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Investigation into the Productivity of Single- and Mixed-Species, Second-growth Stands of Western Hemlock and Western Redcedar

Introduction

In BC, it is required that harvested areas be regenerated with a mixture of tree species whenever appropriate to the site. This policy is based upon the assumption that increases in stand productivity, reliability, and/or biodiversity can be achieved in mixed-species stands. However, the knowledge justifying this policy is at best incomplete.

Differences in forest productivity of mixed-species stands have been attributed mostly to competition. However, an increasing number of studies are providing evidence to support alternate theories, in which positive plant interactions play a major role. Positive plant interactions are divided into two components: (i) competitive reduction through structural and physiological differences in above and below ground structures, and (ii) facilitation through any positive effect on the growing environment of one plant species by another. These theories have yet to be tested in forest ecosystems. The objectives of this study, with respect to naturally established, unmanaged, second-growth stands of western hemlock (Hw) (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (Cw) (*Thuja plicata* Donn ex D. Don in Lamb.), and their mixtures, were: (1) to review the mechanisms of positive plant interactions and their potential to occur in these mixtures, and (2) to compare the productivity of these three stand types, using relative and absolute yield.

Study Stands and Methods

Study stands were located in three areas: Capilano River Valley (Capilano), University of British Columbia Malcolm Knapp Research Forest east of Vancouver (Knapp), and Mission Tree Farm License No. 26 (Mission). 18 stands were selected for the study: 7 hemlock stands, 4 Cw stands, and 7 Hw-Cw stands. The stands were naturally regenerated, unmanaged, closed-canopied, and even-aged (53 to 65 years @ bh), and represented the end of the stem exclusion stage of stand development. All stands were within the Submontane Very Wet Maritime Coastal Western Hemlock (CWHvm1) variant, and were located on fresh, nutrient-medium sites.

Within each stand a 30 x 30 m (0.09 ha) sample plot uniform in topography, vegetation, and soil was established. Diameter at breast height (dbh) and height were measured. Each live tree was assigned into one of four crown classes: dominant, codominant, intermediate, or suppressed. Species, dbh, total height, and crown height (distance from the ground to the lowest live branch) were recorded for all trees taller than 1.3 m. The breast height ages of three dominant trees of Cw and hemlock per plot were determined from increment cores. Site index of Cw and Hw was estimated using standard equations.

The relative yields of the mixed- and single-species stands were compared using the mean annual increment of each stand, based on the sum of individual tree volumes (inside bark, gross volume from stump to tree top) divided by the mean age at breast height of three dominant trees of each predominant species per stand. Relative yield comparisons were made with and without the volume contributions of non-study species. Comparisons were calculated for mixtures of species X and Y, relative yield (RY) and total relative yield (RYT).

Productivity was compared among stand types using mean annual increment (MAI). These comparisons were augmented with stand volume and basal area. Productivity comparisons among stand types were made using regression and analysis of variance (ANOVA). Despite controlling as much as possible for tree age, site quality, and stand density, some variation in these factors could not be avoided and was addressed by adding covariates to ANOVA models. To help explain differences or similarities in productivity among stand types, the individual characteristics of both Cw and Hw trees were compared in the single- versus the mixed-species stands. The mean dbh, height, height to live crown, and MAI of Cw trees in Cw stands were compared to those of the Cw in the mixed stands. The same comparison was made among Hw trees in Hw and mixed stands.

Results and Discussion

Positive plant interactions and their potential in hemlock-redcedar mixtures

Although naturally occurring mixtures of Hw and Cw are very common in the CWH and southern ICH, the productivity and growth dynamics of these mixtures have been little studied. Theory on the mechanisms of competitive reduction suggests that Hw and/or Cw may benefit in mixtures through: (1) belowground physiological separation via the preferential uptake of different forms of nitrogen, and (2) aboveground spatial and temporal separation of canopies via differences in growth habit, spatial arrangement, and longevity. Theory on the mechanisms of facilitation suggests that Hw and Cw may benefit in mixtures through: (1) resource modification whereby Cw increases forest floor base cation concentrations, pH levels, and microbial populations, (2) substrate stabilization where Cw can enhance the windfirmness of Hw, and (3) herbivory reduction where each species shields the other from their common, specific defoliators. Other studies suggest that Hw and Cw may experience positive interactions through: (1) vertical canopy separation and a random spatial pattern of trees, (2) preferential uptake of different nitrogen forms, and (3) Cw increasing forest floor pH levels, Ca and K concentrations, and microbial populations.

