GROWTH AND YIELD OF DOUGLAS-FIR & WESTERN HEMLOCK IN PURE AND MIXED PLANTED STANDS: RESULTS AT AGE 12 FROM THE SMC TYPE III TRIALS

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SILVICULTURE ▪ NUTRITION
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COLLEGE OF FOREST RESOURCES
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SEATTLE WASHINGTON 98115-2100

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MARIANO M. AMOROSO, MS.

ERIC C. TURNBLOM, ASSOCIATE PROFESSOR, AND SMC SILVICULTURE PROJECT LEADER

DAVID G. BRIGGS, PROFESSOR, AND SMC DIRECTOR

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ABSTRACT

The objectives of this study were to assess differences in growth and productivity between Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) growing both in pure and mixed plantations across a wide range of planting densities. Two type III installations, each consisting in a set of monocultures and 50/50 mixtures of Douglas-fir and western hemlock, were studied at two locations on the Olympic peninsula in the state of Washington. This research examined growth and yield performance for the first 12 growth seasons after establishment at three density levels (200, 450 and 700 TPA).

At age 12, as components of the mixed stands, Douglas-fir exhibited greater height, diameter, and individual tree volume than western hemlock at all densities. Compared with performance in pure stands, Douglas-fir exhibited greater diameter and height growth at the 700 TPA density level while western hemlock, in contrast, experienced reduced growth at all densities. At 200 and 450 TPA the monocultures resulted in higher volume per acre than the mixed stand, but at 700 TPA the mixed stand appeared to be just as productive as the pure stands. At 700 TPA, Douglas-fir in the mixture averaged the same volume per acre as the pure hemlock stand. The increase in productivity by the mixture at high densities seems to have been a result of the partial stratification observed and probably to a better use of the site resources. Because of this, less interspecific competition was probably experienced in the mixed stand than intraspecific competition in the pure stands. Even when interactions occurred at low and medium densities, they may not have been of large enough magnitude to cause the mixture to outyield the pure plantations. This shows the important role density plays on the productivity of mixed stands, and thus in comparing mixtures and pure stands.

CHAPTER 1: INTRODUCTION

When timber production is the primary objective of management, there is a clear tendency to favor monocultures of the most productive species. The main reason for this is the simplification of management by the use of a single component in the stand, but also, and no less important, because less is known about planted mixed stands and the interactions between species. In contrast, when mixed species stands are favored, the objectives usually include wildlife conservation, aesthetics, resistance to wind damage, risk reduction or compensatory growth, and protection from disease and insect outbreaks. A sacrifice in productivity is usually assumed to occur as a consequence of the use of mixed species stands (Kelty 1992).

This research examines the validity of this assumption including the possibility of achieving equal or greater total yields when using mixed species planted stands as opposed as monocultures of equal densities. Ecological theory suggests that species in a mixture may exploit resources of a site more completely and efficiently than a single species would be able to do, leading to a greater overall productivity (Vandermeer 1989). Even though this has been found to be possible in many situations, it is not always likely to happen. In order to achieve greater productivity in mixed stands, the species comprising the stands need to show differences in their requirements (niches) and the way they use site resources, and/or positively affect the growth of each other (Vandermeer 1989). This concept of niche separation implies that if two species are too similar in their requirements they would eventually compete intensely to exclude one from another, but if competition is sufficiently weak, the two species may coexist (Harper 1977).

The principal mechanism that has been used in forestry to increase production in mixed stands is to increase nutrient availability (Kelty and Cameron 1995) primarily through the introduction of nitrogen-fixing species in mixtures (Binkley 1983, 1992, DeBell et al., 1997, Khanna 1997, Bauhus et al., 2000, Balieiro et al., 2002). Furthermore, different photosynthetic efficiency of foliage in the tree species present in a mixture along with differences in height growth patterns, form, phenology, and root structure have been suggested as possible causes leading to a mixed stand having overall productivity greater than a monoculture (Kelty 1992). As a consequence of this difference in shade tolerance, the stand may experience less intense interspecific than intraspecific light competition with a subsequent increase in the productivity. Such a stratified canopy with shade tolerant species underneath a shade intolerant species would, in theory, maximize the use of light, because of the increase in light interception and light efficiency (Kelty 1992), leading to greater total productivity than pure stands (Smith et al., 1986). This type of response has been found in studies by Assmann (1970), Wierman and Oliver (1979), Kelty (1989), Brown (1992), Montagnini et al., (1995), DeBell et al., (1997), and Man and Lieffers (1999).

Previous research has found that Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) differ in their response of photosynthesis to irradiance, i.e. shade tolerance (Lewis et al., 2000) and height growth. When growing together, Douglas-fir, as a shade intolerant species, tends to occupy the upper part of the canopy, while western hemlock, capable of living at lower light levels (shade tolerant behavior), develops in the understory (Oliver and Larson 1996). This stratified canopy structure, even in even-aged stands, tends to develop naturally because sun-adapted species generally have greater rates of juvenile height growth than shade tolerant species (Kelty 1992, Oliver and Larson 1996, Smith et al., 1997). There is abundant evidence of this different height growth pattern, and consequent stratification, for the two species in natural stands (King 1958, Scholz and Smith 1975, Oliver and Larson 1996). Wierman and Oliver (1979) found that in even-aged mixed natural stands of these two species, Douglas-fir dominated western hemlock by becoming significantly taller after about 20 years, Douglas-fir suppressed competing hemlocks, and that basal area per acre averaged more in the mixed stands than the pure stands; the authors also conclude that mixed stands appeared to yield greater volume per acre than pure stands.

In accordance to what previous studies have shown, it is likely for these two species to exhibit “ecological combining ability” and have greater productivity in a mixed stand than the pure stands of its components. However, all of the previous research on Douglas-fir and western hemlock mixtures has examined natural stands. The questions are whether the patterns of stratification and growth of these species observed in natural stands also occur in plantations, and how trees may be influenced by stand density; both questions have not been addressed yet.

The objectives of this study were to assess differences in growth and productivity between Douglas-fir and western hemlock growing both in pure and mixed plantations across a range of planting densities. This study, consisting of pure Douglas-fir, pure western hemlock, and a 50/50 mixture of these two species combined with three density levels, provides a wide array of competitive regimes.

CHAPTER 2: OBJECTIVE AND HYPOTHESES

The objective of this study was to assess for differences in growth and productivity between Douglas-fir and western hemlock growing both in pure and mixed plantations at three density levels. Specifically this study will either prove or disprove the following null hypotheses:

1. Douglas-fir and western hemlock have equal initial height growth rates growing both in single species and mixed planted stands, and do not stratify in plantations.

2. The allometry of the species does not change at different densities and age, nor does it when they grow together in comparison with their growth in pure stands.

3. Tree crowns do not respond to different levels of growing space (i.e., to different light environments resulting from the different structure in single and mixed species stands).

4. Interspecific and intraspecific competition are the same in pure and mixed planted stands and are not affected differently when density changes.

5. Mixed species plantations are not as productive as single species plantations.

6. Initial density does not affect interactions between species, i.e., the yield of mixed plantations is equal to the sum of the expected yield for each component across all densities.

CHAPTER 3: METHODOLOGY

A. Experimental Sites

This study was conducted at two sites (Brittain Creek and Forks) located on the Olympic peninsula in the state of Washington, US. Brittain Creek is located in Gray's Harbor County (47º13' N and 123º52' W), while Forks is located in Clallam County (48º2' N and 124º23' W). Brittain Creek has a mean annual precipitation of approximately 114.25 inches (with 79.34 inches concentrated between the months of September and February) and a mean annual temperature of 49.5 F (Western Regional Climate Center 1997). The site is located at an elevation of 360 feet, and the site index is 125 ft at 50 years corresponding to a site class II (King 1966). The soil at this site, a Willaby silt loam 1-15 % slope, consists of very deep, moderately well drained soils from the Willaby series formed in glacial drift (Pringle 1986). Forks has a mean annual precipitation of approximately 119.95 inches (with 83.34 inches concentrated between the months of September and February) and a mean annual temperature of 49.7 F (Western Regional Climate Center 1997). This site is located at an elevation of 400 feet, and the site index is 120 ft at 50 years corresponding to a site class of II (King 1966). The soils at this site are classified as part of the Klone-Ozette-Tealwhit complex 0-15% slope from the Klone series, and are characterized as very deep, well drained soils formed in poorly sorted glacial outwash (Halloin 1987).

The region where both sites are located is ecologically classified by Franklin and Dyrness (1973) as "the *Picea stichensis* Zone". It is described as coniferous forest stands mainly composed of *Picea stichensis*, *Tsuga heterophylla*, *Thuja plicata*, and *Pseudotsuga menziesii*. In recently disturbed areas, *Alnus rubra* appears as one of the most abundant tree species. The understory composition, mainly composed of ferns, cryptogams, shrubs and dicotyledonous herbs, varies depending on the site.

These two study sites are part of a number of research installations established by the Stand Management Cooperative (SMC) across the Pacific Northwest with the objective of designing, establishing, and maintaining a regional program of integrated research on various aspects of intensive stand management (Maguire et al., 1991). Within this program are Type III installations; areas operationally planted at a wide range of spacings to provide experimental material for future research. The two installations chosen for this study were established and planted in January 1990 on land that was scheduled for reforestation and received no or uniform site preparation. The planting stocks used at both sites were 2-1 Douglas-fir and 1-1 western hemlock seedlings. Plantation establishment was intended to apply the best available technology (site preparation, genetically improved stock, and brush control) so that the future development of these plantations will be typically of the best regeneration practices presently available.

B. Experimental Design

At each of the experimental sites, a block containing three installations (sub-blocks) was established. Species composition, consisting of pure Douglas-fir, pure western hemlock, and a 50/50 mix of these two species, was then randomly assigned among the three installations. Within each of these installations, six areas of at least three acres in size were delineated. These areas were as contiguous as site uniformity permitted, and were laid out to achieve maximal uniformity within and among installations. Boundaries were flagged and plot corners were set with stakes. One of six initial desired planting densities (100, 200, 300, 440, 680, and 1210 trees per acre) was randomly assigned to each area (experimental units), giving the experiment a Complete Randomized Block Split Split-Plot Design. In each of these experimental units, a one acre-plot was located yielding 36 plots between both sites. The 1-ac plots include a buffer strip and a Measurement Sample Plot (MSP), the size of which varies depending on the target spacing in each spacing block. The MSP dimensions, shown in Table 3.1, were selected as multiples of the target spacing for each block (Maguire et al., 1991).

Table 3. 1: Measurement Sample Plot size by spacing.

Spacing	Trees per acre	# Rows	Plot side (ft)	Plot size (acres)	# Trees
21	100 (99)	7	147	.496	49
15	200 (194)	8	120	.331	64
12	300 (303)	9	108	.268	81
10	440 (435)	10	100	.230	100
8	680 (681)	13	104	.248	169
6	1210 (1210)	16	96	.212	256

C. Measurements and Field Data Collection

Basal diameter and diameter at breast height (DBH) were measured on all trees. Basal diameter was measured 7 inches above the ground line using a caliper until trees reached breast height, while DBH measurements were done by caliper and d-tape (to the nearest 0.1 inch). Total height (to the nearest 0.1 foot), height to the base of the live crown (to the nearest 0.1 foot), and crown width (two crown widths one in the east-west plane and the other in the north-south plane were measured to the nearest 0.1 foot) were also measured on a sub sample of 42 trees drawn from the diameter distribution including the smallest and the largest trees on each plot. Mortality and its possible causes were recorded as well as any other relevant comment on each tree. Four measurements taken on a 2-year cycle and a last one on a four-year cycle were available for analysis.

During the last measurement, some plots at higher densities could not be measured for crown width because the crowns of adjacent trees were very close to each other making the determination of tree crown limits difficult.

D. Data Analysis

As already noted, recent measurements of crown width at higher densities could not be taken. In these cases, crown widths were predicted using the equations suggested by Paine and Hann (1990), and Hann (1997). To be sure the predictions were accurate, crown widths for all trees with actual measurements were predicted and plotted against the measured values to check for deviations.

Heights for all the trees in each plot were estimated from non-linear height-diameter equations fit by species to the 42 height trees measured in the plot at any given time.

