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However, some forests contain gaps that appear to have persisted for long periods of time, are associated with no obvious gap-maker, demonstrate little difference in edaphic characteristics compared to the adjacent forest (Spies et al., 1990; Ehrenfield et al., 1995; Ogden, 1996) and have little or no regenera-

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Vine maple gaps were sighted from existing transects (McGhee, 1996), which ran upslope, from east to west, at 50 m-intervals within the study site. Gap sites that met the following criteria were selected: at least one healthy vine maple clone beneath the canopy opening, no obvious gap makers or apparent edaphic characteristics, and no other deciduous tree species present. Paired canopy plots were located randomly in the nearby forest matrix, sufficiently far away (> 20 m) to exclude light and site effects associated with the persistent gap and with no obvious gap maker or apparent edaphic characteristics. See the work of Wardman (1997) for a more detailed description of the sampling design.

The expanded gap size was defined by the boles of the trees whose foliage defines the edge of the canopy opening (Lertzman, 1992). Eight radii were measured from the gap center, the results were charted, and a planimeter was used to estimate the expanded gap area (McGhee, 1996). A regression equation was developed to estimate canopy gap size using data for five vine maple gaps from Ogden (1996): canopy gap size =  $0.30 + 0.278$  (expanded gap size);  $r^2 = 0.78$ ,  $n = 5$ ,  $p = 0.046$ .

### 2.3. *Douglas-fir morphology*

The height of the 58 study trees and the diameter  
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Differences in site chronologies were tested by creating a 'difference' chronology, created by subtracting the mean canopy BAI chronosequence from the gap BAI chronosequence (Young et al., 1995). The 'difference' chronology was compared to a theoretical normal distribution with the same standard

Table 1

Characteristics of gap and closed canopy Douglas-fir (means of plot means,  $n = 10$  each for gap and canopy,  $p$ -values given; plot means were calculated from three trees per plot).

| Characteristic   | Gap         | CC          | Gap:CC | $p$ -values |
|--|-------------|-------------|--------|-------------|
| Breast-height tree age (yr)  | 62.8 (1.2)  | 63.5 (1.1)  | 0.99   | 0.17        |
| Tree DBH (cm)  | 60.5 (6.2)  | 49.8 (5.4)  | 1.21   | 0.002       |
| Tree BA (m <sup>2</sup> )  | 0.29 (0.06) | 0.20 (0.04) | 1.46   | 0.002       |
| Crown radius (m)   | 4.40 (1.2)  | 2.94 (0.5)  | 1.50   | 0.001       |
| Crown length (m)   | 22.0 (4.5)  | 17.7 (3.3)  | 1.24   | 0.03        |
| Crown volume (m <sup>3</sup> )   | 535 (154)   | 190 (73)    | 2.82   | 0.001       |
| Tree height (m)  | 48.4 (2.5)  | 46.1 (1.9)  | 1.05   | 0.06        |
| Site index   | 42.6 (2.5)  | 40.2 (1.9)  | 1.06   | 0.05        |
| Potential growing space (m <sup>2</sup> )                                  | 44.0 (13.4) | 27.4 (6.8)  | 1.61   | 0.05        |
| Site BA (m <sup>2</sup> ha <sup>-1</sup> )                                 | 69.7 (15.7) | 76.9 (23.4) | 0.91   | 0.41        |
| Recent BA productivity (m <sup>2</sup> ha <sup>-1</sup> yr <sup>-1</sup> ) | 1.07 (0.28) | 1.02 (0.31) | 1.05   | 0.67        |

The Gap:CC ratio denotes the value of the gap variable divided by the value of the closed canopy variable.

Values in parentheses are standard deviations.

Paired  $t$ -tests were used for all variables, except site index (Wilcoxin signed-rank test).

expanded gap sizes followed an exponential decay curve due to the high number of smaller gaps and relatively few larger gaps in the stand. Estimated canopy gap size ranged from 15 to 52 m<sup>2</sup> with a mean of 25 m<sup>2</sup>. All sampled Douglas-fir regenerated within a narrow, 7-year-period. The ages of Douglas-fir on both gap and canopy plots were normally distributed.

