

INVESTIGATION INTO THE PRODUCTIVITY OF SINGLE- AND MIXED-SPECIES,
SECOND-GROWTH STANDS OF WESTERN HEMLOCK AND WESTERN REDCEDAR

by

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ABSTRACT

In order to evaluate if mixed-species stands of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western redcedar (*Thuja plicata* Donn ex D. Don) were more productive than single-species stands of either species, I: (1) reviewed the theory of positive plant interactions and integrated it with the silvical characteristics of hemlock and redcedar to determine if positive interactions are feasible among these species, (2) located even aged, unmanaged, second growth, single- and mixed-species stands of hemlock and redcedar on intermediate (fresh and nutrient medium) sites, within the perhumid mesothermal climate of southern coastal British Columbia, (3) compared the productivity of each stand type using relative and absolute yield comparisons, and (4) evaluated the mixed-species stands to determine if increasing productivity was associated with physical separation of the species, as suggested by the findings in (1).

Theory on positive plant interactions logically divides the mechanisms of these interactions into two components: competitive reduction, and facilitation. When applied to existing mixed-species stands of hemlock and redcedar, the mechanisms of competitive reduction and facilitation suggest that hemlock and redcedar may experience positive interactions through: (1) vertical canopy separation and a random spatial pattern of trees, and (2) preferential uptake of different nitrogen forms.

The relative yield of hemlock and redcedar was lower in mixture, as compared to single-species stands, due to the effects of competition with each other and non-study species. Mean annual increment and wood volume production increased with increasing presence of hemlock. Basal area increased with increasing presence of redcedar, and the redcedar stand type was also the densest. Redcedar trees in the redcedar stand type were similar in height, diameter, and mean annual increment, relative to those in the hemlock-redcedar stand type. Hemlock trees in the hemlock stand type were taller, had larger diameters, and had higher mean annual increments, than those in the hemlock-redcedar stand type. These differences in hemlock and redcedar

growth in each stand type are thought to be responsible for the differences in mean productivity detected among stand types.

In the mixed-species stands, increasing productivity was associated with increasing vertical separation of hemlock and redcedar canopies, where the area of hemlock canopy overtopping that of redcedar, and crown depths of both species, were maximized. Increased productivity was not associated with increasing levels of randomness in stand spatial tree patterns, but was associated with decreasing stand density, and a tendency towards regularity in the stand spatial tree patterns. Maximum productivity in fully stocked hemlock-redcedar mixtures can be attained with low density stands in which hemlock does not experience an establishment lag.

Given the choice between single- and mixed-species stands of hemlock and redcedar, hemlock stands should be established if maximum wood production is the management objective. If maintaining a mixture, or improving site nutrient status, is the management objective, then hemlock-redcedar stands should be established. Maximum wood production in a hemlock-redcedar stand will be achieved where stands are fully stocked, but established at low numbers of stems per hectare. These recommendations are for intermediate (blueberry) sites in the Submontane Very Wet Maritime Coastal Western Hemlock (CWHvm1) variant, for stands less than 80 years old.

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B.C.

1. GENERAL INTRODUCTION

British Columbia (BC) forest policy recommends that harvested areas be regenerated with a mixture of tree species, rather than with a single species, wherever a mixture is suited to the site (Anonymous 1995). This policy is based on the assumptions that stand productivity, reliability, or biodiversity will all be enhanced in mixed-species stands. Analogous assumptions have been made in most European countries, including, in Germany, the assumption that mixed-species stands will also enhance aesthetic values (Burschel *et al.* 1992). Tree species composition has impacts on all stand characteristics, including productivity, structure, and nutrient cycling, and the BC Ministry of Forests has implemented tree species selection guidelines recognizing these impacts (Klinka 1977; Green *et al.* 1984; Klinka and Feller 1984; Green and Klinka 1994). However, the knowledge justifying the policy of regenerating a mixture of tree species, and the practice of choosing an appropriate mixture, is at best incomplete, and at worst anecdotal. Current policy is to mimic naturally occurring mixtures, however, the *de facto* assumption that mixtures are generally beneficial is yet to be demonstrated. Studies determining how effectively different mixtures meet specific value objectives are required to guide regeneration policy.

Traditionally, the population dynamics, distribution rates and patterns, and productivity of plants have been attributed mostly to competition (Connell 1983; Fowler 1986; Aarssen & Epp 1990). A large body of complex, experimental evidence exists supporting the role and mechanisms of competition. This is the basis, either implicitly or explicitly, of most general conceptual ecological models (Callaway 1995). However, an increasing number of studies are providing evidence to support alternate theories, in which positive plant species interactions also play a major role in the reproduction, distribution, diversity, and productivity of plant communities (Hunter & Aarssen 1988; DeAngelis *et al.* 1986; Grace and Tilman 1990; Wang

1997). Positive plant interactions are meaningfully divided into two components (Vandermeer 1989; Kelty 1992; Callaway 1995):

1. *competitive reduction* through structural and physiological differences in above and below ground structures, (this mechanism is also known as niche separation), and
2. *facilitation* through any positive effect on the growing environment of one plant species by another species.