Based on the variables measured in the field, the following individual tree attributes were derived: basal area, crown base area, crown volume, height-diameter ratio, crown ratio, and tree volume. Crown cross-sectional shape was assumed to be circular and the crown diameter used was the geometric mean of the two crown widths taken in the two cardinal directions. Crown volume was calculated assuming the crown as a paraboloid based on field observations and what has been suggested in the literature for young trees (Mawson et al., 1976, Biging and Wensel 1990, Roeh and Maguire 1997). Tree volume was calculated using the following equations depending on the species:

<u>For Douglas-fir (Bruce and de Mars 1974)</u>

$$\textbf{Volume (V)} = k * (DBH)^2 * Ht * f$$

Where:

V = total volume including stump and top (cubic feet)

k = 0.005454154 (feet ^{2}/inches ^{2})

DBH= diameter at breast height (inches)

Ht = total height (feet)

f = form factor

with

$$f = (0.406098 * (Ht - 0.9)^2) / (Ht - 4.5)^2 - (0.0762998 * DBH * (Ht - 0.9)^3) / (Ht - 4.5)^3 + (0.00262615 * DBH * Ht * (Ht - 0.9)^3) / (Ht - 4.5)^3$$

for trees between 6.5 and 18 feet tall, and

$$f = 0.480961 + (42.46542 / (Ht)^2) - (10.99643 * DBH / (Ht)^2) - (0.107809 * DBH / Ht) - (0.00409083 * DBH)$$

for trees taller than 18 feet.

<u>For western hemlock (Flewelling and Raynes 1993)</u>

$$\textbf{Volume (V)} = e^{(-6.464 + 1.914 * (\log (DBH)) + 1.173 * (\log (Ht)) - 0.0115 * DBH)}$$

Where:

V = total volume including stump and top (cubic feet)

DBH= diameter at breast height (inches)

Ht= total height (feet)

Mean values by plot and measurement number were calculated for all the variables described previously, as well as for basal area per acre, volume per acre, quadratic mean diameter (QMD) and Stand Density Index (Reineke 1933, Stage 1968).

Because the targeted planting densities were met with variable success in the field at the two sites, comparisons among plots with the same density at the six fixed initial planting densities were not possible. Instead, a regression analysis approach was used in which models for the variables under analysis would be built to predict values at any given year and density within the range of final densities and the time frame of the study. The independent variables in the models were Trees per acre and Age (since planting). In addition, because one of the objectives of this study was to assess the behavior of each species in both pure and mixed stands, two categorical (dummy) variables were included in the model; one corresponding to “species” to differentiate between Douglas-fir or western hemlock in the pure stands, and another one corresponding to “component” to differentiate between the two species when growing within the mixtures. The full quadratic response surface models included the independent and categorical variables mentioned above and all the possible interactions among them. The general model is presented as follows:

$$\mathbf{Y = b_0 + b_1 (c1) + b_2 (c2) + b_3 (sp1) + b_4 (sp2) + b_5 (tpa) + b_6 (age) + b_7 (c1*tpa) + b_8 (c2*tpa) + b_9 (sp1*tpa) + b_{10} (sp2*tpa) + b_{11} (c1*age) + b_{12} (c2*age) + b_{13} (sp1*age) + b_{14} (sp2*age) + b_{15} (tpa*age) + b_{16} (tpa*tpa) + b_{17} (age*age) + b_{18} (c1*tpa*age) + b_{19} (c2*tpa*age) + b_{20} (sp1*tpa*age) + b_{21} (sp2*tpa*age) + b_{22} (c1*tpa*tpa) + b_{23} (c2*tpa*tpa) + b_{24} (sp1*tpa*tpa) + b_{25} (sp2*tpa*tpa) + b_{26} (c1*age*age) + b_{27} (c2*age*age) + b_{28} (sp1*age*age) + b_{29} (sp2*age*age)}$$

Where:

Y = response (dependent) variable (mean diameter at breast height, or quadratic mean diameter, or mean total height, or mean crown length, or mean crown area, or mean individual tree volume, or basal area per acre, or volume per acre)

c1 = dummy variable used to indicate Douglas-fir as a component of the mixed stands (1 = Douglas-fir in mixture, 0 otherwise).

c2 = dummy variable used to indicate western hemlock as a component of the mixed stands (1 = western hemlock in mixture, 0 otherwise).

sp1 = dummy variable used to indicate Douglas-fir as the single component in the pure stands (1 = pure Douglas-fir stands, 0 otherwise).

sp2 = dummy variable used to indicate western hemlock as the single component in the pure stands (1 = pure western hemlock stands, 0 otherwise).

tpa = density expressed in number of trees per acre.

age = plantation age in years.

$\mathbf{b_1}$ to $\mathbf{b_{29}}$ = ordinary least squares parameter estimates for each variable and interaction terms.

Using this general model form, quadratic response surfaces were fit using multiple regression analysis to the dependent variables. The plot of the residuals against predicted values indicated that all the models needed transformation of the response variable due to non-constant variance. Models for all the variables involved in the analysis were found to be highly significant. The largest statistically significant hierarchical models with their corresponding coefficients and significance levels for all the terms present in the model are shown in the Appendix.

Utilizing these models, values for three chosen density levels (200, 450 and 700 trees per acre) were initially predicted at three ages (4, 8 and 12); additional analyses required predictions for other densities as well as for other ages. Because one of the hypotheses was to test differences among treatments not only at a single density but also across the three proposed densities, simultaneous confidence intervals were constructed using Bonferroni's procedure at the 0.05 significance level. Statistical analyses were made using the SAS package for Windows V8 (SAS Institute 1999-2001).

The yield of pure and mixed stands is usually compared on a relative basis, thus the effects of combining the two species were evaluated by comparing the yield of each species in the mixture with its yield in monoculture as per Harper (Harper 1977). Yield variables for this analysis were basal area and volume per acre. The relative yield (RY) of each species and the relative yield total (RYT) were calculated as:

$$\mathbf{RY}_{\text{Douglas-fir}} = \frac{\text{yield of Douglas-fir in mixture}}{\text{yield Douglas-fir in monoculture}}$$

$$\mathbf{RY}_{\text{western hemlock}} = \frac{\text{yield of western hemlock in mixture}}{\text{yield of western hemlock in monoculture}}$$

$$\textbf{Relative Yield Total (RYT)} = \mathbf{RY}_{\text{Douglas-fir}} + \mathbf{RY}_{\text{western hemlock}}$$

CHAPTER 4: RESULTS

This paper presents results for individual tree and stand development in terms of height, diameter, crown volume, basal area, and volume. Additional results and factors studied, mortality patterns, crown ratio, crown width, growth efficiency, stand density index, are reported elsewhere (Amoroso 2004).

A. General

Table 4.1 summarizes mean growth statistics at age 12 for the two pure stands and the mixed stand at the three chosen densities. At this age, as expected, diameter had an inverse relationship with density in all situations. Height, instead, was found to have different responses with density depending on the stand composition. Both basal area and volume per acre increased with density and there were changes in terms of the most productive stand composition at different densities. More detailed and deeper analyses for all the variables studied are presented later in the sequel.

In what follows, pure Douglas-fir stands will be denoted as DF, pure western hemlock stands as WH, and the mixed stands as MIX. Douglas-fir and western hemlock as components of the mixed stands will be denoted as df/MIX and wh/MIX respectively.

Table 4.1: Mean stand characteristics at age 12 by species composition at three density levels, 200, 450 and 700 trees per acre (TPA).

Density	Composition	Height (feet)	DBH (inches)	BA (feet²/acre)	Volume (feet³/acre)
200 TPA	Douglas-fir	33.6	5.88	42.8	553
	Western hemlock	29.1	4.99	25.0	378
	Mixture	29.1	5.20	29.8	380
450 TPA	Douglas-fir	33.0	5.23	83.0	1122
	Western hemlock	29.8	4.91	73.1	1178
	Mixture	29.8	4.74	63.3	855
700 TPA	Douglas-fir	32.8	4.84	106.2	1486
	Western hemlock	32.0	4.60	80.8	1350
	Mixture	32.0	4.63	107.1	1554

B. Patterns of Height Growth

It is known that height is affected only at extreme ranges of density, however some differences were found to be significant at age 12 for the range of densities used in this study (Figure 4.1). It seems that in pure stands the height of Douglas-fir is less affected than that of western hemlock over the range of densities examined. Western hemlock trees growing at a density of 700 trees per acre (TPA) were significantly taller than hemlock at lower densities. Comparisons between the two species show that Douglas-fir was significantly taller than western hemlock by 4 feet at 200 TPA; however differences in total mean heights for the two species were insignificant at 700 TPA. There were no significant height differences at age 8 or at age 4 for any density in the pure stands.

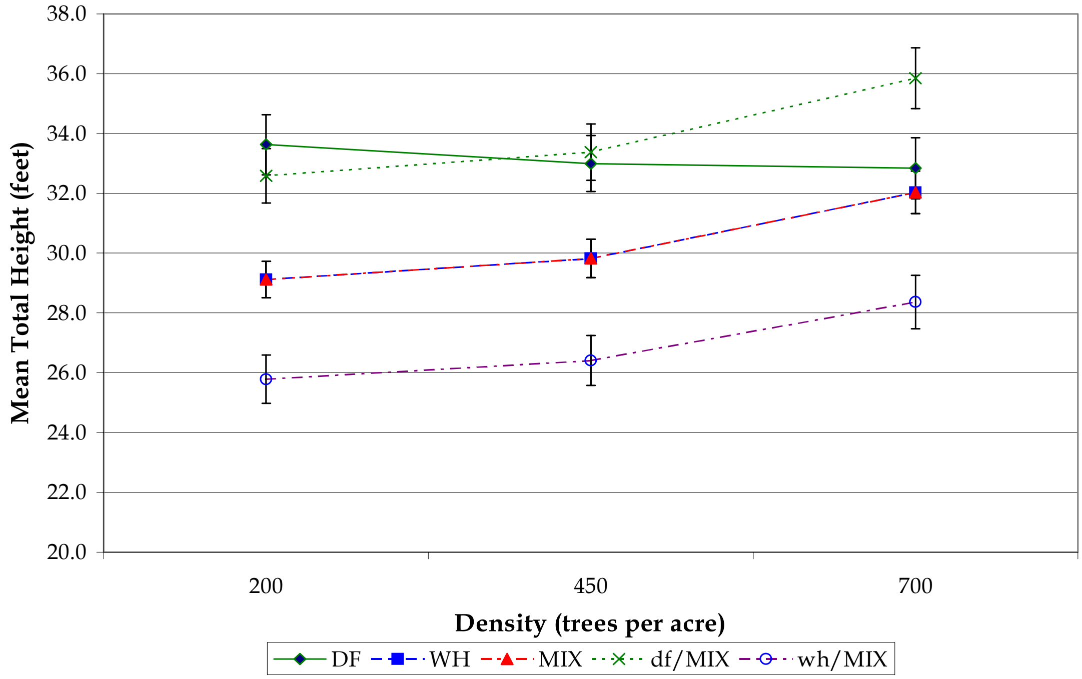

Figure 4.1: Mean Total Height by treatment at age 12 for three density levels. Bars represent 95% confidence intervals. Note: the trend line for the mixed stand lies on top of the line for pure hemlock.

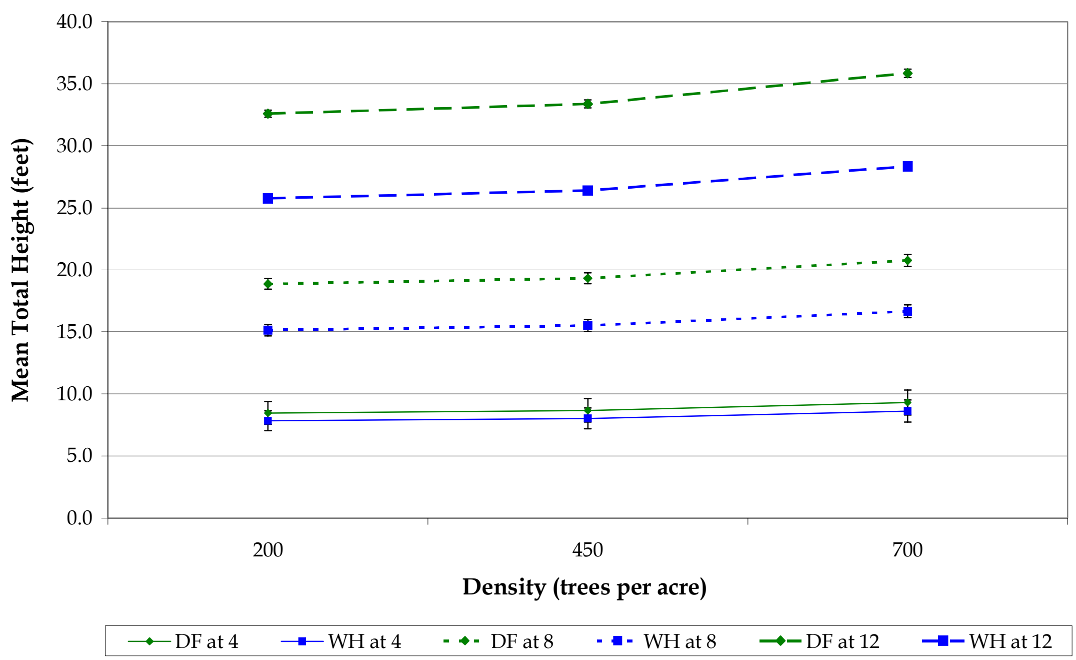

Figure 4.2: Mean Total Height by density for Douglas-fir and western hemlock growing in mixed stands at three ages: 4, 8 and 12. Bars represent 95% confidence intervals.