The productivity of single- and mixed-species hemlock and redcedar stands using relative and absolute yield.

Uncorrected MAI and quadratic mean diameter increased, while stocking decreased with increasing presence of Hw (Table 1), suggesting greater annual volume growth per tree in Hw stands. The highest mean basal area was also found in Hw stands, although this may be misleading considering the influence of stand H7, which has substantially higher basal area than the other Hw stands. Excluding this stand, the mean basal area of the Hw stands was intermediate (80.0 ± 5.5 m^2 ha^{-1}) between the mixed and Cw stands.

Table 1. Selected characteristics of study stands, stratified according to stand type (H - hemlock, M (mixed) - hemlock-redcedar, C - western redcedar; *se* is the stand type standard error of the mean.

Stand	Dominant tree height (m)	Dominant tree age at 1.3 m	Site index (m) (Cw/Hw)	Stems per hectare	Quadratic mean diameter (cm)	Relative density	Basal area (m^2 ha^{-1})	Volume (m^3 ha^{-1})	MAI (m^3 ha^{-1} yr^{-1})
H1	37.3	65	29.5	1000	32.0	20.1	80.6	999.8	15.4
H2	35.2	57	28.4	989	33.2	21.0	85.4	1002.6	17.6
H3	38.7	61	31.7	767	37.4	19.7	84.0	1061.0	17.4
H4	46.9	65	35.0	744	35.3	17.5	72.7	1044.0	16.1
H5	39.3	66	31.9	1033	30.1	18.9	73.8	1037.4	15.7
H6	38.8	61	34.5	822	36.0	20.0	83.8	1105.4	18.1
H7	47.8	70	39.8	500	63.5	30.1	158.3	1619.0	23.1
mean	**40.6**	**64**	**33.0**	**837**	**38.2**	**21.1**	**91.2**	**1121.2**	**17.6**
se	(4.8)	(4)	(3.9)	(190)	(11.4)	(4.1)	(30.0)	(221.1)	(2.6)
M1	33.2	60	26.6/31.1	978	32.2	19.9	79.6	850.7	14.2
M2	31.8	51	24.6/28.9	944	35.0	21.9	90.8	935.0	15.5
M3	37.6	55	24.4/31.0	1356	26.5	20.1	74.5	830.1	15.1
M4	33.5	50	30.0/32.0	822	34.3	18.5	76.1	730.1	14.6
M5	32.2	51	27.6/32.6	989	29.7	17.6	68.4	680.8	13.4
M6	33.2	58	27.2/29.0	1000	32.7	20.8	84.0	935.3	16.1
M7	32.9	58	26.3/29.9	944	30.8	17.9	70.5	713.6	12.3
mean	**33.5**	**56**	**26.7 30.6**	**1005**	**31.6**	**19.5**	**77.7**	**810.8**	**14.4**
se	(1.9)	(4)	(1.9/1.4)	(166)	(2.9)	(1.6)	(7.8)	(104.7)	(1.3)
C1	28.0	58	23.6	1100	29.7	19.6	76.0	699.9	12.1
C2	31.8	55	26.3	1478	27.4	23.1	87.0	796.3	14.5
C3	38.0	55	26.3	767	39.6	21.7	94.7	762.6	13.9
C4	32.4	57	28.5	967	33.1	20.5	83.2	786.5	13.8
mean	**32.6**	**56**	**26.2**	**1078**	**32.5**	**21.2**	**85.2**	**761.3**	**13.6**
se	(4.1)	(2)	(2.0)	(300)	(5.4)	(1.5)	(7.8)	(43.3)	(1.0)

The relative yields of Hw and Cw were higher in mixtures when the effect of non-study species was removed. Both species had RY > 0.5, implying that mixtures are more productive than single-species stands of either species. However, when this effect was accounted for, the relative yields of Hw and Cw were lower in mixtures compared to single-species stands, due to the effects of intraspecific competition. Although Hw still achieves the same yield in mixture with Cw as it would in alone, Cw achieves lower yield in mixture with Hw than it would in a monoculture. This impact of competition on Cw yield decreases total relative yield in Hw-Cw mixtures below 1.0, indicating that the mixtures are experiencing competitive inter-species interactions.

Increasing Hw presence in a stand was associated with increasing MAI (Table 2). Differences in MAI among stand types became increasingly prominent with the complexity of the density covariate used in ANOVA models (complexity: sph < qdbh < relative density). The model using relative density explained the most variation in stand type mean annual increment, and significant differences in increasing productivity were found for each stand type, with increasing presence of Hw. Wood volume also increased with increasing presence of Hw in progression from the Cw to the Hw-Cw to the Hw stand types (Table 2). Increasing proportions of the variation in volume was explained as the complexity of the density covariate increased, although significant differences among stand types were only found using relative density.

