

RELATIONSHIPS AMONG FOLIAR PHENOLOGY, RADIAL GROWTH RATE, AND XYLEM DENSITY IN A YOUNG DOUGLAS-FIR PLANTATION

*Warren D. Devine**

Research Forester

Constance A. Harrington

Research Forester

Olympia Forestry Sciences Laboratory
USDA Forest Service PNW Research Station
3625 93rd Avenue SW
Olympia, WA 98512

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Abstract. We related intra-annual patterns in radial growth rate and xylem density to foliar phenology and second growth flushes in a young Douglas-fir plantation in western Washington. Three foliar maturity classes were defined: (1) shoots and needles elongating; (2) elongation complete, needles maturing; and (3) needles mature. Diameter growth rate had two peaks, one about the time of budbreak and one when foliage was in maturity Class 2. There was a limit to the maximum periodic density of xylem formed at a given rate of diameter growth; as growth rate increased, maximum periodic density decreased. Although xylem density profiles varied widely among individual trees, xylem density differed significantly among foliar maturity classes, increasing 16% from Class 1 to 2 and 60% from Class 2 to 3. Diameter growth rate of second-flushing trees was significantly greater in July compared with trees with no second flush, but we detected no relationships between second-flushing and xylem density patterns or false rings. Although the young trees in this study did not show distinct earlywood-latewood transitions, fully mature foliage (Class 3) was associated with formation of xylem exhibiting characteristics of latewood: greater density, reduced diameter growth rate, reduced tracheid radial diameter, and less interannual growth variation.

Keywords: Phenology, foliage, xylem density, radial growth, second flushing, Douglas-fir, soil water, vegetation control.

INTRODUCTION

Cambial phenology and xylem formation are regulated by hormones such as auxins that are produced by the tree's crown (Sundberg et al 2000). Production of these hormones is influenced by environment and foliar phenology (Larson 1969; DeYoe and Zaerr 1976; Caruso et al 1978). Although xylem formation in Douglas-fir has been researched extensively, foliar phenology is less often studied, and the relationship between the two is seldom examined in studies of either subject. Our focus in this study is the relationship between foliar

development in Douglas-fir and xylem growth rate and density.

Environmental variables have both direct and indirect effects on xylem formation (Larson 1963; Kramer and Kozlowski 1979). Variables such as soil water availability and air temperature affect xylem formation directly through their influences on cell division (Larson 1963). Indirect effects of environment on xylem formation occur through environmental influences on foliar phenology, which affect foliar hormone production. For example, environmental cues affect the timing of spring bud swelling in Douglas-fir, which in turn is associated with hormone production linked to the annual initiation of cambial activity and radial growth

* Corresponding author: wdevine@fs.fed.us.

(Lavender and Hermann 1970; Brix and Mitchell 1980; Li and Adams 1994).

Tracheid radial diameter, one of the variables that differentiates earlywood from latewood, is under hormonal control and is therefore influenced by crown development (Larson 1969; Ugglä et al 2001). Earlywood is characterized by large-diameter tracheids with relatively thin walls; in North American pines (*Pinus* spp.), these tracheids are formed during the period of foliar expansion in the early part of the growing season (Larson et al 2001). Latewood tracheids, formed after foliar expansion is complete, are smaller in radial diameter and are characterized by a greater degree of secondary wall thickening. During earlywood formation, the — growing crown is the primary photosynthate sink. During latewood formation, the new foliage has matured, and tracheid wall thickening becomes the primary sink for photosynthates produced by the mature foliage (Larson 1994). Owing to the higher density of latewood, the primary factor determining mean annual xylem density is the timing of the cambium's transition from earlywood to latewood formation (Vargas-Hernandez and Adams 1994; Grotta et al 2005). An early transition to latewood, resulting in a relatively long period of latewood production, results in high mean xylem density for the year, although often at the cost of reduced tree diameter growth. The timing of the earlywood-latewood transition is often related to a summer decline in soil water availability (Kennedy 1961; Kraus and Spurr 1961; Zahner 1962; Reukema 1965; Brix 1972; Robertson et al 1990).

Several conifer species have exhibited a relationship between the period of shoot elongation and the timing of the transition from earlywood to latewood. In red pine (*Pinus resinosa* Ait.), the period of terminal shoot elongation was related to high levels of auxin production and the formation of large-diameter tracheids (Larson 1960, 1962). A correlation between the cessation of shoot growth in summer and the transition from earlywood to latewood production has been reported for loblolly pine (*Pinus taeda* L.) (Zahner 1962; Jayawickrama et al

1997) and Douglas-fir (Emmingham 1977). However, a recent study did not detect a relationship between cessation of shoot elongation and initiation of latewood in 5-yr-old Douglas-fir (Renninger et al 2006). The authors speculated that, in Douglas-fir, foliar development stage had a greater influence on xylem formation than the timing of shoot elongation. This conjecture was based in part on research in pines that linked the period of needle expansion to that of earlywood formation (Larson 1963, 1969). In herbaceous plants, auxin synthesis in new leaves was shown to be substantially greater during the period of cell division than during subsequent cell expansion (Ljung et al 2001), supporting the idea that foliar maturation may be hormonally linked to cambial activity.

In addition to the unquantified relationship between foliar maturation and Douglas-fir xylem formation, there is a question of what effect multiple flushing has on cambial activity. After an initial period of fixed growth during which needles originate from overwintered primordia, Douglas-fir typically enters a period of free growth that may include multiple flushing (Cline and Harrington 2007). Multiple flushing in Douglas-fir often occurs when unfavorable environmental conditions (eg short-term drought) induce bud set but then are followed by conditions favorable for additional growth (eg soil water recharge). In pines, initiation of each growth flush is associated with low-density earlywood production (Larson et al 2001).