When comparing the two species as components of the mixed stands, results were different. Douglas-fir was on average 7 feet taller than western hemlock across densities. These differences in the height growth pattern started between age 4 and 8 (Figure 4.2). This can also be visualized as the differences in height growth rate for the two species (Table 4.2); right after age 4 Douglas-fir started growing nearly a foot faster in height than western hemlock.

Comparison of the behavior for both species growing in pure and mixed stands showed that western hemlock was on average 3 feet taller growing in pure stands. Douglas-fir, instead, had the same height both in pure and mixed stands when it grew at 200 and 450 TPA but became about 3 feet taller at 700 TPA. This change in the growth pattern seems to be more evident starting from age 8. The overall trends through time of all the patterns described above can be visualized in the set of graphs at two different densities (Figure 4.3).

Table 4.2: Periodic annual increment (PAI) in mean total height for Douglas-fir and western hemlock growing in pure and in mixed stands for three growth periods, 0-4, 4-8 and 8-12 year old.

Growth Period	Species	Density (trees per acre)		
		200	450	700
0 – 4 years	DF	2.08	2.04	2.03
	WH	2.10	2.15	2.31
	df/MIX	*2.11*	*2.17*	*2.33*
	Wh/MIX	*1.96*	*2.00*	*2.15*
4 – 8 years	DF	2.67	2.62	2.61
	WH	2.34	2.40	2.58
	df/MIX	*2.60*	*2.67*	*2.86*
	Wh/MIX	*1.83*	*1.87*	*2.01*
8- 12 years	DF	3.65	3.58	3.56
	WH	2.83	2.90	3.11
	df/MIX	*3.43*	*3.51*	*3.77*
	Wh/MIX	*2.66*	*2.72*	*2.93*

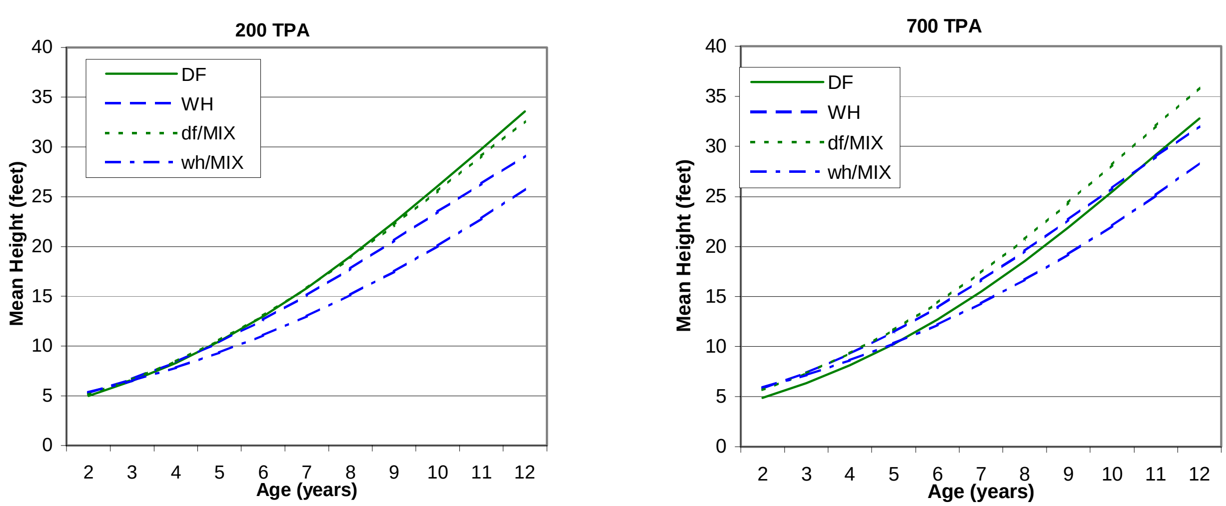

Figure 4.3: Mean Total Height over time by species for two density levels: 200 and 700 trees per acre.

C. Patterns of Diameter Growth

Density and species composition had a strong effect on mean diameter at age 12. As it was expected, diameter had an inverse relationship with density, and it appears that the two species may respond to density differently (Figure 4.4). Growing in pure stands, Douglas-fir was 1 inch greater when it grew at 200 than at 700 TPA. Western hemlock instead, did not show significant diameter differences across the three density levels. Differences between the two single species stands were significant at 200 TPA, however, they became insignificant at 700 TPA; it seems that Douglas-fir is more affected in its potential growth at higher densities than western hemlock. Mean diameter of the mixture did not show significant differences from western hemlock at any of the densities and was statistically equal to Douglas-fir at the high density level. The described differences were already established at age 8.

When comparisons between the species as components of the mixed stands were made, results were again different. At age, 12 Douglas-fir was on average 1.5 inches greater than western hemlock at all densities (Figure 4.5). Furthermore, these differences appeared early in the stand development and were already on the order of 1 inch at age 8 at all densities. Growth rates for the two species at different ages also showed this pattern (Table 4.3).

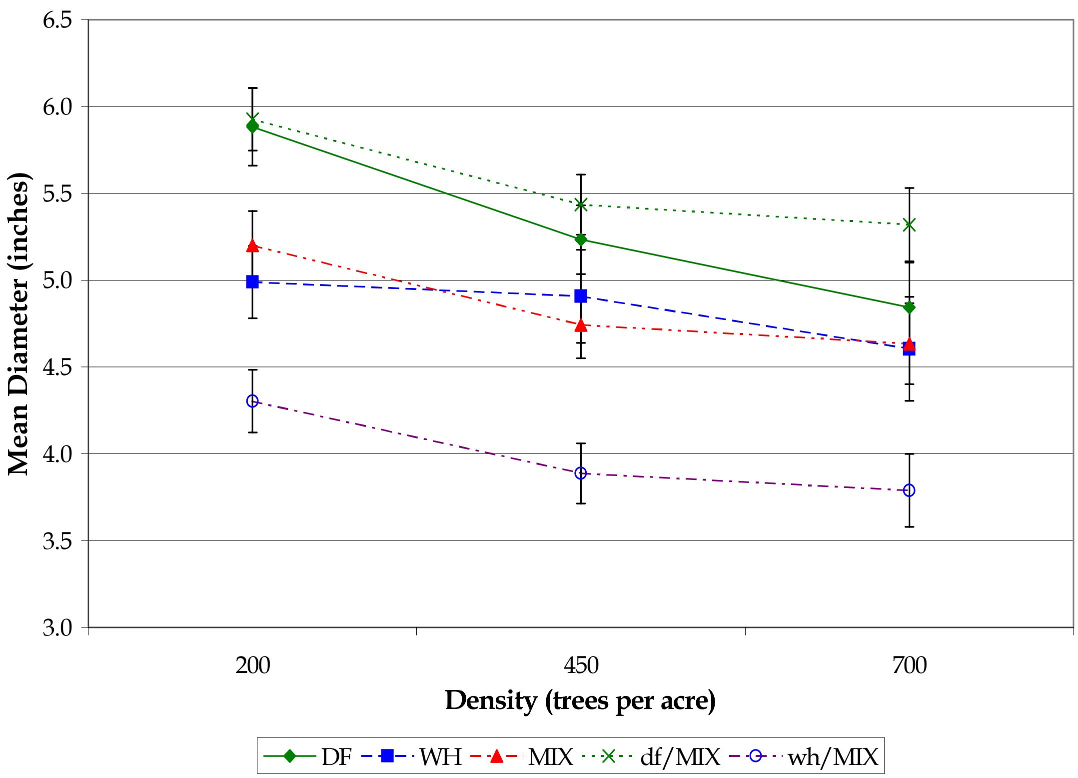

Figure 4.4: Mean Diameter by treatment at age 12 for three density levels. Bars represent 95% confidence intervals.

Table 4.3: Periodic annual increment (PAI) in mean diameter for Douglas-fir and western hemlock growing in pure and in mixed stands for three growth periods, 0-4, 4-8 and 8-12 year old.

Growth Period	Species	Density (trees per acre)		
		200	450	700
0 – 4 years	DF	0.70	0.62	0.56
	WH	0.64	0.59	0.54
	Df/MIX	*0.70*	*0.63*	*0.59*
	Wh/MIX	*0.50*	*0.44*	*0.41*
4 – 8 years	DF	0.56	0.50	0.47
	WH	0.48	0.47	0.45
	Df/MIX	*0.56*	*0.52*	*0.51*
	Wh/MIX	*0.39*	*0.35*	*0.34*
8- 12 years	DF	0.23	0.21	0.21
	WH	0.15	0.18	0.18
	Df/MIX	*0.24*	*0.23*	*0.26*
	Wh/MIX	*0.11*	*0.11*	*0.13*

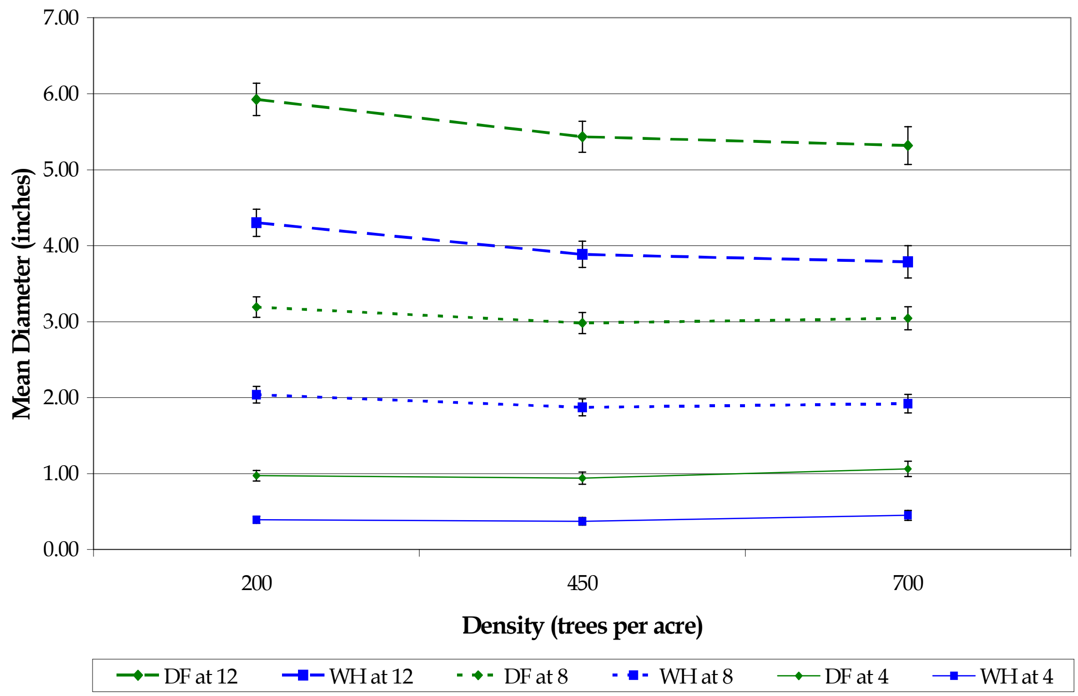

Figure 4.5: Mean Diameter by density for Douglas-fir and western hemlock growing in mixed stand at three ages: 4, 8 and 12. Bars represent 95% confidence intervals.

