Comparing productivity of pure and mixed Douglas-fir and western hemlock plantations in the Pacific Northwest

M.M. Amoroso and E.C. Turnblom

Abstract: We studied pure and 50/50 mixtures of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) plantations to compare attained total yields between mixed-species stands as opposed to monocultures of equal densities. Whether overall stand density influences this outcome has not been adequately investigated, and to address this we included three density levels (494, 1111, and 1729 trees/ha) in the analysis. 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. At 494 and 1111 trees/ha the monocultures had a higher volume per hectare than the mixed stand, but at 1729 trees/ha the mixed stand appeared to be just as productive as the pure stands. The increase in productivity by the mixture at high densities seems to have resulted from the partial stratification observed and most likely also from 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. This study shows the important role density plays in the productivity of mixed stands and thus in comparing mixed and pure stands.

Résumé : Les auteurs ont étudié des peuplements purs et mélangés (50/50) de douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) et de pruche de l’Ouest (*Tsuga heterophylla* (Raf.) Sarg.) en plantation pour comparer les rendements totaux obtenus en peuplements mélangés comparativement à des monocultures de même densité. Ils ont inclus dans l’analyse trois niveaux de densité (494, 1111 et 1729 tiges/ha) étant donné que l’effet de la densité globale du peuplement sur le rendement n’a pas été adéquatement étudié. À l’âge de 12 ans, en peuplements mélangés, la hauteur, le diamètre et le volume des tiges individuelles de douglas de Menzies étaient supérieurs à ceux de la pruche de l’Ouest peu importe la densité. Avec 494 et 1111 tiges/ha, les monocultures avaient un volume à l’hectare plus élevé que le peuplement mélangé mais avec 1729 tiges/ha le peuplement mélangé semblait tout aussi productif que les peuplements purs. L’augmentation de productivité dans le mélange à haute densité semble être le résultat de la stratification partielle qui a été observée et fort probablement aussi d’une meilleure utilisation des ressources du site. À cause de cela, il y avait probablement moins de compétition interspécifique dans le peuplement mélangé que de compétition intraspécifique dans les peuplements purs. Cette étude montre l’importance du rôle que joue la densité sur la productivité des peuplements mélangés et, par conséquent, dans la comparaison des peuplements purs et mélangés.

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Introduction

When timber production is the primary objective of management, there is a clear tendency to favor monocultures of the most productive species. This is mainly because of the simpler management of monocultures (easier and cheaper establishment, planning and marketing), but also, though 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, compared to the most productive species, 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 comparable or greater total yields when using mixed-species planted stands as opposed to 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 greater overall productivity (Vandermeer 1989). Even though this has been observed in many situations, it is not always likely to happen. To achieve greater productivity in mixed stands, the species constituting 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 the other, but

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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, photosynthetic efficiency of foliage, 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).The mixed stands may experience less intense interspecific than intraspecific light competition as a consequence of the differences in shade tolerance among species. Such a stratified canopy would, in theory, maximize the use of light because of increased light interception and light-use efficiency (Kelty 1992), leading to greater total productivity than in pure stands (Smith et al. 1997). This type of response has been found in studies by Assmann (1970), Wierman and Oliver (1979), Kelty (1989), Brown (1992), Montagnini et al. (1995, 2000), DeBell et al. (1997), Man and Lieffers (1999), and Garber and Maguire (2004).

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

In accordance with what previous studies have shown, these two species are likely to exhibit "ecological combining ability" (Harper 1977) and to have greater productivity in a mixed stand than in pure stands of their respective components. However, all the previous research on Douglas-fir and western hemlock mixtures has only examined natural stands. Questions remain as to whether the patterns of stratification and growth of these species observed in natural stands also occur in plantations and how stand growth, yield, and structural development depend on initial stand density.

The objectives of this study were to assess differences in growth and productivity between Douglas-fir and western hemlock growing in both 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 and replicated at two sites, provides a well-designed field experiment testing the effects of widely varying spacing and species composition.

Methodology

Experimental sites

This study was conducted at two sites (Brittain Creek and Forks) located on the Olympic Peninsula in the state of Washington, USA. The Brittain Creek site is located in Gray's Harbor County (47°13′N and 123°52′W), while the Forks site is located in Clallam County (48°02′N and 124°23′W). Brittain Creek has a mean annual precipitation of approximately 2902 mm and a mean annual temperature of 9.7 °C (Western Regional Climate Center 2003). The site is located at an elevation of 110 m, and the site index is 38 m (125 ft) at 50 years, corresponding to a site class of II (King 1966). The site has a 1%–15% slope, and the soil, a Willaby silt loam, 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 3047 mm and a mean annual temperature of 9.8 °C (Western Regional Climate Center 2003). This site is located at an elevation of 122 m, and the site index is 37 m (120 ft) at 50 years, corresponding to a site class of II (King 1966). The site has a 0%–15% slope, and the soils are classified as part of the Klone–Ozette–Tealwhit complex from the Klone series and characterized as very deep, well-drained soils formed in poorly sorted glacial outwash (Halloin 1987).

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). The two installations chosen for this study were established and planted in 1990 with Douglas-fir 2–1 stock and western hemlock 1–1 stock.

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 to the three installations. Within each of these installations, six areas (experimental units) of at least 3 acres (1 acre = 0.404 686 ha) in size were delineated, where one of six initial desired planting densities (245, 479, 748, 1074, 1682, and 2989 trees/ha) was randomly assigned to each experimental unit, giving the experiment a randomized complete block split-plot design. In each of these experimental units, a 0.405 ha plot was located. Each plot includes 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 1, were selected as multiples of the target spacing for each block (Maguire et al. 1991). Thus, there are 36 MSPs, and it should be emphasized that the MSPs are the experimental units; therefore, they are to be treated as the independent observations, because they represent the stage at which randomization of planting densities occurred (Oehlert 2000). Kelty and Cameron

Table 1. Sample plot size and characteristics by targeted planting spacing.