The primary objective of this study was to relate intra-annual radial growth rate and xylem density to foliar phenology and second flushing in Douglas-fir. We hypothesized that the visible maturation of foliage is an indication of the density of currently forming xylem. If these variables are linked, it would be possible to quickly estimate the stage of xylem formation by examining foliage. This could potentially be used to make field assessments of the influence of factors such as microsite, genetics, and climate on xylem formation. We evaluated Douglas-fir in the seventh and eighth years after plantation establishment in vegetation control

treatments that created differences in soil water availability and tree growth rate.

MATERIALS AND METHODS

Study Site

The study took place in southwestern Washington, in the Coast Range (46°43' N; 123°24' W; elevation 300 m). The site is in the western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] vegetation zone, and the plant association is *Tsuga heterophylla* (Raf.) Sarg./*Polystichum munitum* (Kaulfuss) K. Presl-*Oxalis oregana* Nutt. (Franklin and Dyrness 1988). The site slopes gently (10%) toward a westerly aspect. Mean annual air temperature is 9.4°C. January mean minimum and August mean maximum temperatures are 2.4 and 22.8°C, respectively (data from on-site weather station). Mean annual precipitation at the study site from 2001 to 2006 was 1711 mm with approximately 11% of this precipitation occurring annually between 1 June and 30 September. Soils are very deep and well-drained, formed in basalt residuum with volcanic ash present in the surface horizons. Soils are of the Boistfort series, a medial over clayey, ferrihydritic over parasesquic, mesic Typic Fulvudand (Soil Survey Staff 1999; Ares et al 2007b). Age-50 site index for Douglas-fir is 41 - 43 m (King 1966).

Study Design

This study is part of the Fall River Long-Term Site Productivity Study that was established to evaluate the effects of various silvicultural treatments on soil processes, nutrient budgets, the microenvironment, and tree growth (Ares et al 2007b). The area was planted in March 2000 with 1 + 1 Douglas-fir seedlings at a spacing of 2.5 x 2.5 m. The seed source was a mixed lot of 23 first-generation Douglas-fir half-sib families with a known percentage of seed from each family. The study reported here follows a randomized complete-block design with two treatments (a subset of 12 treatments in the larger study), each replicated on 2 plots (30 x 85 m) in each of the study's 4 blocks for a total of 16 plots.

The two treatments were presence (+VC) vs absence (-VC) of competing vegetation control. These treatments were selected for this study because they resulted in significant differences in soil water availability (Devine and Harrington 2006), a variable known to strongly influence xylem formation (Kramer and Kozlowski 1979). On +VC plots, vegetation was treated with a combination of broadcast- and spot-applied herbicides from before planting through the fifth year of the study (Ares et al 2007b). As a result, coverage of competing vegetation averaged 4% during this 5-yr period on these plots. On - VC plots, coverage of competing vegetation was 32% in Year 1 and >80% in subsequent years.

Data Collection

This study involved intensive measurements of the growth and phenology of 64 trees during 2006 and 2007 (Years 7 and 8 postplanting). Thirty-two trees were located in each VC treatment with 4 from each of the 16 plots. Trees were located adjacent to established soil monitoring locations, which were randomly placed near each plot center in study Year 3. Sample trees were restricted to: 1) trees that had no major defects influencing height growth; and 2) trees with a minimum diameter of 6.0 cm at a height of 0.3 m (the minimum diameter for which a band dendrometer would function properly). Thus, our sample was not representative of the entire plantation in that we did not sample the smallest 8% of trees in the - VC treatment and the smallest 3% of trees in the +VC treatment. Before and after each growing season, trees were measured for total height and for diameter at 0.3 m above ground. All diameter measurements were made at a 0.3-m height because breast height diameter of most trees was too small for installation of the dendrometers used in this study. Before each growing season, diameters of the four adjacent trees in cardinal directions from each study tree were recorded. Manual band dendrometers (DB20; EMS Brno, Brno, Czech Republic) were installed on the 64 study trees on 25 April of Year 7. Dendrometers measured tree cir-

cumference with a 0.1-mm resolution (results reported here as diameter). Dendrometer readings were recorded at approximate 2-wk intervals during the months of May through October, once during April and November, and once in January of Year 8.

During the growing season of both study years, budbreak status, foliar maturity, and presence/absence of second flushing were recorded for all study trees on the same dates as the band dendrometer readings. Three separate portions of each tree were assessed: the terminal bud/shoot, the highest whorl, and the remainder of the crown. Budbreak status was classified as broken, swollen, or not swollen (Bailey and Harrington 2006). After buds had broken, foliar maturity was assigned one of three classes: 1) needles and shoot still elongating, needles light in color, tuft of needles at terminal end; 2) elongation of needles and shoot complete, needles medium green in color, tuft of needles at terminal end; or 3) elongation complete, needles dark green without a dense tuft around the terminal bud. While coding foliar maturity, field personnel used a reference sheet with color photographs showing examples of each class. For the highest whorl and the remainder of the crown, the percentage of branch tips in each foliar maturity class were visually estimated to the nearest 10%. During data analysis, foliar maturity class for a given tree and measurement period was assigned based on the classification of the majority of the tree's crown. A tree was classified as second flushing if the terminal shoot or at least 10% of branch tips had a second growth flush.

