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Distribution of epicormic branches and foliage on Douglas-fir as influenced by adjacent canopy gaps

John W. Punches and Klaus J. Puettmann

Abstract: The influence of adjacent canopy gaps on spatial distribution of epicormic branches and delayed foliage (originating from dormant buds) was investigated in 65-year-old coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco). Sample trees were selected across a broad range of local densities (adjacent canopy gap sizes) from a repeatedly thinned stand in which gaps had been created 12 years prior to our study. Lengths and stem locations of original and epicormic branches were measured within the south-facing crown quadrant, along with extents to which branches were occupied by sequential (produced in association with terminal bud elongation) and (or) delayed foliage. Epicormic branches, while prevalent throughout crowns, contributed only 10% of total branch length and 2% of total foliage mass. In contrast, delayed foliage occupied over 75% of total branch length, accounted for nearly 39% of total foliage mass, and often overlapped with sequential foliage. Canopy gap size did not influence original or epicormic branch length and location. On original branches, larger gaps may have modestly negatively influenced the relative extent of sequential foliage on branches and (or) slightly positively influenced delayed foliage mass. Delayed foliage appears to contribute substantially to Douglas-fir crown maintenance at this tree age, but canopy gap size had a minor influence, at least in the short term.

Key words: epicormic, delayed, reiteration, gap, crown.

Résumé : L'influence de trouées adjacentes dans le couvert forestier sur la distribution spatiale des pousses adventives et du feuillage tardif (issus de bourgeons dormants) a été étudiée chez le douglas de Menzies (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) côtier âgé de 65 ans. Les arbres échantillons ont été choisis parmi un large éventail de densité locale (taille des trouées adjacentes) dans un peuplement éclairci à plusieurs reprises et dans lequel les trouées avaient été créées 12 ans auparavant. La longueur et la position sur la tige des branches originales et adventives ont été mesurées dans le quadrant de la cime exposé au sud. On a aussi noté dans quelle mesure les branches étaient garnies de feuillage séquentiel (produit à la suite de l'élongation du bourgeon terminal) ou tardif. Les branches adventives, bien que répandues partout dans la cime, représentaient seulement 10 % de la longueur totale des branches et 2 % de la masse totale de feuillage. Par contre, le feuillage tardif occupait plus de 75 % de la longueur totale des branches et représentait près de 39 % de la masse totale de feuillage; il chevauchait souvent le feuillage séquentiel. La taille des trouées n'influençait pas la longueur ni la localisation des branches originales ou adventives. Dans le cas des branches originales, les plus grandes trouées pourraient avoir eu une influence légèrement négative sur l'étendue relative du feuillage séquentiel sur les branches ou une influence légèrement positive sur la masse du feuillage tardif, et possiblement les deux à la fois. Le feuillage tardif semble contribuer substantiellement au maintien de la cime du douglas de Menzies à cet âge mais la taille des trouées dans le couvert forestier aurait peu d'influence, du moins à court terme. [Traduit par la Rédaction]

Mots-clés : adventive, tardif, réitération, trouée, cime.

Introduction

Trees normally produce shoots and branches sequentially, with new growth produced in the year of, or in the year immediately following, development of the source bud. Many tree species, however, have significant capacity to produce epicormic branching or sprouting, as each flush produces not only active buds, but also dormant buds that can activate after some period of delay (Morisset et al. 2012). Epicormic branching and sprouting has been extensively studied in angiosperms, especially with respect to its implications for leaf area maintenance, tree vigor, crown form, and wood quality (Rey-Lescure 1982; Stubbs 1986). Conifer species have received less attention in this regard, but several temperate coniferous species have been observed to develop epicormic branches (herein referring to as primary branches originating

from the main stem) and shoots (originating from primary branches or secondary stems) at a variety of ages. Examples include Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mayr) Franco; Bryan and Lanner 1981), coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco; Ishii et al. 2000), western larch (*Larix occidentalis* Nutt.; O'Hara and Valappil 2000), black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.; Bégin and Filion 1999), Sitka spruce (*Picea sitchensis* (Bong.) Carrière; Deal et al. 2003), white fir (*Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr.; Hanson and North 2006), and coast redwood (*Sequoia sempervirens* (Lamb. ex D. Don) Endl.; O'Hara and Berrill 2009).

Epicormic branch development and epicormic shoots on existing branches (collectively known as delayed adaptive reiteration) have been suggested to play essential roles in maintenance of old-growth Douglas-fir crowns (Ishii et al. 2007). Epicormic

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branches repopulate segments of stems that have lost their original branches. In contrast, epicormic shoots (branchlettes formed on existing branches) add new, young, leaf area to both original and epicormic branches. Epicormic initiation and success has been attributed to a variety of factors, including light, temperature, stress, and tree vigor, with much variation among and within species (Meier et al. 2012); however, "there is no well-established theory explaining how adaptive [epicormic] reiteration is initiated" (Ishii et al. 2007, p. 457). Epicormic branches appear to be more prevalent after treatments that open up canopies such as thinning or gap creation (Erdmann and Peterson 1972), leading to concerns about wood quality (Rey-Lescure 1982; Quine 2004).

The contribution of delayed adaptive reiteration to leaf area and (or) crown maintenance in younger conifers has received less attention. Short-lived epicormic shoots have been noted in 30-year-old Douglas-fir (Hollatz 2002), and epicormic branching in young Douglas-fir stands (dominant height averaging 9 m) have been examined with respect to pruning and stand density (Collier and Turnblom 2001). Delayed reiteration of shoots and foliage appears, however, to play a more important role than epicormic branching itself in maintaining the species' leaf area (Ishii and Wilson 2001; Kennedy et al. 2004).

We investigated epicormic branch production and delayed reiteration of foliage in approximately 65-year-old coastal Douglas-fir in a stand that had been repeatedly thinned and in which canopy gaps had been intentionally created 12 years prior to our study. Our objectives were to evaluate the effect of adjacent canopy gaps on (i) the occurrence of epicormic branches on tree stems and (ii) the extent of delayed adaptive reiteration within branches. Lastly, we propose a general model for branch and foliage distribution within Douglas-fir crowns, contrasting the roles of original vs. epicormic branches and sequential vs. delayed foliage, where "sequential" denotes foliage produced in close association with the activity of a terminal bud and "delayed" is foliage that arose from buds that had lain dormant for at least one full growing season (for additional details, see Methods).

