Patterns of Gap-Phase Replacement in a Subalpine, Old-Growth Forest

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Ecology, Vol. 73, No. 2. (Apr., 1992), pp. 657-669.

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PATTERNS OF GAP-PHASE REPLACEMENT IN A SUBALPINE, OLD-GROWTH FOREST[1]

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Abstract. Small-scale natural disturbances involving the death of one to a few trees and creating gaps in the forest canopy are key processes in the population and community ecology of many forests. I examined the patterns of replacement in gaps in a subalpine old-growth forest in southern coastal British Columbia to assess their role in the forest community. I found no evidence that self replacement or reciprocal replacement act to maintain the current community composition. Gapmaker–gapfiller comparisons indicated preferential replacement of all species by Pacific silver fir (*Abies amabilis*), suggesting that the community is undergoing successional change. Nor did gap size, location within a gap, or local canopy composition appear to exert a strong influence on the species composition of regeneration within the gap. The only circumstance where Pacific silver fir was not overwhelmingly dominant among gapfillers was on stumps, where almost all successful western hemlock (*Tsuga heterophylla*) gapfillers were located. These patterns suggest that neither species-specific interactions between gapmakers and gapfillers nor variability in gap environments is adequate to maintain the current composition of the forest canopy. However, caution is indicated in projecting a long-term trend from this short-term assessment of community trajectory.

Key words: Abies amabilis; *British Columbia; coexistence; forest; gaps; succession; transitions;* Tsuga heterophylla.

INTRODUCTION

Two classes of hypotheses have been proposed to explain patterns of tree-by-tree replacement in gap-phase regenerating forests. The first class relates the species of trees whose mortality creates gaps (gapmakers) to the species of the trees that replace them (gapfillers). The second class attempts to explain gapfiller species in relation to variable characteristics of the gap environment. In a gap-regenerating forest, the net result of the individual transitions of space from gapmakers to gapfillers determines whether or not there is a net change in species composition over time. The patterns of replacement of gapmakers can thus be used to assess whether, in sum, the current regime of disturbance to the canopy is sufficient to maintain the forest community or whether periodic larger scale disturbances are necessary (Harcombe and Marks 1978, Runkle 1981, Veblen 1986).

Processes of gap creation and filling are thought to play a central role in species coexistence in a variety of forests (Denslow 1980, 1987, Orians 1982, Canham 1989, Poulson and Platt 1989, Whitmore 1989). Variation in the physical environment within and among gaps can provide opportunities for species that could not establish under a closed canopy. Hypotheses of coexistence stress the differential ability of species to exploit gaps of different sizes and different portions of larger gaps. Alternatively, if most of the successful recruits in gaps were present before the gapmakers died, the role of gaps may be more distinct at a population than a community level, and their effect more one of reorganization than colonization (Glitzenstein et al. 1986).

In this paper, I examine the relationships of gapfiller species to gapmaker species and gap environment in a coastal subalpine forest in Cypress Provincial Park, southwest British Columbia. Fundamentally, I would like to know whether the replacement processes occurring in gaps act to maintain the current canopy composition or change it. Community composition could be maintained by either specific nonrandom gapmaker–gapfiller relationships (i.e., reciprocal replacement; Fox 1977), or by reversals of competitive asymmetries in particular parts of gaps, or gaps of different sizes (Denslow 1987). The data presented here will be examined with respect to the following (mostly not mutually exclusive) hypotheses:

Hypotheses about the identity of gapfillers: gapmaker–gapfiller comparisons

1) Self replacement by each species will maintain the current canopy composition.

2) Reciprocal replacement of canopy dominants will maintain current canopy composition. Reciprocal replacement has been proposed as a mechanism of long-term co-existence in several temperate forests domi-

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[1] Manuscript received 31 July 1990; revised 6 June 1991; accepted 11 June 1991.

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nated by two species (Fox 1977, Woods 1979, 1984, Runkle 1981).

3) Replacement of most gapmakers, irrespective of species, by one species of gapfiller will result in succession: a directional change in species composition over time (Drury and Nisbet 1973, Connell and Slatyer 1977, Horn 1981).

4) Random transitions between gapmakers and gapfillers will result in a slowly drifting community composition (Hubbell 1979, Chesson and Warner 1981, Chesson 1986, Hubbell and Foster 1986*a*).

Hypotheses about the identity of gapfillers: gap-environment–gapfiller interactions

5) Species will vary in the size of gaps in which they are most successful, leading to a partitioning of gaps among species by size (Denslow 1980, 1987, Bazzaz 1983, Brokaw 1985*a, b,* Hubbell and Foster 1986*b,* Whitmore 1989).

6) Due to an abundance of local seed sources, each species will be most successful in gaps where it is most abundant in the surrounding canopy (Sousa 1984).

7) Certain species will be most successful as gapfillers in particular locations within gaps (i.e., center vs. periphery; Orians 1982, Putz 1983, Brokaw 1985*a*, Beatty and Stone 1986).

8) Certain species will be most successful on particular substrates within gaps (Putz 1983, Christy and Mack 1984, Lawton and Putz 1988).

In the Cypress Park forest, one species, Pacific silver fir, occurs as a much higher proportion of the understory sapling population than of the canopy individuals (Lertzman 1989). For a variety of reasons, one cannot conclude from this alone that its canopy abundance is increasing (White et al. 1985). In particular, abundance in the understory prior to gap creation does not necessarily lead to abundance among the relatively few individuals successful in filling canopy gaps. In terms of the hypotheses presented above, I will first examine whether the gapmaker–gapfiller comparisons support a hypothesis indicating a net change in species composition or not (hypotheses 1–4), and then look for circumstances in the gap environment (i.e., particular sizes of gaps or substrates) where this dominance by firs is mitigated (hypotheses 5–8).

MATERIALS AND METHODS

Study sites

This research was carried out at Cypress Provincial Park in the Coast Range of southwestern British Columbia, just north of the city of Vancouver (49°25′ N, 123°12′ W). The forests are in the lower range of the Forested Subzone of the Mountain Hemlock Zone where it grades into montane forests of the Wetter Maritime Subzone of the Coastal Western Hemlock Zone (Brooke et al. 1970, Green et al. 1984, Pojar et al. 1987). This corresponds 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 the snow-free period is often <150 d. 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 [*Abies amabilis* (Dougl.) Forbes, Pinet.], western hemlock [*Tsuga heterophylla* (Raf.) Sarg.], mountain hemlock [*Tsuga mertensiana* (Bong.) Carr.], and Alaska yellow-cedar [*Chamaecyparis nootkatensis* (D. Don) Spach]. No other species of trees are common in the forested areas, though western white pine (*Pinus monticola* Dougl.) occurs sporadically. These stands are above the elevational limit for Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*]. They are near the upper elevational limit for western hemlock and the lower elevational limits for mountain hemlock and yellow-cedar.