Because the young study trees were producing juvenile wood, in which the earlywood-latewood transition was diffuse (McKimmy 1959; Larson et al 2001), we did not base our analyses on an estimated earlywood-latewood transition point, which would have, in turn, been based on a predefined density value or other calculation. Defining a transition point was not practical given the gradual transition to latewood exhibited by many of our study trees; instead, we analyzed intra-annual xylem density and growth rate within each 2-wk interval.

In February of Year 9, 5-mm dia stem cores were extracted horizontally from two of the study trees on each plot (32 total) at 0.3 m above ground level from a random azimuth. Sixteen trees were selected from each VC treatment to achieve a sample in which approximately one-half of the trees exhibited second flushing in at least one of the study years; aside from this constraint, tree selection was random within each plot. A 2-mm thick strip was sawn from each extracted core, and the density profile (0.1-mm intervals) was determined by X-ray analysis (QMS density profiler; Quintek Measurement Systems, Knoxville, TN) at Weyerhaeuser Technology Center, Federal Way, WA. Density values are reported as oven-dry mass per green Volume. After analysis, the strip extracted from each core was examined using a stereomicroscope (Leica MZ75; Leica Microsystems Inc., Bannockburn, IL) and the presence of false rings (Kramer and Kozlowski 1979) during Years 7 and 8 was recorded to determine whether false rings were related to multiple growth flushes.

A centrally located on-site weather station recorded hourly air temperature, RH, photosynthetically active radiation (U-190 Quantum sensor; LI-COR, Lincoln, NE), and cumulative precipitation at 2 m above ground level (Fig 1). Temperature was measured using a type-T thermocouple. Weather station data were recorded by a CR10X data logger with a reference thermistor at the panel (Campbell Scientific, Inc., Logan, UT). Because there was significant variability in soil water content at a microsite (ie submeter) scale (Devine and Harrington 2006), soil water sensors were installed at multiple locations across the study site. Four Ech2o EC-20 probes (Decagon Devices, Pullman, WA) were installed at each of 8 trees in the vicinity of our study trees, 4 trees in each VC treatment. At each of the 8 trees, 2 pairs of probes were installed; pairs were 1 m apart and 1 m from the base of the tree. Within each pair, probes were installed horizontally at 0.1- and 0.5-m soil depths. Probe millivolt readings were recorded at 15-min intervals (CR10X data log-

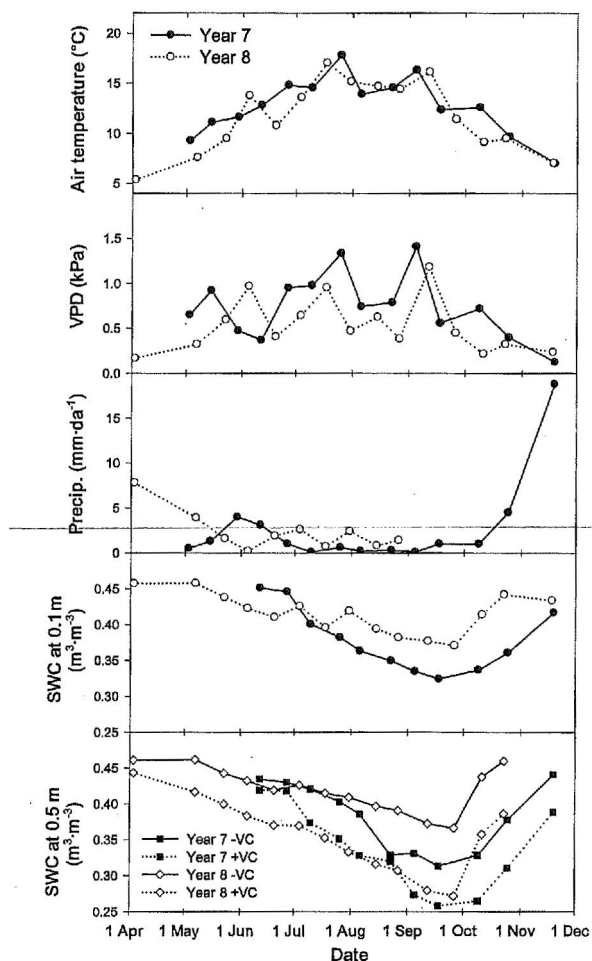


Figure 1. Mean air temperature, daytime vapor pressure deficit (VPD), daily precipitation, and mean soil water content (SWC) at 0.1- and 0.5-m depths during each dendrometer measurement period. Because SWC differed by vegetation control (VC) treatment at 0.5 m, both treatments are shown.

gers) and converted to volumetric soil water content using a soil-specific equation developed earlier (Devine and Harrington 2006).

Data Analysis

Dependent variables included diameter growth per 2-wk measurement period (expressed as mm/da) and mean xylem density per measurement period (kg/m³). Xylem density per measurement period was calculated using dendrometer data to determine what fraction of growth in each year

occurred in each measurement period for each tree. Then these fractions were applied to the density profile of the annual growth ring of that tree, and the xylem density within each 2-wk fraction was averaged. Because band dendrometers were not installed until 25 April of Year 7, a small amount of growth had occurred before the first measurement. Therefore, data from the same period of Year 8 as well as data from five continuously recording electronic dendrometers (not shown) were used to estimate the amount of growth missed at the beginning of Year 7.

