

INFLUENCE OF RED ALDER COMPETITION ON CAMBIAL PHENOLOGY AND LATEWOOD FORMATION IN DOUGLAS-FIR

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SUMMARY

To better understand the influence of competition on wood formation and wood quality in Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), patterns of cambial growth and latewood production were examined for one growing season in 15-year-old plantations with similar densities but differing Douglas-fir/red alder (*Alnus rubra* Bong.) ratios. The treatments consisted of plots having different proportions of Douglas-fir vs. red alder, different red alder planting dates, and one of two total planting densities. Cambial growth was tracked using the pinning method. Cambial activity in most trees began between May 12 and May 23, and ended between August 27 and September 10. Mean date of transition to latewood was July 6. In the treatment with the highest mean red alder basal area, Douglas-fir trees began radial growth later and ended earlier in the year than those in pure Douglas-fir stands. There was no evident effect of competition from red alder on the duration of cambial activity in treatments with intermediate to low red alder basal areas. In all treatments, the duration of radial growth was shorter in smaller-diameter trees. Early transition to latewood production was also associated with higher red alder basal area. Percent latewood was unaffected by treatment, but it was dependent on the date of a tree's transition to latewood production.

Key words: Cambial growth, Douglas-fir, latewood, phenology, red alder.

INTRODUCTION

Because Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) wood is used in structural applications, density is of fundamental importance among its wood quality attributes. Wood density is a function of xylem cell diameter and wall thickness, both of which are highly variable within a growing season. Factors such as physiological processes, environmental effects and resource availability that influence the rate of cell production

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and development at various times during the season thus can affect overall ring density. Neighboring plants certainly affect a target plant's environment and availability of resources, but the effect of neighbors on xylem phenology has never been investigated.

Some environmental influences on cambial activity in conifers have been well documented and thorough reviews are available elsewhere (Creber & Chaloner 1990; Horacek *et al.* 1999). Higher ambient temperatures are associated with increased ring width (Larson 1967), earlier cambial growth initiation in spring (Kozłowski *et al.* 1991), increased rates of cell production and reduced radial cell diameter (Jenkins & Shepherd 1972). Increased precipitation appears to extend the period of cambial growth (Creber & Chaloner 1990; Antonova & Stasova 1993) whereas a water deficit can end the growing season (Horacek *et al.* 1999). The length of the cambial growing season is also known to be influenced by photoperiod (Larson 1962; Creber & Chaloner 1990).

In contrast, the effects on cambial activity of other environmental variables, such as light intensity, are poorly understood. Light intensity affects the rate of photosynthesis (Kozłowski *et al.* 1991), which can affect the rate of cambial growth (Philipson *et al.* 1971). Furthermore, in a forest stand with a deciduous component, not only the light intensity but also the phenology of its availability can differ from a pure evergreen forest.

Latewood, characterized by thick-walled, narrow-radial-diameter tracheids, is dense relative to earlywood; consequently the percentage of latewood formed each year is the main driver of overall wood density (Zobel & Van Buijtenen 1989). Latewood production in Douglas-fir is highly variable from year to year (Kennedy 1961), and its control is complex. For example, percent latewood has been reported to increase with cambial age (Megraw 1986) and spring precipitation (Kennedy 1961; Robertson *et al.* 1990), and decrease with wider spacing within a plantation (Smith 1980), following thinning (Erickson & Lambert 1958) or fertilization (Brix & Mitchell 1980), or with pollution-related needle loss (De Kort 1993). In addition, Vargas-Hernandez and Adams (1994) demonstrated that latewood percentage is at least partially genetically controlled. Larger percentages of latewood correlate with longer periods of latewood formation (Kennedy 1961); furthermore, in Douglas-fir, both an earlier date of latewood transition (Vargas-Hernandez & Adams 1994) and a prolonged growing season (Chalk 1930 *cited in* Creber & Chaloner 1990) result in larger latewood percentages. To assess latewood production, one thus needs to consider factors affecting both the timing of the transition to latewood and the length of time during which it is produced relative to earlywood.

Several physiological processes are involved in the transition to latewood, because separate mechanisms control xylem radial diameter and wall thickness (Brown 1970). In Douglas-fir, the transition to latewood occurs near the time when shoot elongation ends (Emmingham 1977), or before bud set (Rensing & Owens 1994). When primary (extension) growth ceases, photosynthates are translocated to the stem and thicker xylem cell walls are thus formed (Larson 1969). Reduced auxin concentration in the cambium at the time shoot elongation ends is related to reduced radial cell diameter (Kennedy 1961). Processes that influence the period of shoot growth, therefore, also could have an indirect effect on the transition to latewood production.

