

AN ABSTRACT OF THE THESIS OF

Amy T. Grotta for the degree of Master of Science in Wood Science and Forest Science presented on July 18, 2002.

Title: Competitive Interactions in Young, Coastal Douglas-fir/Red Alder Mixtures: Implications for Wood Quality

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When Douglas-fir and red alder grow in mixture, interactions between the two species can be competitive, facilitative, or a combination of both over time. A number of factors have recently led to increased interest in managing these two species together for commercial production, and ongoing investigations are yielding important information about how interactions between the two species affect stand structure and productivity.

Many wood quality attributes are ultimately controlled by physiological processes, which in turn are affected by competition within a forest stand. This research addressed how stand structure in young, mixed red alder/Douglas-fir plantations was associated with variations in growth form and wood quality.

Branch attributes and cambial growth patterns in Douglas-fir and stem form attributes in red alder were analyzed as a function of species proportion and timing of establishment in 15-year-old mixed plantations in the Oregon coast range. When the two species were planted simultaneously, only mixed stands with low (10% of total stand density) proportions of red alder had low Douglas-fir mortality. In these stands, red alder stem form was poor, with a high incidence of multiple stems, low live crown bases, and considerable stem lean and sweep. Douglas-fir trees had a relatively short season of cambial growth and many were highly suppressed.

When red alder planting was delayed five years, Douglas-fir trees had a short cambial growth season when the proportion of red alder in the stand was high (75%). Douglas-fir crown base height was low when the proportion of red alder was high, but branch sizes were relatively consistent across species proportions. Percent latewood in Douglas-fir was not affected by species proportion. Red alder stem form was consistent across all levels of species proportion.

It is suggested that the differences observed are a result of differential juvenile growth rates of the two species and subsequent different levels of light availability to individual tree crowns through stand age 15. Simultaneous planting of the two species at these spacings results in either unacceptable Douglas-fir growth and mortality rates or poor red alder stem form, depending on species proportion. Delayed planting of red alder appears to improve red alder stem form and results in acceptable Douglas-fir wood quality attributes, if red alder proportion is 50% or less. Because these stands are not yet of harvestable size, further

monitoring is needed to assess how the patterns of growth and wood quality described would affect eventual product recovery.

Competitive Interactions in Young, Coastal Douglas-fir/Red Alder
Mixtures: Implications for Wood Quality

by
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COMPETITIVE INTERACTIONS IN YOUNG, COASTAL DOUGLAS-FIR/RED ALDER MIXTURES: IMPLICATIONS FOR WOOD QUALITY

CHAPTER 1 : INTRODUCTION

INTERACTIONS BETWEEN DOUGLAS-FIR AND RED ALDER

Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and red alder (*Alnus rubra* [Bong.]) are both early successional species that commonly regenerate on the same sites in the Pacific Northwest. Management of the resulting mixed conifer/hardwood stands has generated much interest over the last several decades, especially because red alder has expanded into cutover areas that it historically did not occupy (Puettmann and Hibbs 1996). Potential advantages of these species mixtures over monospecific stands include increased nitrogen availability (Tarrant 1961), greater nutrient cycling, greater abundance and diversity of wildlife, aesthetic appeal (Puettmann and Hibbs 1996), and, depending on site characteristics and management decisions, increased overall productivity (Tarrant 1961, Miller and Murray 1978, Binkley 1983).

Interactions between red alder and Douglas-fir can be competitive, facilitative, or a combination of both over time (Tarrant 1961, Cole and Newton 1986, 1987, Shainsky and Radosevich 1991, 1992). On nitrogen-limited sites, red alder appears to enhance conifer growth through addition of nitrogen to the forest system (Tarrant 1961, Miller and Murray 1978), and the interaction is largely facilitative. However, on fertile sites, particularly where nitrogen is not limited,

competition for light and soil moisture drives the development of these mixed stands (Shainsky and Radosevich 1992). On these sites, red alder has a much higher initial growth rate than Douglas-fir, mainly due to its superior ability to capture light (Chan et al. submitted). On the other hand, Douglas-fir exhibits a more conservative strategy, yet is better able to withstand drought limitation (Shainsky and Radosevich 1991). Because these two species differ in their efficiency at capturing and utilizing limited resources, the relative density and proportion of each species is an important factor in the growth of the other. For instance, with a high proportion of red alder in a stand, Douglas-fir light capture is reduced due to shading (Newton and Cole 1994); with a high proportion of Douglas-fir, red alder water stress increases (Shainsky and Radosevich 1992).

Several long-term studies have examined or modeled the effect of interspecific interference between red alder and Douglas-fir on stand structure, growth and yield (Miller and Murray 1978, Cole and Newton 1986, Comeau and Sachs 1992, Miller et al. 1999, Radosevich et al. in progress). From these studies, it is apparent that the density of each species in early stand development has lasting impacts on stand structure. If the conifers are able to persist in the red alder understory, they may eventually succeed the shorter-lived hardwoods, but conifer succession is dependent on the limitation of red alder competition (Newton et al. 1968). Delayed establishment of red alder has been proposed as a means of counteracting its suppressive effect in early stand development and enhancing Douglas-fir competitive ability (Newton et al. 1968, Comeau and Sachs 1992,

Newton and Cole 1994). The long-term experimental stands in which the study described here was carried out were designed in part to test this hypothesis (Radosevich et al. in progress). Data collection from this experiment, currently in its 17th year, is ongoing.

THE CONCEPT OF WOOD QUALITY AND ITS BIOLOGICAL UNDERPINNINGS

Worldwide, wood quality in harvested logs is changing, as a greater proportion of the timber supply is coming from fast-growing plantations. Therefore, it is becoming more important to predict how plantation management affects wood quality. Wood quality is defined by the end user, but common indicators include knot characteristics, stem form, density, and fiber characteristics. The physiological processes of tree growth shape all of these features. In turn, the rates of these physiological processes are affected by resource availability. For instance, light availability affects photosynthesis within the crown, which controls the rate of crown recession, which in turn controls knot size, distribution, and quality. As another example, wood density is partially a function of earlywood/latewood ratio, which is affected by a host of tree growth processes (Larson 1969, Zobel and van Buijtenen 1989).

Many have observed that wood quality has deteriorated with the increase of plantation-grown wood (Zhang 1997). At the same time, plantation forests are under pressure not only to generate high volumes of fiber, but also to adhere to socially acceptable standards of biodiversity and environmental health. For this

reason, innovative forest management techniques that result in both improved wood quality and increased biodiversity while also maintaining high yield are needed.

Mixed-species forests are known to improve biodiversity, and have the potential to attain production levels at or above those of monospecific forests, but the impacts of interspecific management on wood quality are still largely unstudied.

This study merges two fields of research: the study of interspecific competition in conifer/hardwood mixtures with the analysis of wood quality and its controls. Chapter 2 discusses knots, a key wood quality feature of Douglas-fir structural products, and their relationship to crown recession and resource availability as a function of stand structure. Chapter 3 analyzes red alder stem form and size, factors that affect product value, in relation to its own planting density and spatial relationships, and the planting density of Douglas-fir. Finally, in Chapter 4 patterns of cambial growth in Douglas-fir are investigated in relation to resource availability, which differs with stand structure and the influence of neighboring trees. It is hoped that this work will add a biological dimension to the prediction of wood quality attributes and lend a practical dimension to the understanding of competition and stand structure in mixed forests. The information presented here should also help forest managers to make more informed choices about the management of red alder and Douglas-fir mixtures.

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CHAPTER 2 : INFLUENCE OF INTRASPECIFIC VS. INTERSPECIFIC COMPETITION FROM RED ALDER ON DOUGLAS-FIR BRANCH SIZE, FREQUENCY AND VITALITY

ABSTRACT

The relationships among branch characteristics, stand structure and light availability were explored for the basal 5 m bole of 15-year-old Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) growing in mixed Douglas-fir/red alder (*Alnus rubra* [Bong.]) plantations. Treatments included a range of species proportions, and red alder was either planted simultaneously with Douglas-fir or after five years. Both replacement effects and additive effects of red alder competition were considered. The timing of red alder planting resulted in few differences in branch characteristics that could not be attributed to differences in tree size. When red alder planting was delayed, height to the base of the Douglas-fir live crown decreased with increasing red alder proportion, resulting in a larger number of live branches on the basal 5 m stem as stands approached a red alder monoculture. However, neither the total number of branches nor the mean diameter of the largest four branches per tree was affected by species proportion. The additive effect of tree density differed with species; whereas increasing Douglas-fir density increased the height to the base of the Douglas-fir live crown, there was no such effect as a result of the addition of red alder. It is suggested that differences in branch characteristics are a function of differences in light transmittance. Light transmittance to the lower portion of the Douglas-fir crown was higher with a

higher proportion of red alder in the stand, which would reduce crown recession rates. Douglas-fir lumber quality may be affected by the changes in knot characteristics associated with these different patterns of crown recession.

INTRODUCTION

Knots are one of the most important features determining softwood lumber grade; while knot size is of prime importance, knot frequency and tightness are also considered in determining lumber value. For example, only tight knots less than two inches in diameter are allowable for No. 2 or better dimension Douglas-fir lumber; loose knots are only allowed if they are much smaller (WWPA 1998). Knot size and frequency is related directly to branch size and number; thus, silvicultural practices that affect the number, size, and longevity of branches can influence the quality of lumber eventually recovered. Crown dynamics of the tree dictate how long branches live, and subsequently their eventual size. Consequently, in order to optimize wood quality, it is important to understand crown growth and recession patterns and how these patterns are affected by factors such as tree spacing and thinning.

There has been substantial research investigating silvicultural influences on branch characteristics. It is well known that branch retention is inversely related to stand density (Grah 1961, Carter et al. 1986, Ballard and Long 1988). In widely-spaced stands, tree crowns recede slowly, resulting in longer-lived, larger branches. Knots created from such branches exist over a large proportion of the bole radius, a

result of two mechanisms: longer-lived live branches, and branch stubs that take longer to occlude because they are larger in diameter.

Individual branches are thought to be autonomous with respect to carbohydrates (Sprugel et al. 1991); that is, branches that photosynthesize at low rates (i.e. low carbon producers) generally do not import carbon from other sources within the tree in order to meet the respiratory demands of living tissue. Therefore, when shading from upper branches causes the photosynthetic production of a branch to drop below its maintenance needs, the branch dies. Thus recession of the live crown is related directly to light availability in the lower canopy.

Light levels and quality differ below the canopies of different tree species. Also, the vertical pattern of light transmission through a canopy is related to crown morphology and leaf area distribution (Sinclair and Knoerr 1982, Ellsworth and Reich 1993, Parker et al. 2002), both of which differ among tree species and stand attributes. Because of the different canopy structures of deciduous hardwoods and conifers, the quality, quantity and vertical pattern of light transmittance through the two types of canopies differ (Borghetti and Vendramin 1986, Ellsworth and Reich 1993, Koike et al. 2001, Parker et al. 2002). Moreover, light transmittance patterns through deciduous canopies change seasonally with the expansion and shedding of leaves. These factors have important implications when considering light availability to individual trees in mixed conifer/hardwood stands.

While most research on the influences of silvicultural practices on branching patterns has focused on monocultures, less is known about the

relationships between interspecific competition and branch characteristics. Trees growing in species mixtures may exhibit different crown growth and recession patterns than trees in monocultures, depending on the variability of resource capture among species in the mixture. For example, a shade tolerant tropical tree, *Hyeronima alchorneiodes*, developed a larger crown but grew less in height when grown in a three-species mixture than when grown in monoculture (Menalled et al. 1998); it was hypothesized that because the other two species in the mixture had a lower leaf area index (LAI) than *Hyeronima*, sufficient light was transmitted through the canopy of the other species to allow *Hyeronima* trees in the mixture to develop a large crown.

In the Pacific Northwest, red alder (*Alnus rubra* [Bong.]) and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) often co-exist on the same site, because they both commonly regenerate in disturbed areas. Leaf area index (LAI) in closed Douglas-fir stands is higher than in closed stands of many deciduous hardwoods, including red alder (Giordano 1990, Vose et al. 1995, Parker et al. 2002): where LAI in a closed red alder stand has been estimated at 2.5 to 3.0 (DeBell and Giordano 1994), the LAI under a mature conifer canopy can be 5.0 or greater (Parker et al. 2002). Given the differential capacity of these two species to capture and absorb light, it is possible that the presence of red alder alters the quantity and quality of light to co-occurring Douglas-fir, which may affect Douglas-fir crown development. The purpose of this study was to characterize branch characteristics of young Douglas-fir trees as a function of intraspecific competition vs.

interspecific competition from red alder. We hypothesized 1) that in a mixture of Douglas-fir and red alder, the amount of light available to a Douglas-fir tree growing amidst taller red alder is related to the species proportion in the mixture if total stand density is held constant; 2) that Douglas-fir crown recession rates and other related branch characteristics are related to species proportion; and 3) that an increase in total stand density would affect branch characteristics differently as a function of which species was added. Such information would be useful in predicting relative knot sizes and frequencies in future sawlogs from similarly managed natural stands or plantations.

MATERIALS AND METHODS

Site Description

The study site is in the Oregon Coast Range 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. The site was originally 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 and Binkley 1992).

The study was conducted on experimental plots established in 1985 as part of a long-term study of Douglas-fir/red alder interactions (D. Hibbs and S.

Radosevich, principal investigators). The plots are a randomized block replacement series of Douglas-fir and red alder (Radosevich et al. in progress). In 1985, the site was clearcut and the following year trees were planted at a fixed spacing of 3 m x 3 m (1109 trees per hectare). Combinations of the two species ranged from 100% Douglas-fir to 100% red alder, with intermediate combinations of 90:10, 75:25, 50:50, and 25:75 (Table 2.1). Each combination is represented by two series: one in which seedlings of both species were planted in year 1 (1986), and one in which red alder planting was delayed five years (1991). Another treatment consisted of a 50:50 mixture with the red alder removed after five years (1991). Finally, additional monocultures of each species were established at 4.2 m x 4.2 m spacing (555 trees per hectare), to represent the same within-species density found in the 50:50 mixture, with the absence of the other species.

Each treatment was replicated in three blocks, for a total of 45 plots. Each plot consisted of 9 trees in 9 rows for a total of 81 trees, except in treatments 14 and 15, where only 41 trees were planted due to the wider spacing. The inner 25 trees within each plot became the permanent measurement trees, while the outer two rows serve as a buffer between treatments. Trees that died were replaced for the first three growing seasons. Volunteer trees and shrubs were hand-removed until year five. Trees were 15 years old (10 if they were red alder planted in the delayed treatments) at the time of this study.

Table 2.1 Replacement series treatment descriptions. An asterisk (*) after the treatment number indicates that the treatment was used in the current study.

Treatment	Douglas-fir percent	Red alder percent	Red alder planting ⁺	Spacing (m)	Red alder removed
1*	100	0	Immediate	3 x 3	--
2*	90	10	Immediate	3 x 3	No
3*	90	10	Delayed	3 x 3	No
4	75	25	Immediate	3 x 3	No
5*	75	25	Delayed	3 x 3	No
6	50	50	Immediate	3 x 3	No
7*	50	50	Delayed	3 x 3	No
8*	50	50	Immediate	3 x 3	After 5 yrs
9	50	50	Immediate	3 x 3	After 10 yrs
10	25	75	Immediate	3 x 3	No
11*	25	75	Delayed	3 x 3	No
12*	0	100	Immediate	3 x 3	No
13	0	100	Delayed	3 x 3	No
14*	100	0	--	4.2 x 4.2	--
15	0	100	Immediate	4.2 x 4.2	No

⁺Red alder planting date: immediate = year 1 (1986); delayed = year 6 (1991)

Eight treatments within the replacement series were included in this study (Table 2.1). In each plot, five Douglas-fir trees were selected randomly from the inner 25 trees of the plot. Forked trees and trees with missing neighbors were excluded. With three replicate plots per treatment, a total of 24 plots and 120 trees were studied.

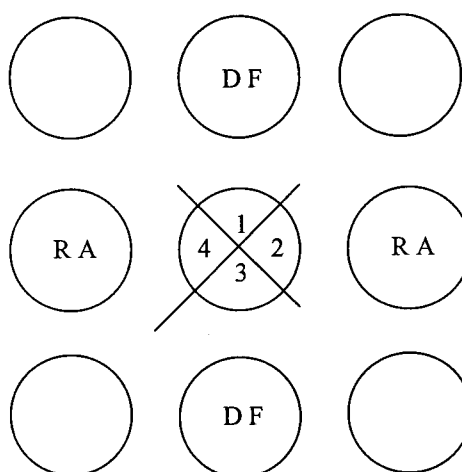
Branch Measurement

All measurements were taken in June or July 2001. Sample trees were divided into vertical quadrants, with each quadrant directly facing the nearest neighboring tree (Figure 2.1). The species of neighbor tree, red alder or Douglas-fir, was recorded for each quadrant. Branches within each quadrant were counted to

a height of 5.2 m (the length of the first 16 ft log with a 1 ft stump allowance). For each branch we then recorded its quadrant, whether it was alive or dead, and its size class: large (outside-bark diameter just distal to the branch collar > 4 cm), medium (diameter between 2 and 4 cm), or small (diameter between 0.5 and 2 cm).

Branches smaller than 0.5 cm in diameter were not counted. A branch was categorized as “alive” if any current-year needles were present; otherwise, the branch was categorized as “dead”, even if green needles from previous years persisted. Previous research suggests that branches in the lower crown may live for many years without increasing in diameter before mortality occurs (Robbins 2000). Thus for this study, dead branches were all those that had presumably reached their maximum size.

Figure 2.1. An example of the location of quadrants (1-4) on the study tree (center) with respect to its nearest neighbors. DF = Douglas-fir; RA = red alder.



Additionally, the diameter of the largest branch in each quadrant was determined with a digital caliper. Two perpendicular measurements were taken just distal to the branch collar and were averaged. The mean of the diameters of the four largest branches (one per quadrant) per tree is a common branch size index (Fahey et al. 1991, Maguire et al. 1991) and was used for this study. Finally, the height to the lowest live branch in each quadrant was measured with a height pole, and diameter at breast height (DBH) was measured.

Light Measurement

Light penetration through the upper canopy was measured on a clear day in July 2001. A quantum sensor (Model LI-190SA, Li-Cor, Lincoln, NE) was affixed to the top of a telescoping pole, which was positioned 1 m from the uphill side of the base of each of six randomly selected Douglas-fir trees in each plot. The sensor was attached to a weighted gimbal so that it remained level. The pole was raised to three heights, 3.9 m, 5.1 m and 6.2 m. These heights were arbitrarily chosen but were situated approximately in the lower, middle, and upper-middle sections of the Douglas-fir crowns, respectively. At each height, the average of five consecutive sensor readings taken at 1-second intervals was recorded. Open-sky readings were simultaneously recorded in a nearby field; these readings were recorded once per minute and consisted of 12 readings taken at 5-second intervals. Each canopy measurement was then converted to a fractional transmittance value, consisting of the ratio of the canopy reading to the open-sky reading taken at the corresponding

time. Thus, a measure of relative photosynthetically active radiation (PAR) was obtained for the three heights for each tree crown. This process was also repeated in the 100% red alder treatment to quantify light in a pure red alder stand; light measurements were not taken in the treatment where red alder was removed after five years.