Diameter growth data were analyzed within each year by repeated measures analysis of variance (ANOVA) with the VC treatment as a fixed effect, block as a random effect, and measurement date as the within-subject repeated effect (proc Mixed; SAS 2005). Analysis of variance also was used to compare periodic diameter growth and xylem density among foliar maturity classes and between trees with or without second flushes in each year. In these ANOVA models, which did not include VC treatment as a source of variation, the sum of the prestudy (ie end of Year 6) cross-sectional stem area of the four adjacent trees was used as a covariate to account for the effect of neighbor competition on each study tree. Mean soil water content at 0.1- and 0.5-m depths was compared between VC treatments for each dendrometer measurement period using repeated measures ANOVA. Assumptions of homoscedasticity and normality of residuals were met in each model. All tests were performed at the 95% confidence level.

RESULTS

Vegetation Control Effects and Temporal Trends

Trees in the +VC treatment began the study significantly larger in diameter and height than trees in the -VC treatment (Table 1). Total annual diameter and height growth during the two study years were not significantly affected by the VC treatment, with the exception of Year 8, when diameter growth was significantly greater in the -VC treatment.

Table 1. Tree diameter (at 0.30 m above ground) and height at study initiation (with standard error) and annual diameter growth and annual height growth at plantation ages 7 and 8 for 64 Douglas-fir trees without (-VC) and with (+VC) vegetation control.^a

Treatment	Study initiation		Second flush	n	Year 7 growth		n	Year 8 growth	
	Diameter (mm)	Height (m)			Diameter (mm)	Height (m)		Diameter (mm)	Height (m)
-VC	84.7 ± 2.2 a	4.4 ± 0.1 a	No	18	15.9 ± 0.7 a	1.0 ± 0.1 a	26	25.4 ± 0.9 a	1.0 ± 0.1 a
			Yes	14	15.6 ± 0.7 a	1.0 ± 0.1 a	6	29.0 ± 1.7 a	1.2 ± 0.1 a
+VC	98.0 ± 2.2 b	4.9 ± 0.1 b	No	14	14.2 ± 0.7 a	1.0 ± 0.1 a	23	20.5 ± 0.9 b	1.0 ± 0.1 a
			Yes	18	13.7 ± 0.7 a	1.1 ± 0.1 a	9	20.5 ± 1.5 b	1.1 ± 0.1 a

^a Values within each column accompanied by the same letter do not differ ($p \geq 0.05$).

Soil water content at the 0.1-m depth did not differ significantly between the -VC and +VC treatments at any point during study Years 7 or 8; however, soil water content at 0.5 m was affected by the VC treatment in both study years (Fig 1). In Year 7, soil water content in the +VC treatment was significantly lower than that in the -VC treatment in early October ($p = 0.04$). In Year 8, soil water content in the +VC treatment was significantly lower than that in the -VC treatment throughout August ($p = 0.04$) and in early October ($p = 0.04$). The maximum volumetric soil water difference between treatments at the 0.5-m depth was $0.09 \text{ m}^3/\text{m}^3$, which occurred in late August and early September.

Diameter growth began before May in both study years with a growth rate of greater than 0.05 mm/da for the measurement period ending in early May (Fig 2). For both treatments and years, an average of 17% of the annual diameter increase occurred before budbreak. Growth rate was greatest from late July through August in Year 7. In Year 8, growth rate remained high from June through August with two peaks for the 2-wk periods ending in early June and mid-July. In Year 7, trees in the -VC and the +VC treatments grew 0.014 and 0.012 mm/da , respectively, during the final measurement period (26 October through 20 November). In Year 8, the final measurement period in which diameter growth was observed was 12 - 24 October, and

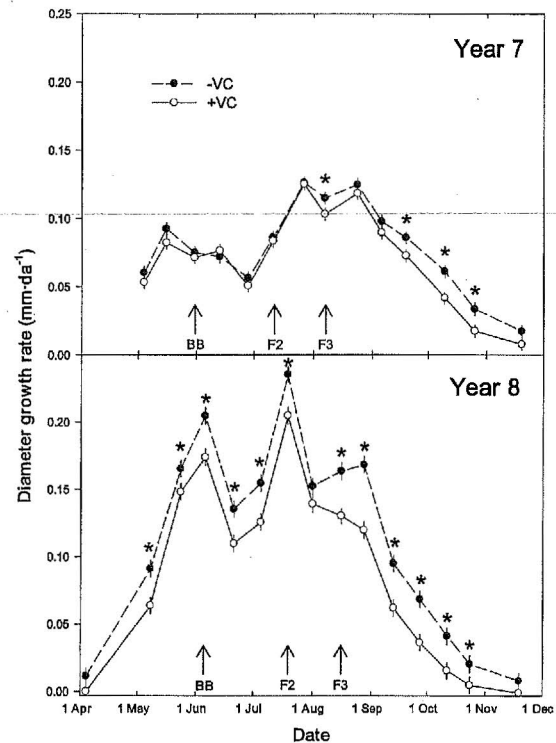


Figure 2. Periodic diameter growth rate (with standard error) for Douglas-fir at plantation ages 7 and 8 without (-VC) or with (+VC) vegetation control through age 5. Asterisks denote significant differences between treatments ($p < 0.05$). Dates at which 75% of trees across both treatments reached terminal bud burst (BB) and foliar maturity Classes 2 (F2) and 3 (F3) are noted.

averaged 0.38 mm between 20 November and 29 January after the Year 7 growing season and $.025 \text{ mm}$ between 19 November and 22 February

after the Year 8 growing season.

only the -VC treatment grew during this interval (0.016 mm/da). Across both VC treatment and years, approximately 1% of annual growth occurred after the late October measurement date. All study trees increased slightly in diameter during winter; the diameter increment

During Year 7, periodic diameter growth was similar in the two VC treatments through July, but beginning in August, periodic growth in the

-VC treatment was usually significantly greater than that in the +VC treatment. During Year 8, periodic diameter growth in the -VC treatment was greater than that in the +VC treatment for nearly the entire growing season.

