

Gap-phase structure of a subalpine old-growth forest

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We examined four stands in a subalpine old-growth forest in the Coast Mountains of southwestern British Columbia for gap-phase structure. Though the stands varied in the proportions of each species, all had a similar distribution of area under closed canopy and in gaps (overall means: 29% closed canopy, 52% expanded gap, 18% canopy gap). Median areas of canopy gaps and expanded gaps were 41 and 203 m², respectively. Most gaps (90%) had more than one gap maker, and gap makers within a gap were often from mortality events separated in time. Half of all gap makers died standing, and only 13% were windthrown. Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) was represented among gap makers in a much higher proportion than among canopy trees in general (64 vs. 45%). The estimated forest turnover time varied from 280–1000 years, depending on assumptions about the time taken for gaps to be filled. Distinctive features of gap-phase structure and dynamics in this forest are the high proportion of area in gap, small gap size, multiple gap makers of varying stages of decay, and long tenure of gaps before they are filled.

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Nous avons étudié l'aspect des trouées dans quatre peuplements d'une vieille forêt subalpine située dans la région côtière du sud-ouest de la Colombie-Britannique. Quoique les peuplements variaient quant aux proportions de chaque espèce, ils démontraient une distribution similaire des superficies de couvert fermé et de trouées (moyennes globales : 29% sous couvert fermé, 52% de trouées en évolution et 18% en clairières). Les superficies médianes du couvert et des trouées en développement étaient de 41 et 203 m², respectivement. La plupart des trouées (90%) présentaient plus d'une tige morte et cette réduction du couvert était généralement due à des événements causant une mortalité échelonnée dans le temps. La moitié des tiges sont mortes debout, tandis que seulement 13% étaient renversées par le vent. Le sapin amabilis (*Abies amabilis* (Dougl.) Forbes) était représenté dans une plus grande proportion parmi les tiges créant les trouées qu'à l'intérieur du couvert en général (64 vs. 45%). Le temps estimé pour une rotation de la forêt varie de 280 à 1000 ans, tout dépendant des estimations du temps nécessaire pour combler les trouées. Les principales différences au niveau de la physionomie des trouées et de la dynamique des forêts sont la grande superficie occupée par les trouées, la petite dimension des trouées, le nombre de tiges à différents stades de décrépitude et le temps nécessaire pour que les trouées soient comblées.

[Traduit par la rédaction]

Introduction

In forests where large, stand-destroying disturbances are infrequent, small-scale disturbances associated with the mortality and replacement of individual trees are a primary source of heterogeneity in forest structure and composition. When a canopy tree dies in such forests, the removal of its crown from the canopy creates a gap (Jones 1945; Watt 1947; Bray 1956) in which species are able to establish or recruit that could not do so under a closed canopy (Runkle 1981, 1982, 1985; Brokaw 1985a, 1985b; Denslow 1980, 1985; Whitmore 1989). In this way, gaps may contribute to the maintenance of species diversity in a variety of communities (Grubb 1977; Connell 1978; Denslow 1980, 1985; 1987). Much of the response to gaps is associated with changes in the light, temperature, and water regimes on the forest floor (Bazazz and Pickett 1980; Chazdon and Fletcher 1984; Collins et al. 1985; Denslow 1987), but the belowground status of gaps is poorly understood (Vitousek and Denslow 1986; Mladenhoff 1987). Fallen trees create a variety of substrates not otherwise available (Orlans 1982; Bazazz 1983), and windthrow events can exert a long-term and substantial influence on both soil structure and

chemistry (Lutz 1940; Stephens 1956; Beatty and Stone 1986).

Gap-phase processes have been described most extensively for the mixed hardwood forests of eastern North America (Runkle 1981, 1982, 1985; Romme and Martin 1982) and the moist to wet neotropics (Hartshorn 1978; Brokaw 1985a, 1985b; Hubbell and Foster 1986a, 1986b). The old-world tropics have also received attention (Aubreville 1938; Poore 1968), as have some Southern Hemisphere temperate forests (Veblen 1985, 1989; Cullen 1987; Armesto and Fuentes 1988) and Asian coniferous and mixed forests (Naka 1982; Nakashizuka 1983; Taylor and Zisheng 1988a, 1988b).

Gap-forming disturbances have received considerably less attention in the coniferous forests of western North America. This is probably due to the clear and often overwhelming impact of the catastrophic disturbances, mainly fires, to which many stands owe their origin (Franklin and Hemstrom 1981; Hemstrom and Franklin 1982; Spies and Franklin 1989; Spies et al. 1990). However, even in a matrix of younger, even-aged stands, there are frequently patches of multiple-aged old growth persisting on north-facing slopes, in protected hollows, or wet pockets, that predate the surrounding forest (Eis 1962; Hemstrom and Franklin 1982). In these stands, and other areas that have escaped catastrophic disturbance for long periods, we might expect processes occurring at the spatial scale of one to a few trees

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to play an important role in forest structure and composition.

In midelevation old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests in the western Cascade Range of Oregon, canopy gaps are required for the replacement of the early seral Douglas-firs by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) (Stewart 1986a, 1986b; Spies and Franklin 1989; Spies et al. 1990). Differences in canopy structure between species, stand age, and disturbance history all affect both the development of advanced regeneration under intact canopies and the response of vegetation to the creation of a gap. The presence of Douglas-fir, with its large dimensions and long tenure, exerts a profound influence on the vertical and horizontal structure of these stands, and on the time dynamics of succession (Stewart 1986a, 1986b; Spies et al. 1990).

At higher elevations in the Cascade Range, above the range of Douglas-fir, the autecology of the dominant species (true firs, hemlocks, and cedars), combined with a cool, wet climate and infrequent fires, suggests the potential importance of gap-phase processes. Though patterns of succession and stand development have been well described (Thornburgh 1969; Kotar 1972; Long 1976), gap-phase processes have not yet been examined explicitly. Where regeneration in canopy openings has been observed in higher elevation forests (Kotar 1972; Long 1976), the abundance and growth rates of Pacific silver fir and western hemlock were greater in the openings than under a closed canopy, and gaps in the canopy were considered necessary for recruitment.

The montane to subalpine forests of southern coastal British Columbia are similar floristically and climatically to those of the western Cascade Range (Krajina 1970; Brooke et al. 1970; Franklin and Dyrness 1973; Franklin et al. 1988). However, the roles of gap-phase processes have not been examined there. In this paper we describe gap-phase structure of an old-growth, subalpine forest just north of Vancouver, British Columbia. We focus on the overall structure of the forest and on the patterns of mortality that give rise to gaps, gap size, and geometry. Subsequent papers will examine forest composition, the patterns of tree replacement in gaps, and the longer term consequences of replacement patterns for forest dynamics.

Study sites and methods

Study sites and species

This research was conducted at Cypress Provincial Park in the North Shore Mountains of the Coast Mountains of southwestern British Columbia (Fig. 1; 49°25'N, 123°12'W). The study sites are in the Mountain Hemlock Zone of British Columbia's biogeoclimatic classification system (Brooke et al. 1970; Green et al. 1988; Pojar et al. 1987). The stands examined are at the lower range of the Mountain Hemlock Zone, where it grades into montane stands of the Wetter Maritime Subzone of the Coastal Western Hemlock Zone. The Mountain Hemlock Zone can be divided into a Parkland Subzone at higher elevations, and a Forested Subzone at lower elevations. This research was conducted entirely in the Maritime Forested Subzone (Green et al. 1988).

Plant associations and vegetation-environment relationships of the Mountain Hemlock Zone have been described extensively by Brooke et al. (1970). These forest classes correspond roughly to the upper range of the *Abies amabilis* Zone and the lower range

of the *Tsuga mertensiana* Zone of the Cascade Range to the south (Franklin and Dyrness 1973).

The Mountain Hemlock Zone is characterized by a cool, wet climate, with significant precipitation every month of the year, and a substantial amount of the precipitation in the form of snow (Brooke et al. 1970). Late winter snow depths of >3 m are not uncommon, and even within the Forested Subzone, the snow-free period is usually less than 150 days (Brooke et al. 1970). Small changes in slope position, slope angle, aspect, and elevation can have a pronounced influence on microclimate and vegetation. A compacted or cemented glacial till with varying mixtures of rock types is the predominant parent material for soils. Podzolization and gleization are the predominant soil forming processes, and Humic and Humus Podzols are the zonal soils (Brooke et al. 1970; Ugolini 1982).

Dominant tree species at Cypress Provincial Park are Pacific silver fir, western hemlock, mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.), and Alaska yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach). The Cypress Provincial Park sites are above the local elevational limit for Douglas-fir (*P. menziesii* var. *menziesii*).

The forests at Cypress Provincial Park are typical in composition of upper montane - lower subalpine old growth on well-drained, productive sites on the south and central British Columbia coast. They are fairly typical structurally as well, except that the distinction between gaps and adjacent closed canopy areas is unusually well defined at Cypress Provincial Park.

