

AN ABSTRACT OF THE DISSERTATION OF

John W. Punches for the degree of Doctor of Philosophy in Forest Ecosystems and Society presented on August 15, 2017.

Title: Contributions of Epicormic Branches and Delayed Adaptive Foliage in Coastal Douglas-fir under Variable Density Management Regimes.

Abstract approved: _____

Klaus J. Puettmann

The contribution of delayed adaptive reiteration to crown maintenance was explored across a wide range of adjacent open space conditions in early-mature (approximately 60 year old) Douglas-fir located on the eastern slope of Oregon's Coast Range. The stands had experienced uniform thinning in 1964-65 and 1980-81 to release dominant and codominant trees, and again in 1993 to create a wide range of stand density and spatial uniformity conditions. A subset of plots had been re-thinned in 2001 to return them to target densities. A combination of ground-based, in-crown, and needle cohort measurements were employed to characterize branch and foliage characteristics.

Epicormic branches were present throughout tree crowns but contributed less than 10 percent of total branch length and only 2.4 percent of foliage mass. Very few epicormic branches occurred below the base of the regular crown in the sample trees, and those present were too small to impact log or lumber quality. However, reiteration of foliage from dormant buds (delayed adaptive reiteration) was ubiquitous, occupying 60 percent of total branch length and accounting for more than 40 percent of total foliage mass. The extent of adjacent open space did not influence patterns of branch length or location for either original or epicormic branches, nor did it affect the proportion of branch length occupied by delayed foliage.

Increasing adjacent open space may have had a modest negative impact on the proportion of sequential (regular) foliage occurring on original branches ($p=0.0548$).

Paired samples of delayed and sequential (regular) foliage were compared to determine if they differed in structure or physiological performance. Regardless of crown position, delayed foliage had higher average specific leaf area (SLA) and exhibited higher levels of discrimination against ^{13}C ($\Delta^{13}\text{C}$), lower intrinsic water use efficiency (iWUE), and higher $\delta^{18}\text{O}$, than sequential foliage. The results indicated that delayed foliage was, on average, more shade adapted than sequential foliage. In addition, cohorts of both types of foliage demonstrated distinct reductions in average SLA with increasing age of their leaf cohort, a result attributed to more rapid shedding of high-SLA needles. Year-to-year variation in $\Delta^{13}\text{C}$, iWUE, and $\delta^{18}\text{O}$ was correlated with weather conditions, but trends were complicated by the integration of isotope signals across multiple growth seasons.

Delayed foliage provides Douglas-fir with an ongoing source of new leaf area and the capacity to adapt to changing growth conditions. It provides a significant proportion of the species' photosynthetic capacity, and very likely increases its ability to recover from crown damage, foliage disease, and herbivory. It may allow Douglas-fir to more readily utilize the increased levels of CO_2 available in the earth's atmosphere, and to respond positively to other environmental changes at both local (site-level) and global (climatic) scales.

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Contributions of Epicormic Branches and Delayed Adaptive Foliage in Coastal Douglas-fir under
Variable Density Management Regimes

by
John W. Punches

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

John W. Punches, Author

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DEDICATION

To Michelle, Abby, and Will, who stuck with me through this very long process;

and,

to Mom and Dad, for their never-failing faith and support.

CHAPTER 1: INTRODUCTION

Coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) is an important commercial timber species and a major component of western North American forests. It grows under a variety of climate conditions and has been introduced successfully into other temperate regions. It can reach great age; specimens of 500 years are not uncommon and trees have been identified that exceed 1,000 years (the oldest known tree was documented at more than 1,400 years of age, Hermann and Lavender 1990). Coastal Douglas-fir regenerate under a wide range of natural conditions, from relatively even-aged stands in which it may be the dominant species, to mixed aged and/or mixed species stands that may have required 100 or more years to become fully established (Spies 1991, Tappeiner et al. 1997, Poage et al. 2009, Freund et al. 2014, Freund et al. 2015). Substantial height growth is maintained for more than 200 years, and trees in excess of 75 meters (250 feet) height and 1.8 meters (6 feet) in diameter are common in old-growth forests (Hermann and Lavender 1990). Although considered an early seral species, Douglas-fir is common in old-growth Pacific Northwest forests, where its long life and great size potential allow it to persist in conjunction with more shade tolerant late seral or climax species such as western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*) (Hermann and Lavender 1990, Spies 1991, Spies and Franklin 1991, Poage et al. 2009, Freund et al. 2014.)

The ability of woody plants to achieve such large size and maintain themselves over long periods of time requires ongoing capacity to capture solar energy and produce carbohydrates as sources of energy and raw materials. Photosynthesis in leaves is the primary mechanism by which trees meet their carbohydrate needs. Leaves are arranged on trees to make effective use of available sunlight, with branches serving as “scaffolds” to distribute leaf area with crowns (Ishii et al. 2002). Light intensity varies within crowns, with leaves lower in the crown typically

receiving less light. Many species compensate through production of sun leaves and shade leaves (leaves tailored to be effective under specific light regimes). Below some minimum threshold, however, the respiratory and other maintenance requirements of shaded foliage exceed its photosynthetic contributions and the tree either sheds this foliage or allows entire branches to die (Givnish 1988, Witowski 1996, Ishii and Ford 2001, Taiz & Zeiger 2002 p177, Hikosaka 2005, Newton et al. 2012). Thus, the tree's limited resources are allocated to prioritize the areas of its crown most efficient at providing a positive return on its morphological and physiological investment.

The typical crown development process of coastal Douglas-fir serves as an illustration of this trade-off. Healthy, open-grown trees often possess living crowns for all or much of their height. As the trees grow in height and branch length, their stands become denser and each tree competes for increasingly scarce access to sunlight and other resources. Lower limbs become shaded and the crowns recede as excessively-shaded foliage dies. Thus, in stands experiencing significant competition for light, tree crowns tend to be short relative to the tree's height. Conversely, trees grown in more open conditions tend to maintain longer, broader crowns (Larson 1962, Carter et al. 1986, Hermann & Lavender 1990).

Numerous tree growth and simulation models recognize relationships between crown size and tree height and diameter. Many of these models use the relationship between crown size, leaf area and associated photosynthesis to predict tree growth. The focus of these models has often been on predicting diameter growth, but recent models also predict the number, size, location and other characteristics of branches under varying stand conditions as indicators of wood quality, as well as other stand features (see Burkhardt and Tomé 2012 p106 for extensive references).

Maintaining an effective crown over time (one capable of effective photosynthesis) requires trees to allocate resources to getting taller and wider by expanding foliage in areas with abundant sunlight; to replace aging, less effective foliage with newer leaves; and ideally to have some mechanism for replacing crown components lost to ice, wind, insects/disease or other damage mechanisms. Douglas-fir has been shown to accomplish these objectives through a combination of sequential and delayed reiteration (Ishii and Ford 2001, Barthélémy and Caraglio 2007).

Sequential reiteration is the tree's normal process of replicating its basic architectural units through the activity of apical buds (Hallé et al. 1978, Ishii, Ford and Kennedy 2007). It is responsible for production of new foliage at the growing axes of stem and branch tips, and until constrained by limitations in space or resources it ensures an ever increasing area of new foliage.

Douglas-fir is an evergreen, but while its crown as a unit retains live foliage indefinitely, individual needles mature, lose effectiveness over time, die and are shed. Coastal Douglas-fir commonly holds three to nine years of needles, with trees under higher levels of stress holding a greater number of age groups (Reich et al. 1995, Van Pelt and Stille 2008, Zhao et al. 2011). The process of adding new needles to branch tips, while losing older needles more proximal to branch bases, should be expected to result in Douglas-fir crowns resembling cones of foliage a few age layers in depth, with foliage occurring distally on branches. The inside of the lower crown would be relatively devoid of foliage. Indeed, many Douglas-fir trees can be observed to demonstrate such hollow crowns.

In an old growth Douglas-fir, the interiors of tree crowns have been shown to refoliate through a process describe as delayed adaptive reiteration (Ishii, Ford and Dinnie 2002, Ishii,

Ford and Kennedy 2007, Kennedy and Ford 2009). Dormant buds on existing branches are activated and produce new shoot clusters populating available branch space, allowing trees to maintain a stable population of branchlets with associated foliage. Delayed reiteration can occur at the main stem as epicormic branches, or from older branch axes (basal reiteration). Ishii and colleagues contend that “there is no well-established theory explaining how adaptive reiteration is initiated” (Ishii, Ford and Kennedy 2007 p457), and note that delayed adaptive reiteration is evident in many tree species, and across a wide range of tree ages.

The ability of Douglas-fir to replace old, lost or damaged foliage and branch support structures is arguably a key factor in its ability to remain viable in forests for hundreds of years (Ishii and Ford 2001, Ishii, Ford and Dinnie 2002, Ishii, Ford and Kennedy 2007). Adaptive reiteration’s role in younger stands has received less attention. Short-lived epicormic shoots have been noted in 30-year old Douglas-fir (Hollatz 2002) and the implications of epicormic branching in young Douglas-fir stands (dominant height averaging 9.1 meters) examined (Collier and Turnblom 2001), but the work of Ishii and colleagues suggests delayed reiteration of shoots on existing branches (rather than epicormic branching itself) plays the more important role in maintaining the species’ leaf area (Ishii and Wilson 2001, Kennedy et al. 2004).

Until recently, the common method of managing Douglas-fir stands focused on timber production and relied heavily on even-aged management with stand density fine-tuned to balance stand growth and individual tree growth and quality with the goal of maximizing profit (Curtis et al. 2007). Today’s forest management paradigms are evolving toward (or some might argue, returning to) a greater emphasis on ecosystem services: seeking opportunities to pair wood production with habitat management, plant and animal species diversity, soil productivity management, water quantity and quality and other goals (Puettmann, Coates and Messier 2009

px, O'Hara, Hasenauer and Kindermann 2007). In this context stand management is shifting, at least on some fronts, toward methods that utilize greater variation in stand density to induce complexity into existing stands (Dodson, Ares and Puettmann 2012, Gray, Spies and Pabst 2012, Puettman et al. 2016).

Douglas-fir has demonstrated the capacity to maintain and/or rebuild crowns over potentially multi-century lifespans, but little information is available about the age at which delayed foliage reiteration becomes important or how management practices influence this phenomenon. The new stand management approaches are often initiated at the time of the first commercial thinnings (Cissel et al. 2006) and rely on younger trees that regenerated under even-aged conditions to respond effectively to newly opened canopy spaces. Research is needed to identify tree crown responses to variable density management (i.e., gap creation), and the roles of epicormic branches and delayed adaptive foliage in Douglas-fir during its early stages of maturity. To this end, this study seeks to address the following questions:

1. How prevalent are epicormic branches in early-mature (approximately 60 year-old) Douglas-fir across a wide range of stand densities, in stands undergoing transition from relatively uniform density to variable density or "gappy" stand structures? What contribution does the foliage of these branches make to trees' overall leaf area?
2. To what extent do young Douglas-fir undergo delayed adaptive reiteration of foliage on original branches? What is the role of this foliage in maintenance of crown leaf area?
3. How do the characteristics of sequentially reiterated foliage compare and contrast to delayed-reiterated foliage, with respect to needle area and mass, photosynthetic efficiency and water use efficiency?

This thesis is organized in the manuscript document format, and consists of two manuscripts intended for publication. The first manuscript addresses elements of the study related to quantities and locations of epicormic branches and extents of sequential and delayed foliage and their relationship to adjacent open space (questions 1 and 2, above). It relies primarily upon direct measurements of tree and crown properties. The second manuscript addresses issues of foliage quality – the relative capacities of sequential and delayed foliage to make use of light and water resources (question 3). The latter manuscript relies upon paired analysis of C and O stable isotopes, along with observations of specific leaf area, at the branch and leaf cohort levels.

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CHAPTER 2: DISTRIBUTION OF EPICORMIC BRANCHES AND FOLIAGE ON EARLY-MATURE DOUGLAS-FIR AS INFLUENCED BY CANOPY OPENINGS

Potential journals: CJFR, FEM, CJB

Abstract

The contributions of delayed adaptive reiteration (including epicormic branches and foliage formed from activation of dormant buds) were investigated for early-mature (approximately 60 year old) Douglas-fir growing on the eastern flank of the Oregon Coast Range, across a wide range of adjacent open space conditions. The stands had experienced multiple thinning operations, initially to maintain uniformity and release dominant and codominant trees, but later to introduce canopy gaps. Hemispherical photography was utilized to assess open space, and trees were climbed to allow detailed, in-crown measurements of branches and foliage extent. Measurements were focused on the south-facing quadrant of the trees' crowns. Epicormic branches were prevalent throughout crowns but contributed less than 10 percent of total branch length and only 2.4 percent of total foliage mass. In contrast, delayed adaptive foliage (formed from delayed activation of previously dormant buds on existing branches) occupied 60 percent of total branch length and accounted for more than 40 percent of total foliage mass. The extent of adjacent open space did not influence patterns of branch length or location for either original or epicormic branches, nor did it affect the proportion of branch length occupied by delayed foliage. Increasing adjacent open space may have had a modest negative impact on proportion of sequential (regular) foliage occurring on original branches ($p=0.0548$). The results suggest delayed adaptive reiteration of foliage contributes substantially to the maintenance of early-mature Douglas-fir crowns.

Introduction

Trees utilize a variety of strategies to adapt to changes in their environment. Examples include crown expansion and recession, root extension and die-back, a wide range of foliar responses, development and abandonment of vascular structures, investments in defensive chemicals and structures, and a host of other species-specific responses (Hallé et al. 1978). Many trees exhibit the capacity to develop epicormic branches, allowing them to repopulate segments of stem that have experienced branch mortality/loss (Bryan and Lanner 1981, Meier et al. 2012). They produce new shoots and foliage through the action of apical meristems and the associated, sequential action of lateral meristems: processes that allow for regular, recurring leaf area development. They may also activate dormant meristems on existing branches to produce epicormic shoots and foliage which repopulate sparsely-foliated branch segments (Barthélémy and Caraglio 2007, Ishii and Ford 2001). Collectively, these structures and processes allow trees to adjust resource uptake relative to their physiological needs, within the scope of their genetic potential.

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, Miller 1996, Nicolini et al. 2003, Fontaine et al. 2004, Colin et al. 2008). Several temperate coniferous species (including Douglas-fir, redwood, spruce, true firs and larch) have been observed to develop epicormic branches and shoots at a variety of ages (Bryan and Lanner 1981, Ishii et al. 2000, O'Hara and Valappil 2000, Collier and Turnblom 2001, Deal et al. 2003, Hanson and North 2006, O'Hara and Berrill 2009). Many tree species have significant capacity to produce epicormic features, as each flush also produces dormant buds that can later emerge as epicormic shoots or branches (Morisset et al. 2012).

Epicormic branch development and epicormic shoots on existing branches (collectively known as delayed adaptive reiteration) can play essential roles in maintenance of old-growth Douglas-fir crowns (Ishii, Ford and Kennedy 2007, Kennedy et al. 2010). Epicormic branches repopulate segments of stem that have lost their original branches. In contrast, epicormic shoots (branchettes 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, Ford and Kennedy 2007 p. 457). Epicormic branches appear to be more prevalent on trees adjacent to canopy openings – a feature of interest in modern silviculture because of wood quality concerns (Trimble and Seegrist 1973, Rey-Lescure 1982, Quine 2004).

Delayed adaptive reiteration’s role in younger trees has received less attention. Short-lived epicormic shoots have been noted in 30-year old Douglas-fir (Hollatz 2002) and the implications of epicormic branching in young Douglas-fir stands (dominant height averaging 9 meters) examined (Collier and Turnblom 2001). However, delayed reiteration of shoots and foliage appears to play a more important role than epicormic branching itself in maintaining the species’ leaf area (Ishii and Wilson 2001, Kennedy et al. 2004).

On many ownerships forest management paradigms are evolving toward greater emphasis on the variety of ecosystem services provided: pairing wood production with habitat management, plant and animal species diversity, soil productivity management, water quantity and quality and other goals (Puettmann, Coates and Messier 2009 p. x, O’Hara, Hasenauer and Kindermann 2007). In response to these changes, silvicultural practices that lead to greater

spatial and structural variability in existing stands have garnered attention (Dodson, Ares and Puettmann 2012, Gray, Spies and Pabst 2012).