Xylem density was greater in the -VC treatment than in the +VC treatment from July through September of Year 7 and in May of Year 8 (Fig 3a - b); xylem density was similar between treatments for the remainder of Year 8. Although the rate of xylem density change fluctuated during each growing season, it remained positive beginning in June, indicating continual increases in

density during each year (Fig 3c - d). Combining both years and treatments, diameter growth rate increased from April through June -with little increase in xylem density (Fig 4). Xylem density increased in July and August, whereas the growth rate was generally between 0.1-0.2 mm/da. After August, growth rate declined and xylem density increased to an average of approximately 600 kg/m^3 at the end of the growing season. When data from the entire growing season were plotted together, it was clear that all of the data points fell below the dashed line in Fig 4, suggesting that there was an absolute cap on xylem density at any diameter growth rate and that this cap declined as growth rate increased.

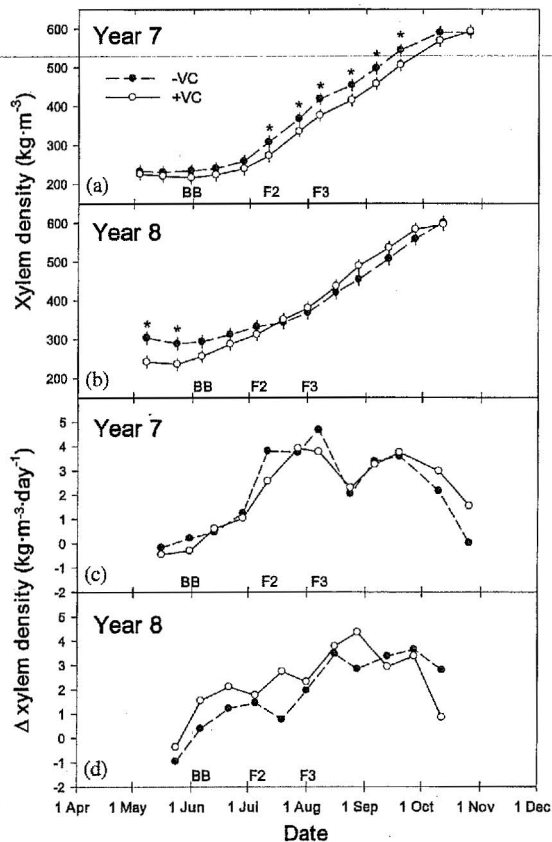


Figure 3. Periodic xylem density (with standard error; a and b) and periodic change in xylem density (c and d) for Douglas-fir at plantation ages 7 and 8 without (-VC) or with (+VC) vegetation control through age 5. Asterisks denote significant differences between treatments ($p < 0.05$). Dates at which 75% of trees across both treatments reached terminal budbreak (BB) and foliar maturity Classes 2 (F2) and 3 (F3) are noted.

Foliar Phenology and Xylem Properties

In both years, budbreak occurred predominantly between mid-May and early June (Table 2; Figs 2 and 3). Foliage remained in maturity Class 1 until the second half of June in Year 7 and until early July in Year 8. The transition from foliar maturity Class 2 - 3 was nearly complete by

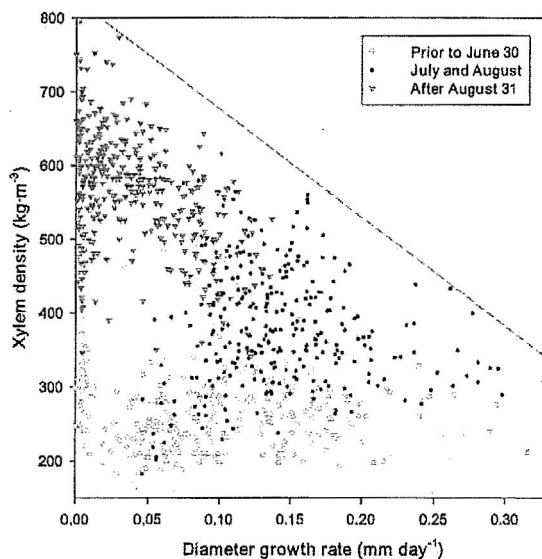


Figure 4. Relationship between diameter growth rate and xylem density for Douglas-fir during two growing seasons; each point represents an approximate 2-wk measurement period for one tree. Data trended in a counterclockwise pattern throughout the growing season; for clarity, the growing season has been divided into three periods.

Table 2. Percentage of trees, by date, classified by budbreak status of terminal shoot, crown foliar maturity class, and presence of second flushing.

