of number of saplings per 100 m$^2$ (SE in parentheses) of species in gaps and under canopies in mature and old-growth stands

| | Mature | | Old-growth | |
|---|---|---|---|---|
| | Gap ($n=20$) | Canopy ($n=10$) | Gap ($n=20$) | Canopy ($n=10$) |
| Tsuga heterophylla | 16 (3) | 6 (2) | 8 (2) | 1 (<1) |
| Abies amabilis | 0 | 0 | 1 (1) | 0 |
| Abies grandis | <1 (<1) | 0 | 0 | 0 |
| Thuja plicata | 2 (1) | 0 | 0 | 0 |
| Taxus brevifolia | <1 (<1) | 0 | <1 (<1) | 0 |

under canopies. In the mature stand seedlings were about three times more common in gaps than under canopies.

Total density of tree regeneration in gaps in both stands was better correlated with measures of gap age, than gap size. In the mature stand, stepwise regression of regeneration density (RDEN) on time since earliest recorded disturbance (ERD), time since most recent disturbance (RD), and the log of the square root of the area (LSRA), yielded the model

$$RDEN = 0.155 + 0.0093ERD - 0.1196LSRA$$

$$p < 0.015$$

The partial $R^2$ of ERD in the model was 0.37 ($p < 0.02$) and the partial $R^2$ of LSRA was 0.14 ($p < 0.09$). It is interesting to note that RDEN is negatively, though weakly, correlated with LSRA.

In the old-growth stand, only RD entered into the model selected by stepwise regression

$$RDEN = 0.115 - 0.0019RD, \qquad p < 0.03$$

In contrast with the model for the mature stand, the age variable (RD) was negatively correlated with RDEN ($R^2 = 0.30$). The fact that ERD was selected in the regression for the mature stand and RD in the regression for the

old-growth stand may be related to the time it takes regeneration to establish and reach the minimum measurable size (1 m tall). Events in the mature stand, many of which were less than 15 years old, may have been too recent to allow establishment and growth to 1 m. Most initial events, in the old-growth stand, were over 50 years ago, which may be sufficient to allow some of the regeneration to enter the overstory class (>25 cm dbh). Consequently, our measure of regeneration response is more closely correlated with gap events 15 to 50 years ago than with either earlier or later events.

In both stands, over 85% of the tree seedlings in the canopy gaps were western hemlock (Table 4). Other species included western red cedar and Pacific silver fir. No Douglas-fir regeneration had attained 1 m height. Western hemlock was the only species encountered in plots under canopies in both stands. Of the seedlings judged to have the best chance of filling the gaps, 88.4 and 89.4% were western hemlock in the mature and old-growth stands, respectively. These percentages exceed only slightly the overall percentages of western hemlock in the regeneration.

## Discussion

### Gap dynamics

Estimates of canopy gap formation rates in both the mature and old-growth stands were lower than the annual mortality rates of large overstory trees. This occurs because the two rates are measures of different properties of stand dynamics and are calculated in different ways. If gap for-

mation rates were based on total crown area rather than total stand area, and if no overlap occurred among crowns, then canopy tree mortality rates would be more similar, if not identical, to annual canopy tree mortality rates. However, since a stand is composed of both crowns and gaps, and tree crowns overlap, when a tree dies the proportion of the total stand area opened to the sky will be less than the proportion of the total number of canopy trees that died. The amount of overlap among tree crowns varies with species and stand conditions. The crown maps indicated that within a canopy stratum, tree crowns are distributed in a way that minimizes overlap. For example, tree crown overlap in crown projection maps from two 0.13-ha plots in a mature and an old-growth stand was 15 and 30%, respectively, with much of the overlap in the old-growth stand resulting from overlap of dominant Douglas-fir and subdominant western hemlock (unpublished data collected by the senior author).

Gap dynamics in Douglas-fir/western hemlock forests appear to operate more slowly than in other forest ecosystems. The rates of gap formation in old-growth Douglas-fir/western hemlock forests are at the low end or below the range of 0.5–2.0% reported for temperate deciduous forests (Runkle 1985a) and tropical forests (Brokaw 1985a, 1985b). The slow rates may suggest episodic gap formation on scales longer than the 8- to 10-year periods examined here, although similar rates were found in gap surveys of events during the last 25 years. Thirty-six years of mortality data from an old-growth stand in the Washington Cascades (Franklin and DeBell 1988) revealed two mortality episodes 24 years apart of about 1% or more per annum. Large-scale disturbances, such as windstorms and insect outbreaks, that did not occur in the old-growth stands during the time intervals studied, could result in higher long-term gap formation rates than were observed.