Apparently some changes in the allometry of the species occur when they grow in pure as opposed to mixed stands. Western hemlock was 1 inch greater when it grew in pure stands compared to mixed, and this was consistent across all densities. Douglas-fir, on the other hand, became half inch greater when it grew at high densities in the mixture even though these differences were not found to be significant at the 95% confidence level. This may actually be due to the fact that in this situation the actual number of Douglas-fir trees growing is around 350 per acre, closer to the low-to-medium density values.

The overall trends through time for all the patterns described above can be visualized in the set of graphs at the different densities (Figure 4.6).

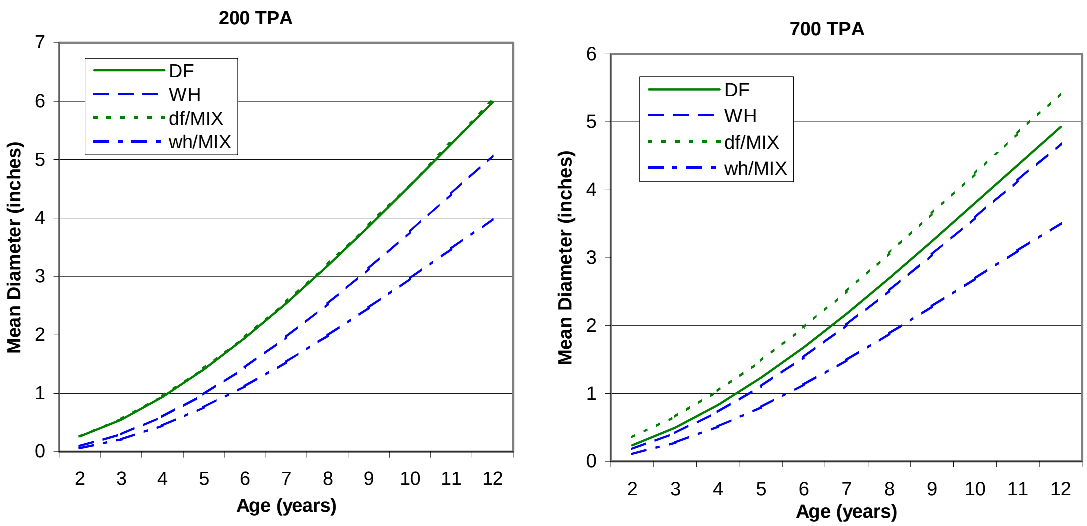

Figure 4.6: Mean Diameter over time by species for two density levels: 200 and 700 trees per acre.

D. Height – Diameter Ratio

It has been suggested that the use of mixtures may provide more resistance to wind damage through the improvement in physical stability (Kelty 1992, Man and Lieffers 1999). One simple way to study this is through the analysis of the height to diameter ratio (h/d). Figure 4.7 shows that even though some significant differences in diameter and height growth were evident at age 12, the h/d ratio at this age was very low and was not significantly different among the treatments over the range of densities studied. Western hemlock growing in the mixture seems to be developing slightly greater h/d at this stage.

E. Crown Development

One of the hypotheses to be tested is to examine if the crown of one species is affected by the presence of the other, and to examine what role density plays on this. We could expect that a shade-intolerant species such as Douglas-fir would allocate more to branch growth than a shade-tolerant species such as western hemlock. The intolerant Douglas-fir will attempt to grow crowns quickly, thereby capturing more light and dominate a mixed stand early. We propose here to study this through the analysis of the crown development.

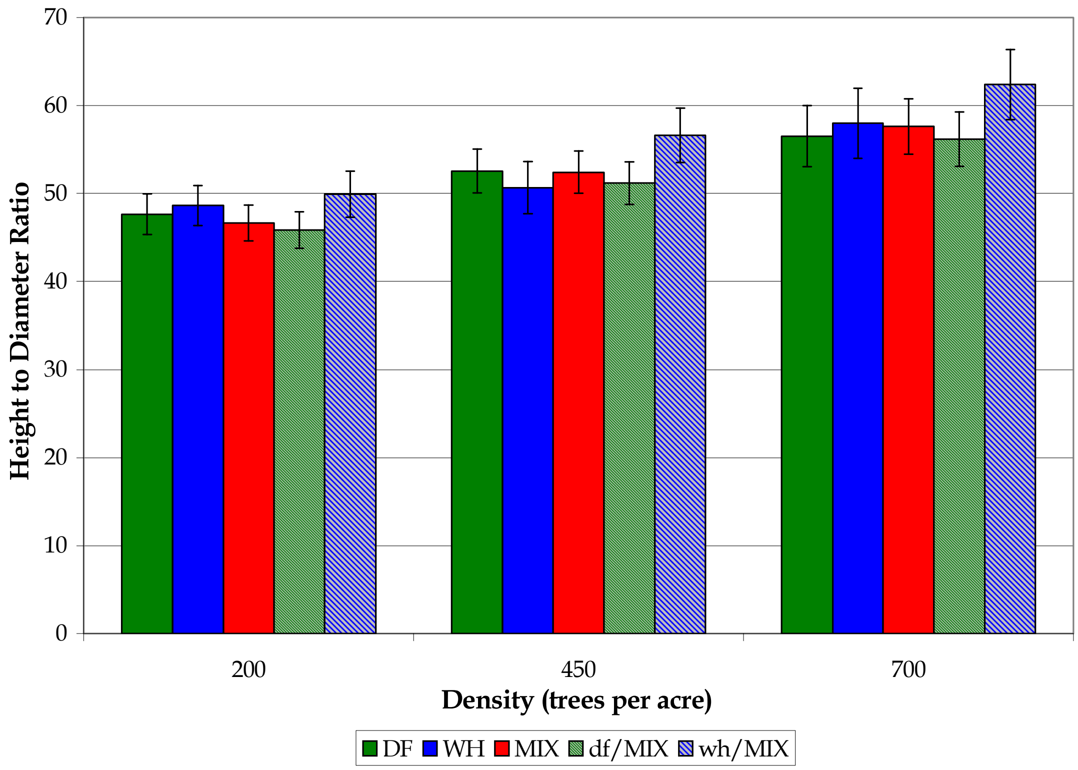

Figure 4.7: Height to diameter Ratio by treatment at age 12 for three density levels. Bars represent 95% confidence intervals.

Even though crown development analyses were assessed through the changes in live crown length (used to calculate the crown ratio), crown width and crown volume, only results for crown volume are presented here (Figure 4.8). The comparison of the crown volume for each species growing as components in the mixed stands was found to be significantly different than tree crown volumes when growing in pure stands at the same density (i.e. actual number of trees of each of the components in the mixture density against same number of trees in a pure stand). While Douglas-fir in the mixed stand significantly increased its crown volume compared to Douglas-fir in pure stands, western hemlock in mixed stands significantly reduced crown volume by about 50 %. As it was pointed out before, Douglas-fir seems to develop its crown independently of the presence of western hemlock. In contrast, western hemlock was severely affected by the presence of Douglas-fir.

F. Individual Tree Volume Growth

At the three density levels, Douglas-fir trees in pure stands had significantly larger mean tree volume than western hemlock trees in pure stands. It is interesting to note that even though at 700 TPA both height and diameter were not significantly different between the two species, Douglas-fir mean tree volume was significantly greater than that of western hemlock. Although the individual tree volume for both species in pure stands decreased significantly with density from 200 to 450 TPA, there was no significant change from 450 to 700 TPA (Figure 4.9).

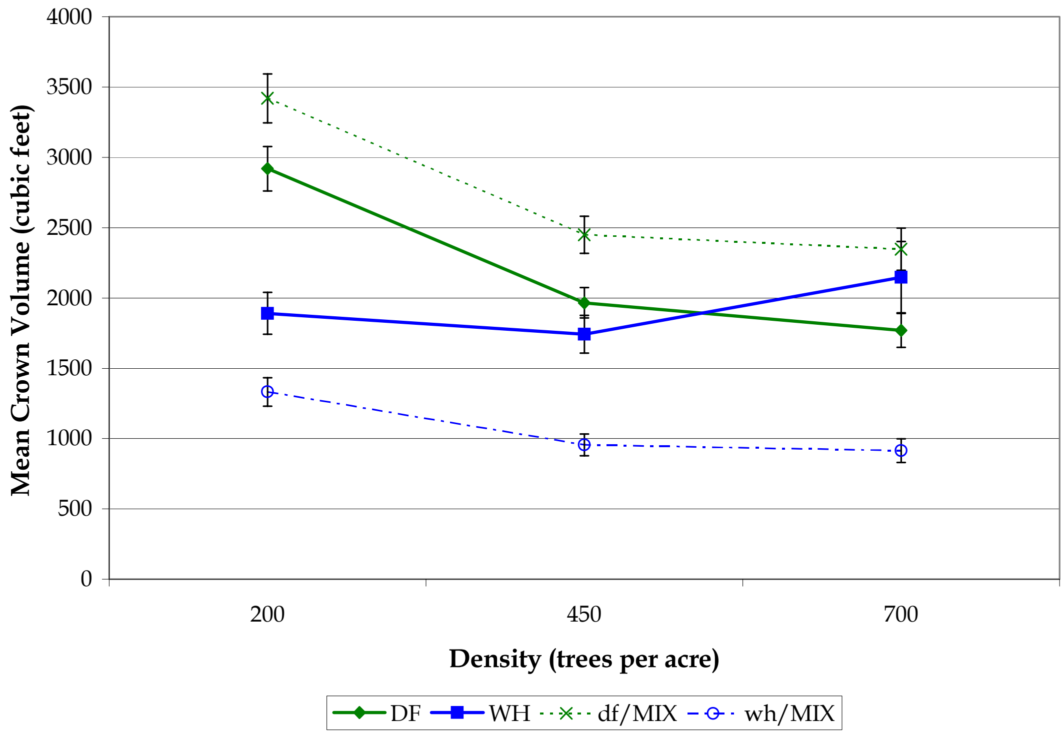

Figure 4.8: Mean Crown Volume by treatment at age 12 for three density levels. Bars represent 95% confidence intervals.

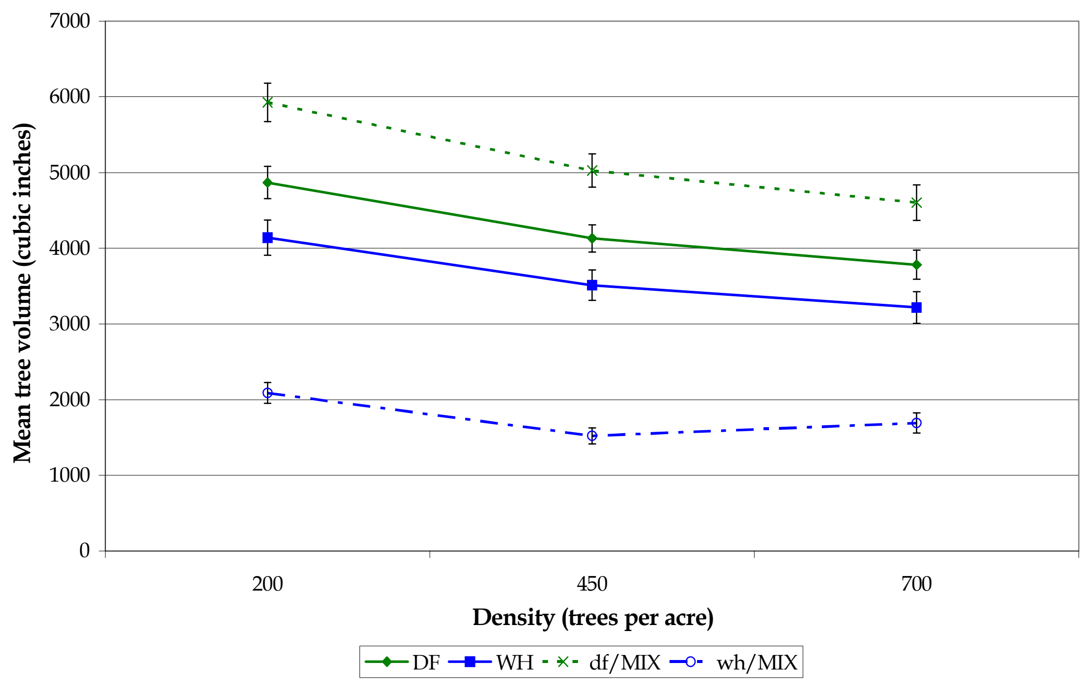

Figure 4.9: Mean Tree Volume by treatment at age 12 for three density levels. Bars represent 95% confidence intervals.

