

Growth and form of Douglas-fir adjacent to persistent vine maple gaps in southwestern British Columbia

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Abstract

Vine maple is distinct in its ability to prevent conifer establishment and create persistent gaps. The goal of our research was to determine the influence of persistent vine maple gaps on the morphology, basal growth, and the productivity of Douglas-fir within a temperate rainforest. On 10 paired plots, gap size, Douglas-fir crown and bole size, site chronologies and site productivity were examined in a 75-year-old, second-growth stand. Median gap size was 80 m². Douglas-fir on the gap edge had 61% greater growing space, 182% larger crowns and 46% larger boles than Douglas-fir in the forest matrix. Crown expansion into the gap and the long-term presence of the canopy gap has resulted in crowns on the side of the tree adjacent to the gap that were 62% wider and 36% deeper than closed canopy crowns, resulting in crown volumes of Douglas-fir adjacent to gaps that were 182% greater than for trees in the closed canopy. Annual basal area increments (BAI) for Douglas-fir on gap plots exceeded BAI for Douglas-fir in the closed canopy by as much as 70%. Site index was significantly higher on gap plots when compared to closed canopy plots, indicating vine maple may play an important role in the long-term fertility of forest ecosystems where it is a dominant component in the understory. Site BA and recent BA productivity did not significantly differ between gap and canopy plots. Persistent gaps in Douglas-fir stands offer an opportunity for silviculturists to incorporate biodiversity and stand structural objectives into silvicultural systems without significant trade-offs in timber production. © 1998 Elsevier Science B.V.

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1. Introduction

Developmental gaps, openings in the forest canopy associated with the mortality of one to many trees, are common in many ecosystems and have received

considerable attention from researchers (Mladenoff, 1987; Canham et al., 1990; Spies et al., 1990; Lertzman, 1992; Orwig and Abrams, 1994; Lertzman et al., 1996). Developmental gaps fill over time by a combination of lateral expansion of adjacent conifers towards the gap center (Frelich and Martin, 1988), the release of understory saplings (Veblen, 1986) and/or seedling establishment within the gap (Spies et al., 1990; Lertzman, 1992).

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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 regeneration within the gap (McGhee, 1996). The ability of some of these gaps to persist may be due to a well-developed shrub layer which appears to be able to perpetuate the canopy opening (McGhee, 1996) or to intense localized fires which consumes the litter layer (Ehrenfield et al., 1995).

Spies et al. (1990) were the first to document a unique gap in Douglas-fir (*Pseudotsuga menziesii*) forests of the Pacific Northwest for which no obvious gap-forming process could be identified. Vine maple (*Acer circinatum*) was growing within the gap. McGhee (1996) argues that many canopy gaps, which are occupied by vine maple, do not result from vine maple invading pre-existing gaps, but occur due to vine maple's ability to establish dense mats of foliage during stand initiation (Haeussler et al., 1990) and resist the invasion of conifers through several seral stages. These gaps are referred to as persistent gaps.

Vine maple is a shade-tolerant, multi-stemmed, small, deciduous tree commonly found in the understory of conifer forests from California to southwestern British Columbia (Haeussler et al., 1990). Vine maple is present during all stages of stand development with its greatest abundance occurring during early seral stages and in mature and old growth stands that it occupies (Anderson, 1969; O'Dea et al., 1995).

A number of researchers have studied the morphology and demography of vine maple (Anderson, 1969; Tappeiner and Zasada, 1993; O'Dea et al., 1995; McGhee, 1996), but no researchers have addressed the influence of persistent vine maple gaps on adjacent, mature conifer growth and form. Our research focuses on the influence of persistent vine maple gaps on the bole size; the width, depth, and volume of crowns; radial and basal growth rates; site index and basal productivity of Douglas-fir surrounding the gaps. This research helps to determine if the inclusion of vine maple gaps within Douglas-fir stands leads to losses in merchantable timber production.