Spacing (m)	Trees/ha	No. of rows	Plot side (m)	Plot size (ha)	Trees per plot
6.4	245	7	44.8	0.20	121
4.6	479	8	36.6	0.13	158
3.7	748	9	32.9	0.11	200
3.0	1074	10	30.5	0.09	247
2.4	1682	13	31.7	0.10	417
1.8	2989	16	29.3	0.09	632

(1995) discuss other individual-tree study designs, which are for many reasons not appropriate for the type of analyses presented here.

Measurements and field data collection

Basal diameter and diameter at breast height (DBH) were measured on all trees. Basal diameter was measured 18 cm above the ground line using calipers until trees reached breast height, while DBH measurements were done by caliper or diameter tape (to the nearest 0.25 cm). Total height and height to the base of the live crown were measured with a laser hypsometer to the nearest 0.03 m on a sample of 42 trees drawn from the diameter distribution, including the smallest and the largest trees on each plot. Crown width (average of two crown widths: east–west and north–south, measured to the nearest 0.03 m) was also measured on the same subsample of trees. Four measurements taken on a 2-year cycle and an additional measurement on a 4-year cycle were available for analysis.

Data analysis

Trees without measured heights in each plot were given a height estimate from a nonlinear height–diameter equation fit by species to all 42 height trees measured in the plot at any given time. We used a functional form recommended by Martin and Flewelling (1998), because they found it to be properly parameterized and unbiased when tested on inventory data sets from western Washington. The following individual-tree attributes were derived from diameter and height: basal area, height/diameter (*h*/*d*) ratio, crown ratio, and tree volume. Douglas-fir tree volumes were calculated using the method of Bruce and de Mars (1974), and western hemlock volumes were estimated using the method of Flewelling and Raynes (1993).

Mean values for each plot and measurement number were calculated for all the variables described previously, as well as for basal area per hectare, volume per hectare, and quadratic mean diameter.

The targeted planting densities were met with variable success in the field. The density on a few of the plots varied so widely from their target density that they actually matched the next higher or lower planting density. Further, measurements on the two research sites, Forks and Brittain Creek, began 1 year apart. So, comparisons among plots with the same density at the six fixed initial planting densities at a specific age either were not possible or would be imprecise at best. Therefore, to enhance precision of the comparisons among stands, regression analysis was used, in which models for the variables under analysis were built to predict values at any given year and density within the range of final densities and the time frame of the study. The two primary independent variables in the models were trees per hectare (the actual trees per hectare at each measurement) and age (time 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 variables were included in the model: one corresponding to “species”, to differentiate between Douglas-fir and 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 previously and all possible interactions among them. A quadratic response surface model was chosen because it is a well-known standard analysis technique for well-designed experiments and is relatively easy to interpret (Oehlert 2000). It allows dependent variables to exhibit level, linear, and (or) curvilinear responses to both the experimentally manipulated variables of species composition and density and to the covariate age. It also allows for testing of interaction effects between all independent variables. Higher order response surfaces, such as the cubic, which are capable of identifying more complex nonlinear responses, were not considered necessary, given the young age of the plantations. The general model form is presented in the Appendix.

Separate quadratic response surface models were fit to each dependent variable using multiple regression analysis. Residual plots indicated that all response variables needed to be transformed because of non-constant variance and non-normality. Square-root (for DBH) and logarithmic transformations (for remaining variables) were sufficient to stabilize variance and improve normality in all cases. The final models for all response variables contained only those predictor variables with $p \leq 0.05$. Possible autocorrelation effects with the use of age as a covariate were not assessed. Rather, we relied on the analytical heuristic that when the number of independent observations (36 plots in this case) exceeds the number of repeat measurements (5 in this case), the effects of autocorrelation are very likely to be minimal (Crowder and Hand 1996).

Utilizing these models, values for three chosen density levels (494, 1111, and 1729 trees/ha) were initially predicted at three ages (4, 8, and 12 years). The low- and high-density levels correspond to the range of actual density values within which all three stand types were represented; the situation is analogous for the three ages. All comparisons made in the results were conducted by computing 95% confidence intervals on the predicted responses at the chosen levels of the independent variables, taking any nonoverlapping intervals as sufficient evidence of statistical significance. Combined type I error rates were controlled using Bonferroni's procedure, so that all the confidence intervals constructed for any given response variable (height, DBH, volume, etc.) hold simultaneously, meaning confidence coverage is at least 95% for any single predicted response (Oehlert 2000). Statistical analyses were made using the SAS package for Windows, version 8 (SAS Institute Inc. 1999–2001).

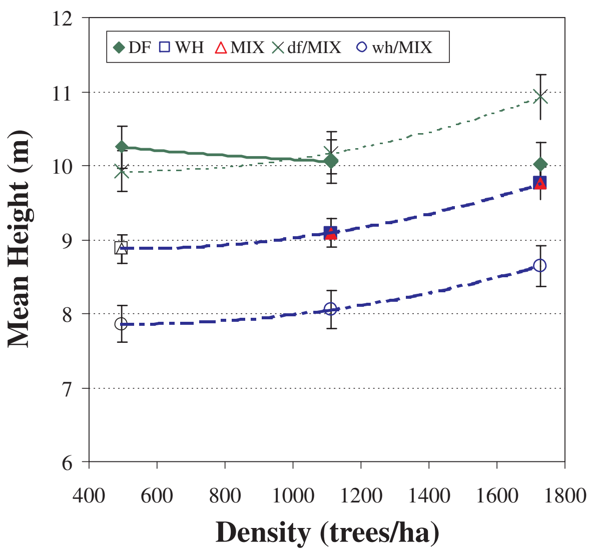
The yield of pure and mixed stands is usually compared on a relative basis; thus, the effects of combining the two species were evaluated by comparing the yield of each species

Table 2. Mean stand characteristics predicted at age 12 by species composition and the three density levels chosen for analysis.

Density (trees/ha)	Composition	Height (m)	DBH (cm)	Basal area (m^2/ha)	Volume (m^3/ha)
494	Douglas-fir	10.2	14.94	9.8	39
	Western hemlock	8.9	12.67	5.7	26
	Mixture	8.9	13.21	6.8	27
1111	Douglas-fir	10.1	13.29	19.1	78
	Western hemlock	9.1	12.46	16.8	82
	Mixture	9.1	12.04	14.5	60
1729	Douglas-fir	10.0	12.30	24.4	104
	Western hemlock	9.8	11.70	18.6	94
	Mixture	9.8	11.77	24.6	109

Note: The density levels chosen for the analyses are well within the range of the six targeted planting densities displayed in Table 1.