Those mixtures of plant species in which competition is reduced, or one species facilitates the growth of the other, are said to have high ecological combining ability (Harper 1977; Kelty 1992), increasing the efficiency of plants to utilize a limited resource pool (Kelty 1992). A mixed stand of plant species with high ecological combining ability should be more productive than single-species stands of either component species. Mixtures may also increase pest and disease resistance, increase biodiversity values, and reduce the risk of crop failure. However, silvicultural practice generally favours high-value monocultures, and mixed-species stands are usually only established where the associated benefits are deemed necessary to reduce risk to the species of high commercial value (Kelty 1992).

In recent decades interest in the productivity of mixed-species stands has intensified. Some naturally occurring mixtures have been investigated to determine whether potential productivity advantages can be gained by growing mixed-species stands. Mixtures have been found to be both more or less productive than their component species in monocultures, depending on both the species and site in question (Kelty 1992; Binkley *et al.* 1992; Burschel *et al.* 1992; Callaway 1995; DeBell *et al.* 1997). The results of these studies suggest that no *a priori* assumptions should be made about the productivity advantages or disadvantages of a particular species mixture.

A complex balance between competition and positive interactions exists between plant species occurring in mixtures. This balance may be affected by the life stage of the species involved, environmental harshness, and the degree to which resources required for growth are limited (Callaway 1995). It is necessary to study the productivity of each mixture relative to a particular site type and life stage of both species.

The objectives of this study, with respect to naturally established, unmanaged stands of hemlock, redcedar, and their mixtures, are: (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 yield and absolute yield, and (3) to determine if increased productivity in these mixtures is associated with competitive reduction, through the vertical separation of hemlock and redcedar canopies, or increasing spatial randomness in tree spatial patterns.

2. STUDY AREA AND STANDS

This study was conducted in southern British Columbia, in the foothills of the Coastal Mountains. The areas under study were within the Submontane Very Wet Maritime Coastal Western Hemlock (CWHvm1) variant, characterized by a perhumid, cool mesothermal climate (Klinka *et al.* 1991).

Candidate stands were located in three areas: Capilano River (Capilano), University of British Columbia Malcolm Knapp Research Forest (Malcolm Knapp), and Mission Tree Farm No. 26 (Mission) (Table 2.1).

Table 2.1 Latitude, longitude, and elevation of study areas in southern coastal British Columbia.

Study area	Latitude	Longitude	Elevation (m)
Capilano	49° 28' N	123° 08' W	308
Malcolm Knapp	49° 17' N	122° 36' W	362
Mission	49° 21' N	122° 21' W	371

The selection criteria required study stands to be as similar as possible in history, site quality, and structure (i.e., age, species composition, stocking, density, spatial (horizontal and vertical) tree distribution). Within each area (location), 3 stands were selected in each of 3 stand types: 3 hemlock, 3 redcedar, and 3 mixtures (with approximately equal proportions of hemlock and redcedar), for a total of 27 study stands. Final assignment of each stand to one of the 3 stand types was based on basal area. Those stands with greater than 66% basal area contribution of either species were assigned to the hemlock or redcedar stand types; those stands with less than 16% difference in basal area contributions by hemlock and redcedar were assigned to the hemlock-redcedar stand type. Those stands with more than 15% basal area contribution by non-

study species were excluded from the study. These criteria resulted in the selection of 18 stands for the study: 4 redcedar stands, 7 hemlock stands, and 7 hemlock-redcedar stands (Table 2.2).

Table 2.2 Percentage of basal area contribution to each stand, stratified according to stand type.

Stand type	Stand Identification	Basal area contribution (%)		
		Redcedar	Hemlock	Non-study species
Redcedar	C1	75	15	10
	C2	73	26	1
	C3	69	27	4
	C4	67	33	0
Hemlock-Redcedar	M1	55	39	6
	M2	52	40	8
	M3	52	43	5
	M4	48	52	0
	M5	42	58	0
	M6	40	51	9
	M7	39	52	9
Hemlock	H1	16	73	11
	H2	12	73	15
	H3	10	76	14
	H4	6	90	4
	H5	4	94	2
	H6	2	95	3
	H7	0	95	5