2. Methodology

2.1. Study site

The research was carried out in a 75-year-old Douglas-fir stand, in the Seymour Demonstration Forest in North Vancouver, British Columbia (49°22'30"N, 123°00'25"W). The stand is situated on the southeast facing, moderate slopes (10° to 28°) of the glacially-carved Seymour Valley. This submontane site, which ranges in elevation from 227 m to 290 m, is transitional between the Moist Maritime and Dry Maritime subzones of the Coastal Western Hemlock (CWH) biogeoclimatic zone (Meidinger and Pojar, 1991). Mean annual precipitation is approximately 2088 mm (Meidinger and Pojar, 1991), of which less than 15% falls as snow. The majority of precipitation occurs during the mild winter months (October–March), with a distinct hot, dry period often occurring in late summer (Meidinger and Pojar, 1991). The dominant soils have developed from glacial till and are moderately well to well-drained Orthic Ferro-Humic Podzols and Duric Ferro-Humic Podzols (Luttmerding, 1980).

Western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) are present in the stand but occur less frequently than Douglas-fir. The occurrence of red alder (*Alnus rubra*) is generally restricted to riparian sites. The associated understory shrub and herb communities contain a good representation of vine maple, salal (*Gaultheria shallon*), and swordfern (*Polystichum munitum*).

2.2. Sampling design and gap measurement

Measurements were taken for 10 plots in persistent vine maple gaps paired with 10 plots in the surrounding conifer forest. For each plot, measurements were made on three Douglas-fir which were randomly selected from the population of Douglas-fir showing no signs of suppression, deformities, insect or pathogen infestation, substantial leaning, or other damage (Stokes and Smiley, 1968; Biondi et al., 1992). For one paired plot, measurements were made on only two trees due to a lack of trees which met the above criteria. Measurements were, thus, made for a total of 58 Douglas-fir which will be referred to as study trees.

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 at breast-height (DBH) of the study trees and surrounding conifers were measured and basal area (BA) was calculated. Two crown widths and two crown depths were measured parallel to the topographic contours for trees in the closed canopy and through an imaginary line which bisected the center of the gap for trees adjacent to the gap. A gap-side crown is the half-crown portion of a Douglas-fir adjacent to a gap which extends towards the gap center and a canopy-side crown is the half-crown portion which extends away from the gap and into the surrounding canopy. Canopy crown values were calculated by averaging crown dimensions for the north and south side of each closed canopy tree. Crown volume was estimated using the volumes for each of the half-cones generated by the data.

2.4. Site chronologies

Two increment cores were removed at breast-height from each study tree at about 180° from each

other and parallel to the topographic contours (Stokes and Smiley, 1968; Jorsa, 1988). Coring procedures, handling, mounting and sanding followed the guidelines outlined by Stokes and Smiley (1968), Jorsa (1988), and Fritts and Swetnam (1989). A high resolution stereomicroscope was used to determine tree age and annual ring widths (to the nearest 0.002 mm). Radial increments were measured with a tree ring measuring device (Velmex 6000) equipped with a video camera and monitor. The Velmex 6000 was linked to a digital encoder and microcomputer which contained software capable of storing ring width measurements by year for each core. The data sets were then transferred to Microsoft Excel 5.0. Cores from the same tree were visually cross-dated against each other and against the site chronology, constructed using mean annual radial width from all plots (Young et al., 1995). We used 1953–1955 (three relatively good consecutive growing years), 1969 (poor growing year), and 1991 and 1993 (relatively poor growing years) as signature years (Jenkins and Pallardy, 1995). Cores were double-checked for accuracy. Given the easily discernible annual rings and sensitivity of the response in the majority of cores, we consider the core data to be highly accurate.