We investigated epicormic branch production and delayed adaptive reiteration of foliage in approximately 60-year-old Douglas-fir in stands that had been managed using thinning to create canopy gaps. Our objectives were to: 1) evaluate how prevalent epicormic branches were on trees across a wide range of growing conditions, as expressed through adjacent canopy openings; and 2) determine the extent to which delayed adaptive shoots and foliage populated original and epicormic branches throughout tree crowns, and their reaction to adjacent open space. Lastly, we propose a general model for branch and foliage development within Douglas-fir tree crowns, contrasting the roles of original and epicormic branches and sequential and delayed foliage.

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 (Lat. 44.65° N, Long. 123.27° W). In 2005 it was predominantly occupied by even-aged stands of 63-68 year-old Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) with scattered grand fir (*Abies grandis* 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 percent, typically west to northwest facing. Annual precipitation was approximately 1,500 mm (mostly as rain from October to May) and experienced moderate temperatures. The stands on the study site had experienced uniform thinning in 1964-65, and again in 1980-81, to release dominant and codominant trees. In 1993 the site was thinned again to create a wide range of

stand density and spatial uniformity conditions. A subset of plots were re-thinned in 2001 to return them to target densities (Newton and Cole 2006).

The treatments resulted in trees growing at a wide range of local densities. Growing conditions for individual trees varied from trees that were fully surrounded by neighboring trees to trees adjacent to gaps. One hundred and eight (108) dominant or codominant trees were systematically selected such that the resulting sample represented a broad gradient of adjacent open space.

Hemispherical photos were taken adjacent to each tree using a Nikon Coolpix 5000 camera with a calibrated fish-eye lens. We focused our measurements on the 90° quadrant centered on true south to best capture the impact of openings on available photosynthetically active radiation (Schoettle and Smith 1991, Van Pelt and North 1996, Burke 2015). The camera was mounted on a tripod one meter above the ground, situated one meter due south of the tree stems, and leveled. All photos were taken between May 23 and June 7, 2005, between the hours of 6:00 a.m. and 10:00 a.m. or between 4:00 p.m. and 6:00 p.m. to avoid having the sun appear within the target quadrant of the photo.

Several digital photos were taken at each tree and a single photo with optimal contrast selected from each series for further analysis. Several series were unusable due to incorrect camera settings or because hardwood species obscured the Douglas-fir canopy. Ultimately, 94 photos were analyzed for open space adjacent to target trees, within their south-facing 90° quadrants. For initial sample selection we limited the opening to 30° from true vertical and used a dot grid to estimate percent open sky as an indicator of conditions in tree crowns (e.g., light availability, temperature) relevant to epicormic branch or delayed foliage development.

Trees were ranked and stratified into four groups of equal range of open sky, and six trees selected from each strata for branch and foliage sampling. One tree was later dropped after field-verifying that it had been incorrectly coded as Douglas-fir, but was in fact a grand fir. The resulting sample included 23 trees, ranging in height from 34.2 to 45.8 meters, with associated south-quadrant canopy conditions ranging from nearly closed (1.5 percent open) to over 76 percent open (Table 2.1).

For the statistical analysis, more precise calculations of open space were made using WinSCANOPY 2005c. Photos were rotated to true north, a mask was applied to restrict analysis to the south-facing quadrant, and percent gap fraction (amount of area in canopy gap) calculated for openings of 22, 34 and 43 degrees from vertical (WinSCANOPY, Regent Instruments Inc.). Examples are available in Appendix A.

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 trunk 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 relative branch diameter (Ishii and Wilson, 2001). See Figure 2.1 for examples.
- branch location (whorl or between whorls, where a whorl was a cluster of original branches located within a 10cm vertical range, presumed to be the location of a previous terminal bud).
- branch diameter (outside bark, outside collar – using calipers and/or diameter tape).
- branch length (straight-line distance from stem intersection to branch tip – using optical range finder or measuring tape/pole).

- branch height above ground (using tape stretched along 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 branch tip pointed, referenced to true north).
- starting and ending points of sequential foliage on branch (measured from tree stem surface), where “sequential” was defined as foliage produced during, or in close association with, elongation of the shoot apex (Figure 2.2).
- starting and ending points of delayed foliage on branch (measured from tree stem surface), where “delayed” was foliage arising from dormant buds that could be determined to be at least two seasons younger than its adjacent sequential foliage (Figures 2.3 and 2.4).



Figure 2.1. Epicormic branches on Douglas-fir



Figure 2.2. Sequential foliage on Douglas-fir



Figure 2.3. Delayed foliage on Douglas-fir



Figure 2.4. Delayed foliage on Douglas-fir

Between March and September of 2006 a subsample of branches was harvested from 15 of the 23 trees: nine trees in March, prior to bud break, and six trees between July and September, after bud break). Crowns were segmented into three sections (high, mid and low). For this subsample, the location of the longest branch was used to separate low and medium crown segments on the assumption that branches above that point would be actively elongating while those below may have entered maintenance or die-back modes. The branches above the longest branch were split equally in number to separate mid and high crown sections. Within each section we harvested two regular branches from whorls, two regular 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, then frozen to maintain freshness until processing.

In the lab, each sample was divided into foliage years (based on the location of shoot nodes and/or bud scale scars). Samples were then dried at 70°C for 96 hours, screened to remove woody material, and weighed. Total masses for each combination of branch and foliage type were estimated by extrapolating the results, within each branch category, from sample branches to the total number of branches for which foliage proportions were measured. We then summed across categories to estimate total foliage mass.

Tree illustrations were created in Maple 10. Branch starting points were set at the surface of the stem at their recorded heights above ground. Branch end points were calculated from associated branch length, aspect and angle. Branches were assumed to be straight for the purposes of these illustrations. Extent of sequential foliage has been indicated using its starting and ending points, offset slightly to show it just below and parallel to the branch. Delayed foliage has been plotted similarly, but offset slightly to the top of the branch.

Table 2.1. Sample tree characteristics. Low density treatment = 17.2 – 19.5 m² BA, Medium = 21.8 – 24.1, High = 26.4 – 28.7, Ultrahigh = 29.8 – 32.1. Medium and High were re-thinned in 2001 to original basal area. Additional detail in Appendix B.

Tree Number*	Height (m)	Treatment History	% Open Sky (ocular est.)
2496	42.4	Gap/Clump, Ultrahigh Density	1.5
332	34.2	Uniform, Ultrahigh Density	4.3
2360	35.5	Gap/Clump, Ultrahigh Density	6.0
1945	38.7	Gap/Clump, High Density	11.9
458	35.3	Uniform, Ultrahigh Density	13.0
1935	40.9	Gap/Clump, High Density	17.9
3144	39.5	Uniform, Ultrahigh Density	22.4
2001	40.8	Gap/Clump, Med Density	23.9
850	36.2	Gap/Clump, Med Density	24.6
1824	40.9	Gap/Clump, High Density	28.4
115	41.1	Uniform, High Density	29.0
175	41.6	Uniform, Med Density	36.2
826	35.9	Gap/Clump, Med Density	37.7
2804	42.7	Uniform, Low Density	38.8
2518	36.1	Uniform, High Density	40.3
1785	40.0	Gap/Clump, High Density	40.3
89	42.2	Uniform, High Density	44.9
2118	37.2	Gap/Clump, Med Density	55.2
1172	41.0	Gap/Clump, High Density	58.2
2832	45.8	Uniform, Low Density	58.2
3409	37.6	Uniform, Med Density	59.7
2077	39.0	Gap/Clump, Med Density	68.7
1487	42.0	Gap/Clump, Low Density	76.1

* Trees permanently numbered (Newton and Cole 2006)

Analysis

SAS 9.4 was utilized to apply a series of mixed models to assess the impact of adjacent open space on branch length and extent of sequential and delayed foliation. Relative crown position was treated as a covariate. Since trees varied in height and crown length, relative crown position was calculated based on the total length 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 last living regular branch had relative crown positions exceeding 1. Intercept, crown position, and adjacent open space (gap) were treated as fixed effects. Tree was treated as a class variable, and intercepts and crown positions were allowed to have random effects between trees. 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 two 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 model adequately accounted for spatial autocorrelation.

The impact of open space on original branch length was modeled as follows:

$$[2.1] \quad \ln Y_{ij} = (\beta_0 + b_{0i}) + (\beta_1 + b_{1i})\text{Crwn}_{ij} + (\beta_2 + b_{2i})\text{Crwn}_{ij}^2 + \beta_3\text{Gap}_i + e_{ij}$$

where $\ln Y_{ij}$ was the natural log of branch length at crown position j within tree i ($i = 1, 2, \dots, 23; j = 1, 2, \dots, j_i$), β_0 was the overall intercept, b_{0i} was the random effect on intercept associated with tree i where $b_{0i} \sim N(0, \sigma_{b0}^2)$, β_1 was the overall slope coefficient for crown position, b_{1i} was the random effect on slope associated with tree i where $b_{1i} \sim N(0, \sigma_{b1}^2)$, Crwn_{ij} was crown position j in tree i , β_2 and b_{2i} were the equivalent overall slope and random effects for Crwn^2 with $b_{2i} \sim N(0, \sigma_{b2}^2)$, β_3 was slope coefficient for the fixed effect of Gap_i , Gap_i was the percent of open space associated with tree i , e_{ij} was the random error associated with the model, where $e_{ij} \sim N(0, \sigma_e^2)$.

Epicormic branches longer than 1 meter were modeled as:

$$[2.2] \quad Y_{ij} = (\beta_0 + b_{0i}) + (\beta_1 + b_{1i})\text{Crwn}_{ij} + \beta_2\text{Gap}_i + e_{ij}$$

where Y_{ij} was the branch length at crown position j within tree i ($i = 1, 2, \dots, 23; j = 1, 2, \dots, j_i$), β_2 the slope coefficient for the fixed effect of gap, and all other components per [2.1].

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

$$[2.3] \quad Y_{ij} = (\beta_0 + b_{0i}) + \beta_1 \text{Gap}_i + e_{ij}$$

Similar mixed models were utilized to assess responses of the two foliage types to adjacent open space. We used the proportion of each branch's length occupied by sequential or delayed foliage as the response variable, as it standardized the foliage measurement by adjusting for differing branch lengths and facilitated comparison of the relative importance of the two types of foliage. Thus, foliage proportions ranged from 0 to 1 per branch. (We converted these values to a percentage basis for figures and results/discussion.)

The relationship of sequential foliage proportion on regular living branches was determined, via scatterplots, to be approximately linear with its major explanatory variables. It was modeled as:

$$[2.4] \quad Y_{ij} = (\beta_0 + b_{0i}) + (\beta_1 + b_{1i})\text{Crwn}_{ij} + \beta_2\text{Gap}_i + e_{ij}$$

Variables for this model were as noted in [2.1], except that Y_{ij} was the proportion of branch length in sequential foliage at crown position j within tree i ($i = 1, 2, \dots, 23; j = 1, 2, \dots, j_i$), and the squared term was omitted.

Delayed foliage on regular living branches was most prevalent in the middle of the crown, suggesting the quadric form of the model. A Box-Cox transformation to Y ($\lambda=3$) was required to ensure residuals were normally distributed. Delayed foliage was modeled as:

$$[2.5] \quad (Y_{ij}^3 - 1)/3 = (\beta_0 + b_{0i}) + (\beta_1 + b_{1i})\text{Crwn}_{ij} + (\beta_2 + b_{2i})\text{Crwn}_{ij}^2 + \beta_3\text{Gap}_i + e_{ij}$$

Where Y_{ij} was the proportion of branch length in delayed foliage at crown position j within tree i ($i = 1, 2, \dots, 23; j = 1, 2, \dots, j_i$) and all other variables were as in equation [2.1]. In this form residuals were approximately normally distributed, although still slightly left-skewed.

On epicormic branches, distribution of sequential and delayed foliage was bimodal and we were unable to analyze it using linear or mixed models. Results are discussed in more general terms.

Results

Branch patterns and response to open space

The 23 sample trees possessed nearly 900 branches with over 2.5 km of total branch length within the south facing quadrants (truncated at a 10 cm stem diameter; Figure 2.5 and Table 2.2). Original branches at whorls accounted for 64 percent of branches and nearly 89 percent of total branch length. Very few original branches originated between whorls (just eleven branches on seven trees). Epicormic branches were common (34 percent of total branches) but contributed only 10 percent of the total branch length. Unlike original branches, epicormic branches most commonly originated between whorls.

Original and epicormic branch length displayed differing patterns relative to crown position. Original branches reached their maximum length in the lower half of the crown (approximately 75 percent of relative crown depth; Figure 2.5A). Epicormic branches had two overlapping patterns: many short branches (less than 1 meter) scattered throughout the crown, plus other branches that increased in length lower in the crown (Figure 2.5B). The amount of adjacent open space did not significantly impact length of branches in any of the three branch categories (Table 2.3).

The number of branches on individual trees was not influenced by the amount of adjacent open space. 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 percent adjacent open space (R^2 for each model less than 0.01).

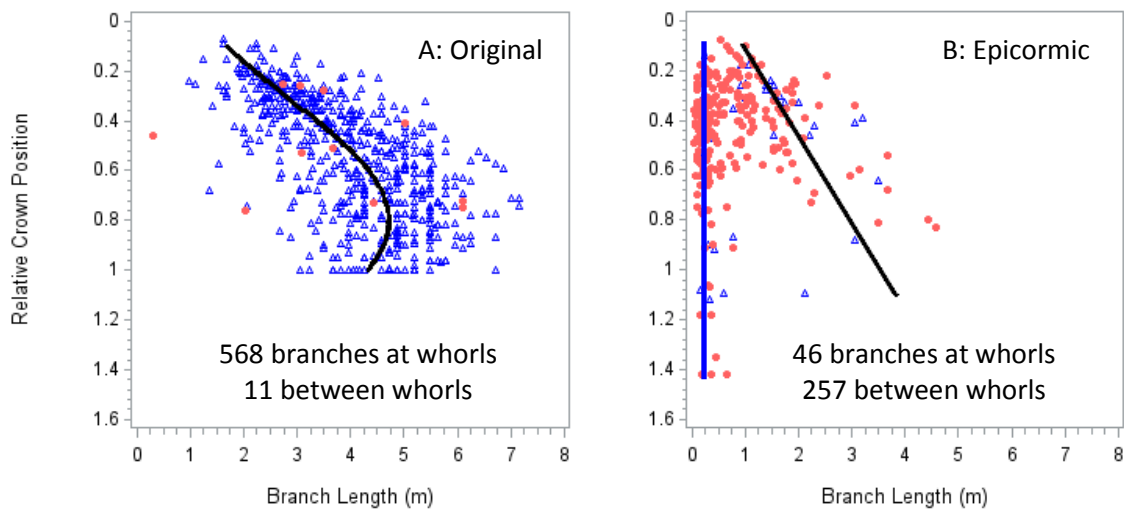


Figure 2.5. Length of living, unbroken branches by relative crown position. Blue triangles: branches initiating from whorls. Red points: branches originating from between whorls. The top of the crown has a relative position of 0 and the base of the regular crown (lowest living original branch) is at 1.0. Epicormic branches located below the base of the regular crown have relative crown positions exceeding 1.0. Fit lines per Table 2.3, with gap held constant at 36.9 percent (the observed average), back-transformed for original branches. Data for south-facing quadrants of sample trees. No branches measured above 10cm stem diameter.

When examined by crown segment, over 45 percent of branch length appeared in the mid-third of the measured crowns, just under 37 percent in the lower-third, and less than 18 percent in the upper-third (Table 2.2). As the lowest living original branch was utilized as the reference point for the base of the crown, epicormic branches appearing below that point are noted in the tables in the column labeled “below base of regular crown.” Epicormic branches in this lowest crown segment accounted for just 0.2 percent of total branch length.

Table 2.2. Total branch length and percentage by branch type and crown segment. All percentages are expressed as percent of the total branch length.

	Total length (m)	% of total length	% total length by crown segment			
			Upper 3rd of Measured Crown	Mid 3rd of Measured Crown	Lower 3rd of Measured Crown	Below Base of Regular Crown
Original at whorl	2,258.1	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	2,541.9	100.0%	17.9%	45.2%	36.7%	0.2%

Table 2.3. Parameter estimates for models of branch length (with standard errors in parentheses) for mixed models applied to living, unbroken branches in three categories: original, epicormic greater than one meter in length, epicormic less than or equal to one meter in length. Detailed statistical results available in Appendix C. Results back-transformed for figures and discussion.