The fact that the majority of gaps were over 25 years old suggests that the low rate of gap formation is paralleled by a slower rate of gap filling relative to other forests (Runkle 1982; Brokaw 1985b; Veblen 1985). A similar slow rate of filling also occurs in subalpine old-growth forests in British Columbia (Lertzman 1989). The slow rate of gap filling explains the relatively high percentage of area in gaps in the old-growth and mature stands. The percentage of land area in gaps fell within the range of 3.2 to 24.2% reported for deciduous old-growth forests (Runkle 1982) and within the range of 3 to 25% reported for tropical forests (Brokaw 1985a); however, it is at the high end of these ranges and we have observed many mature and old-growth forests with more gaps per unit area than the two surveyed stands.

Whether these gaps are truly open (i.e., have available resources) or are closed to additional seedling establishment by shading of understory foliage cover, root competition, or both is not known. Many of the gaps were occupied by understory shrubs and lacked coarse woody debris seedbeds. Since seed sources of western hemlock and Douglas-fir are common, the limitation may have to do with the characteristics and dynamics of resources within the gaps particularly at the scale of the germinating seedling.

## Douglas-fir regeneration

The absence of Douglas-fir reproduction under canopy gaps is consistent with other studies (e.g., Stewart 1986; Franklin and Hemstrom 1981). Shade-intolerant species

reportedly reproduce in gaps 300 to 1000 m$^2$ in size (Runkle 1985a; Brokaw 1985a). We encountered only four gaps larger than 250 m$^2$ in this study, so our sample size is too small to support conclusions about the lower threshold of gap size for Douglas-fir. However, our results suggest conditions in these small gaps are unsuitable for gap-phase regeneration of Douglas-fir. Since the majority of canopy trees died standing or by stem breakage, gap events did not create gaps in the lower strata (shrub/herb layer, forest floor, rooting zone) and expose mineral soil, which is a favorable site for Douglas-fir seed germination and seedling establishment (Minore 1979; Isaac 1943). Furthermore, the dominants are tall trees with narrow crowns, and old-growth stands have a high leaf area of codominant western hemlock; this creates a structural context in which the death of one or a few trees may not increase light levels enough for the growth and survival of shade-intolerant species (Canham et al. 1990). Gaps sufficiently large to have high light intensities at ground level are uncommon. For example, a gap of 1000 m$^2$ would require the death of 15 to 25 trees in many mature stands and 5 to 10 trees in many old-growth stands. Few disturbances kill this many adjacent trees.

We do know that gaps of sufficient size for regenerating Douglas-fir do occur in forests in this region (Franklin and Dyrness 1973; Spies and Franklin 1989). These are most frequently observed on dry sites but can also be infrequently encountered on very productive moist habitats, such as the coastal forests of the western Olympic Peninsula. Minimum gap sizes for Douglas-fir establishment on more mesic sites appear to be about 750 to 1000 m$^2$.

## Role of gaps in forest succession and regeneration of western hemlock

Differences between the density of hemlock reproduction in gaps and under canopies in the two stands suggest that gaps are important in the regeneration of this species and that the spatial distribution of the regeneration changes with succession. In mature stands, western hemlock seedlings are widely dispersed and not limited to the projected area of canopy gaps; this is probably because Douglas-fir canopies transmit relatively high amounts of light in a diffuse pattern. Douglas-firs are tall, support relatively low leaf areas (Grier and Logan 1977), and have crowns that are well above the forest floor. Furthermore, as canopies thin from suppression mortality and other causes, numerous small gaps form, raising light levels over a relatively large percentage of the forest floor. Small gaps forming during the development of a well-stocked young stand will probably fill from horizontal branch growth, whereas later in stand development, when trees are near their maximum size and more widely spaced, lateral branch growth probably does not play as important a role in a gap filling. At this latitude, light radiation through a gap can extend well beyond the expanded gap (Canham et al. 1990). In old-growth stands, where overstory canopies are dominated by western hemlock, regeneration tends to be limited to the immediate area of the gap because light levels are very low under the shorter western hemlocks with relatively dense canopies (Grier and Logan 1977) that often extend to within a few meters of the forest floor.

The absence of a relationship between regeneration and gap size in the old-growth stand has been observed in other

forests (Brokaw 1985b; Uhl et al. 1988). Brokaw (1985b) suggested that lack of correlation of shade-tolerant regeneration density to gap size in a wet tropical forest fits Connell and Slayter's (1977) prediction for late successional species for low severity disturbances. If western hemlock has a low gap size threshold for establishment as this study suggests then it is not surprising that a relationship between gap size and sapling density was lacking in the old-growth stand. This does not mean, however, that growth rates would not differ across the gap sizes. The absence of a relationship between regeneration density and gap site may also mean that other factors, such as the presence of suitable organic seedbeds and belowground competition, may be the primary controls of seed germination and seedling survival. It is well documented that western hemlock seedling establishment is much more successful on rotted logs and other organic substrates (Mckee et al. 1982; Harmon and Franklin 1989) than on the forest floor.