The mean annual ring width for each tree was calculated prior to constructing the radial growth chronologies for gap and canopy plots. The annual ring width data and the core radius at the time of sampling (Jenkins and Pallardy, 1995) were used to calculate BA increment (BAI) for each year between 1945–1994 (Visser, 1995). The radius r of the core at annual intervals was calculated by subtracting the mean radius for year t from the mean radius of the following year ($t + 1$). BAI, in cm^2 , was derived using the following equation (adapted from the work of Visser, 1995):

$$\text{BAI}_t = \pi r_{(t+1)}^2 - \pi r_t^2 \quad (1)$$

where r is in cm. When the pith was not present, we used a pith locator (converging concentric circles drawn the same width apart as the inner rings of the core) to determine the core radius (Jenkins and Pallardy, 1995). Symmetrical growth was assumed for all trees.

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 deviation, but with a mean of zero. To determine if differences between gap and canopy BAI occurred at specific times during stand development, the mean annual BAI for gap and canopy plots were calculated for the five decadal periods between 1945–1994 (Jenkins and Pallardy, 1995). No standardization procedures were used as we were testing for differences between means (Biondi et al., 1992).

The radial growth rates of saplings were calculated using a subsample of 10 trees randomly selected from the population which had cores that penetrated the pith, and were greater or equal to 63 yr in age (to maximize the time span). Mean radial chronologies from 1932–1945 for gap and canopy trees were tested in a similar fashion as the 1945–1994 BAI chronologies.

2.5. Site productivity

Because height growth occurs largely independent of stand density, site index (a measure of dominant tree height at 50 yr breast-height age) is a widely accepted measure of site quality (Carmean, 1975). Breast-height tree age was determined by counting the number of rings from the pith to year 1994. For cores that did not contain the pith, we used a pith locator to estimate breast-height age. Cores were aligned for best fit on the pith locator and age was estimated by adding the number of concentric circles between the last recorded date on the core and the expected pith location on the pith locator (Jenkins and Pallardy, 1995). We calculated site indices using ‘Freddie’, a site index estimation program (Polsson, 1993).

We attempted to quantify the spatial influence of vine maple on each study tree in order to determine if variations in site quality were associated with differences in the percentage of vine maple cover around Douglas-fir. Within 5 m of each study bole, the percent area covered by the vertical projection of vine maple foliage onto the ground was visually estimated, for each of four quadrants.

Stand productivity is generally defined as the increase in plant mass or volume per unit area per unit time (Wenger, 1984; Kimmins, 1988). To avoid error associated with converting tree dimensions to timber volumes (Kimmins, 1988), we chose to represent site BA as the BA per unit ground area ($\text{m}^2 \text{ha}^{-1}$) and recent BA productivity as the mean annual increase in BA per unit ground space for the period of 1985–1994 ($\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$). To determine the amount of ground area each tree potentially uses, we used the weighted area potentially available (WAPA) index. An area potentially available index (APA) was initially defined by Brown (1965) as a measure of point density, or growing space. The WAPA index is the area of the polygon formed by weighted inter-tree bisectors, based on the proportional BA size of the study tree to surrounding conifers (Moore et al., 1973). The compass bearing and size of all trees (greater than 20 cm in diameter) within 10 m of each study tree and all conifers whose crowns were directly adjacent to the study tree were recorded. Manual plotting methods and a planimeter were used to determine the WAPA index.

2.6. Statistical analyses

Paired *t*-tests were used to determine if differences existed between gap plots and the surrounding forest matrix. Functional relationships were detected using model II linear regression and covariance checked using Pearson correlations. Prior to analysis, all data were tested for normality using normal probability plots (Wilkinson, 1990). Gap size, BA and potential growing space (WAPA) were log transformed and crown volumes were square-root transformed. Decadal BAI were compared using a Wilcoxin signed-rank test. To test the difference chronology against a theoretical distribution, a one-sample Kolmogorov–Smirnov (KS) test was used. All data were analyzed with Systat, versions 5.0 and 6.0 (Wilkinson, 1990).