Research stands

The locations of the four focal stands are indicated in Fig. 1. Three stands are located along the Howe Sound Crest Trail on the southwest to northwest slopes of Mount Strachan. Two are adjacent to each other: STRACHAN1 is above the trail, and STRACHAN2 is below the trail in the Howe Sound Overlook area. A third, STRACHAN3, is several hundred metres farther north along the trail and downhill from it. Stand HOLLY1 (Hollyburn 1) is on the western slope of Hollyburn Mountain, above the trail between the cross-country and downhill skiing facilities (about 2 km from the other stands).

The stands are all near 1000 m elevation (950-1145 m) and vary from south southwest to northwest in aspect (Table 1). STRACHAN1, STRACHAN3, and HOLLY1 are on slopes (20°-30°), and STRACHAN2 is on a nearly level bench. In this area, cold air pools on flat areas, creating a microclimate more similar to higher elevation forests where the Forested Subzone begins to grade into the Parkland Subzone. This can cause substantial small-scale heterogeneity in vegetation. STRACHAN2 is similar in structure and composition to stands on benches above STRACHAN1, STRACHAN3, and HOLLY1. Details of the composition of each stand can be found in Lertzman (1989).

All four stands are part of a contiguous band of montane to subalpine forest stretching for many kilometres up Howe Sound and along the North Shore Mountains. In many places this band of mature forest is elevationally restricted by an extensive logging history at lower elevations. Within this forest, some stands are delimited by local topographic features that are reflected in forest structure and are of clearly limited area. For instance, STRACHAN2 is on a 2-3 ha nearly level bench in a midslope position. STRACHAN1 is bounded by a clearcut along its south side, and STRACHAN2, on its downhill (west) side. The other two focal study sites are part of a large block (>100 ha) of more or less continuous forest that grades into subalpine parkland at higher elevations.

Based on the estimated ages of large trees growing on large uncharred stumps (Lertzman 1989) and on preliminary analysis of pollen and charcoal in the soil profile (K.P. Lertzman and L.B. Brubaker, unpublished data), these stands have not experienced a major fire for 1500+ years. Many individuals approach or exceed published age records for their species, and gap-phase processes appear to have been important in shaping canopy structure for a long time (Lertzman 1989).

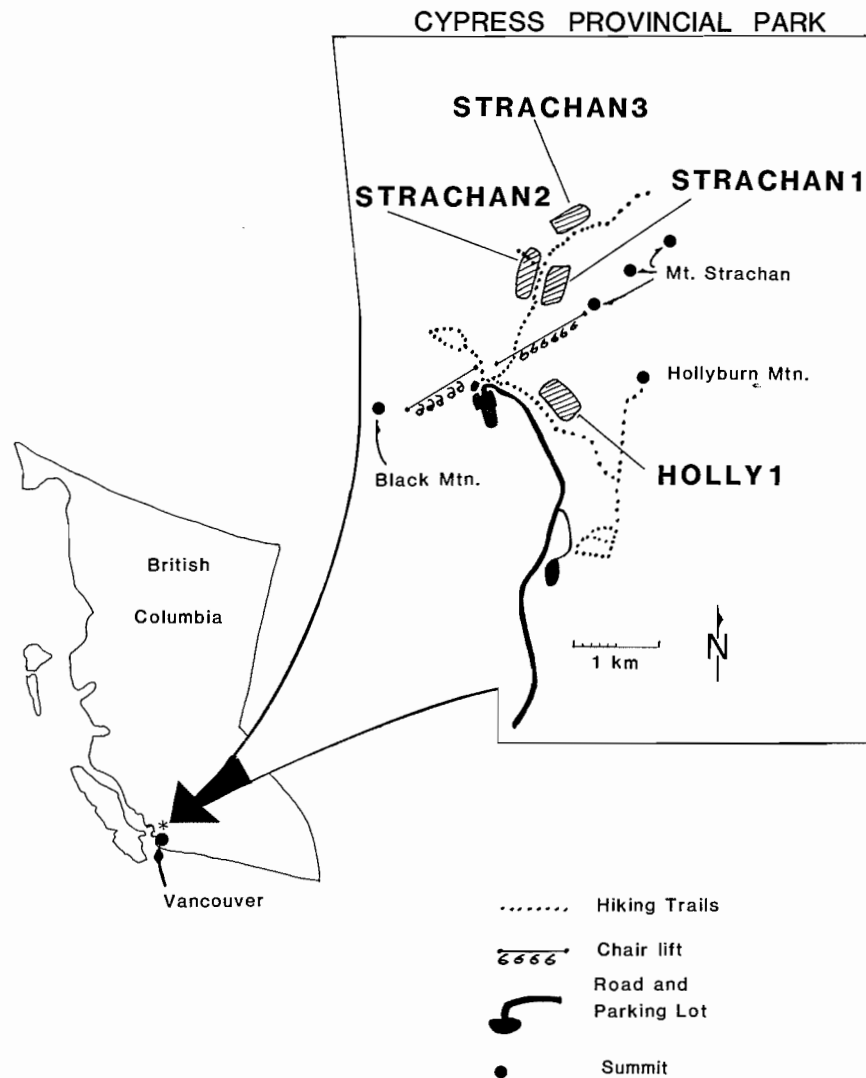


FIG. 1. Location of Cypress Provincial Park and the focal study stands.

TABLE 1. Characteristics of the four focal stands

Stand	Elevation (m)	Aspect (degrees)	Slope (degrees)	Soil moisture regime
STRACHAN1	1085-1145	221-260	21-31	Moist
STRACHAN2	1040-1050	180-240	0-17	Fresh
STRACHAN3	1000-1030	225-315	21-30	Moist
HOLLY1	950-1000	242-282	18-24	Moist

NOTE: Soil moisture regimes are as defined in Green et al. (1988).

Sampling for canopy structure

The methods used to estimate the proportion of the forest represented by gaps, and to locate a population of gaps for more detailed description, are similar to those of Runkle (1982) and Veblen (1985). This sampling was done in the summers of 1985, 1986, and 1987.

We established permanently marked 50- or 100-m transects following constant elevational contours in each stand. Transects were at least 100 m from the clearcut edge in STRACHAN1, where the boundary was characterized by increased windthrow of edge trees. Transects were at least 50 m from the clearcut edge in STRACHAN2, where the boundary has been stable. STRACHAN3 and HOLLY1 were much farther than 100 m from any major forest edge.

Parallel transects were separated by 30-m intervals (ground distance). Thirty metres was enough distance between transects that all but the largest gaps were not contacted by more than one transect, but few, if any, small gaps were missed between transects. If stream beds, rocky outcrops, or other major exogenous discontinuities in forest structure were encountered, the transect was terminated or continued on the other side of them. Such discontinuities accounted for a small proportion of the land surface area. A total of 350 m of transect was sampled in STRACHAN1, and 300 m each in STRACHAN2, STRACHAN3, and HOLLY1, for a total of 1250 m.

At 1-m intervals along each transect, we classified canopy status as canopy gap, expanded gap, or closed canopy. A canopy gap is the vertical projection onto the ground of the opening in the forest canopy caused by the mortality of a tree; for an opening to be considered a gap, the remains of a gap maker (see later) must be present. A point on the transect was considered in canopy gap if, in sighting vertically above it (using a clinometer to insure a vertical sighting), no foliage of canopy trees was encountered. For this and all subsequent discussion, a canopy tree was defined as 22 cm dbh or greater and at least 10 m in height.

The boundary of the expanded gap (Runkle 1982; Veblen 1985) is defined by the boles of the trees whose canopies define the canopy gap. A point was considered in expanded gap if it was underneath the foliage of these trees. With increasing latitude, and especially on slopes, an increasing amount of direct beam radiation enters

TABLE 2. Decay classes for gap makers

Class	Characteristic					
	Small branches	Large branches	Bark	Heartwood	Sapwood	Log
Young	Present	Present	Intact	Solid	Solid	Present
Medium	Absent	Present	Sloughing ^a	Friable	Shell ^b	Present
Old	Absent	Absent	Absent ^c	Variable ^d	Variable	Decayed ^e
Very old	Absent	Absent	Absent	Variable	Variable	Absent

^aThe subcategories young-medium and medium-old were distinguished largely on how much bark had sloughed off; young-medium, 25%; medium, 50%; medium-old, 75%.

^bThe heartwood of standing dead trees rotted first, leaving a hard exterior shell (Thornburgh 1969). The pattern was the opposite for logs on the ground, as in Triska and Cromack (1979) and Sollins (1982).

^cBark is sometimes present on stumps of old and very old gap makers, but never on the logs associated with the stumps. Bark persisting on the stumps of most old and all very old gap makers was waterlogged and covered by decomposing litter.

^dPortions of old and very old gap makers below ground or covered with leaf litter and moss were often waterlogged and sound, with distinct ring structure, though heavily stained and soft.

^eLogs associated with old gap makers were being incorporated into the forest floor and are well characterized by the descriptions of class 5 logs in Triska and Cromack (1979) and Sollins (1982).

a gap at angles other than 90° relative to the forest canopy. This results in light from a gap passing beneath the canopies of the trees bordering the canopy gap, suggesting that the expanded gap may be a more appropriate measure of the effective opening than the canopy gap (Canham 1988b).