Fig. 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.



in the mixture with its yield in monoculture as per Harper (1977). Yield variables for this analysis were basal area and volume per hectare. The relative yield (RY) of each species and the relative yield total (RYT) were calculated as

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

$$\mathrm{RY}_{\text{Western hemlock}} = \frac{\text{Yield of western hemlock in mixture}}{\text{Yield of western hemlock in monoculture}}$$

$$\text{Relative yield total (RYT)} = \mathrm{RY}_{\text{Douglas-fir}} + \mathrm{RY}_{\text{Western hemlock}}$$

If both species use resources in identical ways, and hence compete for these resources, the expected RY of each species will be equivalent to its proportional contribution in the mixture, and an expected RYT = 1. An RYT > 1 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 < 1 indicate an 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 each species having an expected RY = 0.5 and an RYT = 1.0.

Results

Mean stand characteristics at age 12 for the two pure stands and the mixed stand at the three chosen densities are summarized in Table 2. 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 hectare increased with density, and there were changes in terms of the most productive stand composition at different densities. Hereafter, pure Douglas-fir stands will be denoted DF, pure western hemlock stands WH, and mixed stands MIX. Douglas-fir and western hemlock as components of the mixed stands will be denoted df/MIX and wh/MIX, respectively. More detailed and deeper analyses for all the variables studied are presented in what follows.

Patterns of height growth

Ninety-five percent of the total variation in the logarithm of height was explained by the following predictor variables: Douglas-fir component indicator (C1), the western hemlock component indicator (C2), the Douglas-fir species indicator (SP1), TPH, AGE, C1 × AGE, C2 × AGE, SP1 × AGE, TPH × TPH, AGE × AGE, SP1 × AGE × AGE, and C2 × AGE × AGE, where TPH is trees per hectare (see Appendix for full model form).

Height is known to be 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 (Fig. 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 1729 trees/ha were significantly taller than hemlock at lower densities. Comparisons between the two species show that Douglas-fir was significantly taller than western hemlock by more than 1 m at 494 trees/ha; however, differences in total mean heights for the two species were in-

Fig. 2. Mean total height over time by species for two density levels: 494 and 1729 trees/ha.

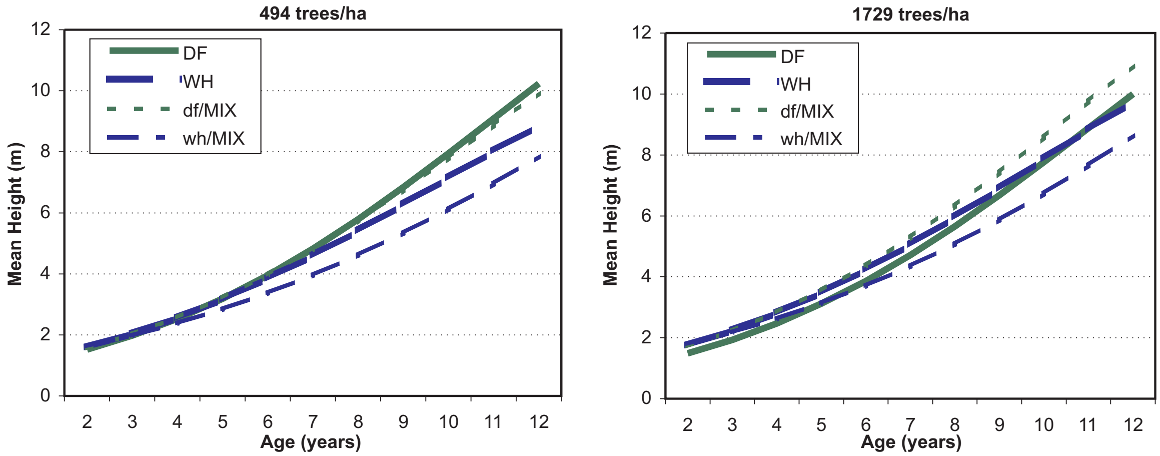
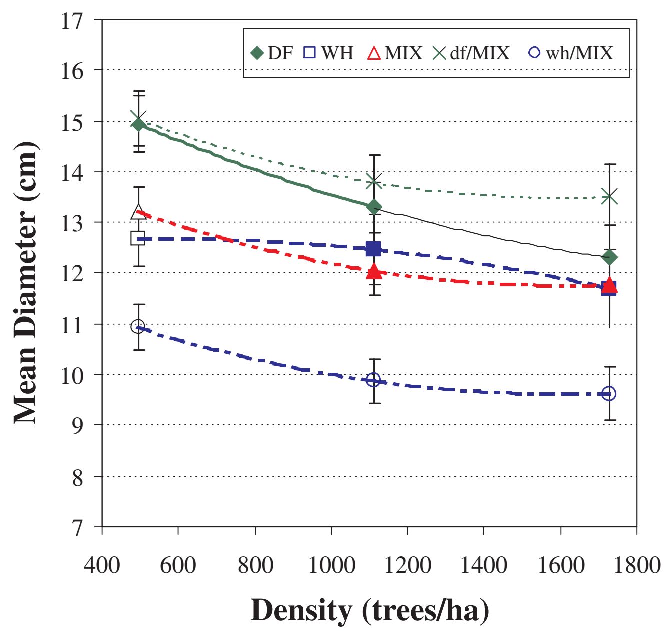


Table 3. Periodic annual increment in mean total height (m) for Douglas-fir (DF) and western hemlock (WH) growing in pure and in mixed stands for three growth periods.

		Density (trees/ha)		
Growth period (years)	Species	494	1111	1729
0–4	DF	0.63	0.62	0.62
	WH	0.64	0.66	0.70
	df/MIX	0.64	0.66	0.71
	wh/MIX	0.60	0.61	0.66
4–8	DF	0.81	0.80	0.80
	WH	0.71	0.73	0.79
	df/MIX	0.79	0.81	0.87
	wh/MIX	0.56	0.57	0.61
8–12	DF	1.11	1.09	1.09
	WH	0.86	0.88	0.95
	df/MIX	1.05	1.07	1.15
	wh/MIX	0.81	0.83	0.89

Note: df/MIX and wh/MIX denote Douglas-fir and western hemlock, respectively, as components of the mixed stands.