All second growth study stands were naturally regenerated after clearcutting and slashburning of old-growth stands, were unmanaged, fully stocked (Hamilton and Christie 1971), and even-aged (where <20 years at breast height age difference existed between all stands' site trees). Study stands were located on the most commonly occurring, intermediate (zonal) HwBa-Blueberry (*Vaccinium ovalifolium* Sm.) sites (Green and Klinka 1994); selection of study stands with fresh and medium soil moisture and nutrient regimes kept the edaphic conditions of all sample plots within a narrow range. Study stands were free of disease and insect problems, and represented a late stem exclusion stage of stand development (Oliver and Larson 1996). This development stage allowed sufficient time for the overstory to influence forest floor nutrient

properties, but preceded the understory reinitiation stage and the influence this understory vegetation may have on forest floor nutrient properties. Forest floor depths ranged from 2 to 23 cm, and potential rooting depths ranged from 50 to over 100 cm; soils were typically mid-slope, coarse-skeletal, Humo-Ferric or Ferro-Humic Podzols (Soil Classification Working Group 1998), with textures ranging from sandy to loamy, derived from glacial till and underlain by granitic rocks, and coarse fragment contents ranging from 10 to 70%. Humus forms were generally thick (6 to 14 cm) Mors in hemlock stands, and Mormoders in redcedar stands and hemlock-redcedar stands. Although the study stands varied somewhat in the individual physical properties (Table 5.1), such as topographic and soil characters, because of the compensating effects of environmental factors, they were considered to be ecologically-equivalent, i.e., to provide the same growing conditions and to have the same vegetation potential (Cajander 1926; Bakuziz 1969; Major 1977).

Table 2.3 Selected characteristics (means) of the study stands stratified according to study area and stand types (H – western hemlock, HC – hemlock-redcedar, C – redcedar).

Study area Stand	Capilano			Malcom Knapp			Mission		
	H	HC	C	H	HC	C	H	HC	C
Number of stands	3	3	3	3	3	3	3	3	3
Slope gradient (%)	25	20	35	28	32	34	37	33	26
Forest floor (cm)	17	19	9	13	14	5	7	10	4
Content of coarse fragments (%)	25	32	40	20	25	30	30	33	30
Rooting depth (cm)	35	25	33	45	72	65	70	58	53
Cover of understory vegetation (%)	21	27	28	62	35	44	36	2	3
Forest floor cover (%)	65	62	65	72	71	69	65	55	53
Decaying wood cover (%)	22	22	13	25	23	20	30	28	35
Coarse fragment cover (%)	13	11	20	5	6	11	5	13	10
Mineral soil cover (%)	0	1	2	0	0	0	1	4	2

3. MATERIALS AND METHODS

3.1 Data Collection

Within each study stand a 30 x 30 m (0.09 ha) area, uniform in structural, topographic, and soil characteristics, was established. The understory vegetation and environment of each study stand was described. The vegetation description included strata coverage of the tree, shrub, herb and moss layers, and coverage of component species within each stratum, expressed as percent ground cover. The environmental description included elevation, slope gradient, aspect, slope position, microtopography, parent materials, surface substrate, humus form, potential rooting depth, soil texture and structure, coarse fragment content, thickness and sequence of soil horizons, and soil identification.

The corners of each study stand were marked with painted stakes, and a 5 m x 5 m grid was established within the stand. The grid perimeter and grid intersection points were marked with labeled flagging pins. The species, height, height to live crown, diameter at breast height (dbh), and position relative to the grid (within 0.1 m), of all live and dead trees taller than 1.3 m were recorded. The ages at breast height (1.3 m) of the three dominant trees of each leading species per stand were determined through increment coring techniques.

3.2 Productivity Analyses

3.2.1 Relative Yield

The relative yields of the mixed- and single-species stands were compared using the mean annual increment ($\text{m}^3\text{ha}^{-1}\text{yr}^{-1}$) of each stand, based on the sum of individual live 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 leading species per stand. Relative yield comparisons

were made with and without the volume contributions of non-study (inclusion) species. For mixtures of species X and Y, relative yield (RY) and total relative yield (RYT) comparisons were calculated:

$$RY_X = \text{Yield}_X \text{ in mixture} / \text{Yield}_X \text{ in monoculture} \quad [3.1]$$

$$RYT = RY_X + RY_Y \quad [3.2]$$

If both species use resources in mixture identically to that in monoculture, the RY of each should be 0.5 and the RYT should be 1.0. Where competition is reduced or species are facilitated, RYT values greater than 1.0 are expected. Where competitive interactions are dominant among the species, RYT values of less than 1.0 are expected.

3.2.2 Yield

Productivity was compared among stand types using mean annual increment. These comparisons were augmented with comparisons using stand volume and basal area.