Equation	Parameter estimates*				Random effects
	Intercept	CrwnPos	CrwnPos ²	Gap	
2.1**: ln length of original branches	<u>0.1625</u> (0.1336) P=0.2372	+3.3564 (0.4298) P<0.0001	-2.1006 (0.3291) P<0.0001	<u>+0.001318</u> (0.001928) P=0.5018	Yes
2.2: length of epi branches >1m	<u>-0.02839</u> (0.1572) P=0.8586	+1.4185CrwnPos (0.2319) P<0.0001		<u>-0.00214</u> (0.003508) P=0.5486	No
2.3: length of epi branches ≤1m	-0.8460 (0.2222) P=0.0011			<u>-0.00958Gap</u> (0.005656) P=0.1057	No

*underline denotes parameter estimate not significantly ($p>0.05$) different from 0.

**equation 2.1 included a natural log transformation to the response variable (back transformed in Figure 2.5A)

Foliage patterns and response to open space

A bit more than half of combined length of original and epicormic branches was occupied by sequential foliage (1,351 meters of 2,542 total) and sequential foliage was most

extensive in the mid-third of the measured crown (Table 2.4). This coincided with the point at which branches were close to their maximum length and still largely populated with foliage. In comparison to mid-crown branches, those in the lower-third were often shorter and had less of their length occupied by sequential foliage.

Table 2.4. Sequential foliage by branch type and crown segment. All percentages are expressed as percent of the total branch length occupied by sequential foliage.

	Total length (m)	% of total length	% total length by crown segment			
			Upper 3rd of measured crown	Mid 3rd of measured crown	Lower 3rd of measured crown	Below base of regular crown
Original at whorl	1,190.4	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	1,350.8	100.0%	22.9%	48.9%	27.9%	0.4%

Our sample trees had more foliated branch length in delayed foliage than in sequential foliage (1,920 meters vs. 1,350 meters; Table 2.5). Nearly 92 percent of the delayed foliage length occurred on original branches at whorls. Roughly five percent occurred on epicormic branches between whorls, with the remainder split between the other two branch categories. Relative to sequential foliage, a greater percentage of delayed foliage length occurred in the lower-third of the measured crown, and smaller percentages in the upper, middle, and below base segments.

Table 2.5. Delayed foliage by branch type and crown segment. All percentages are expressed as percent of the total branch length occupied by delayed foliage.

	Total length (m)	% of total length	% total length by crown segment			
			Upper 3rd of measured crown	Mid 3rd of measured crown	Lower 3rd of measured crown	Below base of regular crown
Original at whorl	1,764.2	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	1,919.8	100.0%	15.7%	46.7%	37.4%	0.2%

Original living branches near the top of trees' crowns had nearly all of their length occupied by sequential foliage (Figure 2.6A). That proportion decreased in a linear fashion at points lower in the crown. Increasing open space may have led to lower proportions of sequential foliage; its p-values only slightly exceeded 0.05 (Table 2.6). The open space measurements utilized in our model ranged from 8 to 63 percent, which when multiplied by the model parameter suggested open space could have reduced the foliage percentage by as much as 13 percent.

There were meaningful changes in percent of sequential foliage among trees, as evidenced by the significance of random effects in model [2.4]. Most trees had 70 to 90 percent of their branch length occupied by sequential foliage in the uppermost parts of their crowns, but only 15 to 55 percent at their crown bases (Figure 2.7). One tree (2518) had much less variation in sequential foliation percentage (note the line with the steepest slope on Figure 2.7). 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 stable foliage pattern, and as such it was included in the analysis reported herein.

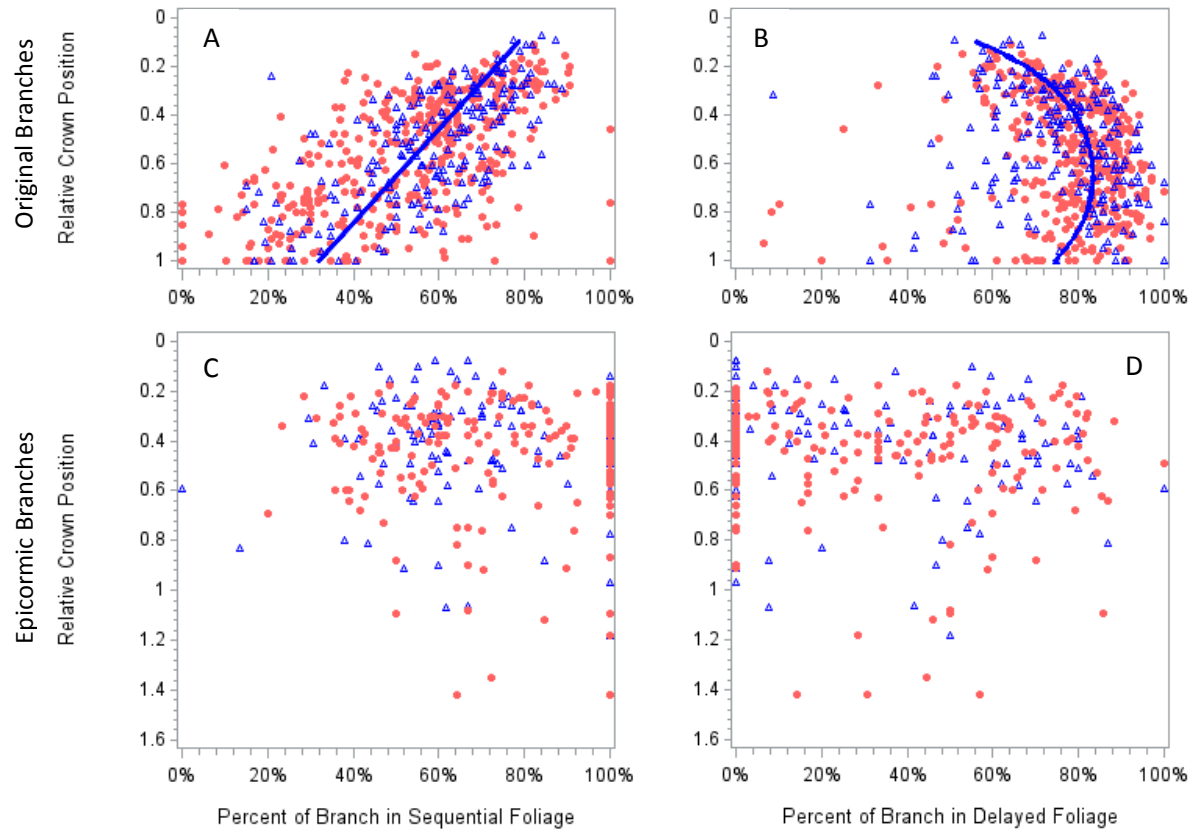


Figure 2.6. Foliar distribution by relative crown position. The top of the crown has a relative position of 0 and the base of the regular crown (lowest living original branch) is at 1. Epicormic branches located below the base of the regular crown have relative crown positions exceeding 1. The horizontal axis denotes the percentage of branch length occupied by each type of foliage. 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 2.6, with gap held constant at 36.9 percent (the observed average). Blue triangles are from trees in plots re-thinned in 2001. Rose points are those not subjected to the 2001 thinning. Data for south-facing quadrants of sample trees. No branches measured above 10cm stem diameter.

Delayed foliage on original living branches followed a different pattern (Figure 2.6B). At the top of crowns these branches had about half of their length occupied by delayed foliage. Percent foliation increased rapidly lower in the crown until just below the crown's midpoint, then decreased to about 70 percent. Variation in extent of delayed foliation increased at points lower in the crown. The pattern was modeled per equation [2.3]. Fixed effects of intercept and crown position (including the squared term) were all highly significant (Table 2.6). Adjacent

open space did not appear to influence the percentage of delayed foliation. The trend in delayed foliation on original branches was similar across all trees in our sample (i.e., random effects were not significant). While we obtained measurements only in the sample trees' south-facing quadrants, we observed delayed foliation to be ubiquitous throughout crowns on regardless of aspect.

Table 2.6. Parameter estimates, proportions of foliated length for mixed models of sequential and delayed foliation on original living branches. Standard errors in parentheses. Detailed statistical results available in Appendix C. Results converted to percentages for figures and discussion.

Equation	Intercept	Parameter estimates*			Random effects
		CrwnPos	CrwnPos ²	Gap	
2.4 sequential	0.9111	- 0.5191		<u>- 0.00199</u>	Yes
	(0.04186)	(0.04068)		(0.00098)	
	$p < 0.0001$	$p < 0.0001$		$p = 0.0548$	
2.5** delayed	-0.3472	+ 0.5821	-0.4489	<u>+0.000524</u>	No
	(0.01925)	(0.05870)	(0.05120)	(0.000309)	
	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p = 0.1045$	

*underline denotes parameter estimate not significantly ($p > 0.05$) different from 0.

**equation 2.5 included a Box-Cox ($\lambda = 3$) transformation to the response variable (back-transformed in Figure 2.6B).

Epicormic branches had different patterns of foliation. Many epicormic branches had either 100 percent of their length occupied by sequential foliation (Figure 2.6C) and/or were entirely devoid of delayed foliation (Figure 2.6D, Appendix D). The remaining branches were clustered between relative crown positions of 0.2 and 0.6, held 30 to 90 percent of their length in sequential foliation, and zero to 90 percent in delayed foliation. Neither relative crown position nor associated open space explained this pattern. The branches that were either entirely populated with sequential foliation, and/or devoid of delayed foliation, were much shorter on average than other branches (Table 2.7). This observation held for branches located at, and between, whorls.

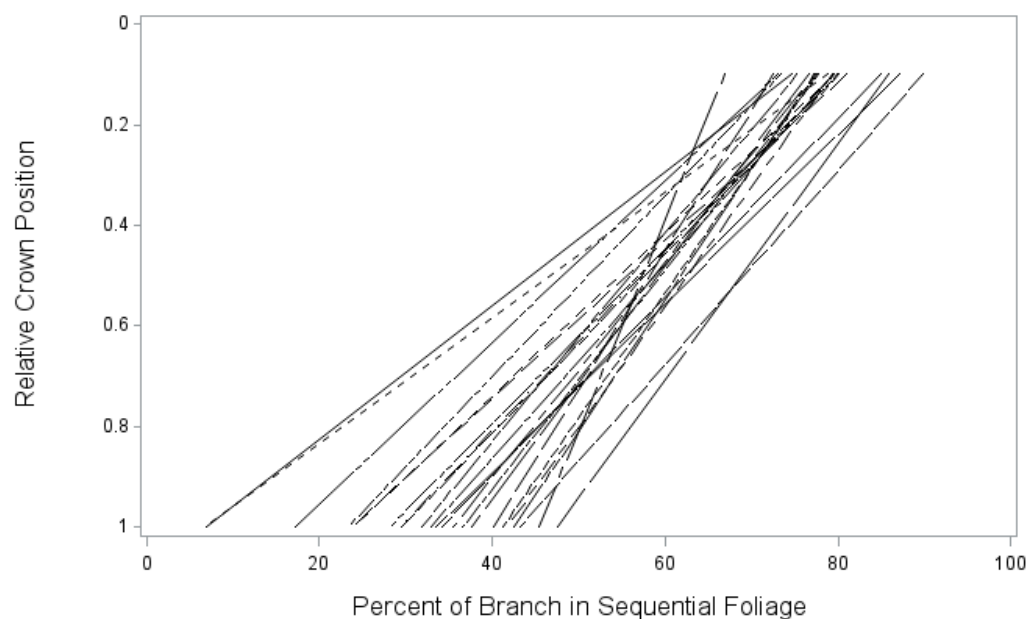


Figure 2.7. Sequential foliage distribution on original living branches, by relative crown position. The top of the crown is assigned a value of 0 and the base of the regular crown a value of 1. The horizontal axis denotes the percentage of branch length occupied by foliage. Each line corresponds to a different tree (n=23), and is adjusted for its gap.

Table 2.7. Mean length of living epicormic branches, by foliation extent and whorl locations. Branch length in meters.

Foliage extent	Location	N Obs	Mean	Std Dev	Minimum	Maximum
100% Sequential	whorl	8	0.50	0.69	0.09	2.13
	between whorls	76	0.20	0.11	0.03	0.67
<100% Sequential	whorl	38	1.23	0.93	0.12	3.51
	between whorls	181	0.99	0.80	0.09	4.57
0% Delayed	whorl	8	0.26	0.18	0.09	0.67
	between whorls	67	0.26	0.19	0.03	0.85
>0% Delayed	whorl	38	0.48	0.22	0.03	0.87
	between whorls	190	0.46	0.24	0.03	1.00

We segmented our data and repeated our analyses to specifically examine impacts of adjacent open space on branches located in the lowest portions of the crowns. No evidence was

found to suggest that open space (gap) had a meaningful impact on either sequential or delayed foliage percentages in lower crowns.

Foliage mass

Nearly all foliage in our sample trees occurred on original branches at whorls (Table 2.8). This was true for sequential and delayed foliage. In contrast, epicormic branches supported a tiny fraction of the total foliage mass. Delayed foliage, however, played a substantial role, accounting for over 41 percent of total foliage mass.

Table 2.8. Percent of total foliage mass by branch and foliage type. Extrapolated from a sample of 160 branches harvested from 15 trees. Total dry mass harvested = 82 kg. Total dry mass as extrapolated = 530 kg.

	Branch type				Total
	Original at whorl	Original between whorls	Epicormic at whorl	Epicormic between whorls	
Sequential foliage	56.3%	0.6%	0.1%	1.7%	58.7%
Delayed foliage	39.6%	1.1%	0.1%	0.5%	41.3%
Total foliage	95.9%	1.7%	0.2%	2.2%	100.0%

General model of foliage distribution

A general model for branch development and foliage distribution on Douglas-fir trees approaching maturity (approximately 60-years old) is illustrated in Figure 2.8. 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 the tree held its foliage (Zhao et al. 2011). Delayed foliage overlapped with sequential foliage and also occupied branch area that would otherwise have been vacant of foliage. It provided 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. They held true for both original and

epicormic branches. Illustrations of foliage patterns for all samples trees are available in

Appendix E.

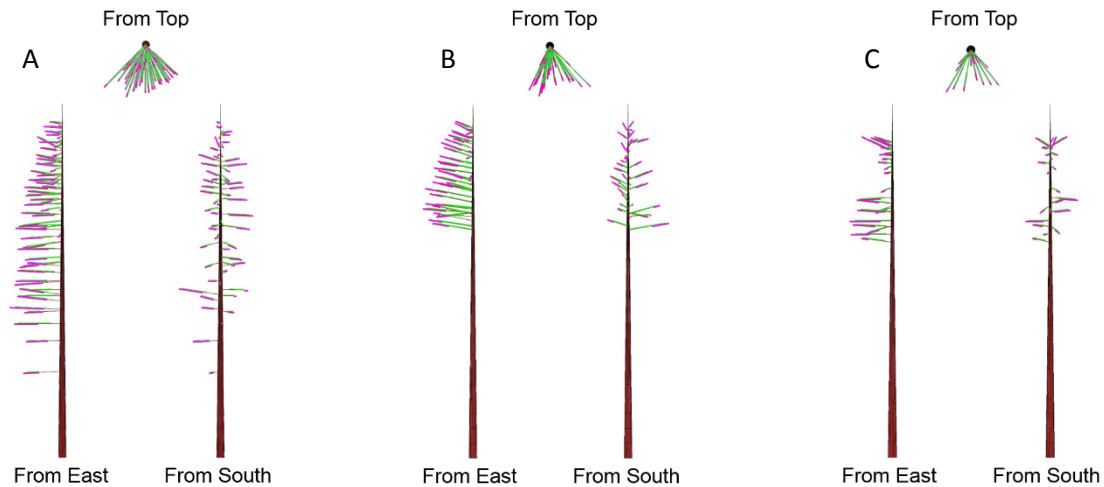


Figure 2.8. Sequential and delayed foliage distribution within crowns of three representative early-mature Douglas-fir trees. Purple represents the extent of sequential foliage and green the extent of delayed foliage. Measurements were not taken in the crown located above the point at which the stem measured 10 cm in diameter. A: long crown. B: short crown. C: damaged crown.