Data Analysis

The diameter of the largest branch and height to the lowest live branch were determined for each tree quadrant. Total number of branches, number of branches within each size class, average diameter of the largest branch in each of the four quadrants (BD₄), percentage of branches that were alive, and average height to the lowest live branch were then determined for each sample tree. Data for each tree were averaged by plot to result in plot means for each variable. Multiple linear regression was used to determine whether each of these variables was correlated with the proportion of Douglas-fir in the stands where alder planting was delayed; that is, in treatments 1, 3, 5, 7, and 11 (Table 2.1). Percent Douglas-fir (0-100) of total tree density was treated as a continuous variable in these cases. Initial exploration revealed that most branch size and frequency variables correlated strongly with DBH; thus, DBH (mean of all sample trees within a plot) was initially included as an covariate in all models, and subsequently dropped from the analysis if found not to be significant. Initial regression models took the form:

$$[\text{response variable}] = \beta_0 + \beta_1[\text{percent Douglas-fir}] + \beta_2[\text{DBH}] + \beta_3[\text{block}]$$

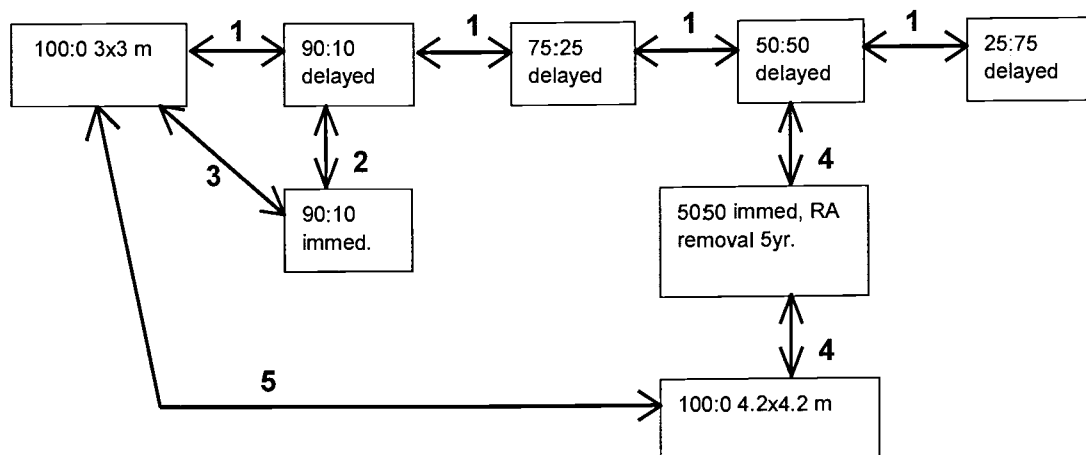
where β_1 and β_2 are regression coefficients for the continuous effects of species proportion and tree size, and β_3 is a coefficient for the random block effect.

Other comparisons of interest (Figure 2.2) were evaluated with analysis of covariance (ANCOVA). These comparisons included: treatments 2 and 3, to investigate the effect of alder planting time; treatments 1 and 3, to evaluate the effect of having immediately-planted alder in the stand; treatments 7, 8 and 14, to compare the effect of the presence of alder in the stands where total relative density of Douglas-fir is 50%; and treatments 1 and 14, to compare the effect of spacing within a monoculture. Block-treatment interactions were tested and rejected in all models describing branch characteristics. Final ANCOVA models took the form:

$$[\text{response variable}] = \beta[\text{DBH}] + \gamma[\text{treatment}] + \lambda[\text{block}] + \varepsilon$$

where β is the continuous effect of DBH, γ is the fixed effect of the level of treatment (combination of species proportion and timing of red alder planting), λ is the random effect of block, and ε is the random variation among plots. The Fisher procedure for multiple planned comparisons was used to correct confidence interval widths for estimated effects.

Figure 2.2. Comparisons of interest in the study of Douglas-fir branch characteristics. Proportions are % Douglas-fir:% red alder. Treatments linked by arrows with the same number were evaluated as a group.



The effect of species proportion in treatments on light attenuation was evaluated by fitting an exponential regression of fractional transmittance as a function of percent Douglas-fir and canopy height. The 100% immediately-planted red alder treatment and the close-spaced, 100% Douglas-fir treatment were included for comparison along with all treatments with delayed red alder planting. The model equation was:

$$\ln(FS) = \beta_0 + \beta_1 * DFP + \beta_2 * L + \beta_3 * M + \beta_4 * DFP * L + \beta_5 * DFP * M$$

where FS = fractional PAR transmittance, DFP = percent Douglas-fir of total stand density, L = indicator variable for measurements at 3.9 m (1 if at 3.9 m, 0 if otherwise), and M = indicator variable for measurements at 5.1 m (1 if at 5.1 m, 0 if otherwise).

All statistical analyses were performed with SAS 8.0 (SAS Institute, Cary, NC) or S-Plus 2000 (MathSoft Inc., Cambridge, MA) software packages.

RESULTS

Branch Frequency

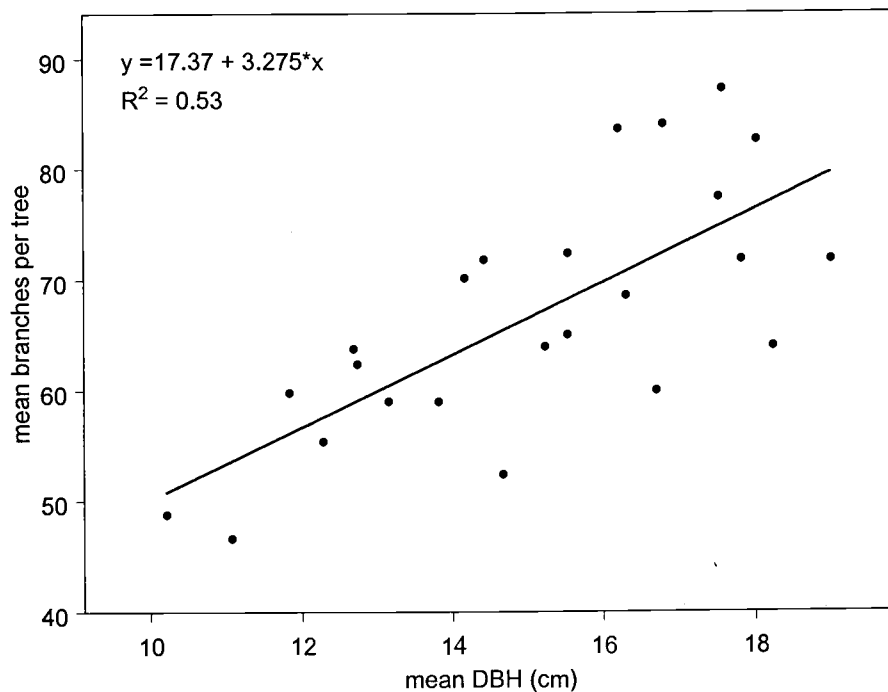
The total number of branches per tree (basal 16 ft stem length) ranged from 29 to 104 (5.9 to 21.3 branches/m of stem), with an overall mean across all experimental units of 66.7 (13.7 branches/m). Treatment means ranged from 61 to 73 branches per tree, and 10.6 to 15.0 branches/m (Table 2.2). Branch frequency was correlated with DBH ($P < 0.001$, simple linear regression; Figure 2.3).

Among the treatments with delayed alder planting, the total number of branches was not correlated with Douglas-fir proportion after accounting for DBH ($P = 0.84$, data not shown). No other significant contrasts were detected.

Table 2.2. Branch characteristics of Douglas-fir trees in Douglas-fir/red alder mixtures at two spacings and with either simultaneous planting of both species ("immediate") or a 5-year delay in alder planting ("delayed"). Trees were planted at 3 x 3 m spacing unless noted otherwise. Total number of branches, branches/m, BD₄, HLC, percent live branches, DBH (mean \pm SE, n = 15 trees per treatment).

Treatment DF:RA	Branches (no.)	Branches/m	BD ₄ (cm)	HLC (m)	% live branches	DBH (cm)
100:0 3x3 m	70.7 (4.2)	14.5 (0.9)	2.6 (0.1)	3.44 (0.27)	33.2 (4.6)	16.6 (0.7)
100:0 4.2x4.2 m	71.7 (3.5)	14.7 (0.7)	3.1 (0.1)	1.87 (0.12)	73.0 (2.5)	17.5 (0.8)
90:10 immediate	51.7 (3.1)	10.6 (0.6)	2.1 (0.1)	3.26 (0.27)	45.0 (6.5)	11.0 (1.0)
90:10 delayed	72.6 (3.9)	14.9 (0.8)	2.5 (0.1)	3.16 (0.19)	40.5 (4.8)	14.5 (0.7)
75:25 delayed	61.1 (3.5)	12.5 (0.7)	2.6 (0.2)	3.34 (0.30)	33.5 (5.1)	15.2 (0.9)
50:50 delayed	73.4 (4.3)	15.0 (0.9)	2.8 (0.1)	2.28 (0.16)	54.7 (3.6)	15.0 (0.8)
25:75 delayed	63.2 (3.5)	13.0 (0.7)	2.5 (0.1)	2.59 (0.29)	58.8 (6.2)	13.9 (0.6)
50:50 removal	69.4 (4.2)	14.2 (0.9)	3.3 (0.3)	1.65 (0.10)	79.8 (2.8)	16.8 (0.9)
Overall mean	66.7 (1.5)	13.7 (0.3)	2.7 (0.1)	2.70 (0.10)	52.3 (2.2)	15.1 (0.3)

Figure 2.3. Number of branches per tree as a function of DBH. Plotted points are plot means.



Branch Size

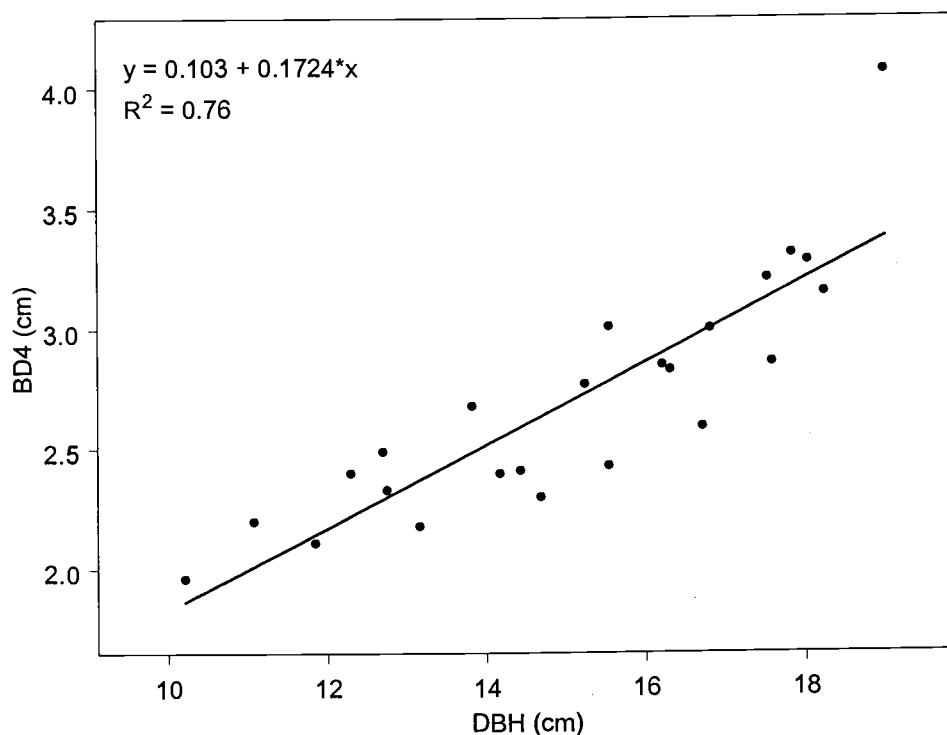
Across all treatments, trees had a mean of 44.9 small branches ($SE = 1.2$), and 21.7 medium branches ($SE = 1.5$). With the exception of one individual, no tree had more than three large branches and the majority had none.

BD_4 (average of the diameters of the largest branch in each quadrant) was strongly correlated with DBH ($r^2 = 0.76$, $P < 0.001$, simple linear regression; Figure 2.4). BD_4 ranged from 1.4 cm to 7.3 cm, with an overall mean of 2.7 cm (Table 2.2). The 50:50 mixture with the red alder removed after five years had the highest mean BD_4 (3.3 cm) of all treatments; however, one tree with unusually large

branches influenced this mean. Without this outlier, the mean BD_4 for this treatment was similar to that of the 100% Douglas-fir treatment at wide spacing (3.1 cm). Across all treatments, the 90:10 mixture with immediately-planted red alder had the lowest mean BD_4 (2.1 cm).

BD_4 was not associated with Douglas-fir proportion in the plots where alder planting was delayed ($P = 0.14$, data not shown). No significant differences in BD_4 were associated with timing of red alder establishment, tree density in the two pure Douglas-fir treatments, or among the treatments with Douglas-fir at 4.2 x 4.2 m spacing.

Figure 2.4. Mean diameter of the largest branch in four quadrants (BD_4) as a function of DBH. Plotted points are plot means.



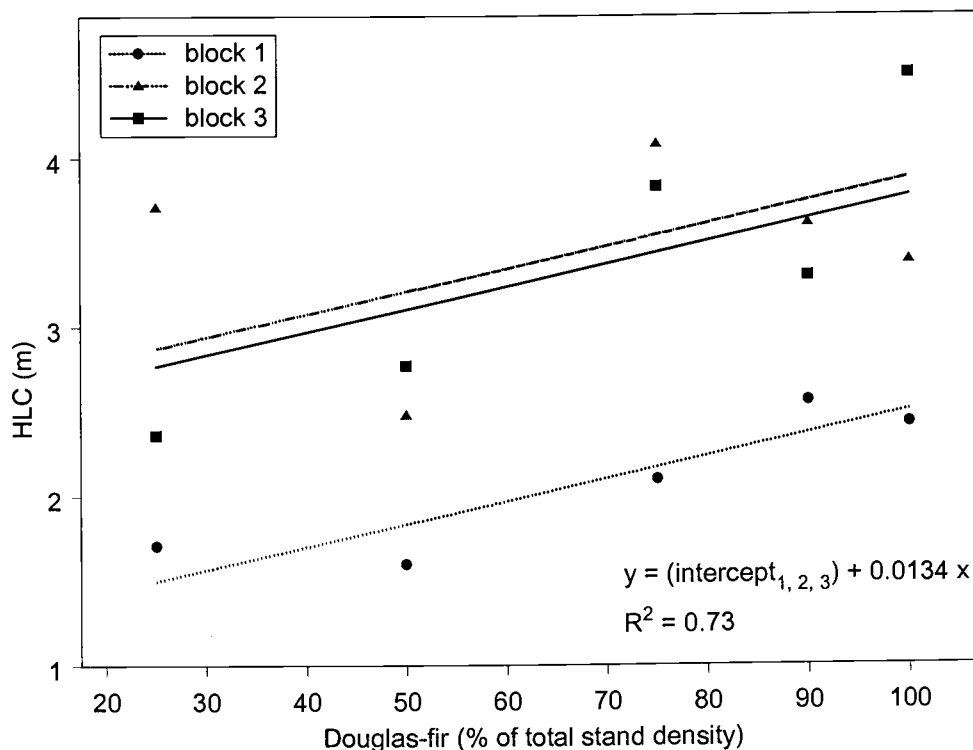
Branch Vitality

Height to the base of the live crown (HLC) was calculated as the average of the heights to the lowest live branch measured in each of the four quadrants. Across all trees, HLC ranged from 0.8 m to 5.5 m, with a mean of 2.7 m (SE = 0.1 m). Treatment means ranged from 1.7 to 3.4 m (Table 2.2). The block effect was significant in explaining HLC (Figure 2.5), presumably due to differences in slope among blocks. Mean plot DBH did not affect mean plot HLC ($P = 0.20$); thus the DBH variable was dropped from models describing HLC.

HLC increased with Douglas-fir proportion in treatments where red alder planting was delayed ($F_{3,11} = 9.7$, $P = 0.02$, Figure 2.5). A 10% increase in the proportion of Douglas-fir was associated with an 0.1 m increase in the height to the base of the live crown (95% CI = 0.03 to 0.2 m).

As expected, HLC increased with stand density between the two Douglas-fir monoculture treatments (Figure 2.6). The mean HLC of the treatment planted at 3 x 3 m was about 1.6 m higher than that of the treatment planted at 4.2 x 4.2 m ($P = 0.001$, 95% CI = 0.7 to 2.4 m). However, there was no statistically significant difference in HLC between the 50:50 mixture and the pure, widely-spaced Douglas-fir treatment, indicating that there was no additive effect of red alder density on Douglas-fir HLC (Figure 2.6). Also, no difference was detected in HLC as a function of timing of red alder planting, or between the treatment with 10% immediately-planted alder and the closely-spaced Douglas-fir monoculture.

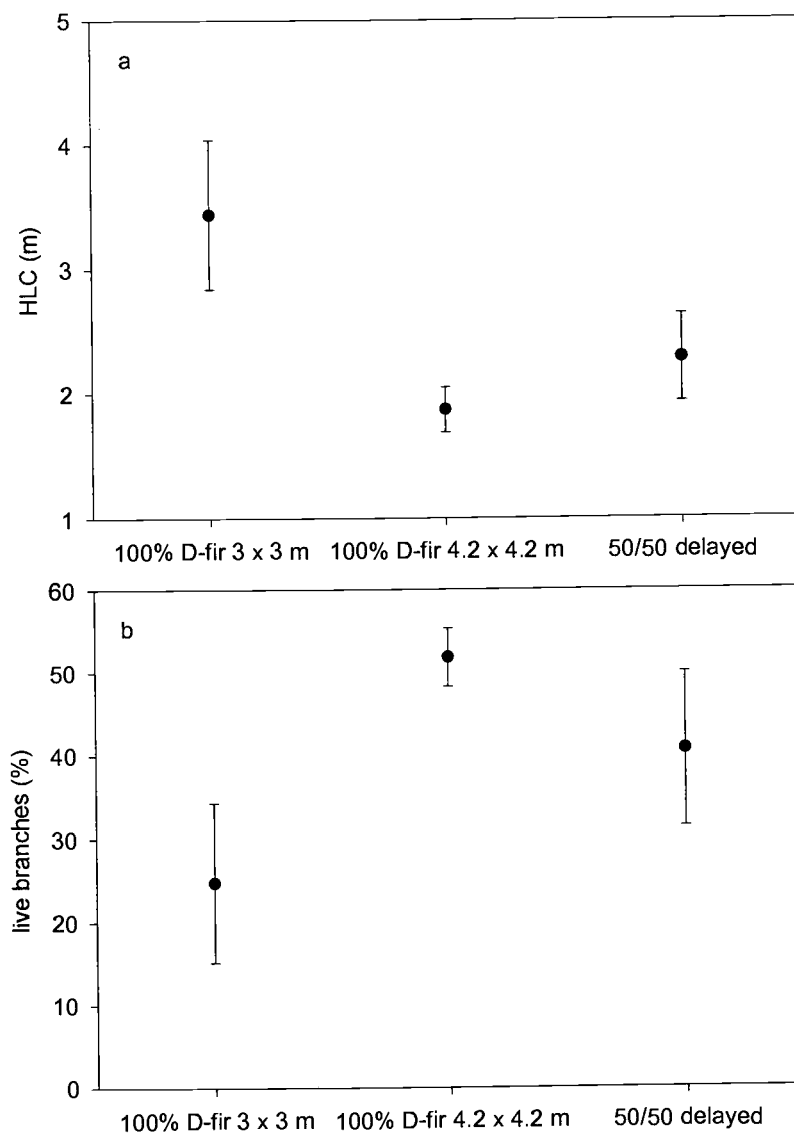
Figure 2.5. Observed values and fitted regression lines for HLC as a function of Douglas-fir proportion in stands where alder planting was delayed. Lines and symbols represent different blocks; plotted points are plot means.