Methods

Site and sample description

The study site was located on the Oregon State University McDonald-Dunn Research Forest in the Willamette Valley foothills (eastern flank of Oregon Coast Range) near Corvallis, Oregon (latitude 44.65°N, longitude 123.27°W). In 2005, it was predominantly occupied by even-aged stands of 63- to 68-year-old coastal Douglas-fir (Pseudotsuga menziesii var. menziesii) with scattered grand fir (Abies grandis (Douglas ex D. Don) Lindl.) and bigleaf maple (Acer macrophyllum Pursh). The site had moderately deep, basalt-derived, clay loam soils with good drainage on slopes ranging from 10% to 50%, typically facing west to northwest. Annual precipitation was approximately 1500 mm (mostly as rain from October to May), and the site experienced moderate temperatures. As part of an earlier study (Newton and Cole 2006), the site had been thinned uniformly in 1964–1965 and again in 1980–1981 to release dominant and codominant trees. In 1993, the site was thinned again to create a wide range of stand density, with spatially uniform conditions in some areas and canopy gaps in others. Portions of the stand were re-thinned in 2001 to return them to target densities. The treatments resulted in trees growing with variable sizes of adjacent canopy gaps. Growing conditions for individual trees varied from trees that were fully surrounded by neighboring trees to trees adjacent to gaps. To ensure that the sample included trees with a wide range of adjacent canopy gap sizes, we selected 23 trees ranging in height from 34.2 m to 45.8 m with adjacent canopy gaps varying from nearly closed to substantially open. As such, the trees could be expected to have experienced differing light and bark temperature regimes, which have

been suggested as being responsible for epicormic branching (Wignall and Browning 1988).

Measurements

Hemispherical photos were taken adjacent to each tree using a Nikon Coolpix 5000 camera with a calibrated fish-eye lens. We focused the measurements on the 90° quadrant centered on true south to best capture the impact of canopy gaps on available photosynthetically active radiation (Schoettle and Smith 1991). The camera was mounted on a tripod 1 m above the ground, situated 1 m due south of the tree stems, and leveled. All photos were taken between 23 May and 7 June 2005, between 0600 and 1000 or between 1600 and 1800 to avoid sun interference. Canopy gap size was calculated using WinSCANOPY (Regent Instruments Inc., available from http://regent.qc.ca/assets/winscanopy_system. html, accessed 25 February 2018). Photos were rotated to true north, a mask was applied to restrict analysis to the south-facing quadrant, and percent gap fraction (the percentage of the adjacent area in an open condition, i.e., canopy gap) was calculated for an opening of 34° from vertical.

Sample trees were climbed in August–September of 2005. All living branches in the south-facing quadrant (135° to 225° azimuth), from the bottom of the live crown up to a stem diameter of 10 cm, were characterized and measured as follows:

- branch type (original or epicormic) based on bark texture, angle of insertion, associated dead or dying branches, shape of branch clusters, callus-like swell as branch origin, and branch diameter relative to adjacent branches (Ishii and Wilson 2001);
- branch location (whorl or between whorls, where a whorl was a cluster of original branches located within a 10 cm vertical range, presumed to be the location of a previous terminal bud);
- branch length (the straight-line distance from stem intersection to branch tip, using an optical range finder or a measuring tape or pole);
- branch height above ground (using tape stretched along the stem);
- branch slope (immediately distal of branch collar, using clinometer);
- branch orientation (point of origin on stem surface, referenced to true north);
- branch aspect (primary direction toward which a branch tip pointed, referenced to true north);
- starting and ending points of sequential foliage on branches (measured as the straight-line distance from the branch–stem interface), where "sequential" is defined as foliage produced during, or in close association with, elongation of the shoot apex;
- starting and ending points of delayed foliage on branches (measured as the straight-line distance from the branch–stem interface), where "delayed" is defined as foliage arising from dormant buds that could be determined to be at least two seasons younger than its adjacent sequential foliage.

Note that delayed foliage was often interspersed with sequential foliage such that the extents of the two foliage types along the branch axis often overlapped.

Between March and September of 2006, a subsample of branches was harvested from 15 of the 23 trees: nine trees in March (prior to budbreak) and six trees between July and September (after budbreak) to obtain measurements of foliage mass. Crowns were segmented into three sections (upper, mid, and lower), with the location of the longest branch being used to separate low and mid crown segments based on the assumption that branches above this point would be actively elongating, while those below may have entered maintenance or dieback modes. The crown above the longest living branch was divided into upper and mid segments such that each included one half of the remaining measured crown length. Within each section, we harvested two

original branches from whorls, two original branches from between whorls, and two epicormic branches (at or between whorls), for a maximum of 18 branches per tree. Not all trees had sufficient branches of each type in each crown segment, resulting in a total sample of 160 branches (83 original branches at whorls, six original branches between whorls, 14 epicormic branches at whorls, and 57 epicormic branches between whorls).

Branches were harvested using a handsaw and placed in protective bags to avoid damage while lowering. On the ground, shoots were characterized as sequential or delayed foliage, clipped from their main branch, and sealed in doubled plastic bags. They were placed in coolers for short-term storage and then frozen to maintain freshness until processing.

In the lab, each sample was divided into foliage years based on location of shoot nodes and (or) bud scale scars. Samples were dried at 70 °C for 96 h, screened through a sieve to remove woody material, and weighed.

Analysis

SAS software (version 9.4, 2013, SAS Institute Inc., Cary, North Carolina, U.S.A.) was utilized to apply a series of mixed models to assess the influence of gap fraction on branch length, the relative extent of sequential and delayed foliation along individual branches, and foliage mass. Models were specified based on known hierarchical relationships within the dataset and on observed relationships identified after plotting potential explanatory variables against the response variables. Relative height within crown was treated as a covariate. Because trees varied in total height and crown height, relative height within crown was calculated based on the total height of the crown, from tree tip (0) to crown base (1). As a few trees had some small epicormic branches located well below the lowest living original branch, we used the lowest living original branch as the base of the crown. Epicormic branches located below the lowest living original branch had relative heights within crown exceeding 1. Intercept, relative height within crown, gap fraction, and the natural log of foliated length were treated as fixed effects, where applicable. Tree was treated as a class variable. For models of branch length and relative extents of foliated length, intercepts and relative height within crown were allowed to have random effects between trees. Models of foliage mass were allowed to have random intercepts, but the foliage mass dataset was not of sufficient size to accommodate the added complexity associated with inclusion of relative height within crown as a random variable. We specified an unstructured covariance matrix. Residuals were examined to affirm normality assumptions, and natural log and (or) Box–Cox transformations to the dependent variables were required in some cases to address increasing magnitudes of residuals with increasing predicted values of the dependent variable. Semivariograms of residuals, using branch height above ground and branch orientation as coordinates, indicated that each of the models for branch length and relative extent of foliage on branches adequately accounted for spatial autocorrelation. Spatial autocorrelation was apparent in the foliage mass data, and the respective models were adjusted accordingly through application of a spatial (Gaussian) correction to the covariance matrix.