Discussion

Gap creation did not seem to have a major influence on the branch length of adjacent trees, 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, and to a lesser extent in *Pinus strobus* and *Tsuga canadensis* (Young and Hubble 1991, Muth and Bazzaz 2002, Newton et al. 2012). Some trees have also been noted as developing longer branches with increasing access to light in general (Sterch and Bongers 2001). Our choice to include trees from some plots that had been recently thinned may have masked the gap effect, as the trees in these plots may not have had sufficient time to respond to their new conditions (Seidel et al. 2016). Our trees had also grown

under uniform stand density conditions for many years prior to implementation of variable density management in the stands. This said, the wide range of open space conditions present in our sample should have been sufficient to allow detection of a gap effect if it was present. This reinforces the observation that the primary response of Douglas-fir to gaps may be 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, Seidel et al. 2016). It is also possible that our choice to measure open space solely in the south facing quadrant may have masked the effect of open space in other quadrants. We assumed a direct relationship between open space and branches growing into that space, but recent LIDAR mapping suggests that Douglas-fir crowns in 50 to 70 year old stands respond to gap openings by extending relatively uniformly in all directions, rather than becoming longer only in the direction of the gap (Seidel et al. 2016).

In our study, epicormic branches appeared to form regardless of original branch condition or associated open space, rather than forming as replacements of lost or damaged original branches. This finding reinforces observations that some tree species form epicormic shoots even in the absence of external stimuli (Bryan and Lanner 1981, Ewers 1983, Connor and Lanner 1987). Epicormic branches have been identified as playing significant roles in maintenance of old-growth Douglas-fir, and as being prevalent in other conifer species (Bryan and Lanner 1981, Bégin and Filion 1999, Ishii and Ford 2001, Ishii et al. 2002, Deal et al. 2003, Hanson and North 2006, Ishii et al. 2007, Kennedy and Ford 2009, O'Hara and Berrill 2009). They are often cited as forming in response to some exogenous stimulus, such as wounding/pruning, increased light, stress, defoliation or herbivory (Carroll et al. 1993, Wilson and Kelty 1994, Kozlowski and Pallardy 1996, O'Hara and Valappil 2000, Attocchi 2013, Desrochers et al. 2015).

Epicormic branches in old-growth Douglas-fir trees have been noted as occurring principally in the lower-crown (Spies and Franklin 1991, Franklin et al. 2002, Ishii and McDowell 2002). In contrast, in our early-mature 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 they should remain similarly common lower in the crown. However, the relative scarcity of epicormic branches lower in the crown, and their short lengths, indicates 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 (Kerr and Harmer 2001, Hollatz 2002, Ishii et al. 2007). 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 wide-spread manner but retained only if they provide a meaningful benefit to the tree (in keeping with the “branch autonomy” theory; Sprugel et al. 1991). This may represent a form of developmental plasticity 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 regular 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 (Hibbs et al. 1989, Stubs 1986, Farooq et al. 1995, 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 (Spies and Franklin 1991, Franklin et al. 2002, Ishii and McDowell 2002), and our study 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 key finding of this study was the extent to which delayed foliage contributed to the leaf area of Douglas-fir in its early stages of maturity: 40 percent of total foliage mass and almost 60 percent of total foliated branch length. This rivals the contributions of delayed foliage in old-grown Douglas-fir crowns (Ishii and Ford 2001, Ishii et al. 2002). Interestingly, delayed foliage was present throughout crown, not just on lower branches, and it was often intermixed with and overlapped sequential foliage. This suggests that delayed foliage is not simply a response to branch area that has lost sequential foliage, rather its development is ongoing and ubiquitous (a finding similar to that of several long-lived pine species; Connor and Lanner 1987). Of note is that delayed foliage on original branches made a far greater contribution to overall leaf area than foliage of either type located on epicormic branches. Apparently, delayed adaptive reiteration is not just an old-growth phenomenon in Douglas-fir, nor is it confined to trees that have reach maximum canopy size or face suppression (Ishii and Ford 2001, Ishii and Wilson 2001, Ishii et al. 2002). Rather, Douglas-fir trees utilize delayed reiteration throughout their lifespans to continuously repopulate branch area with new foliage.

Conclusion

The combined production of delayed foliage, and to a lesser extent, epicormic branches, affords Douglas-fir a significant capacity to replenish leaf area. These processes appear to be ubiquitous and ongoing, rather than responsive to triggers. The result is a ready supply of foliage to replace that lost to aging, wind or ice events, herbivory and/or disease. Heterogeneity of stand conditions, e.g., gap creation, does not appear to influence these processes, although

crown lift may be (Siedel 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, Ishii et al. 2007).

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

Our trees had a history of over 50 years of management under uniform spacing prior to the creation of canopy gaps. One might assume that had the trees been initiated or exposed to heterogeneous stand conditions at significantly earlier ages their crowns would have ended up in much different conditions. We also acknowledge that the geographic range of our sample was limited. However, our study, and those of others cited, indicate that the most distinct difference would likely have been in the amount of crown recession – more open grown trees would retain longer crowns (Seidel et al. 2016) while the impact on amounts and types of foliage present and the number and size of lower-crown epicormic branches would be minimal (Muth and Bazzaz 2002, Ishii et al. 2007).

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CHAPTER 3: COMPARATIVE ANATOMY AND INDICATORS OF PHOTOSYNTHETIC ACTIVITY AND WATER USE EFFICIENCIES OF SEQUENTIAL AND DELAYED FOLIAGE IN EARLY-MATURE COASTAL DOUGLAS-FIR

Potential journals: Tree Phys, CJFR, CJB

Abstract

Paired samples of sequential (regular) and delayed adaptive (epicormic) foliage from approximately 60-year-old coastal Douglas-fir trees were compared to determine if they differed in structure or physiological activity. Regardless of crown position, delayed foliage had higher average specific leaf area (SLA), higher $\Delta^{13}\text{C}$, lower intrinsic water use efficiency (iWUE), and higher $\delta^{18}\text{O}$ than did sequential foliage on the same branch and within the same foliage cohort. The results indicated that delayed foliage was, on average, more shade adapted than sequential foliage. The SLA of both types of foliage decreased with increasing foliage age, a result attributed to more rapid shedding of high-SLA needles. Year-to-year variation in $\Delta^{13}\text{C}$, iWUE, and $\delta^{18}\text{O}$ was correlated with weather conditions, but trends were complicated by the integration of the isotope signals across multiple growth seasons. Delayed foliage provides Douglas-fir with an ongoing source of new leaf area, well adapted to changing growth conditions.

Introduction

Leaves are responsible for the vast majority of photosynthesis in most tree species, and as such provide the resource base for tree growth, defense, reproduction and other physiological functions (Šesták 1985). Thus, leaf area is included in many tree growth and crown development models as a proxy for photosynthetic capacity, growth potential or hydrological processes (Waring et al. 1982, Waring 1983, Kershaw and Maguire 1995, West et al. 1999,

McDowell et al. 2002, Berrill and O'Hara 2007, Sattier and Comeau 2016). While information about leaf area is adequate for many model uses, it offers a rather simplified perspective. For example, it ignores variation in foliage structure within crowns (e.g., sun vs. shade adaptations, specific leaf area) and that associated with the aging of needles and trees (Hager and Sterba 1984, Givnish 1988, Abrams and Kubiske 1990, Apple et al. 2002, Ishii et al. 2002, Marshall and Monserud 2003) or differences in foliage vascular connections (Maton and Gartner 2005). Furthermore, overall foliar water use efficiency (WUE) and photosynthetic activity levels change within crowns and over time (Freeland 1952, Day et al. 2000, Uberia and Marshall 2011, Wyka et al. 2012). In other words, not all foliage is equal in its contributions to a tree's performance.

In recent years the contributions of delayed adaptive reiteration (i.e., epicormic branches and epicormic shoot/foliage production) on tree performance have received increased attention (Connor and Lanner 1987, Ishii and Ford 2001, Nicolini et al. 2001, Ishii et al. 2002, Ishii, Ford and Kennedy 2007, Kennedy and Ford 2009). This represents a shift from the more traditional focus on epicormic branches as sources of concern from a log grade/wood quality perspective (Trimble and Seegrist 1973, Stubs 1986, Hibbs et al. 1989, Farooq et al. 1995, Meadows and Burkhardt 2001, Attocchi 2013). Recent work has shown that crowns of older (Ishii and Ford 2001, Ishii et al. 2002) and younger (Punches 2017) Douglas-fir include large proportions of delayed shoots and foliage. However, it is not known whether foliage produced from delayed activation of buds is functionally equivalent to sequential (regular) foliage. If the two types of foliage exhibit differing levels of physiological activity, e.g., photosynthetic activity and/or water use efficiency, a distinction between the leaf areas of the two foliage types may improve upon existing growth models and our general understanding of tree physiology.

For many years naturally occurring stable isotope data has been used to advance understanding of plant functions and their relationships to environmental conditions (Peterson and Fry 1987). Particular emphasis has been paid to ^{13}C (Farquhar et al. 1982, Dawson et al. 2002). Under favorable growing conditions C3 plants discriminate against ^{13}C during photosynthesis, preferring the lighter and far more abundant ^{12}C isotope. Under conditions of water stress and/or high rates of photosynthesis they are forced to utilize a larger proportion of the less desirable ^{13}C . Numerous studies have utilized the ratio of ^{13}C to ^{12}C in plant matter to make inferences about photosynthetic activity and water use efficiency (Farquhar et al. 1989, Hultine and Marshall 2000, Linares and Camarero 2012, Leonardi et al. 2012, Tutua et al. 2014, Cornejo-Oviedo et al. 2017). However, the $^{13}\text{C}:^{12}\text{C}$ ratio by itself has limited information value as the observed values could have occurred through increased photosynthetic rates, decreased stomatal conductance, or both (Scheidegger et al. 2000).

Paired observation of $^{13}\text{C}:^{12}\text{C}$ and $^{18}\text{O}:^{16}\text{O}$ ratios offers opportunities to more precisely elucidate foliar activity by sorting out the effects of photosynthesis and leaf conductance (Scheidegger et al. 2000, Dawson et al. 2002, Powers et al. 2009, Ramírez et al. 2009, Flanagan and Farquhar 2014). When water evaporates, the more common ^{16}O isotope is lost at a higher rate than its heavier ^{18}O form, resulting in enrichment of ^{18}O in the remaining liquid water. This phenomenon is observed not only in surface water, but also in leaf water where rates of evaporation are primarily a function of stomatal conductance (Gonfiantini et al. 1965, Barbour 2007). The ^{18}O enrichment in leaf water is attributable primarily to the vapor pressure differences between H_2^{18}O and H_2^{16}O (Dongmann et al. 1974). Also $\delta^{18}\text{O}$ enrichment of leaf water increases at low relative humidity of surrounding air and/or high air temperature (ibid). Thus, the addition of $^{18}\text{O}:^{16}\text{O}$ ratio data in plant physiology studies allows for more information

about photosynthetic activity by providing an indication of the roles of stomatal conductance and relative humidity at the time the plant matter was formed.

This study focused on the relative photosynthetic contributions of sequential and delayed foliage in Douglas-fir. While differences between the two foliage types has the potential for great impact on trees' physiological performance, little information exists on the matter. Ishii et al. (2007) noted differences in water use efficiency (WUE, photosynthesis per unit stomatal conductance) between delayed foliage near branch bases and sequential foliage at branch tips, based on measurements of $^{13}\text{C}:^{12}\text{C}$ ratios. Differences in WUE were attributed to higher water stress in more distal foliage, but stomatal conductance was not reported. Unpublished data by Ford (Brookes 2015) compared leaf void carbon concentration, photosynthetic rates, stomatal conductance and $\delta^{13}\text{C}$ for foliage from the branch apex and lateral (sequential) and epicormic (delayed) shoots from a single branch. Results were largely inconclusive, but suggested that maximum photosynthetic rates in delayed foliage were less than those for lateral sequential foliage. Both the Ishii and Ford studies were conducted in old growth Douglas-fir at Wind River, Washington.

Specific leaf area (SLA; leaf surface area per unit dry mass) has been shown to be correlated with key plant traits such as nitrogen and phosphorous content, maximum photosynthetic rate, dark respiration rates, and leaf lifespan across a broad range of plant species (Westoby et al. 2002, Wright et al. 2004, Osnas et al. 2013). Leaves with higher SLA consistently have more nitrogen and phosphorous per unit mass and greater maximum photosynthetic rates, but have lower leaf construction costs coupled with lower leaf longevity (ibid). These trade-offs represent differing plant strategies; longer lived, low-SLA leaves are more resource intensive to produce more but they retain their nutrients and function for longer

periods of time and may result in greater overall accumulation of leaf area; while shorter-lived, high-SLA leaves are less-resource intensive to produce and offer the plant greater adaptability to changing environmental conditions through increased rates of leaf turnover (Westoby et al. 2002, Burns 2004).

Old-growth Douglas-fir leaves vary in SLA as a function of relative crown position location, with higher SLA leaves occurring at the base of the crown (Ishii et al. 2002), while low-SLA leaves are prominent in crown areas more exposed to light (Chen et al. 1996, Warren et al. 2003). This is consistent with the broadly noted trend that low-SLA leaves are more sun-adapted than are high-SLA leaves (Givnish 1988). Low-SLA leaves have thicker layers of mesophyll and fewer stomata; while high-SLA needles are broader and thinner, with less mesophyll thickness and more stomata per unit of surface area (ibid). We would, therefore, expect to observe differing levels of carbon isotope discrimination and intrinsic water use efficiency relative to crown position, based on expected differences in leaf photosynthetic rates and stomatal conductance.

Old growth Douglas-fir leaves have also been observed to decrease in average SLA as leaf cohorts become progressively older (Ishii et al. 2002). This suggests that the leaves either become progressively more massive per unit area in successive years, or that the ratio of high- to low-SLA needles remaining within each cohort decreases over time. Douglas-fir needles add little or no secondary tissue after reaching maturity (Owens 1968) and long-term accumulation of non-structural materials does not appear to occur within temperate conifers (Krueger 1967, Krueger and Trappe 1967, Little 1970, Turunen and Huttunen 1990, Webb and Kilpatrick 1993, Schaberg et al. 2000). Thus, an increase in leaf mass over time (after leaf maturity) is unlikely. On the contrary, the proportion of Douglas-fir needles remaining within any particular cohort

has been shown to decline substantially from one year to the next (Silver 1962, Mitchell 1974), and it has been postulated that the age effect on SLA in another conifer species could be attributed to preferential shedding of high-SLA (more shade adapted) needles, leading to their underrepresentation in older cohorts (Hagar and Sterba 1985). Differences in SLA, and relative rates of high-SLA retention, among delayed and sequential foliage could have significant implications for Douglas-fir's overall performance and its ability to adapt to changing local environmental conditions.

As forest management paradigms evolve toward greater emphasis on ecosystem services, balancing wood production and habitat management, species diversity, soil productivity management, water quantity and quality and other goals (Puettmann, Coates and Messier 2009 *px*, O'Hara, Hasenauer and Kindermann 2007), silvicultural practices that lead to greater spatial and structural variability in existing stands have garnered attention (Dodson, Ares and Puettmann 2012, Gray, Spies and Pabst 2012). Thus, consideration of crown structure within Douglas-fir needs to be made within the context of variable density management, and the level of adjacent open space becomes an important consideration when studying leaf morphology and function.

Our study focused on trees in early maturity, and measured relative changes in $^{13}\text{C}:^{12}\text{C}$ and $^{18}\text{O}:^{16}\text{O}$ ratios between paired samples of sequential and delayed foliage, from twelve Douglas-fir trees, in three separate foliage age categories. Our primary object was to determine if delayed and sequential foliage differed in photosynthetic activity and/or levels of moisture stress and as they aged. Carbon isotope discrimination, intrinsic water use efficiency, and oxygen isotope deviation were employed as indicators of physiological processes. We also investigated several factors potentially responsible for the observed foliage patterns, including

leaf morphology (specific leaf area), needle retention as needles age, relative crown position, adjacent open space (gap), and weather patterns.

Methods

Site and sample description

The study site was located on the eastern flank of the Oregon Coast Range, on the McDonald-Dunn Research Forest (Oregon State University), near Corvallis, Oregon (Lat. 44.65° N, Long. 123.27° W). In 2005, it was occupied by relatively even-aged stands of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) ranging in age from 63 to 68 years, with scattered grand fir (*Abies grandis* Lindl.) and bigleaf maple (*Acer macrophyllum* Pursh.). The site featured moderately deep, basalt-derived clay loam soils with good drainage. Slopes ranged from 10 to 50 percent and were west to northwest facing. Annual precipitation averaged 1,500 mm and occurred primarily as rainfall from October to May; temperatures were moderate. The stands on the study site had experienced uniform thinning to release dominant and codominant trees in 1964-65 and again in 1980-81. The site was thinned again in 1993 to create a wide range of stand density and spatial uniformity conditions, and a subset of plots were re-thinned in 2001 to return them to target densities (Newton and Cole, 2006).