Most environmental and silvicultural influences on wood formation are related ultimately to the availability of resources for growth. Competition from neighboring trees limits resource availability, and resource depletion varies both with stand density and by species (Cole & Newton 1986; Shainsky & Radosevich 1992; Chan *et al.* 2003). In mixed stands, red alder (*Alnus rubra* Bong.) competes with Douglas-fir for light and soil moisture (Cole & Newton 1986; Shainsky & Radosevich 1992). Light transmittance through pure red alder and Douglas-fir canopies differs, with less light reaching the understory in conifer stands, but variable light transmittance seasonally through the deciduous canopy (DeBell & Giordano 1994; Parker *et al.* 2002; Grotta 2002). Light transmittance through mixed canopies is intermediate between the two types of pure stands (Grotta 2002). Thus, if light intensity affects cambial growth, then red alder density in a mixed stand could affect Douglas-fir cambial activity through this mechanism. Similarly, soil moisture available to Douglas-fir trees in a mixed stand may be different than in a pure stand, and this too could affect cambial growth.

In a mixed stand, red alder could also impact Douglas-fir growth ring attributes through its effect on Douglas-fir growth rate. Investigations of effects of growth rate on Douglas-fir wood density have shown mixed results (reviewed in Zobel & Van Buijtenen 1989), although many of the oldest studies confounded growth rate and cambial age. Several recent studies point to a negative relationship between growth rate and latewood proportion. Fabris (2000) found that suppressed or closely-spaced Douglas-fir trees had higher latewood proportions than similarly-aged trees with faster growth. Additionally, Gartner *et al.* (2003) found that across a range of sites, ring width and latewood percent were negatively correlated. These findings imply that in mixed stands, where Douglas-fir can become suppressed by faster-growing red alder (Cole & Newton 1987), Douglas-fir latewood percent may be increased by interplanted red alder.

This study examined whether the period of cambial growth in Douglas-fir was influenced by the abundance of red alder in a mixed stand. We also investigated whether the timing of the transition to latewood and the amounts of earlywood and latewood formed were associated with red alder competition.

MATERIALS AND METHODS

Site description and experimental design

The study site is in the Cascade Head Experimental Forest near Lincoln City, Oregon (45° 02' N, 123° 58' W), within five km of the Pacific Ocean and at 330 m elevation. Originally, the site was dominated by old-growth Sitka spruce (*Picea sitchensis* [Bong.] Carr.) and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.). Mean annual precipitation is about 250 cm, with the majority occurring between November and April. Average minimum and maximum temperatures are 2.2 °C and 20.9 °C, respectively. Soils are well drained and deep (up to 1 m), and highly fertile (Rhoades & Binkley 1992).

The study was undertaken in 2001 on experimental plots established in 1985 for a study of Douglas-fir/red alder interactions. Fifteen treatments were randomly assigned to 30 × 30 m plots, but only five treatments were included in the current study (Table 1). In 1985, the site was clearcut, and the following year trees were planted at a fixed

spacing of 3×3 m (1109 trees/ha), with the exception noted below. The first treatment, a pure Douglas-fir stand, was considered a control for the current study. The second treatment was 90% Douglas-fir and 10% red alder. Two more species mixtures were included, with proportions of 50 : 50 and 25 : 75 Douglas-fir/red alder. Unlike the 90 : 10 mixture, in these two treatments the red alder trees were planted five years after the Douglas-fir, in 1991 (skips in the planting rows were left in 1986 for eventual red alder planting). In all three mixtures, the red alder trees were evenly dispersed within the plots. Finally, an additional pure Douglas-fir treatment was planted at 4.2×4.2 m; this treatment had half the density (555 trees/ha) of the first monoculture. Each treatment was replicated in three blocks. Each plot of each treatment consisted of 9 rows for a total of 81 trees, except in the monoculture planted at 4.2×4.2 m, where only 41 trees were planted due to the wider spacing. Trees that died after planting were replaced for the first three years. Volunteer shrubs and trees were hand-removed through 1991. At the time of this study, Douglas-fir trees were 15 years old, and alders were either 10 or 15 years old.

Because the age of the red alder trees varied among treatments, the proportion of trees in the stand that were red alder did not accurately reflect a comparable measure of the competitive pressure exerted on Douglas-fir trees by red alder. For example, in the treatment where both species were planted simultaneously, the red alder trees, though few in number, were quite large, overtopped the conifers, and fully occupied the canopy. However, in the treatments where red alder planting was delayed, the red alder trees were smaller in diameter and about the same height as the Douglas-fir trees in the same plots. Basal area of each species in each treatment is given in Table 1.

Table 1. Description of treatments, showing proportions of Douglas-fir and red alder, whether red alder planting was simultaneous with Douglas-fir vs. delayed by five years, initial tree spacing, diameter (mean and SE) and sample size of the Douglas-fir trees sampled, red alder and Douglas-fir basal area (BA), and percentage of total BA that is red alder, by treatment (mean of three plots and SE). On red alder trees with multiple stems, all stems with diameters >10 cm that resulted from a fork below breast height were measured (from Grotta *et al.* 2004).