The impact of gap fraction on original branch length was modeled as

$$(1) \qquad \mathrm{Ln}Y_{ij} = (\beta_0 + b_{0i}) + (\beta_1 + b_{1i})\mathrm{Crwn}_{ij} + (\beta_2 + b_{2i})\mathrm{Crwn}_{ij}^2 + \beta_3\mathrm{Gap}_i + e_{ij}$$

where $\mathrm{Ln}Y_{ij}$ is the natural log of branch length at relative height within crown j of tree i ($i = 1, 2, \ldots, 23; j = 1, 2, \ldots, j_i$); β_0 is the overall intercept; b_{0i} is the random effect on intercept associated with tree i, where $b_0 \sim N(0, \sigma_{b0}^2)$; β_1 is the overall slope coefficient for relative height within crown; b_{1i} is the random effect on slope

associated with tree i, where $b_1 \sim N(0, \sigma_{b1}^2)$; Crwn_{ij} is the relative height within crown j of tree i; β_2 and b_{2i} are the equivalent overall slope and random effects, respectively, for Crwn^2, where $b_2 \sim N(0, \sigma_{b2}^2)$; β_3 is the slope coefficient for the fixed effect of Gap_i, where Gap_i is the gap fraction associated with tree i; and e_{ij} is the random error associated with the model, where $e_{ij} \sim N(0, \sigma_e^2)$.

Attempts to model length of epicormic branches using the above-described approach were unsuccessful. Plots revealed many short branches scattered throughout the crown with lengths that did not vary predictably as a function of relative height within crown. In contrast, other, longer branches did demonstrate such a relationship. Based on the values of the observed variables, the two groups were separated at a dividing point of 1 m of branch length and different models were developed for each group.

Epicormic branches longer than 1 m were modeled as

$$(2) \qquad \mathrm{Ln}Y_{ij} = (\beta_0 + b_{0i}) + (\beta_1 + b_{1i})\mathrm{Crwn}_{ij} + \beta_2\mathrm{Gap}_i + e_{ij}$$

where β_2 is the slope coefficient for the fixed effect of Gap, and all other components are as noted for eq. 1.

The model for epicormic branches less than 1 m long included terms for only the intercept and Gap.

$$(3) \qquad \mathrm{Ln}Y_{ij} = (\beta_0 + b_{0i}) + \beta_1\mathrm{Gap}_i + e_{ij}$$

In each of the branch length models, residuals were approximately normal in distribution, although slightly negatively skewed.

Similar mixed models were utilized to assess responses of the two foliage types to gap fraction. For each branch, we calculated the relative extent of its length occupied by sequential or delayed foliage as the response variable, as it standardized the measurement by adjusting for differing branch lengths and facilitated comparison between the two foliage types. Relative extents ranged from 0 (devoid of foliage) to 1 (fully foliated) per branch for each foliage type.

Relative extent of sequential foliage on original branches was determined, via scatterplots, to be approximately linear with its major explanatory variables. It was modeled as

$$(4) \qquad Y_{ij} = (\beta_0 + b_{0i}) + (\beta_1 + b_{1i})\mathrm{Crwn}_{ij} + \beta_2\mathrm{Gap}_i + e_{ij}$$

Variables for this model are as noted in eq. 1, except that Y_{ij} is the relative extent of the branch occupied by sequential foliage at relative height within crown j of tree i ($i = 1, 2, \ldots, 23; j = 1, 2, \ldots, j_i$), the squared term is unnecessary, and β_2 is the slope coefficient for the fixed effect of Gap. Residuals for the model were approximately normal.

Delayed foliage on original living branches was most prevalent around mid-heights of crowns, suggesting the quadratic form of the model. A Box–Cox transformation to Y ($\lambda = 3$) was required to ensure that residuals were normally distributed. Delayed foliage was modeled as

$$(5) \qquad \frac{Y_{ij}^3 - 1}{3} = (\beta_0 + b_{0i}) + (\beta_1 + b_{1i})\mathrm{Crwn}_{ij}$$
$$+ (\beta_2 + b_{2i})\mathrm{Crwn}_{ij}^2 + \beta_3\mathrm{Gap}_i + e_{ij}$$

where Y_{ij} is the relative extent of delayed foliage at relative height within crown j of tree i ($i = 1, 2, \ldots, 23; j = 1, 2, \ldots, j_i$) and all other variables are as in eq. 1. In this form, residuals were approximately normally distributed, although still slightly negatively skewed.

On epicormic branches, the relative extent of sequential and delayed foliage was bimodal and we were unable to analyze it

Fig. 1. Length of living, unbroken branches by relative height within crown: (A) original; (B) epicormic. Triangles denote branches occurring at whorls; circles denote branches occurring between whorls. The top of the crown has a relative height within crown of 0, and the base of the original crown (lowest living original branch) is at 1. Epicormic branches located below the base of the original crown have relative heights within crown exceeding 1. Fit lines per Table 2, with gap fraction held constant at 36.9% (the observed average), back-transformed. Data are for south-facing quadrants of sample trees. No branches were measured above 10 cm stem diameter.
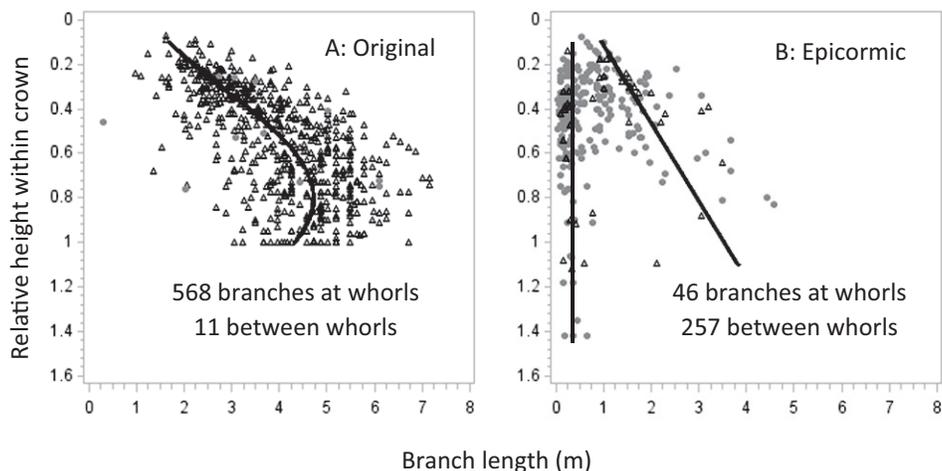
using linear or mixed models. Results are discussed in more general terms.

Foliage mass was modeled in two ways: first, from an inferential perspective to determine the influence of gap fraction, and second from a predictive perspective to allow extrapolation from the subsample of branches on which foliage mass was measured to the full complement of branches measured within the south-facing quadrant of the 15 sample trees. As noted above, the foliage mass dataset was not of sufficient size to allow integration of random effects for relative height within crown into the models.