Across all trees, the percentage of live branches on the lowest 5.2 m of the bole ranged from 0 to 98.8%, with an overall mean of 52.3%. Treatment means ranged from 33.2 to 79.8% (Table 2.2).

The percentage of branches that were alive was negatively correlated with proportion of Douglas-fir among the treatments where alder planting was delayed ($r^2 = 0.69$, $F_{3, 11} = 8.31$, $P < 0.05$). A 10% decrease in proportion of Douglas-fir was associated with a 2.1% increase in the number of branches that were alive (95% CI = 0.1 to 4.1 %). Timing of red alder planting did not affect the percent live branches in the two plots with 90:10 proportions of the two species. Also, there was

Figure 2.6. (a) HLC and (b) percent live branches for selected treatments (mean of three plots \pm SE).



no difference in the percent live branches among the treatments with the same Douglas-fir density (4.2 x 4.2 m spacing) but with differing alder treatments, indicating that there was no additive effect of red alder density (Figure 2.6). However, the additive effect of Douglas-fir density was to decrease the proportion

of live branches, since trees in the widely-spaced pure Douglas-fir stand had 27% more live branches than trees in the closely-spaced Douglas-fir stand (95% CI = 7 to 47%, Figure 2.6).

Canopy Light Transmittance

At all three measured heights, the distribution of fractional PAR transmittance values was highly skewed, with most values below 0.05, but as height increased the frequency of higher transmittance values increased slightly. Due to the non-normal data distribution, transmittance values were log-transformed for statistical analysis. At 3.9 m, the highest mean light transmittance (0.065) was found in the 100% red alder treatment, whereas the lowest mean transmittance (0.005) was in the 90% Douglas-fir treatment with delayed alder planting. At 5.1 and 6.2 m, the highest mean transmittance values were found in the widely-spaced, Douglas-fir monoculture (0.274 and 0.402, respectively). The 90% Douglas-fir treatment with immediately-planted alder had the lowest mean transmittance (0.001) at 5.1 m, while at 6.2 m the lowest mean value (0.053) was in the 25% Douglas-fir treatment with delayed alder planting (Table 2.3, Figures 2.7, 2.8).

Douglas-fir proportion significantly affected light transmittance at all heights, but the trend differed with height ($P = 0.001$, $F_{7, 46} = 10.6$, Table 2.4). At 3.9 m and 5.1 m, fractional PAR transmittance decreased with increasing Douglas-fir proportion. However, at 6.2 m, transmittance increased with increasing Douglas-fir proportion (Figures 2.7, 2.8).

Table 2.3. Fractional PAR transmittance (in %) at three canopy heights (Mean \pm SE). Species proportions are Douglas-fir:red alder.

Treatment	3.9 m		5.1 m		6.2 m	
100:0 3x3 m	0.84	(0.6)	4.92	(1.4)	20.32	(7.1)
90:10 delayed	0.54	(0.1)	8.02	(5.3)	22.20	(6.8)
75:25 delayed	5.01	(4.4)	6.18	(5.3)	11.10	(4.7)
50:50 delayed	1.95	(0.7)	6.11	(4.8)	16.92	(9.2)
25:75 delayed	0.58	(0.1)	2.23	(0.6)	5.32	(3.2)
0:100 3x3 m	6.50	(1.7)	6.44	(1.8)	9.14	(3.3)
100:0 4.2x4.2 m	3.87	(1.3)	27.38	(3.6)	40.19	(4.6)
90:10 immediate	2.02	(0.8)	1.14	(0.3)	6.21	(2.1)

Table 2.4. Regression coefficients for model describing light penetration to different heights in red alder/Douglas-fir canopies. *DFP* = Douglas-fir proportion; *L* = indicator for 3.9 m (1 if measurement taken at 3.9 m, 0 if otherwise); *M* = indicator for 5.1 m (1 if measurement taken at 5.1 m, 0 if otherwise). Response variable = $\ln(\text{fractional transmittance})$.

Effect	Coefficient	SE	P
Intercept	0.921	0.338	0.009
<i>DFP</i>	0.008	0.005	0.12
<i>L</i>	-0.232	0.478	0.63
<i>M</i>	-0.119	0.478	0.80
<i>DFP*L</i>	-0.027	0.007	0.001
<i>DFP*M</i>	-0.014	0.007	0.06

Figure 2.7. Observed values (open symbols) and fitted regression lines for fractional PAR transmittance at three heights as a function of Douglas-fir proportion where red alder planting was delayed. (100% red alder plot was planted immediately.)

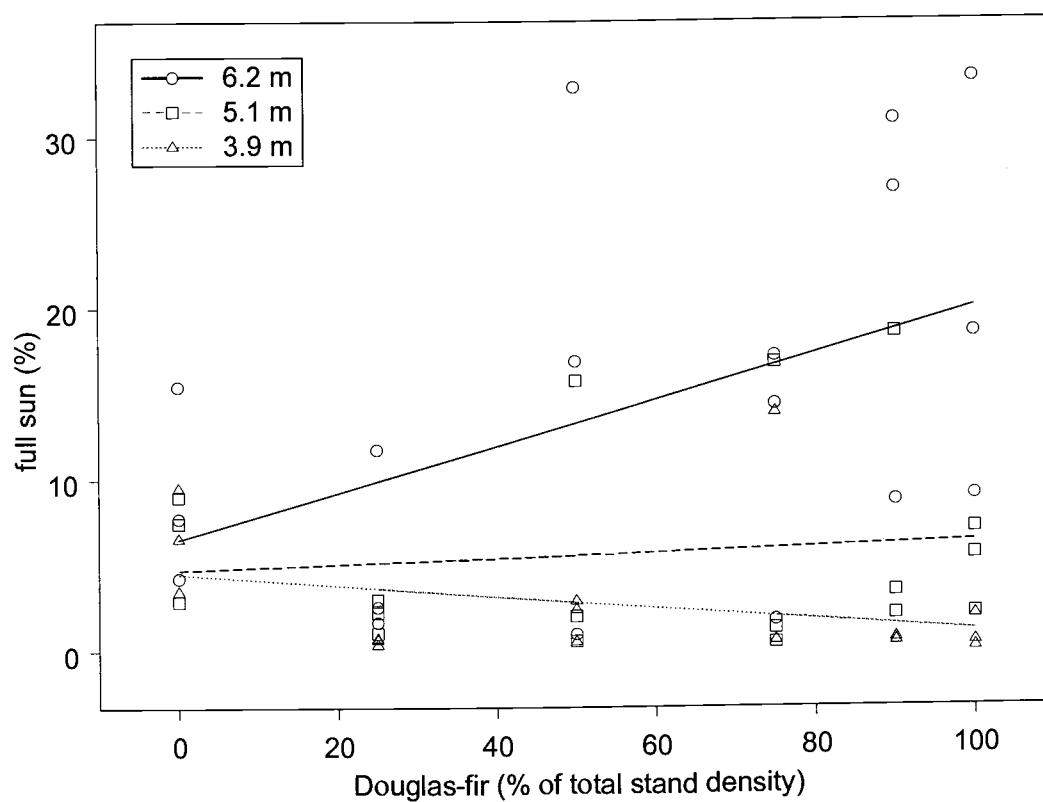
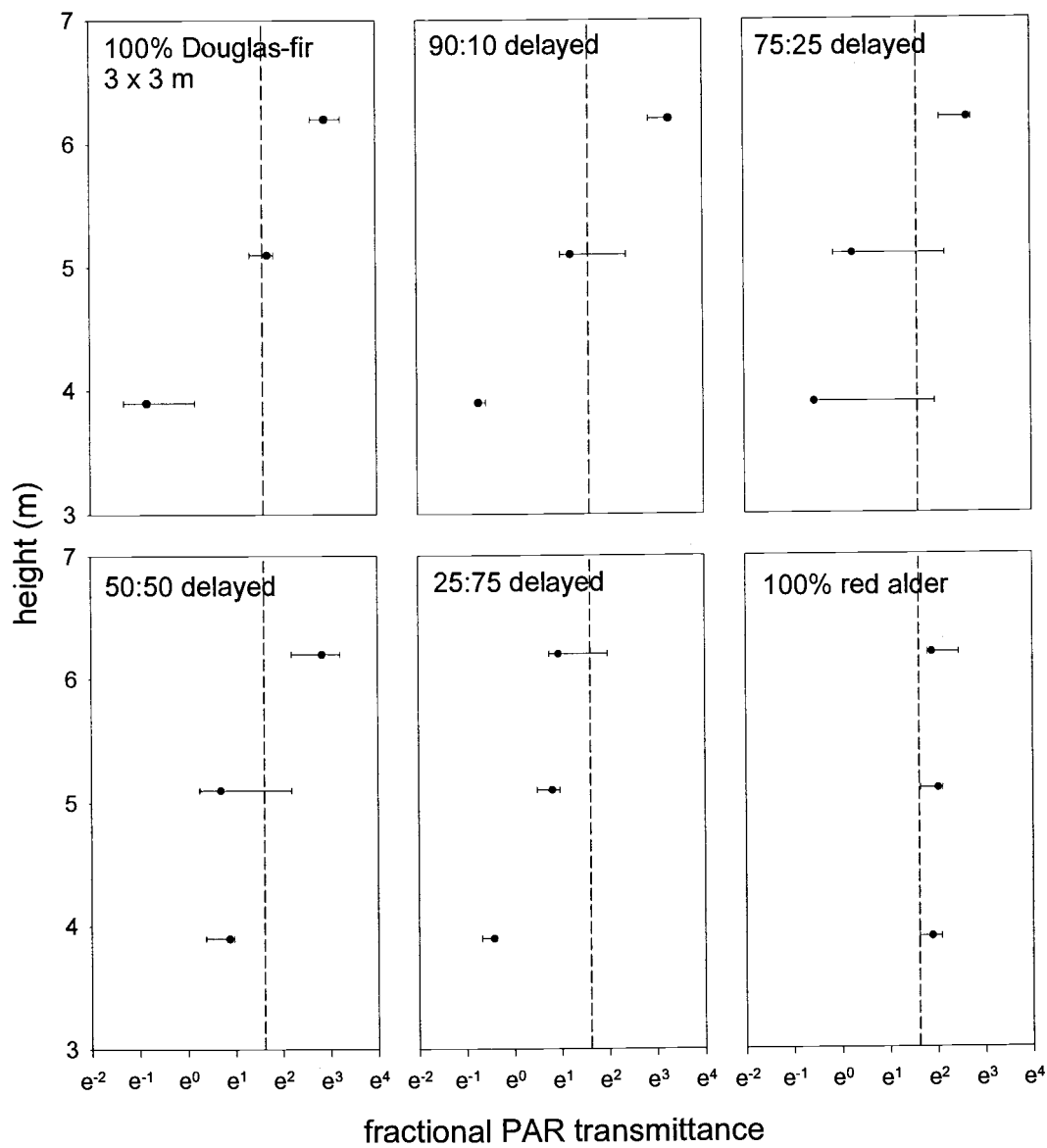


Figure 2.8. Vertical profile of PAR transmittance through the canopies of selected treatments. Dots are median values and horizontal bars represent 1st and 3rd quartiles. Vertical reference line is at 5% fractional PAR.



DISCUSSION

Branch Frequency

Variation in the number of branches per tree was related mainly to tree diameter, whereas responses of this variable to treatments were insignificant. Previous studies on young Douglas-fir in monoculture have found no relationship between branch count and stand density (Briggs and Turnblom 1999), a finding supported by the lack of difference detected between the two monoculture treatments in this study. We found that stand density influenced stem diameter and thus the number of branches per tree, however for a given tree size, the number of branches was constant across stand densities.

A number of other factors aside from stand density and/or competition can also influence branch frequency. The number of branches on a particular stem length can be attributed partially to the number of branch whorls on that section of stem, which in turn is directly related to a tree's annual height growth. Trees with greater height growth will have fewer branch whorls per meter (Maguire et al. 1991), and thus may be expected to have fewer total branches for a given stem length. The number of whorls per 16-foot stem length was not measured in this study; however, mean Douglas-fir tree height at age 15 was not statistically different among treatments with varying species proportions (A. D'Amato unpub. data). Thus, it is likely that the number of branch whorls per meter was also similar, because all trees were the same age. The most reasonable explanation for the differences observed in branch frequency is that larger tree diameter is an indicator

of greater tree vigor. More vigorous trees would have more photosynthate available for the production of branches, leading to the positive association between tree diameter and branch frequency. The increase in the number of branches on larger trees is likely a result of an increased number of branches per whorl, or at least an increase in the number of branches per whorl that met the minimum size criteria for measurement in this study.

Because the number of branches was unaffected by treatment, it appears that species proportion can be manipulated without a significant reduction in Douglas-fir lumber grade due to the number of knots. Furthermore, the position of knots relative to one another affects lumber grade more than the total number of knots within a piece (WWPA 1998). Too many knots within a short linear distance can devalue the product. For this reason, the number of branches per whorl is probably a better indicator of future lumber quality than the number of total branches on a log. Previous studies in monoculture stands have found a tendency toward an increase in the number of branches per whorl with increased spacing (Carter et al. 1986). Future work in mixed stands should examine this variable as well.

Branch Size

It is important to note that branch sizes reported here overestimate knot sizes, because branch diameters were measured outside the bark. However, outside-bark diameter provides an index of the relative inside-bark diameters.

As with branch frequency, branch size was most strongly associated with tree size, and not associated with the level of treatment. Again, it is likely that this relationship is a function of tree vigor. Larger, more vigorous trees are able to allocate photosynthates to branches, whereas suppressed trees use more of their photosynthates for maintenance activities.

At 15 years of age, 95 of 120 trees had a BD_4 greater than 2.2 cm, the upper knot size limit for Select Structural grade 2 x 4 lumber. Only one tree in the entire sample had branches that were larger than 5.1 cm in diameter, the maximum knot size allowed for No. 2 dimension 2 x 4 lumber (WWPA 1998). Slightly older Douglas-fir trees (19-21 years) at spacings comparable to those in this study had a similar range of maximum branch diameters (Robbins 2000). Middleton and Munro (1989) reported a mean BD_4 of 4.4 cm in intensively managed Douglas-fir trees ranging from about 45-65 years old, and found that oversized knots caused almost 30% of lumber to be downgraded from Select Structural. Though inferences from data from other sites and experimental designs must be made cautiously, these data provide insight on what the future trajectory of the stands described in this study might be. However, from the data presented here it is not possible to predict what eventual branch sizes will be when trees reach harvest size. Such a model would need to consider patterns and differences in crown recession and diameter growth. Because in this study Douglas-fir grew in conjunction with red alder, patterns of crown recession in the future may be different from those typical of a monoculture, and future branch sizes also may be affected differently.

Branch Vitality and Canopy Light Transmittance

Light transmittance values calculated for the pure red alder treatment were comparable to those found in other deciduous hardwood forests (Ellsworth and Reich 1993, Vose et al. 1995), while transmittance in the pure Douglas-fir treatment was similar to that found in other, similarly-aged conifer stands (Sinclair and Knoerr 1982, Parker et al. 2002). Transmittance values in the species mixtures were intermediate between the two types of pure stands.

The proportion of live branches on the basal 16-ft stem increased as the proportion of Douglas-fir in a stand decreased, even though total stand density remained constant. Thus, with a greater proportion of red alder, Douglas-fir crown recession slowed, despite the fact that Douglas-fir trees across treatments were similarly sized (as expressed by DBH). Though the red alder trees were planted five years after the Douglas-fir, by stand age 15 the alder were as tall or taller than the Douglas-fir (personal observation).

This relationship supports the hypothesis that Douglas-fir crown recession is affected differently by interspecific competition from red alder than by intraspecific competition. Crown recession occurs when insufficient light becomes available for lower branches to produce enough carbohydrates to be photosynthetically self-sufficient. A comparison of the trends in HLC and light transmittance among stands with different species proportions reveals that the difference in light availability in the lower canopy could explain the differences found in HLC. In the pure red alder stand, light transmittance was similar at all

three measured heights, indicating that the bulk of the red alder leaf area was above the heights where light was measured. However, in the pure Douglas-fir stand, the difference in light transmittance between the upper and lower heights was much more pronounced, with relatively high transmittance in the upper portion of the crown and quite low light penetration to the lower portion. Correspondingly, as Douglas-fir proportion increased in the species mixtures, less light was available at the height corresponding with the lower third of the Douglas-fir canopy. The reduction in light, though estimated to be only a few percentage points in terms of the fraction of incident radiation, could be sufficient to accelerate branch mortality in the lower crown.

In stands with a high proportion of red alder (i.e. 75%), Douglas-fir crowns were relatively deep at age 15. Because there is little evidence of intraspecific Douglas-fir competition for light in these stands at present, it is likely that this trend will continue for a number of years. This combination of species could eventually result in logs with a higher number of large knots over a greater proportion of the bole, or in logs that would be less suitable for veneer due to a larger-diameter knotty core. However, verification of this assumption would require continued observation of these stands for a longer period of time. Also, the eventual effect, if any, on lumber grade cannot be predicted without future data.

CONCLUSIONS

Douglas-fir branch characteristics are affected by species proportion in young, mixed Douglas-fir/red alder stands where red alder is planted five years after Douglas-fir. Increasing the proportion of red alder does not significantly alter branch frequency or size over the lower portion of the bole, however the height to the Douglas-fir crown base is reduced, resulting in a larger proportion of live branches. This finding may be linked to the higher light availability in the lower canopy associated with high proportions of alder. Assuming that this trend were to continue as the stand ages, the size of the knotty core in Douglas-fir logs from stands with a high proportion of alder would be expected to be larger than in stands with mostly Douglas-fir, if diameter growth rates in the two types of stands continue to be similar. Validation of such an assumption requires further monitoring of the experiment.

In pure Douglas-fir stands, branch size increased with tree spacing whereas the height to the base of the live crown decreased with tree spacing. Both findings confirm that increased spacing in pure stands can compromise wood quality due to poorer knot characteristics.

The addition of red alder (without reducing Douglas-fir density) does not significantly change the height to the base of the Douglas-fir live crown or decrease the proportion of live branches on the lower bole. This effect is different than the additive effect of increased Douglas-fir density. Again, the effect can be linked to the difference in light penetration through red alder and Douglas-fir crowns.