Table 2. Least squares means and standard errors (in parentheses) of MAI and volume of 18 study stands, stratified according to density covariate and stand type. Values in the same row with different superscripts are significantly different (p <0.05).

Productivity measure	Density covariate	Stand productivity according to stand type		
		Hemlock (n = 7)	Hemlock-redcedar (n = 7)	Redcedar (n = 4)
Stand MAI ($m^3 ha^{-1} yr^{-1}$)	Stems per hectare	16.3^{a} (0.7)	14.9^{a} (0.6)	14.3^{a} (0.8)
	Quadratic mean diameter	16.5^{a} (0.6)	$15.1^{a,b}$ (0.5)	14.1^{b} (0.7)
	Relative density	17.0^{a} (0.4)	15.1^{b} (0.3)	13.5^{c} (0.4)
Stand volume ($m^3 ha^{-1}$)	Stems per hectare	954.8^{a} (72.1)	911.6^{a} (41.0)	874.2^{a} (46.1)
	Quadratic mean diameter	949.1^{a} (62.6)	915.2^{a} (37.5)	876.3^{a} (37.9)
	Relative density	1053.3^{a} (38.0)	881.2^{b} (21.0)	766.4^{c} (28.1)

The Cw in the Cw stands were similar in most respects to those in the mixed stands (Table 3). No significant differences (a = 0.05) in mean dbh, tree height, height to live crown, and MAI were found in Cw of either stand type. The mean height to live crown of Cw in the Hw-Cw stands was significantly greater than in the Cw stands. In contrast, Hw in the Hw stands had greater MAI, and significantly greater mean diameter, height, and height to live crown, than the Hw in mixed stands (Table 3).

Table 3. Mean individual tree characteristics, and standard errors of the means (in parentheses), stratified according to species and stand type. Values in the same row with the same superscript are not significantly different (p >0.05).

Tree species	Redcedar		Hemlock	
Stand type	Redcedar	Hemlock-redcedar		Hemlock
Total height (m)	22.2^{a} (5.7)	22.8^{a} (5.3)	26.6^{b} (6.5)	31.0^{a} (6.6)
Height to live crown (m)	13.0^{a} (3.4)	14.4^{b} (3.5)	15.3^{b} (4.5)	18.1^{a} (4.1)
Mean annual increment ($m^3 ha^{-1} yr^{-1}$)	0.012^{a} (0.013)	0.011^{a} (0.011)	0.017^{a} (0.013)	0.022^{a} (0.017)
Diameter at 1.3 m (cm)	28.4^{a} (14.1)	28.1^{a} (11.6)	29.4^{b} (10.9)	33.3^{a} (11.5)

Silvicultural Implications

Foresters need to know whether a mixture of two or more tree species will be more productive than single-species stands of these species. Taking into account the lack of canopy stratification in single-cohort, Hw-Cw mixtures, and the improved growth of Hw with decreasing presence of Cw, we propose that pure Hw stands appear to be the most productive tree species option on the study sites.

Conclusions

Contrary to other conclusions arrived on the mechanisms of positive plant interactions and their potential to occur in Hw-Cw mixtures, the relative yields of each species in single- versus mixed-species stands appear to suffer from competitive interactions. MAI and wood volume increased with increasing presence of Hw, while basal area increased with increasing presence of Cw. The Hw stands were most productive because Hw height growth was greater than Cw, and its height and diameter growth were greater in Hw stands. This greater diameter growth may be due to the superior ability of Hw to self-thin on these sites. The Cw stand type was the least productive due to dense stocking of slender, short stems. Although Hw was shorter and of smaller diameter in mixed-species stands, Cw grew equally well in mixed- and single-species stands. Maximum wood volume production on similar sites would be achieved by establishing Hw stands with a minimal component of other species.

Reference

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Editor: Karel Klinka (klinka@interchange.ubc.ca)
Research: Brad Collins (brad@locin.com)
Production and design: Christine Chourmouzis (chourmou@interchange.ubc.ca)
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For more information contact: Brad Collins

Copies available from:
www.forestry.ubc.ca/klinka or
K. Klinka, Forest Sciences Department, 3036-2424 Main Mall,
UBC, Vancouver, BC V6T 1Z4