The inferential models for foliage mass on individual branches were

$$(6, 7, 8, 9 \text{ full}) \quad \text{Ln}Y_{ij} = (\beta_0 + b_{0i}) + \beta_1\text{Crwn}_{ij} + \beta_2\text{Crwn}_{ij}^2 + \beta_3\text{LnFollength}_{ij} + \beta_4\text{Gap}_i + e_{ij}$$

where $\text{Ln}Y_{ij}$ is the natural log of foliage mass for a branch at relative height within crown j of tree i ($i = 1, 2, …, 23$; $j = 1, 2, …, j_i$); β_3 is the slope coefficient for the fixed effect of LnFollength_{ij}, where LnFollength_{ij} is the natural log of the foliated length (in metres, not relative extent) of branch j of tree i; β_4 is the slope coefficient for the fixed effect of Gap_i; and remaining variables and parameters are as in eq. 1. Residuals for each of the models using the four combinations of branch and foliage type (sequential foliage on original branches, delayed foliage on original branches, sequential foliage on epicormic branches, and delayed foliage on epicormic branches) were approximately normal but slightly negatively skewed. Three outliers, representing branches that had very low foliage mass for their respective foliated lengths, were removed from the dataset. Upon examination of the data, these appeared to be instances where there were small sections of foliage at the extreme ends of the branches while the midsections of the branches were devoid of foliage. Thus, their foliated lengths were reported as higher than was appropriate — an artifact of the measurement protocol.

For prediction of foliage mass, fit statistics (–2 Res Log Likelihood, AIC, AICC, BIC) were utilized to identify the most effective reduced model for each combination of foliage and branch type. In each case, the best fit was obtained when the term for gap fraction was removed. This resulted in the following models:

$$(6, 7, 8, 9 \text{ reduced}) \quad \text{Ln}Y_{ij} = (\beta_0 + b_{0i}) + \beta_1\text{Crwn}_{ij} + \beta_2\text{Crwn}_{ij}^2 + \beta_3\text{LnFollength}_{ij} + e_{ij}$$

The fixed effects components of the reduced models where then utilized to predict foliage mass for each branch within the measured portions of the crowns of the 15 sample trees. Goodness of fit of these models was approximated using a model R^2 statistic for fixed effects per Jaeger et al. (2017). Note that the statistic could be calculated for versions of the models including random intercepts, but the approximation was unable to accommodate the residual spatial autocorrelation correction.

Results

Distribution of original vs. epicormic branches within crowns

Original branches occurring at whorls accounted for 64% of branches and nearly 89% of total branch length (Fig. 1; Table 1). Very few original branches occurred between whorls (just 11 branches on seven trees). Epicormic branches were common (34% of the total number of branches) but contributed less than 10% of the total branch length. Unlike original branches, epicormic branches most commonly occurred between whorls.

Original and epicormic branch length differed with respect to relative height within the crown. Original branches reached their maximum length in the lower half of the crown (relative height within crown approximately 0.75; Fig. 1A). Epicormic branches had two distinct patterns: many short branches (less than 1 m) scattered throughout the crown, and another set of branches that increased in length lower in the crown (Fig. 1B). Gap fraction did not significantly influence the length of branches in any of the branch categories (Table 2).

The number of branches on individual trees was not influenced by gap fraction. This was true for original branches, epicormic branches, and the total number of branches per tree, as assessed using simple linear regression of branch numbers against gap fraction (R^2 values for these models were less than 0.01).

When examined by crown segment, over 45% of total branch length appeared in the mid third of the measured crowns, just under 37% in the lower third, and less than 18% in the upper third (Table 1). The few epicormic branches occurring below the lowest

Table 1. Total branch length and percentage by branch type and crown segment (all percentages are expressed relative to total branch length).

Branch type	Total length (m)	% of total length	% total length by crown segment			
			Upper 3rd	Mid 3rd	Lower 3rd	Below base of original crown
Original at whorl	2258.1	88.8	14.1	39.9	34.8	0.0
Original between whorls	40.0	1.6	0.4	0.5	0.7	0.0
Epicormic at whorl	50.6	2.0	0.8	0.9	0.2	0.1
Epicormic between whorls	193.3	7.6	2.5	3.9	1.0	0.1
Total	2541.9	100.0	17.9	45.2	36.7	0.2

Note: No branches were measured above 10 cm stem diameter. The lowest living original branch was treated as the base of the original crown. Some epicormic branches occurred below that point.

Table 2. Parameter estimates for fixed effects of mixed models; natural log length of branches in three categories: original, epicormic greater than 1 m in length, epicormic less than or equal to 1 m in length (standard errors in parentheses).

Model	Intercept	Crwn	Crwn^2	Gap
1: original	0.1625 (0.1336), $p = 0.2372$	+3.3564 (0.4298), $p < 0.0001$	−2.1006 (0.3291), $p < 0.0001$	+0.001318 (0.001928), $p = 0.5018$
2: epicormic >1 m	0.02839 (0.1572), $p = 0.8586$	+1.4185 (0.2319), $p < 0.0001$		−0.00214 (0.003508), $p = 0.5486$
3: epicormic ≤1 m	−0.8460 (0.2222), $p = 0.0011$			−0.00958 (0.005656), $p = 0.1057$

Note: Crwn, the relative height within crown, where 0 is the tree leader tip and 1 is the lowest living original branch; Gap, the gap fraction (percentage of open space) in the south-facing quadrant. Each model included a natural log transformation to the response variable (results back-transformed for figures and discussion). Model 1 exhibited significant ($p < 0.05$) random effects for Intercept, Crwn, Crwn^2, and their covariances, i.e., results varied by tree. Models 2 and 3 exhibited no significant ($p < 0.05$) random effects. Detailed statistical results are available in Supplementary Material S1[1].

Table 3. Foliated branch length, by branch and foliage type, by crown segment (percentages relative to total branch length within each foliage category).

Branch type	Total foliated length (m)	% of foliated length	% of foliated length by crown segment			
			Upper 3rd	Mid 3rd	Lower 3rd	Below base of original crown
Sequential foliage						
Original at whorl	1190.4	88.1	18.6	43.1	26.4	0.0
Original between whorls	19.2	1.4	0.5	0.5	0.4	0.0
Epicormic at whorl	29.0	2.1	0.9	0.9	0.2	0.2
Epicormic between whorls	112.3	8.3	2.9	4.4	0.8	0.2
Total sequential	1350.8	100.0	22.9	48.9	27.9	0.4
Delayed foliage						
Original at whorl	1764.2	91.9	13.4	42.7	35.8	0.0
Original between whorls	31.6	1.6	0.3	0.5	0.8	0.0
Epicormic at whorl	26.8	1.4	0.5	0.6	0.1	0.1
Epicormic between whorls	97.3	5.1	1.5	2.9	0.7	0.1
Total delayed	1919.8	100.0	15.7	46.7	37.4	0.2

Note: No branches were measured above 10 cm stem diameter. Total branch length = 2541.9 m (Table 1).

original living branch accounted for just 0.2% of total branch length.

Distribution of sequential vs. delayed foliage within branches

Slightly more than half of the total length of original and epicormic branches was occupied by sequential foliage (1350.8 m of 2541.9 m), and sequential foliage was most extensive in the mid third of the measured crown (Table 3). This coincided with the point at which branches were close to their maximum length. In comparison with mid-crown branches, those in the lower third were often shorter and had less of their length occupied by sequential foliage (Figs. 1 and 2).