Treatment	Douglas-fir proportion	Red alder proportion	Red alder planting*	Spacing (m)	Douglas-fir DBH (cm)	# trees sampled	Red alder BA (m ² /ha)	Douglas-fir BA (m ² /ha)	% Red alder BA
1	100	0	-	3×3	15.5 (0.9)	17	0.0 (0.0)	0.0 (0.0)	25.3 (0.9)
2	90	10	imm.	3×3	11.0 (0.8)	17	19.7 (1.2)	68.5 (2.6)	9.1 (0.7)
3	50	50	del.	3×3	18.0 (1.0)	18	8.4 (2.2)	43.3 (10.5)	11.1 (2.6)
4	25	75	del.	3×3	13.5 (1.0)	11	10.4 (1.2)	69.4 (6.5)	4.6 (1.0)
5	100	0	-	4.2×4.2	17.4 (1.2)	16	0.0 (0.0)	0.0 (0.0)	15.8 (3.0)

* Immediate (imm.) = planted in year 1 (1986); Delayed (del.) = planted in year 6 (1991).

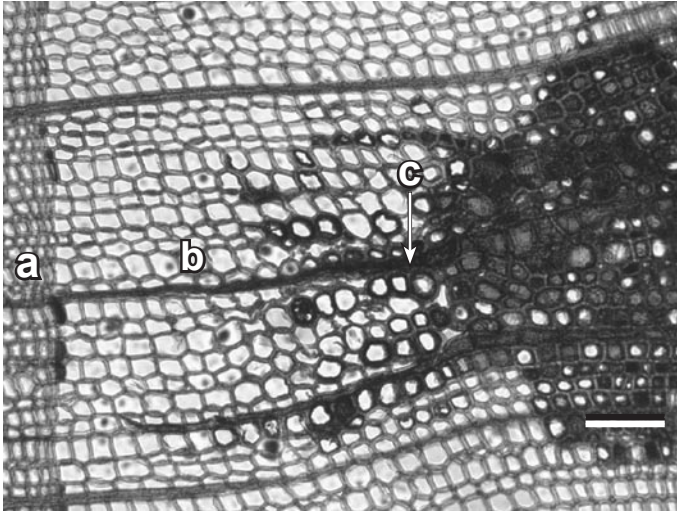


Fig. 1. Transverse section ($\times 10$ magnification) indicating location of cambium on the date of pinning. a: latewood of previous year (2000); b: normal earlywood formed prior to pinning; c: estimated location of cambium on date of pinning. The section in this example was pinned on 14 June 2001. — Scale bar = 100 μm .

Pinning method

Six Douglas-fir trees in each plot were selected randomly for sampling from the second-outermost row of trees. These trees were chosen to avoid the permanent measurement trees in the inner five rows, because the methods used in this study involved semi-destructive sampling. This sampling protocol resulted in a total possible sample of 90 trees; however, in some plots with a low proportion of Douglas-fir, six suitable trees could not be identified, so in these cases, five were used. Thus only 79 trees were sampled.

To track incremental radial growth over the course of the growing season, the cambial pinning method (Wolter 1968) was used. An insect mounting pin (0.5 mm diameter) was inserted into each sample tree at breast height so that it penetrated the bark and reached the cambial zone. Pins were labeled with the date and then left in the tree. The tip of the pin stimulated the formation of abnormal tissue in the cambial zone, marking the position of the cambium at the time of pinning (Fig. 1). The process was repeated at 7- to 10-day intervals from mid-March to mid-September 2001. On each tree, the pins were inserted in one internode and within one axial quadrant; they were placed at least 1 cm away from one another. Overbark diameter at breast height (DBH) was also recorded for each tree.

Sample analysis

In October–November 2001, wood samples were extracted using a chisel and mallet. The samples consisted of strips of wood surrounding numerous pins and were at least one annual ring deep. The pins were removed and using a band saw, the wood sam-

ples were then cut into smaller pieces, each containing one pin mark. Using a sliding microtome, 30 μm -thick transverse sections of each pinned area were prepared. They were then stained with safranin and mounted permanently.

Sections were analyzed with a light microscope connected to a video monitor using NIH Image 1.60 (NIH, Bethesda, MD). For each section, we measured the total radial width of the 2001 increment as well as the distance from the inner edge of the 2001 increment to the pin wound. Measurements among samples were standardized by dividing the distance to the wound by total ring width to obtain the percentage of annual radial growth already completed by the date of pinning.

For each sample tree, percent latewood in the 2001 increment was determined. Latewood was defined according to Mork's definition (Denne 1989), as cells in which the double-cell wall thickness in the radial direction is at least twice the radial diameter of the lumen when viewed in cross section. Percent latewood along two radial files at least 1 mm apart tangentially were averaged for each sample tree. Earlywood and latewood widths were then calculated from percent latewood and total ring width.