All other points were under more or less continuous canopy and were considered closed canopy. There were occasionally small openings in the canopy where the crowns of adjacent trees did not quite meet, or where a very old gap had not quite filled. If these were, by visual estimate, less than half the diameter of the average canopy tree crown in that area, then they were still considered closed canopy. Although interstitial spaces between adjacent crowns were frequent, we never had any difficulty distinguishing these from canopy gaps as defined earlier. Other than those around stream courses or rocky outcrops (see earlier), there were no openings exceeding this size criterion that were not associated with canopy gaps.

We estimated the proportion of surface area in the forest represented by each canopy category by calculating the proportion of the total metres of transect sampled that were classified as that category. The proportion of area in gaps could also be calculated by dividing the sum of the areas of individual gaps (17 150 m² of expanded gap) by the total area sampled (1250 × 30 m). The value arrived at (46%) is less than that found from the transect data, suggesting that the census of gaps was not complete.

Description of individual gaps

All gaps with canopy gap or expanded gap intersecting the transects were enumerated and marked for further study. Line transects do not sample gaps of different sizes without bias; larger gaps are more likely to be sampled relative to their abundance (Runkle 1982). The inclusion of gaps whose expanded gap intersected the transects, rather than only those with canopy gaps intersecting the transects, partially corrects for this bias. To further correct for this, we also included small gaps encountered during sampling that did not intersect any transect and would otherwise have been missed. Most of these were very small gaps that occurred wholly between transects. Apparently, this still did not achieve a complete census of gaps within the sampled area.

A gap maker is a tree whose mortality contributed to the creation of a gap. A gap filler is a tree growing in a gap.

For each gap we recorded aspect, slope, orientation of the long axis of the gap, canopy height, mode of mortality for each gap maker (uprooted, standing dead, etc.), expanded gap area, and, where possible, species and dbh of the gap maker. For data collected in 1987 (all gaps in STRACHAN1 and STRACHAN3, and most in STRACHAN2), we also measured canopy-gap area and gap aperture (after Lawton and Putz 1988). Note that this results in

TABLE 3. Frequency of canopy gap (CG), expanded gap (EG), and closed canopy (CC) among the four stands

Stand	%CG	%EG	%CC	N
STRACHAN1	21 ± 6	50 ± 15	29 ± 20	4
STRACHAN2	22 ± 4	47 ± 19	28 ± 19	3
HOLLY1	20 ± 6	51 ± 4	29 ± 9	3
STRACHAN3	12 ± 6	60 ± 6	28 ± 11	4
Overall mean	18 ± 7	52 ± 12	29 ± 14	14

NOTE: Values are means among transects in each stand ± 1 SD. N is the number of transects; each parallel transect within each stand is a datum, and 50- and 100-m transects are not weighted differently. The stands do not differ significantly, ANOVA (on arcsine square root transformed data); CG, $p = 0.13$; EG, $p = 0.54$; CC, $p = 0.99$.

an unequal sample size for canopy-gap areas and expanded-gap areas (37 and 60, respectively). A variety of types of data on gap fillers and gap maker - gap filler relationships were also collected, but are not examined here (discussed in Lertzman 1992; Lertzman 1989). We were unsuccessful in an attempt to obtain dates for the origins of gaps by counting the number of years of released height growth on Pacific silver firs greater than 1 m in height (see later).

The time since mortality of gap makers was estimated qualitatively using a decay class system based on morphological characters observable in the field. This system differs from that used by Triska and Cromack (1979), Sollins (1982), Graham and Cromack (1982), and Means et al. (1985) because of the predominance of snags rather than fallen logs, and the need to include stumps that persist after the logs associated with them are not detectable. Table 2 shows the criteria used in classifying gap-maker decay class.

Young gap makers are recently dead trees with all or most of their canopy branch structure intact and little or no evidence of decomposition in the bole or stump. Medium gap makers have lost smaller branches, but may retain larger ones, have sloughing bark, and show substantial signs of decay in heartwood (for standing dead) or sapwood (for logs on the ground), but are able to support their own weight. Old and very old gap makers were classified solely on characters of the stumps; logs from old gap makers are mostly incorporated into the forest floor, and logs from very old gap makers are indistinguishable. Thus, the old and very old categories could rarely be assigned a mortality class; they appear as snapped off stumps irrespective of the original mode of mortality. Old gap makers had some sound wood protruding above the surface of the forest floor. This sound wood varied from a substan-

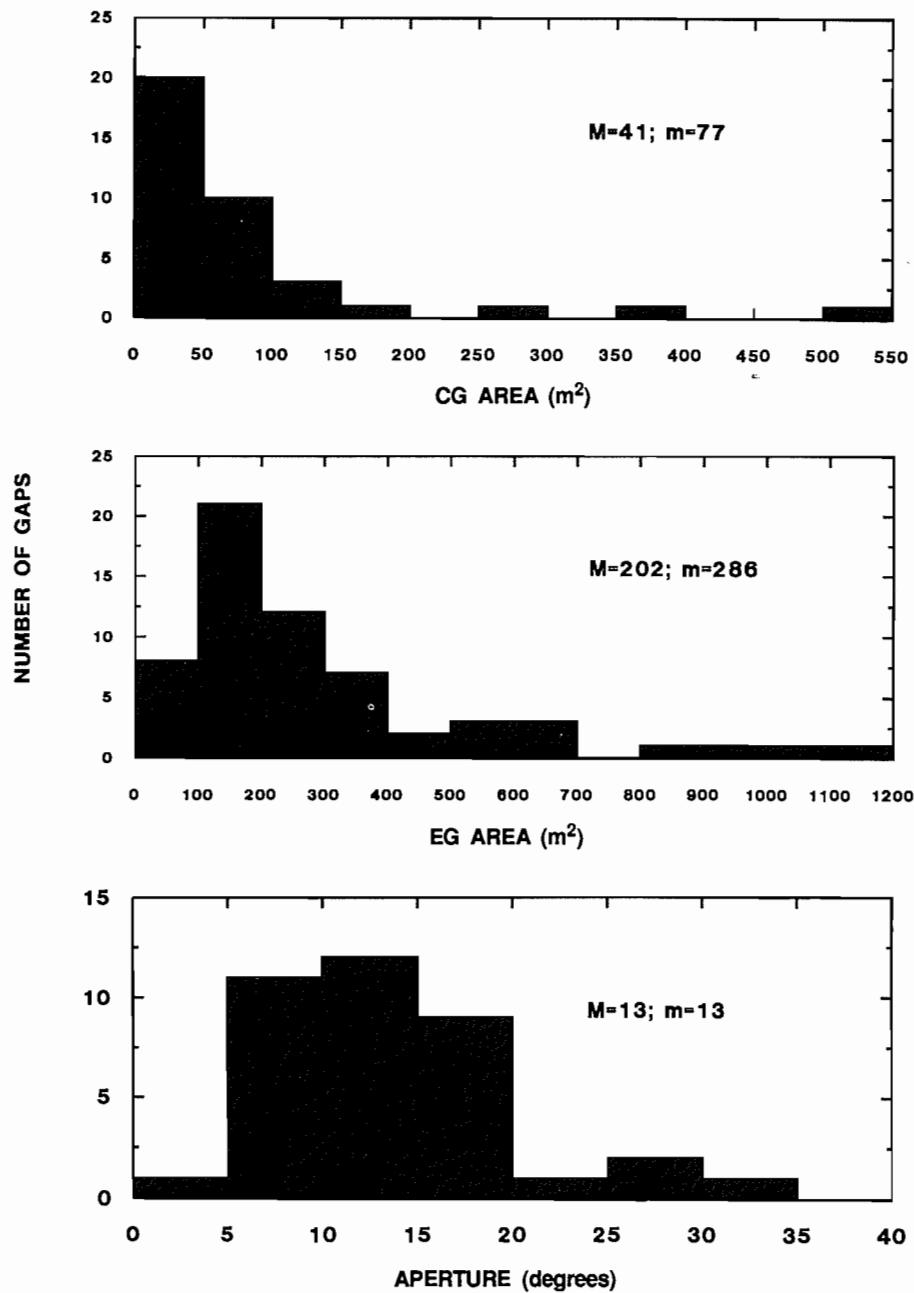


FIG. 2. Size frequency distributions for canopy gaps (CG), expanded gaps (EG), and gap aperture. *M*, median; *m*, mean.

tially intact stump, representing the full basal diameter of the tree, to a narrow central core of sound heartwood. Very old gap makers are visible as a mound in the forest floor mostly or entirely covered by leaf litter and moss, and usually supporting a substantial growth of conifers and shrubs.

Young and medium gap makers correspond roughly to Triska and Cromack's (1979) and Sollins' (1982) classes 1-3. Old and very old gap makers correspond to Triska and Cromack's (1979) and Sollins' (1982) classes 4 and 5, and a stage beyond their class 5 where stumps are present but logs are no longer detectable.