The four dominant species vary in life history characters that might lead one to expect, a priori, differential ability to occupy gaps. All are classed as shade tolerant (Fowells 1965, Krajina 1970, Franklin and Dyrness 1973, Minore 1979), but the tolerance of Pacific silver fir exceeds that of the others. Despite their broad similarity in shade tolerance when compared with intolerant species, the four species do differ substantially in the life history characters and physiological parameters used to distinguish regeneration guilds. They vary in drought and snow tolerance, maximum growth rate, in the frequency of reproduction, seed size, and longevity (Fowells 1965, Kotar 1972, USDA 1974, Long 1976, Arno and Hammerly 1977, Waring and Franklin 1979, Franklin and Waring 1980, Grant 1980, Lassoie et al. 1986).

Data were collected from four stands at Cypress Park, all at 1050 ± 100 m elevation (Lertzman 1989, Lertzman and Krebs 1991). STRACHAN1, STRACHAN3, and HOLLY1 are on slopes (20°–30°) and have substantial components of western hemlock in their canopies. STRACHAN2 is on a nearly level bench and has a higher proportion of mountain hemlock than western hemlock.

Within the focal stands at Cypress there is no evidence of logging or of recent natural disturbance other than gap formation. Many large, old trees show evidence of having germinated on the uncharred stumps of other large trees, and the growth histories of canopy trees show evidence of having established and recruited under a gap-phase regeneration regime (Lertzman

TABLE 1. Number of gaps and gapmakers from each stand used to construct the matrix of transition frequencies.

Stand	Number of gaps	Number of definitive gapfillers
STRACHAN1	15	49
STRACHAN2	16	77
STRACHAN3	19	64
HOLLY1	10	36
Total	60	226

1989). The most recent layer of charcoal in the soil profile has been estimated at >1500 yr in age (K. P. Lertzman and L. Brubaker, *unpublished data*).

Trees of all species are broadly represented among age and size classes, with individuals of Pacific silver fir and both hemlock species exceeding published age records (maximum age at stump height for firs: 697 yr; for hemlocks: 944 yr; Lertzman 1989). Mean diameters were near 1m, depending on species and stand, with large individuals approaching 2 m at breast height.

Data on the gap size distribution and geometry, and other structural features of the Cypress Park forests are presented in Lertzman and Krebs (1991).

General gap sampling scheme

The gaps on which this data set is based were located by establishing permanently marked transects in the four stands and recording all expanded gaps (see definition below) intersecting the transects. This protocol is similar to that of Runkle (1982) and Veblen (1985). Transects were either 50 or 100 m long (depending on topographic and other discontinuities) and followed constant elevational contours. Transects were separated by 30 m and at least 300 m were sampled in each stand for a total of 1250 m. Further details on the transects are provided in Lertzman (1989).

Two of the four stands did not have substantial components of mountain hemlock (STRACHAN1 and STRACHAN3), and mountain hemlock was well represented among canopy trees in the remaining two (STRACHAN2 and HOLLY1). Though there are more gaps in the sample from the first category, there are equal numbers of definitive gapfillers from each (see below for definition of "definitive"). In the analyses presented here, data from the four stands are combined and dealt with as a single data set for the forest as a whole. I collected data on a total of 60 gaps, 23 in 1985 and 1986 and 37 in 1987. Table 1 shows the number of gaps and definitive gapfillers from each stand.

In 1987 I obtained estimates of canopy gap area (the central portion of the gap, defined by the vertical projection of the opening in the canopy onto the forest floor), expanded gap area (the peripheral portion of the gap, underneath the foliage of the trees whose canopies defined the edge of the canopy gap; Runkle 1982, Veblen 1985), the species composition of trees surrounding each gap, the proportion of area occupied by different substrates, and gap aperture (Lawton and Putz 1988). In 1985 and 1986 I did not measure canopy gap area or gap aperture.

Gapfiller data and definitions

I classed gapfillers in two categories in the field: the overall population of gapfillers (all trees >1 m and <10 m in height), and definitive gapfillers. Definitive gapfillers are those which, by virtue of their height, growth rate, and location, are those individuals deemed most likely to successfully occupy the open space in a gap. These were not simply the largest gapfillers because those individuals sometimes had broken tops or were located in the periphery of a gap. Because Pacific silver fir has a determinate growth form, their recent growth history could be easily assessed visually. There were usually one to a few individuals that were substantially taller than the rest of the gapfillers, were growing faster, and could be classed as definitive with little fear of error. Where two or more gapfillers could not be distinguished in terms of dominance, I considered them all definitive. Definitive gapfillers could be in canopy gap or in expanded gap. However, I did not consider gapfillers as definitive that were on the outer edge of the expanded gap and were therefore truly marginal to the gap, having little chance of growing foliage that would occupy part of the canopy gap.

Some gaps had no definitive gapfillers. This could occur in gaps that were recently created or in very small gaps that are filled by lateral growth of adjacent canopy trees (Runkle 1981, Runkle and Yetter 1987). All gaps in this study that lacked definitive gapfillers were being filled laterally by canopy trees.

For each gapfiller I recorded whether it was in the canopy or expanded portion of the gap (roughly center or periphery), rooting substrate (stump, log, forest floor), and associated gapmaker(s).

Gap characteristics

I estimated gap area by measuring at least eight radii from a point at the visual center of each gap. Where gaps were irregularly shaped, more radii were added as needed. For expanded gaps, these radii extended to a line between the centers of the boles of trees that defined the gap edge. For canopy gaps, radii extended to the edge of the canopies of the trees whose boles defined the expanded gap. Estimates of expanded gap area thus include the canopy gap portion. Gap aperture is the average of the four angles from the zenith to the edge of the canopy, along the main axes of a gap (Lawton and Putz 1988). I measured gap aperture at eye level.

For each gap in the sample, I counted the number of canopy trees of each species among the individuals whose canopies defined the canopy gap. These data are the estimate of local canopy composition for each gap.

To estimate the proportion of each gap represented by stumps, I censused line transects along the two major axes of gaps, recording substrate class at 1-m intervals.

Where statistical tests were conducted on proportions, for instance a regression of the proportion of a species among gapfillers on the proportion of gap area occupied by a particular substrate, all proportions were arcsine square root transformed.

Constructing the species-specific transition matrix

To establish gapmaker–gapfiller pairs, I identified the gapmaker with which each gapfiller was associated. In most cases, this was the gapmaker whose base was closest to the gapfiller. In multiple-gapmaker gaps (which were quite common; Lertzman and Krebs 1991), however, there were gapfillers that could not be associated exclusively with one gapmaker. For all cases where gapfillers appeared associated with > 1 gapmaker, I recorded all gapmakers with which the gapfiller appeared associated.