Twelve dominant or codominant trees were selected such that a wide range of adjacent open space conditions were represented. Open space was measured using hemispherical photographs, taken for each tree, in a sector constrained to the 90° quadrant centered on true south (Schoettle and Smith 1991, Burke 2015) and limited to 34° from vertical. Trees were climbed in August-September, 2005, and branch height above ground, branch length, and other descriptors measured (see Punches 2017, for details).

Weather data for the years 2000 to 2005 (the years of our needle cohorts plus the immediately-preceding years), along with the 30-year average from 1971 to 2000, were obtained from ClimateNA_MAP (www.climatewna.com; Wang et al. 2016), for the study area. Details along with a brief description of weather patterns in each year appear in Table 3.1.

Table 3.1. Annual and summer weather conditions for years impacting study foliage samples. Summer (June-Aug) in parentheses, where applicable. Precip = precipitation (mm). MSP = May to September precipitation (mm). T_{ave} = Average Temperature ($^{\circ}\text{C}$). CMD = Climate Moisture Deficit (mm). MAR = Mean Annual Solar Radiation ($\text{MJ m}^{-2} \text{d}^{-1}$). Interpretations relative to 30-year average (1971-2000). From ClimateNA_MAP (Wang et al. 2016).

	2000	2001	2002	2003	2004	2005	1971-2000
Precip	1119 (41)	1116 (88)	1414 (43)	1484 (16)	1078 (79)	1240 (67)	1427 (71)
MSP	143	143	121	83	183	198	179
T_{ave}	10.6 (17.1)	11.0 (17.0)	11.1 (17.9)	11.7 (18.6)	11.8 (18.9)	11.3 (18.1)	10.8 (17.3)
CMD	474 (362)	476 (303)	531 (376)	545 (411)	445 (337)	424 (341)	435 (342)
MAR	13.3 (23.2)	13.3 (22.1)	13.9 (22.7)	13.3 (23.5)	13.4 (22.3)	13.2 (22.5)	13.2 (22.3)
Inter-pretation	Dry year Dry summer Norm temp CMD slightly elevated Normal radiation	Dry year Slightly increased summer precip Norm temp Low CMD Normal radiation	Normal annual precip Dry summer Slightly elevated temp CMD slightly elevated Elevated radiation	Slightly wet year Very dry summer Elevated temp High CMD Elevated summer radiation	Dry year Above norm summer precip Elevated temp Norm CMD Normal radiation	Dry year Above norm summer precip Elevated temp Norm CMD Normal radiation	Ref. period

Sample harvest and preparation

In 2006 a subsample of branches was harvested from the trees: nine in March prior to bud break, and three in July and August, after bud break. Crowns were segmented into three sections (high, mid and low), with the location of the longest branch used to delineate low and medium crown segments. The branches above the longest branch were split equally in number to separate mid and high crown sections. Within each section we harvested two regular (non-epicormic) branches located at whorls, and where possible up to two more regular branches located between whorls. Not all trees had sufficient branches of each type in each crown segment, resulting in a total sample of 62 branches.

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, then frozen to maintain freshness until processing.

In the lab, each sample was divided into foliage years based on the location of shoot nodes and/or bud scale scars. There were typically obvious differences in needle length and width between age cohorts, so where the terminal growth had been damaged or lost it was possible to assign remaining foliage to its associated age cohort. Foliage formed in the 2005 growth season was considered to be age cohort one. For branches harvested in the fall of 2006, that year's foliage cohort was considered "year-0" and excluded from analysis.

Needles were removed from their branchettes and a subsample (target size 50 or more needles) scanned on a flatbed optical scanner and analyzed using ImageJ (Rasband 1997-2016) to obtain the one-sided surface area. The subsample was then dried at 70°C for 96 hours and weighed, allowing calculation of specific leaf area (SLA; cm² surface area per gram dry weight).

For this study, sequential foliage was defined as that developed by the annual process of branch and branchlette elongation. It is characterized by its ordered, recurring pattern and arises from annual buds at shoot apices, set at the end of a growth season, which activate in the spring producing new leaders and associated lateral branchlettes. The branchlettes supporting this foliage orient themselves into relatively flat planes along the main branch. Once the foliage has aged and been discarded or otherwise lost, that portion of the branch/branchlettes becomes devoid of sequential foliage. As a result, sequential foliage is concentrated toward the distal ends of branches (Punches 2017).

Delayed foliage, elsewhere described as epicormic shoots (Ishii and Ford 2001) or delayed adaptive reiteration (Ishii et al. 2007), arises from dormant buds, out of sync with the sequential foliation process. For this study, we characterized foliage as delayed when it arose two or more years after the associated sequential foliage at a specific location on a branch. Delayed foliage generally originates from the top of the main branch, and often lacks the ordered appearance of sequential foliage (Ishii and Ford 2001, Ishii et al. 2007). Delayed foliage most frequently repopulates sections of branches that have lost their sequential foliage, but is not exclusive to those areas. In our study trees, delayed foliage was commonly intermixed with sequential foliage (Punches 2017).

Up to ten foliar years were present on some branches in our study, with years one through five most prevalent. Our analysis focused on the foliage cohorts for years one, three and five. Healthy Douglas-fir trees have been previously reported to hold up to ten foliage cohorts (years) in British Columbia and seven in western Oregon and Washington (Silver 1962, Mitchell 1974), while those infected with Swiss needle cast often hold just one to three years of

foliage (Zhao et al. 2011, Zhao et al. 2012, Shaw et al. 2014). Silver (1962) found 90 percent of foliage was accounted for in the youngest five foliage cohorts in Douglas-fir in British Columbia.

Isotopic analysis and models

Dry needle samples were ground to a fine powder using a small coffee grinder followed by mortar and pestle, and 370 pairs of samples were submitted to the Stable Isotope Core Lab, Washington State University, Pullman Washington. Each pair included separate samples of sequential and delayed foliage from a single branch, for one of the three targeted age cohorts. Each pair was analyzed for both ^{13}C and ^{18}O .

Samples for ^{13}C isotopic analysis were converted to CO_2 and other gasses in an elemental analyzer (ECS 4010, Costech Analytical, Valencia CA), while those for ^{18}O were converted to CO and associated gasses in a pyrolysis elemental analyzer (TC/EA, ThermoFinnigan, Bremen). The respective gas products were then separated via GC column and analyzed by a continuous flow isotope ratio mass spectrometer (Delta PlusXP, ThermoFinnigan, Bremen). Isotopic reference materials were interspersed with samples for calibration, and the contribution of ^{17}O corrected for by IRMS software using the Santrock correction. ^{13}C values are reported relative to the Vienna Pee Dee belemnite (VPDB) reference and ^{18}O relative to Vienna Standard Mean Ocean Water (VSMOW) in ‰ according to the formula:

$$\delta^{13}\text{C} \text{ or } \delta^{18}\text{O} = 1000 \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right)$$

where R was the ratio of ^{13}C to ^{12}C atoms, or ^{18}O to ^{16}O , of the sample and standard. The 2-sigma uncertainty results were 0.5‰ and 0.4‰ for carbon and oxygen, respectively, per the Stable Isotope Core Laboratory, 2017.

The value of $\delta^{13}\text{C}$ at any point in time is influenced by the ratio of ^{13}C to ^{12}C in the ambient air. We corrected for this effect by converting $\delta^{13}\text{C}$ (deviation) to $\Delta^{13}\text{C}$ (discrimination) per the following equation (Farquhar et al. 1982):

$$\Delta^{13}\text{C} = \frac{\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{leaf}}}{1 + \delta^{13}\text{C}_{\text{leaf}}/1000}$$

Values for $\delta^{13}\text{C}_{\text{air}}$ were obtained from the NOAA Mauna Loa observatory by averaging the reported monthly values for May through September, for reference years 2001, 2003, and 2005 (White et al. 2015). We then calculated intrinsic water use efficiency (iWUE) using the following two equations (Farquhar et al. 1989, Brooks and Mitchell 2011):

$$\text{iWUE} = \frac{A}{g_s} = \frac{(c_{\text{air}} - c_{\text{leaf}})}{1.6}$$

where A is net photosynthetic activity, g_s is stomatal conductance, c_{air} and c_{leaf} the CO_2 concentrations ($\mu\text{mol mol}^{-1}$) in ambient air and the leaf intercellular space, respectively, and 1.6 is the ratio of diffusivity of water and CO_2 in air. We obtained annual average CO_2 concentration for ambient air from NOAA's Mauna Loa observatory (NOAA 2017) and calculated c_{leaf} per:

$$\Delta^{13}\text{C} = a + (b - a)\left(\frac{c_{\text{leaf}}}{c_{\text{air}}}\right)$$

where a is the fractionation that occurs during diffusion (4.4‰) and b is the fractionation from carboxylation (27‰). This approach assumed that ^{13}C concentrations in chloroplasts (c_c), the actual site of carboxylation, were adequately represented by c_{leaf} , and that mesophyll conductance did not limit net photosynthetic activity (Seibt et al. 2008). Our model also assumed that air mixing within the canopy was sufficient to dissipate any CO_2 concentration gradient that would otherwise have been expected to arise from leaf photosynthetic and respiratory processes, an assumption supported by Buchmann et al. (2002).

Statistical analysis

SAS 9.4 was utilized to apply a series of mixed models to assess impacts of foliage type (delayed vs. sequential), foliage cohort (1, 3 or 5), and adjacent open space on $\Delta^{13}\text{C}$, $\delta^{18}\text{O}$, iWUE, and SLA, respectively. Relative crown position was treated as a covariate. Since trees varied in height and crown length, relative crown position was calculated based on the total length of the crown, from tree tip (0) to crown base (1). The lowest living original branch was used as the crown base. Intercept, crown position, adjacent open space (gap), foliage type, foliage year and the interaction of foliage type with year were treated as fixed effects. Tree, branch, foliage type, and year were treated as a class variables. Intercepts and crown positions were allowed to have random effects between trees, and intercepts to have random effects among branches. We specified an unstructured covariance matrix, and approximated degrees of freedom using the Satterthwaite method. Residuals were examined to test normality assumptions.

The models followed the form:

$$[3.1] \quad Y_{ijk} = (\beta_0 + b_{0i} + c_{0j(i)}) + (\beta_1 + b_{1i})\text{Crwn}_{ij} + \beta_2\text{Gap}_i + \beta_3\text{Type}_{ijk} + \beta_4\text{Year}_{ijk} + \beta_5(\text{Type}_{ijk} \times \text{Year}_{ijk}) + e_{k(jj)}$$

where Y_{ijk} was the dependent variable ($\Delta^{13}\text{C}$, $\delta^{18}\text{O}$, iWUE, or SLA) for observation k on branch j within tree i ($i = 1, 2, \dots, 12; j = 1, 2, \dots, j_i, k = 1, 2, \dots, k_{ij}$), β_0 the overall intercept, b_{0i} the random effect on intercept associated with tree i , $c_{0j(i)}$ the random effect on intercept associated with branch j within tree i , β_1 the overall slope coefficient for crown position, b_{1i} the random effect on slope associated with tree i , Crwn_{ij} was crown position of branch j on tree i , β_2 the slope coefficient for the fixed effect of Gap_i (the percent of open space associated with tree i), β_3 the effect of Foliage Type (where Type is an indicator variable for delayed or sequential foliage), β_4 the effect of Foliage Year (where Year is an indicator variable for foliage cohort year-1, year-3, or

year-5), β_5 was the effect of the Type by Year interaction, and $e_{k(ij)}$ was the random error associated with the model, where $b_{0i} \sim N(0, \sigma_{b0}^2)$, $b_{1i} \sim N(0, \sigma_{b1}^2)$, $c_{0i} \sim N(0, \sigma_{c0}^2)$, and $e_{k(ij)} \sim N(0, \sigma_e^2)$.

Results

Differences between foliage types

Delayed foliage exhibited higher mean $\Delta^{13}\text{C}$, and lower iWUE than sequential foliage (Figure 3.1, Table 3.2). The results indicated that delayed foliage was either less actively engaged in photosynthesis or experienced higher rates of stomatal conductance than sequential foliage. Delayed foliage's mean $\delta^{18}\text{O}$ was slightly higher than the ratio for sequential foliage, suggesting delayed foliage experienced higher temperature and/or lower internal relative humidity at the time of oxygen incorporation into needle mass. SLA was slightly higher in delayed than in sequential foliage.

Differences over time: foliage year/cohort

Year-1 foliage had higher $\Delta^{13}\text{C}$ and lower iWUE than foliage from years 3 or 5, but there was no discernable difference between years 3 and 5 (Figure 3.2, Table 3.3, Table 3.4). Conversely, year-5 foliage had a distinctly lower $\delta^{18}\text{O}$ than did foliage in years 1 and 3, but foliage from years 1 and 3 did not differ from each other significantly. SLA of foliage was much higher in year 1 than in years 3 and 5, and there was an apparent trend of decreasing SLA across the three needle cohorts.

To expand the analysis of annual changes in SLA we plotted and analyzed data for seven consecutive needle cohorts (rather than just the three used in the isotope analysis). Sequential and delayed foliage had the same consistent trends, with highest SLA in the youngest cohort and decreasing values in older needles (Figure 3.3). The trend appeared to stabilize by year-6. Note, that we had up to ten needle cohorts on some branches, but the number of needles per cohort

was very low beyond year-7. Further analysis indicated that the trend in SLA was driven by changes in average dry mass per needle, which increased with age, and not by changes in average needle area, which remained more or less constant (Table 3.5). For both sequential and delayed foliage, the percentage of needle mass per cohort declined in progressively older cohorts (Table 3.6).

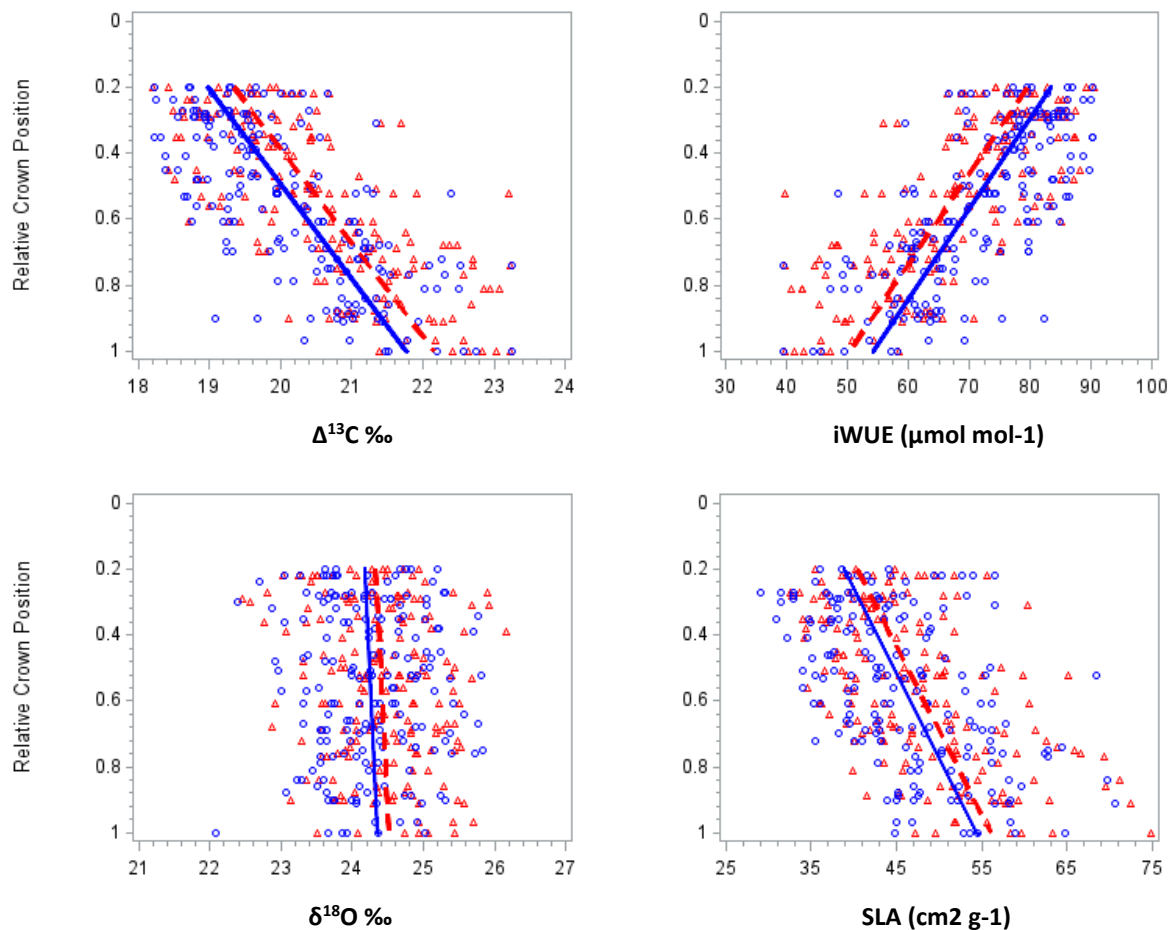


Figure 3.1. Carbon isotope discrimination, intrinsic water use efficiency, deviation of ^{18}O , and specific leaf area by relative crown position and foliage type. Plotted points include the three foliage age cohorts for which isotope data were collected. Triangles and red dashed line = delayed foliage. Circles and blue line = sequential foliage. Crown position 0 refers to the tip of the stem and crown base as 1. No branches were collected from above 10 cm stem diameter. Trend lines plotted with g fixed at its observed average value of 37.39.