Gap makers intermediate in character were classified as young-medium or medium-old. During analysis, we found that those gap makers classified in the field as old - very old had the same distribution of species and modes of mortality as very old gap makers (mostly unidentifiable in both cases), and therefore the two classes were combined.

To measure canopy-gap and expanded-gap size, we laid perpendicular 50-m tapes along the two main axes of a gap, with their

intersection as close to the visual centre of the gap as possible. For each of these four radii, and four additional radii at angles equidistant between them, the distances from the gap centre to the edges of the canopy gap and the expanded gap were measured. The edge of the expanded gap was defined by a line drawn between the centres of the boles of trees whose canopies defined the canopy-gap edge. In irregularly shaped gaps, we measured additional radii as needed. Gap area and perimeter were obtained from scale maps of each gap with a digitizer. When presenting data on gap area, each expanded gap includes the canopy gap, whereas in the estimation of how much space in the forest is represented by each category, canopy gap and expanded gap are mutually exclusive categories.

Gap aperture may be a better proxy for estimating the light available in a gap than gap size (Lawton and Putz 1988). Gap aperture is the average of the four angles from the zenith to the edge of the canopy, along the two main axes of a gap. Gap aperture was measured at eye level in the centre of each gap.

TABLE 4. Summary statistics for gap size measures

	CG area (m ²)	CG perimeter (m)	EG area (m ²)	EG perimeter (m)	Aperture (degrees)
<i>N</i>	37	37	60	60	37
Min.	5	9	25	20	5
Max.	525	143	1127	176	33
Median	41	31	203	56	13
Mean	77	40	286	67	13
SD	108	29	244	34	6

NOTE: CG, canopy gap; EG, expanded gap.

Stand- versus forest-level analyses

We will present the basic description of gap-phase structure (percent canopy gap, expanded gap, and closed canopy) on both a stand by stand basis and averaged over the four study stands within Cypress Provincial Park. All discussion of the characteristics of gap makers and gaps as populations (e.g., gap-maker species and mortality patterns, gap size, and geometry) will be presented as one data set combining data from the four stands.

Results

Percent of forest in each canopy and substrate category

Of 1250 m sampled on 14 transects in the 4 stands, 18% was in canopy gap, 52% was in expanded gap, and 29% was in closed canopy (Table 3). The four stands did not differ significantly in the amount of each canopy class (Table 3). In fact, the mean amounts of closed canopy and total gap (canopy + expanded gap) were remarkably similar between stands. Though its total percent gap (canopy plus expanded) was similar to the others, more of STRACHAN3 was in expanded gap than the other stands. This is probably because a greater proportion of the gaps in this stand were older than in the other stands, and, as gaps age, canopy gap is converted into expanded gap.

Leaf litter was the predominant substrate in the forest, accounting for 67% of the sampled points. Logs represented 8.6% of the sampled surface; root mounds, 3.5%; and stumps, 3%. Miscellaneous dead woody debris (e.g., branches, highly decomposed old logs incorporated into the forest floor) made up an additional 17%, and 1% was boles, rocks, roots, and bark. The relative paucity of large woody substrates (~15%) is significant because of their importance as a rooting substrate for western hemlock (Lertzman 1989).

Gap size and geometry

Canopy-gap sizes varied from 5 to 525 m², with a median of 41 m², and exhibited a distribution that was negative exponential in form (Fig. 2, Table 4). Expanded gaps varied from 25 to 1127 m² in area, with a median of 203 m², and more closely approached a lognormal distribution, with an intermediate modal size. Gap apertures were even more symmetrically distributed, with a median and mean of 13°. Gap aperture was the least variable of the three measures (CV = 0.48), and canopy-gap area the most variable (CV = 1.4 for canopy gaps and 0.85 for expanded gaps). Though most gaps are small, large gaps contribute disproportionately to the total gap area in the forest. The five largest canopy gaps (14% of the total number of canopy gaps) contained 52% of the canopy gap area, and the 10 largest expanded gaps (16% of the expanded gaps) contained 44% of the expanded gap area.

In some forests, gap shape is well approximated by an ellipse (Runkle 1982, 1990; Veblen 1985), but at Cypress,

both canopy gaps and expanded gaps are often quite irregular in shape, and especially for larger gaps, the relationship between perimeter and area deviates substantially from that predicted for a circle (Fig. 3). With increasing size, gaps become increasingly irregular. This is consistent with the multiple gap maker origin of most gaps (see later): while the crown of a single tree may be roughly represented by an ellipse, the intersecting crowns of several trees are unlikely to be.

Lawton and Putz (1988) suggested that gap aperture is much better correlated with photosynthetically active radiation in the centre of a gap than is gap area *per se*. Gap aperture integrates projected gap area with stand stature and slope. Incident light in the gap will be a complex function of how these three interact with canopy geometry and latitude. Gap aperture was strongly correlated with gap area and perimeter ($0.77 < r^2 < 0.82$ for all comparisons between gap aperture and the area and perimeter of canopy and expanded gaps). Of these, gap aperture was best correlated with canopy-gap perimeter ($r^2 = 0.82$).

Number of gap makers per gap and mode of mortality

Gap makers can be separated into those of primary and secondary importance in each gap. A primary gap maker was one whose crown was judged to have represented a substantial portion of the current canopy gap. Secondary gap makers are on the edge of the expanded gap (thus the removal of their crown did not greatly contribute to the current gap), are smaller trees knocked down by primary gap makers, or represent earlier mortality events whose influence on gap geometry has been overwhelmed by the more recent mortality of a primary gap maker.

Most gaps are a result of the mortality of more than one tree: 90% of the gaps had more than one gap maker, and 63% had more than one primary gap maker. Many gaps had several gap makers, to a maximum of 16 (8 primary and 8 secondary; Fig. 4). The mean numbers (± 1 SD) of primary, secondary, and total gap makers per gap were 2.8 ± 1.9 , 3.0 ± 2.5 , and 5.7 ± 3.8 , respectively. The gap makers in a each gap were often of different decay classes (primary gap makers usually more recent, secondary gap makers usually older), suggesting a long residence time for many gaps. Primary gap makers had a larger mean diameter than secondary gap makers (0.92 ± 0.31 vs. 0.68 ± 0.28 m, $N = 91$ and 52 , respectively; *t*-test, $p < 0.001$).

Gap makers were classed as standing mortality, uprooted, snapped off along their stem, or of unknown mode of mortality (Table 5). Of the 143 gap makers for which the mode of mortality could be identified (95 primary gap makers), 55% died standing (64% of primary gap makers). Only 13% of the total gap makers were uprooted (13% of primary gap

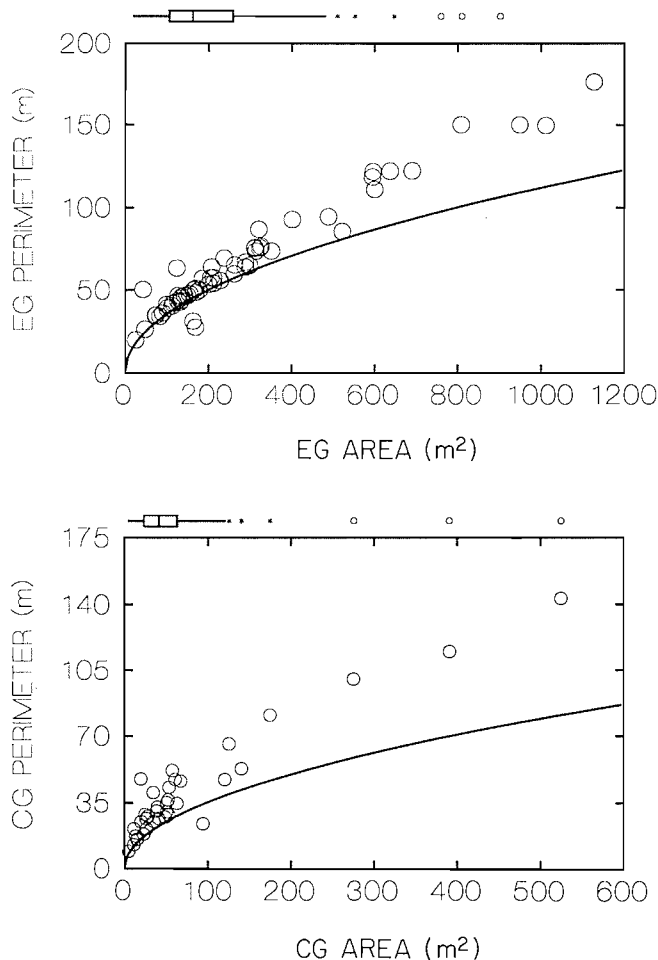


FIG. 3. Area-perimeter relationships for expanded gaps (EG) and canopy gaps (CG). Solid lines plot the area-perimeter relationship for circles. Marginal box plots indicate median (central vertical line), quartiles of the distribution, and outlying values. Outlying values shown by asterisks represent values that fall farther than 1.5 times the interquartile range from the ends of the box, and those shown by circles represent values that fall farther than 3 times the interquartile range (the interquartile range = 75th quartile - 25th quartile) (Wilkinson 1988a, 1988b; Chambers et al. 1983).

makers). The remaining 31% (23% of primary gap makers) had snapped between 2 and 10 m above the ground. Some of the gap makers classified as snap-off mortality probably died standing intact and snapped later.