Fig. 3. Mean diameter by treatment at age 12 for three density levels. Bars represent 95% confidence intervals.



significant at 1729 trees/ha. There were no significant height differences at age 8 or age 4 for any density in the pure stands.

When comparing the two species as components of the mixed stands, results were different. Douglas-fir was on average 2 m taller than western hemlock across densities. These differences in the height growth pattern started at around age 5 (Fig. 2) and were a consequence of the differences in height growth rate for the two species (Table 3); right after age 4 Douglas-fir started growing faster in height than western hemlock.

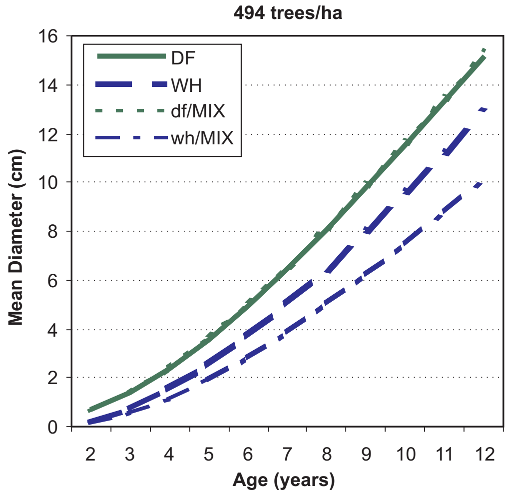
Compared with stands growing in a mixture, western hemlock was on average 1 m taller growing in pure stands. Douglas-fir, instead, had the same height both in pure and in mixed stands when it grew at 494 and 1111 trees/ha but became about 1 m taller at 1729 trees/ha. This change in the growth pattern seems to be more evident beginning at age 8. The overall trends through time of all the patterns described previously can be visualized in the set of graphs at two different densities (Fig. 2).

Patterns of diameter growth

Ninety-four percent of the total variation in the square-root of DBH was explained by the following predictor variables: Douglas-fir component indicator (C1), the western hemlock component indicator (C2), the Douglas-fir species indicator (SP1), the western hemlock species indicator (SP2), TPH, AGE, SP2 × TPH, C2 × AGE, TPH × AGE, TPH × TPH, AGE × AGE, SP1 × TPH × TPH, and SP2 × TPH × TPH (see Appendix for full model form).

Density and species composition had a strong effect on mean diameter at age 12. As was expected, diameter had an inverse relationship with density, and it appears that the two species responded to density differently (Fig. 3). Growing in pure stands, Douglas-fir was about 2.5 cm greater when it grew at 494 than at 1729 trees/ha. Western hemlock, instead, did not show significant diameter differences across the three density levels, though a slight trend is observed that qualitatively matches that for Douglas-fir. Differences between the

Fig. 4. Mean diameter over time by species for two density levels: 494 and 1729 trees/ha.



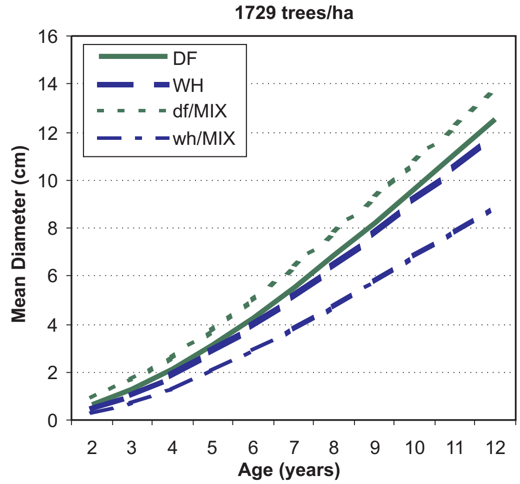


Table 4. Periodic annual increment in mean diameter (cm) for Douglas-fir (DF) and western hemlock (WH) growing in pure and in mixed stands for three growth periods.

		Density (trees/ha)		
Growth period (years)	Species	494	1111	1729
0–4	DF	1.8	1.6	1.4
	WH	1.6	1.5	1.4
	df/MIX	1.8	1.6	1.5
	wh/MIX	1.3	1.1	1.0
4–8	DF	1.4	1.3	1.2
	WH	1.2	1.2	1.1
	df/MIX	1.4	1.3	1.3
	wh/MIX	1.0	0.9	0.9
8–12	DF	0.6	0.5	0.5
	WH	0.4	0.5	0.5
	df/MIX	0.6	0.6	0.7
	wh/MIX	0.3	0.3	0.3

Note: df/MIX and wh/MIX denote Douglas-fir and western hemlock, respectively, as components of the mixed stands.

two single-species stands were significant at 494 trees/ha; however, they became insignificant at 1729 trees/ha; 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 with that from western hemlock at any of the densities and became statistically indistinguishable from Douglas-fir at the high-density level. The described differences were already established at age 8.

Comparisons between species as components of the mixed stands produced different results than pure stand comparisons. At age 12 Douglas-fir had a DBH that was on average 4 cm more than that of western hemlock at all densities (Fig. 3). Furthermore, these differences appeared early in stand development and were already on the order of 3 cm at age 8 (Fig. 4). Growth rates for the two species at different ages support this pattern (Table 4).

Apparently some changes in the growth pattern of the species occur when they grow in pure as opposed to mixed stands. Western hemlock was 2.5 cm greater in DBH when it grew in pure stands, and this was consistent across all densities. Although these differences were not found to be significant at the 95% confidence level, Douglas-fir became more than 1 cm in DBH greater when it grew at high densities in the mixture. The overall trends through time for all the patterns described previously can be visualized in the set of graphs at the different densities (Fig. 4).

Height/diameter ratio

The height/diameter ratio (*h*/*d*) was compared among species while growing alone and together at each of the density levels (Fig. 5). Even though some significant differences in diameter and height growth were evident at age 12, the *h*/*d* ratio at this age is very low and is not significantly different among the treatments over the range of densities studied. Western hemlock growing in the mixture seemed to be developing a slightly greater *h*/*d* ratio than other stand types at this stage.