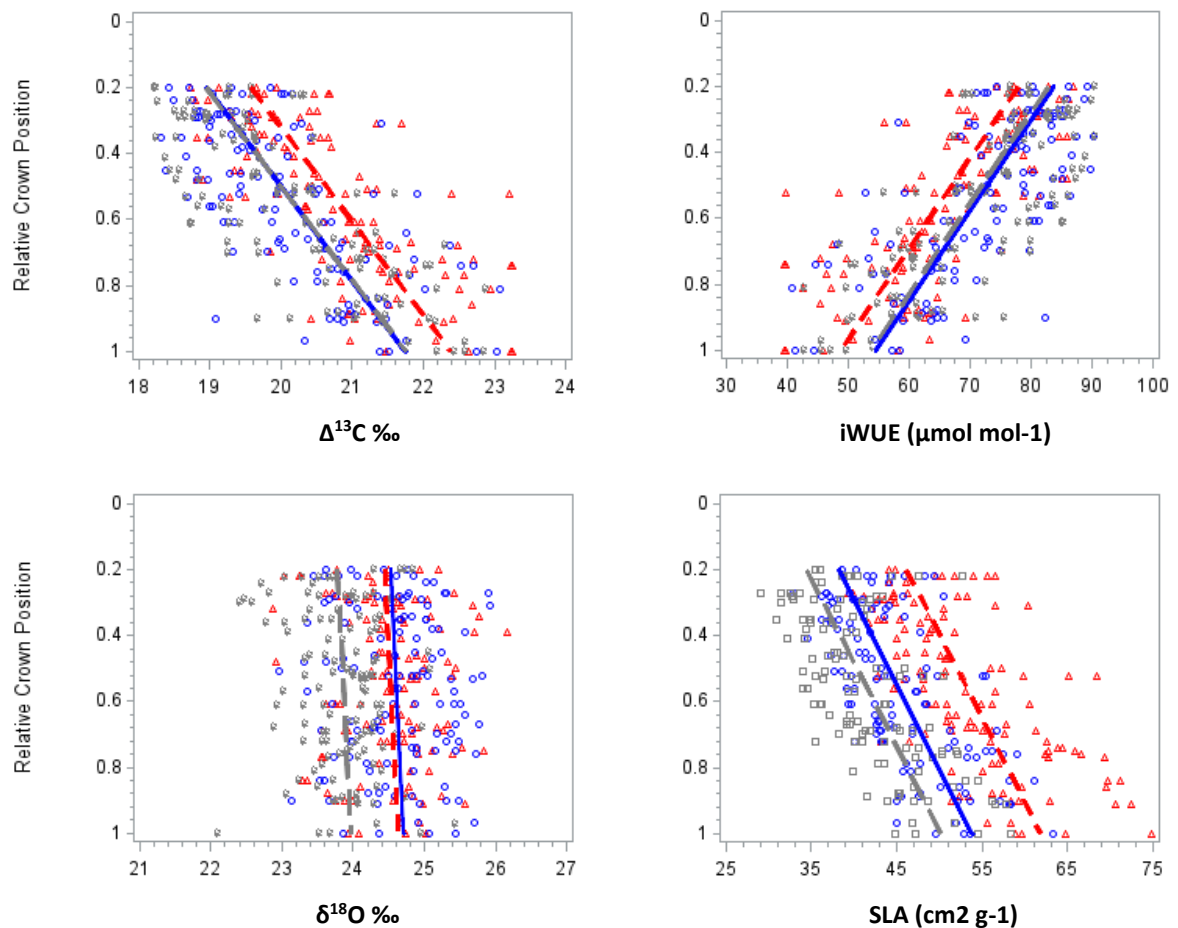


Figure 3.2. Carbon isotope discrimination, intrinsic water use efficiency, deviation of ^{18}O , and specific leaf area by relative crown position across three foliage cohorts. Triangles and red dashed line = Y1 (2005). Circles and blue solid line = Y3 (2003). Squares and grey long dashed line = Y5 (2001). Plotted points include both delayed and sequential foliage types. Crown position 0 refers to the tip of the stem and crown base as 1. No branches were collected from above 10 cm stem diameter. Trend lines plotted with gap fixed at its observed average value of 37.39. Note that trend lines for carbon isotope discrimination and iWUE nearly overlap in years 3 and 5.

Table 3.2. Foliage type differences (delayed vs. sequential) in mean $\Delta^{13}\text{C}$, iWUE, $\delta^{18}\text{O}$, and SLA. Per SAS LSMeans procedure, at observed average crown position of 0.55 and gap of 37.39.

	Difference	SE	DF	P
$\Delta^{13}\text{C}$	0.37	0.05	304	<0.0001
iWUE	-3.82	0.38	304	<0.0001
$\delta^{18}\text{O}$	0.16	0.06	304	0.0053
SLA	1.50	0.29	294	<0.0001

Table 3.3. Foliage cohort differences in mean $\Delta^{13}\text{C}$, iWUE, $\delta^{18}\text{O}$, and SLA. Per SAS LSMeans procedure, at observed average crown position of 0.55 and gap of 37.39. P-values adjusted for multiple comparisons using Tukey method.

	Difference	SE	DF	P
$\Delta^{13}\text{C}$				
Y1-Y3	0.62	0.05	304	<0.0001
Y1-Y5	0.63	0.05	304	<0.0001
Y3-Y5	0.01	0.05	304	0.9876
iWUE				
Y1-Y3	-5.77	0.42	304	<0.0001
Y1-Y5	-4.97	0.42	304	<0.0001
Y3-Y5	0.82	0.42	304	0.1946
$\delta^{18}\text{O}$				
Y1-Y3	-0.08	0.07	304	0.4301
Y1-Y5	0.66	0.07	305	<0.0001
Y3-Y5	0.75	0.07	305	<0.0001
SLA				
Y1-Y3	7.87	0.36	294	<0.0001
Y1-Y5	11.69	0.36	295	<0.0001
Y3-Y5	3.81	0.36	295	<0.0001

Foliage type x foliage year interaction

None of our models had significant foliage type-by-year interactions. P-values for fixed effects in full models are available in Table 3.4.

Crown influence

Discrimination against ^{13}C was lowest in branches located near the top of tree crowns and increased in a linear fashion at progressively lower crown positions (Figure 3.1). This suggests that lower-crown leaves had greater access to carbon and could be more selective about the carbon isotope utilized. Intrinsic water use efficiency was greatest at the top of crown and decreased at lower crown levels. $\delta^{18}\text{O}$ may have been slightly lower in the upper crown than in the lower crown, but this trend was not statistically significant (Table 3.4). Thus, the $\delta^{18}\text{O}$ results suggest that average relative humidity in the leaf intercellular spaces was similar

regardless of height in the crown. There were significant random effects for $\delta^{18}\text{O}$ at several levels. The overall intercept varied by tree, the effect of crown position varied by tree, and the intercept was further affected at the individual branch level. This could indicate that relative humidity varied at a localized level, or that other unmeasured factors confounded our results. SLA was lowest at the top of the crown and became progressively greater at points lower in the crown.

Stand structure influence

No evidence of an effect of adjacent open space (gap) was noted for any of the foliage performance indicators. P-values and other statistical results are summarized in Table 3.4.

Table 3.4. P-values from F tests for model fixed effects: for carbon isotope discrimination ($\Delta^{13}\text{C}$), intrinsic water use efficiency (iWUE), oxygen isotope deviation from standard ($\delta^{18}\text{O}$), and specific leaf area (SLA) per equation [3.1]. Denominator degrees of freedom in parentheses, per Satterthwaite method.

	Crown Position	Gap	Foliage Type	Foliage Year	Type x Year
$\Delta^{13}\text{C}$	<0.0001 (49.6)	0.1908 (9.74)	<0.0001 (304)	<0.0001 (304)	0.2807 (304)
iWUE	<0.0001 (49.6)	0.1882 (9.75)	<0.0001 (304)	<0.0001 (304)	0.2477 (304)
$\delta^{18}\text{O}$	0.4620 (10.7)	0.3459 (9.97)	0.0053 (304)	<0.0001 (304)	0.2565 (304)
SLA	<0.0001 (10.6)	0.9867 (9.86)	<0.0001 (294)	<0.0001 (295)	0.9817 (294)

Figure 3.3. Specific leaf area across seven foliage age cohorts, by foliage type, in original branches. Error bars include variation attributable to crown position and gap, as well as foliage cohort.

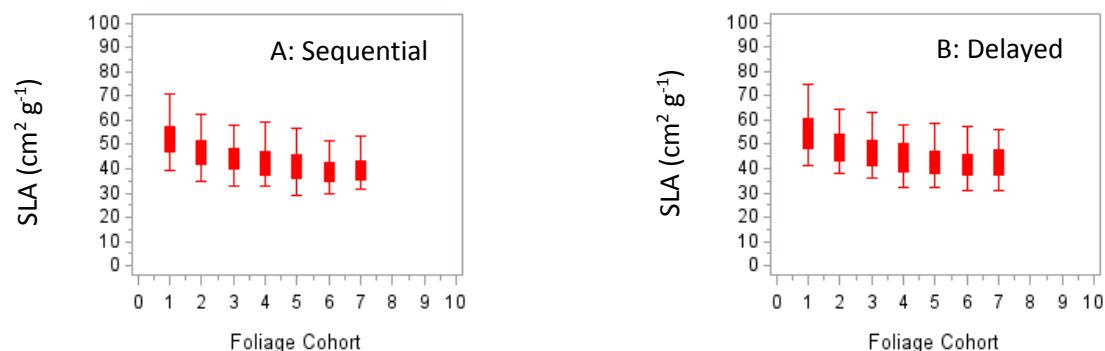


Table 3.5. Mean SLA, average area per needle, and average mass per needle by foliage cohort for original branches. Standard errors in parentheses. Estimated at the observed average relative crown position of 0.58 and gap of 37.18. N=880. Cohorts with no superscript letters in common indicate significant difference at $P < 0.05$.

Needle cohort	SLA ($\text{cm}^2 \text{g}^{-1}$)	Area per needle (mm^2)	Mass per needle (mg)
1	53.86 (1.15) ^a	30.37 (0.97) ^{cb}	5.81 (0.36) ^a
2	47.86 (1.15) ^b	30.03 (0.97) ^{ab}	6.42 (0.36) ^b
3	45.89 (1.15) ^c	29.18 (0.97) ^a	6.52 (0.36) ^b
4	43.68 (1.15) ^d	30.43 (0.97) ^{bd}	7.15 (0.36) ^c
5	42.06 (1.15) ^e	30.62 (0.97) ^{be}	7.51 (0.36) ^d
6	39.93 (1.15) ^f	31.25 (0.97) ^{cde}	8.01 (0.36) ^e
7	39.05 (1.17) ^f	29.83 (0.99) ^{ab}	7.78 (0.36) ^{de}

Table 3.6. Percent of needle mass by foliage type and cohort. Percentages calculated by branch, excluding immature (year-0) needles and those in cohorts older than 7.

Foliage type	Needle cohort	Mean %	Std Dev	N
Sequential	1	32.4	14.8	121
	2	28.8	7.5	120
	3	16.6	5.4	112
	4	13.1	6.4	108
	5	6.8	4.9	95
	6	2.9	2.5	79
	7	1.3	2.3	57
Delayed	1	36.1	17.8	92
	2	28.6	6.2	89
	3	17.1	7.2	87
	4	10.7	4.4	82
	5	5.2	3.4	76
	6	2.5	3.5	64
	7	0.9	1.7	40

Discussion

Delayed foliage more shade adapted than sequential foliage

Delayed foliage in our Douglas-fir sample trees appeared to be, in general, more shade adapted than did sequential foliage at equivalent positions within the crowns, as evidenced by delayed foliage's higher average SLA and $\Delta^{13}\text{C}$, and lower average iWUE. Previous studies have shown that Douglas-fir needles in crown areas less exposed to light have higher SLA (Chen et al. 1996, Warren et al. 2003) and are broader and thinner with less mesophyll and more stomata per unit of surface area, while low-SLA needles are more sun-adapted and have thicker layers of mesophyll and fewer stomata (Givnish 1988). Thus, high-SLA needles would be expected to experience 1) lower levels of iWUE (less photosynthesis per unit of stomatal conductance) and 2) greater ability to discriminate against ^{13}C (higher $\Delta^{13}\text{C}$), relative to the low-SLA needles. This sun/shade trend appears to be general and has been documented for various plants and plant

communities, with the prevailing response that plants in more shaded growing environments exhibited higher specific leaf areas (e.g., Burns 2004, Dwyer et al. 2014).

The $\Delta^{13}\text{C}$ and iWUE changes we observed (in both delayed and sequential foliage) at varying positions within crowns have been documented for a variety of conifers and typically have been attributed to moisture stress (Scheidegger et al. 2000, Winner et al. 2004, Ishii, Ford and Kennedy 2007, Li and Zhu 2011). Water has a longer path, and a greater gravitational gradient to overcome, to reach the upper crown than it would to reach lower crown foliage (Taiz and Zeiger 2002 p63). Higher moisture stress in the upper part of the crown has been deduced to lead to increased stomatal closure relative to conditions in lower crowns, which in turn reduces CO_2 availability and forces upper-crown leaves to utilize less desirable ^{13}C (Warren et al. 2003). Our data support this explanation, as the observed $\Delta^{13}\text{C}$ in our study was higher (and iWUE lower) in lower crown foliage than that in upper crowns. Also, needles carrying out photosynthesis in upper crowns under lessened moisture access demonstrated a higher level of photosynthate production relative to their stomatal conductance, leading to decreased $\Delta^{13}\text{C}$ and increased iWUE.

The SLA, $\Delta^{13}\text{C}$ and iWUE results obtained in our study were consistent with observations that delayed foliage in our sample trees occurred at positions slightly more interior within the crown, while sequential foliage was clustered toward the distal ends of branches (Punches 2017). Needles in parts of the crown most likely to have received the highest light intensities had the most sun-adapted leaves (lowest SLA) and their $\Delta^{13}\text{C}$ and iWUE results reinforced this interpretation.

Delayed foliage in our study exhibited higher $\delta^{18}\text{O}$ than that noted for sequential foliage, a result that would seem to contradict the interpretation that delayed foliage was more shade

adapted and experienced lower levels of moisture stress than sequential foliage. Studies using $\delta^{18}\text{O}$ to estimate relative moisture stress levels have generally been conducted across site gradients where changes in precipitation, temperature and relative humidity would be expected (Saurer et al. 1997, Scheidegger et al. 2000, Cabrera-Bosquet et al. 2011, Ramírez et al. 2009). In those studies, higher $\delta^{18}\text{O}$ was equated with sites experiencing greater moisture stress and/or lower relative humidity. In contrast, our study compared paired samples of delayed and sequential foliage, each from a specific needle cohort on a specific branch. Each pair of samples would reasonably have experienced similar atmospheric relative humidity and temperature, and under these conditions the leaves capable of the highest transpiration rates (i.e., those with greatest stomatal conductance) could be expected to exhibit the highest enrichment of ^{18}O , rather than those under the highest levels of moisture stress. We noted precisely this pattern between sequential and delayed foliage, where delayed foliage exhibited higher $\delta^{18}\text{O}$.

