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Tree growth at stand and individual scales in two dual-species mixture experiments in southern Washington State, USA

Heather E. Erickson, Constance A. Harrington, and David D. Marshall

Abstract: Planting with mixtures of tree species rather than single species is often considered during reforestation because of the potential increased productivity and other benefits. We examined tree growth at the stand and individual tree scales in two experiments contrasting monocultures with a 1:1 mixture of tree species: (1) Douglas-fir *(Pseudotsuga menziesii* (Mirb.) Franco) with a conifer of similar shade tolerance (western white pine *(Pinus monticola* Dougl. ex D. Don)) and (2) Douglas-fir with a more shade-tolerant conifer (western hemlock *(Tsuga heterophylla* (Raf.) Sarg.)). There was no effect of mixture on growth or yield in the Douglas-fir – western white pine combination. In the Douglas-fir – western hemlock combination, yields in the mixture equaled those in Douglas-fIr stands because of the enhanced performance of Douglas-fir in the mixture. For Douglas-fIr, the height/diameter *(hid)* ratio was significantly less in mixture, suggesting reduced competition for light when grown with western hemlock. In contrast, the *hid* ratio for western hemlock was significantly greater in mixture, suggesting increased competition for light when grown with Douglas-fir. Neighborhood analyses showed that tree growth was directly related to initial size and inversely related to relative neighbor size and that the *hid* ratio was positively related to relative neighbor size. In general, the size of a neighboring tree influenced growth more than species identity. Relationships between *hid* ratios and growth rates suggest that growth differences between Douglas-fir and western hemlock in mixture will eventually increase.

Résumé : La plantation d'un melange de plusieurs especes d'arbre plut6t que d'une seule est souvent envisagee à cause de l'augmentation potentielle de la productivite et d'autres bénéfices. Nous avons étudié la croissance des arbres aux echelles du peuplement et de l'arbre à partir de deux experiences comparant des monocultures à des melanges formes de deux especes en proportion égale : (1) Ie douglas de Menzies *(Pseudotsuga menziesii* (Mirb.) Franco) avec un conifere de tolerance similaire à 1'ombre (Ie pin blanc de l'Ouest *(Pinus monticola* Dougl.ex D. Don)) et (2) le douglas de Menzies avec un conifere plus tolerant à 1'ombre (la proche de 1'Ouest *(Tsuga heterophylla* (Raf.) Sarg.)). La combinaison du douglas de Menzies et du pin blanc de 1'Ouest n'a pas eu d'effet sur la croissance ou la production. Dans le cas du mélange de douglas de Menzies et de proche de l'Ouest, la production de la plantation mixte était égale à celle des peuplements purs de douglas de Menzies à cause d'une meilleure performance du douglas de Menzies en plantation mixte. Pour Ie douglas de Menzies, Ie rapport entre la hauteur et Ie diametre *(hid)* était significativement plus petit dans la plantation mixte, ce qui indique une diminution de la competition pour la lumiere dans la plantation mixte. Toutefois, dans Ie cas de la proche de 1'Ouest, Ie rapport *hid* était significativement plus grand dans la plantation mixte, ce qui indique une augmentation de la competition pour la lumiere lorsque la proche se developpe avec Ie douglas de Menzies. Des analyses de voisinage ont montre que la croissance des arbres était directement reliee à leur taille initiale et inversement reliee à la taille relative des arbres voisins, et que Ie rapport *hid* était positivement relié à la taille relative des voisins. En général, la croissance était davantage influencee par la taille que par 1'espece d'un arbre voisin. La relation entre Ie rapport *hid* et Ie taux de croissance indique que les differences de croissance entre Ie douglas de Menzies et la pruche de 1'Ouest plantes ensemble vont eventuellement augmenter.

[Traduit par la Redaction]

Introduction

For forest managers worldwide, the decision to reforest with one or several tree species is an important one. In many areas of the world, planting single-species stands was the norm for many years. For example, in coastal areas of the Pacific Northwest region of the United States and in British Columbia in Canada, single species, often Douglas-fir *(Pseudotsuga menziesii* (Mirb.) Franco), were planted on cutover or burned areas. Now mixed-species are being seri-

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ously considered because of potential benefits to wildlife (Varga et al. 2005), reduced market risk with diversification (Hartley 2002), possible increased protection from insect and disease outbreaks (Kelty 2006), and potentially more efficient use of resources, leading to greater stand productivity (Vandermeer 1989; Kelty 2006). Despite these potential benefits, studies comparing single- and mixed-species plantations are limited to a few species combinations (Kelty 2006).

Highly productive stands are sought after for a number of reasons, including meeting the demand for timber and wood products and increasing carbon stocks. Theoretical (Vandermeer 1989; Kelty 2006) and empirical evidence (e.g., Garber and Maguire 2004; Amoroso and Tumblom 2006; Piotto 2008) suggest that under certain ecological circumstances, mixed-species stands may be more productive than single-species stands. Neighboring trees have long been known to influence individual tree performance (cf. Harper 1977), and whether a neighbor is of the same or a different species may determine the outcome of an interaction. For example, interspecific competition may be less than intraspecific competition if the species have dissimilar resource requirements and obtain their resources in unique ways. With reduced competition as a result of this resource complementarity (cf. Haggar and Ewel 1995) in mixed species systems, overall stand productivity might be enhanced.

Kelty (2006) suggests that more of a site's available resources may be captured by mixtures of tree species differing in height growth, crown structure, phenology, or shade tolerance. Obvious differences in these traits occur between broadleaved and coniferous trees. However studies comparing conifers with more subtle trait differences are rare. The fast-growing Douglas-fir, classified as intermediate in shade tolerance (Minore 1979), often forms an overstory above the slower-growing, very shade-tolerant western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), throughout much of its range (Franklin and Dyrness 1973), suggesting complementary resource use. Such canopy stratification appears to be a characteristic of mixed-species conifer stands with greater yields than single-species stands (Chen et al. 2003; Garber and Maguire 2004; Forrester et al. 2006), though not all stratified canopies are more productive than single-canopy stands (Chen et al. 2003).

In the late 1970s, a series of experimental plantations was established on the west side of the Cascade Mountains in southern Washington state to examine the effect of neighbor composition and tree spacing on growth. In this paper, we analyzed tree growth for the first 20+ years of growth for two combinations of conifer species at a single spacing: Douglas-fir with western white pine *(Pinus monticola* Dougl. ex D. Don), both species classified as intermediate in shade tolerance (Minore 1979), and Douglas-fir with western hemlock. In addition to examining the effect of mixtures on average yields, we also examined various neighborhood attributes on growth at the individual tree scale.

We asked three questions: (1) How do mixed-species stands compare with single-species stands with respect to tree and stand attributes (e.g., height, diameter, basal area)? (2) How is average performance of a given species affected by growing in a mixed-species versus a single-species stand? (3) How is individual tree performance influenced by size and identity of neighbors? Following Kelty (2006), we predicted yield will be greater in mixed stands combining species that differ in shade tolerance than in their respective single-species stands, but that yield will not be greater in mixed stands combining species with similar shade tolerance. We also expected that relatively large neighbors will have a greater (negative) effect on growth than relatively small neighbors.

Methods

Experimental plantations

The study was conducted on Trout Creek Hill (TCH) (45°50'05"N, 121°59'45"W, elevation 790 m a.s.l.), a Quaternary-aged shield volcano within the Wind River Experimental Forest. TCH is located on the west side of the southern Washington Cascades near the Columbia River, in the *Tsuga heterophylla* zone (Franklin and Dyrness 1973). Old-growth forests in the area contain Douglas-fir, western hemlock, western redcedar *(Thuja plicata* Donn. ex D. Don), Pacific yew *(Taxus brevifolia* Nutt.), Pacific silver fir *(Abies amabilis* (Dougl. ex Louden) Dougl. ex Forbes), grand fir *(Abies grandis* (Dougl. ex D. Don) Lindl.), and noble fir *(Abies procera* Rehd.) (Shaw et al. 2004). Western white pine was previously a component of these forests prior to widespread mortality by white pine blister rust *(Cronartium ribicola).* The 50 year site index (cf. King 1966) averages 34.7 m.

The region has a wet climate with dry summers; over 90% of the 2800 mm annual precipitation falls from 1 October through 31 May (climate data from the PRISM model developed by Daly et al. 1994). The mean annual, mean minimum January, and mean maximum August temperatures are 8.7, -2.5, and 25 °C, respectively (30 year averages from 1971 to 2000). Snow is common in winter. Slopes are gentle to moderate, ranging up to 30%. Soils are well-drained, deep loams derived from residual material weathered from andesites and basalts, in the Stabler Series (Soil Survey Staff 2007).