Delayed foliage occupied more total branch length than did sequential foliage (1919.8 m vs. 1350.8 m; Table 3), and it was common for delayed and sequential foliage to overlap. Nearly 92% of total branch length occupied by delayed foliage occurred on original branches at whorls. Roughly 5% occurred on epicormic branches between whorls, with the remainder split between the other two branch categories. Relative to sequential foliage, a greater percentage of total branch length occupied by delayed foliage occurred in the lower third of the measured crown, and smaller percentages occurred in the upper, middle, and below-base segments.

Original living branches near the top of trees' crowns were nearly fully occupied by sequential foliage (Fig. 2A). The relative extent of sequential foliage decreased in a linear fashion lower in the crown. The relative extent of sequential foliage may have been negatively influenced by gap fraction (Table 4, $p = 0.0548$). Measurements of gap fraction utilized in the model ranged from 8% to 63%. When multiplied by the model parameter, this suggested that changes in gap fraction could have reduced relative extent of sequential foliage by as much as 0.13.

There were meaningful changes in the way that relative height within crown influenced the relative extent of sequential foliage among trees, as evidenced by the significance of the random effects for Crwn in model 4 (Table 4). The branches of most trees had

Fig. 2. Relative extent of foliage by relative height within crown. The top of the crown has a relative height within crown of 0, and the base of the original crown (lowest living original branch) is at 1. Epicormic branches located below the base of the original crown have relative heights within crown exceeding 1. The horizontal axis denotes the relative extent of each branch occupied by each type of foliage, where 1 indicates fully occupied and 0 indicates a branch devoid of the foliage type in question. (A) Sequential foliage on original branches; (B) delayed foliage on original branches; (C) sequential foliage on epicormic branches; (D) delayed foliage on epicormic branches. Fit lines per Table 4, with gap fraction held constant at 36.9% (the observed average), back transformed in B. Triangles denote trees in plots re-thinned in 2001; circles are those not subjected to the 2001 thinning. Data are for south-facing quadrants of sample trees. No branches were measured above 10 cm stem diameter.
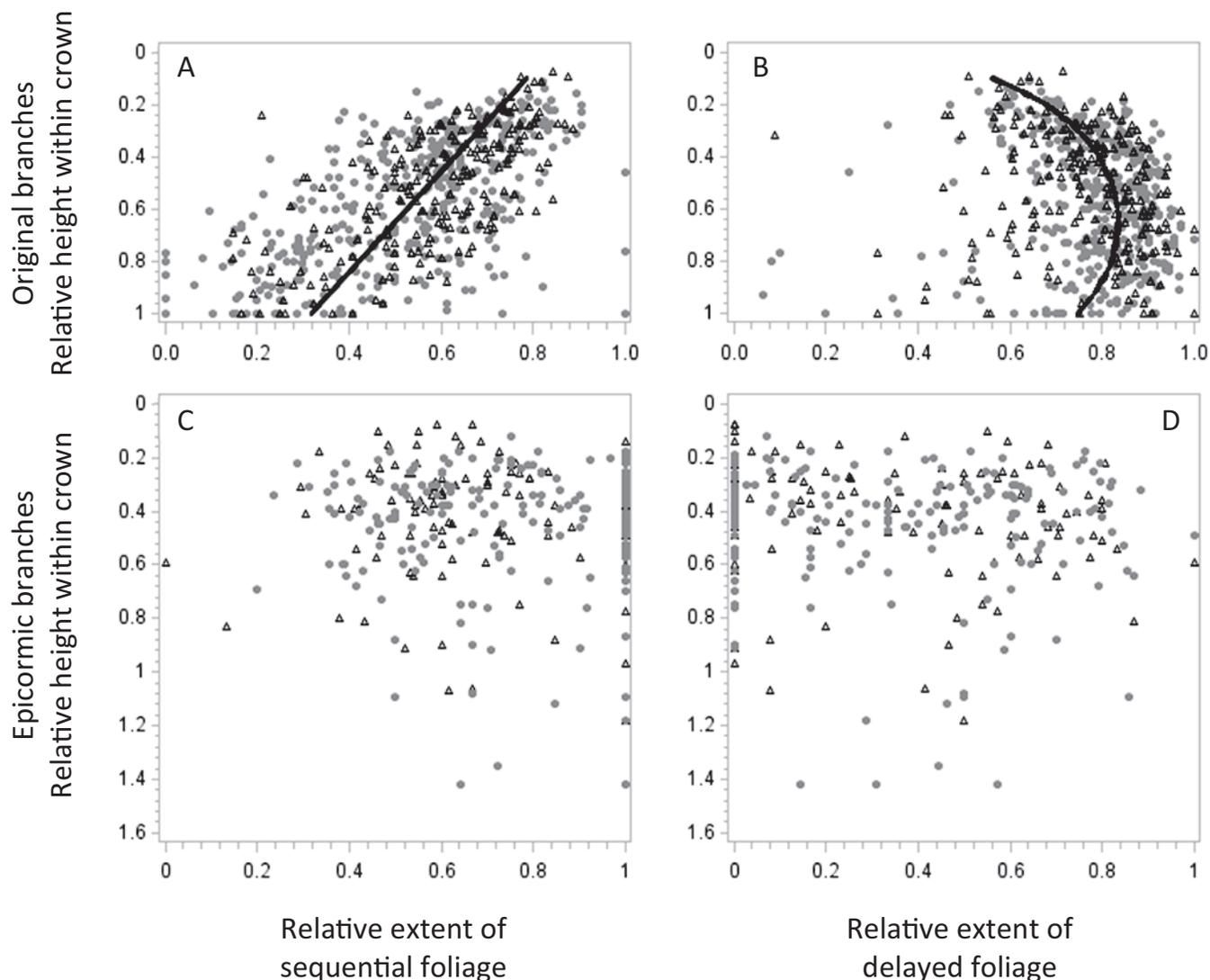

Table 4. Parameter estimates for fixed effects of mixed models; relative extent of sequential and delayed foliage on original branches (standard errors in parentheses).

Model	Intercept	Crwn	Crwn^2	Gap
4: sequential	0.9111 (0.04186), $p < 0.0001$	−0.5191 (0.04068), $p < 0.0001$		−0.00199 (0.00098), $p = 0.0548$
5: delayed	−0.3472 (0.01925), $p < 0.0001$	+0.5821 (0.05870), $p < 0.0001$	−0.4489 (0.05120), $p < 0.0001$	+0.000524 (0.000309), $p = 0.1045$

Note: Crwn, the relative height within crown, where 0 is the tree leader tip and 1 is the lowest living original branch; Gap, the gap fraction (percentage of adjacent open space) in the south-facing quadrant. Equation 5 included a Box–Cox ($\lambda = 3$) transformation to the response variable (back-transformed in Fig. 2B). Model 4 exhibited a significant ($p < 0.05$) random effect for Crwn, i.e., the influence of Crwn varied by tree (see Fig. 3). Model 5 exhibited no significant ($p < 0.05$) random effects. Detailed statistical results are available in Supplementary Material S2[1].

relative extents of sequential foliage ranging from 0.70 to 0.90 in the uppermost parts of their crowns, but only 0.15 to 0.55 at their crown bases (Fig. 3). One tree (tree 2518) had much less variation in the relative extent of sequential foliage among its branches (note the line with the steepest slope on Fig. 3); however, removing tree 2518 from the dataset had only minimal impact on parameter

estimates. We could identify nothing specific to tree 2518 that would explain the more uniform foliage distribution and thus included it in the analysis reported herein.