The negative correlation between regeneration density and gap size in the mature stand has also been observed in other forests. Runkle and Yetter (1987) attributed the negative correlation with gap size in temperate deciduous forests to increased area of fallen stems and branches in large gaps. We do not know if this explanation also fits Douglas-fir forests. Given that the correlation is marginally significant, observations of within-gap environmental and resource controls on seedling establishment are needed.

The positive correlation of regeneration density with gap age in the mature stand and the negative correlation in the old-growth stand further reflect the differences in understory light conditions and forest structure in the two stands. In the mature stand where tree saplings are sparse, gaps may continue to be sites of new seedling establishment because understory resources are still available in gaps surrounded by relatively open upper and midcanopy layers. In the old-growth stand, where canopy-sized hemlocks and tall Douglas-firs surround many gaps, light and belowground resources may be so low that the first seedlings established in the gaps preempt resources and retard further seedling establishment. In addition, where sapling density is relatively high, self-thinning within the patch of regeneration will also reduce seedling and sapling density.

*Distinctive features of canopy gaps in Douglas-fir/western hemlock forests*

This study suggests that Douglas-fir/western hemlock forests fit the paradigm that gap disturbances and vegetation response are important driving forces in forest dynamics. However, gaps in these forests also suggest that the gap paradigm must be broadened to incorporate other factors such as forest structure, the nature and severity of the disturbance, within gap heterogeneity, and the interaction between large catastrophic and small canopy disturbances.

Forest structure provides an important context for gap dynamics. Unlike eastern deciduous forests (Poulson and Platt 1989), the death of one or a few narrow-crowned conifers in tall Douglas-fir/western hemlock forests may not transmit enough light for the regeneration of shade-intolerant species (Spies and Franklin 1989; Canham et al. 1990). Gaps may play this role for Douglas-fir and other early seral species in other forests with shorter and less dense canopies, such as mixed-conifer forests (Franklin and Dyrness 1973; Spies and Franklin 1989).

The apparent slow rates of gap formation in the old-growth forests may be a distinctive feature that results from the life history characteristics of the trees, the disturbance regime, and the structure of the stands. The relatively low rates of mortality, which contribute to the low gap formation rates, may be a consequence of the great longevities of the dominant species such as Douglas-fir, which have a potential life span of 1200 years (Franklin and Waring 1980). The infrequency of strong winds in the Cascade Range may also play a role in the apparent low rate of gap formation. The multistoried nature of the old-growth stands, with a seral dominant over a shade tolerant, also contributes to low gap formation rates. The lower canopies of western hemlock often overlap the projected areas of the crowns of the emergent Douglas-firs. Therefore, gaps created by the standing death of a large Douglas-fir are smaller than the area of the Douglas-fir crown. In addition, since the Douglas-firs often die standing, when then eventually fall to the ground as a partly decomposed tree they may not damage or knock down hemlocks and create gaps.

The nature and severity of disturbances play an important role in vegetation response to gaps. In coniferous forests of the Cascade Range, gap formation infrequently disrupts the forest floor, thereby limiting colonization opportunities for species, such as Douglas-fir, that prefer mineral soil for establishment (Minore 1979). The kind and heterogeneity of seedbeds, structures, and resources within gaps is also important in gap dynamics in these forests. The slow filling of gaps may be a distinctive feature that is related to the limited availability of seedbeds, competition from clonal understory shrubs, and summer drought.

Fine- and coarse-scale disturbances are not independent (Lorimer 1989; Spies and Franklin 1989). The frequency of large disturbances probably controls the importance of small canopy gaps; where large disturbances are frequent small gaps may be relatively unimportant in forest dynamics. In addition, large gaps created by fires may fill very slowly, so even old forests have unfilled canopy openings. This may be the case in many Douglas-fir forests where many canopy openings are not associated with evidence of tree mortality. This kind of gap has been noted for eastern deciduous forests (Barden 1989), but not quantified. The role of these unfilled canopy openings in forest dynamics and in the maintenance of community diversity is not clear. They may be areas that are just slowly filled by trees, or they may be semipermanent shrub and herb patches in the forest.

In conclusion, much more information is needed on the role and importance of gaps in coniferous forests. In particular, the role of small, low intensity fires in small gap dynamics needs to be evaluated. Comparative studies of coniferous and deciduous forest ecosystems are needed to identify variation in gap dynamics and develop a more general gap paradigm.

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