We used data from two units that are located ~2 km apart, have similar soils, but differ somewhat in elevation, aspect, planting date, and species planted. One unit, planted with Douglas-fir and western white pine in 1982 (hereafter DF-WWP), faces west and averages 700 m a.s.l. The second unit (DF-WH) was planted with Douglas-fir and western hemlock in 1981, faces south-southeast, and averages 550 m a.s.l. Both units were machine piled and burned after clear-cut harvesting.

The units were divided into multiple square 0.4 ha plots, with stand-level treatments (either single species or 1:1 mixtures) randomly assigned and applied to the entire plot. The number of plots varied by unit and stand-level treatment (Table 1), mostly because we added plots that were part of spacing trials or intended for manipulations that did not happen. The distance between trees was 3 m. Measurements were made on 196 trees in an internal area of 14 rows and 14 columns, leaving a three-row buffer of trees beyond the internal block. Tree density, based on the internal area of 1764 m^2, is about 1111 trees/ha. In mixed plots, species were alternated such that each tree was surrounded on four

Table 1. Patterns of mortality and recruitment for DF-WWP in 2002 and DF-WH in 2005, the final year measurements were taken.

Unit	Plot type*	No. of plots	% Cumulative mortality	% Living trees that are recruits	No. of live trees	% DF in plot by the final year	% Basal area contributed by recruits
DF–WWP	DF	3	8.9 (2.8)	5.3 (2.4)	191 (3)	99.8 (0.3)	0.9 (0.2)
	WWP	6	28.8 (6.6)	16.4 (8.9)	168 (13)	15.6 (8.3)	3.9 (2.8)
	DF–WWP mixture	3	20.1 (5.2)	8.8 (6.5)	172 (4)	58.5 (1.9)	0.9 (0.7)
DF–WH	DF	10	10.8 (8.0)	3.3 (1.7)	181 (16)	99.8 (0.3)	3.1 (2.4)
	WH	4	27.3 (4.3)	18.9 (10.9)	178 (21)	11.1 (6.5)	16.2 (9.6)
	DF–WH mixture	4	35.3 (16.7)	22.4 (12.3)	161 (17)	68.4 (10.5)	20.0 (9.4)

Note: Values are means (standard deviations in parentheses).

*Plot types are as follows: DF, planted with Douglas-fir; WWP, planted with western white pine; DF-WWP mixture, planted as a 1:1 mixture of Douglas-fir and western white pine; WH, planted with western hemlock; and DF-WH mixture, planted as a 1:1 mixture of Douglas-fir and western hemlock.

sides by the other species, yielding a fine-grained spatial pattern.

Density control, to offset mortality during the first several years, was maintained by replanting with the original species. Thereafter, mortality was partly offset by keeping some of the natural recruitment, regardless of species. Natural regeneration not viewed as potentially offsetting mortality was periodically removed.

Data collection and measurements

At DF-WWP, data were collected at the end of the growing season after 7, 10, 15, and 20 years of growth. As a preventative measure against white pine blister rust, in year 10 branches were removed from the lower third of white pine crowns. Douglas-fir trees were treated similarly to avoid any potential confounding of pruning on tree growth. Branches within 2 m of the ground were removed again in year 15.

At DF-WH, data were collected at the end of the growing season after 8, 11, 16, 20, and 24 years of growth. No trees were pruned in this unit.

Tree height was measured on all trees until a height of 1.3 m was reached; thereafter, height and height to live crown were measured on every fourth to fifth tree, except in mixed-species plots where the height sample was doubled. Crown width was measured on ~ one-third of height trees. Diameter at breast height (dbh) was measured on all trees >1.3 m tall. Disease or defects were noted for every live tree and mortality tallied.

Calculations

The ratio of live crown length to total tree height, i.e., crown ratio, was calculated only at DF-WH because of pruning at DF-WWP. Crown ratios and height/diameter *(hid)* ratios were calculated only for trees with measured heights, ~ 25% of all trees.

Several tree- and stand-level attributes were derived from the measurements made on a subset of trees. Individual tree volume was calculated for the final two measurement periods using species-specific equations for western white pine (Browne 1962), Douglas-fir (Bruce and DeMars 1974), and western hemlock (Flewelling and Raynes 1993). For these calculations, we estimated height for non-height trees by developing separate linear regressions of height versus diameter ($\ln(h - 1.3) = a + b(1/d)$) for each species, plot, and year combination. Because outliers can greatly influence regression coefficients and lead to incorrect predictions, regression residuals (Studentized) for each combination were examined for outliers (> 121)and removed. Also, because of the continuing regeneration of Douglas-fir at DF-WWP, separate regressions for each year were developed for these trees across all plots. At DF- WH, where most of the Douglas-fir natural regeneration occurred prior to 1992, a single regression was developed for these trees. Basal area and volume were calculated for all trees and summed by plot.

Stand- and species-level analyses at the plot scale

At each unit, the stand-level treatments are the different stand (or plot) types, i.e., single species or species mixtures, which are replicated on the plots, the experimental units. Stand-level summaries are based on all living trees, including the recruited trees, and thus represent actual stand conditions. To examine differences in tree size among these stand-level treatments, we used a nested ANOVA reflecting the hierarchy of trees nested in plots and plots within treatments (Underwood 1997); plots were modeled as a random effect. Highly skewed variables (crown ratio and *hid* ratios) were ln-transformed to meet assumptions of ANOVA. Differences among means were assessed with the post-hoc Tukey-Kramer's test ($P < 0.05$), appropriate for unbalanced designs. To examine the effect of treatment on variables summed by plot (stand-level basal area and volume), differences were assessed with a one-way ANOVA followed by the Tukey's multiple comparison.

We also compared the effect of mixture for each species ("species treatment") using a nested ANOVA. Natural regeneration was not included in these analyses. Moreover, because of high mortality and shifts in intended species ratios (see Results), only trees with the correct number and identity of neighbor were used in the species treatment tests, preserving the original design.

While our main objective was to contrast the patterns in the final measurement periods, we present the data from the younger trees to highlight a few general trends.

Individual tree scale: species comparisons

To examine neighborhood interactions at the individual tree scale, we calculated a size-ratio competition index, CI (modified from Lorimer (1983)),based on basal area, BA, of the four neighboring trees relative to a subject tree. Specifically,

[1] $\mathrm{CI} = (\text{the sum of } \mathrm{BA}_{\text{neighbors}}/4)/\mathrm{BA}_{\text{subject tree}}$

A CI >1 means the average neighbor tree is larger in diameter than the subject tree; conversely a CI <1 means the average neighbor tree is smaller than the subject tree. Mortality is accounted for in the calculation by assigning a basal area of 0 to a dead tree but still counting that tree as one of four in the neighborhood, appropriately reducing the CI.

A linear mixed-effects approach was used to model tree growth and to test the effect of neighbors on tree growth. Because trees are clustered in plots, and plots differ in mortality, recruitment, and perhaps productivity, a hierarchical structure was indicated (cf. Fox et al. 2001). Thus plot, nested within treatment (single-species or mixed-species stand), and initial size and CI nested within plots were treated as random effects. Initial size has been shown to be a strong predictor of conifer tree growth (e.g., Monserud and Sterba 1996; Wagner and Radosevich 1998). We also included a squared term for size, which allows growth rates to decrease as size increases (e.g., Monserud and Sterba 1996), and a squared term for CI, which allows for some amount of growth at high CI values.

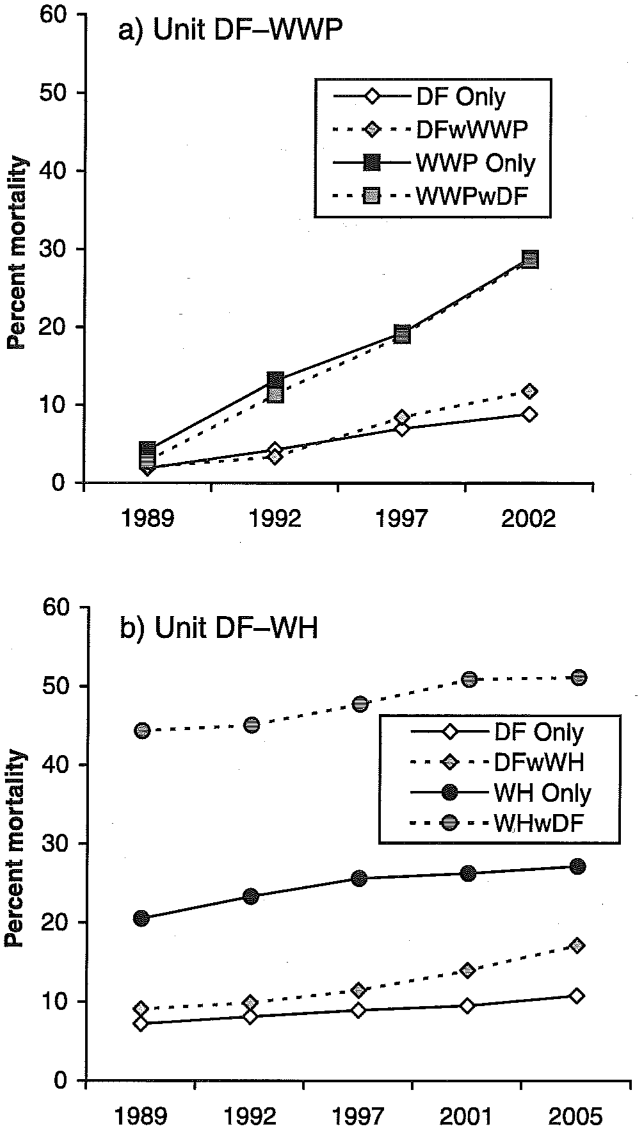
To test the hypothesis that neighbor identity, i.e., same species or not, affects tree growth, an indicator variable, X, was used to specify whether a species was growing in a single-species (X = 1) or mixed-species (X = 0) plot. The interaction between X and CI, to test whether the effect of relative neighbor size depended on species, was also included in the models. The effect of neighbor identity was examined at each unit for annual diameter, height, and volume increment over the last two measurement periods and for the *h/d* ratio the final year. The general fixed-effects equation for growth (or *h/d* ratio) was