Many of the snapped and uprooted trees were small individuals knocked down by larger trees when they fell (note the lower proportion of primary gap makers in these mortality types). Thus wind was not often the direct causative agent in the uprooting of trees in these stands. Mean diameters did not differ significantly between gap makers experiencing different modes of mortality (ANOVA; $p = 0.09$), but the mean diameters of uprooted or snapped trees were smaller than those of trees that had died standing (means = 0.71 ± 0.35 , 0.76 ± 0.37 , and 0.92 ± 0.36 m; $N = 6, 30$, and 50 , respectively).

Though many gap makers could not have a mode of mortality assigned to them (57% of all gap makers; 41% of primary gap makers; Table 5), almost all of the more recent gap makers had an identifiable mode of mortality (98% of

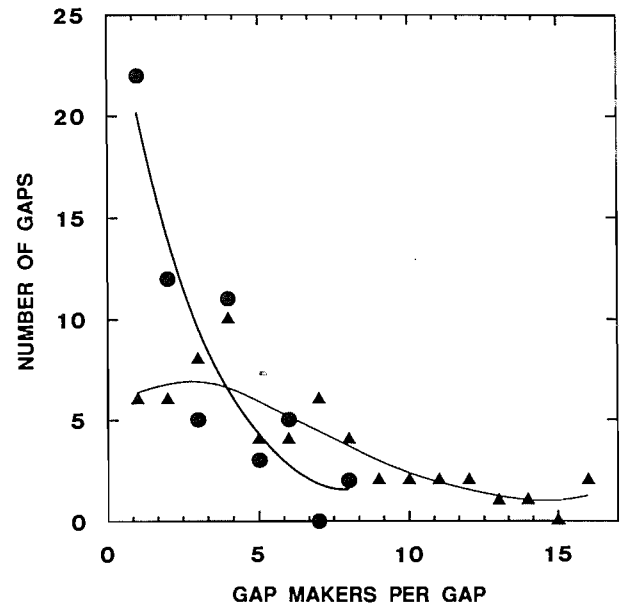


FIG. 4. Frequency distribution of the number of primary and total gap makers per gap. Triangles and the thinner line represent total gap makers; circles and the thicker line represent primary gap makers. Lines are distance weighted least squares smoothings of the data (Wilkinson 1988b).

the young, young-medium, and medium age-class gap makers; gap maker age classification scheme, Table 2; data, Table 6). When only these more recent gap makers are considered, the proportion of standing dead increases to 62% (71% of primary gap makers) owing to a reduction in the proportion of snapped gap makers. This suggests that an even higher proportion of all gap makers died standing than Table 5 indicates, and that many of the primary gap makers that now appear as snap-off mortality died standing.

Uprooted gap makers were all complete plate and ball "hinge-type" tree falls (*sensu* Beatty and Stone 1986). Almost all the uprooted gap makers were Pacific silver fir (17 out of 19; Table 5), though these represented only 20% of all Pacific silver fir gap makers overall and 18% of Pacific silver fir primary gap makers.

Of the 160 gap makers identified at least to genus (101 primary gap makers), 64% were Pacific silver fir and 23% western hemlock (56 and 27% of primary gap makers; Table 5). Pacific silver fir thus occurs as a gap maker in a much higher proportion than its representation in the canopy (Lertzman 1992). The mean diameter of western hemlock gap makers was greater than that of Pacific silver fir gap makers (1.1 ± 0.31 vs. 0.70 ± 0.29 m, $N = 31$ and 55 , respectively; t -test, $p < 0.001$), consistent with the higher proportion of western hemlock gap makers that were primary (73% of the western hemlock vs. 56% of the Pacific silver fir).

Does the species composition of gap makers change with gap maker age-class? Figure 5 shows the ratio of Pacific silver fir to (i) western hemlock and (ii) all hemlocks for young through old age-classes. There are roughly double the number of fir per hemlock for medium-aged gap makers than there are for both younger and old gap makers. Two alternative hypotheses could explain this pattern: (i) a pulse of mortality among Pacific silver fir in the past or (ii) a general increase in the representation of hemlocks among

TABLE 5. Number of gap makers of each species, by type of mortality

Species	Type of mortality				Total
	Uprooted	Snapped	Standing	Unknown ^a	
Pacific silver fir	17 (10)	21 (8)	49 (35)	15 (4)	102 (57)
Western hemlock	1 (1)	9 (5)	20 (19)	7 (2)	37 (27)
Mountain hemlock	0 (0)	1 (0)	3 (2)	1 (1)	5 (3)
Hemlock ^b	0 (0)	7 (5)	3 (3)	3 (3)	13 (11)
Yellow-cedar	0 (0)	0 (0)	1 (1)	2 (2)	3 (3)
Unknown ^a	1 (1)	7 (4)	3 (1)	165 (54)	176 (60)
Total	19 (12)	45 (22)	79 (61)	193 (66)	336 (161)

NOTE: Values are totals for primary plus secondary gap makers (in parentheses are numbers of primary gap makers).

^aIndividuals in a sufficiently advanced state of decay that their species or the original mode of mortality could not be determined.

^bIdentifiable only to the genus.

TABLE 6. Number of gap makers in each decay class, by type of mortality

Class	Type of mortality				Total
	Uprooted	Snapped	Standing	Unknown ^a	
Young	4 (2)	6 (2)	20 (16)	0 (0)	30 (20)
Young-medium	4 (2)	5 (2)	28 (23)	0 (0)	37 (27)
Medium	9 (7)	15 (7)	22 (16)	2 (1)	48 (31)
Medium-old	1 (0)	13 (8)	5 (4)	12 (6)	31 (18)
Old	0 (0)	6 (3)	4 (2)	86 (25)	96 (30)
Very old	1 (1)	0 (0)	0 (0)	93 (34)	94 (35)

NOTE: Values are totals for primary plus secondary gap makers (in parentheses are numbers of primary gap makers). See Table 2 for explanation of decay classes. Column totals are the same as those in Table 5.

^aIndividuals in a sufficiently advanced state of decay that their original mode of mortality could not be determined.

gap makers (leading to a lower fir:hemlock ratio among younger gap-maker age-classes), combined with a more rapid rate of decay for Pacific silver fir (leading to a lower ratio among older age-classes). There are no data with which to evaluate the first hypothesis, but the second is consistent with a gradual increase in fir in the canopy (Lertzman 1992). Since the same pattern holds for the comparison of fir to both mountain and western hemlock, the higher proportion of fir among medium gap makers is less likely to be a result of a directional change in climate.

With increasing time since mortality of the gap maker, an increasing proportion of the individuals were stumps that could not be assigned to a mortality class (Table 6). These older age-classes of gap makers were only common as primary gap makers in STRACHAN2. Gap filling in STRACHAN2 may be delayed by persistent spring snowpack because snow persists longer in the spring in this stand than in the others.

Patterns of release dates among saplings less than 5 m in height were not useful as indicators of the dates of gap creation. They were highly variable within a gap and broadly consistent among gaps. Averaged over all gaps, there was a mean number of years of released height growth of 10.4 years (SD = 3.4, $N = 250$). Most gap fillers that showed released sapling height growth were released within a few years of 10 years ago, even in gaps that were clearly very old based on the decay status of gap makers. This inconsistency may be due to the multiple gap maker origin of most gaps (i.e., the releases may date the most recent gap maker to contribute to the gap). However, it was often difficult to establish a clear correspondence between releases in particular gap fillers and individual recent gap makers.

Discussion

Percent of the forest in each canopy category

The 18% canopy gap observed at Cypress Provincial Park is near the mean observed for temperate forests, and higher than the mean for tropical forests (Lertzman 1989), but comparable to some of the stands in the American Pacific Northwest examined by Spies et al. (1990). There are fewer studies that have reported values for expanded gap, but the 52% reported here is higher than has been reported elsewhere (Runkle 1982; Veblen 1985). The closest reported value is 42%, calculated for mature Douglas-fir forest by Spies et al. (1990). The amount of open space in a forest at steady state is a balance between the rate of creation of gaps and filling in of gaps (Runkle 1982). The high overall percent gap in the forest at Cypress Provincial Park (canopy gap + expanded gap = 70%) probably results from a lower rate of filling in of gaps, leading to a longer mean residence time for open space and a higher steady state percent gap. We could not directly estimate the age of gaps (sensu Runkle 1981, 1990; Spies et al. 1990), but a low rate of filling (and consequent long tenure) is consistent with the decay states of gap makers and observed growth rates of saplings.