Differences between the two species became more evident in the mixed stands. Douglas-fir as a component of the mixed stands produced about 22% higher mean tree volumes at all densities when compared with Douglas-fir growing in pure stands at the same total stand density. In contrast, western hemlock in mixed stands had mean tree volume reduced by 50, 43 and 53 percent at 200, 450 and 700 TPA respectively.

The individual tree volume of the two species growing in mixed stands was also compared with those of the species growing in pure stands but at the same density of each component in the mixture (i.e. half of the total stand density of the mixture). Mean tree volume of Douglas-fir was apparently not affected, but western hemlock mean tree volume in the mixture was reduced by 55 and 60 % at 350 (half of 700 TPA) and 225 TPA (half of 450 TPA) respectively.

G. Basal Area per Acre Accumulation

Basal area accumulation expresses the change of both the diameter and the number of trees growing in a stand through time. Figure 4.10 presents basal area per acre at age 12 for the pure and the mixed stands, as well as its components. From this figure the following points can be observed.

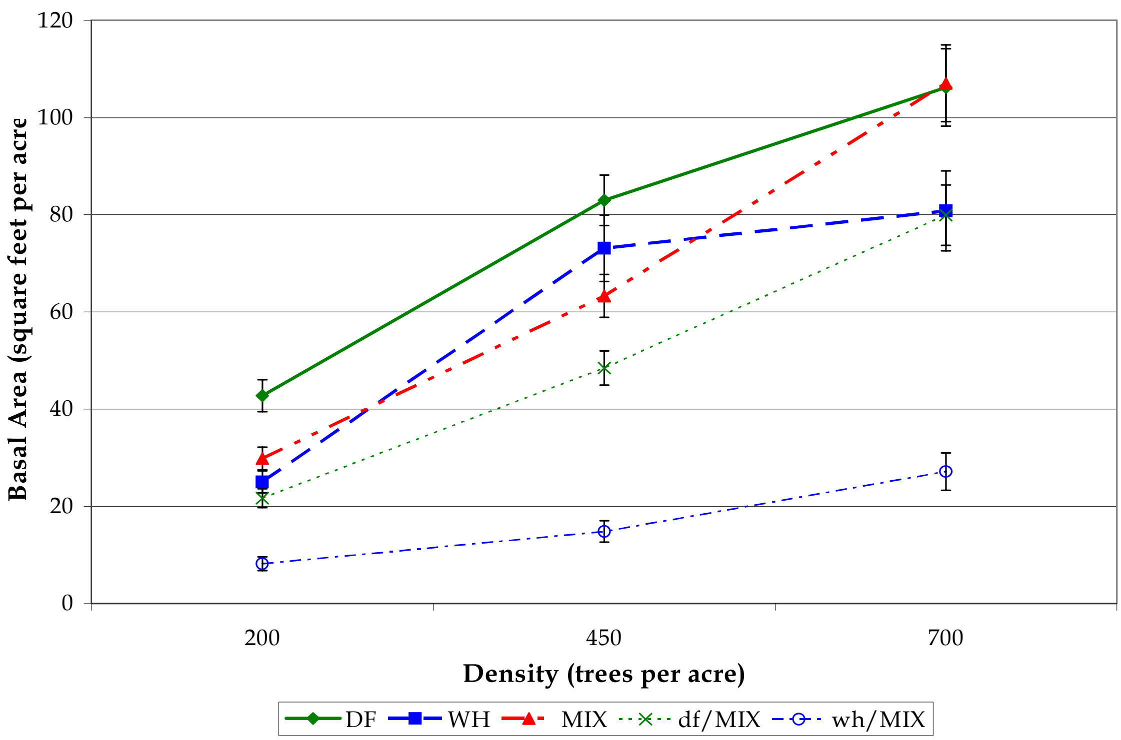

Figure 4.10: Basal Area per acre by treatment at age 12 for three density levels. Vertical bars represent 95% confidence intervals.

Douglas-fir pure stands

Basal area per acre increased with increasing density, and each density was significantly different from the others.

Western hemlock pure stands

Basal area per acre increased significantly from 200 to 450 TPA, but there was a non significant increase from 450 to 700 TPA.

Pure Douglas-fir vs. pure western hemlock

Douglas-fir resulted in higher basal area per acre than western hemlock at all densities; differences were significant at 200 and 700 TPA but not at 450 TPA.

Mixed stands

Basal area per acre in the mixed stands increased with increasing density, and differences were significant from each other. Compared with the pure stands, values for the mixed stand were significantly lower than Douglas-fir at 200 and 450 TPA but not at 700 TPA. With respect to western hemlock, basal area per acre in the mixture was significantly higher at 200 and 700 TPA, and not significantly different at 450 TPA. Differences are summarized in table 4.4.

Table 4.4: Statistical differences * (0.05) in mean basal area per acre: Mixed stands vs. pure stands.

Mixed stand density	Pure Douglas-fir	Pure western hemlock
200 TPA	lower *	higher *
450 TPA	lower *	no differences
700 TPA	no differences	higher *

Douglas-fir as component in the mixed stand

As a component, Douglas-fir basal area per acre was about the same as that in the pure stands with same number of trees (i.e. parallel lines).

Western hemlock as component in the mixed stand

The trend for western hemlock as a component in the mixed stands was not parallel to the pure stand trend; furthermore it had lesser slope indicating poorer basal area per acre for same number of trees when in mixture.

H. Volume per Acre Accumulation

Results for volume per acre at age 12 for the pure and the mixed stands, as well as its components, are presented in Figure 4.11. From this, the following patterns were observed.

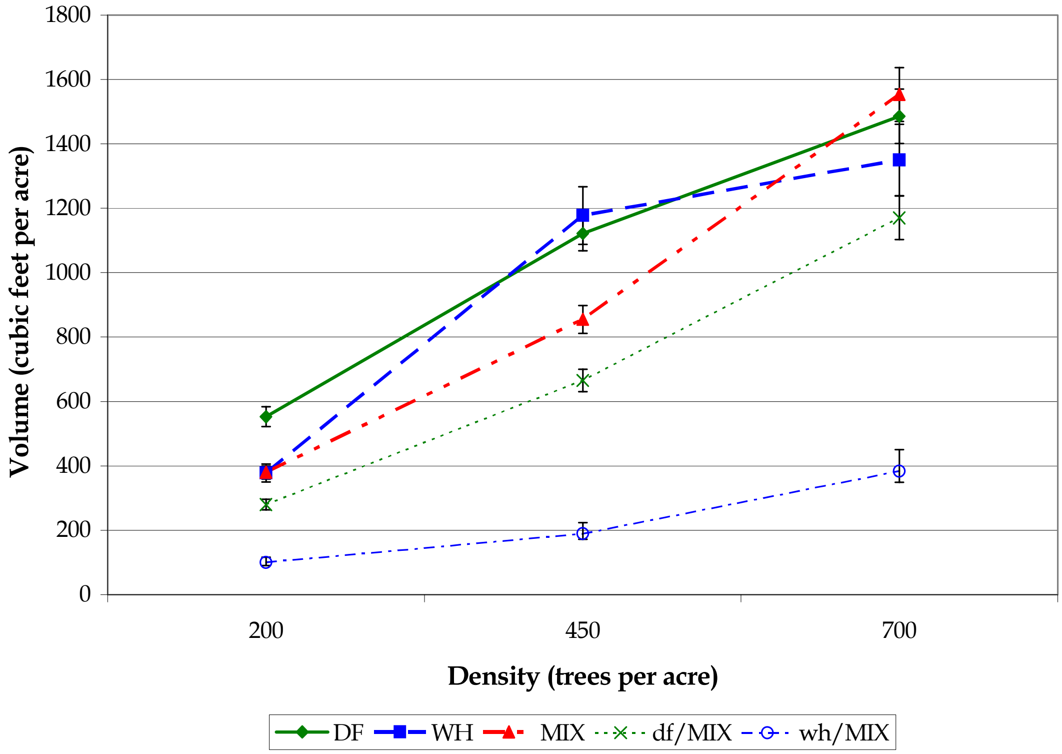

Figure 4.11: Volume per acre by treatment at age 12 for three density levels. Bars represent 95% confidence intervals.

Douglas-fir pure stands

Volume per acre increased with increasing density, and each density was significantly different from the others.

Western hemlock pure stands

Volume per acre increased significantly from 200 to 450 TPA, but there was a non significant increase from 450 to 700 TPA.

Pure Douglas-fir vs. pure western hemlock

Douglas-fir resulted in higher volume per acre than western hemlock at 200 and 700 TPA and lesser at 450 TPA; differences were only significant at 200 TPA.

Mixed stands

Volume per acre in the mixed stands increased with increasing density, and differences were significant from each other. Compared with the pure stands, values for the mixed stand were significantly lower than pure Douglas-fir and equal to pure western hemlock at

200, lower than either pure Douglas-fir or pure western hemlock at 450 TPA, and equal to pure Douglas-fir and significantly higher than pure western hemlock at 700 TPA. Statistical differences are summarized in table 4.5.

Table 4.5: Statistical differences (0.05) in mean volume per acre: Mixed stands vs. pure stands.

Mixed stand density	Pure Douglas-fir	Pure western hemlock
200 TPA	lower *	no differences
450 TPA	lower *	lower *
700 TPA	no differences	higher *

Douglas-fir as component in the mixed stand

As found for basal area, Douglas-fir volume per acre as a component in the mixture was about the same as that in the pure stands with same number of trees (i.e. parallel lines).

The percentage contribution of Douglas-fir to the mixture total volume was higher across densities, ranging from 74% to 78%.

Western hemlock as component in the mixed stand

The trend for western hemlock as a component in the mixed stands was not parallel to pure stand trend; over the range of densities between 200 to 450 TPA the slope was lower indicating that for the same number of trees, western hemlock in the mixture had less volume per acre compared to the pure stand. In contrast, from 450 to 700 TPA the slope was similar to that in the pure stands; however it takes about 350 western hemlock trees in the mixture (700 total TPA) to equal the volume per acre of 200 TPA in the pure stand. The percentage contribution of western hemlock to the mixture total volume was lower than its proportion to the total density (50%), ranging from 22% to 26% across the range of densities.

I. Productivity: Periodic and Annual Increments

A simple way to follow the evolution of a stand is through the analysis of the periodic and mean annual increments (PAI and MAI). These increments for the three stands were calculated for the three density levels, but because competition and changes from one stage of development to another are usually accelerated with increasing density, PAI and MAI for just the highest density (700 TPA) are presented (Figure 4.12). Douglas-fir and the mixture apparently reached their maximum PAIs at around age 11. In contrast, western hemlock was still growing at increasing rates after 12 years. We could presume the Douglas-fir stand will eventually reach the MAI culmination before the western hemlock and mixed stands. These results also suggest that while both the Douglas-fir and the mixed stands have reached canopy closure and probably the maximum leaf area index, western hemlock has not.

Culmination of MAI for all stand type likely will not occur in the near future. We have no reason to suspect at this stage, that patterned changes in PAI/MAI relationships observed in past research after treatments have been applied will not hold here, as well.

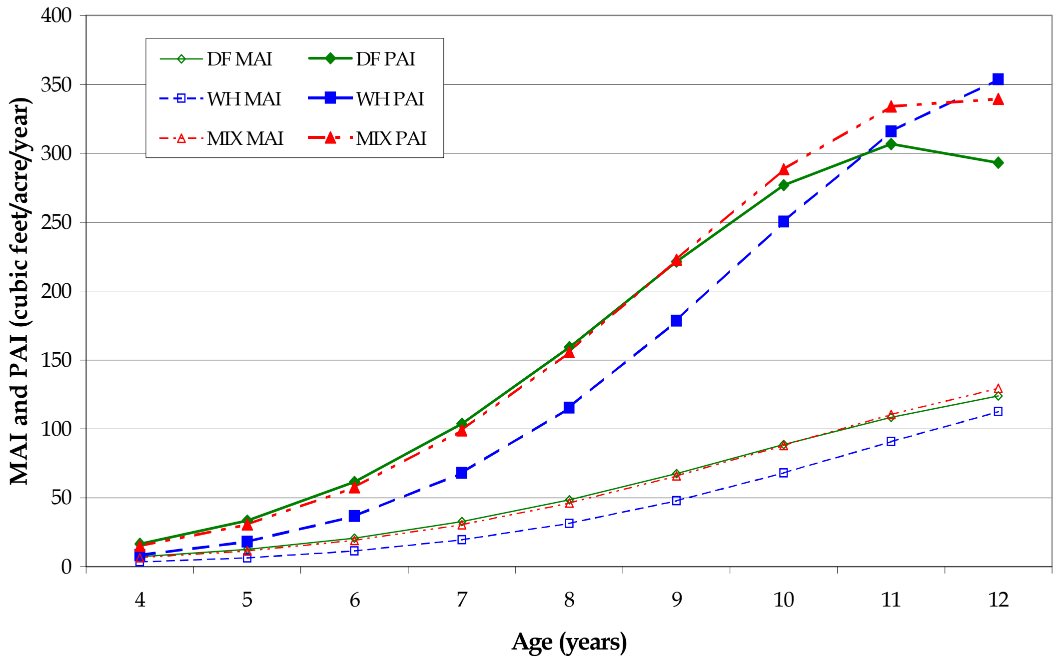

Figure 4.12: Periodic and Mean Annual Increment in Volume per acre by treatment through time at 700 trees per acre.