Individual-tree volume growth

Ninety-four percent of the total variation in the logarithm of mean tree volume was explained by the following predictor variables: Douglas-fir component indicator (C1), the western hemlock component indicator (C2), the Douglas-fir species indicator (SP1), the western hemlock species indicator (SP2), TPH, AGE, C2 × TPH, C2 × AGE, SP2 × AGE, TPH × AGE, TPH × TPH, AGE × AGE, and C2 × TPH × TPH (see Appendix for full model form).

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 1729 trees/ha 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 494 to 1111 trees/ha, there was no significant change from 1111 to 1729 trees/ha (Fig. 6).

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

Fig. 5. Height/diameter ratio by treatment at age 12 for three density levels. Bars represent 95% confidence intervals.

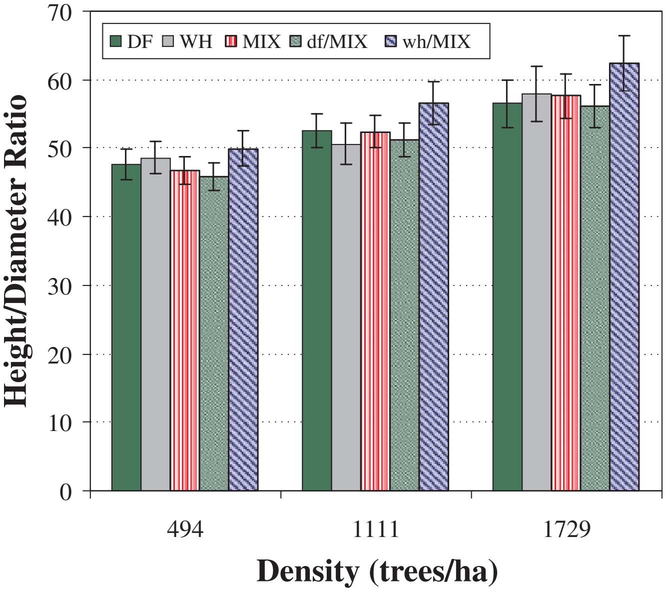
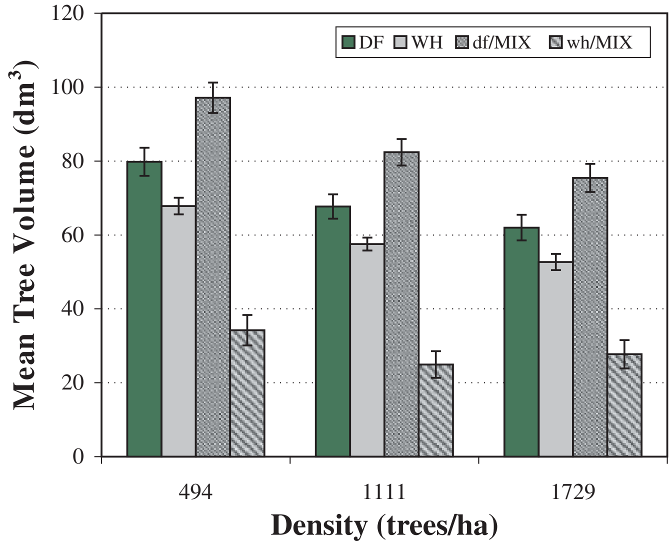


Fig. 6. Mean tree volume by treatment at age 12 for three density levels. Bars represent 95% confidence intervals.



stands at the same total stand density. In contrast, western hemlock in mixed stands had mean tree volume reduced by 50%, 43%, and 53% at 494, 1111, and 1729 trees/ha, 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 did not exhibit significant differences. Western hemlock mean tree volume, on the other hand, experienced a statistically significant decrease in the mixture of 55% and 60% at 865 trees/ha (half of 1729 trees/ha) and 555 trees/ha (half of 1111 trees/ha), respectively.

Per-hectare volume accumulation

Ninety-three percent of the total variation in the logarithm of volume per hectare was explained by the following predictor variables: Douglas-fir component indicator (C1), the western hemlock component indicator (C2), the Douglas-fir species indicator (SP1), the western hemlock species indicator (SP2), TPH, AGE, C2 × TPH, SP2 × TPH, C2 × AGE, SP2 × AGE, TPH × AGE, TPH × TPH, AGE × AGE, C2 × TPH × TPH, SP1 × TPH × TPH, and SP2 × TPH × TPH (see Appendix for full model form).

At low densities, pure Douglas-fir had higher volume per hectare at age 12 than the pure western hemlock and the mixed stand (Fig. 7). At 1111 trees/ha both the Douglas-fir and western hemlock monocultures had significantly higher volume per hectare than the mixture. At 1729 trees/ha volume per hectare was statistically indistinguishable among the three stands. These results are consistent with what was found at this density for the height and diameter growth patterns where no significant differences were found among stand types. Another interesting result was that at 1729 trees/ha, Douglas-fir, as a component of the mixture, resulted in volume per hectare statistically indistinguishable from that of the pure hemlock stand. Results at age 8 were similar to those found for basal area at age 12, with the only difference that volumes in the western hemlock stands were lower than those for Douglas-fir at all densities.

The percentage contribution of Douglas-fir to the mixture total volume was higher across densities, ranging from 74% to 78%. Western hemlock contributed the balance of 22%–26%.

It appears that at densities higher than 1500 trees/ha, volume per hectare was no longer significantly different among the three stands. This result was paralleled by an increment in productivity of the Douglas-fir component in the mixed stands, which at the density of 1729 trees/ha accounted for 25% more volume than the same number of Douglas-fir trees growing in pure stands.

Volume per hectare in the western hemlock stands did not result in significantly different values at 1111 and 1729 trees/ha. To examine this more closely, volume per hectare for intermediate densities was estimated (Fig. 8). With this new resolution, volume per hectare for western hemlock was no longer significantly affected by densities greater than 1200 trees/ha.