I recorded the species of each gapmaker that could be identified in the field. The longer the time since the gapmaker died, the less likely I was to be able to identify it. Many of the hemlock stumps could not be identified to species in the field, and it is not possible to separate mountain hemlock (M HEM) from western hemlock (W HEM) based on microscopic wood anatomy (Panshin and de Zeeuw 1980).

To construct the matrix of species-specific transition probabilities, I tallied the number of gapmakers of each species that were replaced by definitive gapfillers of each species. I represented each definitive gapfiller by a transition of the form: (gapmaker species) → (gapfiller species). Definitive gapfillers that were associated with > 1 gapmaker of different species were given a fractional transition for each gapmaker species. For instance, if a Pacific silver fir (PSF) was associated as a definitive gapfiller with two gapmakers, a western hemlock and a Pacific silver fir, then I tallied two transitions: 0.5(W HEM → PSF) and 0.5(PSF → PSF). After tallying all definitive gapfillers in this way, I summed the transitions for each species pair.

I treated separately the transitions that involved hemlock gapmakers only identified to genus. For gaps where 100% of the hemlocks in the surrounding canopy were of one species, I assumed that gapmakers recorded as generic hemlocks were of that species. Similarly, where the proportions of the two hemlock species were equal, and proportional transitions could be allocated equally within a gap, generic hemlock (HEM) gapmakers were allocated species in proportion to their abundance among the canopy trees surrounding a gap (biasing the results toward a conclusion of no change).

This left 14 "unit" transitions: 2 HEM → W HEM transitions, 1 HEM → AYC transition, 1 HEM → M HEM transition, and 10 HEM → PSF transitions. Since I recorded no other M HEM → W HEM transitions, but many W HEM → W HEMs, I assumed the 2 HEM → W HEMs were W HEM → W HEMs. There were no precedents for transitions from either hemlock species to Alaska yellow-cedar, so I assumed that the single HEM → AYC was a M HEM → AYC on the basis of edaphic factors. Because there were no examples of M HEM → W HEM, I made the HEM → M HEM a M HEM → M HEM. Finally, the remaining 10 HEM → PSF were allocated among the two hemlock species in the overall proportions in which they occurred in the canopy surrounding the gaps in which the transitions occurred (11 W HEM:16 M HEM).

A total of 56 of 118 transitions (56 of 75 transitions involving hemlock gapmakers) involved extrapolation of hemlocks from the genus to the species level.

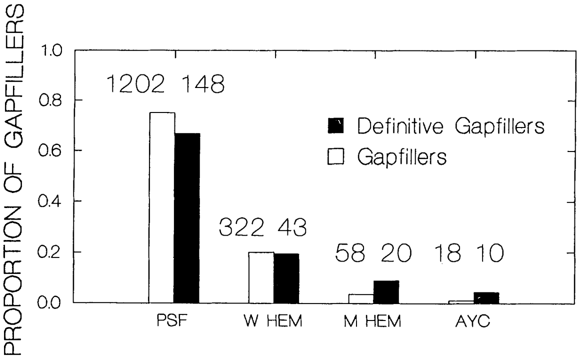

FIG. 1. Proportion of each species among definitive gapfillers and the overall gapfiller population. Number of individuals making up each proportion is above each column.

RESULTS

Composition of the overall gapfiller population

Pacific silver fir dominated the overall population of gapfillers with 75% of the individuals (Fig. 1). This represents an increase of 31.9% relative to its presence in the canopy (Lertzman 1989). Western hemlock, mountain hemlock, and yellow-cedar decreased among general gapfillers 15.5, 11.4, and 5.2%, respectively, relative to their presence in the canopy. Pacific silver fir loses slightly and mountain hemlock and yellow-cedar gain slightly when definitive gapfillers are considered rather than the overall gapfiller population (Fig. 1). The proportion of western hemlock remains almost the same when the general gapfiller population is compared with the definitive gapfillers. The difference between the two distributions in Fig. 1 is statistically significant ($\chi^2 = 44.0$; df = 3; $P < .001$), with the major contributions to the estimated chi-squared value coming from mountain hemlock and yellow-cedar.

Gapmaker–gapfiller transition matrix: hypotheses 1–4

Table 2 presents the species-specific transition frequencies based on gapmaker-gapfiller comparisons. The

TABLE 2. Matrix of transition frequencies between species of gapmakers and gapfillers. PSF = Pacific silver fir (*Abies amabilis*), W HEM = western hemlock (*Tsuga heterophylla*), M HEM = mountain hemlock (*Tsuga mertensiana*), AYC = Alaska yellow-cedar (*Chamaecyparis nootkatensis*). Matrix entries are the proportion of gapmakers of each species replaced by a given species of definitive gapfiller (rows sum to 1).

Gap-makers	Gapfillers				
	PSF	W HEM	M HEM	AYC	*N*
PSF	.61	.31	.08	0	48
W HEM	.77	.21	.02	0	47
M HEM	.69	0	.23	.08	13
AYC	.50	0	.25	.25	4
N	76	25	9	2	112

gapfiller species were not distributed randomly with respect to gapmaker species ($\chi^2 = 24.7$; df = 9; $P < .005$; though note that cells for yellow-cedar and mountain hemlock had low expected frequencies). All species were replaced by Pacific silver fir with a greater frequency than they replace themselves. Thus hypothesis 1, self replacement, can be rejected for all species but Pacific silver fir, and hypothesis 4, random replacement, can be rejected for the community as a whole.

There were few transitions between the low elevation species (western hemlock) and the two high elevation species (mountain hemlock and yellow-cedar). Western hemlock never replaced mountain hemlock or yellow-cedar, and was rarely replaced by them, suggesting that there is edaphic or topographic differentiation between these species on a local scale. In fact, definitive gapfillers of mountain hemlock and yellow-cedar were distributed nonrandomly among the stands sampled: stand STRACHAN2 was represented by only 13 out of the 60 gaps sampled, but contained 12 of 20 mountain hemlock definitive gapfillers and 7 of 10 yellow-cedar definitive gapfillers. The areas in the other stands where yellow-cedar or mountain hemlock definitive gapfillers were found were small patches similar to STRACHAN2 in forest openness or stature: either flat benches or slopes adjacent to stream courses (both of which consistently retained snowpack later in the spring than the surrounding forest). This differentiation in species composition of gapfillers among stands is consistent with variation in the canopy composition of those stands (Lertzman 1989).