At stand age 15, few trees had branches large enough to negatively affect lumber grade, and few trees were yet of merchantable size. However, the trends in branch patterns described here may result in differences in lumber grade as the stand grows. Because competition between red alder and Douglas-fir is dynamic through time, such predictions can only be verified through monitoring and measurement of older stands.

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CHAPTER 3 : RELATIONSHIPS BETWEEN SPECIES PROPORTION, PLANTING DATE, AND RED ALDER STEM FORM IN DOUGLAS- FIR/RED ALDER MIXTURES

ABSTRACT

Red alder (*Alnus rubra* [Bong.]) stem form attributes were analyzed as a function of species proportion and timing of red alder planting in 15-year-old replacement series experimental plots of red alder and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco). Treatments included a range of species proportions at 3 x 3 m spacing, and red alder was either planted simultaneously with Douglas-fir or after five years. Lean, sweep and multiple stem formation were interdependent. When the two species were planted simultaneously, a low proportion of red alder resulted in red alder trees with many multiple stems, low live crown bases, and higher amounts of lean and sweep. Trees with multiple stems also produced individual boles that were smaller in diameter than single-stemmed trees. When red alder planting was delayed, stem form was consistent regardless of species proportion. It is suggested that the patterns observed are a result of different rates of growth between the two species during the first 15 years of stand development. Low crown bases and the stem defects associated with the presence of multiple stems could lead to reduced product recovery and value.

INTRODUCTION

In the Pacific Northwest, red alder (*Alnus rubra* [Bong.]) often grows in association with Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), because both species tend to colonize recently disturbed areas. For many years, red alder was considered a species with low crop value (Tarrant 1978); perhaps as a consequence, little attention was paid to factors that influence wood quality or recovery in this species. More recently, red alder has grown in commercial value, and interest in managing red alder has increased. In order to manage red alder most effectively, it is important to understand how its wood quality is affected by its growing conditions.

Early research on red alder focused mainly on naturally regenerated, pure stands (see Bormann 1985, Hibbs et al. 1989). More recently, studies have included red alder plantations, and have yielded important conclusions about the effects of spacing (Knowe and Hibbs 1996, Hurd and DeBell 2001), thinning (Hibbs et al. 1995), irrigation (Hurd and DeBell 2001), and other management techniques on red alder stand development and yield (Hibbs and DeBell 1994). Nonetheless, knowledge about the impacts of plantation management on red alder wood quality is limited. Because stem form and log quality in red alder is highly variable, such information potentially could drive management decisions.

Red alder tends to lean toward open areas with more light (Bormann 1985, Newton and Cole 1994), which can cause a number of deviations from ideal stem form and associated wood quality attributes. For example, leaning hardwoods

produce tension wood (Wilson and Gartner 1996) as a compensatory mechanism to counteract the lean. Wilson and Gartner (1996) found that 10% of red alder in natural stands leaned more than 22°. There was variable tension wood formation with lean angles of 9-26°, but above 26° all trees had tension wood. Tension wood fibers are less desirable for pulp and paper processing than normal wood, and also have shrinkage properties that differ from normal wood fibers (Zobel and van Buijtenen 1989). Radial shrinkage is greater in red alder trees with greater amounts of lean, although the role of tension wood in this finding is unclear (Lowell and Krahmer 1993).

A leaning tree also may have variable amounts of sweep (curvature) in its stem, which can affect recoverable log volume. Mills may have greater difficulty processing logs that are not straight, and transportation costs may also increase because fewer logs can be hauled per load. To avoid such problems, alder logs are merchantable in lengths as short as 8 feet. Willits et al. (1990) showed that in red alder, neither lean nor sweep affected lumber recovery when logs were milled to 10 ft. However, they did not specify the maximum amount of lean or sweep analyzed. In other studies, red alder trees have been documented with over 40° of deviation from vertical (Wilson and Gartner 1996).

Lean in red alder is most pronounced in irregularly spaced, natural stands, where crown development is greater in sunny gaps than in shaded areas (DeBell and Giordano 1994). Control of tree spacing through stand management or plantations can result in straighter trees. Several studies have attempted to

determine exactly how tree spacing affects stem form in red alder plantations. Trees that are initially established at spacings greater than 4 x 4 m have poorer stem form than trees established at denser spacings (DeBell and Giordano 1994). Conversely, thinning dense natural stands seems to reduce lean (Bormann 1985); trees leaned more in dense (2.4 x 2.4 m) stands than in those that had been thinned at 7 years to 3.7 x 3.7 m or 4.9 x 4.9 m.

Whereas significant steps have been taken toward understanding stem form responses to spacing in single-species plantations, similar responses in a mixed species plantation cannot be predicted easily from monoculture data. In a mixed species stand, even if all trees are evenly spaced, differential growth rates of different species can produce a non-uniform canopy. For example, red alder has a much higher juvenile growth rate than Douglas-fir, and so in the early years of plantation establishment red alder overtops the conifers (Cole and Newton 1987). The area occupied by the conifer, then, represents a canopy gap into which a neighboring red alder tree could be expected to lean. This response has not been documented and to do so was one objective of this study.

Although much red alder wood is used for pulp and non-aesthetic applications like pallets, red alder lumber is also used for furniture and other fine applications. Thus, clear, knot-free wood is highly desirable and commands a price premium. Because the rate of crown recession determines the size, abundance, and depth of knots, a good understanding of crown dynamics is needed to optimize the production of clear alder wood.

When open-grown, red alder has the tendency to produce multiple stems (Newton and Cole 1994), which are associated with a number of negative wood quality attributes. Because the multiple stems from an individual tend to grow away from one another, lean, sweep, and tension wood may be more pronounced. Also, because bole biomass must be distributed to more than one dominant, each individual stem is likely to be smaller than if all the biomass were allocated to one stem. Potentially, this could result in a higher number of low-grade logs at the time of harvest due to reduced diameters. Open-grown trees also have reduced rates of crown recession, resulting in larger and more frequent knots.

Recently, a number of studies investigating the stand structure and yield of red alder/Douglas-fir mixtures have become old enough to study (Newton and Cole 1994, Miller et al. 1999, Radosevich et al. in progress). This work along with modeled experiments (Comeau and Sachs 1992) show that competitive interactions between the two species are complex and that they change with time. Depending on stand age, planting density, species proportion, and site characteristics, one species or the other will dominate and affect the growth of the other at different stages in stand development. Because red alder stem form and wood quality appear to be dependent on resource availability (primarily light), these attributes are likely to be affected by conifer competition, and differently than by intraspecific competition.

The objectives of this study were to quantify stem form attributes—lean, sweep, length of clear bole, and multiple stems—in red alder and to assess patterns of these attributes as a function of mixture with Douglas-fir. We hypothesized that

1) the amount of red alder in a stand drives variation in stem form, when total stand density is kept constant; 2) multiple-stemmed trees have a greater amount of stem defect (i.e. lean, sweep); and 3) the timing of red alder establishment relative to Douglas-fir affects stem form. This information will help landowners evaluate whether associations with species mixture have an effect on product quality.

MATERIALS AND METHODS

Site Description

The study site is located in the Oregon Coast Range 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 above sea level. The site was originally 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 and Binkley 1992).

The study was conducted in August 2001 on experimental plots established in 1985 as part of a long-term study of Douglas-fir/red alder interactions (D. Hibbs and S. Radosevich, principal investigators). The plots are a randomized block replacement series of Douglas-fir and red alder (Radosevich et al. in progress). In 1985, the site was clearcut and trees were planted at a fixed spacing of 3 m x 3 m (1109 trees per hectare). The plots were combinations of the two species ranging

from 100% Douglas-fir to 100% red alder, with intermediate combinations of 90:10, 75:25, 50:50, and 25:75 (Table 3.1). Each combination is represented by two series: one in which seedlings of both species were planted in year 1 (1986), and one in which red alder planting was delayed five years (1991). Another treatment consisted of a 50:50 mixture with the red alder removed after five years (1991). Finally, additional monocultures of each species were established at 4.2 m x 4.2 m spacing (555 trees per hectare), to represent the same within-species density found in the 50:50 mixture, with the absence of the other species. Thus, at the time of study, Douglas-fir trees were 15 years old and red alder trees were 10 or 15 years old.

Each treatment was replicated in three blocks, for a total of 45 plots. Each plot consisted of 9 trees in 9 rows for a total of 81 trees, except in treatments 14 and 15, where there were only 41 trees due to the wider spacing. The inner 25 trees within each plot became the permanent measurement trees, while the outer two rows serve as buffer rows. Trees that died after planting were replaced for the first three years. Volunteer shrubs and trees were removed by hand until year five. Trees were 15 years old at the time of measurement (10 years for red alder trees in treatments with delayed planting).

Table 3.1. Replacement series treatment descriptions. An asterisk next to the treatment number indicates that the treatment was included in this study.

Treatment	Douglas-fir percent	Red alder percent	Red alder planting ⁺	Spacing (m)	Red alder removed
1	100	0	Immediate	3 x 3	--
2*	90	10	Immediate	3 x 3	--
3*	90	10	Delayed	3 x 3	--
4*	75	25	Immediate	3 x 3	--
5*	75	25	Delayed	3 x 3	--
6*	50	50	Immediate	3 x 3	--
7*	50	50	Delayed	3 x 3	--
8	50	50	Immediate	3 x 3	After 5 yrs
9	50	50	Immediate	3 x 3	After 10 yrs
10*	25	75	Immediate	3 x 3	--
11*	25	75	Delayed	3 x 3	--
12*	0	100	Immediate	3 x 3	--
13*	0	100	Delayed	3 x 3	--
14	100	0	--	4.2 x 4.2	--
15*	0	100	Immediate	4.2 x 4.2	--

⁺Red alder planting date: immediate = year 1 (1986); delayed = year 6 (1991)

Experimental Design

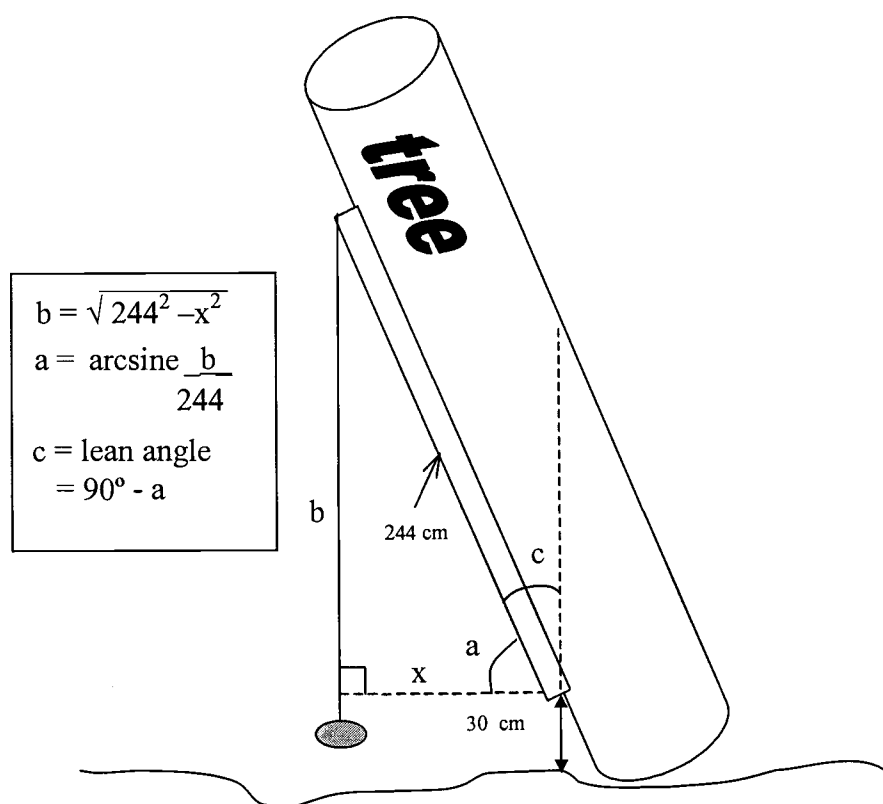
Eleven treatments within the replacement series were included in this study (Table 3.1). All red alder trees within the inner permanent plots were measured; thus, depending on the species proportion within the treatment, 6 to 25 trees per plot were measured. With three replicate blocks, a total of 31 plots and 391 trees were measured (for treatment 13, only one plot was measured).

Tree Measurement

To calculate lean, a 2.44 m (8 ft) pole with a plumb line attached to the top was held against the bole, with the base of the pole resting 30 cm (1 ft) above the

ground. The horizontal distance between the weight at the end of the plumb line and the pole was measured. The sine of the angle produced by the base of the tree and the ground could thus be calculated and subsequently the lean angle in degrees determined (Figure 3.1).

Figure 3.1. Method for measuring and calculating lean angle.



The amount of sweep was also measured for the lower 8 ft segment of each stem (after leaving a 1 ft stump allowance). This length was chosen to reflect conventional milling lengths for red alder (Willits et al. 1990). The 8 ft pole was

positioned against the bole, and the widest perpendicular distance between the bole and the pole was measured. Finally, height to the base of the live crown (HLC) was measured using a laser sensor. HLC was calculated as the lowest point on the stem below which there were live branches on three of the four quadrants of the tree.

The number of multiple stems, defined as stems greater than 10 cm in diameter at breast height (DBH), was recorded for each tree. A tree was considered to have multiple stems if it was forked below breast height. If multiple stems were present, then all other measurements (except for height to crown base) were taken on each individual stem greater than 10 cm DBH. These included DBH, lean, and sweep.

Data Analysis

The incidence of multiple stems was treated as a binomial response variable with a Bernoulli distribution (0 for a single stem, 1 for more than one stem). A logit transformation of the data resulted in estimated probabilities of trees developing multiple stems at a given proportion of red alder in the stand. Separate analyses were carried out for the two series where red alder was planted immediately or after five years. A similar analysis was carried out to determine whether the presence of sweep (0 for no sweep, 1 for sweep > 0) was associated with treatment.

Multiple linear regression was used to determine whether the amount of lean, sweep, and the height to the base of the live crown were correlated with the proportion of red alder in both the delayed-planted and the immediately-planted

series. Data for each tree were averaged by plot to result in plot means for each variable. Percent red alder (0-100) of total stand density was treated as a continuous variable in these cases; the best-fitting regression models were those where the explanatory variable for red alder proportion was log-transformed. Initial regression models took the form:

$$[\text{response variable}] = \beta_0 + \beta_1[\ln(\text{percent red alder})] + \beta_2[\text{block}]$$

where β_1 is a regression coefficient for the continuous effect of species proportion, and β_2 is a coefficient for the random block effect. Separate analyses were performed for those treatments where red alder was planted immediately and those where it was planted five years later than Douglas-fir (Figure 3.2).

Tests of the effect of timing of planting were performed with analysis of variance (ANOVA). Additionally, the wide-spaced red alder monoculture was compared to the 50:50 mixture with immediately-planted red alder, to compare the additive effect of Douglas-fir density while keeping red alder density constant.

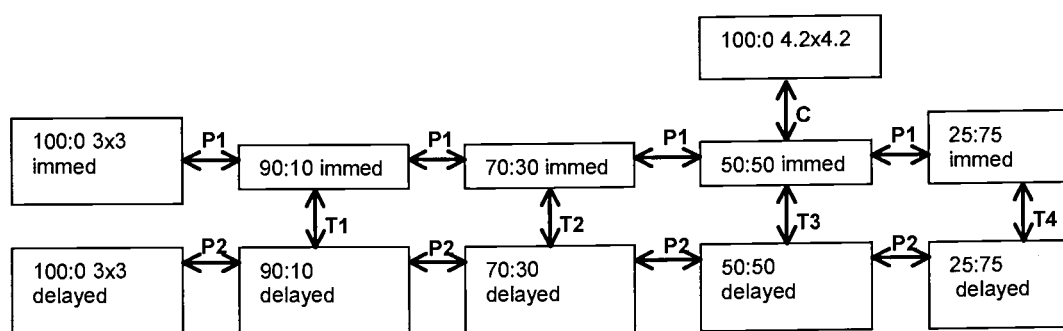
ANOVA models took the form:

$$[\text{response variable}] = \gamma[\text{treatment}] + \lambda[\text{block}] + \varepsilon$$

where γ is the fixed effect of the level of treatment (combination of species proportion and timing of red alder planting), λ is the random effect of block, and ε is the random variation among plots. Figure 3.2 shows the specific analyses performed. The Fisher procedure for multiple comparisons was used to correct confidence interval widths for estimated effects. All statistical analyses were

carried out with SAS 8.0 (SAS Institute, Cary, NC) or S-Plus 2000 (MathSoft, Inc., Cambridge, MA) statistical software.

Figure 3.2. Comparisons of interest in the study of red alder stem form. Proportions are % red alder:%Douglas-fir. Comparisons designated with a T are tests of the effect of timing of planting; those designated with a P are tests of the effect of species proportion, and that with a C is a test of the effect of Douglas-fir additivity.



RESULTS

Lean

Lean in individual stems ranged from 0 to 43° (Table 3.2), though the distribution of lean was highly skewed with most trees having between 0 and 8° of lean. All treatments had some trees with no lean, except for the 75% red alder, delayed-planted treatment, where the minimum lean angle was 1.6°.

Multiple linear regression indicated that there was a negative association between red alder proportion and the magnitude of lean in plots where alder was planted immediately ($F_{3,11} = 3.1$, $P = 0.01$, Figure 3.3). If the proportion of red alder were doubled, it was predicted that lean would decrease by 1.5° (95% CI =

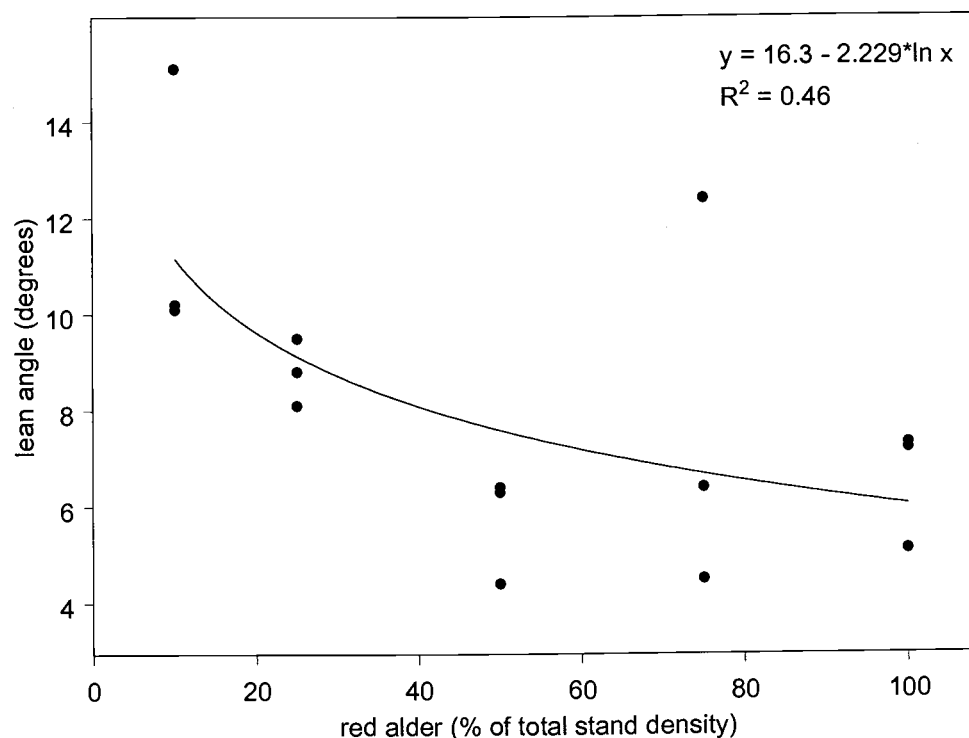
0.4 to 2.7°). Our model thus predicted that the mean lean angle in stands with 10% red alder would be 11.2°, whereas in a pure red alder stand it would drop to 6.0°.