[2] $$\text{Growth} = \text{initial size} + (\text{initial size})^2 + \mathrm{CI} + \mathrm{CI}^2 + X + X{*}\mathrm{CI}$$

where initial size refers to dbh, height, or volume.

Maximum likelihood estimates of model parameters were obtained using Proc Mixed, PC-SAS (SAS Institute Inc. 2004). In building models, first, size and CI variables were added if significant, and then the indicator variables were tested. The final model contained only significant variables (based on a partial *F* test) and was nearly always coincident with the lowest Akaike's Information Criterion, AIC (low AIC values indicate good model fits). Transformations (ln) of response and predictor variables were considered as a way to linearize the data and normalize residuals. Trees with stem damage and an occasional extreme outlier (less than 5% of any run) were removed to improve normality. Diameter and height growth were modeled as untransformed responses; *h/d* ratios and volume growth were ln transformed. CI was ln (+1) transformed. Only originally planted trees, excluding trees in border columns and rows (which had trees beyond them that were not measured), were used as subject trees if neighbor identity was correct. In the pure plots, to avoid any potential lack of independence with a tree functioning as both subject tree and neighbor, only every other tree was used as a subject tree in analyses.

Fig. 1. Cumulative percent mortality of originally planted trees at DF-WWP *(a)* and DF-WH *(b)*. Treatment codes: DF Only, Douglas-fir in single-species plots; DFwWWP, Douglas-fir with western white pine; WWP Only, western white pine in single-species plots; WWPwDF, western white pine with Douglas-fir; DFwWH, Douglas-fir with western hemlock; WH Only, western hemlock in single-species plots; WHwDF, western hemlock with Douglas-fir.



Results

Patterns of mortality

Despite efforts to control blister rust at DF-WWP, mortality was high; by year 20, nearly 30% of the original white pine had died (Fig. *1a*).[3] Mortality and replacement were not equal across the treatments (Table 1). At DF-WWP, as expected, cumulative mortality was greatest in the WWP plots, where most recruitment took place. Yet recruitment was not complete; after 20 years there were only 85% of

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[3] Actual mortality rates are somewhat higher, as these calculations do not include mortality that was offset by replanting during the first several years.

Table 2. Mean stand-level characteristics at DF-WWP averaged across stand (plot) types for all living trees, including natural regeneration.

		Mean (SE)		
Variable	Plot type	1992 (10 years old)	1997 (15 years old)	2002 (20 years old)
dbh (cm)	DF	6.7 (0.5)	10.8 (0.6)	13.7 (0.7)
	WWP	7.6 (0.3)	10.5 (0.4)	13.5 (0.4)
	Mixture	6.9 (0.5)	10.6 (0.6)	13.6 (0.5)
Height (m)	DF	4.9 (0.4)	8.4 (0.5)	11.9 (0.7)
	WWP	5.1 (0.2)	8.0 (0.4)	11.3 (0.5)
	Mixture	4.8 (0.3)	8.0 (0.6)	11.3 (0.5)
Top height (m)*	DF	6.0 (0.5)	10.1 (0.6)	14.2 (0.8)
	WWP	6.3 (0.1)	9.8 (0.3)	13.5 (0.3)
	Mixture	6.1 (0.2)	9.7 (0.4)	13.5 (0.3)
Stand volume (m^3/ha)	DF	—	44.3 (6.3)	95.8 (14.1)
	WWP	—	44.7 (2.9)	84.3 (3.5)
	Mixture	—	39.9 (4.4)	82.8 (6.5)
Basal area (m^2/ha)	DF	4.3 (0.6)	11.2 (1.0)	17.5 (1.7)
	WWP	4.9 (0.2)	10.7 (0.5)	15.0 (0.4)
	Mixture	4.3 (0.5)	10.1 (0.7)	15.4 (0.8)

Note: For each variable, there were no significant differences ($P < 0.05$) among plot types within each year. DF, Douglas-fir; WWP, western white pine. The number of plots for each plot type is listed in Table 1.

*Based on 40 of the tallest trees per plot.

the original 196 trees (Table 1). Most of the recruits were Douglas-fir, resulting in Douglas-fir increasing in proportion to 58% and 16% in mixed and single-species WWP plots, respectively.

Mortality for western hemlock at DF-WH was high; close to 35% of originally planted trees were dead by year 24 (Fig. *1b)*. Most of the mortality occurred by 1989, and for western hemlock, mortality was more than two times higher in the mixed-species plots compared with the single-species plots. Given the small size of the trees at age 8, this high mortality was likely not due to neighborhood effects, and we can only speculate that perhaps field crews were not as careful initially replanting in mixed plots. Recruitment followed but did not completely compensate for mortality (Table 1). Most of the recruits were Douglas-fir, which again resulted in a shift in the original species ratios; by age 24 the mixed- and single-species plots had about 68% and 11% Douglas-fir, respectively (Table 1). Because mortality occurred earlier at DF-WH than at DF-WWP (Fig. 1), the recruits contributed ~ 20% of the total basal area in the mixed plots at DF-WH versus <2% of the total basal area of the mixed plots at DF-WWP (Table 1).

Plot-scale analyses: stand comparisons

At DF-WWP, none of the size metrics (dbh, height, top height, stand volume, and basal area) differed by plot type (Table 2). By age 20, mean diameter and height at the unit were 13.6 cm and 11.6 m, respectively, and stand volume averaged 88 m^3/ha.

In contrast, at DF-WH, average dbh, height, top height, stand volume, and basal area were significantly greater in the Douglas-fir and the DF-WH mixed plots than in the western hemlock plots (Table 3). This response was consistent over the 13 year measurement period (Table 3). After 24 years, stand volume in the Douglas-fir and DF-WH stands averaged 141 m^3/ha. Top height in the mixed plots equaled that in the Douglas-fir only plots, not surprising given the tallest trees in the mixed plots were Douglas-fir.

Plot-scale analyses: species comparisons

At DF-WWP, Douglas-fir and western white pine were essentially the same size in terms of height and diameter after 20 years of growth (Table 4). (Trees included in the species comparisons contain the right identity and number of neighbors.) White pine blister rust was visually noted in about 10% of the white pines at DF-WWP, yet we found no differences in diameter or height between visually infected and uninfected trees ($P > 0.05$, data not shown). For either species, growing in mixture (effect of species treatment) had minimal influence on growth and *hid* ratios (Table 4). The *hid* ratio for white pine increased over the 10 year period but always remained less than the average *hid* ratio for Douglas-fir of ~86 ($P < 0.01$). After 15 years of growth, mean crown width was close to the designed spacing of 3 m for all treatments (Table 4), indicating crown closure had been reached.

At DF-WH, Douglas-fir was consistently taller than western hemlock (Table 5). After 24 years, Douglas-fir height was more than 50% and individual tree volume more than twice that of western hemlock. The mixture had clearly stratified by height; of the originally planted trees with correct neighbors, 75% of the Douglas-fir were taller than 17.3 m, while 75% of the western hemlock were shorter than 12.9 m.

Species of neighbor influenced tree growth at DF-WH, notably so for Douglas-fir (Table 5). After 24 years, diameter, crown width, and individual tree volume were 33%, 25%, and nearly 100% greater, respectively, for Douglas-fir in a western hemlock neighborhood versus a Douglas-fir neighborhood. Douglas-fir had a greater *hid* ratio in the

Table 3. Mean stand-level characteristics at DF-WH averaged across stand (plot) types for all living trees, including natural regeneration.