Growth rates in gaps, especially in the smaller size classes of saplings, are very slow compared with most other gap-regenerating systems that have been studied (compare Lertzman 1989 with Runkle 1982; Brokaw 1985b; Runkle and Yetter 1987; Canham 1988a; Uhl et al. 1988). Snow persists in gaps up to several weeks longer in the spring than in the adjacent closed canopy areas (in each of the four stands, in every year of the study, spring snowmelt under a closed canopy preceded adjacent gap areas by 1–3 weeks),

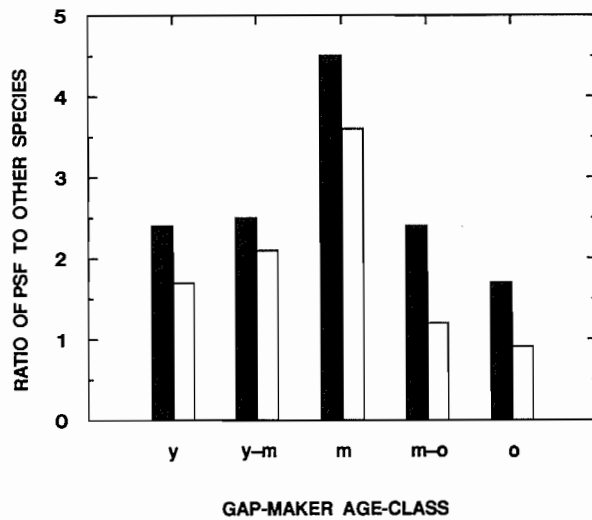


FIG. 5. Ratio of Pacific silver fir (PSF) to other species among gap makers of different age-classes. Open bars show the ratio of fir to both species of hemlock combined, and solid bars show the ratio of fir to western hemlock only. *y*, young; *m*, medium, *o*, old.

and until trees are tall enough to extend above the snowpack, this reduces their growing season substantially. A prolonged delay between the creation of a gap and it being filled can also be inferred from the distribution of decay classes of primary gap makers (many gaps may not have been filled even after 100–200+ years; see below). The large proportion of gap in the forest is thus a consequence of the long tenure of gaps before they are filled, which is in turn a consequence of short overall growing season, slow growth rates of young trees, and initial suppression of growth in gaps by persistent snowpack.

Spies et al. (1990) observed a slow rate of gap filling in old-growth Douglas-fir forests in the American Pacific Northwest where there was also a high percent of stand area in gap. In both their system and the one studied here, competition from the dense shrub layer that can develop in gaps remains an untested hypothesis for the cause of delays in gap filling (though preliminary results indicate that this could be important, K.P. Lertzman, unpublished results).

Size of gaps

The canopy gaps studied here are small relative to those of many other forests (Naka 1982; Romme and Martin 1982; Runkle 1982; Brokaw 1985a), though comparable to those found by Spies et al. (1990). Expanded-gap areas are similar to those of other forests where they have been measured (Runkle 1982; Veblen 1985). A predominance of small canopy gaps is consistent with the high frequency of standing mortality, which should form smaller gaps than uprooting (Putz et al. 1983; Spies et al. 1990). The size of expanded gaps should be less dependent on the mode of gap-maker mortality because it is a function of the spacing of the canopy trees that remain after the gap has formed. Also, with time after the formation of a gap, bordering trees grow laterally to fill a canopy gap (Runkle 1982; Runkle and Yetter 1987), so that the canopy gaps of the very old gaps will have shrunk substantially relative to their original size. Expanded-gap size will only be affected by mortality among bordering trees, or recruitment of new bordering individ-

TABLE 7. Forest turnover times (years) calculated as T_{fill} divided by the proportion of the forest in gap, given 18% canopy gap in the forest

T_{fill}	T_{res}	Turnover time
25	114	139
50	228	278
100	456	556
150	683	833
200	911	1111

NOTE: T_{fill} , time for a newly created gap to fill to the point where it is no longer gap; T_{res} , time that a tree is resident in the canopy after filling a gap. Turnover time, $T_{\text{fill}} + T_{\text{res}}$ (see text for further explanation).

uals to canopy size classes, and will thus be less affected by time since gap formation.

The disproportionate contribution of large gaps to the total gap area in the forest has been observed in other systems (Lawton and Putz 1988). This should be particularly important where gap-colonizing species have a threshold size for gaps in which they can successfully recruit (Brokaw 1985a, 1985b; Denslow 1980).

Both negative exponential (Brokaw 1982a; Foster and Reiners 1986; Lawton and Putz 1988; Spies et al. 1990) and lognormal (Naka 1982; Runkle 1982; Hubbell and Foster 1986b; Spies et al. 1990) patterns of gap size distributions have been observed. To some extent, different processes of gap formation may account for differences in the shape of size distributions. For instance, in many tropical forests, branch falls create many small gaps (Brokaw 1982a; Lawton and Putz 1988), but branch fall appears not to be a significant gap-forming process in temperate forests. Such differences in the shape of gap size distributions may also result from differences in gap definitions (Brokaw 1982b), which may exclude branch fall created gaps or limit consideration to gaps created by the mortality of single trees.

Gap makers: mode of mortality and number per gap

The stands at Cypress Provincial Park are unusual in the degree to which standing mortality dominates the gap-forming processes. Most studies that have examined the mode of mortality and its consequences among gap-forming trees have focussed on windthrow and snapping of boles (Brewer and Merritt 1978; Putz and Milton 1982; Naka 1982; Romme and Martin 1982; Foster and Reiners 1983; Orians 1982; Putz et al. 1983; Brokaw 1985a; Veblen 1985; Lawton and Putz 1988; Uhl et al. 1988). However, standing death has been reported as an important mode of mortality in a variety of tropical and temperate gap-regenerating forests (Lieberman et al. 1985; Veblen 1986; Armesto and Fuentes 1988; Martinez-Ramos et al. 1988; Taylor and Zisheng 1988b; Spies et al. 1990), and it is increasing in importance among high-elevation spruce in north eastern North America, possibly as a consequence of air pollution (Foster and Reiners 1986). Windthrow or wind-related breakage appear to be dominant forms of noncatastrophic mortality in many other coniferous forests of northwestern North America (Franklin et al. 1987; Franklin and DeBell 1988) as well.

A gap disturbance regime dominated by standing mor-

tality produces regeneration opportunities very different from a regime dominated by uprooting. Uprooting occurs suddenly, and just as suddenly it changes the moisture and temperature regimes at the soil surface, and the competitive regimes above and below ground. A tree succumbing to pathogens may die over a number of years, slowly losing foliage and root volume. Standing mortality differs not only in the rate of mortality, but also in the intensity of disturbance. Standing mortality creates relatively small gaps slowly and favours tolerant species, such as Pacific silver fir, that are able to take advantage of intermediate light environments. It also favours those individuals already present relative to those that germinate after gap formation (Putz et al. 1983). In such a system, species dependent on woody substrates that do not become available until some time after gap formation are at a disadvantage.

The forests at Cypress Provincial Park are also unusual in the predominance of multiple gap makers (though see Armesto and Fuentes 1988; Taylor and Zisheng 1988b; Spies et al. 1990). This is particularly notable, because while some gap makers died at the same time, most gaps represent the combined results of different gap making events separated substantially in time. Repeat disturbance and expansion of canopy gaps by mortality among peripheral trees have been observed in other systems (Foster and Reiners 1986; Runkle and Yetter 1987; Runkle 1990), and in one tropical forest, new gaps were shown to occur closer to old ones than expected by chance (Lawton and Putz 1988). However, the slow rate of filling in at Cypress Provincial Park enhances the consequences of such processes. Though tree falls can be more frequent at the edges of gaps (Hubbell and Foster 1986b; Lawton and Putz 1988), sequential gap-making episodes appear to be less often of primary importance in the tropics, where turnover times and rates of filling in of gaps tend to be faster (for instance, compare Runkle (1985) with Brokaw (1985a), and Runkle (1982) and Runkle and Yetter (1987) with Brokaw (1985b) and (1987)).

Forest turnover time

It would be useful to be able to summarize data on the creation and filling of gaps in a single statistic that represented the overall rate of turnover of space in the forest. Forest turnover time can be calculated in several ways (Hartshorn 1978; Runkle 1982; Romme and Martin 1982; Bongers et al. 1988; Lertzman 1989). We used a method based on the proportionality between the amount of forest in gap and canopy phases and the amount of time spent in each phase: the turnover time equals the time taken for a gap to be filled (T_{fill}) divided by the proportion of the forest in gap (P_{gap}). Table 6 shows turnover times given the observed 18% of the forest in gap, and a range of estimates for the time taken to fill gaps (T_{fill}). T_{res} is the length of time that trees are resident in the canopy after filling a gap. Since the turnover time is also equal to $T_{\text{fill}} + T_{\text{res}}$, T_{res} can be obtained as well.

If, on average, gaps take 125 years to fill, mean turnover time for this forest should be in the neighborhood of 694 years, and residence times for canopy trees should be near 569 years. If this turnover time is accurate, it would be among the longest that has been reported for a gap-regenerating forest.