3. Results

3.1. Gap size and tree ages

Expanded gap size ranged from 53 to 187 m^2 with a mean of $90 \pm 39 \text{ m}^2$. The distribution of

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^2)	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^3)	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^2)	44.0 (13.4)	27.4 (6.8)	1.61	0.05
Site BA ($m^2 ha^{-1}$)	69.7 (15.7)	76.9 (23.4)	0.91	0.41
Recent BA productivity ($m^2 ha^{-1} yr^{-1}$)	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^2 with a mean of 25 m^2 . 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 around their means (63 yr for both sites, Table 1). No significant differences were detected

for mean breast-height tree age between gap and canopy plots (Table 1).

3.2. Douglas-fir morphology

The mean DBH of trees on gap plots was significantly greater than trees on closed canopy plots (Table 1). Linear increases in diameter results in exponential increases in BA (Wenger, 1984). Diame-

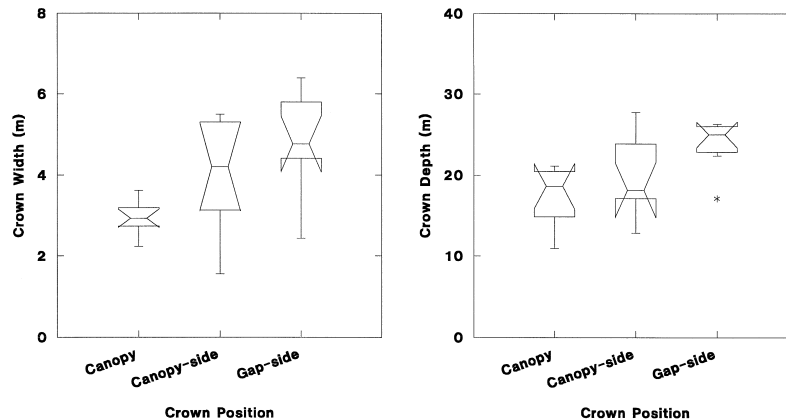


Fig. 1. Box plots showing gap-side, canopy-side and mean closed canopy crown width and crown depth of Douglas-fir. The central horizontal lines represent medians, and where the boxes reach full width represents the 95% confidence interval. The upper and lower horizontal lines delimit the central 50% of the data (Lertzman, 1992; Wilkinson, 1990). The * represents a gap-side crown depth that exceeds the area of the 3rd quartile (bottom of box) by 150%.

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

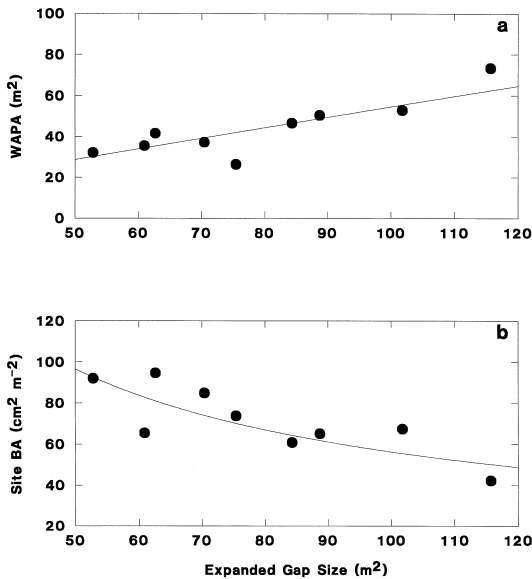


Fig. 2. Significant regressions of: (a) potential growing space vs. expanded gap size for Douglas-fir on gap peripheries ($r^2 = 0.68$, $n = 9$, $p = 0.006$), and (b) site BA ($r^2 = 0.60$, $n = 9$, $p = 0.01$) vs. expanded gap size. The largest expanded gap size was left out of these analyses due its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