		Mean (SE)			
Variable	Plot type	1992 (11 years old)	1997 (16 years old)	2001 (20 years old)	2005 (24 years old)
dbh (cm)	DF	6.5 (0.2)a	11.3 (0.4)a	13.6 (0.4)a	16.0 (0.4)a
	WH	2.3 (0.4)b	5.9 (0.6)b	9.0 (0.7)b	12.3 (0.7)b
	Mixture	5.5 (0.4)a	10.1 (0.6)a	13.0 (0.7)a	15.8 (0.7)a
Height (m)	DF	4.8 (0.2)a	8.3 (0.3)a	10.8 (0.4)a	14.3 (0.50)a
	WH	1.9 (0.3)c	3.9 (0.4)c	5.5 (0.6)b	8.7 (0.7)b
	Mixture	4.0 (0.3)b	6.9 (0.4)b	9.3 (0.6)a	12.3 (0.7)a
Top height (m)*	DF	6.2 (0.2)a	10.5 (0.3)a	13.6 (0.4)a	16.8 (0.4)a
	WH	3.5 (0.2)b	6.0 (0.5)b	8.2 (0.6)b	11.1 (0.6)b
	Mixture	6.2 (0.3)a	10.3 (0.5)a	13.5 (0.6)a	16.7 (0.6)a
Stand volume (m^3/ha)	DF	—	—	88.1 (8.0)a	147.9 (11.6)a
	WH	—	—	24.1 (4.5)b	61.2 (8.6)b
	Mixture	—	—	74.7 (15.6)a	133.2 (26.8)a
Basal area (m^2/ha)	DF	4.1 (0.3)a	11.8 (0.8)a	16.9 (1.1)a	23.1 (1.4)a
	WH	0.5 (0.1)b	3.6 (0.5)b	7.9 (1.0)b	14.4 (1.6)b
	Mixture	3.0 (0.6)a	9.8 (1.8)a	15.0 (2.3)a	21.3 (3.1)ab

Note: For each variable, significant differences among plot types within each year ($P < 0.05$) are indicated by different letters. The number of plots for each plot type is listed on Table 1. DF, Douglas-fir; WH, western hemlock.

*Based on 40 of the tallest trees per plot.

Table 4. Mean (least squares) species-level characteristics by species treatment (single or mixed species) for originally planted trees (i.e., no recruitment) with correct neighborhoods (see text for an explanation) at DF-WWP.

		Mean (SE)		
Variable	Species treatment*	1992 (10 years old)	1997 (15 years old)	2002 (20 years old)
dbh (cm)	DF only	6.8 (0.1)	11.3 (0.1)	14.2 (0.2)
	DFwWWP	5.8 (0.2)	10.3 (0.3)	13.5 (0.6)
	WWP only	7.8 (0.1)	11.6 (0.1)	14.9 (0.2)
	WWPwDF	8.1 (0.1)	12.0 (0.2)	15.3 (0.3)
Height (m)	DF only	5.0 (0.1)	8.7 (0.2)	12.2 (0.3)
	DFwWWP	4.3 (0.2)	7.8 (0.3)	11.1 (0.6)
	WWP only	5.2 (0.1)	8.2 (0.2)	11.6 (0.4)
	WWPwDF	5.3 (0.1)	8.5 (0.2)	12.1 (0.2)
Crown width (m)	DF only	—	3.4 (0.2)	3.3 (0.2)
	DFwWWP	—	3.1 (0.2)	3.1 (0.3)
	WWP only	—	3.0 (0.2)	3.1 (0.4)
	WWPwDF	—	2.8 (0.2)	2.2 (0.3)
Individual tree volume (dm^3)	DF only	—	42.4 (1.1)	93 (2.3)
	DFwWWP	—	30.9 (2.4)	73 (7.7)
	WWP only	—	46.2 (1.3)	103 (3.8)
	WWPwDF	—	51.0 (1.8)	112 (4.2)
Height/diameter ratio	DF only	83.5	80.0	87.5
	DFwWWP	79.9	76.7	84.9
	WWP only	68.1	71.9	77.6
	WWPwDF	67.8	70.8	78.4

Note: For each variable, there were no significant differences ($P < 0.05$) among species treatments within each year. The number of plots for each plot type is listed in Table 1.

*DF only, Douglas-fir with Douglas-fir; DFwWWP, Douglas-fir with western white pine; WWP only, western white pine in single-species stands; WWPwDF, western white pine with Douglas-fir.

single-species versus mixed-species plots, and Douglas-fir crowns reached the 3 m spacing sooner than hemlock crowns (Table 5).

For western hemlock, only crown ratios and *h/d* ratios were influenced by neighbor identity (Table 5). Growing in mixture with Douglas-fir diminished crown ratios by about 7%. In contrast to Douglas-fir, the *h/d* ratio for western hemlock was significantly greater in mixed-species rather

Table 5. Mean (least squares) species-level characteristics by species treatment (single or mixed species) for originally planted trees (i.e., no recruitment) with correct neighborhoods (see text for an explanation) at DF-WH.

Variable	Species treatment*	Mean (SE) 1992 (11 years old)	 1997 (16 years old)	 2001 (20 years old)	 2005 (24 years old)
dbh (cm)	DF only	6.5 (0.1)	11.3 (0.4)	13.5 (0.1)a	16.0 (0.2)a
	DFwWH	7.2 (0.6)	13.3 (1.0)	17.6 (1.1)b	21.3 (1.3)b
	WH only	2.9 (0.3)	6.8 (0.3)	9.5 (0.4)	12.6 (0.5)
	WHwDF	2.6 (0.4)	6.1 (0.5)	9.0 (0.8)	11.1 (1.0)
Height (m)	DF only	4.8 (0.1)	8.4 (0.2)	10.7 (0.2)†	14.4 (0.3)
	DFwWH	5.5 (0.5)	9.5 (0.8)	13.6 (1.1)†	17.4 (1.6)
	WH only	2.6 (0.3)	4.3 (0.4)	5.6 (0.3)	9.0 (0.8)
	WHwDF	2.6 (0.3)	4.6 (0.4)	6.5 (0.8)	9.2 (0.8)
Crown width (m)	DF only	—	3.4 (0.2)	3.7 (0.2)	3.9 (0.3)‡
	DFwWH	—	4.0 (0.5)	4.4 (0.5)	5.0 (0.7)‡
	WH only	—	2.1 (0.3)	2.6 (0.4)	3.6 (0.6)
	WHwDF	—	1.8 (0.3)	2.6 (0.5)	2.9 (0.7)
Crown ratio	DF only	—	—	0.80 (0.006)	0.70 (0.008)
	DFwWH	—	—	0.84 (0.033)	0.75 (0.042)
	WH only	—	—	0.92 (0.006)a	0.92 (0.014)a
	WHwDF	—	—	0.88 (0.015)b	0.86 (0.014)b
Individual tree volume (dm^3)	DF only	—	—	82.3 (2.0)a	141 (14)a
	DFwWH	—	—	143 (16)b	261 (26)b
	WH only	—	—	26.5 (2.8)	64.1 (5.5)
	WHwDF	—	—	28.7 (5.9)	58.1 (12.0)
Height/diameter ratio	DF only	86.9	78.9	84.2a	83.6a
	DFwWH	79.4	67.4	72.8b	68.3b
	WH only	221	104	100	75.1a
	WHwDF	162	110	105	88.4b

Note: Significant differences within year ($P < 0.05$) for each species are shown with different superscripts. The number of plots for each plot type is listed in Table 1.

*DF only, Douglas-fir with Douglas-fir; DFwWH, Douglas-fir with western hemlock; WH only, western hemlock with western hemlock; WHwDF, western hemlock with Douglas-fir.

$^{\dagger}P = 0.07$.

$^{\ddagger}P = 0.08$.

than single-species plots. Overall, the greatest *hid* ratios (>150) were for the youngest (age 11) western hemlock.. Importantly, growing with Douglas-fir did not reduce volume for western hemlock (Table 5).

Individual tree scale: species comparisons

Diameter and height increment

In both units, annual diameter increment was positively influenced by initial size, except for western hemlock, and negatively affected by the relative size of neighbors (CI) (Table 6). For all species, when diameter growth was low, increasing the size of neighbors relative to the subject tree did not further reduce growth, as indicated by the positive coefficients for CI^2 (Table 6). At unit DF-WWP, Douglas-fir diameter increment was greater adjacent to white pine than adjacent to other Douglas-firs, indicated by the negative coefficient for the indicator variable X.