Relative yield analysis

The effects of combining two species in a mixture were analyzed by comparing the yield of each species in mixture with its yield in a pure stand (Harper 1977). Relative yield (RY) and relative yield total (RYT) were calculated for basal area and volume per hectare, but because the results were similar, only those for volume are presented (Fig. 9). 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 1111 and 1729 trees/ha. It is clear that the mixture of the two species benefitted the Douglas-fir at 1111 and 1729 trees/ha as judged by its volume yield. Combined RYT was less than 0.8 for both 494 and 1111 trees/ha but, although not statistically different, was higher than 1.0 at 1729 trees/ha. Thus, it appears that at the highest density significant niche separation between these species may exist. Even though this suggests it might be a potential advantage for the mixture compared to the monocultures,

Fig. 7. Volume per hectare by treatment at age 12 for three density levels. Bars represent 95% confidence intervals.

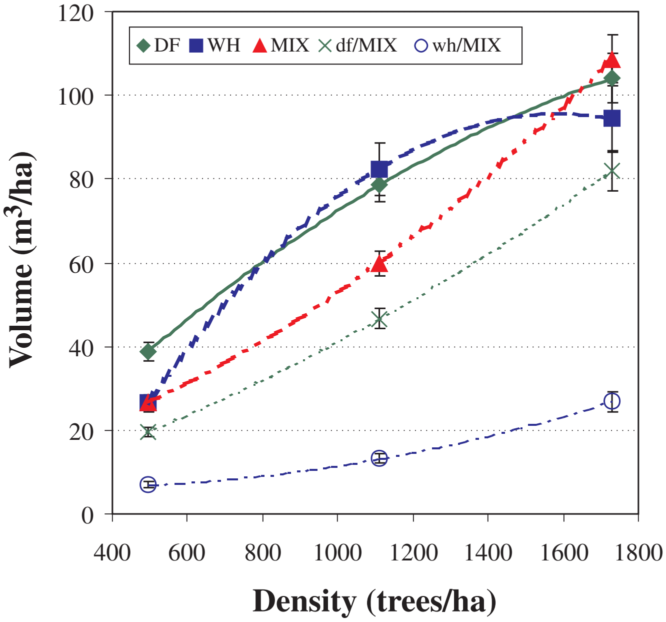
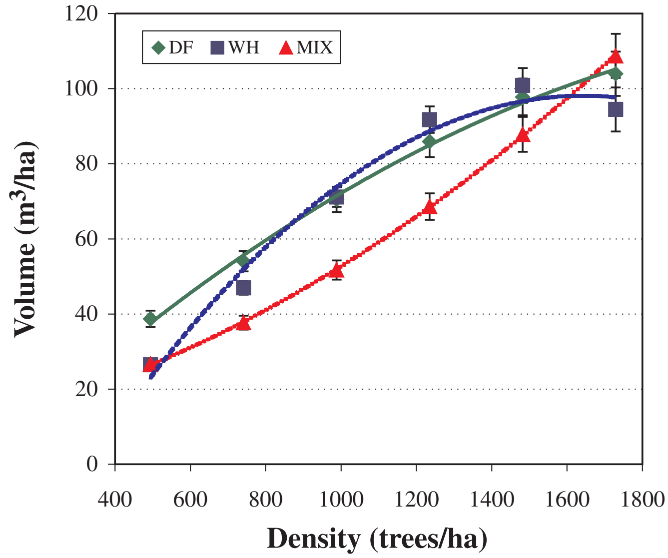


Fig. 8. Volume per hectare by treatment at age 12 across all density levels. Bars represent 95% confidence intervals.



absolute yield values should be compared to identify the highest yielding stand (Kelty 1992). This comparison is shown in Fig. 10, which combines the results found for absolute and relative yield at the three proposed densities. This shows that at 1729 trees/ha both the relative and the absolute yield (volume per hectare) for the mixture were statistically indistinguishable from that of the two monocultures.

Discussion

Height growth pattern and stratification

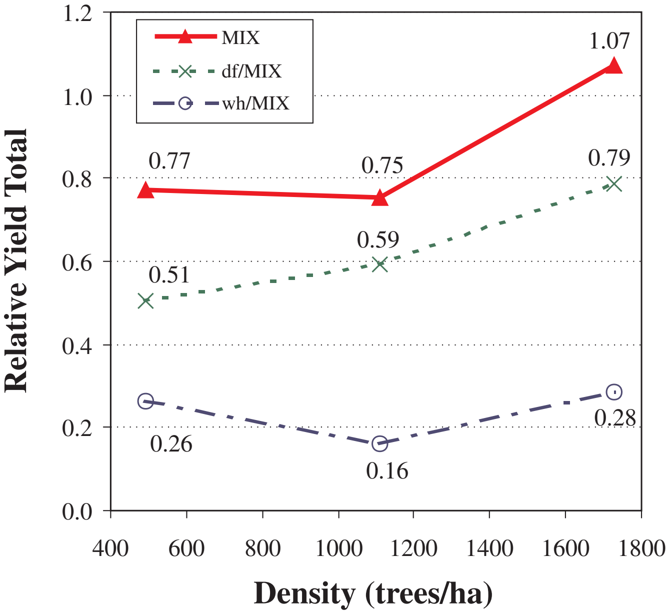
The relationship between juvenile height growth rates and shade tolerance among species plays an important role in determining development patterns of mixed stands (Menalled et al. 1998). Stratified canopies in mixed stands tend to develop naturally because shade-intolerant species generally have greater rates of juvenile height growth than shade-tolerant species, and shade-tolerant species are able to survive in reduced light environments (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. However, whether Douglas-fir would similarly outgrow western hemlock in mixed plantations and this stratification pattern occurs was not certain. This plantation study shows that by age 12 Douglas-fir has outgrown western hemlock by an average of 2 m across all densities. Since the Douglas-fir trees were 1 year older than the hemlock trees at planting, admittedly it may have had some small advantage, but no data or evidence is available to suggest an initial height difference at time of planting. Differences in height growth were quite small starting around age 4, but were almost 1 m at age 8 (Fig. 2). These height growth rates demonstrate that the difference between the two species has been increasing over the period of time measured, and though this trend is expected to continue in the near future, western hemlock may later catch up with Douglas-fir (Larson 1986). Even though the evidence of stratification at this point is partial, the increasing juvenile height growth observed and the height differences already established for the two species in the mixed plantations support the conclusion that stratification, even though not present yet, is developing.