No proportion effect was detected when red alder planting was delayed ($P = 0.30$, data not shown). Also, ANOVA showed no difference in lean angle as a function of timing of red alder planting at any level of species proportion ($P = 0.65$, data not shown).

Table 3.2. Angle of lean (°) by treatment. Values are the means (\pm SE) of three plots for each treatment.

Treatment	Mean	SE
(2) 10% red alder/immediate	11.8	1.7
(3) 10% red alder/delayed	7.6	1.3
(4) 25% red alder/immediate	8.8	0.4
(5) 25% red alder/delayed	9.8	2.7
(6) 50% red alder/immediate	5.7	0.7
(7) 50% red alder/delayed	6.2	1.0
(10) 75% red alder/immediate	7.8	2.4
(11) 75% red alder/delayed	8.0	2.3
(12) 100% red alder/immediate	6.5	0.7
(13) 100% red alder/delayed	4.7	---
(15) 100% red alder/wide spacing	6.3	1.0
TOTAL	7.7	0.5

Figure 3.3. Observed values and fitted regression line for lean angle as a function of red alder proportion in plots where planting was immediate. Plotted points are plot means.



Sweep

Of the 489 stems measured (on a total of 391 trees), 143 stems had no measurable sweep. Of the 346 stems with measurable sweep, mean sweep was 3.7 cm and the maximum sweep measured was 27.2 cm (Table 3.3). The frequency of stems without any sweep was unrelated to species proportion ($P = 0.4$). Though stems from immediately-planted trees were less likely to have measurable sweep than stems from delayed-planted trees ($F_{1,27} = 4.78$, $P = 0.04$), the magnitude of

sweep was not different between the two timing treatments (t-test, $P = 0.46$). Sweep was also positively correlated with lean angle ($F_{3, 27} = 11.1$, $P < 0.0001$, $R^2 = 0.55$).

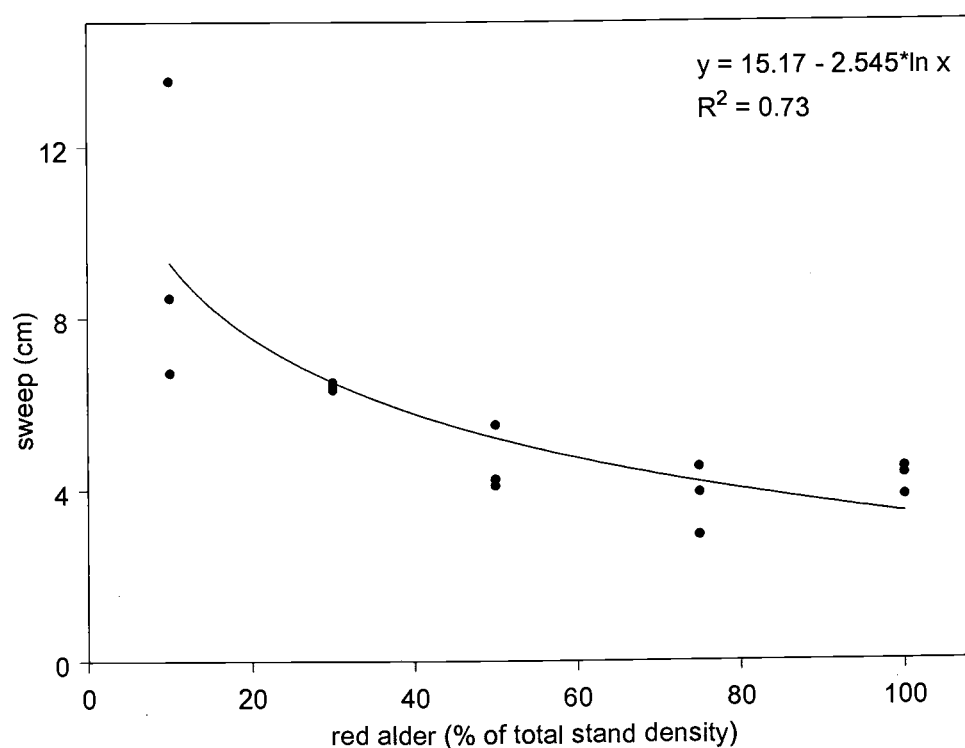
Table 3.3. Summary statistics for sweep measurements of red alder stems by treatment. Sweep is measured in cm deviation from straight. Values are the means of three plots per treatment.

Treatment	% stems with sweep	Mean sweep (stems without sweep included)	Mean sweep (stems without sweep excluded)	Max. sweep	<i>n</i>
(2) 10% red alder/immediate	61.8	6.0	9.6	27.2	42
(3) 10% red alder/delayed	94.4	5.1	5.4	24.5	18
(4) 25% red alder/immediate	51.7	3.3	6.4	15.6	46
(5) 25% red alder/delayed	79.0	4.9	6.0	16.5	24
(6) 50% red alder/immediate	76.8	3.5	4.6	14.2	52
(7) 50% red alder/delayed	66.0	3.1	4.7	16.6	39
(10) 75% red alder/immediate	73.8	2.8	3.8	9.0	61
(11) 75% red alder/delayed	87.4	4.3	4.8	12.5	52
(12) 100% red alder/immediate	63.2	2.6	4.2	13.7	83
(13) 100% red alder/delayed	69.6	3.4	4.8	10.8	23
(15) 100% red alder/wide	69.0	4.1	5.8	19.9	49
TOTAL	72.2	3.9	5.5	27.2	489

In the immediately-planted series, sweep decreased as red alder proportion increased, considering only stems that had measurable sweep ($F_{3, 11} = 10.1$, $P < 0.001$, Figure 3.4). By doubling the proportion of red alder, it was estimated that sweep would decrease by 1.8 cm (95% CI = 1.0 to 2.5). Thus, the mean sweep value for stems in the 10% red alder treatment was predicted to be 9.3 cm, whereas in a 100% red alder stand, the predicted mean sweep value was only 3.4 cm (Figure 3.4). However, in the delayed-planted series, there was no relationship between red alder proportion and sweep ($P = 0.5$). Additionally, no additive effect of Douglas-

fir density was detected in influencing sweep (i.e. there was no difference in sweep between the 50:50, immediately planted and the 100% red alder, widely spaced treatments).

Figure 3.4. Observed measurements and fitted regression for sweep as a function of red alder proportion in plots where red alder was planted immediately. Plotted points are plot means.



Multiple Stems and Associated Effects

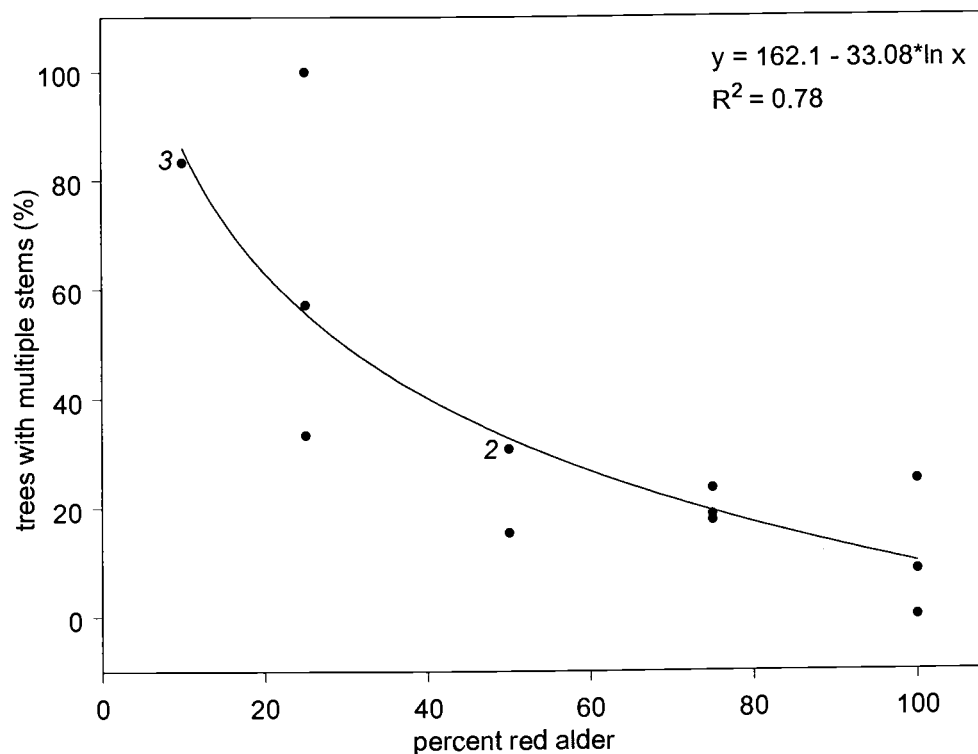
The percentage of trees within a treatment with multiple stems (stems larger than 10 cm DBH) ranged from 0 (10% and 75% red alder, delayed planting) to 83.3% (10% red alder, immediate planting) (Table 3.4). In the immediately-planted

treatments, the incidence of red alder trees with multiple stems increased as red alder proportion decreased ($F_{3,11} = 13.4$, $P < 0.001$, Figure 3.5). Doubling the proportion of red alder was predicted to result in 22.9% fewer trees developing multiple stems (95% CI = 15.0 to 30.9%). No significant effect of red alder proportion was detected where red alder planting was delayed ($P = 0.10$). In this case, the probability of multiple stems was estimated at less than 0.1 at all proportions of red alder. Finally, there was no difference in the probability of the occurrence of multiple stems between the wide-spaced pure alder stand and the 50:50, immediately-planted stand, indicating that there was no additive effect of Douglas-fir density.

Table 3.4. Percentage of trees with multiple stems larger than 10 cm DBH and the number of trees observed in each treatment. Percentage values are the means of three plots per treatment.

Treatment	% trees with multiple stems	<i>n</i>
(2) 10% red alder/immediate	83.3	18
(3) 10% red alder/delayed	0.0	18
(4) 25% red alder/immediate	63.5	25
(5) 25% red alder/delayed	3.7	23
(6) 50% red alder/immediate	25.6	39
(7) 50% red alder/delayed	5.6	37
(10) 75% red alder/immediate	20.0	50
(11) 75% red alder/delayed	3.6	52
(12) 100% red alder/immediate	11.1	73
(13) 100% red alder/delayed	9.5	21
(15) 100% red alder/wide spacing	28.5	35
TOTAL	24.0	391

Figure 3.5. Observed values and fitted regression of the likelihood of a red alder tree developing multiple stems as a function of red alder proportion in the immediately-planted series. Plotted values are plot means; numbers in italics indicate multiple points for the same value.



Individual stems coming from multiple-stemmed trees were smaller than those from single-stemmed trees in all treatments (ANCOVA, $F_{1,35} = 66.3$; $P < 0.0001$). Across all trees measured in immediately-planted treatments, stems from single-stemmed trees were on average 3.5 cm bigger in diameter than stems from multiple-stemmed trees; however, the difference in size was greater when red alder proportion was low (Figure 3.6). On the other hand, total cross-sectional area of multiple-stemmed trees was greater than that of single-stemmed trees (ANCOVA, $F_{1,23} = 16.9$, $P < 0.001$, Table 3.5). So, assuming that tree heights were similar,

multiple-stemmed trees produced a greater total volume of wood per tree, however the size of each stem on these trees was smaller than that of normal trees.

Figure 3.6. Observed (symbols) and fitted regression lines for DBH of single- and multiple-stemmed trees as a function of red alder proportion in plots where red alder was planted immediately. Plotted points are plot means.

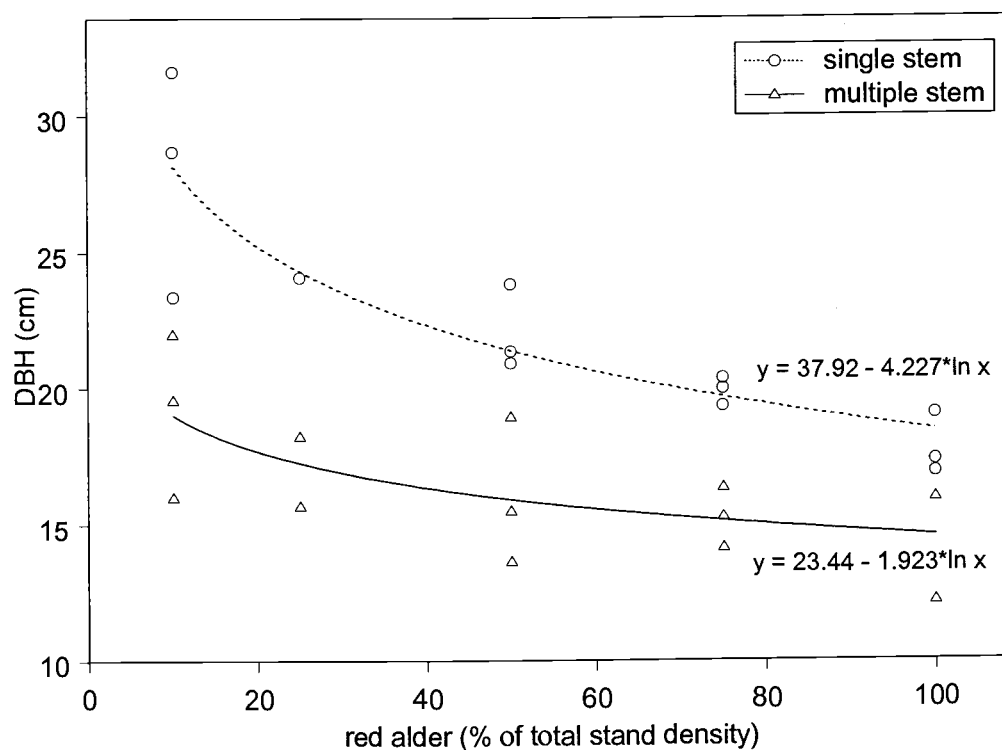


Table 3.5. Total cross-sectional area of all stems on multiple-stemmed trees compared to cross-sectional area of single-stemmed trees in treatments where red alder was planted immediately (mean \pm SE). Cross-sectional area was calculated from DBH values for individual stems.

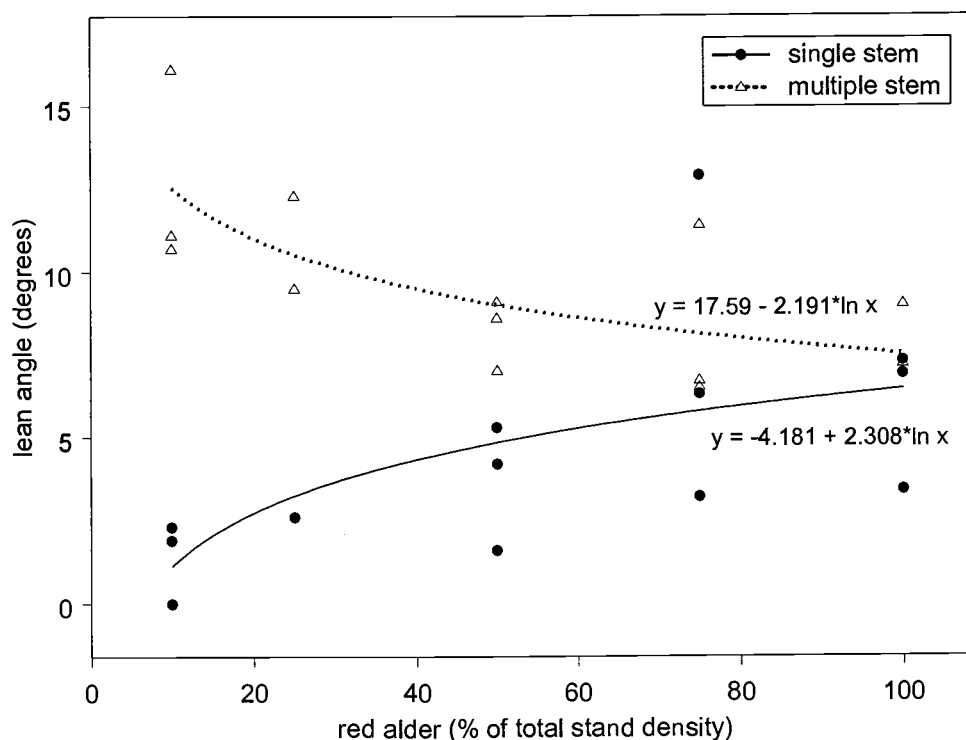
Treatment	Area (cm ²)	
	Multiple-stemmed	Single-stemmed
100% red alder	311 (38)	253 (10)
90% red alder	767 (48)	620 (104)
75% red alder	629 (34)	465 (60)
50% red alder	455 (42)	384 (18)
25% red alder	404 (38)	321 (18)
100% red alder/wide spacing	533 (76)	392 (29)

Lean angle was positively associated with multiple stems ($P < 0.01$, t-test, Table 3.6). When red alder was planted immediately, stems from multiple-stemmed trees leaned more than single-stemmed trees, but the difference varied with species proportion (multiple linear regression, $F_{5,20} = 10.8$, $R^2 = 0.73$, $P < 0.001$, Figure 3.7). With 10% red alder, our model predicted an 11.5° difference in lean angle between single-stemmed trees and stems from multiple-stemmed trees (Figure 3.7). In a pure red alder stand, the predicted difference dropped to 1.0°. There was no such relationship in plots where red alder planting was delayed; however, because the incidence of trees with multiple stems in these treatments was quite low, such a comparison was difficult to make.

Table 3.6. Sweep (cm) and lean angle (°) for stems from trees with and without multiple stems (mean \pm SE).