Gross tree volume equations were obtained from the BC Ministry of Forests (Anonymous 1976), in accordance to the appropriate age and forest inventory zone. The gross volume equations utilized were:

$$\log_{10} V_{\text{Hemlock}} = -4.418820 + 1.867780 \log_{10}(\text{dbh}) + 1.099890 \log_{10}(\text{Ht}) \quad [3.3]$$

$$\log_{10} V_{\text{Redcedar}} = -4.139118 + 1.716770 \log_{10}(\text{dbh}) + 1.0047420 \log_{10}(\text{Ht}) \quad [3.4]$$

$$\log_{10} V_{\text{Pacific silver fir}} = -4.266202 + 1.782960 \log_{10}(\text{dbh}) + 1.103820 \log_{10}(\text{Ht}) \quad [3.5]$$

$$\log_{10} V_{\text{Douglas-fir}} = -4.319071 + 1.813820 \log_{10}(\text{dbh}) + 1.042420 \log_{10}(\text{Ht}) \quad [3.6]$$

where dbh is measured in centimeters, and Ht represents tree height measured in meters.

Individual tree volumes were back-transformed from log volumes before summing the stand total for further analysis. Stand volume totals included non-study tree species for which

volume equations were available, namely Pacific silver fir (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) (equations [3.5] and [3.6]). These inclusions contributed an average basal area of 5.6% overall, with inclusions in the hemlock stand type at 7.7%, the hemlock-redcedar stand type at 5.3%, and the redcedar stand type at 3.8%. Hardwood species in the shrub layers (<10 m height) were not included in stand volume calculations.

Productivity comparisons among stand types (hemlock, hemlock-redcedar, and redcedar) were performed with analysis of covariance (ANCOVA) models, according to the general equation:

$$Y_{ij} = \mu. + \tau_i + \gamma_1 (X_{ij1} - \bar{X}_{..1}) + \gamma_2 (X_{ij2} - \bar{X}_{..2}) + \dots + \varepsilon_{ij} \quad [3.7]$$

where Y_{ij} is the value of the productivity measure of the j th stand in the i th stand type, $\mu.$ is the overall mean of that measure, τ_i are the fixed stand type effects, γ_1 is the regression coefficient for the relation between Y and the first model covariate X_{ij1} , X_{ij1} represents the value of the first model covariate for the j th stand in the i th stand type, $\bar{X}_{..1}$ is the overall mean of the first model covariate, and ε_{ij} are independent. Additional model covariates were added according to the specific analysis, as detailed in the remainder of this section. Productivity measures from each stand type were assessed for normality with probability plots and subjected to variance homogeneity tests via Bartlett's test (Bartlett 1937) ($\alpha = 0.05$). Tests for outliers were conducted with studentized residual analysis (Neter *et al.* 1996). Interactions were not detected between stand types and covariates in ANCOVA models, indicating stand type response variables were close to parallel. Volume was the only productivity measure with non-homogenous variance among stand types, and model coefficients were fitted via iteratively re-weighted least squares procedures until stable coefficients were attained (Neter *et al.* 1996).

Despite controlling as much as possible for tree age, site quality, and stand density during the selection of study stands, some variation in these factors could not be avoided. Since tree age, site quality, and stand density all affect productivity, variation in these factors was addressed by adding these covariates to analysis of covariance models. Adding model covariates for age, site, and density provided estimates of productivity in which the means were adjusted to reflect trends in stand productivity for equivalent age, site, and density.

Within each stand, tree age was measured as mean age at breast height (Table 2.3), based on three dominant trees of each leading species per stand. Dominant trees were selected as those trees, free from damage or disease, of largest dbh in the stand. Site was measured as site index (Table 2.3), which, in the hemlock-redcedar stand type, represents a modified site index for each stand. The site indices of both hemlock and redcedar, and the proportion of contribution of both hemlock and redcedar to stand basal area, were determined for each stand. Each species' site index was then weighted by the proportion of basal area contribution of that species to the stand total, and then summed to give a pooled site index for each stand. Density was measured as number of stems per hectare (SPH), quadratic mean diameter (QDIA), and Curtis' relative density index (1982) (RD):

$$QDIA = \sqrt{\frac{\sum_{i=1}^n dbh_i^2}{n}} \quad [3.8]$$

$$RD = \frac{BA}{(QDIA)^{0.4}} \quad [3.9]$$

Quadratic mean diameter reflects the diameter of trees of average basal area (BA) in the stand, and thus contains information on basal area and stems per hectare in the model. Curtis' (1982)

relative density index provides a density index independent of stage of stand development, as basal area is divided by the diameter of tree of average basal area in the stand.