Furthermore, while $\delta^{18}\text{O}$ has been shown to be higher in sites experiencing greater moisture stress (as noted above), we found no such trend within this study's tree crowns. Mean $\delta^{18}\text{O}$ did not vary significantly with crown position, even though results for $\Delta^{13}\text{C}$ and iWUE indicated greater water-stress in the upper portions of the crowns. We postulate that the trees exercised sufficient stomatal control to maintain conductance levels adequate for the needles' local environments, resulting in relatively uniform rates of conductance relative to localized atmospheric humidity.

SLA decreased in older cohorts, other results mixed

Patterns of variation among needle cohorts in this study were most evident in SLA, with an apparent decline in SLA with increasing cohort age. Light availability did not appear to drive these changes, as solar radiation incident upon the trees varied only slightly between 2001 and

2005 (Table 3.1), and the two summers with elevated radiation did not correspond to trends in the trees' photosynthetic rates (i.e., $\Delta^{13}\text{C}$) or moisture stress. Seven of our sample trees had experienced a thinning operation in 2001 (our year-5), which may have increased the amount of adjacent open space to which they were exposed. Thinning in 2001 should have increased light incident upon the trees and induced them to produce more sun adapted needles. That may in fact have been the case, as SLA decreased from 2001 to 2003 and 2005. The lack of a gap effect, however, calls the effect into question.

In the more inclusive 7-year SLA dataset the year-to-year trend in SLA reduction (Figure 3.3) confirmed observations by Ishii (2002). SLA was highest in youngest foliage and decreased with age. This was true of sequential and delayed foliage (sampled from original/non-epicormic branches). While a preponderance of studies have noted that longer-lived leaves have lower SLA (or higher leaf mass per area) than shorter-lived leaves (Westoby et al 2002, Meinzer 2003, Burns 2004, Wright et al 2004, Osnas et al 2013), it is unlikely the leaves on our trees changed dramatically in mass as they aged past maturity (Krueger 1967, Krueger and Trappe 1967, Owens 1968, Little 1970, Turunen and Huttunen 1990, Webb and Kilpatrick 1993, Schaberg et al. 2000). Our results support the observation that conifers experience preferential loss of high-SLA leaves within leaf cohorts over time, leading to lower average SLA in older cohorts (Hagar and Sterba 1985).

Our study found no discernable year-to-year pattern in average foliage area per needle, while average mass per needle increased in progressively older cohorts (with the possible exception of the 7th cohort; Table 3.5). Chrosciewicz (1986) demonstrated that leaf moisture content in several conifer species declined in a predictable manner as foliage aged, and this suggests that reductions in moisture content could result in concurrent reductions in leaf

surface area, but our results do not support this mechanism. Furthermore, while our study's average needle mass increased in progressively older cohorts, Owens (1968) detailed study of Douglas-fir leaf initiation and development indicated that needles add little or no secondary tissue after reaching maturity and entering their first dormancy period. Any increase in needle mass over time would, therefore, need to be attributed to accumulation of non-structural materials. While several studies have documented seasonal fluctuations in leaf carbohydrates (sugars and starch), long-term accumulation of these products does not appear to occur within temperate conifer needles (Krueger 1967, Krueger and Trappe 1967, Little 1970, Webb and Kilpatrick 1993, Schaberg et al. 2000.) Similarly, it does not appear that proteins or fats accumulate across seasons (Krueger and Trappe 1967), nor does it appear that epicuticular wax builds up in a manner that would add significant mass to aging conifer needles, as the waxes have been shown to erode rather than accumulate (Turunen and Huttunen 1990). Astrosclereids (large, non-living cells intermixed in leaf mesophyll) have been observed to be more numerous in old-growth Douglas-fir than in saplings (Apple et al. 2002), but no evidence was presented that these structures expand or increase in frequency as needles age (only that they are more common on older trees).

Our results provide more compelling evidence that the ratio of low- to high-SLA leaves increases within cohorts as they age. They support Hagar and Sterba's (1985) hypothesis that the age effect on specific leaf area in Norway spruce could be attributed to the preferential shedding of shade-adapted (high-SLA) needles, leading to their underrepresentation relative to more sun-adapted needles in older cohorts. Furthermore, our results also support findings that the proportion of Douglas-fir needles remaining within any particular cohort decline substantially from one year to the next (Silver 1962, Mitchell 1974).

The difference in $\Delta^{13}\text{C}$ and iWUE between needle age cohorts appears to have been more heavily influenced by growth conditions at the time of needle formation than by changing proportions of high- and low-SLA needles. If only the trends in SLA described above were influential, $\Delta^{13}\text{C}$ would have increased and iWUE decreased over time. Instead, year-1 had the highest $\Delta^{13}\text{C}$ and lowest iWUE, while years 3 and 5 were essentially equivalent. Our results suggest the hypothesis that conditions at time of needle formation may be at least partially responsible for this trend. Growing season (May to September) precipitation was best correlated with differences in $\Delta^{13}\text{C}$ and iWUE among cohorts (Table 3.1). Other unmeasured physiological factors could change as needles age, but they were beyond the scope of this study.

$\delta^{18}\text{O}$ differences among needle cohorts appeared to have been influenced primarily by summer temperatures during the year of primordia formation and the year of shoot flush. Only the two-year summer temperature averages (see Table 3.3) corresponded well with the observed differences in $\delta^{18}\text{O}$ among the cohorts (Figure 3.2). The abundance of ^{18}O in leaf matter is reflective of evaporative conditions at time of needle development (Wright and Leavitt 2006, Barbour 2007) and isotope's presence in source water (DeNiro and Epstein 1979, Yakir and DeNiro 1990). Our results suggest that changes in source water, as impacted by prevailing temperatures, drove the $\delta^{18}\text{O}$ changes observed among needle cohorts. $\delta^{18}\text{O}$ of rainwater can be used as a proxy for temperature (Gat 1996). ^{18}O precipitates preferentially from atmospheric water, so as cloud systems move further from their original water source they become increasingly depleted in ^{18}O . Cold temperatures exaggerate this effect by hastening precipitation (Barbour 2007). As no fractionation of oxygen occurs in plant roots, xylem water and soil water have equivalent $\delta^{18}\text{O}$ values (Gonfanti et al. 1965, Wershaw et al. 1966). Enrichment occurs within the leaf water as $\delta^{16}\text{O}$ has higher vapor pressure and evaporates more easily than $\delta^{18}\text{O}$.

Further fractionation occurs during photosynthesis, but then $\delta^{18}\text{O}$ remains relatively stable in plant carbohydrates (Yakir 1992, Barbour 2007). Thus, in our samples the year-to-year $\delta^{18}\text{O}$ changes appear to have been driven primarily by temperature-induced changes in source water oxygen ratios, rather than leaf enrichment of the isotope. This said, we acknowledge that the relative proximity of our study site to its Pacific Ocean moisture source may have limited the extent to which significant release of ^{18}O rich water occurred prior to local rainfall, and that other unmeasured factors may have influenced our results.

Both foliage types could reasonably be assumed to have utilized the same source water. Thus, the lack of direct measurements of oxygen isotope ratios in our study's soil source water should not affect comparisons between delayed and sequential foliage. We were, however, restricted in our ability to interpret trends among leaf cohorts, where year-to-year variation in source water could be a factor.

The overall $\Delta^{13}\text{C}$, iWUE, and $\delta^{18}\text{O}$ results reflected carbon and oxygen incorporated during several stages: 1) cell primordia initiated as part of bud development, 2) additional cell division during leaf maturation following bud break and cell expansion, and 3) the net flux of non-structural carbohydrates over time (Allan and Owens 1972, Yakir 1992, Wright and Leavitt 2006). As such, foliar organic matter contains carbon and oxygen derived from photosynthesis in at least two calendar years (Kozlowski and Keller 1966). Needle primordia in our study most likely demonstrated an isotopic signal representative of the timeframe in which they were produced (for sequential foliage the growth period in the year prior to flush; for delayed foliage a growth period corresponding to the year in which that particular bud formed). Following bud break, maturing cells expanded basipetally through both expansion of existing cells and production of new cells (Owens 1968, Wright and Leavitt 2006), and likely utilized carbon

assimilated by neighboring mature needles in the current and preceding year. Sugar and starch reserves in needles could also have influenced our results. Sugars would have isotopic signatures influenced by fall growing conditions, while starch would reflect primarily the current growing season (Krueger and Trappe 1967, Webb and Kilpatrick 1993, Schaberg et al. 2000).

Our results suggest the hypothesis that production of delayed foliage provides Douglas-fir with an adaptive advantage by favoring new, high-SLA leaves that offset performance declines associated with leaf-aging. Once conifer needles reach maturity, further aging results in loss of photosynthetic capacity (Freeland 1952). Stomata become occluded (Turunen and Huttunen 1990), leading to a presumptive reduction in conductance capacity. Each cohort of leaves includes a range of levels of shade and sun adaptation, which are most readily identified by their specific leaf area. High irradiance (low-SLA) leaves have higher construction costs than low irradiance (high-SLA) leaves, with the cost factor primarily attributed to production of phenolics (Poorter et al. 2006). The low-SLA leaves have been shown to have longer average life spans, but also to have lower net photosynthesis per unit mass, and a lower nitrogen investment per unit mass (Reich et al. 1999).

Furthermore, our results show that Douglas-fir lose high-SLA needles faster than those with low SLA. The low-SLA needles are presumably more robust, but they have higher construction costs and lower photosynthetic efficiency. Recurring production of delayed adaptive foliage replenishes branches with foliage that is better adapted to the branch microsite's changing radiation access. The delayed foliage is higher in SLA, and therefore likely to be lower in construction cost and higher in photosynthetic efficiency. Delayed foliage has been shown to represent as much as 40 percent of a Douglas-fir's total foliage (Punches 2017).

As such, delayed adaptive reiteration of foliage provides substantial adaptive benefit to Douglas-fir, and is undoubtedly a major contributor to its growth capacity.

Conclusion

Delayed foliage was structurally and functionally distinct from sequential foliage in early-mature Douglas-fir trees growing in a stand on the eastern flank of the Oregon Coast Range. Relative to sequential foliage, delayed foliage had higher specific leaf area, greater discrimination against ^{13}C , lower intrinsic water use efficiency, and a greater degree of ^{18}O deviation. These features appear to be functions of a higher degree of shade adaptation in delayed foliage. Douglas-fir foliage cohorts became progressively lower in specific leaf area over time as higher SLA needles were lost while low SLA needles were retained.

The development and physiological characteristics of delayed foliage was not influenced by the adjacent open space proximal to our study trees. As such, maintenance of strict density levels is not necessary to obtain the functional benefits of this foliage type. Douglas-fir is capable of producing delayed foliage under a wide range of stand structures, and forest managers can be confident in the species' ability to maintain effective leaf cohorts under varied stand density systems.

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CHAPTER 4: SUMMARY, IMPLICATIONS AND RESEARCH OPPORTUNITIES

Delayed adaptive reiteration makes substantial contributions to crown maintenance in early-mature Douglas-fir, although not in the traditional context of epicormic branching. While studies of adaptive reiteration in hardwoods has often focused on epicormic branching and its implications for wood quality and/or log grade (Rey-Lescure 1982, Stubbs 1986, Miller 1996, Collier and Turnblom 2001, Nicolini et al. 2003, Fontaine et al. 2004, Colin et al. 2008), in our study trees, epicormic branches were small and rarely occurred below the base of the regular living crown. The contribution of delayed reiteration came in the form of foliage originating from previously dormant buds, populating existing branches. Delayed foliage in our trees was widely interspersed with sequential foliage throughout the crowns, and accounted for nearly 40 percent of total foliage mass and occupied 60 percent of total branch length. Rather than being a response to some external stimulus, the prevalence of delayed foliage suggests it is a ubiquitous and ongoing mechanism of leaf area development.

The delayed foliage in our study trees differed from sequential foliage in some key ways. It had higher average specific leaf area (SLA), higher $\Delta^{13}\text{C}$, lower iWUE, and higher $\delta^{18}\text{O}$. $\Delta^{13}\text{C}$ was lower, and iWUE higher, at the top of the crown relative to the base, trends common to other temperate conifer species and consistent with expected levels of moisture stress throughout the crowns (Scheidegger et al. 2000, Taiz and Zeiger 2002 p63, Warren et al. 2003, Winner et al. 2004, Ishii, Ford and Kennedy 2007, Li and Zhu 2011). $\delta^{18}\text{O}$ did not appear to vary as a function of branch height within the crown, suggesting that stomatal conductance rates remained relatively uniform. The results led to the conclusion that delayed foliage was, on average, more shade-adapted than sequential foliage.

Foliage (both delayed and sequential) declined in SLA over time. Studies of foliage development in conifers (and Douglas-fir specifically) indicate that, once needles reach maturity they do not gain appreciable mass (Krueger 1967, Krueger and Trappe 1967, Owens 1968, Little 1970, Turunen and Huttunen 1990, Webb and Kilpatrick 1993, Schaberg et al. 2000). Thus, the decline in SLA was attributed to more rapid loss of high-SLA foliage, leading to higher proportions of low-SLA needles in the foliage remaining within each cohort (Hagar and Sterba 1985).

Production of delayed foliage provides Douglas-fir with an adaptive advantage by favoring new, high-SLA leaves that offset performance declines associated with leaf-aging (Freeland 1952). The new leaves have higher net photosynthesis, and a lower nitrogen investment, per unit mass (Reich et al. 1999). Recurring production of delayed adaptive foliage replenishes branches with foliage that is better adapted to the branch microsite's changing radiation access.

The extent of open space adjacent to trees did not influence epicormic branching or formation of delayed foliage in our study trees, despite the wide range of open space conditions within our sample. Thus, strict attention to stand density levels does not appear to be necessary to manage epicormic branching (from a wood quality perspective), nor is it necessary to obtain the functional benefits of delayed foliage. Rather, Douglas-fir has the capacity to utilize delayed adaptive reiteration to maintain crowns under a wide range of stand structures, and forest managers can be confident in the species' ability to maintain effective leaf cohorts under varied stand density systems.

Broader Implications

Can delayed foliage help Douglas-fir adapt to global climate change and disease/insect outbreaks? Perhaps, but outcomes will be context-dependent. Consider the following scenarios:

Increasing CO₂ concentration

Global atmospheric CO₂ levels have increased by nearly 25% in the past 60 years, and have now exceeded 400 ppm (Monastersky 2013, NOAA 2017). Higher atmospheric CO₂ concentration generally leads to increased plant growth, although many plant species develop “resistance” to elevated CO₂ over time (Bazzaz 1990, Amthor 1995). Active production of delayed foliage may allow Douglas-fir to develop significantly more total leaf area, and greater ability to capitalize upon the abundance of CO₂, than would be feasible if the trees relied solely upon sequential reiteration. The tree’s ability to expand leaf area would, however, be dependent upon a number of other factors, such as soil nutrient and water availability and the localized climatic response associated with the CO₂ increase (ibid). So while it is possible, and even likely, that delayed foliage would be an advantage under increased CO₂, other factors would likely limit the extent to which foliage area could be increased.

More intense drought

Climate change may lead to more intense drought and its more rapid onset, with responses expected to be localized (Trenberth et al. 2014). Could delayed foliage help Douglas-fir resist the negative effects of drought? The answer depends on whether delayed foliage is produced in response to drought, or if it is produced recurrently regardless of drought. Leaf loss is an adaptive feature utilized by many plant species to reduce transpiration under droughty conditions (Reich and Borchert 1984, Munné-Bosch and Alegre 2004). If the delayed foliage is

produced to replace drought-shed foliage, the new foliage would form under (and presumably be better adapted to) the higher stress conditions (Waring 1987, Abrams and Kubiske 1990). However, our study suggested it is produced recurrently without specific stimuli, and as such the increased leaf area would likely be counterproductive under increased moisture stress. This effect would be mediated, however, by the ability of Douglas-fir to use delayed foliage to replace leaf area more promptly once the drought has passed.

Increased temperature

Global average temperatures, and temperature extremes over land, have increased substantially in the past 60 years (Seneviratne et al. 2014, Fischer and Knutti 2015). Can delayed foliage help Douglas-fir withstand these trends? As air temperature increases, Douglas-fir evapotranspiration demands also increase, resulting in reduced growth rates (Restaino et al. 2016). Delayed foliage may help Douglas-fir recover from short term temperature extremes by replacing lost or damaged foliage, and its contributions to carbohydrate reserves in advance of temperature stress may aid recovery, but it is unlikely to prevent mortality associated with long-term elevated temperature.