	Sweep	Lean
Single-stemmed	2.9 (0.3)	5.7 (0.7)
Multiple-stemmed	4.7 (0.4)	8.6 (0.6)

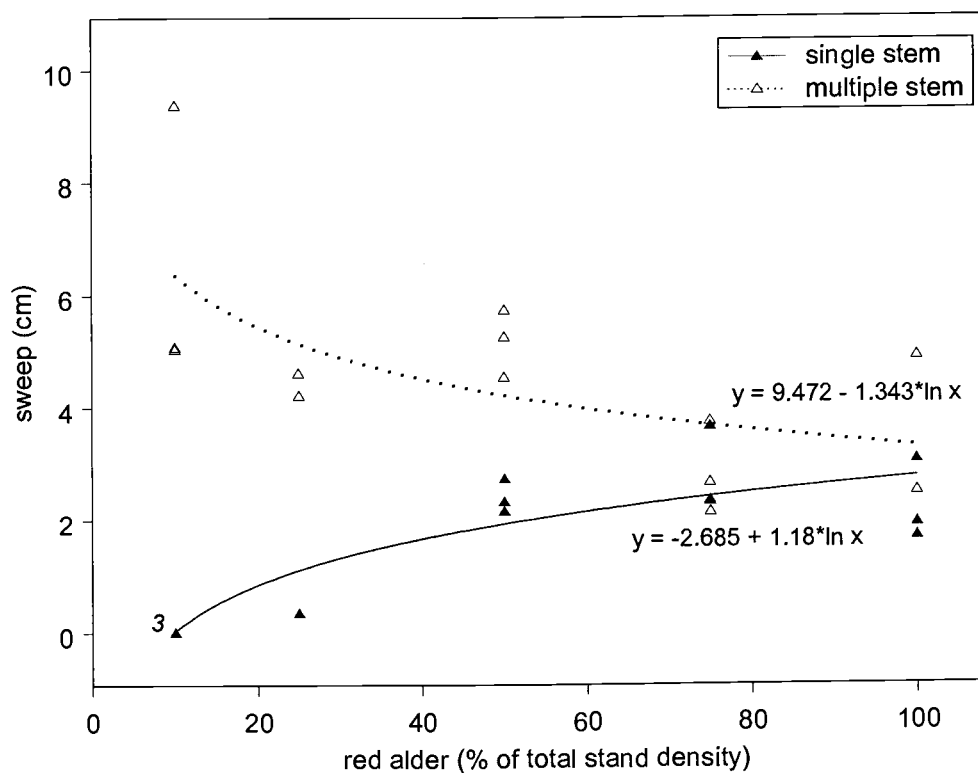
Figure 3.7. Lean angle in single-stemmed red alder trees vs. stems from multiple-stemmed trees in plots where red alder was planted immediately. Plotted points are plot means for single- and multiple-stemmed trees.



Stems that were from multiple-stemmed trees also had greater sweep than single-stemmed trees ($P < 0.01$, t-test, Table 3.6), and the pattern across treatments was quite similar to that of lean angle when red alder was planted immediately (Figure 3.8). In single-stemmed trees, sweep increased with red alder proportion, whereas in multiple-stemmed trees, sweep decreased with alder proportion (multiple linear regression, $F_{5,20} = 12.2$, $R^2 = 0.75$, $P < 0.001$). When red alder made up 10% of total stand density, the difference in sweep between single- and

multiple-stemmed trees was predicted to be 6.4 cm, whereas in a pure red alder stand the estimated difference dropped to 1.4 cm (Figure 3.8).

Figure 3.8. Sweep in single- and multiple-stemmed trees in treatments where red alder was planted immediately. Plotted points are plot means for single- and multiple-stemmed trees. Numbers in italics indicate multiple points at a given location.



Height to the Base of the Live Crown

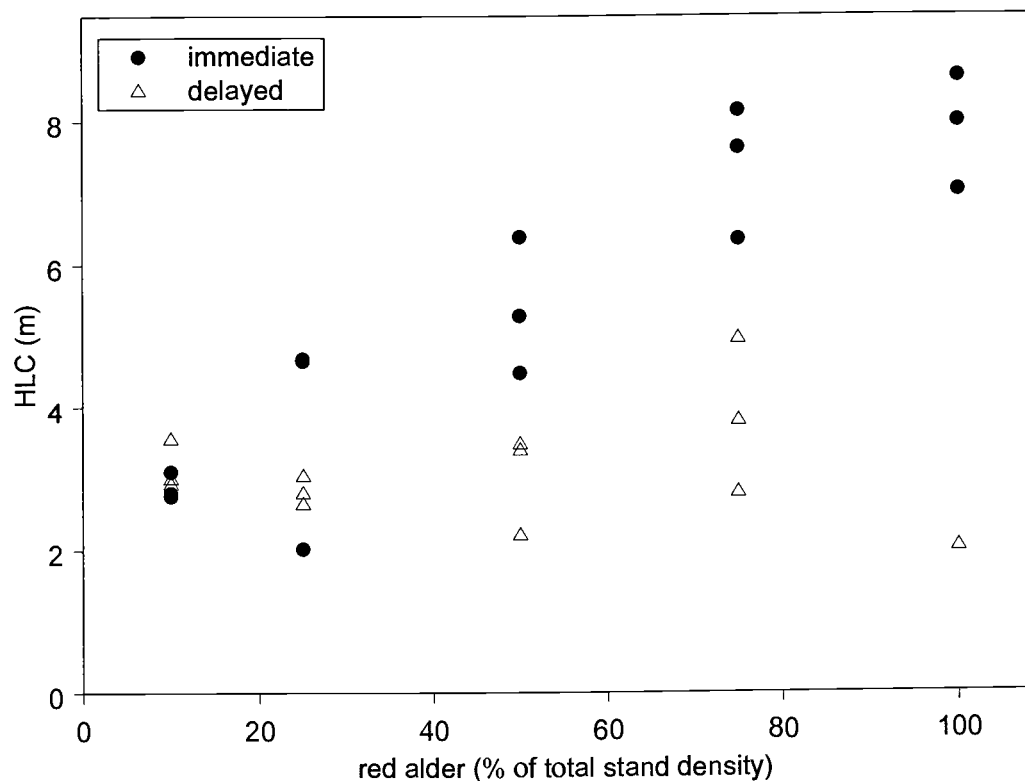
Across all individual trees, height to the base of the live crown (HLC) ranged from 0.8 m to 13.8 m, with a grand mean of 5.0 m. Treatment means ranged from 2.0 m to 7.9 m (Table 3.7).

Table 3.7. Height to the base of the red alder live crown by treatment (mean \pm SE).

Treatment	HLC (m) (mean \pm SE)
(2) 10% red alder/immediate	2.9 (0.1)
(3) 10% red alder/delayed	3.2 (0.2)
(4) 25% red alder/immediate	3.8 (0.9)
(5) 25% red alder/delayed	2.8 (0.1)
(6) 50% red alder/immediate	5.4 (0.6)
(7) 50% red alder/delayed	3.0 (0.4)
(10) 75% red alder/immediate	7.4 (0.5)
(11) 75% red alder/delayed	3.9 (0.6)
(12) 100% red alder/immediate	7.9 (0.5)
(13) 100% red alder/delayed	2.0 (---)
(15) 100% red alder/wide spacing	5.3 (1.0)
TOTAL	4.5 (0.4)

In the series where red alder and Douglas-fir were planted at the same time, red alder live crowns were higher where red alder proportion was greater ($F_{3, 11} = 28.0$, $P < 0.001$, Figure 3.9): a 10% increase in the proportion of red alder in the stand was associated with a 0.6 m increase in HLC (95% CI = 0.4 to 0.7 m). There was no effect of species proportion when red alder planting was delayed ($P = 0.6$, data not shown). Also, there was no difference in HLC between trees in the widely-spaced monoculture and the 50:50 immediately-planted treatment, indicating that there was no additive effect of Douglas-fir density on red alder HLC.

Figure 3.9. Height to the base of the red alder live crown as a function of proportion of red alder in the stand and timing of red alder planting. Plotted points are plot means.



When the percentage of red alder in the stand was low ($\leq 25\%$), there was no difference in HLC in immediately-planted or delayed-planted trees. However, as the proportion of species approached a pure red alder stand, the timing effect on HLC increased (Figure 3.9). The mean HLC for immediately-planted trees were estimated to be 2.1 m, 3.5 m, and 4.8 m higher than for delayed-planted trees for the 50%, 75%, and 100% red alder proportions, respectively (multiple linear regression, $F_{5, 22} = 33.7$, $R^2 = 0.88$, $P < 0.001$).

DISCUSSION

Stem Form

In this study, red alder lean and sweep appeared to be controlled by a combination of two factors: the development of multiple stems and the proportion of red alder of total stand density. When there were few, widely-spaced red alder trees in the stand, multiple-stemmed trees had high amounts of both lean and sweep, whereas single-stemmed trees were near vertical and had very little to no sweep. At these low proportions of red alder, intraspecific tree spacing and biomass allocation are likely factors accounting for the differences observed. Because red alder grew much more rapidly than Douglas-fir through age 15, red alder tree density was more important than competition from the understory conifers in determining resource availability to red alder trees. With abundant light and space available to individual red alder trees, resource levels resembled those available to open-grown trees, enabling the development of wide crowns. The individual stems on multiple-stemmed trees leaned outward in order to fully occupy open canopy space rather than compete with one another. Single-stemmed trees in these stands were larger in diameter than stems of multiple-stemmed trees, since woody biomass was allocated to only one bole. It is possible that as these single-stemmed trees grew larger, any amount of lean and sweep originally present was reduced as new wood was unevenly distributed around the circumference of the tree.

When red alder trees were planted closer to one another (i.e. at high proportions of total stand density), there was no difference in lean or sweep

between multiple- and single-stemmed trees. Additionally, there was a lower incidence of multiple stem development. Again, it appears that any competition from the few understory Douglas-fir trees was irrelevant, and with a more crowded canopy red alder stem form took on characteristics similar to those of a dense monoculture (DeBell and Giordano 1994).

The precise mechanism driving the development of multiple stems is unclear, however Newton and Cole (1994) propose that there may be more than one cause involved. It is thought that widely-spaced alders are more prone to antler rubbing in the first years of growth, resulting in top die-back. Open-grown trees also are more likely to develop basal suckers, which, given adequate light resources, might eventually develop into co-dominant boles. Both of these mechanisms can be supported with data from this study, because there was a clear trend of increased development of multiple stems with increased spacing between red alder trees.

The range and distribution of lean angle in the trees measured in this study was comparable to that found in the literature for trees of similar size in natural stands (Wilson and Gartner 1996), though in older (> 30 years) natural stands with larger trees, lean angles were lower than those found here (Bormann 1985). Wilson and Gartner (1996) found variable amounts of tension wood in leaning red alder trees. However, because in the current study the mean lean angle in all treatments was below the threshold (26°) above which Wilson and Gartner (1996) found tension wood in all trees, it is difficult to predict how the quantity of tension wood

would change with either timing or proportion of red alder planting. Still, when red alder proportion was low, multiple-stemmed trees leaned much more ($> 10^\circ$) than single-stemmed trees, indicating that there is a potential for increased tension wood in the former set of trees. In previous studies, trees growing on steep slopes had greater amounts of lean. Thus, it appears that site characteristics could be as important as stand structure as a factor determining lean in red alder. Though the plots in this study were situated on a wide range of slopes, we did not measure slope as a covariate and thus cannot make inferences as such to our conclusions.

Whether the magnitude of sweep measured in this study could have a significant effect on product quality is also unknown. The greater the amount of sweep, the more likely that a log would be usable only for pulp, and thus command a much lower price. Single-stemmed, large-diameter trees had little sweep, whereas the smaller-diameter multiple-stemmed trees had more. It is possible that if the multiple-stemmed trees were allowed to grow to a harvestable size, the magnitude of sweep may be reduced to an extent where the effect on the logs' value is negligible. In other words, it is difficult to conclude whether the increased sweep detected in smaller-sized trees is a consequence of multiple stem formation, or whether sweep decreases as trees grow. In a study of stem form in several birch species, more sweep was found in stands of with smaller mean tree diameters (Viherä-Aarnio and Velling 1999).

The development of multiple stems is linked not only to other negative stem form attributes, but also to decreased individual stem size. Although the total

volume of wood produced by multiple-stemmed trees was likely greater on average than that of single-stemmed trees, trees with multiple stems produced significantly smaller individual boles. This decrease in diameter potentially could result in logs that do not meet the size minimum for sawlog grade at the time of harvest, if growth rates remain the same. Red alder sawlogs typically must have a minimum 8-inch top (G. Ahrens, pers. comm.). To account for taper, a sawlog needs a minimum DBH of about 10 inches. At the time of measurement, 10% of stems from single-stemmed trees were ≥ 10 inches DBH, while only 2.6% of stems from multiple-stemmed trees were that size.

Height to the Base of the Live Crown

When both species were planted simultaneously, crown bases were highest in stands with high proportions of red alder. Because Douglas-fir trees were not as tall as red alder trees and often were highly suppressed due to severe competition from the alder, canopy gaps formed between individual red alder trees above the Douglas-fir tree planting sites. Lower branches thus have been able to persist longer in cases where a high proportion of Douglas-fir resulted in larger canopy gaps. The modeled difference in red alder HLC between the 50% red alder stand and the pure red alder stand was 2.9 m. This is more than the equivalent of one additional mill-length (8 ft) clear log from each tree in the pure stand, compared to the 50:50 mixture. Thus, assuming that log diameters are sufficient for sawlog grade, and that crown recession follows current patterns, there is a substantial

potential for increased log value from pure stands on the basis of the length of the clear bole.

Delayed Establishment of Red Alder

Delaying the establishment of red alder reduced many of the negative stem form effects that were present when the two species were planted simultaneously. The incidence of multiple stem development was sharply reduced; consequently, although at the time of measurement there was no difference in the magnitude of lean or sweep between immediately-planted and delayed-planted trees, the association of these attributes with multiple stems indicates that as the delayed-planted trees mature, lean and sweep may be lower overall than in immediately-planted trees.

The effect of species proportion on lean, sweep, multiple stems and HLC that was detected in immediately-planted trees was eliminated when red alder planting was delayed. These results indicate that in the delayed series, interspecific competition and intraspecific competition were approximately equal in their effect on red alder stem form. Delaying the establishment of red alder elevated the competitive status of Douglas-fir neighbors, particularly in terms of reducing the availability of space and light to red alder trees.

There has been much speculation about the effect of delayed red alder establishment on total stand productivity (Stubblefield and Oliver 1978, Miller and Murray 1979, Comeau and Sachs 1992, Newton and Cole 1994). From our results,

it appears that this management strategy has potential to improve red alder wood quality. However, red alder trees in the experiment described here are still quite small and the future trajectory of these stands is unclear, making it difficult to draw inferences from the present status to harvest age. Continued monitoring of the experiment would yield information on stand productivity, wood quality and product recovery as a function of delayed alder planting.

CONCLUSIONS

When total tree spacing in mixed red alder/Douglas-fir plantations was 3 x 3 m, the probability of a red alder tree developing multiple stems and the magnitude of sweep and lean increased as red alder proportion decreased. Individual bole diameters were smaller if multiple stems developed. Also, the height to the base of the live crown was lower at low red alder proportions. These effects disappeared when red alder planting was delayed. Thus, it appears that in order to optimize red alder wood quality, low proportions of red alder in mixed conifer/alder stands should be avoided, trees should be planted more densely, or red alder establishment should be delayed. If the two species are established simultaneously, Douglas-fir height growth in the first 15 years of stand development is not sufficient to create the competitive environment needed to produce red alder trees with optimal stem form characteristics.

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CHAPTER 4 : INFLUENCE OF RED ALDER COMPETITION ON CAMBIAL PHENOLOGY AND LATEWOOD FORMATION IN DOUGLAS-FIR

ABSTRACT

To better understand the influence of competition on wood formation and wood quality in Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), annual patterns of cambial growth and latewood production were examined in 15-year-old mixed Douglas-fir/red alder (*Alnus rubra* Bong.) plantations. Cambial growth was tracked using the pinning method. Cambial growth in most trees began between May 12 and 23, and ended between August 27 and September 10. Mean date of transition to latewood was July 5. Competition from red alder was evident in tree size and patterns and quantity of radial growth if the two species were planted simultaneously, or if the proportion of red alder in the stand was high (75%) when it was planted five years after Douglas-fir. In these cases, Douglas-fir trees began cambial growth later and ended growth earlier in the year than in pure Douglas-fir stands or if the proportion of red alder was low. The effect of interspecific competition was confounded with the effect of suppression, as trees with shorter growing seasons were also smaller in diameter in all treatments. Percent latewood was unaffected by competition, but it was dependent on the date of a tree's transition to latewood production. In suppressed trees, latewood production began earlier in the year. Wood specific gravity is likely to be lower in trees not subject to

competition from red alder; however, those with denser wood also have slow diameter growth.

INTRODUCTION

Because Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) wood commonly is used in structural applications, wood density is of prime importance among its wood quality attributes. Wood density is a function of xylem cell diameter and wall thickness, which are highly variable within a growing season, from year to year, and among individuals of the same species. Understanding the physiological and environmental processes affecting xylem development is therefore important for predicting wood density.

Cambial growth in conifers is controlled by a number of biochemical mechanisms, which are in turn affected by environmental variables. As a result, different types and amounts of wood are produced under different environmental conditions. Higher temperatures in the spring indirectly induce cambial activity (Waisel and Fahn 1965), as buds are released from dormancy and auxin flows from them to the vascular cambium (Larson 1969, Sundberg et al. 2000). Warm temperatures also have been shown to increase xylem production throughout the growing season (Larson 1967, Jenkins and Shepherd 1972). Water stress is associated with a slowdown in radial growth (Horacek et al. 1999). The interactive effects of other environmental variables, such as light intensity, with the biochemical controls on cambial activity are less well understood. Light intensity

clearly affects photosynthesis, which can affect the rate of cambial growth (Philipson et al. 1971), and photoperiod is known to affect the initiation and cessation of cambial growth (Larson 1962, Waisel and Fahn 1965). However, the effect of light intensity on the duration of cambial growth and the type of wood produced is largely unknown.

In Norway spruce (Baucker et al. 1998) and red pine (Kozlowski and Peterson 1962), a tree's relative position within the canopy influences patterns of cambial growth. In these cases, suppressed trees begin growing later and end growing sooner than dominant trees. Red alder (*Alnus rubra* Bong.), which grows more rapidly in its juvenile phase than Douglas-fir, can suppress conifer growth when the two species grow in mixture (Stubblefield and Oliver 1978, Tarrant 1978, Cole and Newton 1987). Thus, if the pattern observed in other conifers also holds for Douglas-fir, the presence of red alder in a stand could also influence Douglas-fir cambial activity through suppression. Light levels differ beneath red alder and Douglas-fir canopies (see Chapter 2); thus, the suppressive mechanism of red alder may be through limitation of light to understory Douglas-fir.

Latewood, characterized by thick-walled, narrow-diameter tracheids, has a relatively high density; consequently the percentage of latewood formed within each annual ring is a major influence on overall wood density (Zobel and van Buijtenen 1989). Latewood production is highly variable from year to year (Kennedy 1961), and the identification of the factors influencing it can be complex. Climatic, genetic, silvicultural, and environmental stress-related influences on

percent latewood have all been reported for Douglas-fir (Erickson and Lambert 1958, Kennedy 1961, Brix and Mitchell 1980, Smith 1980, Robertson et al. 1990, de Kort 1993, Vargas-Hernandez and Adams 1994). In summary, some of the most important factors appear to be moisture stress (Robertson et al. 1990), wide spacing (Smith 1980) and fertilization (Brix and Mitchell 1980), all of which are reported to reduce latewood production.