Similar to diameter increment, height increment across the units was positively related to initial size for Douglas-fir and western white pine but not for western hemlock (Table 7). Relative neighbor size had a consistently negative and linear effect on height growth, except for Douglas-fir at DF-WWP. After accounting for size of neighbor, species of neighbor had no effect on height increment (Table 7).

hid ratio

At all units, there was a negative effect of prior size on the *hid* ratio; the smaller a tree's previous dbh, the larger the *hid* ratio in the final year (Table 8). Except for Douglas-fir at DF-WWP, there was a positive effect of relative neighbor size on the *hid* ratio. For Douglas-fir and western hemlock at DF-WH, beyond a certain relative neighbor size, the *hid* ratio no longer increased (indicated by the negative coefficient for CI2). Neighbor identity uniquely influenced the *hid* ratios for two cases: (1) Douglas-fir in mixture with western white pine had lower *hid* ratios than those in monocultures and (2) western hemlock in mixture with Douglas-fir had greater *hid* ratios than those in monocultures (Table 8). These latter findings are consistent with the species comparisons at the plot scale (cf. Tables 4 and 5).

Volume growth

In both experiments, volume growth was positively influenced by initial tree size and negatively influenced by relative neighbor size (Table 9). Volume growth was in general independent of neighbor identity (Table 9). For Douglas-fir at DF-WWP and for western hemlock, the effect of relative neighbor size on volume growth depended on neighbor iden-

Table 6. Maximum likelihood estimates for annual diameter increment (cm/year) for 5 years (1997-2002) at DF-WWP and 4 years (2001-2005) at DF-WH.

Unit	Treatment pair	Intercept	dbh_i	X	ln CI	$\ln CI^2$	N
DF–WWP	DF only – DFwWWP	0.78	0.120	–0.11	–0.524	0.112	216
	WWP only – WWPwDF	0.78	0.012	—	–0.495	0.124	342
DF–WH	DF only – DFwWH	0.51	0.021	—	–0.290	0.051	681
	WH only – WHwDF	1.07	—	—	–0.374	0.045	265

Note: Nonsignificant parameters were removed from the final models and only significant ($P < 0.05$) parameters are shown. The full model considered was annual diameter increment = initial diameter (dbh_i) + dbh_i^2 + ln CI + $\ln CI^2$ + X + X * ln CI, where X, the dummy variable for species treatment, is 1 for growing with the same species and 0 for growing in mixture. For description of treatment pairs see Tables 4 and 5.

Table 7. Maximum likelihood estimates for annual height increment (cm/year) for 5 years (1997-2002) at DF-WWP and 4 years (2001-2005) at DF-WH.

Unit	Treatment pair	Intercept	$\ln Ht_i$	ln CI	N
DF–WWP	DF only – DFwWWP	0.37	0.05	—	52
	WWP only – WWPwDF	0.13	0.30	–0.09*	127
DF–WH	DF only – DFwWH	0.03	0.20	–0.108	117
	WH only – WHwDF	0.65	—	–0.120	101

Note: Nonsignificant parameters were removed and only significant ($P < 0.05$) parameters are shown except where indicated. The full model considered was annual height growth = initial height ($\ln Ht_i$) + $\ln Ht_i^2$ + ln CI + $\ln CI^2$ + X + X * ln CI, where X, the dummy variable for species treatment, 1 for growing with the same species and 0 for growing in mixture. For description of treatment pairs see Tables 4 and 5.

*$P = 0.10$.

Table 8. Maximum likelihood estimates for height/diameter ratios at units DF-WWP (2002) and DF-WH (2005).

Unit	Treatment pair	Intercept	ln dbh	ln CI	$\ln CI^2$	X	N
DF–WWP	DF only – DFwWWP	0.5	–0.31	—	—	0.07*	50
	WWP only – WWPwDF	–1.3	–0.13*	0.12	—	—	243
DF–WH	DF only – DFwWH	4.5	–0.01	0.25	–0.06	—	106
	WH only – WHwDF	4.6	–0.17	0.18	–0.03	–0.15	114

Note: Nonsignificant parameters were removed and only significant ($P < 0.05$) parameters are shown except where indicated. The full model considered was ln (h/d) = ln (previous dbh) + ln CI + $\ln CI^2$ + X + X * ln CI, where X, the dummy variable for species treatment, is 1 for growing with the same species and 0 for growing in mixture. For description of treatment pairs see Tables 4 and 5.

*$P = 0.06$.

Table 9. Maximum likelihood estimates for annual volume increment (dm^3/year) for 5 years (1997-2002) at DF-WWP and 4 years (2001-2005) at DF-WH.

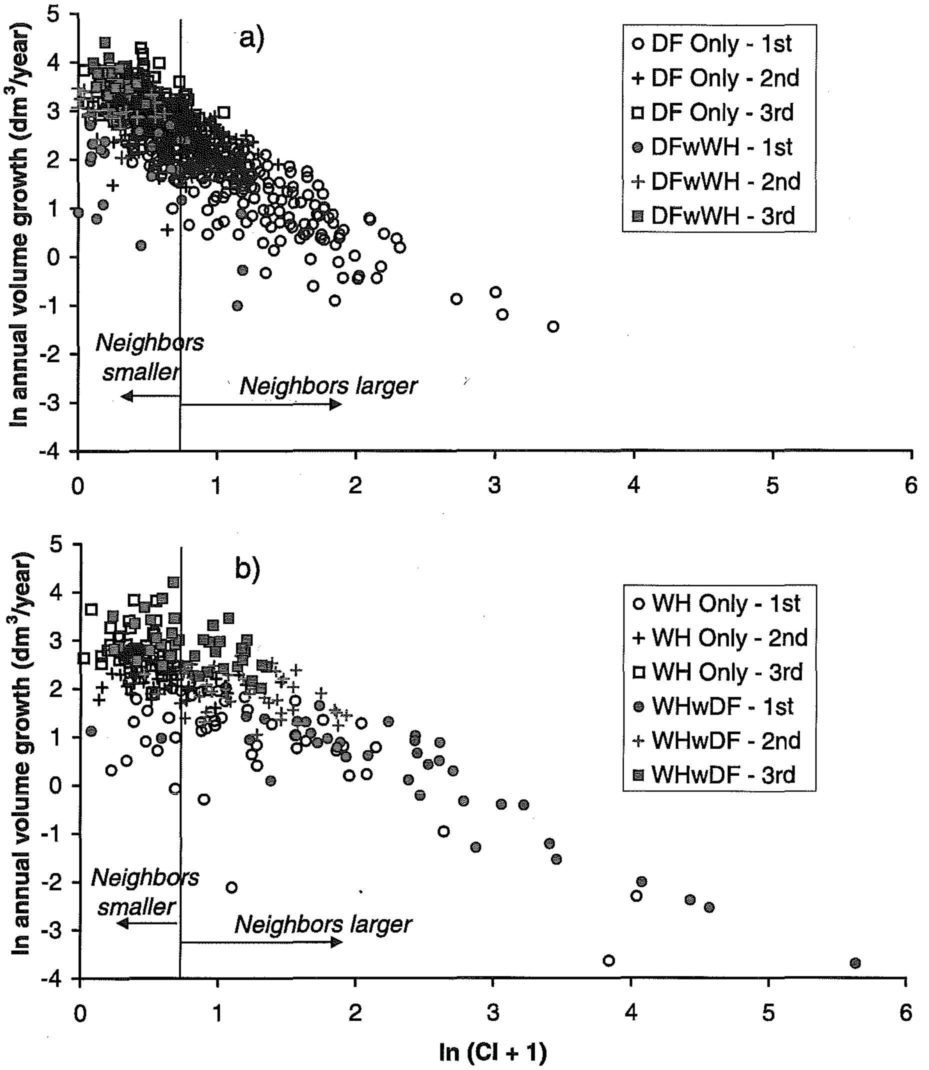
Unit	Treatment pair	Intercept	$\ln dbh_i$	$\ln dbh_i^2$	ln CI	X * CI	N
DF–WWP	DF only – DFwWWP	–1.25	1.74	—	–0.64	–0.21	216
	WWP only – WWPwDF	–1.80	1.89	—	–0.43	—	340
DF–WH	DF only – DFwWH	–2.64	1.99	—	–0.39	—	698
	WH only – WHwDF	–0.14	0.81	0.14	–0.50	0.25	262

Note: Nonsignificant parameters were removed and only significant ($P < 0.05$) parameters are shown. The full model considered was annual volume growth (ln) = initial diameter ($\ln dbh_i$) + $\ln dbh_i^2$ + ln CI + $\ln CI^2$ + X + X * ln CI, where X, the dummy variable for species treatment, is 1 for growing with the same species and 0 for growing in mixture. For description of treatment pairs see Tables 4 and 5.

tity (indicated by the significant interaction term), though the effects were not large.

Figure 2 shows the relationship between annual volume increment and CI by diameter class at DF-WH, where size differences between the species were large. For both species, the trees in the smallest size class had the largest range of relative neighbor size, often with CI values <1, indicating small trees in the population could still be larger than their neighbors. This was especially apparent for Douglas-fir growing with western hemlock (Fig. *2a*). Also, the largest western hem-

Fig. 2. Volume growth from 2001-2005 at DF-WH as a function of relative neighbor size (ln (CI + 1)) for *(a)* Douglas-fir and *(b)* western hemlock, grouped by subject tree diameter class (as thirds, dbh in 2005), with the first third containing the smallest trees. Only subject trees with the correct species of neighbors are included. Values below 0.693 on the *x* axis, left of the vertical line, indicate CI < 1.



locks were often smaller than their Douglas-fir neighbors (Fig. *2b*). For subject trees larger than neighbors (CI < 1), there was a relatively large spread in volume increment.