J. Relative Yield Analysis

A method for analyzing the effects of combining two species in a mixture is by comparing the yield of each species in mixture with its yield in a pure stand (Harper 1977). If both species use resources in identical ways, and hence compete for these resources, the expected relative yield (RY) of each species will be equivalent to its proportional contribution in the mixture, and the expected relative yield total (RYT) will equal 1.0. A RYT greater than 1.0 indicates either niche separation or the existence of some beneficial relationship between species producing a potential productivity gain for the mixture. On the other hand, values of RYT lower than 1.0 indicate antagonistic or competitive relationship between the species in the mixture. In our case, the assumption that 50:50 mixtures of Douglas-fir and western hemlock grow independently would result in the expected RY of each species to be 0.5 and a RYT equal to 1.0. RY and RYT were calculated for basal area and volume per acre, but because the results were similar, only those for volume are presented (Figure 4.13). The relative yield of western hemlock was less than 0.5 at all density levels. Douglas-fir, instead, had RY values substantially greater than 0.5 at both 450 TPA and 700 TPA. It is clear that the mixture of the two species benefited from the yield of Douglas-fir at 450 TPA and 700 TPA. Combined total relative yield was less than 0.8 for both 250 and 450 TPA but was above 1.0 at

700 TPA. Thus, it appears that at the highest density significant niche separation between these species exists. Even though this suggests it might be a potential advantage for the mixture compared to the monocultures, absolute yield values should still be compared to identify the highest yielding stand (Kelty 1992). This comparison is shown in a set of graphs (Figure 4.14) which combine the results found for absolute and relative yield at the three proposed densities. This shows that at 700 TPA both the relative and the absolute yield (volume per acre) were higher for the mixture compared to the two monocultures. This phenomenon has not yet appeared at the lower densities. Continued monitoring in the future is needed to see if and when this occurs at lower densities.

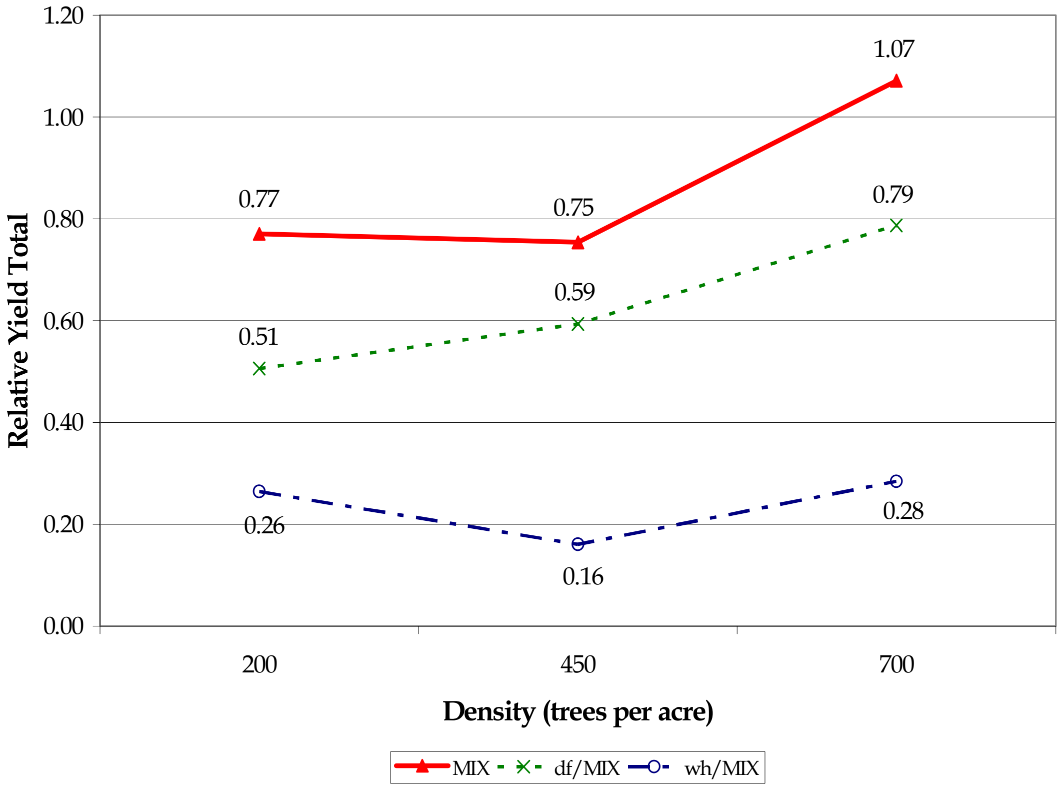

Figure 4.13: Relative yields of Volume per acre at age 12 for Douglas-fir and western hemlock grown in mixed stands at three density levels.

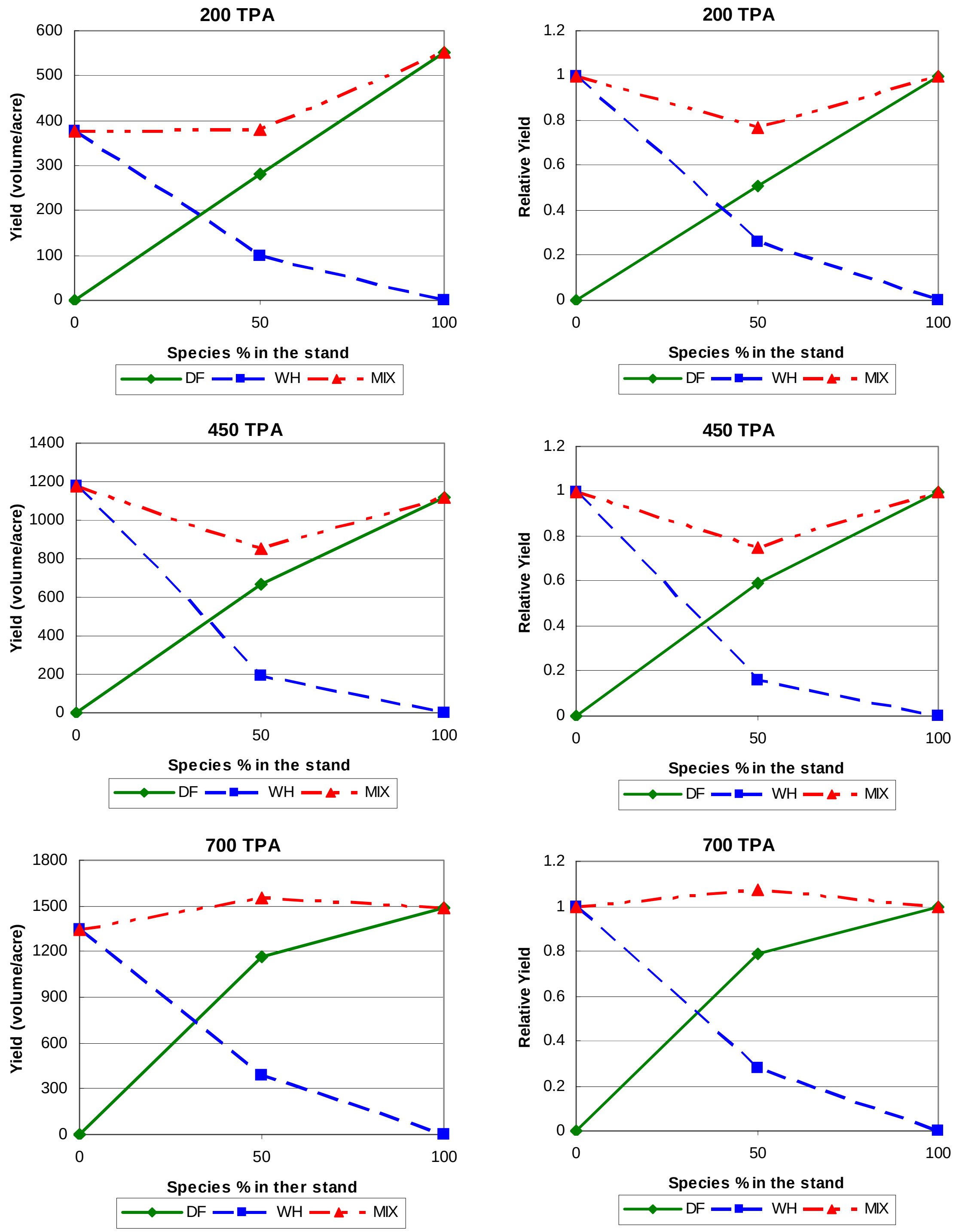

Figure 4.14: Absolute and relative yield for the Douglas-fir and western hemlock monocultures and the 50/50 mixture at three density levels: 200, 450 and 700 TPA.

CHAPTER 5: DISCUSSION

A. Height Growth Pattern and Stratification

The relationship between juvenile height growth rates and shade tolerance among species plays an important role in determining development patterns of mixed stands (Menalled at el., 1998). Stratified canopies in mixed stands tend to develop naturally because shade intolerant species generally have greater rates of juvenile height growth than shade tolerant species (Kelty 1992, Oliver and Larson 1996, Smith et al., 1997). Douglas-fir and western hemlock differ in their tolerance to shade (Lewis et al., 2000), and different height growth patterns along with stratification have been found for the two species in natural stands (King 1958, Scholz and Smith 1975, Oliver and Larson 1996). Working with even-aged mixed natural stands of these two species, Wierman and Oliver (1979) reconstructed the height growth pattern and found that after about 20 years Douglas-fir was significantly taller than western hemlock. These authors also suggested that it was not certain that Douglas-fir would similarly outgrow western hemlock in plantations.

However, this plantation study shows that by age 12 Douglas-fir has outgrown western hemlock by an average of 7 feet across all densities. These differences in height growth initiated around age 4, and were already 3 feet at age 8. These height growth rates demonstrate that the difference between the two species has been increasing over the period of time measured, and this trend is expected to continue in the future. Even though the evidence of stratification at this point is partial, the increasing juvenile height growth observed and the height differences already established in these 50:50 mixed plantations of Douglas-fir and western hemlock support the conclusion that stratification is developing.

Results found for the crown development also support the idea of stratification. Western hemlock exhibited reduced crown length, crown ratio, crown width and crown volume when competing for the light environment with Douglas-fir. In contrast, crowns of Douglas-fir trees were able to expand more in the presence of western hemlock than in pure stands, indicating it is a better competitor for capturing the upper-canopy light environment.

It has been suggested that heights of the upper canopy in a mixed stand are expected to reach the same height as would be achieved in the pure stands (Montagnini et al., 1995). However this study found that at high densities (700 TPA) Douglas-fir was taller in the mixture than in the pure stands. The results are consistent with those found by Menalled et al. (1998). A possible explanation for this height gain is that competition among Douglas-fir trees is more severe in pure stands than in mixture with hemlock at high densities, hence Douglas-fir trees in mixture have more growing space available.

B. Interspecific and Intraspecific Competition

It has been proposed that in some situations more efficient utilization of site resources by species in mixed stands can result in greater yields. This may occur if the component species have characteristics such that interspecific competition is less intense than intraspecific competition (Kelty and Cameron 1995). Stratified canopies reduce competition since the species occupy different niches by capturing light at different intensities and locations within the canopy and would, in theory, maximize the use of light because of the greater overall utilization of light (Kelty 1992). If this happens, a stratified canopy with shade tolerant species underneath a shade intolerant species would collectively intercept more photosynthetically functional light (Kelty 1989), and the stand may therefore experience less intense interspecific than intraspecific competition (competitive production principle).