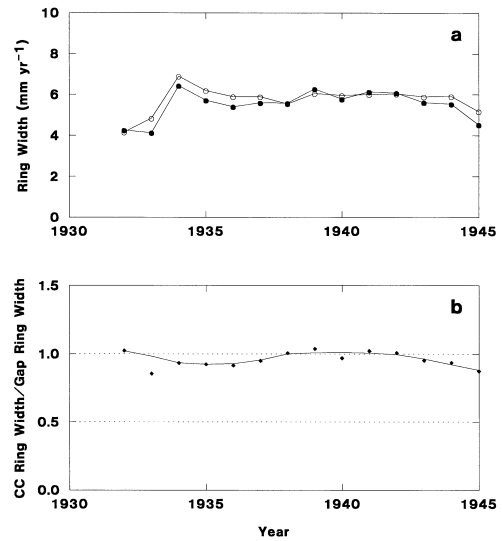


Fig. 3. (a) Mean radial growth of Douglas-fir saplings on gap (○) and closed canopy plots (●) ($n = 10$ each for gap and canopy sites), and (b) the ratio of mean closed canopy (CC) radial growth to mean gap radial growth. A Lowess smoothing function with a tension of 0.4 was applied to the data (Wilkinson,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

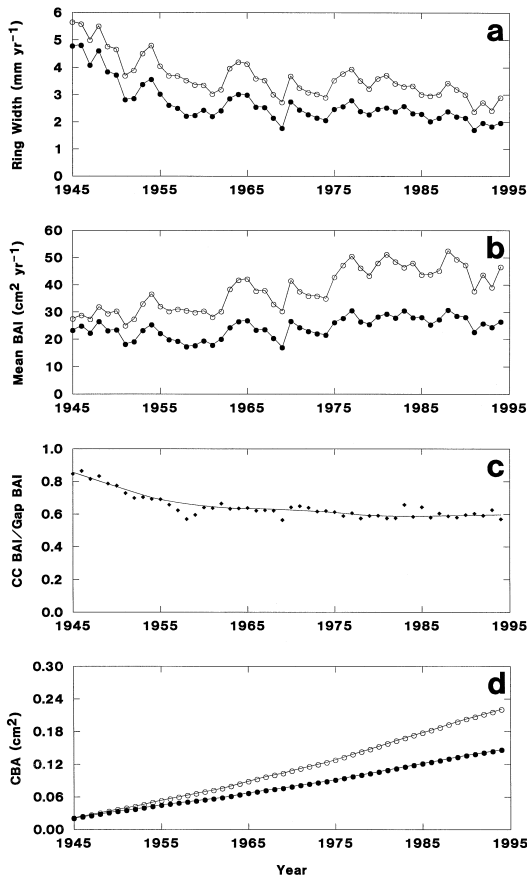


Fig. 4. (a) Radial growth chronologies, (b) BAI chronologies, (c) the ratio of mean canopy BAI to mean gap BAI and (d) cumulative BA (CBA) growth of gap (○) and canopy (●) Douglas-fir for 1945–1994. The numbers of cores representing each data point = 58 (29 trees). A Lowess smoothing function with a 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 bark at the time of sampling is not included, resulting in proportionally lower values of BA when compared to BA calculated using field measurements, which did include bark width. Decadal BAI for trees adjacent to gaps were significantly greater than decadal BAI for canopy trees for all decades

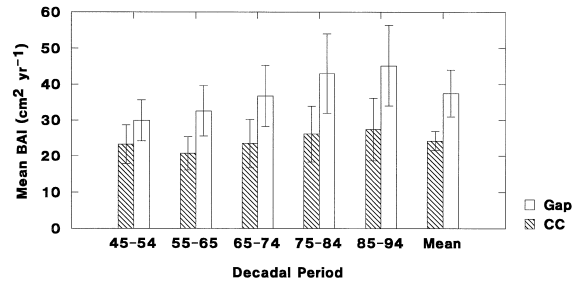


Fig. 5. Mean annual BAI for the last five decadal periods (1945–1994) for gap and closed canopy (CC) sites ($n = 10$). All paired decadal BAI are significantly different ($p < 0.05$; Wilcoxon signed ranks test). Error bars represent 1 standard deviation from the mean.

(Fig. 5). Decadal BAI increased as stand age increased for both gap and canopy plots (Fig. 5).