Discussion

Stand yield in mixed-species versus single-species plots

If trees have different resource requirements, theory suggests that competition should be reduced in mixtures compared with single-species stands, leading to a possible increase in stand yield (Vandermeer 1989; Kelty 2006). Our test of this theory assumes that differences in shade tolerance reflect different light requirements. For Douglas-fir and western white pine, both intermediate in shade tolerance, neither yield nor size increased in mixed stands. This indicates little canopy stratification and supports the idea of similar resource requirements, at least for light. Garber and Maguire (2004) found no differences in yield for *Pinus ponderosa* and *Pinus contorta* (both relatively shade intolerant), at similar densities to our study when grown together in central Oregon (Table 10). Interestingly, Chen et al. (2003) found yield tended to be lower for a nonstratified mixture of *Pinus contorta* and *Larix occidentalis* compared with respective monocultures, which was attributed to the pine being the superior competitor for soil resources on nutrient-poor sites.

Where Douglas-fir was paired with western hemlock, stand yield in the mixtures was not significantly different from yield in the Douglas-fir stands but was greater than yield in western hemlock stands. Also, average diameter, height, and top height for the mixed stands were similar to those in the Douglas-fir stands and greater than in the western hemlock stands. These findings indicate different strategies for resource capture between these species and are consistent with other studies in the region comparing species differing in shade tolerance (Table 10). However, in experi-

Table 10. Studies in the Pacific Northwest and British Columbia comparing yield and performance of single- and mixed-species conifer stands.

Study	Location (stand type)	Species* (shade tolerance)	Yield in mixture
Wierman and Oliver 1979	Olympic Peninsula, Washington (natural stands)	PSME (intermediate in tolerance), TSHE (very tolerant)	Mixed stands "appeared to have greater volume" than pure stands (ages 35–80)
Chen et al. 2003	British Columbia and Alberta, Canada (natural stands)	TSHE, THPL (both very tolerant)	No gains in mixture (ages >50)
		PICO, LAOC (both intolerant)	Slightly reduced gains in mixture (ages >60)
		PICO (intolerant), PIMA (tolerant)	Same as pure "but some were higher" (ages >80)
Garber and Maguire 2004	Central Oregon (dry pumice plain plantations)	PICO, PIPO (both intermediate in tolerance)	No gains in mixture (age 34)
		ABGR (tolerant), PIPO (intermediate in tolerance)	Greater total yield in high density mixture (age 26)
Amoroso and Turnblom 2006	Coastal Olympic Peninsula, Washington (plantations)	PSME (intermediate in tolerance), TSHE (very tolerant)	Lower than monoculture at low densities, similar to monoculture at high densities (age 12)
This study	Cascade Mountains, Washington (plantations)	PSME, PIMO (both intermediate in tolerance)	No gains in mixture (age 20)
		PSME (intermediate in tolerance), TSHE (very tolerant)	Mixtures had greater yield, after accounting for mortality (age 24)

*Species codes are as follows: PSME, *Pseudotsuga menziesii*; TSHE, *Tsuga heterophylla*; THPL, *Thuja plicata*; PIPO, *Pinus ponderosa*; LAOC, *Larix occidentalis*; PIMA, *Picea mariana*; PICO, *Pinus contorta*; ABGR, *Abies grandis*; PIMO, *Pinus monticola*.

mental plantations with Douglas-fir and western hemlock at two coastal sites in western Washington (Amoroso and Turnblom 2006), by age 12, yields in mixed stands were lower than yields in either of the monocultures at low densities (including 3 m spacing) but were similar to monocultures at higher densities. The authors suggest that partial stratification may not have been reached at the lower densities. Tree spacing in our study was 3 m, often the midpoint of many spacing trials and typical of plantations in the Pacific Northwest (e.g., Radosevich et al. 2006). Spacing has a well-known effect on tree growth (Garber and Maguire 2004; Amoroso and Turnblom 2006; Puettmann and Berger 2006) and may influence the temporal pattern over which tree interactions occur.

Because of changes in original species ratios due to differential mortality, we cannot exclude the possibility that total yields in a true 1:1 mixture of the original trees might have been greater than those in single-species Douglas-fir.. Natural regeneration, smaller than the originally planted trees, contributed 20% of the basal area by year 24 in the mixtures at DF-WH and only 3% of the basal area in the single-species Douglas-fir plots. Thus, mortality and uncontrolled natural regeneration can complicate interpretation of long-term forestry studies (cf. Kelty and Cameron 1995).

Species differences at the stand level

Growing together did not influence the growth of Douglas-fir or western white pine (unit DF-WWP) compared with their monocultures. However, when Douglas-fir and western hemlock were grown together (unit DF-WH) several differences emerged compared with growing in single-species stands: Douglas-fir was significantly larger (diameter and individual tree volume), had greater crown width, and a significantly lower *h*/*d* ratio in mixture versus single-species stands. A decreasing *h*/*d* ratio suggests that light competition is decreasing (Opio et al. 2000; Forrester et al. 2004), which is consistent with the increase in tree size and crown width for Douglas-fir in mixture. Taken together, the expanding crowns with reduced competition likely enabled more diameter growth once height requirements were met for Douglas-fir. Similarly, the increased *h*/*d* ratio for western hemlock in mixture supports the idea of increased competition for light with this neighbor, consistent with the smaller crown ratio for western hemlock when growing with Douglas-fir. Thus, for western hemlock, height requirements were likely not met in mixture. The lack of a significant height response for any of the species is consistent with other studies showing diameter growth to be more sensitive to competitive interactions than height growth (Wagner and Radosevich 1998; Simard et al. 2005; Piotto 2008).

Tree-scale summaries based on originally planted trees can reveal the effects of mixtures on tree growth and, by inference, the potential differences in stand yield in the absence of mortality. A commonly used metric to assess yield in mixtures is total relative yield (RYT, Harper 1977; DeBell et al. 1997), defined as

$$[3] \quad \text{RYT} = (\text{yield of species A in mixture/yield of species A in a single-species plot}) + (\text{yield of species B in mixture/yield of species B in a single-species plot})$$

If there is no effect of the mixture, then each species contributes 0.5 for a RYT of 1. Using mean individual tree volumes of Douglas-fir and western hemlock for yield and making the assumption that only half of the volume of a single species would be present in the mixed plots, we can estimate RYT. Note that we base this calculation only on trees conforming to the original design, i.e., having the correct number and species of neighbors, and we consider this the best way to estimate stand-level RYT given the substantial early mortality at this unit. So for DF-WH, species A is Douglas-fir and species B is western hemlock, therefore, RYT is as follows (data from Table 5):

[4] $$(261\ dm^3/2)/141\ \mathrm{dm}^3 + (58\ dm^3 12)/64\ \mathrm{dm}^3 = 0.9 + 0.5 = 1.4$$

This indicates that relative yield for Douglas-fir in mixture is greater than the expected 0.5, while relative yield for western hemlock did not change. Barring mortality then, we might have seen an increase in yield in the mixed plots, due to enhanced Douglas-fir growth. Garber and Maguire (2004) found that RYTs were >1 for mixtures of shade-tolerant grand fir and shade-intolerant ponderosa pine, due primarily to the increase in yield for the intolerant species, which is consistent with our finding. In that study, the shade-intolerant ponderosa pine was able to overtop grand fir in the first several years. After 26 years of growth, RYT was significantly >1 only at the tightest spacing (1.8 m) but not at 3.7 m or higher. Thus, yield enhancement appears to occur at the highest density, similar to a finding for Douglas-fir and western hemlock near coastal Washington (Amoroso and Turnblom 2006).

We found that Douglas-fir had the greatest volume when growing in mixture, as at the coastal site (Amoroso and Turnblom 2006). For Douglas-fir, competition appears to have been reduced when growing with western hemlock (i.e., interspecific competition was less than intraspecific competition). In this case, resource complementarity (cf. Haggar and Ewel 1995; Kelty 2006) likely contributed to the increased yield of Douglas-fir. This was also evidenced by greater crown width and crown ratio and by a lower *hid* ratio for Douglas-fir in mixture compared with these values in the single-species plots. Western hemlock is shorter, has lower average volume, and as indicated by crown width, does not take up as much horizontal space as Douglas-fir.