Date	Budbreak	Foliar maturity class			Second flush
		1	2	3	
Year 7					
4 May	0	100	0	0	0
16 May	31	100	0	0	0
31 May	97	100	0	0	0
13 June	100	100	0	0	0
28 June	100	23	77	0	0
11 July	100	0	98	2	0
27 July	100	0	61	39	5
7 August	100	0	2	98	17
24 August	100	0	0	100	33
6 September	100	0	0	100	39
19 September	100	0	0	100	50
Year 8					
8 May	6	100	0	0	0
24 May	44	100	0	0	0
6 June	100	100	0	0	0
21 June	100	87	13	0	0
5 July	100	67	33	0	0
19 July	100	0	100	0	0
1 August	100	0	72	28	5
16 August	100	0	23	77	8
28 August	100	0	0	100	22
13 September	100	0	0	100	23

7 August in Year 7 but was only 77% complete by 16 August in Year 8. Fifty percent of trees second-flushed in Year 7, whereas 23% second-flushed in Year 8. By the time second flushes were first observed, the needles of the first growth flush on those trees were predominantly in maturity Class 3. At each of the dates listed in Table 2, budbreak, foliar maturity class, and second flushing did not differ significantly between -VC and +VC treatments; thus, overall means are presented.

Xylem density profiles differed widely among sampled trees (Fig 5). Some trees exhibited a gradual transition from earlywood to latewood (eg Tree 106), whereas others showed an abrupt increase in xylem density followed by a plateau of relatively high-density xylem (eg Tree 3633). The most common profile was an intermediate form (eg Tree 1783) with a somewhat less abrupt transition to latewood. Visual examination revealed that 30% of trees had false rings in Year 7, and 8% of trees had false rings in Year 8;

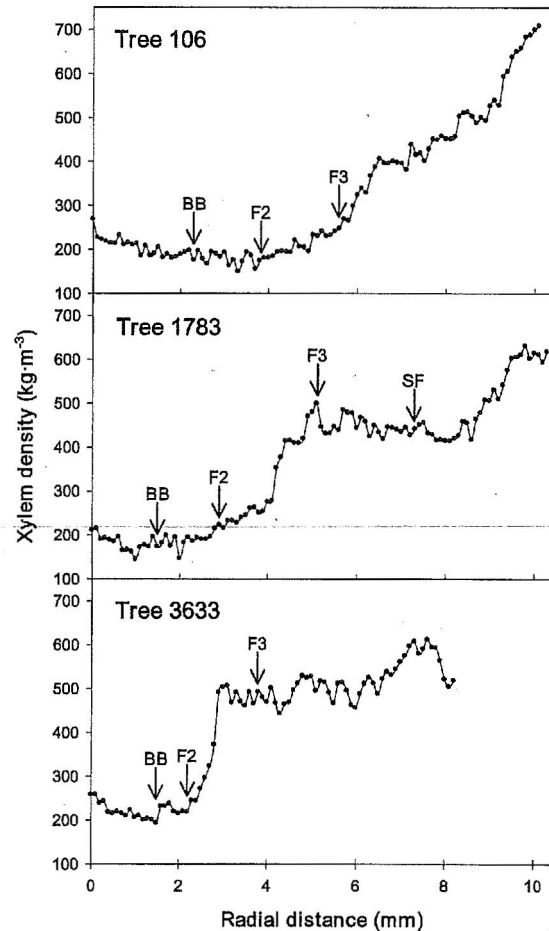


Figure 5. Year-7 xylem density profiles for three trees; these profiles represent the range of xylem density patterns observed. The positions corresponding to the first observation of terminal budbreak (BB), foliar maturity Classes 2 (F2) and 3 (F3), and second flushing (SF), where present, are indicated.

trees with false rings in Year 8 were primarily those without false rings in Year 7. Across both years, 17% of trees with two growth flushes had false rings in the same year, whereas 20% of trees with one growth flush had false rings in the same year.

Mean daily diameter growth did not differ among the three foliar maturity classes in Year 7, but in Year 8, diameter growth was greatest during foliar maturity Class 2 followed by Classes 1 and 3 (Fig 6). In both study years, xylem

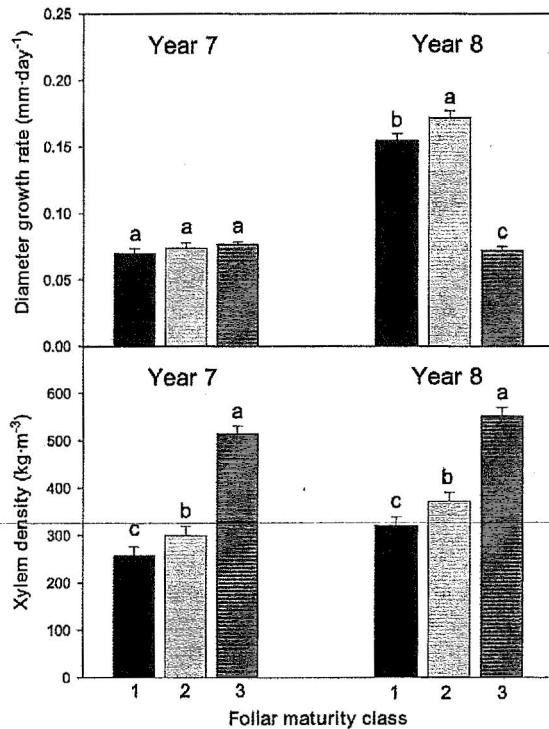


Figure 6. Diameter growth rate and xylem density for Douglas-fir in three foliar maturity classes [shoot elongating (1), shoot elongated and needles maturing (2), and needles fully mature (3)], with standard error bars. Bars accompanied by the same letter within each graph and year do not differ ($p \geq 0.05$).

density increased significantly with each increase in foliar maturity class.

Trees with two growth flushes in Year 7 grew more slowly than trees with one growth flush in late May; however, trees with two flushes also grew more rapidly in early July of that year (Fig 7). In Year 8, trees with two growth flushes again grew more rapidly in early July compared with trees with a single growth flush. Throughout the growing seasons of both study years, xylem density did not differ significantly between trees with two growth flushes and trees with one growth flush.