Data analysis

We considered the dates that 5% and 95% of the total annual radial growth was completed to be the dates that growth began and ended, respectively, because it was impossible to identify the exact date of onset and end of cambial growth with our sampling methods. We also calculated the dates that 25%, 50%, and 75% of radial growth were completed. To estimate the dates corresponding to these thresholds, percent growth and date were linearly interpolated between observed values for consecutive pinning dates. Thus, in our final data set there were five dates for each tree, each corresponding to one of the five specified thresholds of radial growth. In addition, the estimated date of transition to latewood formation was determined by comparing percent latewood with the wood formation phenology data for each tree. The date on which the percent annual growth completed equaled (100 minus latewood percent) was considered to be the date of transition to latewood.

Based on studies showing that suppression affects the duration of cambial growth in other conifer species (Kozlowski & Peterson 1962; Baucker *et al.* 1998), we incorporated a variable into our model to account for the possible effect of competitive status relative to neighboring trees. Two potential variables were tested, relative growth rate (RGR) and diameter at breast height (DBH). Relative growth rate (RGR) is a useful index for characterizing relative competitive status (Hunt 1990), and was defined as the width of the 2001 increment divided by DBH at the end of the 2000 growing season. 2000 DBH was derived from ring width measurements and 2001 DBH measurements. DBH also was presumed to be a good indicator of competitive status, because all Douglas-fir trees were the same age. DBH was chosen over RGR to represent competitive status on the basis of Akaike's Information Criterion (AIC) values for models incorporating each variable.

ANCOVA was used to determine differences among treatments in the dates when each of the five thresholds of radial growth was completed, while accounting for the effect of tree size (Table 1). Also, a repeated measures analysis was included to account for the

effect of repeatedly sampling the same trees; a banded TOEPLITZ covariance structure was selected using AIC. Our statistical model to describe Y_{ijkl} , the day (Jan 1 = 1, Feb 1 = 32, etc.) that the k^{th} tree in the i^{th} rep of the j^{th} treatment at the l^{th} stage, is:

$$Y_{ijkl} = \mu + \rho_i + t_j + \xi_{ij} + \beta^*(\text{dbh}_{ij} - \text{dbh}_{..}) + \gamma_{ijk} + s_l + (\text{st})_{jl} + \beta_l^*(\text{dbh}_{ij} - \text{dbh}_{..}) * s_l + \lambda_{ijkl}$$

where

- μ is the overall mean value of Y_{ijkl}
- ρ_i is the random effect of replicate (block) i
- t_j is the effect of the j^{th} treatment, $j = 1, 2, \dots, 5$
- ξ_{ij} is the random error associated with the i^{th} block within the j^{th} treatment
- β is the slope parameter for the covariate, dbh for each tree
- γ_{ijk} is the random error associated with subsamples (trees) within each block and treatment
- s_l is the effect of the l^{th} stage, $l = 1, 2, \dots, 5$
- ts_{jl} is the interaction of treatment and stage
- β_l is the slope parameter for the covariate, dbh differing for each stage
- λ_{ijkl} is the random error associated with the k^{th} tree in the i^{th} plot within the j^{th} treatment at stage l and is distributed $\sim N(0, \Sigma)$ and Σ is 5×5 variance-covariance matrix with TOEPLITZ(5) covariance structure.

Ring width, earlywood width, latewood width, percent latewood and timing of the transition to latewood were analyzed using the following ANCOVA model:

$$Y_{ijkl} = \mu + \rho_i + t_j + \xi_{ij} + \gamma_{ijk}$$

where

- μ is the overall mean value of Y_{ijkl}
- ρ_i is the random effect of block i
- t_j is the effect of the j^{th} treatment, $j = 1, 2, \dots, 5$
- ξ_{ij} is the random error associated with the i^{th} block within the j^{th} treatment
- γ_{ijk} is the random error associated with subsamples (trees) within each block and treatment.

For each property, estimates for the control treatment were compared to those of each of the other treatments. The Fisher procedure for multiple comparisons was used to protect confidence interval widths for estimated effects (Steel *et al.* 1997). All models met assumptions for normality, so no data transformations were necessary. Statistical analyses were performed using the SAS MIXED procedure (SAS Institute, Cary, NC).

RESULTS

Radial growth

The width of the 2001 growth increment varied among sample trees from 0.2 to 8.3 mm, with a mean of 2.9 mm (SE = 0.3 mm). In the control treatment, the mean ring width was 3.8 mm (Table 2), and radial growth in the 50 : 50 (delayed) treatment was similar. Trees in the widely-spaced Douglas-fir monoculture produced wider rings, with a mean of 4.8 mm, though statistical evidence of a difference between this treatment

and the control was poor ($P = 0.19$). However, in the 90 : 10 (immediate) and 25 : 75 (delayed) treatments, radial growth in 2001 was sharply reduced compared to the control, with averages of only about 1 mm.