The range of estimates for T_{fill} in Table 6 is greater than that reported in most other systems (Romme and Martin

1982; Runkle 1982; Veblen 1985; Bongers et al. 1988). However, Foster and Reiners (1986) estimated a maximum gap age of 100 years for a subalpine forest in New Hampshire, and Spies et al. (1990) found that most gaps in their old-growth stands exceeded 50 years in age and some probably exceeded 150 years. The range of T_{fill} in Table 6 is consistent with the decay class distribution of gap makers, and the values for T_{res} are consistent with the data on tree ages and lengths of suppression at Cypress Provincial Park (Lertzman 1989). The period of suppression observed in canopy trees, however, is not equivalent to the T_{fill} for the gap(s) in which they were recruited; it is probably substantially longer and represents portions of several T_{fill} values for different gaps. Thus, the total longevity of canopy trees will often exceed the turnover time (Runkle 1982).

Without data on decay rates and (or) a detailed stem analysis of gap fillers, it is not possible to estimate accurate T_{fill} values. In addition, gaps will take a variable length of time to fill, and trees will occupy the space filled for a variable length of time, irrespective of how long the gap took to fill. Many combinations of T_{fill} and T_{res} probably occur, and an accurate estimate of the true mean (or median) turnover time could only be calculated if the distribution of T_{fill} were known. The range 50–200 years used in Table 6 should bracket most of the variation in actual T_{fill} .

The accuracy of the turnover time estimate also depends critically on the amount of gap in the forest being at steady state. There are no data with which to assess this directly. However, even if the estimate of 694 years is high by 30%, the stands at Cypress Provincial Park have turnover times well above average for temperate forests (Lertzman 1989), and the general conclusion of slow turnover is holds.

There were several gaps in STRACHAN2 that only contained gap makers in an advanced state of decay, yet had little tree regeneration growing within them. They resembled the shrub meadows of the subalpine parkland 100–200 m higher in elevation. The trees that were present were mostly less than 1 m in height and resembled the young trees invading subalpine meadows in response to the warmer 20th century climate (Brink 1959; Franklin et al. 1971). It may be that the Little Ice Age effectively suppressed tree growth in some gaps in STRACHAN2, maintaining them as persistent gaps with effectively infinite T_{fill} .

In summary, the long turnover time for the Cypress Provincial Park forest reflects the slow time scale of several important component processes of forest turnover. In the absence of major disturbances to the canopy, potential recruits are first suppressed by canopy dominants and then by persistent spring snowpack in gaps, effectively delaying the process of filling gaps. Because canopy gaps are narrow, owing to the primacy of standing death as a mode of mortality, they may often be filled by the lateral growth of adjacent canopy trees before new recruits are able to fill them from below. This results in new recruits requiring several periods of suppression and release in successive gaps before they can recruit to the canopy. As a consequence, the faster growing, more light demanding species, western hemlock, occurs in much fewer numbers in the understory than the slower growing, more shade tolerant Pacific silver fir. The structural aspects of gap dynamics described here influence strongly the current composition of the sapling layer (Lertzman 1989) and the patterns of transitions from gap makers to gap fillers (Lertzman 1992).

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- ARMESTO, J.J., and FUENTES, E.R. 1988. Tree species regeneration in a mid-elevation, temperate rain forest in Isla de Chiloe, Chile. *Vegetatio*, **74**: 151-159.
- AUBREVILLE, A.M.A. 1938. La forêt coloniale : les forêts de l'Afrique occidentale, française. *Ann. Acad. Sci. Colon. Paris*, **9**: 1-245.
- BAZZAZ, F.A. 1983. Dynamics of wet tropical forests and their species strategies. In *Physiological ecology of plants of the wet tropics*. Edited by E. Medina, H.A. Mooney, and C. Vasquez-Yanes. Dr. W. Junk, Publishers, Boston.
- BAZZAZ, F.A., and PICKETT, S.T.A. 1980. The physiological ecology of tropical succession: a comparative review. *Annu. Rev. Ecol. Syst.* **11**: 287-310.
- BEATTY, S.W., and STONE, E.L. 1986. The variety of microsites created by tree falls. *Can. J. For. Res.* **16**: 539-548.
- BONGERS, F., POPMA, J., MEAVE DEL CASTILLO, J., and CARABIAS, J. 1988. Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico. *Vegetatio*, **74**: 55-80.
- BRAY, J.R. 1956. Gap phase replacement in a maple-basswood forest. *Ecology*, **37**: 598-600.
- BREWER, R., and MERRITT, P.G. 1978. Wind throw and tree replacement in a climax beech-maple forest. *Oikos*, **30**: 149-152.
- BRINK, V.C. 1959. A directional change in the subalpine forest-heath ecotone in Garibaldi Park, British Columbia. *Ecology*, **40**: 10-16.
- BROKAW, N.V. 1982a. Treefalls: frequency, timing, and consequences. In *The ecology of a tropical forest: seasonal rhythms and long term changes*. Edited by E.G. Leigh, Jr., A.S. Rand, and D.M. Windsor. Smithsonian Institution Press, Washington, DC.
- _____. 1982b. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica*, **14**: 158-160.
- _____. 1985a. Treefalls, regrowth, and community structure in tropical forests. In *Natural disturbance: an evolutionary perspective*. Edited by S.T.A. Pickett and P.S. White. Academic Press, New York.
- _____. 1985b. Gap-phase regeneration in a tropical forest. *Ecology*, **66**: 682-687.
- _____. 1987. Gap-phase regeneration of three pioneer tree species in a tropical forest. *J. Ecol.* **75**: 9-19.
- BROOKE, R.C., PETERSON, E.B., and KRAJINA, V.J. 1970. The Subalpine Mountain Hemlock Zone. *Ecol. West. North Am.* **2**: 147-349.
- CANHAM, C.D. 1988a. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. *Ecology*, **69**: 786-795.
- _____. 1988b. An index for understory light levels in and around canopy gaps. *Ecology*, **69**: 1634-1638.
- CHAMBERS, J.M., CLEVELAND, W.S., KLEINER, B., and TUKEY, P.A. 1983. Graphical methods for data analysis. Wadsworth International Group, Belmont, CA.
- CHAZDON, R.L., and FLETCHER, N. 1984. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *J. Ecol.* **72**: 553-564.
- COLLINS, B.S., DUNNE, K.P., and PICKETT, S.T.A. 1985. Responses of forest herbs to canopy gaps. In *The ecology of natural disturbance and patch dynamics*. Edited by S.T.A. Pickett and P.S. White. Academic Press, New York.
- CONNELL, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science (Washington, D.C.)*, **199**: 1302-1310.
- CULLEN, P.J. 1987. Regeneration patterns in populations of *Athrotaxis selaginoides* D. Don from Tasmania. *J. Biogeogr.* **14**: 39-51.
- DENSLOW, J.S. 1980. Gap partitioning among tropical rainforest trees. *Biotropica*, **12**(Suppl.): 47-55.
- _____. 1985. Disturbance mediated coexistence of species. In *The ecology of natural disturbance and patch dynamics*. Edited by S.T.A. Pickett and P.S. White. Academic Press, New York.
- _____. 1987. Tropical rainforest gaps and tree species diversity. *Annu. Rev. Ecol. Syst.* **18**: 431-451.
- EIS, S. 1962. Statistical analysis of several methods for estimation of forest habitats and tree growth near Vancouver, B.C. University of British Columbia, Faculty of Forestry, Vancouver. For. Bull. **4**.
- FOSTER, J.R., and REINERS, W.A. 1983. Vegetation patterns in a virgin subalpine forest at Crawford Notch, White Mountains, New Hampshire. *Bull. Torrey Bot. Club*, **110**: 141-153.
- _____. 1986. Size distribution and expansion of canopy gaps in a northern Appalachian spruce-fir forest. *Vegetatio*, **68**: 109-114.
- FRANKLIN, J.F., and DEBELL, D.S. 1988. Thirty-six years of tree population change in an old-growth *Pseudotsuga-Tsuga* forest. *Can. J. For. Res.* **18**: 633-639.
- FRANKLIN, J.F., and DYRNESS, C.T. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8.
- FRANKLIN, J.F., and HEMSTROM, M.A. 1981. Aspects of succession in coniferous forests of the Pacific Northwest. In *Forest succession: concepts and application*. Edited by D.C. West, H.H. Shugart, and D.B. Botkin. Springer-Verlag, New York.
- FRANKLIN, J.F., MOIR, W.H., DOUGLAS, G.W., and WIBERG, C. 1971. Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. *Arct. Alp. Res.* **3**: 215-224.
- FRANKLIN, J.F., SHUGART, H.H., and HARMON, M.E. 1987. Tree death as an ecological process: the causes, consequences and variability of tree mortality. *BioScience*, **37**: 550-556.
- FRANKLIN, J.F., MOIR, W.H., HEMSTROM, M.A., GREENE, S.E., and SMITH, B.G. 1988. The forest communities of Mount Ranier National Park. U.S. Department of the Interior, National Park Service, Washington, DC. *Sci. Monogr. Ser.* **19**.
- GRAHAM, R.L., and CROMACK, K., JR. 1982. Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. *Can. J. For. Res.* **12**: 511-521.
- GREEN, R.N., COURTIN, P.J., KLINKA, K., SLACO, R.J., and RAY, C.A. 1988. Site diagnosis, tree species selection and slash-burning guidelines for the Vancouver Forest Region. B.C. Ministry of Forests, Victoria. *Land Manage. Handb.* **8**.
- GRUBB, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev. Camb. Philos. Soc.* **52**: 107-145.
- HARTSHORN, G.S. 1978. Tree falls and tropical forest dynamics. In *Tropical trees as living systems*. Edited by P.B. Tomlinson and M.H. Zimmerman. Cambridge University Press, Cambridge.
- HEMSTROM, M.A., and FRANKLIN, J.F. 1982. Fire and other disturbances of the forests in Mount Ranier National Park. *Quat. Res.* **18**: 32-51.
- HUBBELL, S.P., and FOSTER, R.B. 1986a. Biology, chance, and history and the structure of tropical rainforest tree communities. In *Community ecology*. Edited by J. Diamond and T.J. Case. Harper and Row, New York. pp. 314-329.
- _____. 1986b. Canopy gaps and the dynamics of a neotropical forest. In *Plant ecology*. Edited by M.J. Crawley. Blackwell Scientific Publications, Oxford. pp. 77-96.
- JONES, E.W. 1945. The structure and reproduction of the virgin forest of the north temperate zone. *New Phytol.* **44**: 130-148.