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ters that were 21% greater for gap vs. canopy plots resulted in mean BA that were 46% greater on gap vs. canopy plots (Table 1).

For Douglas-fir adjacent to gaps, we were unable to detect differences between the mean gap-side crown width (4.7" 1.1 m) and mean canopy-side width (4.1" 1.3 m;  $p = 0.26$ ). However, both were significantly greater in length than the mean crown radius of closed canopy Douglas-fir (2.9" 0.5 m; gap-side:  $p = 0.001$ ; canopy-side:  $p = 0.02$ ; Fig. 1). The gap-side crown (24.1" 2.8 m) was deeper than the canopy-side crown (19.9" 5.0 m;  $p = 0.02$ ) and was also deeper than the mean closed canopy crown (17.7" 3.3 m;  $p = 0.002$ ). No differences were detected between the canopy-side crown depth and the closed canopy crown depth ( $p = 0.30$ ; Fig. 1). The mean crown volume of Douglas-fir next to gaps was 182% greater than the mean volume for closed canopy Douglas-fir (Table 1).

The size of the expanded gap was statistically related to potential growing space ( $r^2 = 0.68$ ,  $p = 0.006$ ; Fig. 2a) and to site BA ( $r^2 = 0.60$ ,  $p = 0.01$ ; Fig. 2b). The largest gap was removed from these two analyses due to the large influence it had on the

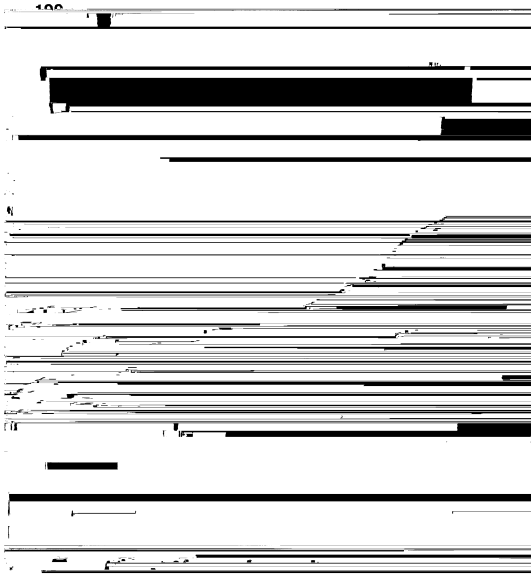


Fig. 2. Significant regressions of: (a) potential growing space vs. expanded gap size for Douglas-fir on gap peripheries ( $r^2 = 0.68$ ,  $n = 9$ ,  $p = 0.006$ ), and (b) site BA ( $r^2 = 0.60$ ,  $n = 9$ ,  $p = 0.01$ ) vs. expanded gap size. The largest expanded gap size was left out of these analyses due its very large influence on the regressions.

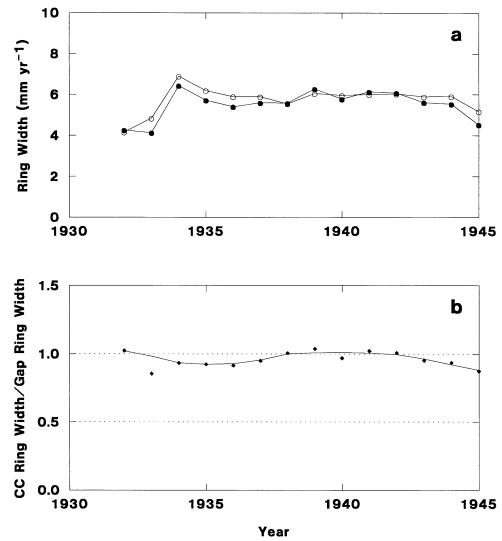


Fig. 3. (a) Mean radial growth of Douglas-fir saplings on gap (○) and closed canopy plots (●) ( $n = 10$  each for gap and canopy sites), and (b) the ratio of mean closed canopy (CC) radial growth to mean gap radial growth. A Lowess smoothing function with a tension of 0.4 was applied to the data (Wilkinson, 1990).

regressions (Wilkinson, 1990). Relationships between gap size and BA ( $r^2 = 0.01$ ,  $p = 0.78$ ) or crown volume ( $r^2 = 0.11$ ,  $p = 0.35$ ) were not detected.