Earlywood width ranged from 0.1 to 6.8 mm among sample trees, with a mean of 1.6 mm (SE = 0.2 mm). Generally, there was less latewood than earlywood, and its variation among trees was also smaller: latewood width ranged from 0.1 to 3.8 mm, with a mean of 1.3 mm (SE = 0.1 mm). The width of the earlywood and latewood ring components followed similar trends among treatments as total ring width (Table 2). Latewood width was greatest in the widely-spaced Douglas-fir monoculture, followed by the control ($P = 0.11$). Earlywood widths in these treatments were not different. Neither earlywood nor latewood width in the 50 : 50 (delayed) treatment differed from the control. In the 90 : 10 (immediate) and 25 : 75 (delayed) treatments, both earlywood and latewood width were far lower than in the control treatment ($P < 0.01$).

Table 2. Width of the 2001 annual increment and earlywood and latewood components by treatment. Mean of three plots (mm, \pm SE), and level of significance (P) of the difference between the treatment and the control (treatment 1) as tested by ANCOVA.

Treatment	Ring width			Earlywood width			Latewood width		
	Mean	SE	P	Mean	SE	P	Mean	SE	P
1 (100 : 0 3 \times 3 m)	3.8	0.8	NA	2.3	0.5	NA	1.5	0.2	NA
2 (90 : 10 immediate)	0.9	0.1	0.01	0.5	0.1	0.01	0.5	0.0	0.01
3 (50 : 50 delayed)	3.5	1.0	0.66	1.9	0.4	0.33	1.6	0.6	0.77
4 (25 : 75 delayed)	1.1	0.0	0.01	0.6	0.1	0.01	0.5	0.1	0.01
5 (100 : 0 4.2 \times 4.2 m)	4.8	0.2	0.19	2.7	0.1	0.38	2.1	0.1	0.11

Phenology of cambial activity

The mean date that radial growth began among all sampled trees was May 17 (SE = 1.2 days), with the dates of initiation ranging from May 1 to June 22. On average, cambial growth ceased on September 5 (SE = 1.3 days), though some trees ceased growth as early as July 28 or as late as September 27. Ring width and duration of cambial growth were well correlated ($r^2 = 0.73$, simple linear regression, $F_{1, 14} = 36.6$, $P < 0.001$), indicating that the overall rate of cell production was rather consistent among plots despite variation in the amount and duration of cambial growth.

Smaller-diameter trees began cambial growth later in the year and ended growth earlier than larger trees, as indicated by the significance of the d*s interaction in the model (Table 3, Fig. 2). This effect was modeled for two trees, 10.6 cm and 19.9 cm DBH, representing diameters one standard deviation below and above the mean DBH for all trees sampled, respectively. The growing season of the larger tree was estimated to be 19 days longer than that of the smaller tree (Fig. 2). Estimates given hereafter are for a tree with a DBH of 15 cm, the mean DBH of all sampled trees.

Differences among treatments in duration of the growing season were indicated by the significance of the s*t interaction in our model (Table 3). Trees in the 90 : 10

Table 3. Results of ANCOVA analysis of the phenology of cambial activity in Douglas-fir trees. Num DF = numerator degrees of freedom; Den DF = denominator degrees of freedom; t = treatment; d = DBH; s = threshold of growth (5%, 25%, 50%, 75%, or 95%).

Effect	Num DF	Den DF	F Value	P
t	4	8	0.40	0.80
d	1	73	1.29	0.26
s	4	255	35.53	< .0001
s*t	16	255	1.99	0.01
d*s	4	255	7.56	< .0001

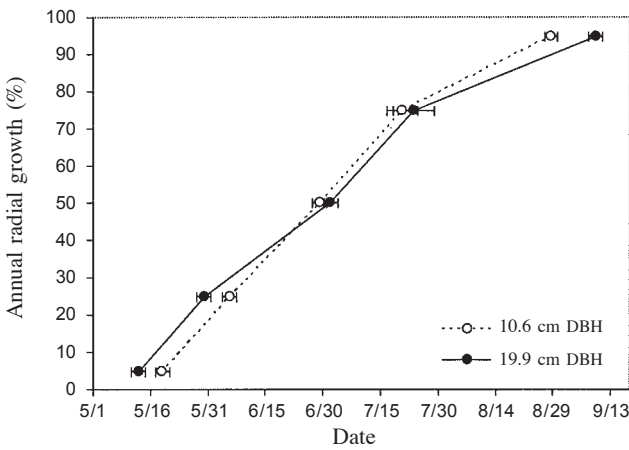


Fig. 2. Modeled dates by which five thresholds of annual radial growth were achieved by trees of two sizes, 10.6 and 19.9 cm DBH (mean ± SE).