In addition to age, site quality, and stand density, productivity differences among Capilano, Malcolm Knapp, and Mission could also affect productivity comparisons among stand types. To determine if productivity comparisons among stand types required correction for location, a two-factor analysis of variance was performed testing stand types, locations, and their interaction. Although mean annual increment was not found to differ significantly among locations, and no significant stand type by location interaction was found, location was inserted as an additional factor in analysis of covariance models in order to reduce model variability.

Mean annual increment (MAI) has an intrinsic age correction factor, therefore the analysis of covariance model [3.7] only required the addition of site index (X_{ij1}), density (X_{ij2}), and location (X_{ij3}) covariates.

Volume (VOL) and basal area (BA) are not age corrected, and the analysis of covariance model [3.7] for each productivity measure included the addition of site index (X_{ij1}), age at breast height (X_{ij2}), density (X_{ij3}), and location (X_{ij4}) covariates. Each of SPH, QDIA, and RD was inserted separately in the analysis of covariance for each productivity measure, generating three sets of estimates of stand type means for each model.

Least squares means were used for final comparisons of productivity among stand types. Means were compared with multiple, pair-wise t-tests, wherein probability levels were adjusted for the number of pairs examined according to the Bonferroni multiple comparison procedure (Neter *et al.* 1996).

To help explain differences or similarities in productivity among stand types, the individual characteristics of both redcedar and hemlock trees were compared in the single-species stands versus the mixed-species stands. The mean values of dbh, tree height, height to live crown, and mean annual increment of redcedar trees in redcedar stands were compared to

those of the redcedar trees in the hemlock-redcedar stands. The same comparison was made among hemlock trees in hemlock and hemlock-redcedar stands.

Variances of mean tree characteristics were subjected to normality and variance homogeneity tests, via probability plots and Bartlett's test (Bartlett 1937) ($\alpha = 0.05$). Where variances were found to be non-homogenous, differences in mean tree characteristics were assessed with the Wilcoxon Rank Sum test (Venables and Ripley 1999). Where variances were found to be homogenous, differences in mean tree characteristics were determined through analyses of variance. Differences in cumulative distribution functions of each tree characteristic were assessed with the Kolmogorov – Smirnov goodness of fit test (Kaluzny *et al.* 1998; Venables and Ripley 1999). Alpha levels were held at 0.05 in all cases, unless otherwise stated.

3.3 Structural Analyses

Each of the hemlock-redcedar stands was evaluated to determine if increasing stand productivity was associated with increasing vertical canopy separation or spatial randomness in tree patterns. The productivity of each hemlock-redcedar stand was assessed by comparing the average mean annual increment of all live hemlock and redcedar trees in each stand. Within each stand, the mean annual increments were calculated for each tree. An analysis of covariance was performed to determine whether significant differences in mean annual increment per tree existed among the mixed-species stands. Site index (X_{ij1}) and nearest neighbour distance (X_{ij2}) covariates were used to correct for variability in site and density in the analysis of covariance model [3.7].

Least squares means were used for comparisons of mean annual increment per tree among hemlock-redcedar stands. Means were compared with multiple, pair-wise t-tests, wherein probability levels were adjusted for the number of pairs examined according to the Bonferroni

multiple comparison procedure (Neter *et al.* 1996). Stands were ranked according to their means, in descending order of productivity.

Canopy stratification, and refined nearest neighbour and combined count and distance (Upton and Fingleton 1985), analyses were conducted on all hemlock-redcedar stands. In the least and most productive stands, the results of each analysis were contrasted and compared.

3.3.1 Canopy stratification

Canopy stratification in mixed-species stands is generally the manifestation of the component species having different shade tolerances (Kelty 1992). Stratification can also occur where two species have established at the same time, but have different height growth rates/patterns, or where species establish at different times due to succession (Man and Lieffers 1999). When a canopy is stratified between two species, each species' crowns should occupy different niches within the canopy. These vertical niches can be distinguished from each other by the differences in tree height, and the amount of crown overlap between the two species.

The height differences between hemlock and redcedar in each mixture were broken into two subcomponents for analysis: (1) the differences in mean tree height of each species in each stand, and (2) the differences in the cumulative height distribution functions of each species in each stand.

Variances of mean tree characteristics were subjected to normality and variance homogeneity tests, via probability plots and Bartlett's test (Bartlett 1937). Where variances were found to be heterogenous, differences in mean tree characteristics were assessed with the Wilcoxon Rank Sum test (Venables and Ripley 1999). Where variances were not found to be heterogenous, differences in mean tree characteristics were determined through analyses of variance. A visual reference of height structure was constructed via height frequency distributions for both hemlock and redcedar in each stand. The cumulative height distribution

functions for hemlock and redcedar in each stand were tested for similarity with a Kolmogorov – Smirnov goodness of fit test (Kaluzny *et al.* 1998; Venables and Ripley 1999).