Sample sizes for estimating transitions involving the two high elevation species are small, especially for yellow-cedar, and observations based on them must be tentative. However, just based on their relative abundances among gapfillers, there should have been more transitions between western hemlock and the two higher elevation species. For instance, based on its abundance as a definitive gapfiller alone (25 out of 112 = 0.22), western hemlock should have replaced mountain hemlock (0.22 × 13) = 2.9 times (Table 2), rather than 0 times. Similarly, mountain hemlocks should have replaced western hemlocks 5.6 times rather than once.

The four cells involving transitions between Pacific silver fir and western hemlock represent 80% of the observed transitions. When transitions between these two species are tested in isolation, the null hypothesis of no interaction between gapmaker and gapfiller species cannot be rejected ($\chi^2 = 1.7$; df = 1; $P = .190$). Most gapmakers of either species are replaced by silver fir. Pacific silver firs represent 72% of the definitive gapfillers (65 out of 90) in this submatrix, and they replace gapmakers in a proportion that doesn't deviate from this significantly. Because gapmaker and gapfiller species are independent for mutual transitions between Pacific silver firs and western hemlocks, hypothesis 2, reciprocal replacement, is not supported.

Of the four gapfiller–gapmaker hypotheses presented in the *Introduction,* the only one supported strongly by these data is hypothesis 3, succession: no species except Pacific silver fir shows strong trends towards self replacement, and all the others are replaced predomi-

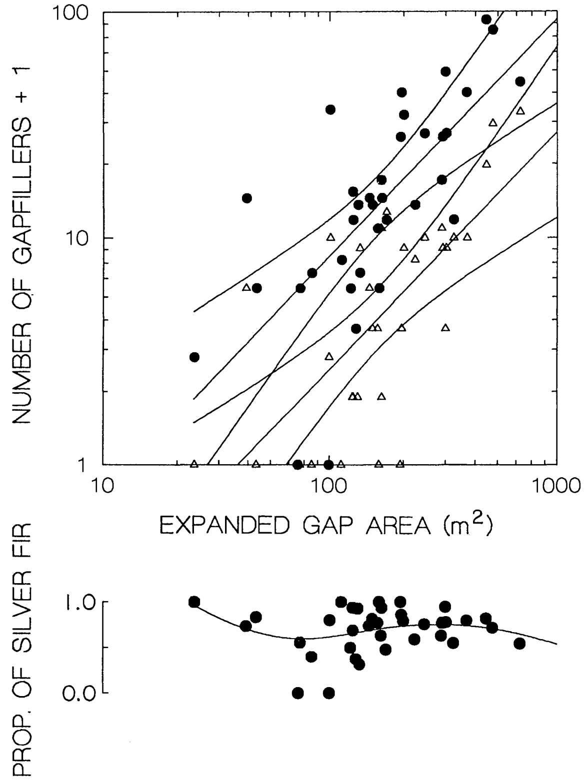

FIG. 2. Number of gapfillers of Pacific silver fir (*Abies amabilis*) and western hemlock (*Tsuga heterophylla*) and the proportion of Pacific silver fir among gapfillers, vs. expanded gap area. ● Pacific silver fir, △ western hemlock. For firs, $r^2 = 0.74$, $P < .001$; for western hemlock, $r^2 = 0.74$, $P < .001$. Linear regressions and their 95% confidence intervals are shown for the number of gapfillers, the line through the proportion of Pacific silver fir is a Distance Weighted Least Squares Smoothing (DWLS; Wilkinson 1988*a, b*).

nantly by firs. However, this is not related to interactions between gapmaker and gapfiller species, but solely to the numerical dominance of firs among the gapfillers.

Gapfiller species and gap size

The number of Pacific silver fir and western hemlock gapfillers both increased loglinearly with gap size, but over the range of measured gap sizes there was little variation in the proportion of Pacific silver fir among the gapfillers (Fig. 2). The densities of Pacific silver fir and western hemlock were also approximately constant over the range of gap sizes (Fig. 3a). Apparently, over most of the range of gap sizes, large gaps do not differ qualitatively from small ones for firs or western hemlocks, they are just larger. There are two differences between firs and western hemlocks. First, in gaps of all sizes, there are usually more firs present, and they are in greater densities than western hemlocks. Second, in very small gaps (expanded gap area < 100 m^2), western hemlocks are rarely present (lower x intercept for firs in Figs. 2, 3a).

For mountain hemlock and yellow-cedar, neither numbers of gapfillers (Fig. 4) or gapfiller density (Fig. 3b) show a consistent relationship with gap size. In both cases zero values dominate the data. When gaps with no yellow-cedar or mountain hemlock gapfillers present are excluded, the coefficients of determination (r^2) in Figs. 3b and 4 increase, but the regression remains nonsignificant.

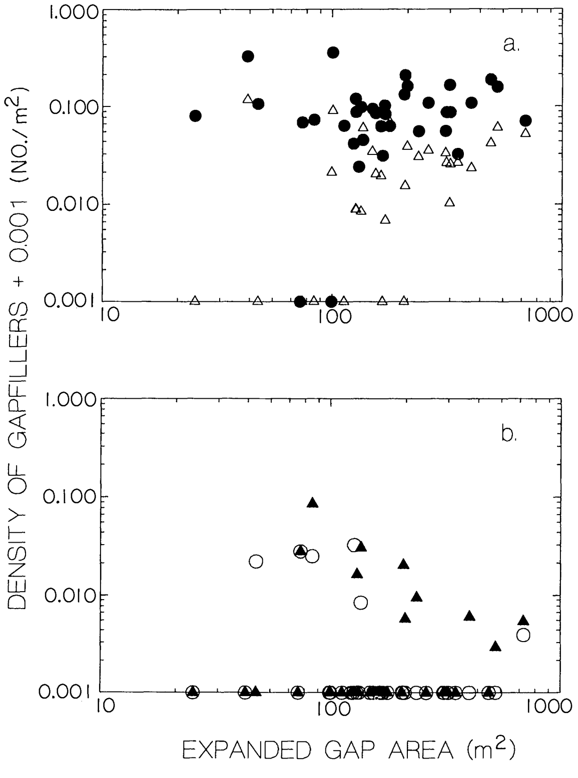

FIG. 3. Density of gapfillers vs. expanded gap area. (a) ● Pacific silver fir and △ western hemlock. (b) ○ Alaska yellow-cedar, ▲ mountain hemlock.

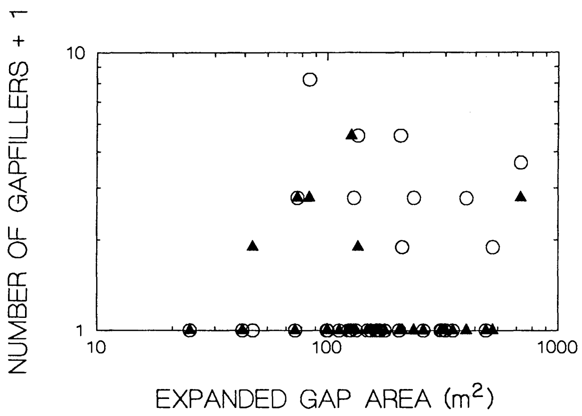

FIG. 4. Numbers of gapfillers vs. expanded gap area for Alaska yellow-cedar and mountain hemlock. ○ Alaska yellow-cedar, ▲ mountain hemlock.