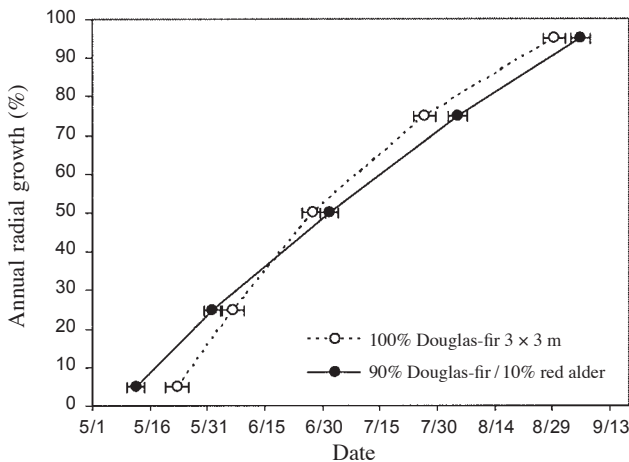


Fig. 3. Estimated patterns of cambial growth of Douglas-fir for selected treatments, adjusted for tree size (estimate ± SE). Species proportions are % Douglas-fir / % red alder.

mixture had a shorter growing season than trees in the control treatment (Tables 4 & 5, Fig. 3). Whereas in the pure stand cambial growth began in mid-May, in the 90 : 10 mixture growth did not begin until about 10 days later, on average. Trees in this mixture also ceased growth earlier than in the pure stand ($P = 0.07$). On the other hand, trees in the other two mixed stands (treatments 3 and 4) showed statistically similar patterns of growth as in the control. The only exception was at the 75% threshold of growth, where trees in both mixtures reached that plateau earlier than in the pure stand (Table 5). There was no difference in patterns of radial growth between the control and the widely-spaced monoculture treatment at any threshold of growth.

Table 4. Estimated date that each calculated percentage of radial growth of Douglas-fir was completed in 2001, by treatment (mean \pm SE, days), modeled for trees 15 cm DBH. Species proportions are Douglas-fir : red alder.

Treatment	Level of growth				
	5%	25%	50%	75%	95%
1 (100 : 0 3 \times 3 m)	May 13 (2.5)	Jun 2 (2.5)	Jul 2 (2.5)	Aug 5 (2.5)	Sep 6 (2.5)
2 (90 : 10 immediate)	May 23 (3.1)	Jun 7 (3.2)	Jun 28 (3.0)	Jul 28 (3.0)	Aug 30 (3.0)
3 (50 : 50 delayed)	May 14 (2.9)	Jun 1 (2.8)	Jul 6 (2.8)	Aug 7 (2.6)	Sep 8 (2.7)
4 (25 : 75 delayed)	May 18 (2.7)	Jun 2 (2.7)	Jun 28 (2.8)	Jul 29 (2.7)	Sep 3 (2.7)
5 (100 : 0 4.2 \times 4.2 m)	May 16 (2.7)	Jun 3 (2.6)	Jun 30 (2.6)	Jul 30 (2.6)	Sep 4 (2.6)

Table 5. Estimated differences between control (100 : 0 3 \times 3 m) and given treatments in the date that five levels of annual radial growth were completed, in days (estimate, lower and upper bounds of 95% confidence interval). Estimates in bold face are significant at $p < 0.05$; in italics significant at $p < 0.10$.

Treatment	5			25			50			75			95		
	Estim.	Lower	Upper	Estim.	Lower	Upper	Estim.	Lower	Upper	Estim.	Lower	Upper	Estim.	Lower	Upper
90:10 immed.	-10.3	-18.2	-2.5	-5.2	-13.2	2.8	4.0	-3.7	11.8	8.3	0.5	16.2	6.6	-1.2	14.5
50:50 delayed	-3.1	-10.2	4.1	-1.3	-8.4	5.9	2.3	-4.7	9.4	6.4	-0.8	13.5	2.2	-4.9	9.2
25:75 delayed	-4.8	-12.2	2.6	-0.2	-7.6	7.1	4.1	-3.5	11.6	7.1	-0.3	14.6	3.3	-4.1	10.6
100:0 4.2 \times 4.2 m	-1.2	-8.8	6.3	1.4	-6.0	8.8	-4.0	-11.4	3.4	-2.0	-9.1	5.2	-2.2	-9.3	5.0

Table 6. Estimated number of days earlier than the control (100 : 0 3 × 3 m) treatment that trees in the given treatment began latewood production (estimate, lower and upper bounds of 95% confidence interval). Estimates in bold face are significant at $p < 0.05$.