### 3.3. Site chronologies

During the earliest stages of stand development, from 1932–1945, approximately 7 yr after seedling establishment and until the saplings were about 20 yr in total age, there were no detectable differences between the radial growth chronologies between gap and canopy plots (KS,  $n = 14$ ,  $p = 0.18$ ; Fig. 3). In the years after 1945, Douglas-fir adjacent to the gap increasingly outgrew those in the closed canopy (Fig. 4). The radial growth chronology for Douglas-fir adjacent to the gap was significantly higher than the radial chronology of closed canopy Douglas-fir (KS,  $n = 50$ ,  $p = 0.001$ ; Fig. 4a). The BAI chronologies also differed for this time period (KS,  $n = 50$ ,  $p = 0.001$ ; Fig. 4b). The ratio of canopy BAI to gap BAI displayed a logarithmic decay curve, starting at 0.84 in 1945 and reaching a minimum of approximately 0.60 in 1994 (Fig. 4c). Differing magnitudes of BAI between the site types led to different cumulative BA

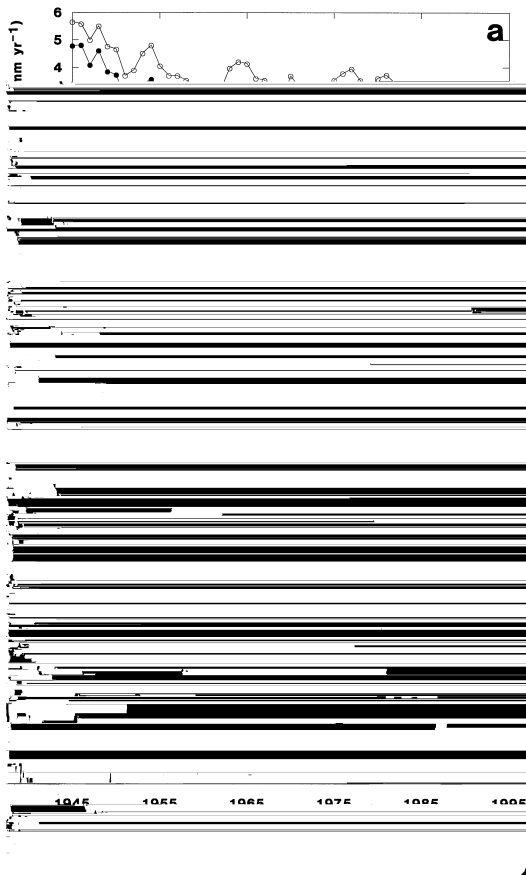


Fig. 4. (a) Radial growth chronologies, (b) BAI chronologies, (c) the ratio of mean canopy BAI to mean gap BAI and (d) cumulative BA (CBA) growth of gap (○) and canopy (●) Douglas-fir for 1945–1994. The numbers of cores representing each data point = 58 (29 trees). A Lowess smoothing function with a tension of 0.4 was applied to the data in (c) (Wilkinson, 1990). Chronologies in (a) and (b) are statistically different (KS,  $n = 50$ ,  $p < 0.001$ ).

(CBA) curves (Fig. 4d). Mean CBA for gap Douglas-fir increased at a greater rate than the CBA of closed canopy Douglas-fir (Fig. 4d), resulting in the BA differences shown in Table 1. By calculating the CBA chronosequence from the core data, the width of the chronosequence .