DISCUSSION

Substantial differences in diameter growth rate occurred between VC treatments. Compared with trees in the +VC treatment, trees in the -VC

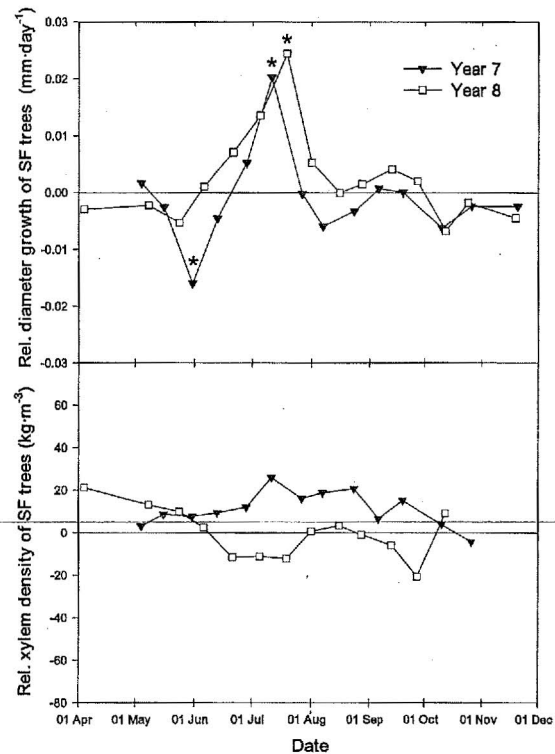


Figure 7. Periodic diameter growth rate and xylem density of second-flushing (SF) Douglas-fir expressed relative to that of trees with no second flush (ie the zero line). Asterisks denote significant ($p < 0.05$) departures from the zero line.

treatment had a higher diameter growth rate late in the Year 7 growing season and throughout the Year 8 growing season. The reduced growth rate in the +VC treatment can be attributed to a higher level of intraspecific competition in that treatment, a result of the fact that trees in the +VC treatment were significantly larger than those in the -VC treatment at Year 7 when the present study began (Devine and Harrington 2006; Ares et al 2007a). This larger Year 7 size was the result of a greater growth rate for +VC trees during the first 5 yr postplanting when competing vegetation was controlled. During the two years of this study, intraspecific competition for both light and soil water was apparently greater in the +VC treatment than in the -VC treatment. In the +VC treatment, crowns were overlapping by Year 7, and the lowest limbs on many of the trees were dying as a result of shading. Lower soil water

content in the +VC treatment suggests that competition for this resource was more intense than in the -VC treatment. During Years 7 and 8, the greatest growth rate differences between treatments occurred late in the growing season when soil water content at the 0.5-m depth was significantly lower in the +VC treatment than in the -VC treatment (Figs 1 and 2). This treatment difference in soil water content is the reverse of that found in the early years of this study (Roberts *et al* 2005; Devine and Harrington 2006) and is presumably a result of greater transpirative water loss by the larger trees in the +VC treatment. A number of conifer species have shown reduced latewood production when soil moisture is deficient (Zobel and van Buijtenen 1989). Given abundant soil moisture, Douglas-fir latewood production continues at least through October, whereas under drier conditions, production may end around August (Worrall 1971; Emmingham 1977; Brix and Mitchell 1980).

Xylem density was significantly greater in the -VC treatment in the latter half of the Year 7 growing season and the beginning of the Year 8 growing season. This pattern appeared despite the fact that xylem density profiles among trees were quite variable as has been shown for the juvenile wood of several conifer species, including Douglas-fir (McKimmy 1959; Barbour *et al* 1997; Koubaa *et al* 2002). Increases in xylem density are generally attributed to reductions in tracheid radial diameter or increased tracheid wall thickness. Radial diameter of tracheids has been positively related to soil water availability during their formation (Larson 1963). Tracheid wall thickness is affected by tree water status through the influence of water availability on the production of photosynthates that contribute to wall thickening (Ooley and Leyton 1968; Larson *et al* 2001). The higher Year 7 July and August xylem density in the -VC treatment was likely the result of greater soil water availability (Fig 1) and greater photosynthate production that contributed to this tracheid wall thickening. Because the timing of foliar maturation was similar between VC treatments, it is

unlikely that the treatment effect on xylem density resulted from a difference in the proportional allocation of photosynthates between foliar growth and xylem formation. In 23-yr-old Douglas-fir, an irrigation treatment influenced the timing of the earlywood-latewood transition but did not affect the timing of shoot growth completion or needle elongation (Brix 1972). It is unclear why there was a treatment difference in xylem density in May of Year 8; early in the growing season, there are rapid changes in the rate of tracheid expansion and in the rate of tracheid wall thickening in Douglas-fir (Dodd and Fox 1990), either of which may have contributed to that treatment difference.