Contrast	Estimate	Lower	Upper
90 : 10 immediate	15.7	8.1	23.2
50 : 50 delayed	9.8	2.2	17.4
25 : 75 delayed	9.5	1.9	17.1
100 : 0 4.2 × 4.2 m	0.6	-6.9	8.2

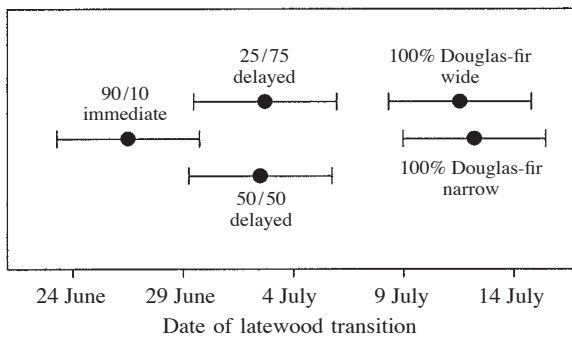


Fig. 4. Mean (\pm SE) date that latewood production began in Douglas-fir trees in five treatments. Species proportions are % Douglas-fir / % red alder.

Latewood production

Trees began producing latewood from about June 2 at the earliest to August 25 at the latest; the mean date was July 6 (SE = 2.3 days). Significant differences existed among treatments in the date of transition to latewood ($F_{4,8} = 8.30$, $P < 0.01$, Table 6, Fig. 4), with trees in all three species mixtures transitioning to latewood production earlier than trees in the two pure Douglas-fir treatments. Trees in the 90:10 (immediate) treatment began latewood production on June 28 on average, while in the two mixed species treatments with delayed alder planting, trees began latewood production around July 3. In both Douglas-fir monoculture treatments, latewood production began on July 12 on average.

Among all trees, percent latewood ranged from 18 to 73%, with a mean of 47% (SE = 1.5%). Treatment means ranged from 43 to 49%. No difference in percent latewood was detected among treatments ($F = 0.81$, $P = 0.55$; data not shown). A higher average latewood proportion was associated with an earlier average date of transition to latewood ($r^2 = 0.58$; $P = 0.03$). However, there was no relationship between the date that growth ceased and percent latewood ($F = 0.02$, $P = 0.90$, data not shown).

At the individual-tree level, percent latewood and ring width were negatively correlated ($F_{1,67} = 11.05$, $P = 0.001$), indicating that slower-growing trees produced more latewood relative to earlywood. There was also a negative association between percent

latewood and earlywood width among individual trees; however, at the plot level, these effects disappeared. There was no relationship between percent latewood and latewood width (Table 7).

Table 7. Simple correlation coefficients (r) and associated p -values for ring width and percent latewood with other ring properties at the tree level ($n = 71$) and at the plot level ($n = 15$).

Explanatory variable	Ring width		Percent latewood	
	Tree level	Stand level	Tree level	Stand level
Percent latewood	-0.33 0.01	-0.10 0.72	–	–
Earlywood width	0.94 < 0.01	0.99 < 0.01	-0.57 < 0.01	-0.21 0.45
Latewood width	0.84 < 0.01	0.98 < 0.01	0.14 0.24	0.04 0.89
Date of latewood transition	0.45 < 0.01	0.49 0.07	-0.80 < 0.01	-0.61 0.01
Date of growth cessation	0.61 < 0.01	-0.74 < 0.01	-0.18 0.14	0.05 0.84

DISCUSSION

Many exogenous and endogenous factors influence cambial phenology, and to separate the effects of these controlling factors can be difficult. Here we present some hypotheses as to how the patterns of wood formation we observed may have been connected to both treatment differences as well as other causal agents. However, because environmental conditions such as temperature and soil moisture were not quantified by treatment for this study, our suggestions are based on findings in the literature and are areas requiring further study to be validated.

Overall, cambial growth in this study began somewhat later (around mid-May) than what has been reported previously for coastal Douglas-fir populations, typically mid-April (Emmingham 1977; Brix & Mitchell 1980; Li & Adams 1994). One possible explanation for this difference is that variations in methods among authors result in different interpretations. However, trees in the current study began producing latewood and ceased cambial growth within the range of dates reported for Douglas-fir in other studies (Kennedy 1961; Emmingham 1977; Brix & Mitchell 1980; Li & Adams 1994; Vargas-Hernandez & Adams 1994), so a systematic misinterpretation of the wound tissue formed by the pinning method is unlikely.

A more plausible explanation for the late onset of growth found in the current study is the unusually dry winter previous to the measurement period. Monthly precipitation at the study site from November 2000 to February 2001 was only about 40 to 50% of the 30-year average for each of those calendar months (Oregon Climate Service 2003). The

dry conditions could have delayed the onset of growth by forestalling the rehydration of the cambial zone in the spring (Savidge 2000). Also, it has been suggested that low rainfall contributes to an early transition to latewood (Voegli & Rinehart 1956 *cited in* Creber & Chaloner 1990; Vargas-Hernandez & Adams 1994). The dry winter could have accelerated the onset of summer water stress, thus producing earlier transitions to latewood production than would otherwise have occurred.