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 and that height is not sensitive to stand density except at extremely wide and narrow spacing (Oliver and Larson 1996). However, the present study found that at the highest density (1729 trees/ha), Douglas-fir was taller in the mixture than in the pure stands. These results are consistent with those found by other authors working with mixed planted stands (Menalled et al. 1998; Garber and Maguire 2004); nevertheless, the height increment of dominant trees in mixed stands is not expected to result as a consequence of a reduction in crown competition due to stratification (Menalled et al. 1998).

Interspecific and intraspecific competition

It has been proposed that in some situations a more efficient utilization of the site resources by different species in mixed stands can result in greater yields compared to pure stands because interspecific competition becomes less intense than intraspecific competition (Kelty and Cameron 1995). This can occur under different mechanisms (competition reduction and facilitation principles). A stratified canopy is one of these mechanisms. Stratified species may experience reduced competition by capturing light at different intensities and locations within the canopy. If this happens, a stratified canopy composed of shade-tolerant species growing underneath a shade-intolerant species would collectively intercept

Fig. 9. Relative yields of volume per hectare at age 12 for Douglas-fir and western hemlock grown in mixed stands at three density levels.



more photosynthetically functional light than a pure stand of the most shade-intolerant species and would maximize the use of it (Kelty 1989). The shade-intolerant component of the stand may, therefore, experience less intense interspecific than intraspecific competition when growing in a pure stand.

Interspecific and intraspecific competition were assessed in this study by changes in the dimensions of each 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, and individual-tree volume in the mixture compared to in the pure stand. In contrast, the opposite effect was found for western hemlock, which experienced a growth reduction due to the presence of Douglas-fir. The effect that western hemlock has on Douglas-fir, seems minimal — growth is similar to that with a wider spacing in pure Douglas-fir stands. Unfortunately, vertical foliage profiles and measurements of light interception were not available to truly assess this; however, the changes in crown size and position (Amoroso 2004) further support the idea of stratification and reduced competition experienced by the Douglas-fir component. This could result in reduced interspecific competition in the mixed stand compared to intraspecific competition experienced by Douglas-fir when growing in a pure stand.

Another possible way to examine the effects of interspecific and intraspecific competition is through the height/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 that in the monoculture is consistent with Wang et al. (2000), who reported that intolerant species growing in mixed stands allocate more carbon to stemwood. In contrast to this, the higher *h*/*d* found for western hemlock in the mixture compared to in the pure stand suggests that interspecific competition is greater than intraspecific competition. This could mean that western hemlock needs to allocate relatively more resources to height growth to participate in the canopy, while Douglas-fir becomes situated in an upper position in the canopy earlier and could allocate more resources to diameter growth.

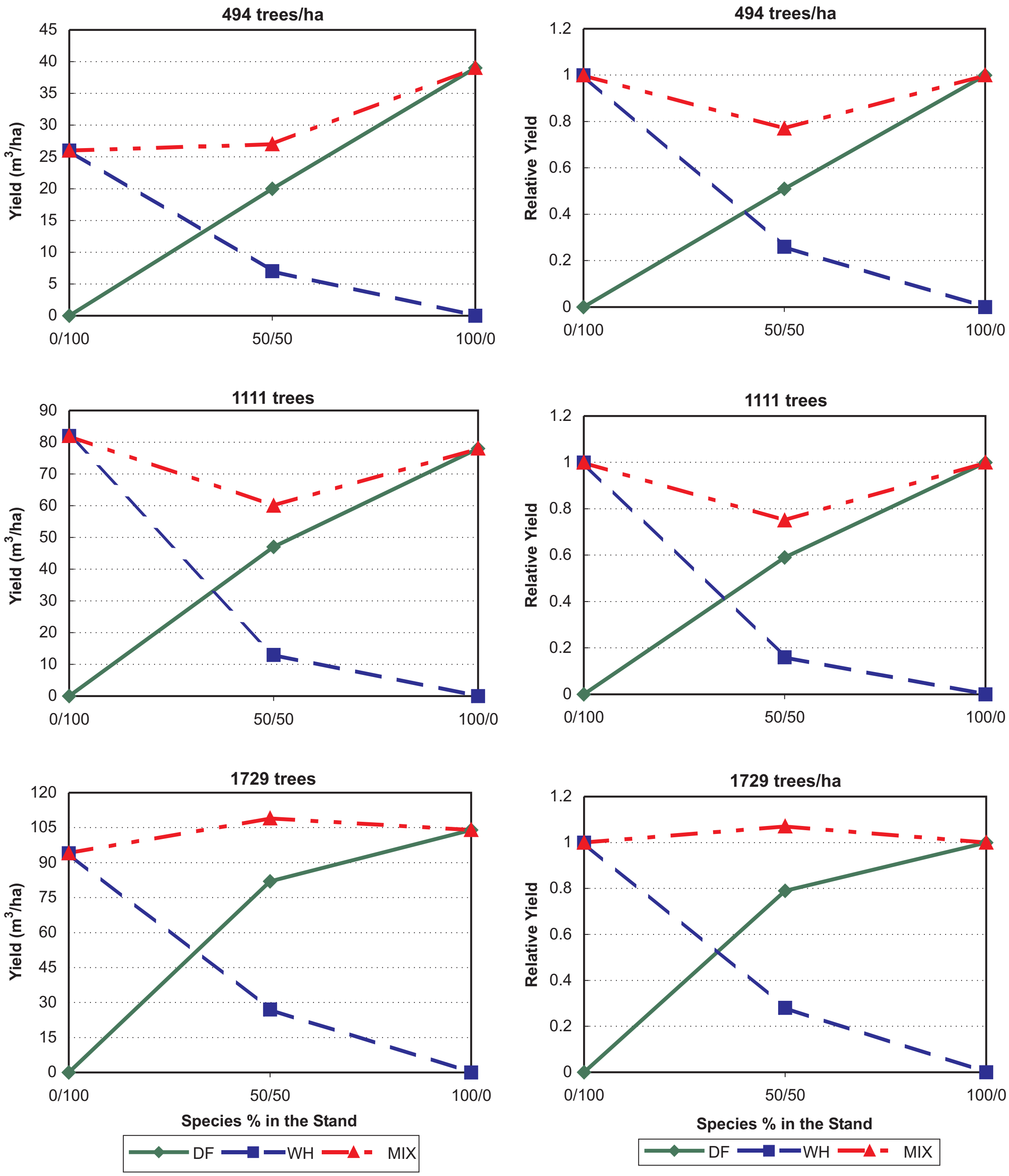
Overall stand productivity: pure versus mixed stands