I regressed numbers and density of total gapfillers, and of each species individually, on expanded gap area, canopy gap area, and gap aperture. No regressions of any of the gapfiller densities on any of the three independent variates were significant ($P > .05$ for each; all $r^2 < 0.1$). In the three cases where regressions of the number of gapfillers on gap area were significant (total number of gapfillers of all species, number of Pacific silver fir, number of western hemlock regressed on measures of gap size; all $P < .001$), the regressions on expanded gap area had higher r^2s than those on either canopy gap area or gap aperture (e.g., for total gapfillers: expanded gap $r^2 = 0.8$; canopy gap $r^2 = 0.69$; gap aperture $r^2 = 0.50$). Therefore, Figs. 2 through 4 plot gapfillers vs. expanded rather than canopy gap area.

Can we conclude from the lack of significant correlations between gapfiller numbers (mountain hemlock and yellow-cedar), and density (all species), and gap area, that no relationship exists? This is equivalent to accepting the null hypothesis, and requires knowledge of the statistical power of the tests (Toft and Shea 1983, Cohen 1987). Statistical power is a function of sample size, the significance level, and the effect size. The effect size in this case is r, the correlation coefficient. Given a sample size of 36–38, a two-tailed test with alpha = .05, and setting 0.8 as a lower limit for acceptable power, one could not confidently expect to detect a relationship unless r was at least ≈0.45 (Cohen 1987: Table 3.3.5). In the above cases, the correlation coefficients were substantially less than this. We can conclude, therefore, that it is very unlikely that strong relationships (i.e., $r > 0.45$) exist between gapfiller densities and gap area, but no inference can be made about the presence of weak relationships.

The relationships between numbers of definitive gap-

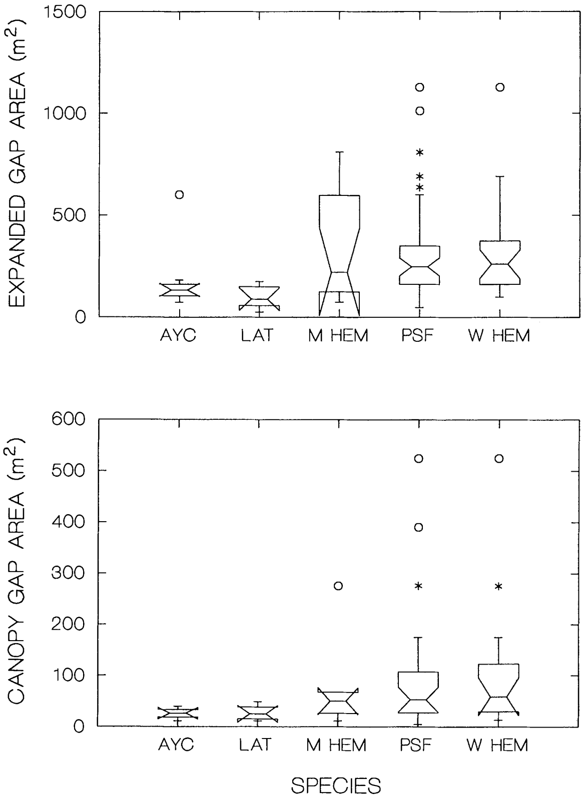

FIG. 5. Boxplots of the size distribution of canopy and expanded gaps containing at least one definitive gapfiller of each species. AYC is Alaska yellow-cedar, LAT are gaps being filled by lateral growth of adjacent canopy trees, M HEM is mountain hemlock, PSF is Pacific silver fir, and W HEM is western hemlock. The horizontal lines in the middle of the boxes are medians, the boxes delimit the central 50% of the data (the horizontal lines marking the box ends are upper and lower quartiles), and the points where the angled sides of the box reach the maximum box width are equivalent to 95% confidence intervals around the medians (Chambers et al. 1983, Wilkinson 1988*a, b*). * and O indicate gaps that exceed the area of the 3rd quartile (top of box) by 150% (*) or 300% (O) of the interquartile range (3rd − 1st quartile). Sample sizes for expanded gaps are (from left to right): 8, 7, 12, 46, 23, for canopy gaps: 4, 5, 6, 27, 16.

fillers and gap area are similar to those for gapfillers in general, but more variable. The numbers of firs and western hemlocks increase with gap size, but much less of the variation in definitive gapfiller numbers is explained by gap size than was the case for the overall gapfiller population ($r^2 = 0.17$ and 0.06, and $P = .001$ and .07, for firs and western hemlock, respectively). The only difference in trend between gapfillers in general and definitive gapfillers, is that while firs represented a high proportion of the general gapfillers in very small gaps (Fig. 2), they represented a smaller proportion of the definitive gapfillers in those gaps. Very small gaps tended to be filled by the lateral growth of adjacent canopy trees (Fig. 5; 4 out of 15 gaps with expanded gaps <100 m^2 in area as opposed to 7 of 60 gaps overall). The numbers of yellow-cedar and mountain hemlock definitive gapfillers show no relationship with gap size.

Another way to pose the question of whether species composition changes with gap size is to examine the distribution of the areas of gaps containing at least one individual of a given species. Fig. 5 presents boxplots (Chambers et al. 1983, Wilkinson 1988*a, b*) of gap area for gaps containing definitive gapfillers of each species, and those gaps being filled by lateral growth of adjacent canopy trees ("LAT"). These boxplots illustrate both the variation in the shape of the distribution of gap areas containing each species and the lack of overall differences among median gap sizes.

The distributions of canopy and expanded gap area for gaps containing Pacific silver fir and western hemlock are almost identical. The other three distributions (mountain hemlock, yellow-cedar, gaps filled by lateral growth of canopy trees) for canopy gap area do not have the long tails at large gap areas, and for yellow-cedar and those filled laterally, the median gap size is smaller. However, for the distributions of canopy gap areas, the 95% confidence intervals for all medians overlap. Considering expanded gap areas does not change the conclusion, though there is more variability in the shape of the distributions. Yellow-cedar was present almost entirely in small gaps, and only small gaps are filled laterally. However, other species were present in the small gaps as well.

Though there appear to be some differences among species in the size of gaps in which they were successful, and larger gaps have more gapfillers in them, hypothesis 5, coexistence promoted by variability in gap size, requires a reversal of the dominance of Pacific silver fir at some gap sizes. Because there is no suggestion of this in any of these data, hypothesis 5 is not supported.