The relative extent of delayed foliage on original branches differed from that of sequential foliage (Fig. 2B). In the upper portions of crowns, original branches had about half of their lengths

Fig. 3. Relative extent of sequential foliage on original living branches, by relative height within crown. The top of the crown is assigned a relative value of 0 and the base of the original crown is assigned a value of 1. The horizontal axis denotes the relative extent of the branch occupied by sequential foliage, where 1 indicates fully occupied and 0 indicates a branch devoid of sequential foliage. Each line corresponds to a different tree ($n = 23$) and is adjusted for the observed gap fraction associated with that tree.
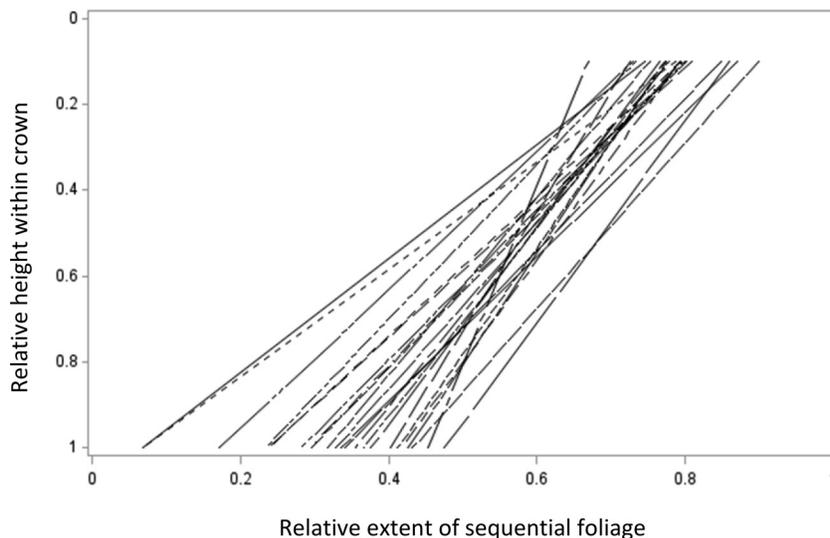

Table 5. Mean length (m) of epicormic branches by foliation extent and whorl locations.

Foliage extent	Location	N	Mean	SD	Min.	Max.
Sequential foliage present along entire length of branch	Whorl	8	0.50	0.69	0.09	2.13
	Between whorls	76	0.20	0.11	0.03	0.67
Sequential foliage present on less than entire length of branch	Whorl	38	1.23	0.93	0.12	3.51
	Between whorls	181	0.99	0.80	0.09	4.57
Devoid of delayed foliage	Whorl	8	0.26	0.18	0.09	0.67
	Between whorls	67	0.26	0.19	0.03	0.85
Delayed foliage present on branch	Whorl	38	0.48	0.22	0.03	0.87
	Between whorls	190	0.46	0.24	0.03	1.00

Note: Sequential and delayed foliage overlapped on many branches. N, number of observations; SD, standard deviation; Min., minimum; Max., maximum. Additional details are available in Supplementary Material S3[1].

occupied by delayed foliage. The relative extent of delayed foliage increased rapidly at points lower in the crown until just below the crown's midpoint and then decreased to about 0.70. Variation in the relative extent of delayed foliage increased at points lower in the crown. The relationship was modeled as per eq. 5. Fixed effects of intercept and relative height within crown (including the squared term) were all highly significant (Table 4). Gap fraction did not appear to influence the relative extent of delayed foliage on original branches (after accounting for the effect of relative height within the crown). The trend in the relative extent of delayed foliage was similar across all trees in the sample (i.e., random effects were not significant). While we obtained measurements only in the sample trees' south-facing quadrants, we observed delayed foliage to be ubiquitous throughout crowns regardless of aspect.

Epicormic branches differed from original branches in their relative extents of foliation and fell into two categories. The first category included the many epicormic branches upon which sequential foliage was present along their entire lengths (but possibly comingled with delayed foliage; Fig. 2C) and (or) were entirely devoid of delayed foliage (Fig. 2D; Supplementary Material S3[1]). The second category included epicormic branches clustered between relative heights within the crown of 0.2 and 0.6, which held relative extents ranging from 0.30 to 0.90 in sequential foliage and from zero to 0.90 in delayed foliage (with the two foliage types overlapping on some branches). Neither relative height within crown nor gap fraction explained these differences (Supplementary Material S2[1]). Branches in the first category were much

shorter on average than those in the second (Table 5). This observation held for epicormic branches occurring at, and between, whorls.

We segmented the data and repeated the analyses to specifically examine impacts of gap fraction on branches located in the lowest portions of the crowns. No evidence was found to suggest that gap fraction had a meaningful influence on relative extents of either sequential or delayed foliage in lower crowns.

Distribution of foliage mass

Over 95% of total calculated foliage dry mass in the 15-tree subsample occurred on original branches at whorls (Table 6). This was true for both sequential and delayed foliage. In contrast, epicormic branches supported only slightly more than 2% of total foliage mass (7.7 of 329.9 kg). Delayed foliage, however, played a substantial role, accounting for nearly 39% of total foliage mass (127.6 of 329.9 kg). For both sequential and delayed foliage, mass was greatest in the mid third of the crowns, but its distribution differed between the foliage types in the upper and lower crowns. Just under 11% of the mass of delayed foliage occurred in the upper crown, compared with 22% for sequential foliage. Over 39% of the mass of delayed foliage occurred in the lower third of the crown, compared with just over 20% for sequential foliage. Epicormic branches located below the base of the original crown accounted for only 0.2% of total foliage mass.

Gap fraction did not appear to significantly influence foliage mass in any of the four branch–foliage type categories, with the possible exception of delayed foliage on original branches ($p = 0.0536$; Table 7;

Table 6. Foliage dry mass, by branch and foliage type, by crown segment (percentages relative to total mass within each foliage category).

Branch type	Mass (kg)	% of mass	% of mass by crown segment			
			Upper 3rd	Mid 3rd	Lower 3rd	Below base of original crown
Sequential foliage						
Original at whorl	193.7	95.7	20.9	55.2	19.6	0.0
Original between whorls	2.6	1.3	0.1	0.7	0.5	0.0
Epicormic at whorl	2.0	1.0	0.4	0.4	0.0	0.2
Epicormic between whorls	4.0	2.0	0.7	1.0	0.3	0.1
Total sequential	202.3	100.0	22.0	57.3	20.4	0.3
Delayed foliage						
Original at whorl	122.0	95.7	10.2	48.3	37.1	0.0
Original between whorls	3.9	3.0	0.2	0.9	1.9	0.0
Epicormic at whorl	0.5	0.4	0.1	0.1	0.0	0.1
Epicormic between whorls	1.2	0.9	0.2	0.6	0.1	0.0
Total delayed	127.6	100.0	10.7	50.0	39.2	0.1

Note: No branches were measured above 10 cm stem diameter. Total calculated foliage dry mass = 329.9 kg. Extrapolated from a sample of 160 branches harvested from 15 trees, per models 6, 7, 8, and 9 reduced (Table 7).