- KOTAR, J. 1972. Ecology of *Abies amabilis* in relation to its altitudinal distribution and in contrast to its common associate *Tsuga heterophylla*. Ph.D. dissertation, University of Washington, Seattle.
- KRAJINA, V.J. 1970. Ecology of forest trees in British Columbia. *Ecol. West. North Am.* 2: 1-146.
- LAWTON, R.O., and PUTZ, F.E. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. *Ecology*, 69: 764-777.
- LERTZMAN, K.P. 1989. Gap-phase community dynamics in a sub-alpine old growth forest. Ph.D. thesis, University of British Columbia, Vancouver.
- _____. 1992. Patterns of gap-phase replacement in a sub-alpine, old-growth forest. *Ecology*. In press.
- LIEBERMAN, M., LIEBERMAN, D., PERALTA, R., and HARTSHORN, G. 1985. Mortality patterns and stand turnover rates in a wet tropical forest in Costa Rica. *J. Ecol.* 73: 915-924.
- LONG, J.N. 1976. Forest vegetation dynamics within the *Abies amabilis* Zone of a western Cascades watershed. Ph.D. dissertation, University of Washington, Seattle.
- LUTZ, H.J. 1940. Disturbance of forest soil resulting from uprooting of trees. *Yale Univ. Sch. For. Bull.* 45.
- MARTINEZ-RAMOS, M., ALVAREZ-BUYLLA, E., SARUKHAN, J., and PINERO, D. 1988. Treefall age determination and gap dynamics in a tropical forest. *J. Ecol.* 76: 700-716.
- MEANS, J.E., CROMACK, K., JR., and MACMILLAN, P.C. 1985. Comparison of decomposition models using wood density of Douglas-fir logs. *Can. J. For. Res.* 15: 1092-1098.
- MLADENHOFF, D.J. 1987. Dynamics of nitrogen mineralization and nitrification in hemlock and hardwood treefall gaps. *Ecology*, 68: 1171-1180.
- NAKA, K. 1982. Community dynamics of evergreen broadleaf forests in southwestern Japan. 1. Wind damaged trees and canopy gaps in an evergreen oak forest. *Bot. Mag. Tokyo*, 95: 385-399.
- NAKASHIZUKA, T. 1983. Regeneration process of climax beech (*Fagus crenata* Blume) forests. III. Structure and development processes of sapling populations in different aged gaps. *Jpn. J. Ecol.* 33: 409-418.
- ORIAN, G.H. 1982. The influence of tree-falls in tropical forests in tree species richness. *Trop. Ecol.* 23: 255-279.
- POJAR, J., KLINKA, K., and MEIDINGER, D.V. 1987. Biogeoclimatic ecosystem classification in British Columbia. *For. Ecol. Manage.* 22: 119-154.
- POORE, M.E.D. 1968. Studies in Malaysian rainforest. *J. Ecol.* 56: 143-189.
- PUTZ, F.E., and MILTON, K. 1982. Tree mortality rates on Barro Colorado Island. In *The ecology of a tropical forest: seasonal rhythms and long term changes*. Edited by E.G. Leigh, Jr., A.S. Rand, and D.M. Windsor. Smithsonian Institution Press, Washington, DC.
- PUTZ, F.E., COLEY, P.D., LU, K., MONTALVO, A., and AIELLO, A. 1983. Uprooting and snapping of trees: structural determinants and ecological consequences. *Can. J. For. Res.* 13: 1011-1020.
- ROMME, W.H., and MARTIN, W.H. 1982. Natural disturbance by treefalls in old-growth mixed mesophytic forest: Lilley Cornett Woods, Kentucky. In *Proceedings of the Central Hardwoods Forest Conference, IV*. Edited by R.N. Muller. University of Kentucky, Lexington. pp. 367-383.
- RUNKLE, J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology*, 62: 1041-1051.
- _____. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology*, 63: 1533-1546.
- _____. 1985. Disturbance regimes in temperate forests. In *The ecology of natural disturbance and patch dynamics*. Edited by S.T.A. Pickett and P.S. White. Academic Press, New York. p. 472.
- _____. 1990. Gap dynamics in an Ohio *Acer-fagus* forest and speculations on the geography of disturbance. *Can. J. For. Res.* 20: 632-641.
- RUNKLE, J.R., and YETTER, T.C. 1987. Treefalls revisited: gap dynamics in the southern Appalachians. *Ecology*, 68: 417-424.
- SOLLINS, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Can. J. For. Res.* 12: 18-28.
- SPIES, T.A., and FRANKLIN, J.F. 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. *Ecology*, 70: 543-545.
- SPIES, T., FRANKLIN, J.F., and KLOPSCH, M. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Can. J. For. Res.* 20: 649-658.
- STEPHENS, E.P. 1956. The uprooting of trees: a forest process. *Soil Sci. Soc. Am. Proc.* 20: 113-116.
- STEWART, G.H. 1986a. Population dynamics of a montane conifer forest, western Cascade Range, Oregon, U.S.A. *Ecology*, 67: 534-544.
- _____. 1986b. Forest development in canopy openings in old-growth *Pseudotsuga* forests of the western Cascade Range, Oregon. *Can. J. For. Res.* 16: 558-568.
- TAYLOR, A.H., and ZISHENG, Q. 1988a. Regeneration patterns in old-growth *Abies-Betula* forests in the Wolong Natural Reserve, Sichuan, China. *J. Ecol.* 76: 1204-1218.
- _____. 1988b. Tree replacement patterns in subalpine *Abies-Betula* forests, Wolong Natural Reserve, China. *Vegetatio*, 78: 141-149.
- THORNBURGH, D.A. 1969. Dynamics of the true fir-hemlock forests of the west slope of the Washington Cascade Range. Ph.D. Dissertation, University of Washington, Seattle.
- TRISKA, F.J., and CROMACK, K., JR. 1979. The role of wood debris in forests and streams. In *Forests: fresh perspectives from Ecosystem Analysis*. Edited by R.H. Waring. Proceedings of the 40th Biology Colloquium, Apr. 1979, Corvallis. Oregon State University Press, Corvallis.
- UGOLINI, F.C. 1982. Soil development in the *Abies amabilis* Zone of the central Cascades, Washington. In *Proceedings of the Biology and Management of True fir in the Pacific Northwest Symposium*, Feb. 1981, Seattle, WA. Edited by C.D. Oliver and R.M. Kenady. University of Washington, College of Forest Resources.
- UHL, C., CLARK, K., DEZZEO, N., and MAQUIRINO, P. 1988. Vegetation dynamics in Amazonian treefall gaps. *Ecology*, 69: 751-763.
- VEBLE, T.T. 1985. Forest development in tree-fall gaps in the temperate rain forests of Chile. *Natl. Geogr. Res.* 1: 162-183.
- _____. 1986. Treefalls and coexistence of conifers in subalpine forests of the central Rockies. *Ecology*, 67: 644-649.
- _____. 1989. *Nothofagus* regeneration in treefall gaps in northern Patagonia. *Can. J. For. Res.* 19: 365-371.
- VITOUSEK, P.M., and DENSLow, J.S. 1986. Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. *J. Ecol.* 74: 1167-1178.
- WATT, A.S. 1947. Pattern and process in the plant community. *J. Ecol.* 35: 1-22.
- WHITMORE, T.C. 1989. Canopy gaps and two major groups of forest trees. *Ecology*, 70: 536-538.
- WILKINSON, L. 1988a. SYGRAPH. SYSTAT, Inc., Evanston, IL.
- _____. 1988b. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, IL.