3.4. Site productivity

The estimated mean site index for the Douglas-fir stand was 41.4 m. This represents the upper range of site index for Douglas-fir in the coastal forests of B.C. (Thrower and Nussbaum, 1991). Site index was significantly higher for Douglas-fir adjacent to gaps than for those in the closed canopy (Table 1). The percentage of vine maple within a 5-m radius of Douglas-fir adjacent to the gap ranged from 0 to 75% with a mean of $32.1 \pm 21.8\%$ (Fig. 6). Site index was not significantly correlated with the transformed percentage of vine maple cover within a 5-m radius ($r = 0.18$, $n = 29$, $p = 0.34$; Fig. 6). How-

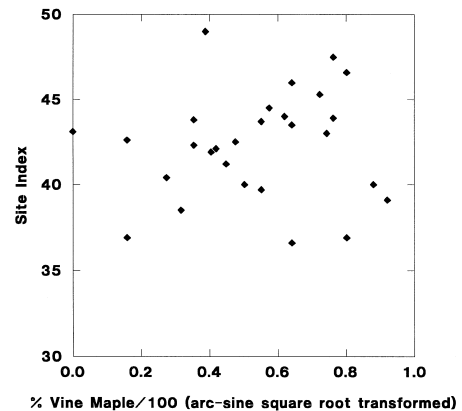


Fig. 6. Relationship between percent cover of vine maple within 5 m of each study Douglas-fir and site index ($n = 29$).

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 m² and for Douglas-fir on canopy plots, values ranged from 19.4 to 39.4 m². 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).

The ratio of site BA was 0.91 and the ratio of recent BA productivity was 1.05 for Douglas-fir on gap plots vs. canopy plots (Table 1). Site BA and recent BA did not significantly differ between gap and canopy plots (Table 1). Douglas-fir on the gap periphery occupy 161% of the growing space of Douglas-fir in the closed canopy (Table 1), and the greater growing space was largely utilized by Douglas-fir to increase its BA.

4. Discussion

Douglas-fir adjacent to gaps had significantly greater potential growing spaces than Douglas-fir in the adjacent closed canopy (Table 1). Since one of

the primary controlling mechanisms for above-ground, net primary productivity in temperate forests is light availability (Law et al., 1992), the wider spacing of conifer stems associated with the presence of a gap would result in greater light interception for trees adjacent to the gap (Oliver and Larson, 1990). The greater the interception of light, the larger the crown that is able to develop, the greater the photosynthate that is produced, and the greater the addition of xylem to the stem (Table 2). Therefore, Douglas-fir on the edge of the gap, though not different in age from Douglas-fir in the closed canopy (Table 1), have developed deeper and wider crowns (Fig. 1) and larger crown volumes (Table 1) than conifers on closed canopy plots. Greater crown volumes generate greater radial and BA growth rates (Long and Smith, 1984; Oliver and Larson, 1990; Table 2; Fig. 4), which resulted in the larger diameter stems on gap plots (Table 1).

Given the height of surrounding canopy trees in this stand (45–50 m), vine maple's ability to persist in relatively small gaps is quite remarkable. In modeling understory light levels in single-tree developmental gaps (~ 75 m²), Canham et al. (1990) found that single-tree gaps in Douglas-fir–hemlock stands had little effect on understory light levels and suggest that a canopy gap size greater than 500 m² would be required to create understory light levels comparable to those in single-tree developmental gaps in northern hardwood forests. The gaps in our stand are similar in size to single-tree developmental gaps reported by Spies et al. (1990) for mature coastal Douglas-fir forests. Spies et al. (1990) found that single-tree developmental gaps dominate in these stands, where the median canopy gap size is 19 m² and most gaps are less than 50 m². In our study, estimated canopy gap size ranged from 15 to 52 m² with a mean of 25 m².