In both treatments, the rate of increase in xylem density increased in each measurement period until about the time that foliage reached maturity Class 3 (Fig 3c - d). At that point, the rate of increase leveled off or declined for the remainder of the growing season. Although the attainment of foliar maturity Class 3 by individual trees was not always closely associated with a sharp increase in xylem density (Fig 5), the overall trend toward greater xylem density at foliar maturity Class 3 appeared to be associated with decreased tracheid diameter. Microscopic examination of the core samples revealed that the abrupt increases in xylem density occurring in some of the trees (eg Tree 3633; Fig 5) were the result of relatively abrupt reductions in tracheid radial diameter. Additionally, foliar maturity Class 3 was associated with a decreasing growth rate (Fig 2) as would be expected during the formation of smaller-diameter tracheids. Other study trees showed a more gradual increase in intra-annual density with no abrupt reduction in tracheid radial diameter (eg Tree 106; Fig 5). The variability among trees was not surprising, because Douglas-fir juvenile wood has a diffuse and variable earlywood - latewood transition (McKimmy 1959). Despite this variability, the significant differences in growth rate and xylem density among foliar maturity classes support our hypothesis that foliar maturity can be used as an indicator of the properties of currently

forming xylem. However, the patterns that we observed were based on a sample of 64 trees. Given the level of variability that we found among individual trees, any foliar-based estimate of xylem stage should be based on a sample mean and not applied to individual trees.

Diameter growth rate of trees with two growth flushes followed a significantly different pattern from that of trees with one growth flush. In both years, second-flushing trees had an increased diameter growth rate in the month of July with the second growth flush generally appearing in the month of August. A possible explanation for this pattern is that increased July growth rates associated with second flushing were caused by a hormonal trigger analogous to that which initiated early growing-season cambial activity at least 1 mon before budbreak (Fig 2). Before this study, we had anticipated that second flushing would be associated with a return to large-celled earlywood production (Larson 1962), presumably with a lower xylem density. This was not the case, however, because we found no relationship between occurrences of second flushing and xylem density patterns (Fig 7). For example, xylem density profiles such as the plateau pattern (Tree 3633 in Fig 5) and midseason density peaks (not shown) were not linked to second flushing and occurred as frequently in trees with only one growth flush. The lack of relationship between second flushing and xylem density also was supported by our visual examination of xylem samples, which showed that false rings occurred at least as frequently on trees with one growth flush (20%) as on trees with two growth flushes (17%).

There appeared to be a relationship, on an intra-annual timescale, between diameter growth rate and the maximum density of xylem formed at a given rate of growth (Fig 4). At a growth rate of 0.10 mm/da, density did not exceed 650 kg/m³, whereas at a growth rate of 0.25 mm/da, density did not exceed 450 kg/m³. This pattern may be the result of a physiological limitation of the cambium reflecting the rate at which photosynthates are produced and allocated to xylem formation. Kennedy (1961) reported that in Douglas-fir, tra-

cheid wall constituents were formed at a constant rate throughout most of the growing season. He found that the cross-sectional area of the tracheid wall remained relatively constant for all of the tracheids formed, but the lumen area was much greater early in the growing season, resulting in low-density earlywood and high-density latewood. On an interannual scale, there is a negative relationship between growth rate and xylem density for Douglas-fir (Brix 1972; Erickson and Harrison 1974). Increased annual diameter growth owing to irrigation, fertilization, and thinning treatments is associated with a greater fraction of low-density earlywood and lower mean annual xylem density.

In both study years, there was a temporary decrease in diameter growth rate in late June. A similar growth pattern was evident in data reported previously for 11- to 13-yr-old Douglas-fir from eight seed sources, including both coastal and inland varieties that were planted in western Oregon (Ernmingham 1977) and, to a lesser extent, in data from 15-yr-old Douglas-fir in Oregon (Li and Adams 1994). In Douglas-fir seedlings, a midseason reduction in diameter growth rate coincided with the period of rapid shoot elongation (Krueger and Trappe 1967). In our study, the timing of this diameter growth lull corresponded to maturity Class 1, the period of shoot elongation after budbreak. This pattern may be a result of the photosynthate requirement of the crown during its phase of rapid expansion. Current-year and 1-yr-old needles of Douglas-fir saplings did not begin to export photosynthates until branch extension was nearly completed in early to midsummer (Ross 1972). The diameter growth lull in our study can likely be explained, at least in part, by the fact that expanding foliage was a net photosynthate sink during the period of shoot and needle elongation (Kruger 1967; Webb 1977).

The substantial differences in diameter growth rate between Years 7 and 8 occurred when foliage was in maturity Classes 1 and 2 but not when foliage was in maturity Class 3. This pattern supports a trend that has been previously reported for Douglas-fir: interannual growth dif-

ferences are primarily a function of differences in the amount of earlywood production, which in turn influence the relative proportion of latewood (Grotta et al 2005). This was evident in 23-yr-old Douglas-fir, in which an irrigation treatment not only increased the rate of earlywood production, but also delayed the transition to latewood by 2 weeks compared with nonirrigated trees (Brix 1972).

In juvenile wood of Douglas-fir, fully mature foliage (i.e., Class 3) was associated with the formation of xylem exhibiting characteristics of latewood. After foliar maturity was reached, radial growth rate declined, tracheid diameter decreased, and xylem density increased. Additionally, interannual differences in growth rate which typically occur during earlywood formation, occurred during the period when foliage had not yet reached maturity. However, because foliar maturity progressed similarly in both VC treatments in each year, we were unable to separate the effects of foliar maturity class from various environmental influences. This underscores the difficulty of finding causative relationships between foliar development and cambial activity in a field study in which both variables are under the influence of environmental cues (Renninger et al 2006). Future research would benefit from examining these variables across multiple sites, where environmental differences could result in phenological differences among trees of similar age. Alternatively, a manipulative study could be designed to alter foliar phenology among trees of the same cohort on the same site. Although it is more difficult to monitor the foliar phenology of larger trees, a study of mature wood formation would be advantageous in that it would eliminate variation in xylem properties associated with juvenile wood.

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