Table 2

Pearson correlation values and Bonferroni probabilities (shown in brackets) showing the interdependence of Douglas-fir crown volume, DBH, mean annual BAI for 1985–1994 (BAI (1985–1994)), and WAPA

|                 | DBH            | Crown volume   | BAI (1985–1994) |
|-----------------|----------------|----------------|-----------------|
| Crown volume    | 0.88 (- 0.001) | –              | –               |
| BAI (1985–1994) | 0.56 (0.01)    | 0.63 (0.003)   | –               |
| WAPA            | 0.90 (- 0.001) | 0.90 (- 0.001) | 0.56 (0.01)     |

ever, several outliers did occur in the data set which may explain why significant results were not obtained, even though the trend was an increase in site index as the percentage of vine maple increased. Three of the outliers occurred on a single, steeply-sloped (21°) plot. When this plot was removed from the analysis, the correlation was significant ( $r = 0.41$ ,  $n = 26$ ,  $p = 0.04$ ).

The mean potential growing space for Douglas-fir on the edge of gaps ranged from 27.0 to 74.1 m<sup>2</sup> and for Douglas-fir on canopy plots, values ranged from 19.4 to 39.4 m<sup>2</sup>. Potential growing space was significantly greater on gap plots vs. canopy plots (Table 1). Crown volume, BA and recent BA were highly correlated with potential growing space. Greater spacing between boles produced trees with larger crowns and boles and higher rates of BA growth (Table 2). The high degree of correlation between these biophysical characteristics and potential growing space lends validity to the WAPA index as an accurate indicator of growing space (Table 2).



due to the retention of lower branches for trees  
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nutrient cycling characteristics of the ground cover and tree species present. Similarly, vine maple appears to be establishing distinct areas of influence. The concentration of several bases (calcium, magnesium and potassium) in the forest directly beneath vine maple is higher than in the adjacent forest matrix (Ogden and Schmidt, 1997). This may be one reason for the higher site index associated with gap sites (Table 1).

Site BA and recent BA productivity were not significantly different between gap and canopy plots. Gap Douglas-fir trees respond to the 61% greater growing space they occupy around gaps by increased BA of 46% over Douglas-fir in the closed canopy (Table 1). Since radial growth on gap sites continues to exceed radial growth for trees in the closed canopy (Fig. 4a), there is no indication that site BA in the closed canopy may become significantly greater than site BA on gap sites.

#### 4.4. Implications for forest management

Site BA and recent BA productivity of Douglas-fir did not significantly differ between gap sites and sites in the adjacent forest matrix suggesting that the inclusion of persistent vine maple gaps within Douglas-fir stands similar to those in this study may not lead to losses in merchantable timber production. Forest managers may be able to realize the benefits of incorporating persistent vine maple gaps into managed stands without having a negative effect on timber production. There are many potential benefits to the inclusion of persistent vine maple gaps in Douglas-fir stands, including enhanced stand structural diversity (McGhee, 1996), retention of distinct habitats for wildlife (Haeussler et al., 1990); a food source for wildlife (Tappeiner and Zasada, 1993), enhanced diversity of bird species (Lertzman, unpublished); and possibly improved site fertility (Ogden and Schmidt, 1997). Persistent vine maple gaps may play a vital role in maintaining structural diversity during the stem-exclusion phase of stand development, when the role of developmental gaps is small (McGhee, 1996).

We recommend that in stands similar to the one in our study, forest managers promote the persistence of vine maple gaps through all successional stages. Allowing vine maple to propagate after harvesting

should lead to the natural development of persistent gaps. However, in some coastal forests in Washington and Oregon, vine maple is prolific and can form dense thickets, preventing merchantable conifers from regenerating (Haeussler et al., 1990). Where vine maple is a significant competitor, vine maple could be manually controlled to prevent the establishment of large persistent gaps. The natural gap size distribution in a stand would likely vary with such factors as slope, aspect, latitude, overstory species and site index. To ensure that gaps persist through stem-exclusion, vine maple clones need to become firmly established prior to canopy closure, because propagation of vine maple rarely occurs during stem-exclusion (O'Dea et al., 1995).

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