Larger percentages of latewood correlate with longer periods of latewood formation (Kennedy 1961). Vargas-Hernandez and Adams (1994) determined that in Douglas-fir, it is not a longer overall active growing season, but an earlier date of latewood transition that causes the period of latewood formation to be longer. Therefore, increased latewood generally comes at the expense of earlywood production (Vargas-Hernandez and Adams 1994). To assess latewood production, one needs to consider factors affecting both the timing of the transition to latewood and the length of time for which latewood 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). When primary (extension) growth is no longer being formed, photosynthates are translocated to create the thicker xylem cell walls characteristic of latewood (Larson 1969). Processes that influence the period of shoot growth, therefore, also could have an indirect effect on the transition to latewood production.

All environmental and silvicultural influences on wood formation processes are related ultimately to resource availability. Competition from neighboring trees limits resource availability, and resource depletion differs not only with stand density, but also by species (Cole and Newton 1986, Shainsky and Radosevich 1992, Chan et al. submitted). In young stands, red alder is superior to Douglas-fir in its ability to capture light, for example. This study examined whether the time period during which cambial growth in Douglas-fir takes place was influenced by the abundance of red alder in a mixed stand, in order to study effects of resource availability on Douglas-fir cambial growth. We also investigated whether the timing of the transition to latewood and the percent latewood formed was associated with red alder competition.

MATERIALS AND METHODS

Site Description and Experimental Design

The study site is in the Oregon Coast Range 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 above sea level. The site was originally 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 and Binkley 1992).

The study was conducted on experimental plots established in 1985 as part of a long-term study of Douglas-fir/red alder interactions (D. Hibbs and S. Radosevich, principal investigators). The plots are a randomized block replacement series of Douglas-fir and red alder. In 1985, the site was clearcut and trees were planted at a fixed spacing of 3 m x 3 m (1109 trees per hectare). Combinations of the two species ranged from 100% Douglas-fir to 100% red alder, with intermediate combinations of 90:10, 75:25, 50:50, and 25:75 (Table 4.1). Each combination was represented by two series: one in which seedlings of both species were planted in year 1 (1986), and one in which red alder planting was delayed five years (1991). Another treatment consisted of a 50:50 mixture with the red alder removed after five years (1991). Finally, additional monocultures of each species were established at 4.2 m x 4.2 m spacing (555 trees per hectare), to represent the same within-species density found in the 50:50 mixture, with the absence of the other species.

Each treatment was replicated in three blocks, for a total of 45 plots. Each plot consisted of 9 trees in 9 rows for a total of 81 trees, except in treatments 14 and 15, where there were only 41 trees due to the wider spacing. The inner 25 trees within each plot are permanent measurement trees. Trees that died after planting were replaced for the first three years. Volunteer shrubs and trees were hand-removed through 1991.

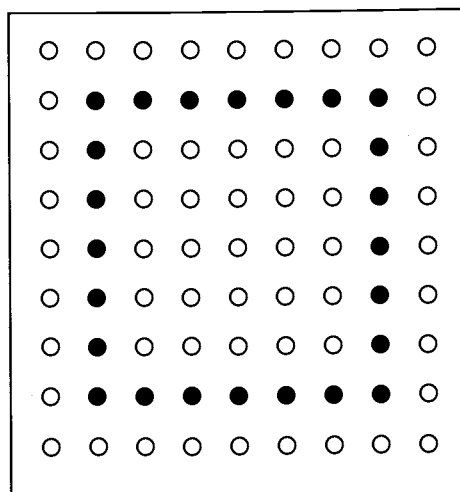
Table 4.1. Replacement series treatment descriptions. Treatments included in this study are marked with an asterisk (*).

Treatment	Douglas-fir proportion	Red alder proportion	Red alder planting ⁺	Spacing (m)	Red alder removed
1*	100	0	Immediate	3 x 3	--
2*	90	10	Immediate	3 x 3	no
3	90	10	Delayed	3 x 3	no
4	75	25	Immediate	3 x 3	no
5	75	25	Delayed	3 x 3	no
6	50	50	Immediate	3 x 3	no
7*	50	50	Delayed	3 x 3	no
8	50	50	Immediate	3 x 3	After 5 yrs
9	50	50	Immediate	3 x 3	After 10 yrs
10	25	75	Immediate	3 x 3	no
11*	25	75	Delayed	3 x 3	no
12	0	100	Immediate	3 x 3	no
13	0	100	Delayed	3 x 3	no
14*	100	0	--	4.2 x 4.2	--
15	0	100	Immediate	4.2 x 4.2	no

⁺Immediate = planted in year 1 (1986); Delayed = planted in year 6 (1991)

Five treatments within the replacement series were included in this study (Table 4.1). Six Douglas-fir trees in each plot were selected randomly for sampling from the second-outermost row of trees (Figure 4.1). These trees were chosen to avoid the permanent measurement trees, because the methods used in this study involved semi-destructive sampling. The outermost row was considered a buffer zone between plots. With six trees sampled within each plot, five plots per block, and three replicated blocks, this sampling protocol resulted in a total possible sample of 90 trees. In some plots with a low proportion of Douglas-fir, six suitable trees could not be identified; in these cases, five were used. Thus only a total of 79 trees were sampled.

Figure 4.1. Location of sample trees within plots. All sample trees were selected randomly from those indicated by solid dots.

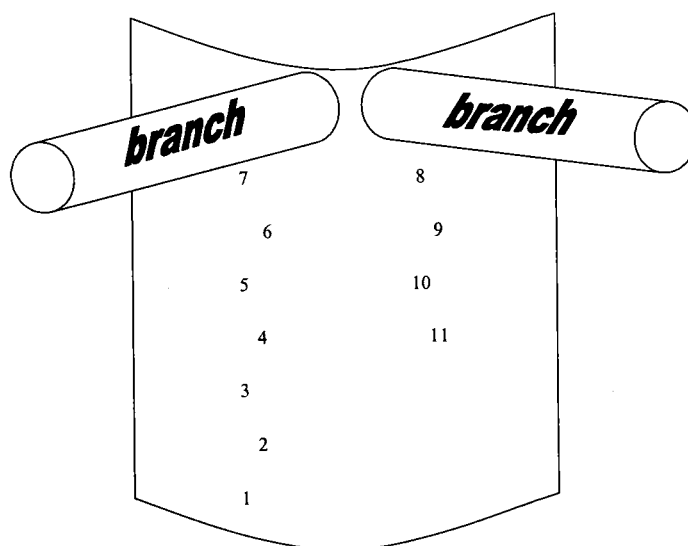


Pinning Method

To track incremental radial growth over the course of the growing season, the cambial pinning method, first described by 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, but did not penetrate already-formed xylem tissue. Pins were labeled with the Julian date (day of the year) 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. The process was repeated at 7- to 10-day intervals from mid-March to mid-September 2001, when the Douglas-fir trees were 15 years old. On each successive pinning day, the pin was inserted approximately 2 cm above and slightly to the left or right of the previous pin. This zigzag pattern continued until a

branch or other obstruction was reached; then the pattern continued downward at another radius approximately 45° around the circumference of the tree (Figure 4.2).

Figure 4.2. Location of pin insertion points in relation to one another. Numbers represent the order in which the pins were inserted.



To determine the approximate date that radial growth had terminated for the year, a band dendrometer was fit at breast height to one sample tree of intermediate size within each plot (Cattellino et al. 1986). Incremental circumferential growth was recorded from the dendrometers on each date of pinning. Pinning ended following three consecutive weeks of zero additional circumferential growth as indicated by the dendrometers.

Sample Analysis

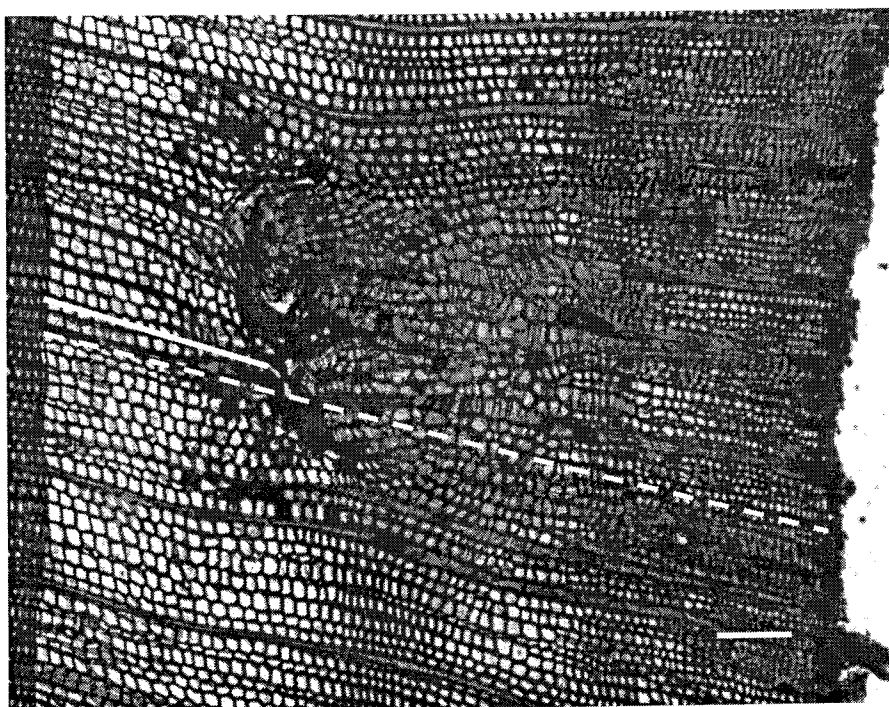
In October-November 2001, wood samples containing the tissue surrounding the pins were extracted using a chisel and mallet. The samples consisted of long strips of wood containing numerous pins and were at least one annual ring deep. The pins were removed and using a band saw, the wood samples were then 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 width of the 2001 annual ring and the distance from the inner edge of the 2001 annual ring to the pin wound (Figure 4.3). Measurements among samples were standardized by dividing the distance to the wound by total ring width to obtain percent total radial growth already completed by the date of pinning.

For each sample tree, percent latewood in the 2001 growth increment was determined. Latewood was defined according to Mork's definition (Denne 1989), as cells in which the double-cell wall thickness is at least twice the radial diameter of the lumen when viewed in cross-section. 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 was equal to (100 minus latewood percent) was considered to be the date of transition to latewood.

Figure 4.3. Method for measuring percent growth completed by date of pinning. The solid line indicates the radial distance from the start of the annual ring to the pin wound. The dashed line indicates the total ring width. Scale bar = 100 μm .

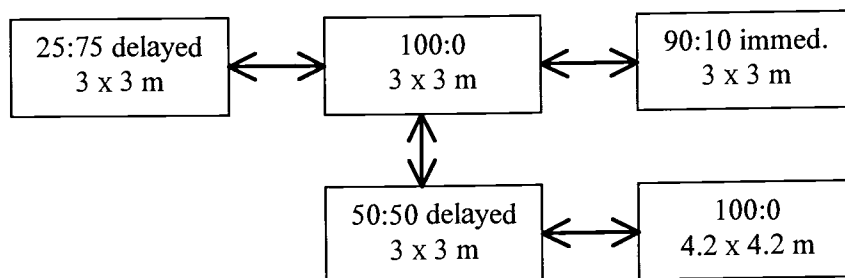


Data Analysis

Four specific comparisons were of interest (Figure 4.4). Two treatments where red alder planting was delayed, and one where red alder was planted immediately were compared to the pure Douglas-fir stand to evaluate the replacement effect of red alder competition on Douglas-fir cambial activity. To

evaluate additive effects of red alder, the 50:50 mixture with delayed red alder planting was compared to the widely-spaced pure Douglas-fir stand.

Figure 4.4. Comparisons of interest in the study of Douglas-fir cambial phenology. Species proportions are % Douglas-fir:% red alder.



Analysis of wood formation phenology was carried out for five thresholds of radial growth: 5%, 25%, 50%, 75%, and 95% of annual growth. To obtain these values, percent growth was linearly interpolated between consecutive pinning dates. The estimated dates that 5% and 95% growth were completed were used to define the dates when cambial growth began and ended, respectively.

Based on findings in other species showing that suppression affects the duration of cambial growth (Kozlowski and Peterson 1962, Baucker et al. 1998), we incorporated a variable to account for the effect of suppression into our model. Two 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 tree vigor, 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 with comparison of regression lines was used to determine differences among treatments in the dates when each of the five thresholds of radial growth were completed, while accounting for the effect of tree size (Table 4.3). Also, a repeated measures analysis was included to account for the effect of repeatedly sampling the same trees; an autoregressive (AR(1)) covariance structure for time series was selected. Percent latewood and timing of the transition to latewood were analyzed using ANCOVA as well. The Fisher procedure for multiple comparisons was used to protect confidence interval widths for estimated effects. Statistical analyses were performed with either SAS 8.0 (SAS Institute, Cary, NC) or S-Plus 2000 (MathSoft Inc., Cambridge, MA) software packages.

RESULTS

Phenology of Cambial Growth

Predicted treatment means (accounting for size and block effects) were all within two days of actual treatment means for all stages of annual radial growth (Table 4.2). Patterns of growth for the close- and wide-spaced monocultures and the 50:50 mixture were quite similar. On average, trees in the two pure Douglas-fir

stands and the 50:50 mixture began cambial growth on May 12 and 13, respectively. In contrast, the average dates of growth initiation in the 90:10 mixture with immediate red alder planting and in the 25:75 mixture with delayed alder planting were May 18 and May 23, respectively (Table 4.2, Figure 4.5).

Table 4.2. Observed and predicted (in italics, accounting for tree size and block effects) Julian date (days since Jan. 1) that each calculated percentage of radial growth of Douglas-fir was completed in 2001, by treatment (mean \pm SE). Species proportions are Douglas-fir:red alder. Values within a column with the same superscript are not significantly different at $\alpha = 0.05$.

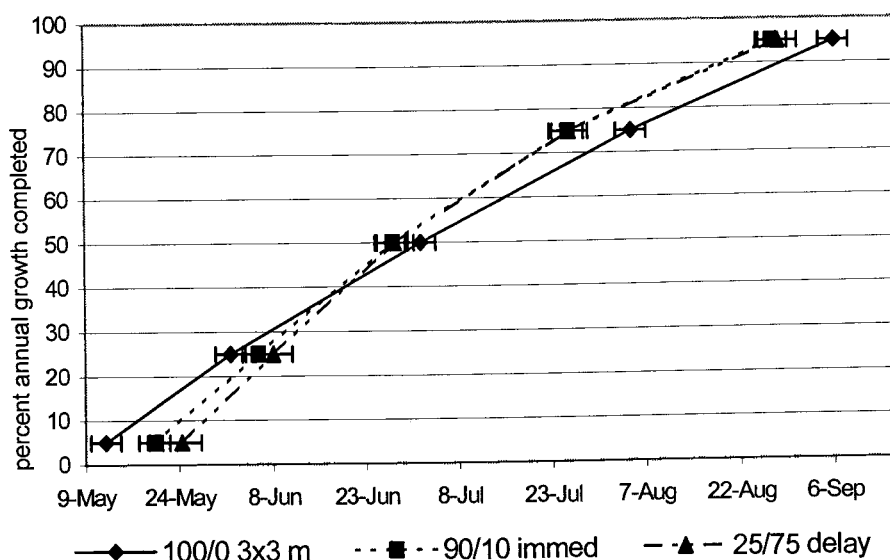
treatment	Level of growth				
	5%	25%	50%	75%	95%
100:0 3 x 3 m	133.1 (1.2) ^a	153.0 (1.7) ^a	183.8 (2.9) ^a	217.7 (2.5) ^{ac}	250.0 (1.4) ^a
	<i>133.2 (2.5)</i>	<i>153.2 (2.5)</i>	<i>183.9 (2.5)</i>	<i>217.8 (2.5)</i>	<i>250.1 (2.5)</i>
90:10 immed	139.7 (2.5) ^b	156.6 (2.0) ^a	177.8 (2.3) ^a	206.2 (3.0) ^b	239.4 (2.9) ^b
	<i>141.0 (2.6)</i>	<i>157.6 (2.6)</i>	<i>179.5 (2.6)</i>	<i>207.8 (2.6)</i>	<i>240.3 (2.6)</i>
50:50 delay	134.0 (2.5) ^a	152.3 (2.3) ^a	182.5 (2.8) ^a	214.9 (2.6) ^a	250.8 (2.4) ^a
	<i>133.4 (2.5)</i>	<i>151.8 (2.5)</i>	<i>181.8 (2.5)</i>	<i>213.2 (2.5)</i>	<i>250.1 (2.5)</i>
25:75 delay	144.9 (4.5) ^b	160.2 (4.1) ^a	179.3 (2.9) ^a	206.9 (3.6) ^b	241.1 (3.8) ^b
	<i>145.4 (3.1)</i>	<i>160.0 (3.2)</i>	<i>179.7 (3.0)</i>	<i>207.9 (3.1)</i>	<i>241.3 (3.1)</i>
100:0 4.2 x 4.2 m	133.5 (1.3) ^a	150.6 (2.3) ^a	190.4 (3.0) ^a	221.8 (2.7) ^c	254.6 (2.1) ^a
	<i>132.2 (2.9)</i>	<i>150.1 (2.7)</i>	<i>187.9 (2.8)</i>	<i>221.2 (2.5)</i>	<i>254.0 (2.6)</i>

No comparisons of interest between treatments were significant for the dates that 25% and 50% growth were completed ($P > 0.09$). However, trees in both the 90:10 (immediate) and 25:75 (delayed) treatments completed 75% of their annual radial growth at least 9 days earlier than trees in the pure Douglas-fir stand at 3 x 3 m spacing (Table 4.2).

On average, Douglas-fir trees in the 90:10 (immediate) and 25:75 (delayed) treatments completed annual growth on August 27 and 28, respectively. Trees in

the pure Douglas-fir stands and in the 50:50 (delayed) mixture continued growing substantially longer: the average date of completion of growth was September 6 for the closely-spaced Douglas-fir monoculture and the 50:50 mixture, and September 10 for the widely spaced monoculture (Table 4.2, Figure 4.5).

Figure 4.5. Estimated patterns of cambial growth of Douglas-fir for selected treatments, standardized for tree size. Species proportions are % Douglas-fir/% red alder and error bars are standard errors.



Results from the full model revealed that DBH accounted for little of the variation in timing of growth ($F_{1,258} = 1.4$, $P = 0.24$, Table 4.3). We hypothesized that the distribution of tree sizes was not independent of treatment, and that DBH and treatment thus were confounded effects in our model. Trees were the smallest on average in the two treatments in which trees had the shortest growing seasons

(Table 4.3). Across all treatments, tree DBH ranged from 7.6 to 25.5 cm, however, of the 11 trees with DBH < 10 cm, 9 were in either the 90:10 (immediate) or the 25:75 (delayed) treatments.

Table 4.3. Diameter at breast height (DBH) of Douglas-fir trees by treatment (mean \pm SE). Species proportions are Douglas-fir:red alder.

treatment	DBH (cm)
100:0 3 x 3 m	15.5 (0.9)
90:10 immed	11.0 (0.8)
50:50 delay	18.0 (1.0)
25:75 delay	13.5 (1.0)
100:0 4.2x4.2 m	17.4 (1.2)

To explore the possibility that DBH and treatment were confounded effects, we tested two reduced models, one in which the treatment variable was removed and one in which the DBH variable was removed. In both cases, the remaining effect was significant in explaining variation in growth (Table 4.4). The reduced model that disregarded tree size as an explanatory variable yielded similar results to the full model, but the magnitudes of the treatment effects were slightly different (data not shown).