Gapfiller species and local canopy composition

There was little relationship between the abundance of either Pacific silver fir or western hemlock in the canopy surrounding gaps, and their representation among definitive gapfillers (linear regressions on transformed proportions: firs: $r^2 = 0.1$, $P = .06$; western hemlocks: $r^2 = 0.07$, $P = .12$; Fig. 6). Yellow-cedar was represented by too few definitive gapfillers for this analysis. However, mountain hemlocks increased in frequency among definitive gapfillers with increasing representation in the canopy (r^2 of 0.50; $P < .001$).

We should be cautious in interpreting this correlation for mountain hemlock as causally related to the canopy composition surrounding the gap. Almost all gaps with a substantial proportion of mountain hemlock among definitive gapfillers were in stand STRACHAN2, where mountain hemlock and yellow-cedar reach their greatest abundance. With these data, the effect of abundant local seed sources cannot be separated from potential microclimatic or edaphic differences among stands. This does, however, suggest that current differences between stands are self maintaining.

Following the reasoning above, we can assess the likelihood that the lack of relationship for firs and western hemlocks is meaningful by examining statistical power. Again, the sample sizes are 36–38, $\alpha = .05$, and 0.8 is the lower limit for acceptable power. There is a very high probability ($\beta < .01$), that if as great a relationship existed for these two species as was seen for mountain hemlock (effect size = $r = 0.7$), that it would have been detected (Cohen 1987: Table 3.3.5). I could not confidently expect to detect relationships with effect size less than ≈ 0.44. Thus for these two species, if there is an effect of local canopy composition, it is weak.

In general, hypothesis 6, the effect of local seed sources, is supported weakly at best. Mountain hemlock is the only species that appears to show a strong effect of local canopy composition on gapfiller species, and true frequency dependence cannot be separated from other factors.

Gapfiller species and location in gap

Though more than twice as many definitive gapfillers were located in canopy gap as in expanded gap, the proportions represented by each species were almost identical between the two populations ($\chi^2 = 0.85$; df = 3; $P = .84$; this test should have been able to detect a fairly small effect size of 0.25 with power = 0.8; Cohen 1987: Table 3.15; Fig. 7). The greater number of definitive gapfillers in canopy gaps is even more striking when the total area available of each class of gap is considered. The total area of all canopy gaps measured was 2842 m^2. The total area for their associated expanded gap was 9226 m^2, 3.2 times as much expanded gap area as canopy gap area (for $N = 37$ gaps). In these gaps, there were 128 definitive gapfillers, 88 in canopy gap and 40 in expanded gap. This is many more in the canopy gap than would be expected on the basis of available area alone ($\chi^2 = 144.1$; df = 1; $P < .001$).

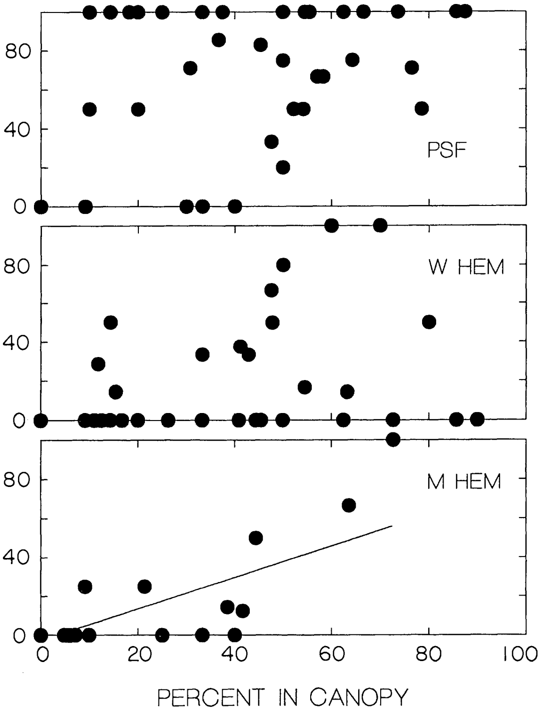

FIG. 6. Percent of each species among definitive gapfillers in each gap vs. its representation in the canopy surrounding the gap. The only species with a significant linear regression is mountain hemlock ($r^2 = 0.50$; $P < .001$).

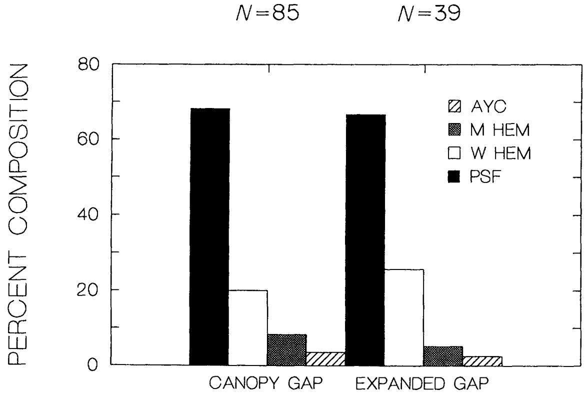

FIG. 7. Species composition among definitive gapfillers in canopy and expanded gaps. Sample sizes (N) refer to the total number of definitive gapfillers in each location.

The abundance of definitive gapfillers in canopy gap is not explained by a greater amount of woody substrate in canopy gap relative to expanded gap. There was no association between the abundance of woody substrates (stumps, logs, root throw mounds) and either class of gap (Lertzman 1989). Woody substrates were distributed among canopy and expanded gap in the same proportions in which the classes of gap occur in the forest (672 m of expanded gap, 342 m of canopy gap; 204 m of woody substrate in expanded gap, 99 m of woody substrate in canopy gap; $\chi^2 = 0.153$; df = 1; $.5 < P < .75$). Further, most of the definitive gapfillers were Pacific silver fir, which were not substrate limited.

Though a disproportionate number of the definitive gapfillers are located in canopy gaps, there is no difference in species composition in the two locations. The center and the periphery of gaps may differ in the levels of critical resources they offer, but they provide no basis for partitioning among the species, and hypothesis 7, partitioning by location in the gap, is not supported.

Gapfiller species and substrate

The different species of definitive gapfillers varied substantially in their distribution among substrates (χ^2

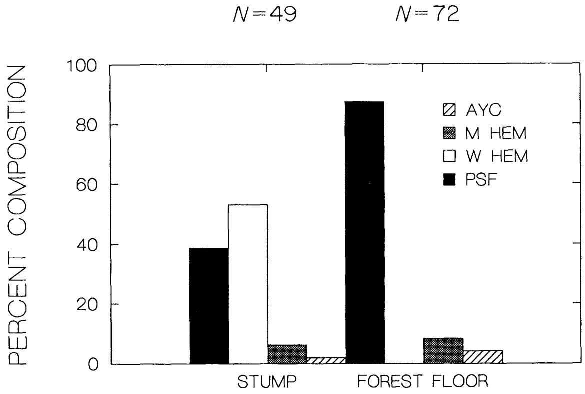

FIG. 8. Species composition among definitive gapfillers on the forest floor and on stumps. Sample sizes (*N*) refer to the total number of definitive gapfillers on each substrate.