However, unlike at the coastal sites (Amoroso and Turnblom 2006), where tree volume for western hemlock was reduced by over 50% when growing with Douglas-fir at 3 m spacing, we found no significant reduction in volume for western hemlock when growing with Douglas-fir at the more interior sites. Overall, greater productivity at the coastal sites may provide a partial explanation for the different responses. After 11 years growth, mean tree heights for Douglas-fir and western hemlock at the coastal plantations were over twice that at the inland TCH plantations. The 50 year site index at the coastal sites was nearly 3 m greater than at TCH (37.5 versus 34.7 m). How these differences in productivity influence competitive interactions between the two tree species is largely unknown. In herbaceous communities, competition has been viewed as being more important in productive sites and decreasing in importance on less productive sites (Grime 1979), but few studies have shown whether this applies to interactions among long-lived trees (Boyden et al. 2005; Coomes and Allen 2007).

Neighbor influences on tree growth

Annual diameter, height, and volume increment were positively related to initial size, as has been shown for conifers in the Pacific Northwest and elsewhere (e.g., Wagner and Radosevich 1998; Wyckoff and Clark 2005; Filipescu and Comeau 2007) and for broadleaved trees (e.g., Boyden et al. 2005). The exception was western hemlock, where initial size only influenced volume increment, which is based on imputed data for most of the trees. This may be because of the limited range in the data (single site, young trees) and the reduced sample size for hemlock due to mortality. The squared term on initial size, which allows for a slowdown in growth as size increases, was essentially unimportant for the trees at TCH, suggesting that at this stage in stand development, size appears to directly correspond to a tree's ability to capture and use resources for growth for the trees.

In both experiments, growth increment was also strongly influenced by neighbor size (Fig. 2 for DF-WH). When neighbor trees were larger than a subject tree, the subject tree was likely shaded by neighbors, and its growth decreased as CI increased. This is particularly true for the smallest trees, which may have been shaded by trees beyond 3 m. Light competition has been used in other studies to explain the decrease in growth rates of subject trees as basal area of neighbor trees increases (e.g., Coomes and Allen 2007).

D'Amato and Puettmann (2004) found that neighborhood interactions were a useful predictor of growth for trees in subordinate canopy positions, while relative dominance was a better predictor of growth for larger trees. We found that the largest diameter trees at TCH were also the fastest growing and tended to have CI values <1 (Fig. 2), suggesting weak neighbor interactions for these trees; this supports the findings of D'Amato and Puettmann (2004) and references therein that suggest neighbor influence on individual tree growth is greatest for subdominant and smaller-sized canopy trees. Interestingly, the largest size class of western hemlock maintained high volume growth with Douglas-fir neighbors that were slightly larger (CI > 1), suggesting minimal neighbor influence on growth.

Large diameter trees with a CI < 1 exhibited a large range in volume growth rates (Fig. 2), and it is likely that factors other than competition for light are limiting growth for these trees. Nutrients are often in short supply in northwest forests and may limit primary production (Stegemoeller and Chappell 1990). Heterogeneity of nutrient supply rates within coniferous forests may create local patches of high and low nutrient availabilities (Erickson et al. 2005; Smithwick et al. 2005). Moreover, burning often increases the spatial heterogeneity of nutrient concentrations in surface soils (Gundale et al. 2006). Given that both units were burned after harvesting, it is not unreasonable to expect spatial variation in available nutrients, and hence growth rates, across the units. Soil water content may also vary spatially in young stands, and likely contributes to differential growth rates of young trees (Devine and Harrington 2006). Moreover, gradients in soil resources have recently been shown to affect both growth rates and neighborhood interactions of trees (Boyden et al. 2005).

Our neighborhood analysis showed that species of neighboring trees, independent of size, did little to influence overall growth rates. In other words, while mean growth rates may differ for Douglas-fir in monoculture versus mixture, after accounting for size difference, the species of neighbor does not matter. This lack of a neighbor identity effect, other than the effect due to size, suggests that belowground interactions may not differ greatly among the species, at least at this stage in stand development. While belowground interactions certainly occur within and between species, currently not much is known about these interactions and complementarity of resource use for Pacific Northwest conifers. This gap remains a limitation in our ability to fully understand mixed-stand dynamics in the Pacific Northwest and elsewhere (cf. Jose et al. 2006).

A possible limitation in our analyses at the individual tree scale is the reduced number of trees with neighbors of the correct identity, particularly for Douglas-fir. Also, in our analyses we did not account for any past contributions currently dead trees likely made to neighborhood interactions when they were alive.

Several lines of evidence (greater *hid* ratio and lower crown ratios) suggest that hemlock was, or will be, under greater competitive pressure in the mixture than in single-species stands (cf. Maguire and Bennett 1996, re: crown ratio as a measure of vigor). Thus, while we found no significant detrimental effects on hemlock growth after 24 years in mixture with Douglas-fir, hemlock growth in mixture may indeed be slowed in the future, as competitive interactions may change with stand age (e.g., Filipescu and Comeau 2007).

Implications for stand management

One concern often expressed in relation to shifting to mixed-species stands is a potential loss of productivity. At the stand level, we found the effect of mixture, with the correct complement of neighbors, was to increase yields of Douglas-fir while causing no change in yield for western hemlock. Barring early-stage mortality in these stands, the potential for increased productivity is likely. However, the contrast between our findings for western hemlock and Douglas-fir in the Cascade foothills and that of Amoroso and Turnblom (2006) for these same species near the coast, where western hemlock productivity decreased in mixture, indicates that extrapolations to other sites and stands of different ages need to be done with caution.

Moreover, the greater range of tree sizes in the western hemlock – Douglas-fir mixture has implications for maintaining biodiversity and facilitating the development of old-growth characteristics. Maximizing tree sizes in managed stands is consistent with natural stand development (Franklin et al. 2002). With greater structural heterogeneity, vertebrate diversity increases (Carey and Wilson 2001), and including western hemlock in mixtures may benefit seed-dependent wildlife because western hemlock produces at least some cones every year (Buchanan et al. 1990).

Planting mixed-species stands will require the development of specific management guidelines for particular site conditions. Spacing, with its well-known effect on tree growth, will need to be considered in designing mixed-species plantings. Mixture ratios can also be altered to favor lower canopy species that may otherwise be suppressed (Kelty 2006). Substituting species that take advantage of natural disease resistance, nitrogen fixing capabilities (DeBell et al. 1997; Forrester et al. 2006; Piotto 2008), or other unique properties of the species can also be considered. For example, in the Douglas-fir region, laminated root rot *(Phellinus weirii)* is prevalent on Douglas-fir. Planting western white pine, which is resistant to root rot, is often recommended in place of Douglas-fir; our findings from the west side of the Cascade Mountains indicate yield would not change with this species substitution. A relatively new management strategy is to plant trees in clumps or patches and often in areas that have not been clear-cut harvested. The experiments at TCH were initiated on lands that were clearcut; nonetheless, our findings suggest a potential for ecological and economic benefits by mixing Douglas-fir and western hemlock within patches.

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References

Amoroso, M.M., and Turnblom, E.C. 2006. Comparing productivity of pure and mixed Douglas-fir and western hemlock plantations in the Pacific Northwest. Can. J. For. Res. 36: 1484-1496. doi:10.1139/X06-042.

Boyden, S., Binkley, D., and Senock, R. 2005. Competition and facilitation between Eucalyptus and nitrogen-fixing Falcataria in relation to soil fertility. Ecology, 86(4): 992-1001. doi:1O.1890/04-0430.

Browne, J.E. 1962. Standard cubic-foot volume tables for the commercial tree species of British Columbia. British Columbia Forest Service, Forest Surveys and Inventory Division, Victoria, B.C.

Bruce, D., and DeMars, D.J. 1974. Volume equations for second-growth Douglas-fir. USDA For. Servo Res. Note RN-PNW-239.

Buchanan, J.B., Lundquist, R.W., and Aubry, K.B. 1990. Winter populations of Douglas' squirrels in different-aged Douglas-fir forests. J. Wildl. Manage. 54: 577-581. doi:1O.2307/3809351.

Carey, A.B., and Wilson, S.M. 2001. Induced spatial heterogeneity in forest canopies: responses of small mammals. J. Wildl. Manage. 65(4): 1014-1027. doi:1O.2307/3803050.

Chen, H.Y.H., Klinka, K., Mathey, A.-H., Wang, X., Varga, P., and Chourmouzis, C. 2003. Are mixed-species stands more productive than single-species stands: an empirical test of three forest types in British Columbia and Alberta. Can. J. For. Res. 33(7): 1227-1237. doi:1O.1139/x03-048.

Coomes, D.A., and Allen, R.B. 2007. Effects of size, competition and altitude on tree growth. J. Ecol. 95(5): 1084-1097. doi:10.1111/j.1365-2745.2007.01280.x.

Daly, C., Neilson, R.P., and Phillips, D.L. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. J. Appl. Meteoro!. 33: 140-158. doi:10.117511520-0450(l994)033<0140:ASTMFM>2.0.CO;2. Available from www.ocs.orst.edu/prism/.