In this study, a shorter period of Douglas-fir radial growth was associated with a relatively high red alder component at the stand level. This suggests that red alder's presence in the stand altered the growing conditions for Douglas-fir such that cambial activity was decreased. Increasing soil temperature is generally thought to trigger the onset of cambial growth in the spring (Creber & Chaloner 1990). Though not measured in this study, it is possible that in the treatment with the highest red alder basal area, soils did not warm as rapidly as in other stands due to a dense alder overstory (T. Zhang *pers. comm.*). Moisture stress induced by alder competition could also be the causal agent for the effects we observed. As an exploitative species, red alder competes with conifers for soil moisture (Cole & Newton 1986), and depletes available soil moisture to a greater degree than does Douglas-fir (Chan *et al.* 2003). In the spring of 2001, red alder leaves developed prior to the onset of Douglas-fir cambial activity in all of the study plots (*pers. obs.*), so presumably soil moisture depletion was already underway, via flux in alder stems, prior to any onset of conifer growth. Therefore, it is possible that in the treatment with the highest red alder basal area, water availability to Douglas-fir during the growth initiation period was even further reduced due to uptake by the red alder trees, thereby causing a late onset (Savidge 2000) and early cessation (Baucker *et al.* 1998) of radial growth.

In all treatments, smaller Douglas-fir trees began growing later and ended growing earlier than larger trees. Studies of other conifer species (Kozlowski & Peterson 1962; Baucker *et al.* 1998) have shown that suppressed trees have a shorter season of cambial growth than dominant trees. It has been suggested that trees with larger, more vigorous crowns have higher auxin availability, increasing cambial production (Larson 1962), whereas the initiation of cambial growth in suppressed trees may be delayed due to auxin deficiency associated with smaller crowns (Kozlowski & Peterson 1962). Though the size of the tree crowns was not measured in this study, it is possible that auxin deficiency was responsible for the late onset of growth in the small-diameter trees. The mechanism driving the earlier cessation of growth among smaller trees is less clear. Water stress is associated with reduced radial growth rates (Horacek *et al.* 1999); one could speculate that small trees became more prone to water stress during late summer if their root systems were less extensive than those of larger trees.

The relationship between growth rate and wood density in Douglas-fir has not been conclusively defined, however in many of the reported cases, wood from slow-growing trees is denser due to increased latewood proportion. In slow-growing trees infected with Swiss needle cast, Johnson *et al.* (2003) found that latewood proportion increased, because earlywood width was lower than in healthy trees; infected trees retained few cohorts of needles over winter with which to produce earlywood in spring. Fabris (2000) also found that the increase in latewood proportion was a result of reduced earlywood

width in slow-growing (suppressed) trees. In the current study, we also found that latewood proportion increased as growth rate (ring width) decreased, when examining the entire sample population as a whole regardless of treatment. Cambial growth in some of the most suppressed trees did not begin until mid- to late June, which was several weeks after other trees had already undergone the transition to latewood production. With a wider variation in earlywood width compared to latewood width among trees, this study provides further evidence for the plasticity of earlywood production leading to variations in percent latewood in Douglas-fir.

Despite the connection between growth rate and percent latewood, we found no treatment effect on percent latewood; while quite variable among trees, there was little variation in percent latewood among treatments. This is likely due to the fact that several changes in cambial phenology were associated with treatments. When red alder basal area was high, cambial growth began later, latewood production began earlier, and cambial growth ceased earlier. The combination of these effects seemingly resulted in no overall change in latewood proportion. Thus from a utilization standpoint, it does not appear that the different management regimes studied here are of consequence in terms of percent latewood or wood density.

Finally, it is important to note the highly limited scope of inference for this study. First of all, it is restricted to the species mixtures and spacings described here, and at one site. Secondly, it applies only to trees that are 15 years old. As the stands develop, the relative dominance of red alder and Douglas-fir in the stands will change; if cambial activity is indeed linked to canopy position, then the patterns observed here will likely change as well. Also, patterns of cambial activity can change as trees mature; at stand age 15, juvenile wood effects may still be present. Finally, repeating this experiment in a different year could produce very different results, because 2001 was a relatively dry year historically, which could have decreased the duration of cambial activity in all trees.

In summary, we found that cambial phenology of Douglas-fir was influenced by the abundance of red alder in mixed stands. When red alder made up a high proportion of the total stand basal area, Douglas-fir cambial growth began late, ended early, and the transition to latewood occurred early. Also, earlywood, latewood and total ring width were low. However, the abundance of red alder did not affect percent latewood.

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