To complete the assessment of canopy stratification, a crown overlap ratio (COR) was calculated for hemlock and redcedar in each mixture:

$$COR = \frac{D}{C}; \quad \text{where: } D = \min(\bar{H}_{Hw}; \bar{H}_{Cw}) - \max(\bar{H}c_{Hw}; \bar{H}c_{Cw}) \quad [3.10]$$

$$C = \max(\bar{H}_{Hw}; \bar{H}_{Cw}) - \min(\bar{H}c_{Hw}; \bar{H}c_{Cw})$$

where *min* and *max* indicate the minimum and maximum values occurring between the adjacent bracketed terms, \bar{H}_{Hw} and \bar{H}_{Cw} are the average heights of hemlock and redcedar in each mixture, and $\bar{H}c_{Hw}$ and $\bar{H}c_{Cw}$ are the average heights of competitive live crown for hemlock and redcedar in each mixture (Figure 3.1).

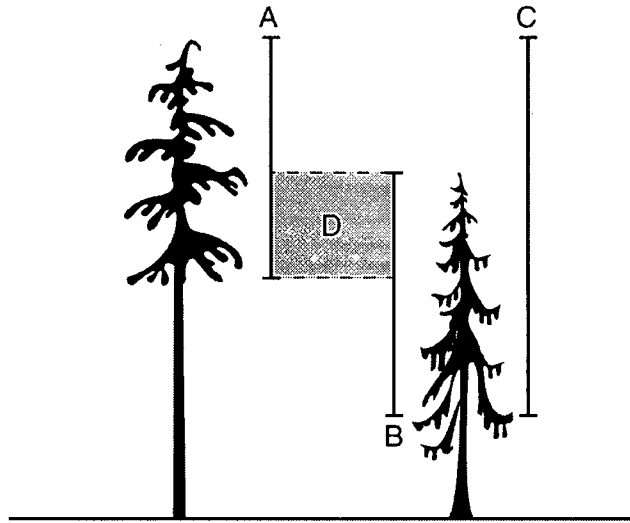


Figure 3.1 Schematic diagram illustrating parameters used in calculating the stand ratio of crown overlap, where: 'A' represents the mean crown depth (from the top of the tree to the closest of: 66% of top height, or height of live crown) of hemlock, 'B' represents the mean crown depth of redcedar, 'C' represents the mean, maximum canopy depth of the stand, and 'D' represents the mean depth of crown overlap between hemlock and redcedar.

Competitive live crown for each tree was defined as 66% of the top height, or the height to live-crown, whichever was closer to the top of the tree. Defining the zone of maximum competition as 66% of tree height is in agreement with the range of values (50% - 75%) determined in other studies (Biging and Dobbertin 1995; Latham *et al.* 1998).

3.3.2 Spatial randomness

Reduced competition for light occurs where different species capture light at different intensities and at different positions in the canopy. Canopy stratification, as described in the previous section, is a two-dimensional characteristic and is not sufficient, in and of itself, to prove above ground competitive reduction in mixtures. In addition to the vertical component, the horizontal arrangement of species on the ground surface is of vital importance to maximize light capture. In addition to canopy stratification, the spatial tree pattern of each species must be considered when evaluating aboveground species interactions.

A spatial tree pattern is said to be regular when the average distance between trees is greater than would be observed when those trees are arranged in a completely random orientation. Alternately, a clustered spatial pattern is characterized by an average inter-tree distance which is less than would be observed in a completely random pattern. When analyzing the spatial patterns of trees, regularity suggests competition, while clustering suggests facilitation (Upton and Fingleton 1985). Where facilitation does not occur, but competition is reduced, a random pattern intermediate between clustering and regularity is expected.

Competitive reduction is maximized with a fine-grained intermixing of species (i.e., trees must be adjacent to trees of a different species) on a two-dimensional plane (Kelty 1992). This type of intermixing is most closely approximated by spatial randomness in the patterns of each species, and the pattern of both species combined, where each species' pattern is independent from that of the other species. A mixture of species exhibiting complete spatial randomness is

characterized by: (1) no interactions between the species' individual spatial point patterns, and (2) a constant intensity (number per unit area) of each species over a bounded region (Diggle 1983; Kaluzny *et al.* 1998).

A random distribution of trees in a stand can be likened to a random spatial point pattern. The probability observing r points (trees) per unit area in a stand of area (A) is defined by the formula:

$$p_r = \frac{\lambda^r e^{-\lambda}}{r!} \quad (r = 0, 1, 2, \dots) \quad [3.11]$$

where λ is the intensity of points (trees) in a unit area. Such a random distribution of trees in a stand is thus referred to as a Poisson process or Poisson forest (Keuls *et al.* 1963; Upton and Fingleton 1985).