= 55.8; df = 6; $P < .001$). Only 23% of the Pacific silver firs, but 96% of the western hemlocks were on stumps. Western hemlocks represented 55% of the population of definitive gapfillers on stumps, but 0% on the forest floor (Fig. 8). Mountain hemlock and yellow-cedar represented a small proportion of the individuals present on both stumps and the forest floor. In addition to the gapfillers shown in Fig. 8, there were two firs and one hemlock that had germinated on logs.

Though there was considerable variability among gaps in the proportion of gap area covered by woody substrates, there was no observable relationship between the proportion of western hemlock among either gapfillers or definitive gapfillers in a gap, and the proportion of gap area covered by woody substrate (for gapfillers: $N = 38$, $r^2 = 0.011$, $P = .52$; for definitive gapfillers: $N = 38$, $r^2 = 0.005$, $P = .69$). Multiple regression of the proportion of western hemlock definitive gapfillers on the proportion of each gap covered in woody substrate and expanded gap area together had nonsignificant slopes and r^2s approaching 0.

These data support hypothesis 8, that differential success among species on different substrates could play a role in maintaining some species in the community that would otherwise not recruit. Western hemlocks outnumber Pacific silver firs in the population of definitive gapfillers on stumps, the only circumstance found where firs were not overwhelmingly dominant among gapfillers. All but one of the western hemlocks in the transition matrix discussed above were on stumps.

DISCUSSION

Hypotheses 1–4: relating gapfiller species to gapmaker species

Either reciprocal replacement (Fox 1977, Woods 1979, 1984) or strong self replacement could act to stabilize community composition. However, I found no evidence that the species of gapmaker exerts an influence on the species of gapfiller. Instead, over the community as a whole, transitions were skewed in favor of one species, Pacific silver fir. As well, for transitions involving just the two most common species (Pacific silver fir and western hemlock, representing 80% of all transitions), gapfiller species were allocated to gapmakers in proportion to their abundance among the gapfillers.

Thus, in most cases, success in capturing space in gaps is proportional to a species' representation in the pool of potential gap colonists. Pacific silver fir is able to dominate this pool by virtue of its ability to persist as a suppressed sapling under a closed canopy and sustain release when a gap is created above it. The main deviations from this pattern do not involve the dominant gapfiller, Pacific silver fir, but rather the lack of mutual transitions between western hemlock and the two less common, high elevation species. The succession model seems well supported and based on gapmaker–gapfiller transitions alone, Pacific silver fir should have a greater relative importance in the canopy in the future.

Predictions for gapfillers and gap environment at Cypress Provincial Park

Based on the dominance of Pacific silver fir among the sapling population in the forest as a whole (Lertzman 1989), we could predict a priori, that unless the gap environments strongly favor the regeneration of another species, the gapfiller population would be dominated by firs. Because it is present in the understory prior to gap creation, Pacific silver fir should occur in gaps of all sizes, but might be expected to be most successful in smaller gaps where relatively rapid canopy closure restricts colonization by new individuals of other species (Hibbs 1982, Runkle 1982, Runkle and Yetter 1987).

Based on their life histories, we would have expected that the species other than firs should do better in larger gaps than small. We could have expected them, especially western hemlock, to experience increasing opportunity with increasing gap size. A variety of studies comparing the biology of Pacific silver fir and western hemlock have emphasized the hemlock's greater drought tolerance, faster juvenile growth rate, greater seed production and dispersal, and in general, its greater ability to colonize open space (Thornburgh 1969, Kotar 1972, Long 1976, Grant 1980, Wagner 1980). Through western hemlock is shade tolerant and occurs commonly in the understory at lower elevations, it appears unable to maintain this role in higher elevation communities.

By the same reasoning, it also seems reasonable to expect Pacific silver fir to be relatively indifferent to location within gaps (because most firs were present before the gap was created), and that the other species should be more successful in the center of gaps than in the periphery. If local seed sources limit gap colonization, it should show most distinctly in the less common species, mountain hemlock and yellow-cedar.

Hypotheses 5–8: relating gapfiller species to gap environment

Pacific silver fir successfully replaces most gapmakers, based primarily on its overall abundance among the gapfillers. Even so, its ability to dominate the community in the future would be limited if, at certain gap sizes, in certain locations in gaps, or on particular substrates, other species recruited to the canopy consistently (Denslow 1987). However, except for western hemlock recruiting on stumps, this is not the case.

There was no evidence that larger gaps differed qualitatively from small ones for the two dominant species: large gaps contained more trees, but not at higher densities or in different proportions. For the two less common species, even the number of individuals present did not increase with gap size. The predictions regarding how species dominance should change with gap size were not supported except for the presence of Pacific silver fir in gaps of all sizes.

The "partitioning by gap size" model has received support in a variety of other forests (Whitmore 1978, 1989, Denslow 1980, 1987, Runkle 1981, 1982, Hibbs 1982, Brokaw 1985*a, b,* Poulson and Platt 1989). Why not here? Though the four species at Cypress are very different in comparison to each other, they would all be classified as members of the same regeneration guild when compared to the diversity of regeneration niches among tropical trees or the mixed deciduous forests of the eastern United States. The range of variation among life history characters and the distinction among regeneration guilds is much greater in the tropical communities discussed by Denslow (1980, 1987), Bazzaz (1983), and Hubbell and Foster (1986*b*; and even they found inconclusive evidence for the gap size model). For instance, in Hubbell and Foster's plot in Panama, the 307 species of canopy trees belong to 58 families (Table 5; Hubbell and Foster 1986*c*), as opposed to two families at Cypress Park. Similarly, in her review of gap-dependent regeneration among a variety of tropical communities, Denslow (1980) tabulated 62 species in 34 families. In particular, the Cypress Park system lacks canopy species belonging to either the seed bank or animal-dispersed guilds, both of which are common among tropical gap colonists (Hubbell and Foster 1986*b*, Denslow 1987, Schupp et al. 1989). However, the low incidence of uprooting (Lertzman and Krebs 1991), and consequently, exposed mineral soil, might limit the effectiveness of buried seeds as a gap colonization strategy at Cypress Park. There are a variety of animal-dispersed herbs and shrubs (e.g., *Vaccinium* spp.) that effectively colonize gaps and are uncommon under a closed canopy, so in principle such a strategy could work, but there are no canopy species that exploit it. In general, Cypress Park lacks tree species that can exploit the short-lived, fast-growing, ruderal niche (such as is filled by red alder [*Alnus rubra*] at lower elevations).