Regardless of treatment, smaller Douglas-fir trees began cambial growth later and completed growth earlier (Table 4.5, Figure 4.6). 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. According to the reduced model, the smaller tree would begin growing 8 days later

and end growing 14 days earlier than the larger tree. These differences are comparable to the differences estimated by the full model for the pure Douglas-fir stand and the 90:10 and 25:75 mixtures.

Table 4.4. Comparison of model effects for three models tested. Variables are defined as follows: *day*, estimated day that the percent growth indicated by the variable *stage* was completed; *dbh*, diameter at breast height; *trt*, treatment; *stage*, an indicator for 5, 25, 50, 75, or 95% growth.

Full Model

$$day = dbh + trt + stage + trt*stage$$

Effect	Num df	Den df	F	P
<i>dbh</i>	1	258	1.40	0.24
<i>trt</i>	4	8	0.61	0.67
<i>stage</i>	4	258	1306.09	< 0.01
<i>trt*stage</i>	16	258	4.03	< 0.01

Reduced Model A

$$day = trt + stage + trt*stage$$

Effect	Num df	Den df	F	P
<i>trt</i>	4	8	1.28	0.35
<i>stage</i>	4	259	1302.08	< 0.01
<i>trt*stage</i>	16	259	4.03	< 0.01

Reduced Model B

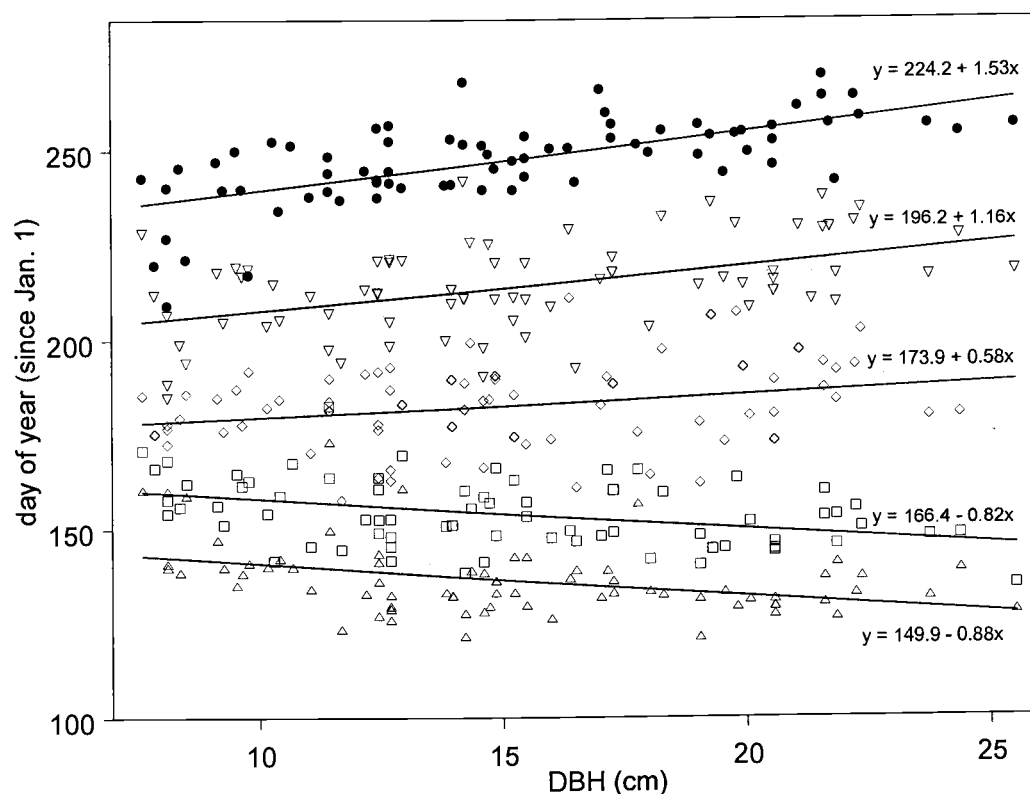
$$day = dbh + stage + dbh*stage$$

Effect	Num df	Den df	F	P
<i>dbh</i>	1	2	3.29	0.21
<i>stage</i>	4	271	56.08	< 0.01
<i>dbh*stage</i>	4	271	17.63	< 0.01

Table 4.5. Regression equations and predicted values for trees of two sizes for the day when five levels of cambial growth were completed. General model is $\text{day} = \text{dbh} + \text{stage} + \text{dbh} * \text{stage}$ where stage is an indicator for the percent growth completed.

stage (% growth)	Equation	P <	R ²	Predicted for dbh of	
				10.6 cm	19.9 cm
5	$\text{day} = 149.946 - 0.885 * \text{dbh}$	0.01	0.17	140.6 (May 19)	132.4 (May 11)
25	$\text{day} = 166.394 - 0.815 * \text{dbh}$	0.01	0.17	157.7 (June 5)	150.1 (May 29)
50	$\text{day} = 173.930 + 0.581 * \text{dbh}$	0.05	0.06	180.0 (June 28)	185.4 (July 3)
75	$\text{day} = 196.198 + 1.164 * \text{dbh}$	0.01	0.20	208.5 (July 26)	219.2 (Aug 6)
95	$\text{day} = 224.233 + 1.534 * \text{dbh}$	0.01	0.41	240.4 (Aug 27)	254.6 (Sep 10)

Figure 4.6. Observed (symbols) and predicted (lines and equations) dates by which various levels of growth were completed as a function of tree size in Douglas-fir. Δ = 5% growth; \square = 25% growth; \diamond = 50% growth; ∇ = 75% growth; \bullet = 95% growth.



Transition to Latewood Formation

Trees began producing latewood from about June 5 at the earliest and August 24 at the latest; the mean date was July 5. Treatment did not affect the timing of latewood transition ($P = 0.28$); however, small trees began producing latewood earlier than large trees ($F_{1,46} = 9.83$, $P < 0.01$, Table 4.6). Our model estimated that 10-cm DBH trees began producing latewood 18 days earlier than 20-cm trees; in the monoculture stand, for instance, the smaller trees would transition to latewood on about July 2, compared to July 21 for the larger trees.

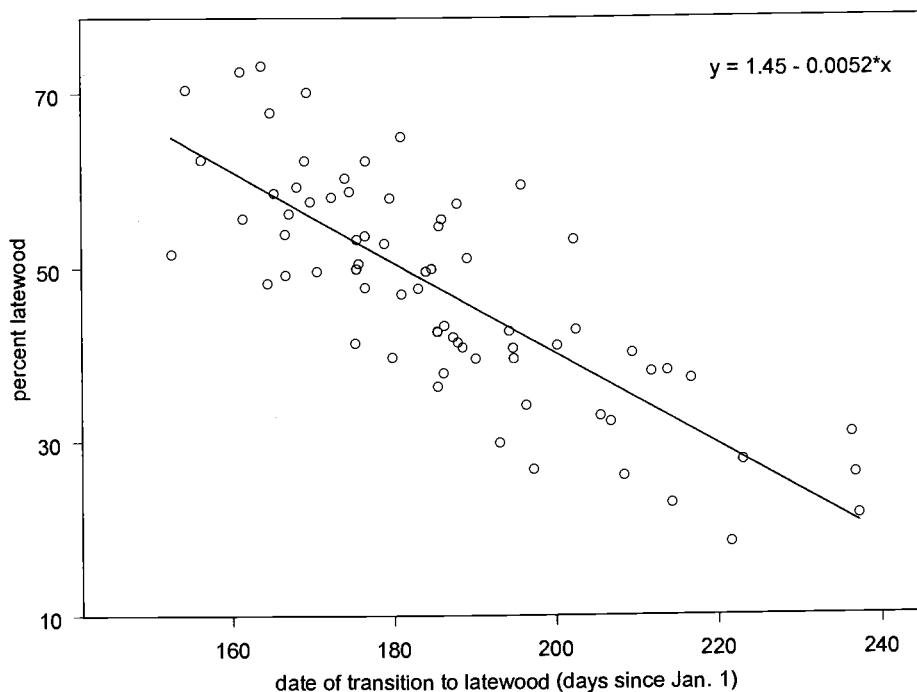
Percent Latewood

Among all trees, percent latewood ranged from 18 to 73%, with a mean of 46%. Treatment means ranged from 38 to 53%. No difference in percent latewood was detected among treatments ($P = 0.46$; data not shown). Percent latewood decreased with increasing tree size ($F_{1,51} = 8.27$, $P < 0.01$, Table 4.6): our model predicted an 11-point difference in percent latewood for 10-cm and 20-cm DBH trees. Thus, in the Douglas-fir monoculture, it was estimated that that a 10-cm DBH tree would have 50% latewood, whereas a 20-cm DBH tree would have only 39% latewood. Percent latewood was strongly and negatively correlated with the date of transition to latewood ($P < 0.0001$, $R^2 = 0.66$, Figure 4.7).

Table 4.6. Model equations, coefficients, and statistical parameters for determining the influence of treatment (TMT) and tree size (DBH) on percent latewood (%LW) and date of latewood transition (DAY). Subscripts for TMT coefficients refer to treatment numbers in Table 4.1.

Model	$\%LW = \beta_0 + \beta_1 \cdot DBH + \beta_2 \cdot TMT$			$DAY = \beta_0 + \beta_1 \cdot DBH + \beta_2 \cdot TMT$		
Coefficient	Value	SE	P <	Value	SE	P <
β_0	66.8	7.9	0.46	152.2	11.7	0.001
β_1	-1.1	0.4	0.006	1.8	0.6	0.003
$\beta_2 \cdot TMT_1$	-5.5	4.2	0.19	12.9	6.1	0.04
$\beta_2 \cdot TMT_2$	-7.8	4.8	0.11	6.8	7.3	0.35
$\beta_2 \cdot TMT_7$	0.0	--	--	0.0	--	--
$\beta_2 \cdot TMT_{11}$	-3.5	4.9	0.48	6.1	7.1	0.39
$\beta_2 \cdot TMT_{14}$	-0.6	4.3	0.88	10.7	6.6	0.11

Figure 4.7. Observed (symbols) and predicted (line) percent latewood as a function of date of transition to latewood.



DISCUSSION

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 and Mitchell 1980, Li and Adams 1994). The reason for this difference is unclear; however misinterpretation of the wound tissue formed by the pinning method is a possibility. Also, drought conditions during the 2000-01 winter could have delayed the onset of growth by forestalling the rehydration of the cambial zone in the spring (Savidge 2000). The dates of cessation of growth were generally intermediate between those reported by Vargas-Hernandez and Adams (1994) and Emmingham (1977).

In the current study, smaller Douglas-fir trees began growing later and ended growing earlier than larger trees. These data concur with the findings in other conifer studies (Kozlowski and Peterson 1962, Baucker et al. 1998), which have shown that suppressed trees have a shorter season of cambial growth than dominant trees. Xylem growth resumes in springtime as auxin is translocated from buds in the live crown to the vascular cambium and triggers cambial cell division (Wilcox 1962). 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 and 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.

Had differences in light intensity, temperature, soil moisture or some other environmental variable been the causal mechanism for the delayed onset of growth, then that effect would have been present in Douglas-fir trees of all sizes within a given treatment, assuming that environmental conditions were consistent within individual treatments.

The mechanism driving the earlier cessation of growth among smaller trees is less clear. Short days and low temperatures are known to cause cambial inactivity (Waisel and Fahn 1965), however, in this experiment these variables would not have been different among treatments. 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 also were less extensive than those of larger trees.

Trees began producing latewood within the range of dates reported for Douglas-fir in other studies (Kennedy 1961, Emmingham 1977, Brix and Mitchell 1980, Vargas-Hernandez and Adams 1994). However, treatment averages for percent latewood were somewhat higher than those reported by others (Kennedy 1961, Brix and Mitchell 1980). Different measurement methods could account for the difference. As reported by Kennedy (1961) and Vargas-Hernandez and Adams (1994), percent latewood was more strongly dependent upon the date of transition to latewood than upon the date that cambial growth (and thus latewood growth) ended. Vargas-Hernandez and Adams (1994) suggested that low rainfall contributes to an early transition to latewood. Drought conditions in the winter of

2000-01 may have accelerated the onset of summer water stress, thus producing earlier latewood transitions than would otherwise have occurred.

Competition from red alder may account for the differences observed in the duration of cambial growth. The smaller trees with shorter growing seasons were concentrated in two treatments, the 90:10 Douglas-fir/red alder mixture with immediate alder planting and, to a lesser degree, the 25:75 mixture with delayed alder planting. In the treatment in which red alder was planted immediately, the red alder rapidly outgrew the conifers. Consequently, the Douglas-fir trees in those plots are now heavily suppressed, despite the low proportion (10%) of red alder. Where red alder planting was delayed, evidence of suppression, in terms of both radial growth patterns and tree size, is present in the 25:75 mixture, but not in the 50:50 mixture. Therefore, it is possible that a threshold of red alder competition below which Douglas-fir growth is reduced may exist somewhere between these two species proportions.

Despite differences in initiation and cessation of cambial growth among these treatments, timing of latewood transition and percent latewood were uniform across them (when considering trees of similar sizes). Though wood density was not measured directly, this result suggests that density would be consistent among Douglas-fir trees regardless of the level of competition from red alder.

From the data in this experiment, we cannot determine whether the differences detected between the pure Douglas-fir stand and the two mixtures are due merely to canopy position or due to the effect of red alder, because the

presence of red alder seems to be associated with smaller Douglas-fir trees. A differently-designed study could control this confounding effect by sampling only trees of similar diameters (perhaps within a 5-cm range rather than a 15-cm range as analyzed here).

This study's scope of inference is highly limited. 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, due to the fact that 2001 was a drought year and that this could have affected the overall duration of cambial activity in all trees.

CONCLUSIONS

Competitive status influenced cambial phenology in 15-year-old Douglas-fir trees. Trees that were suppressed, as indicated by small diameters, initiated cambial growth late and ceased growth early. Both simultaneous planting of red alder and high proportions of red alder planted five years after Douglas-fir resulted in these conditions. Percent latewood was highly variable among trees, though it was higher in smaller trees. This is evidently a result of an earlier transition to

latewood production in smaller trees. However, these differences were consistent across treatments, and thus the effect of competition from red alder on latewood formation was not detected.

Faster-growing trees appear to produce a lower proportion of latewood, which would likely result in a decrease in overall density. However, trees that produced the most latewood grew very little during the year of this study and are likely to succumb to competition pressure if stand development continues along its current trajectory.

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CHAPTER 5 : CONCLUSION

Wood variation is inherent within a species and even within an individual tree, and is a result of many factors. Variations in wood structure become matters of wood quality if they are important to end product function and value. In this study, we examined how some of the aspects of wood structure that are most important in determining the value of red alder and Douglas-fir wood vary with stand structure. In this section I will present a brief synopsis of our results and discuss their practical implications.

Our results indicate several general conclusions with regard to stand management. The decision whether to allow red alder to establish simultaneously with Douglas-fir, or to wait several years has large implications not only in terms of stand structure, but also with respect to wood quality. When red alder and Douglas-fir were planted in the same year, the only treatment in which Douglas-fir growth was satisfactory was that with only 10% red alder. Even in this treatment, many Douglas-fir trees were highly suppressed. For those Douglas-fir trees that were growing well, wood quality attributes (percent latewood and branch/knot characteristics) were similar to those of trees in pure Douglas-fir stands. Thus, if red alder density is low enough to permit Douglas-fir growth, the difference between the effects of interspecific and intraspecific competition on Douglas-fir wood quality is small. Assuming that the suppressed Douglas-fir trees die in the near future, the stand may have the same total tree density as a pure stand that is

precommercially thinned in the next few years, with the residual Douglas-fir trees being similar in wood quality in both treatments.

For a forest manager interested in the productivity of both species, the choice then becomes whether to plant (or permit to regenerate naturally) a very low density of red alder simultaneously with Douglas-fir, or to wait at least five years to plant the alder. The implications of this choice for red alder wood quality are large. Planting red alder immediately results in trees that have a high total wood volume, but poor stem form. There are many multiple-stemmed trees, with each stem smaller in diameter than single-stemmed trees, and crown bases are low. It is likely that these trees will be destined for pulp logs, which have a much lower market value. By delaying the planting of red alder for five years, it appears that most of these negative wood quality effects can be mitigated. This delayed planting may result in red alder logs that can be sold as sawlogs at a higher price. At the same time, at least through stand age 15, delayed red alder planting has few negative impacts on Douglas-fir wood quality. So, the decision whether to delay red alder planting may ultimately rest on the manager's goals and desired management intensity. Delayed red alder planting is more intensive, as it requires an additional stand entry. It is likely to produce red alder material of higher value but lower volume than immediate red alder establishment.

If delayed red alder establishment is chosen, then the decision must be made as to the proportion of each species for which to manage. While species proportion does not seem to affect red alder wood quality (at least through stand age 15) when

alder is planted five years later than Douglas-fir, there are a few considerations with respect to Douglas-fir crown recession and subsequent knot patterns. The proportion of Douglas-fir of total stand density was inversely related to the proportion of live branches on the basal 16-ft Douglas-fir stem. In the pure Douglas-fir stands, crowns had receded to near the top of this stem section, whereas when red alder dominated the species mixture, Douglas-fir crowns were still quite low. The lifespan of a branch affects both the integrity and size of the knot it produces in future years. If dead branches do not self-prune, as is the case with Douglas-fir, then loose knots can form as the stem increases in diameter around the dead branch. The presence of loose knots makes wood unsuitable for high-grade veneer or lumber (WWPA 1998). Conversely, live branches continue to grow in diameter, producing a future knot that is tight (and thus less detrimental to wood strength), yet larger, which could devalue the product. At the time of this study, very few branches were large enough to create knots that would reduce lumber grade. However, in the treatment with the highest proportion of red alder, the fact that nearly half of all the Douglas-fir branches were still alive may mean that the average knot size on those trees will be larger when the trees reach harvest size. At the same time, it can be expected that there will be more small, loose knots on logs coming from stands that are mostly Douglas-fir.

The experimental plots in which this study was carried out were highly controlled in terms of density and tree spacing. As a result, the effects of interspecific and intraspecific competition can be quantified. In a typical managed

stand, it is likely that tree spacing and arrangement would be less uniform, especially if red alder regenerates naturally rather than being planted. Regardless, the results of this experiment can still be relevant to a commercially managed stand.

Finally, it is necessary to reemphasize the importance of site quality and time on these findings. This experiment was carried out on a site with some of the richest soil and highest precipitation levels in the region, making red alder growth especially rapid. On a site with less moisture, or less soil nutrient availability, the interactions between the two species probably would have been quite different. Because the wood quality attributes that we measured are all driven by the trees' competitive status, a similar study on a different site would likely produce quite different results. Also, it is important to keep in mind that all conclusions are based on 15-year-old stands, and that some results may change as stands age and the trajectories of red alder and Douglas-fir growth change.

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