Supplementary Material S4[1]). In the reduced models for each category, foliated branch length was the most significant predictor of foliage mass, but relative height within crown remained a valuable covariate. (Note that while relative height within crown does not appear as a significant explanatory variable in each of the reduced models, removing it from the models consistently resulted in poorer fit, i.e., fit statistics increased in magnitude.)

The dataset for this portion of the study was much smaller than that of the branch length and relative extent of foliage components, and R^2 values for the predictive models were lower than ideal (0.51 for sequential foliage on original branches, 0.28 for delayed foliage on original branches, 0.62 for sequential foliage on epicormic branches, and 0.58 for delayed foliage on epicormic branches). These limitations should be considered when interpreting the foliage mass results.

Discussion

The size of canopy gaps did not seem to have a major influence on branch length, a finding supported by recent research by Seidel et al. (2016) but differing from studies that found branch length asymmetry in the direction of adjacent gaps for several broadleaf species in the tropics and northeastern United States (Young and Hubbell 1991) and to a lesser extent in eastern white pine (*Pinus strobus* L.) and eastern hemlock (*Tsuga canadensis* (L.) Carrière) (Muth and Bazzaz 2002). The choice to include trees from some areas that had been re-thinned in 2001 may have masked the canopy gap effect, as those trees may not have had sufficient time to respond to their new conditions (similar to results noted by Seidel et al. (2016) for other Douglas-fir stands). The sample trees had also grown under spatially uniform stand density conditions for over 50 years prior to creation of canopy gaps. Based on other field observations, one could assume that had the trees been initiated in or exposed to more gappy spatial conditions at significantly earlier ages, their crowns would have ended up in much different forms. However, this approach to stand treatments (start homogenous and increase spatial variability when harvests are profitable) reflects approaches used regionally by the Oregon Department of Forestry and some private landowners. The wide range of canopy gap size present in the sample should have been sufficient to allow statistically significant detection of a short-term canopy gap effect, if it was present.

Our results reinforce previous observations that the primary response of Douglas-fir to canopy gaps is retention of longer crowns (vertical asymmetry) on the side facing the gap, rather than longer branches (horizontal asymmetry) reaching into the gap (Wardman and Schmidt 1998; Muth and Bazzaz 2002). It is also possible that the choice to measure canopy gap size solely in the south-facing quadrant may have masked the effect of canopy gaps in other quadrants. We assumed a direct relationship between canopy gap size and the characteristics of branches growing into that space, but recent LIDAR mapping suggests that Douglas-fir crowns in 50- to 70-year-old thinned stands respond to canopy gaps by extending relatively uniformly in all directions, rather than becoming longer only in the direction of the gap (Seidel et al. 2016).

Epicormic branches appeared to form regardless of original branch condition or associated canopy gap size, rather than forming as replacements of lost or damaged original branches. This finding reinforces observations that some tree species form epicormic branches and shoots even in the absence of external stimuli (Bryan and Lanner 1981; Ewers 1983). Epicormic branches have been identified as playing significant roles in the maintenance of old-growth coastal Douglas-fir crowns (Ishii and Ford 2001) and as being prevalent in other temperate conifers. The presence of epicormic branches is often attributed to or viewed as a response to some exogenous stimulus such as wounding or pruning (O'Hara and Valappil 2000; Attocchi 2013), increased light or stress (Kozlowski and Pallardy 2002), or defoliation or herbivory (Carroll et al. 1993), but our findings suggest such stimuli may not be necessary for epicormic branch and (or) shoot production in Douglas-fir.

Epicormic branches in old-growth Douglas-fir trees have been noted as occurring principally in the lower crown (Ishii and McDowell 2002). In contrast, in our sample trees, they were most prevalent in the upper portion of the crown, an area also densely populated with original branches. If epicormic branches are common high in the crown and if they persist, logic would suggest that they should remain similarly common lower in the crown. However, the relative scarcity of epicormic branches lower in the crown and their short lengths indicate that these branches are short-lived. Indeed, during the data collection process, trees were climbed multiple times and it was common to find that epicormic branches present on an earlier ascent had died or disappeared in the intervening months, an observation supported by other studies (Hollatz 2002). Rather than being produced strictly in response to exogenous stimuli, epicormic branching in Douglas-fir appears to be ongoing and somewhat opportunistic in nature; epicormic branches are produced frequently and in a widespread manner but retained only if they provide a meaningful benefit to the tree (in keeping with the original "branch autonomy" theory; Sprugel et al. 1991). This may represent a form of developmental plasticity

Table 7. Parameter estimates for fixed effects of full and reduced mixed models; natural log mass of sequential and delayed foliage on original and epicormic branches (standard errors in parentheses).

Model	Intercept	Crwn	Crwn²	LnFollength	Gap
6 full: sequential on original	4.3144 (0.5613), $p < 0.0001$	3.2471 (1.5738), $p = 0.0429$	−3.5785 (1.3786), $p = 0.0115$	1.1299 (0.1692), $p < 0.0001$	0.01127 (0.009334), $p = 0.2490$
6 reduced	4.7686 (0.4172), $p < 0.0001$	3.1240 (1.5723), $p = 0.0509$	−3.4710 (1.3774), $p = 0.0141$	1.1240 (0.1694), $p < 0.0001$	
7 full: delayed on original	3.0819 (0.5535), $p < 0.0001$	3.4609 (1.9187), $p < 0.0757$	−2.5491 (1.5651), $p < 0.1080$	0.8333 (0.2167), $p = 0.0003$	0.01621 (0.007636), $p = 0.0536$
7 reduced	3.7714 (0.4484), $p < 0.0001$	3.1515 (1.9262), $p < 0.1064$	−2.2824 (1.5691), $p < 0.1504$	0.8242 (0.2212), $p = 0.0004$	
8 full: sequential on epicormic	4.8700 (0.7564), $p < 0.0001$	−3.0918 (1.8504), $p = 0.1013$	2.0592 (1.2842), $p = 0.1154$	1.7666 (0.2119), $p < 0.0001$	0.009975 (0.01225), $p = 0.4300$
8 reduced	5.2421 (0.5938), $p < 0.0001$	−3.0920 (1.8615), $p = 0.1032$	2.0629 (1.2902), $p = 0.1164$	1.7703 (0.2106), $p < 0.0001$	
9 full: delayed on epicormic	3.3217 (1.3698), $p = 0.0358$	−2.6486 (3.5380), $p = 0.4643$	2.3493 (2.4752), $p = 0.3559$	1.2746 (0.2624), $p = 0.0001$	0.004866 (0.02248), $p = 0.8330$
9 reduced	3.5033 (1.0835), $p = 0.0080$	−2.6158 (3.4773), $p = 0.4622$	2.3253 (2.4200), $p = 0.3501$	1.2745 (0.2584), $p < 0.0001$	