Interspecific and intraspecific competition were assessed in this study by changes in the allometry of tree species growing in the mixture compared to their growth in the monocultures (Menalled et al., 1998). It was found that Douglas-fir trees experienced an increase in diameter, height, crown volume, and individual tree volume in the mixture compared to the pure stand. In contrast, the opposite effect was found for western hemlock which saw its growth reduced by the presence of Douglas-fir. This provides some evidence that interspecific competition on Douglas-fir was likely less than intraspecific competition. A possible explanation is that the different shade tolerance and the ability to utilize efficiently different light environments of the two species reduced the intensity of interspecific competition in mixture compared to the intensity of intraspecific competition in pure stands. The effect of western hemlock on Douglas-fir, which may produce an environment of reduced competition for light, is similar to that of wider spacing within Douglas-fir. Unfortunately, vertical foliage profiles and measurements of light interception were not available; however the changes in crown size and position, and presumably reduced competition, may explain how spatial stratification demonstrates that interspecific competition is less than intraspecific competition in the mixed stands.

Another possible way to examine the effects of interspecific and intraspecific competition is through the height-to-diameter ratio (h/d). This ratio has been used as a measure of competition in even-aged stands (Abetz 1976) because trees allocate more carbon to height than to diameter growth to participate in the canopy (Bauhus et al., 2000). Even though differences were not statistically significant at the 95% confidence level, the slightly lower h/d that Douglas-fir trees exhibited growing in the mixture compared to those in the monoculture is suggesting that interspecific competition decreased in the mixture. In contrast, the higher h/d found for western hemlock in the mixture, compared to the pure stand, is suggesting that interspecific competition is greater than the intraspecific competition. This means western hemlock must allocate relatively more resources to height growth to participate in the canopy, while Douglas-fir, a faster height growing species became situated in an upper position in the canopy earlier and could allocate more resources to diameter growth.

C. Overall Stand Productivity: Pure vs. Mixed Stands

Many studies have shown that both natural and planted mixed stands can yield as much or more than pure stands of the most productive of their components (Wierman and Oliver 1979, Kelty 1989, Brown 1992, Montagnini et al., 1995, DeBell et al., 1997, and Man and Lieffers 1999, Binkley 1983, 1992, DeBell et al., 1997, Khanna 1997, Bauhus et al., 2000, Balieiro et al., 2002). Some cases of increased productivity were the result of species interactions recognized under the facilitation production principle, while others relied on the competitive production principle (Vandermeer 1989). The Douglas-fir – western hemlock interactions examined in this study are explained by the competitive production principle, where species growing in a mixture utilize resources differently, leading to an overall increase in the stand productivity.

The relative yield analysis revealed that at 700 TPA the relative yield total (RYT) of the mixture exceeded 1.0 indicating that some degree of niche separation between the species may exist (Figure 4.15). Although this suggests a potential advantage in productivity for the mixtures compared to pure stands, absolute yield values must be compared to identify the highest yielding stand structure (Kelty 1992). This study found that the mixed stand resulted in statistically similar volume per acre to the pure Douglas-fir at 700 TPA and was significantly greater than the pure western hemlock (Figure 4.12). Furthermore, in terms of absolute volume per acre, the mixed stand resulted in the highest yield. The higher yield observed in the mixed stand was probably driven by the differences in terms of photosynthetic efficiency of foliage and the partial stratification observed. The stratified canopy probably resulted in sufficient radiation interception in the upper canopy to allow higher productivity of the shade intolerant species, and yet adequate transmission of radiation to the shade tolerant species in the lower position of the canopy (Menalled et al., 1998). This might have resulted in a maximization of the light use by the canopy due to increased light efficiency and reduction in the competition for this resource (Kelty 1992). As a result, it appears that the Douglas-fir component was enhanced in the mixture as expressed in a greater mean individual tree volume probably due to an increase in the light interception. In contrast, the yield of western hemlock was disproportionally low as compared with pure western hemlock plantations.

The results obtained for both basal area and volume per acre for western hemlock at high densities requires more discussion. We found that for densities greater than about 400 to 500 TPA, western hemlock productivity no longer showed significantly higher yields and reached an apparent peak around 600 TPA with lower basal area and volume per acre at 700 TPA. This quadratic rather than asymptotic response is not likely to be observed in forest stands. There are no reports in the literature indicating such a reduction in productivity for western hemlock at higher densities. It is our assumption that the model predictions were not as precise at high densities as they were at lower densities. Although the model predictions were within the range of the actual plot density values, the range of densities observed for pure western hemlock was narrower than for the pure Douglas-fir and mixed stands. This comparative deficiency in data points of higher density pure western hemlock may have produced this quadratic artifact (see Appendix, Table A.9).

D. Density and its Effects on Species Interactions and Productivity

The effects of density on tree and stand growth and yield in pure stands are well known; however, species growing in mixed stands would probably have different behavior at different densities compared to pure stands. Kelty and Cameron (1995) suggested that competitive interactions and yield comparisons among mixtures and monocultures would be expected to vary if density changes.

Most of the studies comparing mixtures and monocultures were conducted at a single density. Densities utilized were usually high, and even though it is not clear why these densities were chosen, one could expect that high density stands were chosen to accelerate interactions among individuals and so obtain results in shorter period of time. In an experiment using two densities, Khanna (1997) observed that interactions between the species occurred earlier in the high density treatment and they became evident later in the low density level. Khanna also suggested that positive interactions between species might occur later in wider spacings. Working with Douglas-fir and red alder seedlings, Shainsky and Radosevich (1992) demonstrated that simultaneous manipulation of the densities of the two species produced quantitative changes not only in tree growth, but also in light, soil moisture, and leaf water potential.

This study demonstrates the important role density plays on the productivity of mixed stands, and thus in comparing mixtures and pure stands. It appears that interactions between the species involved in a mixture occur in different degrees depending on the amount of resources they are obligated to share and/or for which they compete. Relative yield analyses at the three densities examined provide a useful way to present and to explain this. Results at 200 TPA show that the RY for Douglas-fir was as expected but, on the other hand, western hemlock had a RY lower than expected; together, they had a combined RYT value of 0.77. At 450 TPA, Douglas-fir RY was slightly higher than expected, while western hemlock RY and RYT still remained below expectation but greater than observed at 200 TPA. However at 700 TPA the combined RYT was 1.07 and that the Douglas-fir RY was much higher than expected. Although a potential productivity advantage for the mixture may exist at 700 TPA, at lower densities the mixture has not exhibited any possible benefit through age 12; western hemlock growth is adversely affected, and beneficial growth of Douglas-fir is only starting to emerge at 450 TPA at age 12.

Even supposing that the results found at 700 TPA would appear in the future at 450 TPA, it is not likely that the 200 TPA density will respond in the same way. Kelty and Cameron (1995) suggest that the use of low densities in mixed stands at establishment may allow species with slow juvenile growth rate to escape early suppression and as a consequence of this, the species may not be able to express differences in niche separation.

CHAPTER 6: CONCLUSIONS

The objective of this study was to determine if mixtures were more productive than monocultures at three different density levels. The six null hypotheses presented in Section 2, all of which were rejected, are summarized below.

Hypothesis 1: Douglas-fir and western hemlock have equal initial height growth rates growing both in single species and mixed planted stands, and do not stratify in plantations.

✓ At age 12 Douglas-fir outgrew western hemlock by an average of 7 feet across all densities. These differences in height growth started around age 4 and were already 3 feet at age 8.

✓ Even though the evidence of stratification at this point is partial, the different juvenile height growth observed and the height differences already established for the two species in the mixed plantations support the conclusion that stratification will eventually occur.

Hypothesis 2: The allometry of the species does not change at different densities and age, nor does it when they grow together in comparison with their growth in pure stands.

✓ Diameter, height and individual tree volume relationships for both species were dependent on density and whether or not they grew in pure or mixed stands.

✓ Height/diameter ratio of western hemlock growing in the mixture was greater than in the monoculture.

Hypothesis 3: Tree crowns do not respond to different levels of growing space.

✓ Western hemlock exhibited reduced crown length, crown ratio, crown width and crown volume when competing for the light environment with Douglas-fir.

✓ In contrast, Douglas-fir tree crowns were able to expand more in the presence of western hemlock than in pure stands.

Hypothesis 4: Interspecific and intraspecific competition are the same in pure and mixed planted stands and different density levels do not affect it.

✓ Douglas-fir trees experienced an increase in diameter, height, crown volume, and individual tree volume in the mixture compared to the monoculture.

✓ Height/diameter ratio was slightly lower for DF and higher for WH in the mixture compared to those in the pure stands.

Hypothesis 5: Mixed species plantations are not as productive as single species plantations.

✓ The relative and absolute yield analyses revealed that at 700 TPA the mixture was as productive as the two monocultures.

✓ We may observe same results at lower densities in the future.

Hypothesis 6: Initial density does not affect interactions between species.

✓ Relative yields were different at different densities, as well as the allometry of the trees.

✓ It appears that interactions between the species involved in a mixture occur in different degrees depending on the amount of resources they are obligated to share and/or for which they compete.

✓ The study here presented supports the important role density plays on the productivity of mixed stands, and thus in comparing mixtures and monocultures.

In terms of ecological theory, it appears that "the competitive production principle" has contributed to superior yields of the mixed planted stands at high densities, achieving as much productivity as the pure stands. This was a result of the partial stratification observed and the presumably better use of the site resources made by the two species in the mixture compared to the pure stands. Because of this, less interspecific competition than intraspecific competition was probably experienced in the mixed stand compared to the pure stands. At low and medium densities, however, interactions between species occurred (as measured by allometry changes) but may not have been of great enough magnitude to cause the mixture to outperform the pure plantations in terms of total yield.

In addition to the result that mixed Douglas-fir – western hemlock planted stands were able to produce as much wood as the pure stands of either species, mixed stands may produce other economic benefits. Wood quality of the Douglas-fir trees may be improved, and this will represented not only by the greater size of the crop trees but also by the improvement in the bole quality as a result of western hemlock trees shading the lower limbs. This might include natural pruning as well as a reduction in limb diameter (knots). It has also been suggested that mixed plantations of these two species may be more wind firm and disease resistant than pure stands (Wierman and Oliver 1979).

Along with the timber production objectives, mixed planted stands can also achieve other management objectives (such as a broader range in wildlife habitats and increased aesthetic value) without the misconceived timber yield sacrifice.

The results presented here reflect responses at an early stage in the stand development. Long-term measurements are expected to show other effects, making the interactions among species more evident. In addition, comparisons among single and mixed species plantations are few, and the advantages and disadvantages may be site specific. Mixtures that could achieve a reduction in interspecific competition might, as a consequence of this, increase their yields over the pure stands of its components. However, this is likely to happen only if the supply of the resource for which competition is reduced is limiting the production in the pure stands (Kelty 1992). For these reasons the results of this study should be understood locally and not be extrapolated widely to other sites.

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APPENDIX: ADDITIONAL TABLES

Table A.1: Model for Mean Diameter at breast height and its corresponding coefficients and significance level for all the terms present in it.

Equation of regression	F value	Pr > F	Adj R-square
Square Root of DBH = $b_0 + b_1$ (c1) + b_2 (c2) + b_3 (sp1) + b_4 (sp2) + b_5 (tpa) + b_6 (age) + b_{10} (sp2*tpa) + b_{15} (tpa*age) + b_{16} (tpa*tpa) + b_{17} (age*age) + b_{24} (sp1*tpa*tpa) + b_{25} (sp2*tpa*tpa)	362.14	<.0001	0.938

Parameter	Estimate	Error	t Value	Pr > |t|
b_0	-.0871970567	0.05198572	-1.68	0.0946
b_1	0.1537438489	0.03059830	5.02	<.0001
b_2	-.2059723300	0.03059830	-6.73	<.0001
b_3	0.1536756314	0.03582361	4.29	<.0001
b_4	-.2072551557	0.06878868	-3.01	0.0028
b_5	-.0003000479	0.00015435	-1.94	0.0529
b_6	0.2665888129	0.01361503	19.58	<.0001
b_{10}	0.0010076565	0.00041453	2.43	0.0157
b_{15}	-.0000430471	0.00001092	-3.94	0.0001
b_{16}	0.0000006231	0.00000013	4.84	<.0001
b_{17}	-.0048129335	0.00089098	-5.40	<.0001
b_{24}	-.0000002153	0.00000009	-2.27	0.0238
b_{25}	-.0000010302	0.00000048	-2.14	0.0328

Table A.2: Model for Quadratic Mean Diameter and its corresponding coefficients and significance level for all the terms present in it.