Thus in a mixture of two species, each species may individually be arranged according to a Poisson process. However, the combined, bivariate spatial point pattern of both species may or may not appear random. It is therefore important to evaluate the bivariate pattern for any interrelation between the individual spatial point patterns of each species (Upton and Fingleton 1985). The interrelation between each species' spatial point patterns can reveal attraction (clustering), independence, or repulsion (regularity) (Upton and Fingleton 1985), supporting arguments for facilitation, competitive reduction, and competition, respectively.

Refined nearest neighbour analysis

Within each hemlock-redcedar stand the spatial point patterns of all stems (live and dead) were subjected to refined nearest neighbour analysis (Roder 1975; Diggle 1979; Upton and Fingleton 1985), examining the complete distribution function of nearest neighbour distances as a function of distance. If trees are arranged according to a Poisson process and the mean intensity of stems per unit area is λ , then the area of a circle centered on tree i , with radius (d_i)

extending to the nearest neighbouring tree, is a random variable defined by the probability density function:

$$g(d) = 2\lambda\pi d_i e^{-\lambda\pi d_i^2} \quad [3.12]$$

The cumulative distribution function based on equation [3.12] describes the probability that a nearest neighbour is within distance (d) of a specified tree (i) in a circular region of area (πd^2) (Moeur 1993):

$$P(d_i \leq d) = G(d) = 1 - e^{-\lambda\pi d_i^2}, \quad d \geq 0 \quad [3.13]$$

The corresponding test statistic (Diggle 1979) was also computed for each study stand:

$$d_i = \sup |G(d) - \hat{G}(d)| \quad [3.14]$$

which represents the largest absolute deviation between the theoretical, random distribution $G(d)$ and the estimated distribution $\hat{G}(d)$. Bias due to edge effects was avoided by calculating the estimated distribution according to the procedure outlined by Upton and Fingleton (1985), which considers only those trees that are closer to their nearest neighbouring trees than they are to any plot boundary:

$$\hat{G}(d) = \frac{\#(b_i > d \geq d_i)}{\#(b_i > d)} \quad [3.15]$$

where $\#$ indicates the number of trees for which the argument within the adjacent brackets is true, and b_i is the distance from tree i to its nearest plot boundary. Plots of $\hat{G}(d) - G(d)$ over d were made for each stand, providing initial evidence of pattern tendencies. Clustering is

indicated where $\hat{G}(d) > G(d)$, independence is indicated where $\hat{G}(d) \cong G(d)$, and regularity is indicated where $\hat{G}(d) < G(d)$.

Combined count and distance analysis

The interrelation between both species' spatial point patterns within each stand was evaluated using Ripley's (1976, 1977) $\hat{K}_{ij}(d)$ and $\hat{L}_{ij}(d)$ functions. Ripley's functions focus on the inter-tree (point to point) distances on a plane, as do the refined nearest neighbour analyses. However, nearest neighbour methods ignore the majority of spatial relations between points in a plane (Clark and Evans 1954). The Ripley functions consider not only nearest neighbour distances, but *all* inter-tree distances on the plane. This allows greater insight into the univariate and bivariate spatial point patterns under investigation, at multiple scales (Upton and Fingleton 1985; Moeur 1993; Chen and Bradshaw 1999).

If trees within a stand are arranged according to a Poisson distribution, and the spatial point pattern is bivariate (there are two tree species within the stand), then that bivariate pattern can be defined by a set of functions whose estimator is calculated from the combined distributions of distances from type 1 trees to type 2 trees, and vice versa (Lotwick and Silverman 1982; Moeur 1993):

$$\hat{K}_{12}(d) = \frac{n_2 \hat{K}_{12}^*(d) + n_1 \hat{K}_{21}^*(d)}{n_1 + n_2}; \quad [3.16]$$

where: $\hat{K}_{12}^*(d) = A \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} \frac{w_{ij}(d)}{n_1 n_2}$, and $\hat{K}_{21}^*(d) = A \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} \frac{w_{ji}(d)}{n_1 n_2}$, for $i \neq j$

where n_1 and n_2 are the number of type 1 and type 2, for all pairs of trees with $d_{ij} \leq d$, A is the total area, and w_{ij} is an edge effect correction factor (Ripley 1977; Moeur 1993). If trees of type 1 and type 2 are independent, then $\hat{K}_{12}(d) = \pi d^2$. Besag [in the discussion of Ripley (1977)]