In addition to the "limited variety of regeneration niches" argument, the range of variation in gap sizes and gap formation processes may be too small for reversal of the competitive asymmetry between Pacific silver fir advanced regeneration and new western hemlock recruits. Wagner (1980) found that in an unburned clearcut in the North Cascades of Washington State (970–1100 m elevation), western hemlock increasingly overtopped Pacific silver fir saplings with greater distance from the stand edge, whereas silver fir growth rate and dominance peaked near the stand edge. Western hemlock reached its greatest growth rate >50 m from the forest edge, where it would have experienced microclimates substantially more "open" than in the largest of the gaps I studied. The clearcuts near the stands at Cypress were free of snow up to a month earlier than any of the forest environments, and spring snowpack remained longer in gaps than in the adjacent understory. A longer growing season combined with more favorable microclimate during the growing season could lead to increased dominance by western hemlock at gap sizes larger than currently occur naturally.

Though gap sizes at Cypress Park are comparable to those in many other gap regenerating forests, large gaps at Cypress are the result of several gap creation events separated widely in time (Lertzman and Krebs 1991). This would give the advantage to a species relying on a pool of suppressed saplings because light levels would increase only gradually to those associated with the current large gap. The most common type of gap formation process at Cypress is slow, standing mortality, which would further contribute to this. Thus the lack of an important effect of gap size on competitive dominance can be attributed to (1) little variation in regeneration niches compared to systems where gap size is an important driving variable, (2) large gaps not being large enough for western hemlock dominance, and (3) large gaps being the result of several small gaps occurring contiguously over a long period, rather than the simultaneous mortality of enough trees to cause a sudden, major alteration of microclimate and light environment.

The cases where mountain hemlock and yellow-cedar were successful were mostly on flat benches that form cold air drainages and maintain late spring snowpack, such as stand STRACHAN2. This provides circumstantial evidence for the role of within-stand topographic variation in maintaining these species within forests at the lower range of their distributions. However, such conclusions must be tentative because of the small number of transitions for these species, especially for yellow-cedar.

Though definitive gapfillers were much more frequently found in the center than the periphery of gaps, the location in expanded or canopy gap did not influence the species composition among the gapfillers. Similarly, local canopy composition did not influence gapfiller species for the two most common species. Mountain hemlock definitive gapfillers tend to be associated with gaps where they have a substantial representation in the canopy, but canopy influence cannot be separated from topographic or edaphic factors in these data. In general, the dominance of Pacific silver firs among gapfillers, and their origin as suppressed saplings whose distribution was established prior to gap creation, obscures the potential impact of local seed sources on gapfiller composition. Because Pacific silver fir can build a pool of suppressed saplings over many decades of seed production, its representation among gapfillers need have little relationship to its abundance among seed sources.

The restriction of successful western hemlock regeneration to stumps may have several causes (Thornburgh 1969, Christy and Mack 1984, Harmon and Franklin 1989). However, its restriction to a low frequency substrate, combined with the current gap size distribution and mode of gap creation limit its ability to recruit in gaps.

In general, many of the relationships, or lack thereof, between gapfillers and gap environment are a consequence of the abundance of Pacific silver fir in the understory prior to gap creation. These individuals account for the majority of gapfillers, and their distribution has little to do with the characteristics of gaps that form around them. Similar lack of correlation between gapfillers and gap environment has been found in other forests where the suppressed sapling population is the primary origin of gapfillers (Uhl et al. 1988).

Gap-phase mediated coexistence?

In these stands, gap-phase processes do not appear to foster coexistence in the tree community. Gaps primarily exert an influence at a population rather than a community level, resulting in a reorganization of the status of pre-existing individuals, rather than facilitating colonization by new species. Gap environments may be necessary for successful recruitment, but are rarely sufficient for any species except Pacific silver fir. Under a changed disturbance regime, (i.e., if the gap size-frequency distribution had a longer upper tail) this might change. Larger scale, or higher intensity disturbances than this stand has experienced in the last several hundred years may be necessary for substantial recruitment of species other than Pacific silver fir.

However, under a changed climatic regime, we might see very different patterns than I found. This forest type appears quite sensitive to minor variation in both micro- and macroclimate. Strong growth responses to the 20th century warming trend have been documented at high elevations in Washington State (Graumlich and Brubaker 1986, Graumlich et al. 1989). As well, invasion of subalpine meadows by trees during the early part of this century has been seen regionally (Brink 1959, Franklin et al. 1971). It is possible that the current dominance of low- to mid-elevation species among gap recruits is a consequence of 20th century climate, and that during the colder period preceding this century, mountain hemlock and yellow-cedar experienced success in a broader range of sites within the stands than the cold air pockets to which they are now largely restricted.

On the one hand then, there is no evidence for strong mechanisms acting today that foster coexistence in this community; on the contrary, all the data indicate a rapid increase in Pacific silver fir at the expense of the other species. On the other hand, the pollen record indicates there has been no local exclusion of species in either the 1500–2000 yr since the last stand-destroying disturbance, or the last 4500 yr of forest history (K. P. Lertzman and L. Brubaker, *unpublished data*).

An alternative hypothesis to gap-phase mediated coexistence, is that coexistence is fostered by climatic variability combined with long life-spans and slow rates of community change relative to environmental change. This would postulate a phenomenon similar to the "storage effect" (Chesson and Warner 1981, Warner and Chesson 1985, Chesson 1986): long-lived individuals could persist through periods unfavorable for recruitment and serve as a source of recruits when better times return. In fact, differential longevity among species has been shown to mitigate dominance among gapfillers in models of other systems (White et al. 1985) and of this one (Lertzman 1989). Studies of gap-phase processes and forest community dynamics have focussed on early life history characters, the "regeneration niche" (Grubb 1977). Since gap-phase replacement reflects patterns of mortality as well as recruitment, it is important to consider later life history characters, the "senescence niche," as well.

ACKNOWLEDGMENTS

This research was submitted in partial fulfillment of the requirements for the Doctoral Dissertation at the University of British Columbia. I would like to thank the College of Forest Resources at the University of Washington, where part of this work was completed. I appreciate the enthusiastic field assistance of C. Trethewey, B. Walters, and E. Kellerhals. C. J. Krebs, J. P. Kimmins, B. McCune, W. E. Neill, T. T. Veblen, P. Zedler, and an anonymous reviewer made helpful comments on previous versions of this work. This research was supported by fellowships from the Killam Foundation, the National Sciences and Engineering Research Council, and the Science Council of British Columbia.

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