Equation of regression	F value	Pr > F	Adj R-square
Square Root of QMD = $b_0 + b_1$ (c1) + b_2 (c2) + b_3 (sp1) + b_4 (sp2) + b_5 (tpa) + b_6 (age) + b_{10} (sp2*tpa) + + b_{12} (c2*age) + b_{15} (tpa*age) + b_{16} (tpa*tpa) + b_{17} (age*age) + b_{24} (sp1*tpa*tpa) + b_{25} (sp2*tpa*tpa)	366.42	<.0001	0.943

Parameter	Estimate	Error	t Value	Pr > |t|
b_0	-.0792372080	0.05053437	-1.57	0.1180
b_1	0.1214806257	0.02918338	4.16	<.0001
b_2	-.0839269192	0.05439942	-1.54	0.1240
b_3	0.1175374686	0.03417760	3.44	0.0007
b_4	-.2103680967	0.06568789	-3.20	0.0015
b_5	-.0002836915	0.00014723	-1.93	0.0550
b_6	0.2780495050	0.01305256	21.30	<.0001
b_{10}	0.0010044509	0.00039575	2.54	0.0117
b_{12}	-.0184766846	0.00665346	-2.78	0.0058
b_{15}	-.0000452761	0.00001042	-4.35	<.0001
b_{16}	0.0000006090	0.00000012	4.95	<.0001
b_{17}	-.0052675422	0.00084979	-6.20	<.0001
b_{24}	-.0000002072	0.00000009	-2.29	0.0227
b_{25}	-.0000010525	0.00000046	-2.30	0.0224

Table A.3: Model for Mean Total Height and its corresponding coefficients and significance level for all the terms present in it.

Equation of regression	F value	Pr > F	Adj R-square
Logarithm of Height = $b_0 + b_1$ (c1) + b_2 (c2) + b_3 (sp1) + b_5 (tpa) + b_6 (age) + b_{11} (c1*age) + b_{12} (c2*age) + b_{13} (sp1*age) + b_{16} (tpa*tpa) + b_{17} (age*age) + b_{24} (sp1*tpa*tpa) + b_{27} (c2*age*age)	454.13	<.0001	0.949

Parameter	Estimate	Error	t Value	Pr > |t|
b_0	0.4947261657	0.02018591	24.51	<.0001
b_1	-.0208103570	0.02133484	-0.98	0.3302
b_2	0.0633371918	0.04050529	1.56	0.1190
b_3	-.0344795311	0.02170024	-1.59	0.1132
b_5	-.0000651119	0.00004645	-1.40	0.1621
b_6	0.1230380737	0.00558929	22.01	<.0001
b_{11}	0.0058127196	0.00276079	2.11	0.0361
b_{12}	-.0306000584	0.01197590	-2.56	0.0111
b_{13}	0.0084750956	0.00278715	3.04	0.0026
b_{16}	0.0000001645	0.00000004	3.82	0.0002
b_{17}	-.0034768812	0.00035078	-9.91	<.0001
b_{24}	-.0000001151	0.00000003	-3.40	0.0008
b_{27}	0.0017434613	0.00077001	2.26	0.0243

Table A.4: Model for Crown Length and its corresponding coefficients and significance level for all the terms present in it.

Equation of regression	F value	Pr > F	Adj R-square
Logarithm of Crown Length = $b_0 + b_2$ (c2) + b_3 (sp1) + b_4 (sp2) + b_5 (tpa) + b_6 (age) + b_9 (sp1*tpa) + b_{12} (c2*age) + b_{13} (sp1*age) + b_{16} (tpa*tpa) + b_{17} (age*age) + b_{28} (sp1*age*age)	423.22	<.0001	0.941

Parameter	Estimate	Error	t Value	Pr > |t|
b_0	0.4954593645	0.01976692	25.07	<.0001
b_2	0.0091519864	0.02103174	0.44	0.6638
b_3	-.0873575398	0.04135519	-2.11	0.0355
b_4	0.0166860800	0.00994830	1.68	0.0946
b_5	-.0000375162	0.00004895	-0.77	0.4440
b_6	0.1198897483	0.00568594	21.09	<.0001
b_9	-.0001077776	0.00003483	-3.09	0.0022
b_{12}	-.0070017532	0.00268819	-2.60	0.0097
b_{13}	0.0327155899	0.01271416	2.57	0.0106
b_{16}	0.0000001160	0.00000004	2.58	0.0103
b_{17}	-.0033224836	0.00036155	-9.19	<.0001
b_{28}	-.0018428169	0.00081288	-2.27	0.0241

Table A.5: Model for Crown Area and its corresponding coefficients and significance level for all the terms present in it.

Equation of regression	F value	Pr > F	Adj R-square
Logarithm of Crown Area = $b_0 + b_1$ (c1) + b_2 (c2) + b_4 (sp2) + b_5 (tpa) + b_6 (age) + b_{10} (sp2*tpa) + b_{12} (c2*age) + b_{14} (sp2*age) + b_{15} (tpa*age) + b_{16} (tpa*tpa) + b_{17} (age*age) + b_{21} (sp2*tpa*age)	215.84	<.0001	0.90

Parameter	Estimate	Error	t Value	Pr > |t|
b_0	0.0734290619	0.06186284	1.19	0.2362
b_1	0.0870474334	0.03157929	2.76	0.0062
b_2	0.0787662170	0.06698742	1.18	0.2406
b_4	0.2627443221	0.10074689	2.61	0.0096
b_5	-.0017080852	0.00017899	-9.54	<.0001
b_6	0.3451400301	0.01662270	20.76	<.0001
b_{10}	-.0004901410	0.00027465	-1.78	0.0754
b_{12}	-.0272304204	0.00856143	-3.18	0.0016
b_{14}	-.0447411169	0.01372573	-3.26	0.0012
b_{15}	0.0000425078	0.00001399	3.04	0.0026
b_{16}	0.0000008936	0.00000015	6.03	<.0001
b_{17}	-.0119171219	0.00106212	-11.22	<.0001
b_{21}	0.0000772621	0.00003512	2.20	0.0286

Table A.6: Model for Mean Tree Volume and its corresponding coefficients and significance level for all the terms present in it.

Equation of regression	F value	Pr > F	Adj R-square
Logarithm of Tree Volume = $b_0 + b_1$ (c1) + b_2 (c2) + b_3 (sp1) + b_4 (sp2) + b_5 (tpa) + b_6 (age) + b_8 (c2*tpa) + b_{12} (c2*age) + b_{14} (sp2*age) + b_{15} (tpa*age) + b_{16} (tpa*tpa) + b_{17} (age*age) + b_{23} (c2*tpa*tpa)	313.66	<.0001	0.936

Parameter	Estimate	Error	t Value	Pr > |t|
b_0	-.7761545605	0.10069235	-7.71	<.0001
b_1	0.2101435813	0.05280646	3.98	<.0001
b_2	-.6169683106	0.12679642	-4.87	<.0001
b_3	0.1247838586	0.05355411	2.33	0.0205
b_4	-.5312779133	0.10041932	-5.29	<.0001
b_5	0.0003379149	0.00027561	1.23	0.2212
b_6	0.6529678286	0.02482453	26.30	<.0001
b_8	-.0010425402	0.00052487	-1.99	0.0480
b_{12}	0.0445602500	0.01266942	3.52	0.0005
b_{14}	0.0487942708	0.01243318	3.92	0.0001
b_{15}	-.0000664172	0.00001878	-3.54	0.0005
b_{16}	0.0000002661	0.00000024	1.11	0.2680
b_{17}	-.0237190991	0.00155483	-15.26	<.0001
b_{23}	0.0000011987	0.00000047	2.52	0.0121

Table A.7: Model for Mean Basal Area per acre and its corresponding coefficients and significance level for all the terms present in it.

Equation of regression	F value	Pr > F	Adj R-square
Logarithm of Basal Area = $b_0 + b_1$ (c1) + b_2 (c2) + b_3 (sp1) + b_4 (sp2) + b_5 (tpa) + b_6 (age) + b_8 (c2*tpa) + b_{10} (sp2*tpa) + b_{12} (c2*age) + b_{15} (tpa*age) + b_{16} (tpa*tpa) + b_{17} (age*age) + b_{23} (c2*tpa*tpa) + b_{24} (sp1*tpa*tpa) + b_{25} (sp2*tpa*tpa)	194.40	<.0001	0.929

Parameter	Estimate	Error	t Value	Pr > |t|
b_0	-2.423100763	0.13838493	-17.51	<.0001
b_1	-0.131012603	0.04181662	-3.13	0.0020
b_2	-0.655422773	0.13040721	-5.03	<.0001
b_3	0.179903417	0.05088451	3.54	0.0005
b_4	-0.368280588	0.11037277	-3.34	0.0010
b_5	0.002834514	0.00028015	10.12	<.0001
b_6	0.500753134	0.03070307	16.31	<.0001
b_8	-0.001080421	0.00045484	-2.38	0.0184
b_{10}	0.001964479	0.00063241	3.11	0.0021
b_{12}	0.022772264	0.01107839	2.06	0.0410
b_{15}	-0.000062058	0.00001609	-3.86	0.0002
b_{16}	-0.000001062	0.00000021	-5.10	<.0001
b_{17}	-0.017325485	0.00173241	-10.00	<.0001
b_{23}	0.000001099	0.00000039	2.83	0.0051
b_{24}	-0.000000382	0.00000013	-2.96	0.0034
b_{25}	-0.000002313	0.00000070	-3.33	0.0010

Table A.8: Model for Mean Volume per acre and its corresponding coefficients and significance level for all the term present in it.

Equation of regression	F value	Pr > F	Adj R-square
Logarithm of Volume = $b_0 + b_1$ (c1) + b_2 (c2) + b_3 (sp1) + b_4 (sp2) + b_5 (tpa) + b_6 (age) + b_8 (c2*tpa) + b_{10} (sp2*tpa) + b_{12} (c2*age) + b_{14} (sp2*age) + b_{15} (tpa*age) + b_{16} (tpa*tpa) + b_{17} (age*age) + b_{23} (c2*tpa*tpa) + b_{24} (sp1*tpa*tpa) + b_{25} (sp2*tpa*tpa)	182.00	<.0001	0.93

Parameter	Estimate	Error	t Value	Pr > |t|
b_0	-1.624422497	0.16475551	-9.86	<.0001
b_1	-0.110653510	0.04905628	-2.26	0.0251
b_2	-0.946843940	0.15488374	-6.11	<.0001
b_3	0.202139002	0.05969411	3.39	0.0008
b_4	-0.728790912	0.16581325	-4.40	<.0001
b_5	0.002788063	0.00032876	8.48	<.0001
b_6	0.517462076	0.03617439	14.30	<.0001
b_8	-0.001251166	0.00053366	-2.34	0.0199
b_{10}	0.002038940	0.00074327	2.74	0.0066
b_{12}	0.048923866	0.01338862	3.65	0.0003
b_{14}	0.036482359	0.01391792	2.62	0.0094
b_{15}	-0.000049858	0.00001898	-2.63	0.0092
b_{16}	-0.000001053	0.00000024	-4.31	<.0001
b_{17}	-0.016828007	0.00203264	-8.28	<.0001
b_{23}	0.000001307	0.00000046	2.87	0.0045
b_{24}	-0.000000427	0.00000015	-2.81	0.0053
b_{25}	-0.000002418	0.00000082	-2.96	0.0034

Table A.9: Range of values for characteristics measured on the plots at age 12 by species composition.

Stand Attributes	Douglas-fir	Western hemlock	Mixture
Stems per acre	90-866	90-758	65-814
DBH (inches)	4.21-7.04	3.92-6.90	4.30-6.33
QMD (inches)	4.31-7.10	4.27-7.02	4.69-6.78
Height (feet)	30.1-36.76	25.18-36.76	28.53-38.80
Basal Area (square feet / acre)	6.78-114.8	19.6-127.5	15.83-135.10
Volume (cubic feet / acre)	244.7-1786.0	191.5-2148	211.5-2329