While in most of the common situations mixtures will not exhibit higher yields than the most productive monoculture, 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; Binkley 1992; Brown 1992; Montagnini et al. 1995; 2000, DeBell et al. 1997; Man and Lieffers 1999; DeBell et al. 1997; Khanna 1997; Bauhus et al. 2000; Balieiro et al. 2002; Garber and Maguire 2004). In some of these cases the increased productivity was the result of species interactions typified by the facilitation production principle, while others were typical of 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, since resources unexploited by one species are used by the other species.

The productivity among the pure and mixed stands was compared both on a relative (relative yield, sensu Harper 1977) and absolute basis (volume per hectare). The relative yield analysis revealed that at 1729 trees/ha the RYT of the mixture was, although slightly higher, statistically indistinguishable from 1.0 (Fig. 9). In terms of absolute volume per hectare, the mixed stand had the same yield as the monocultures. The increased yield observed in the mixed stand at this density was probably driven by the differences 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 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, expressed by a greater mean individual-tree volume, probably due to an increase in the light interception. In contrast, the yield of western hemlock was disproportionately low as compared with that of pure western hemlock plantations.

The volume per hectare response for western hemlock turns down slightly within the range of densities studied, though not significantly so, but may still require some explanation. This response is not likely to be observed in actual 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 this is a modeling artifact caused in part by higher densities for pure western hemlock being less well represented in our data than in the other species mixes, making the western hemlock model less

Fig. 10. Absolute and relative yield for the Douglas-fir (DF) and western hemlock (WH) monocultures and the 50/50 mixture at three density levels: 494, 1111, and 1729 trees/ha. Note that species composition is labeled on the horizontal axis as % DF / % WH.



precise in this range. This is one of the disadvantages of using a quadratic model to represent nonlinearity — the model can peak (or trough) illogically within the range of the data. The downturn probably exacerbated by back-transforming (exponentiating) the fitted volume per hectare response to the original scale. However, based on the observed trend prior to this downturn, there certainly is no evidence suggesting that pure western hemlock stands would have statistically significantly higher volume per hectare than both the pure Douglas-fir and mixed stands. In other words, given a model that behaved more logically within the range of the densities examined, the results of the study would be unchanged.

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).

Most 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 to produce results in a 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 at 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 (*Alnus rubra*) 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. Additionally, Garber and Maguire (2004), working with two mixed-species spacing trials using a range of densities similar to that used in this study, concluded that spacing is an important factor determining species interactions that affect relative performance of individual species.

The study presented here demonstrates the important role density plays in the development and productivity of mixed stands when compared to pure stands of its components. 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 results at 494 trees/ha show that the RY for Douglas-fir was as expected (0.5) but, on the other hand, western hemlock had an RY lower than expected; together, they had a combined RYT value of 0.77. At 1111 trees/ha, Douglas-fir RY was slightly higher than expected, while western hemlock RY and RYT still remained below expectation but greater than observed at 494 trees/ha. However, at 1729 trees/ha the combined RYT was 1.07 and the Douglas-fir RY was much higher than expected. Although a potential productivity advantage for the mixture may exist at 1729 trees/ha, this phenomenon has not yet appeared at the lower densities; western hemlock growth is adversely affected, and beneficial growth of Douglas-fir is only starting to emerge at 1111 trees/ha at age 12. Continued monitoring in the future is needed to see whether and when these interactions do occur at lower densities.

Even supposing that the results found at 1729 trees/ha would appear in the future at 1111 trees/ha, it is not likely that the 494 trees/ha stands 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 a slow juvenile growth rate to escape early suppression, and as a consequence of this the species may not be able to express differences in their ability to use resources (i.e., stratification).

In addition to the result that mixed Douglas-fir – western hemlock planted stands were able to produce as much volume per hectare as the pure stands of either species, mixed stands may produce other economic benefits, though not considered in this study. For example, wood quality of the Douglas-fir trees growing in mixture may be improved, and this will be 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). Along with the timber production objectives, vertical complexity in mixed stands can also provide other benefits such as a broader range in wildlife habitats and enhanced aesthetic values without the often unsubstantiated timber yield trade-off. 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).

Conclusions

It appears that interactions between species growing in a mixed stand occur to different degrees depending on the amount of resources they are obligated to share and (or) for which they compete. The study presented here supports the important role density plays on the productivity of mixed stands.

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 in the pure stands. Because of this, less interspecific competition in the mixed stands than intraspecific competition in the pure stands was probably experienced. At low and medium densities, however, interactions between species did occur (as deduced from dimensional changes), but may not have been of great enough magnitude to cause the mixture to outperform the pure plantations in terms of total yield.

The results presented here reflect responses at an early stage in stand development. Long-term measurements are expected to show other effects, probably 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 too widely to other sites.

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Appendix A

The following standard response surface model was fit to all growth and yield variables:

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

where

Y is a transformation of response variables (square-root for mean DBH; logarithm for mean total height, mean individual tree volume, and volume per hectare);

c1 is a categorical variable indicating Douglas-fir as a component of the mixed stands (1 is Douglas-fir in mixture, 0 otherwise);

c2 is a categorical variable indicating western hemlock as a component of the mixed stands (1 is western hemlock in mixture, 0 otherwise);

sp1 is a categorical variable indicating Douglas-fir as the single component in the pure stands (1 is pure Douglas-fir stands, 0 otherwise);

sp2 is a categorical variable used to indicate western hemlock as the single component in the pure stands (1 is pure western hemlock stands, 0 otherwise);

TPH is density expressed in number of trees per hectare;

age is plantation age in years;

b_0 to b_{29} are ordinary least squares parameter estimates for each variable and interaction term.