D'Amato, AW., and Puettmann, KJ. 2004. The relative dominance hypothesis explains interaction dynamics in mixed species *Alnus rubra/Pseudotsuga menziesii* stands. J. Ecol. 92(3): 450--463. doi:l0.llll1j.0022-0477.2004.00888.x.

DeBell, D.S., Cole, T.G., and Whitesell, C.D. 1997. Growth, development, and yield in pure and mixed stands of Eucalyptus and Albizia. For. Sci. 43(2): 286-298.

Devine, W.D., and Harrington, C.A. 2006. Effects of vegetation control and organic matter removal on soil water content in a young Douglas-fIr plantation. USDA For. Servo Pacific Northwest Research Station, Res. Pap. PNW-RP-568.

Erickson, H.E., Soto, P., Johnson, D.W., Roath, B., and Hunsaker, e. 2005. Effects of vegetation patches on soil nutrient pools and fluxes within a mixed-conifer forest. For. Sci. 51: 211-220.

Filipescu, C.N., and Comeau, P.G. 2007. Competitive interactions between aspen and white spruce vary with stand age in boreal mixedwoods. For. Ecol. Manage. 247(1-3): 175-184. doi:10.1016/j.foreco.2007.04.038.

Flewelling, J., and Raynes, L.M. 1993. Variable-shape stem-profile predictions for western hemlock. Part I. Prediction from DBH and total height. Can. J. For. Res. 23: 520--536. doi:IO.1139/x93-070.

Forrester, D.I., Bauhus, J., and Khanna, P.K 2004. Growth dynamics in a mixed-species plantation of *Eucalyptus globulus* and *Acacia mearnsii*. For. Ecol. Manage. 193(1-2): 81-95. doi: 1O.1016/j .foreco.2004.01.024.

Forrester, D.I., Bauhus, J., Cowie, A.L., and Vanclay, J.K. 2006. Mixed-species plantations of Eucalyptus with nitrogen-fixing trees: a review. For. Ecol. Manage. 233(2-3): 211-230. doi:lO.1016/j.foreco.2006.05.012.

Fox, J.e., Ades, P.K, and Bi, H. 2001. Stochastic structure and individual-tree growth models. For. Ecol. Manage. 154(1): 261-276. doi:l0.1016/S0378-1127(00)00632-0.

Franklin, J.F., and Dyrness, C.T. 1973. Natural vegetation of Oregon and Washington. USDA For. Servo Gen. Tech. Rep. GTR-PNW-8.

Franklin, J.F., Spies, T.A., Pelt, R.V., Carey, AB., Thornburgh, D.A, Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K, and Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. 155(1-3): 399-423. doi:l0.1016/S0378-1127(01)00575-8.

Garber, S.M., and Maguire, D.A. 2004. Stand productivity and development in two mixed-species spacing trials in the central Oregon Cascades. For. Sci. 50(1): 92-105.

Grime, J.P. 1979. Plant strategies and vegetation processes. John Wiley, New York.

Gundale, M.J., Metlen, KL., Fiedler, C.E., and DeLuca, T.H. 2006. Nitrogen spatial heterogeneity influences diversity following restoration in a ponderosa pine forest, Montana. Ecol. Appl. 16: 479-489. doi:10. 1890/l051-0761(2006)016[0479:NSHlDF]2.0.CO;2. PMID:16711038.

Haggar, J.P., and Ewel, J.1. 1995. Establishment, resource acquisition, and early productivity as determined by biomass allocation patterns of three tropical tree species. For. Sci. 41(4): 689-708.

Harper, J.L. 1977. Population biology of plants. Academic Press, New York.

Hartley, M.1. 2002. Rationale and methods for conserving biodiversity in plantation forests. For. Ecol. Manage. 155(1-3): 81-95. doi: 10.1016/S0378-1127(01)00549-7.

Jose, S., Williams, R., and Zamora, D. 2006. Belowground ecological interactions in mixed-species forest plantations. For. Ecol. Manage. 233(2-3): 231-239. doi:1O.1016/j.foreco.2006.05.014.

Kelty, M.J. 2006. The role of species mixtures in plantation forestry. For. Ecol. Manage. 233: 195-204. doi:l0.1016/j.foreco.2006.05.011.

Kelty, M.J., and Cameron, I.R. 1995. Plot designs for the analysis of species interactions in mixed stands. Commonw. For. Rev. 74(4): 322-332.

King, J.E. 1966. Site index curves for Douglas-fir in the Pacific Northwest. Weyerhaeuser Forestry Paper No.8. Centralia, Wash.

Lorimer, C.G. 1983. Test of age-independent competition indices for individual trees in natural hardwood stands. For. Ecol. Manage. 6: 343-360. doi:IO.1016/0378-1127(83)90042-7.

Maguire, D.A., and Bennett, W.S. 1996. Patterns in vertical distribution of foliage in young coastal Douglas-fir. Can. J. For. Res. 26(11): 1991-2005. doi:1O.1139/x26-225.

Minore, D. 1979. Comparative autoecological characteristics of northwestern tree species — a literature review. USDA For. Servo Gen. Tech. Rep. PNW-87.

Monserud, R.A, and Sterba, H. 1996. A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Austria. For. Ecol. Manage. 80(1-3): 57-80. doi: 10.1016/0378-1127(95)03638-5.

Opio, e., Jacob, N., and Coopersmith, D. 2000. Height to diameter ratio as a competition index for young conifer plantations in northern British Columbia, Canada. For. Ecol. Manage. 137(1-3): 245-252. doi:IO.1016/S0378-1127(99)00312-6.

Piotto, D. 2008. A meta-analysis comparing tree growth in monocultures and mixed plantations. For. Ecol. Manage. 255(3--4): 781-786. doi:1O.1016/j.foreco.2007.09.065.

Puettmann, KJ., and Berger, CA. 2006. Development of tree and understory vegetation in young Douglas-Fir plantations in western Oregon. West. J. Appl. For. 21(2): 94-101.

Radosevich, S.R., Hibbs, D.E., and Ghersa, C.M. 2006. Effects of species mixtures on growth and stand development of Douglas-fir and red alder. Can. J. For. Res. 36(3): 768-782. doi:IO.1139/x05-280.

SAS Institute Inc. 2004. Version 9.1. SAS Institute Inc., Cary, N.C.

Shaw, D.e., Franklin, J.F., Bible, K, Klopatek, J., Freeman, E., Greene, S., and Parker, G.G. 2004. Ecological setting of the Wind River old-growth forest. Ecosystems (N.Y., Print), 7: 427--439. doi:IO.1007/s10021-004-0135-6.

Simard, S.W., Hagerman, S.M., Sachs, D.L., Heineman, J.L., and Mather, W.J. 2005. Conifer growth, *Armillaria ostoyae* root disease, and plant diversity responses to broadleaf competition reduction in mixed forests of southern interior British Columbia. Can. J. For. Res. 35(4): 843-859. doi:IO.1139/x05-010.

Smithwick, EAH., Turner, M.G., Mack, M.C., and Chapin, F.S., III. 2005. Postfire soil N cycling in northern conifer forests affected by severe, stand-replacing wildfires. Ecosystems (N.Y., Print), 8(2): 163-181. doi:l0.1007/sI0021-004-0097-8.

Soil Survey Staff. 2007. Natural Resources Conservation Service, United States Department of Agriculture. Official soil series descriptions [online]. Available from http://soils.usda.gov/technicallclassificationlosd/index.html [accessed 14 November 2007].

Stegemoeller, KA., and Chappell, H.N. 1990. Growth response of unthimled and thinned Douglas-fir stands to single and multiple applications of nitrogen. Can. J. For. Res. 20: 343-349. doi:lO.1139/x90-050.

Underwood, A.1. 1997. Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, U.K

Vandermeer, J.R. 1989. The ecology of intercropping. Cambridge University Press, Cambridge, England.

Varga, P., Chen, H.Y.H., and Klinka, K. 2005. Tree-size diversity between single- and mixed-species stands in three forest types in western Canada. Can. J. For. Res. 35(3): 593-601. doi:10.1139/x04-193.

Wagner, R.G., and Radosevich, S.R. 1998. Neighborhood approach for quantifying interspecific competition in coastal Oregon forests. Ecol. Appl. 8(3): 779-794. doi:1O.1890/l051-0761(1998)008[0779:NAFQIC]2.0.CO;2.

Wierman, C.A., and Oliver, C.D. 1979. Crown stratification by species in even-aged mixed stands of Douglas-fir - western hemlock. Can. J. For. Res. 9(1): 1-9. doi:1O.1139/x79-001.

Wyckoff, P.H., and Clark, J.S. 2005. Tree growth prediction using size and exposed crown area. Can. J. For. Res. 35(1): 13-20. doi:1O.1139/x04-142.