Note: Crwn, the relative height within crown, where 0 is the tree leader tip and 1 is the lowest living original branch; LnFollength, the natural log of the foliated length (m) of the branch; Gap, the gap fraction (percentage of adjacent open space) in the south-facing quadrant. Random effects for intercept and spatial autocorrelation (Gaussian) significant ($p < 0.05$) in models 6 full, 6 reduced, and 7 reduced. Random effects for spatial autocorrelation (Gaussian) significant ($p < 0.05$) in models 7 full, 9 full, and 9 reduced. Detailed statistical results are available in Supplementary Material S4[1].
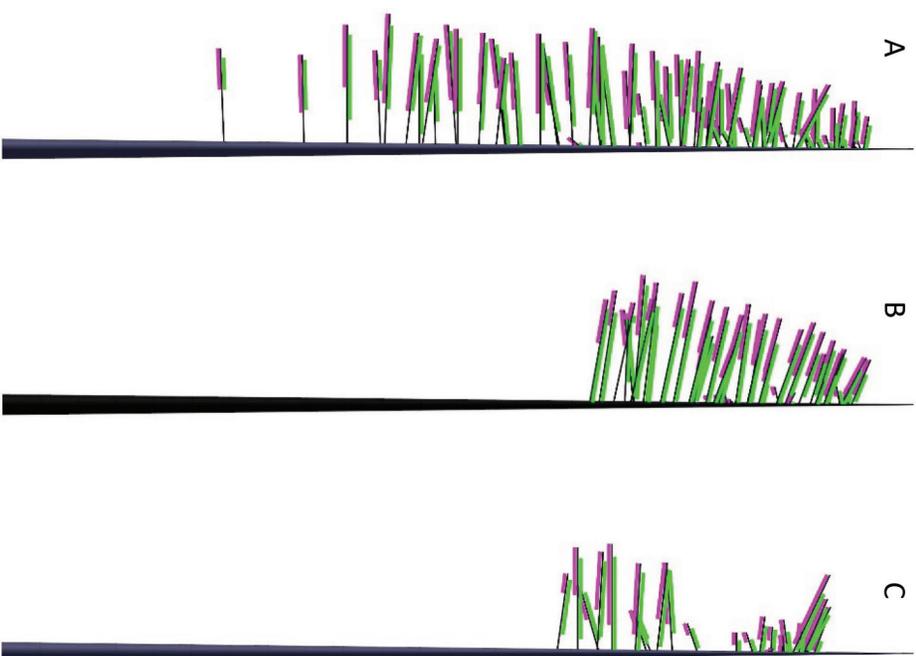
or "bet hedging" that allows Douglas-fir to adjust to environmental change (Meyers and Bull 2002).

Throughout the crown, many epicormic branches were very small, particularly those occurring below the base of the original crown. This may, to an extent, alleviate concerns about negative wood quality implications of epicormic branch development in trees managed under heterogeneous stand conditions. The epicormic branches originating in previously clear portions of the stem were too few and too small to have significant impact on log quality at this point in the trees' life cycles (Collier and Turnblom 2001; Lowell et al. 2014). Note that this finding should not be expected to hold true for trees grown to old-growth ages (Franklin et al. 2002), and we did not attempt to predict the tree age or specific stand conditions under which epicormic branching would start becoming a significant wood quality issue.

A general model for branch development and foliage distribution on Douglas-fir trees approaching maturity (approximately 65 years old) is illustrated in Fig. 4 (in a manner similar to that of Van Pelt and Sillett 2008). Sequential foliage had an obvious and predictable pattern (Jensen and Long 1983); it was focused at the distal ends of branches and its extent was dictated by the number of years that the tree held its foliage (Zhao et al. 2011). Delayed foliage overlapped with sequential foliage and occupied branch area that would otherwise have been devoid of foliage. It provided

Fig. 4. Sequential and delayed foliage distribution within crowns of three representative, approximately 65-year-old Douglas-fir trees. Purple represents the extent of delayed foliage and green represents the extent of sequential foliage. Measurements were not taken in the crown located above the point at which the stem measured 10 cm in diameter. (A) Long crown; (B) short crown; (C) damaged crown. Tree heights are not to scale.

a recurring source of young foliage (Ishii and Ford 2001; Ishii et al. 2002). These trends were apparent in trees with long and short well-formed crowns and in misshapen crowns. The trends held true for both original and epicormic branches. (Illustrations of foliage patterns for all samples trees are available in Punches (2017).)

Conclusion

The production of delayed foliage and, to a lesser extent, epicormic branches affords Douglas-fir a significant capacity to maintain crowns. Douglas-fir appears to produce delayed foliage and epicormic branches without triggers (e.g., aging, wind or ice events, herbivory, and (or) disease). Instead, Douglas-fir appears to develop foliage and branches "in reserve" should their need arise. This suggests that delayed foliage and epicormic branches are not simply responses to loss of sequential foliage or original branches, but rather their development is ongoing and ubiquitous (a finding similar to that of several long-lived pine species; Connor and Lanner 1987), making delayed foliage an integral part of their crowns. Heterogeneity of stand conditions, e.g., canopy gaps, did not appear to influence these processes, although it may influence crown lift (Seidel et al. 2016). Douglas-fir's capacity for delayed reiterative processes is a likely contributor to its ability to recover from physical damage, adapt to ongoing environmental fluctuations, and ultimately achieve great age (Spies and Franklin 1991).

A key finding of this study was the extent to which delayed foliage contributed to the crowns of Douglas-fir in this stage of maturity: nearly 39% of total foliage mass and occupying over 75% of total branch length. This rivals the contributions of delayed foliage in old-growth Douglas-fir crowns (Ishii and Ford 2001). Interestingly, delayed foliage was present throughout crowns, not just on lower branches, and it was often intermixed with and overlapped sequential foliage. Of note is that delayed foliage on original branches made a far greater contribution to overall foliated branch length than foliage of either type located on epicormic branches. Delayed adaptive reiteration is not just an old-growth phenomenon in Douglas-fir, nor is it confined to trees that have reached maximum canopy size or face suppression (Ishii and Ford 2001). Rather, Douglas-fir trees utilize delayed adaptive reiteration throughout their life-spans to continuously repopulate stems with new branches and, perhaps most importantly, branches with new foliage.

Douglas-fir appears well suited to intentional conversion from uniform to heterogeneous (i.e., gappy) stand conditions. Its ability to maintain or replenish branches and foliage gives it ample capacity to respond to or recover from thinning and the plasticity to develop old-growth-like stand and tree structure when managed for those outcomes. Simultaneously, its tendency to form relatively few, large, lower-stem epicormic branches minimizes their effect on log and wood quality in areas below the base of the original crown, at least within the time frames associated with typical, current rotation ages.

Acknowledgements

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