4.1. Douglas-fir morphology

Douglas-fir adjacent to gaps have larger crowns and boles than Douglas-fir in the closed canopy (Table 1). Typically, as canopies close, lower branches do not receive adequate light levels to sustain themselves, and these branches die (Oliver and Larson, 1990). The deep crowns that develop

due to the retention of lower branches for trees adjacent to gaps (Fig. 1) indicate the gaps have existed for a significant period of time. The large width of the gap-side crowns (Fig. 1) are a result of the lateral expansion of the crowns into the gap, and is the primary way that these gaps are filling. Seedlings and saplings, common in developmental gaps (Veblen, 1986; Spies et al., 1990; Lertzman, 1992), are rarely present in persistent gaps (McGhee, 1996).

We expected, a priori, that increasing gap size would result in increasing crown and bole size due to the expected increase in potential growing space on sites with larger expanded gaps. However, BA and crown volume varied little with gap size. Perhaps the relatively small range of gap sizes (~ 50 – 120 m², with one gap 187 m²) made it difficult to detect an influence of gap size on crown and bole growth. Because growing space increased as gap size increased (Fig. 2a) but BA did not, site BA declined as gap size increased (Fig. 2b).

4.2. Site chronologies

In our study stand, vine maple did not appear to affect negatively the radial growth of Douglas-fir saplings on the edge of gaps during stand initiation (1932–1945; Fig. 3). The initial stage of development of an even-aged, single-species stand is characterized by small trees that grow without significant competitive interaction (Oliver and Larson, 1990). As the trees grow and begin to interact, this marks the onset of canopy closure and the growth rate of individual trees is reduced relative to their potential in the absence of intra-specific competition (Long and Smith, 1984). As we were unable to detect any differences in radial growth between gap and canopy sites prior to 1945, but differences in BA growth rates were measured for the 1945–1954 decadal period, it is this time that marks the likely onset of canopy closure.

Competitive interactions between vine maple and conifers were not measured in our study. However, given the decline in radial growth rates following canopy closure for trees on closed canopy sites compared to trees adjacent to vine maple (Fig. 4a), it is likely that competition between conifers is much more prevalent than vine maple–Douglas-fir interac-

tions. This is consistent with studies that suggest that competition for light is one of the driving forces behind radial growth responses of conifers (Law et al., 1992). Since vine maple remains in the understory, it does not compete with mature conifers for light. Similar patterns of conifer growth around understory hardwoods occur in central Arizona. Competition between Ponderosa pine and Gambel oak, a shrubby hardwood is minimal, even on dry sites, when Gambel oak remains in the understory (Biondi et al., 1992). The oak naturally spaced the pine, decreasing intra-specific competition, and increasing the radial growth of pine as the percentage of Gambel oak in the understory increased.

The radial growth releases associated with the formation of a developmental gap have been documented in several ecosystems and are based on suppression and release patterns. In temperate deciduous forests, Henry and Swan (1974) found that a 150% increase in tree-ring width for a period of at least 4 yr marked a release from suppression. This same definition was also used by Veblen (1986) in a temperate spruce–Douglas-fir forest. In developmental gaps, growth responses last from several years to several decades (Orwig and Abrams, 1994), but gap resources are eventually utilized by species colonizing the gap, or crown expansion eventually closes the canopy opening (Frelich and Martin, 1988). The gaps in our study are large enough to have resisted canopy closure by crown expansion for more than 70 yr (McGhee, 1996). The benefits of increased BAI for Douglas-fir adjacent to gaps, which were as high as 70% greater than canopy Douglas-fir growth rates, can be seen in the chronology for approximately the past 50 yr. Chronologies show little indication that the trend in BAI will change in the near future (Fig. 4b), and we expect the difference between CBA between the gap and canopy sites to continue to increase (Fig. 4d).

4.3. Site productivity

The site index for trees adjacent to the gap was higher than for Douglas-fir in the canopy (Table 1). In an eastern hemlock (*Tsuga canadensis*)–tulip poplar (*Liriodendron tulipifera*) stand in eastern Kentucky, Boettcher and Kalisz (1990) found that the soil landscape is a mosaic which reflects the

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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