Swiss needle cast

Swiss needle cast (SNC) is a fungal disease of Douglas-fir that has become endemic along the Pacific Northwest coast (Ritókóvá et al. 2016). The disease causes loss of foliage, with particular impact on older foliage age cohorts (Weiskittel et al. 2006, Shaw et al. 2016). Infected trees often hold just three or fewer cohorts of needles (Shaw et al. 2016). It is likely that delayed foliage accounts for a significant proportion of the functional leaf area of these infected trees and allows them to maintain higher growth rates than would be possible based on the leaf area

contributed by sequential foliage alone. This hypothesis could be readily tested by differentiating among the foliage types in future assessments of needle retention in SNC infected trees.

Research Opportunities

Future research efforts could build upon this study to expand our understanding of delayed adaptive reiteration in Douglas-fir. The follow opportunities may warrant consideration:

LIDAR crown measurements

Advancements in LIDAR have demonstrated that branch characteristics can be obtained without extensive physical measurements (for example, Seidel 2016). If coupled with in-crown examination and branch labeling, LIDAR may provide a mechanism to measure, and differentiate between, original and epicormic branches on a broader scale. The approach holds promise as a way to more effectively and efficiently identify the implications of adjacent open space on branch length and the relative proportions of original and epicormic branches.

Expanded geographic sampling

This study's sample trees all came from a relatively confined sample area and may have had similar genetic predispositions toward production of epicormic branches. Similar studies could be undertaken across a greater expanse of Douglas-fir's range to determine if the responses observed were representative of the species in general. A two-stage approach is suggested. First, assess the predisposition of Douglas-fir to formation of epicormic branches below the regular crown, across one or more representative transects of the species' range. Then identify a subset of locations at which more detailed measurements of epicormic branching and/or foliage development would be obtained (Gregoire et al. 1995).

Proximal foliage sampling

Further efforts are warranted to determine the exact nature of the differences between sequential and delayed foliage in Douglas-fir. This study's comparisons of sequential and delayed foliage performance were conducted at the branch level. More accurate results could likely be obtained by purposefully sampling foliage of the two types, from the same foliage age cohort, growing in close proximity. This would reduce variation in light, temperature, and moisture conditions between paired samples. Adding direct measurements of the foliage location on the branch (distance from stem) would allow total water path distance to be used as a covariate in moisture stress calculations. Furthermore, direct measurement of source (soil) water $\delta^{18}\text{O}$ would allow for more precise interpretation of ^{18}O results, and greater insights into photosynthetic and stomatal conductance processes. These could be coupled with a subsample of more detailed measurements on physiological processes using LI-COR or similar equipment (Stinziano et al. 2017).

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APPENDIX A: EXAMPLE HEMISPHERICAL PHOTOS AND MASKS

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Figure A.1. Example hemispherical photo. Used to assess stand density by measuring open space (red dot indicates south side of tree). 108 trees were assessed, from which sample was drawn to capture wide range of open space tied to photos with unobstructed views of crowns.

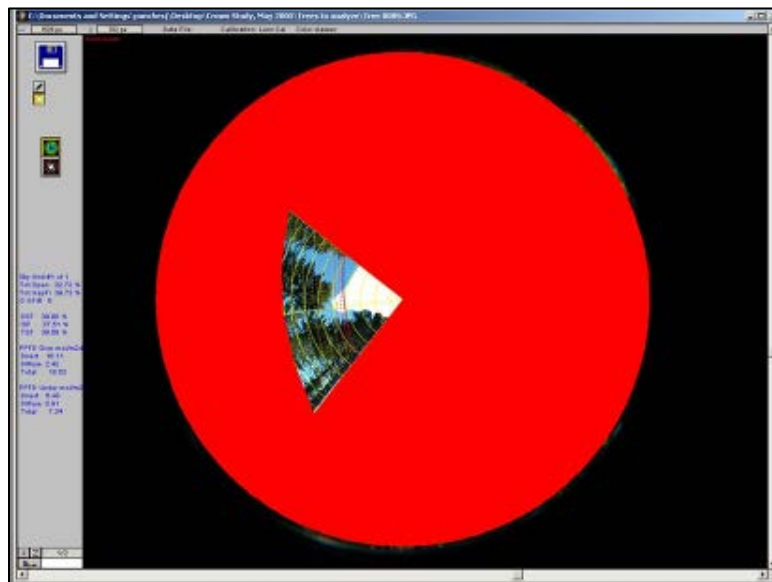


Figure A.2. Example mask procedure. Characterization of open space most likely to impact crown development, restricted to south quadrant (note that photo is not north-oriented). Sample trees ranged from 8 percent (very dense) to 78 percent (very open) in 22° masked segments.

APPENDIX B: CHAPTER 2 SAMPLE TREE DETAILS

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Table B.1. Sample Tree Details. Gap Fraction = the fraction of pixels classified as open (unobstructed by vegetation) in the sky grid region of the image (calculated as a two-dimensional spaces). Open Sky = the fraction (or percent) of open sky (unobstructed by vegetation) in a region of the canopy above the lens (calculated as a three-dimensional space).

Tree ID Number	Height (m)	Height to Lowest Living Branch (m)	<u>43 degree mask</u>		<u>34 degree mask</u>		<u>22 degree mask</u>	
			Total Open Sky	Gap Fraction	Total Open Sky	Gap Fraction	Total Open Sky	Gap Fraction
89	42.2	16.8	28.71	34.99	35.63	44.24	51.76	60.58
115	41.1	24.7	23.36	27.05	28.99	36.28	46.51	45.93
175	41.6	23.0	33.95	31.35	37.81	36.51	39.78	56.27
850	36.2	18.1	25.98	23.79	27.42	29.48	40.69	35.97
826	35.9	17.5	40.08	34.45	41.87	34.52	46.43	62.54
332	34.2	24.4	6.11	7.48	5.67	7.65	7.89	9.70
458	35.3	21.4	7.08	8.89	9.03	12.23	21.93	23.30
1172	41.0	25.0	31.51	29.38	29.44	38.83	60.31	74.50
1487	42.0	20.1	46.62	48.34	60.73	63.23	74.57	87.08
1945	38.7	19.6	22.82	28.94	31.49	36.52	40.00	59.71
2001	40.8	23.8	30.82	40.26	54.35	51.64	58.87	56.43
2077	39.0	25.2	29.85	35.00	32.90	44.17	50.55	73.83
2360	35.5	20.7	7.94	10.83	11.90	16.20	23.67	35.49
2496	42.4	10.3	10.06	13.51	13.45	19.43	27.41	42.46
2804	42.7	22.8	23.37	29.03	30.30	40.08	47.16	61.54
2832	45.8	25.3	31.69	40.56	42.57	53.04	56.03	79.11
2518	36.1	20.1	24.53	31.92	30.50	42.49	57.40	72.17
1824	40.9	12.6	30.01	34.16	35.03	40.13	52.19	52.08
2118	37.2	22.7	27.67	33.44	30.82	39.98	48.97	70.12
1785	40.0	21.9	30.95	40.49	46.83	50.43	65.69	71.98
1935	40.9	26.3	19.59	26.55	28.37	33.56	30.51	42.79
3409	37.6	18.9	28.85	37.73	38.21	53.79	78.28	93.90
3144	39.5	25.5	15.69	19.99	22.79	24.58	25.66	33.65
Average	39.4	21.2	25.10	29.05	31.57	36.91	45.75	56.57

APPENDIX C: CHAPTER 2 DETAILED STATISTICAL RESULTS

APPENDIX C: CHAPTER 2 DETAILED STATISTICAL RESULTS

All models mixed, processed in SAS 9.4, covariance unstructured, estimation method = REML, subject = tree, fixed effects SE method = model-based, degrees of freedom method = between-within.

Model 1: Percentage of branch occupied by sequential foliage, for original living branches.

Covariance Parameter Estimates

Cov Parm	Subject	Estimate	Standard Error	Z Value	Pr > Z
Var (Int)	tree	0.004761	0.003113	1.53	0.0631
Cov (CrwnPos,Int)	tree	-0.00693	0.005291	-1.31	0.1900
Var (CwnPos)	tree	0.02371	0.01145	2.07	0.0192
Residual		0.01762	0.001081	16.30	<.0001

Solution for Fixed Effects

Effect	Estimate	Standard Error	DF	t Value	Pr > t
Intercept	0.9111	0.04186	21	21.76	<.0001
CrwnPos	-0.5191	0.04068	555	-12.76	<.0001
Gap	-0.00199	0.000980	21	-2.03	0.0548

Model 2: Proportion of branch occupied by delayed foliage, for original living branches. Box-Cox transformed dependent (Lambda = 3).

Covariance Parameter Estimates

Cov Parm	Subject	Estimate	Standard Error	Z Value	Pr Z
Var (Int)	tree	0.000585	0.001418	0.41	0.3399
Cov (CrwnPos,Int)	tree	-0.00131	0.005894	-0.22	0.8247
Var (CrwnPos)	tree	0.008710	0.02568	0.34	0.3672
Cov (CrwnPos²,Int)	tree	-0.00015	0.005572	-0.03	0.9781
Cov (CrwnPos²,CrownPos)	tree	-0.00636	0.02390	-0.27	0.7902
Var (CrwnPos²)	tree	0.009030	0.02217	0.41	0.3419
Residual		0.003387	0.000212	16.01	<.0001

Solution for Fixed Effects

Effect	Estimate	Standard Error	DF	t Value	Pr > t
Intercept	-0.3472	0.01925	21	-18.03	<.0001
CrwnPos	0.5821	0.05870	554	9.92	<.0001
CrwnPos²	-0.4489	0.05120	554	-8.77	<.0001
Gap	0.000524	0.000309	21	1.70	0.1045

Model 3: Proportion of branch occupied by sequential foliage, for epicormic living branches, excluding branches with 100 percent sequential foliation.

Covariance Parameter Estimates

Cov Parm	Subject	Estimate	Standard Error	Z Value	Pr > Z
Var (Int)	tree	0.006656	0.008522	0.78	0.2174
Cov (CrwnPos,Int)	tree	-0.00890	0.01648	-0.54	0.5892
Var (CrwnPos)	tree	0.02393	0.03274	0.73	0.2325
Residual		0.02364	0.002495	9.48	<.0001

Solution for Fixed Effects

Effect	Estimate	Standard Error	DF	t Value	Pr > t
Intercept	0.6108	0.05298	21	11.53	<.0001
CrwnPos	-0.05578	0.06724	195	-0.83	0.4078
Gap	0.000540	0.001201	21	0.45	0.6573

Model 4: Proportion of branch occupied by delayed foliage, for epicormic living branches, excluding branches with 0 percent delayed foliation.

Covariance Parameter Estimates

Cov Parm	Subject	Estimate	Standard Error	Z Value	Pr > Z
Var (Int)	tree	0.01120	0.01578	0.71	0.2388
Cov (CrwnPos,Int)	tree	-0.01516	0.02774	-0.55	0.5848
Var (CrwnPos)	tree	0.02788	0.04731	0.59	0.2778
Residual		0.05204	0.005256	9.90	<.0001

Solution for Fixed Effects

Effect	Estimate	Standard Error	DF	t Value	Pr > t
Intercept	0.4095	0.06816	21	6.01	<.0001
CrwnPos	0.1229	0.08517	204	1.44	0.1506
Gap	0.000055	0.001468	21	0.04	0.9702

**APPENDIX D: BRANCH LENGTHS AND PROPORTIONS OF FOLIATION,
BY BRANCH TYPE**

APPENDIX D: BRANCH LENGTHS AND PROPORTIONS OF FOLIATION, BY BRANCH TYPE

Table D1: Lengths (m) of living branches by branch type

Branch Type	Location	N Obs	Mean	Std Dev	Minimum	Maximum
original	whorl	568	3.98	1.21	0.98	7.16
	between whorls	11	3.64	1.73	0.30	6.10
epicormic	whorl	46	1.10	0.93	0.09	3.51
	between whorls	257	0.75	0.76	0.03	4.57

Table D2: Number of living branches by foliation category

Branch Type	Location	Number of branches by foliation category			
		100% original foliation	<100% original foliation	0% delayed foliation	>0% delayed foliation
original	whorl	2	566	0	568
	between whorls	1	10	0	11
epicormic	whorl	8	38	8	38
	between whorls	76	181	67	190

Table D3: Proportion of branch in sequential foliage, for living branches with less than 100 percent foliation

Branch Type	Location	N Obs	Mean	Std Dev	Minimum	Maximum
original	whorl	566	0.55	0.19	0.00	0.90
	between whorls	10	0.52	0.18	0.23	0.74
epicormic	whorl	38	0.62	0.17	0.35	0.91
	between whorls	181	0.61	0.17	0.00	0.97

Table D4: Lengths (m) of living branches with 100 percent sequential foliation

Branch Type	Location	N Obs	Mean	Std Dev	Minimum	Maximum
original	whorl	2	3.28	0.11	3.20	3.35
	between whorls	1	0.30	.	0.30	0.30
epicormic	whorl	8	0.50	0.69	0.09	2.13
	between whorls	76	0.20	0.11	0.03	0.67

Table D5: Lengths (m) of living branches with less than 100 percent sequential foliation

Branch Type	Location	N Obs	Mean	Std Dev	Minimum	Maximum
original	whorl	566	3.98	1.21	0.98	7.16
	between whorls	10	3.97	1.40	2.04	6.10
epicormic	whorl	38	1.23	0.93	0.12	3.51
	between whorls	181	0.99	0.80	0.09	4.57

Table D6: Proportion of branch in delayed foliage, for living branches with more than 0 percent foliation

Branch Type	Location	N Obs	Mean	Std Dev	Minimum	Maximum
original	whorl	568	0.77	0.14	0.06	1.00
	between whorls	11	0.73	0.21	0.25	1.00
epicormic	whorl	38	0.48	0.22	0.03	0.87
	between whorls	190	0.46	0.24	0.03	1.00

Table D7: Lengths (m) of living branches with 0 percent delayed foliation

Branch Type	Location	N Obs	Mean	Std Dev	Minimum	Maximum
epicormic	whorl	8	0.26	0.18	0.09	0.67
	between whorls	67	0.26	0.19	0.03	0.85

Table D8: Lengths (m) of living branches with more than 0 percent delayed foliation

Branch Type	Location	N Obs	Mean	Std Dev	Minimum	Maximum
original	whorl	568	3.98	1.21	0.98	7.16
	between whorl	11	3.64	1.73	0.30	6.10
epicormic	whorl	38	1.28	0.93	0.15	3.51
	between whorl	190	0.93	0.81	0.03	4.57

APPENDIX E: TREE MODELS

APPENDIX E: TREE MODELS

Sequential and delayed foliage distribution within crowns of early-mature Douglas-fir trees.

Purple represents the extent of sequential foliage and green the extent of delayed foliage.

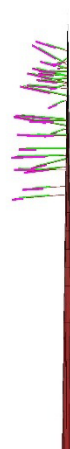
Measurements were not taken in the crown located above the point at which the stem measured 10 cm in diameter. Gap fraction (gap) is the percentage of adjacent open space within 34° of vertical. Arranged from lowest to highest gap fraction. Tree heights not to scale.



Tree 332
Gap 7.7



Tree 458
Gap 12.2



Tree 2360
Gap 16.2



Tree 2496
Gap 19.4



Tree 3144
Gap 24.6



Tree 850
Gap 29.5



Tree 1935
Gap 33.6



Tree 826
Gap 34.5



Tree 115
Gap 36.3



Tree 175
Gap 36.5



Tree 1945
Gap 36.5



Tree 1172
Gap 38.8



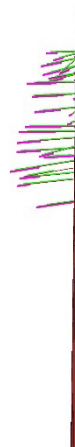
Tree 2118
Gap 40.0



Tree 2804
Gap 40.1



Tree 1824
Gap 40.1



Tree 2518
Gap 42.5



Tree 2077
Gap 44.2



Tree 89
Gap 44.22



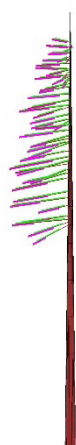
Tree 1785
Gap 50.4



Tree 2001
Gap 51.6



Tree 2832
Gap 53.0



Tree 3409
Gap 53.8



Tree 1487
Gap 63.2