suggested applying a square root transformation to $\hat{K}_{12}(d)$, which linearizes the function, stabilizes its variance, and has an expected value of zero under the Poisson assumption (Moeur 1993; Chen and Bradshaw 1999). The linearized, $\hat{L}_{12}(d)$ function was computed as:

$$\hat{L}_{12}(d) = \sqrt{\frac{\hat{K}_{12}(d)}{\pi}} - d \quad [3.17]$$

The significance of the deviations of $\hat{K}_{12}(d)$ and $\hat{L}_{12}(d)$, from $K_{12}(d)$ and $L_{12}(d)$ respectively, were determined by comparing the Ripley functions against confidence envelopes generated via Monte Carlo procedures. Monte Carlo methods allowed approximate tests for randomness at any point d along the distribution in question, and allowed confidence envelopes to be generated for statistics whose underlying distributions were not necessarily known (Upton and Fingleton 1985; Moeur 1993). The confidence envelopes ($\alpha = 0.05$) for each study stand were generated according to the procedures detailed by Moeur (1993), based on the method detailed by Besag and Diggle (1977). Confidence envelopes for each mixture, and each of hemlock and redcedar within each mixture, were derived from 100 simulations of random, spatial point patterns. Simulations were based on the same numbers of stems as present in the actual study stand.

All spatial analyses were performed with the S-Plus 2000 statistical software package (Mathsoft Inc. 1999) spatial analysis module (Kaluzny *et al.* 1998).

4. POSITIVE PLANT INTERACTIONS – APPLYING CURRENT THEORIES TO MIXED-SPECIES STANDS OF HEMLOCK AND REDCEDAR

Abstract

Theory on positive plant interactions logically divides the mechanisms of these interactions into two components: competitive reduction, and facilitation. Although naturally occurring mixtures of hemlock and redcedar are very common in the coastal and southern interior wet belt of British Columbia (BC), the productivity and growth dynamics of these mixtures have been little studied. Theory on the mechanisms of competitive reduction suggest that hemlock and/or redcedar may benefit in mixtures through: (1) below ground physiological separation via the preferential uptake of different forms of nitrogen, and (2) above ground spatial and temporal separation of canopies via differences in growth habit, spatial arrangement, and longevity. Theory on the mechanisms of facilitation suggests that hemlock and redcedar may benefit in mixtures through: (1) substrate stabilization where redcedar enhances the windfirmness of hemlock, and (2) herbivory reduction where each species shields the other from their respective, common defoliators. When applied to the mixed-species study stands, facilitation among hemlock and redcedar is unlikely due to site and stand selection criteria, but these species may experience competitive reduction through: (1) vertical canopy separation and a random spatial pattern of trees, and (2) preferential uptake of different nitrogen forms.

4.1 Introduction

The study of positive plant interactions has intensified in recent years, providing mounting evidence that these interactions play a major role in the reproduction, distribution, diversity and productivity of plant communities (DeAngelis *et al.* 1986; Hunter & Aarssen 1988; Grace and Tilman 1990; Wang 1997). The mechanisms of positive plant interactions are logically divided into those of competitive reduction, and facilitation (Vandermeer 1989; Kelty 1992; Callaway 1995), and each of which can be subdivided into several components (Table 4.1).

Table 4.1 The mechanisms of positive plant interactions (adapted from: Callaway 1995; Man and Lieffers 1999).

Competitive Reduction	Facilitation
1 Reduction of crown competition - physiological separation - spatial separation - temporal separation	1 Resource modification - light and temperature - soil moisture - soil nutrients
2 Reduction of root competition - physiological separation - spatial separation - temporal separation	2 Substrate modification - aeration / soil oxygenation - substrate supply and stabilization
	3 Mortality agent attenuation - competitor control - herbivory reduction - amelioration of environmental extremes
	4 Additional effects - pollination - propagule concentration

Hemlock and redcedar commonly occur in mixtures in the coastal and southern interior wet belt regions of British Columbia, and each species has been the subject of studies investigating

various aspects of growth and yield. However, how these species grow together in mixture has been the subject of little study. Applying the theory of positive plant interactions to hemlock-redcedar mixtures may provide useful clues to the growth potential of these mixtures. Thus the objectives of this chapter are to: (1) review current theories on the mechanisms of positive plant interactions, and (2) hypothesize the degree to which these mechanisms may occur generally in hemlock-redcedar mixtures, and specifically in the hemlock-redcedar study stands.

4.2 Competitive Reduction

Competitive reduction requires a resource for which competition is reduced to be limiting production (Kelty 1992). When competition is reduced between two species in a mixture relative to what each species would experience in a single-species stand, it can be reduced both above- and belowground. Aboveground competitive reduction is characterized by competition for light, the resource of primary limitation. Belowground competitive reduction is characterized by competition for soil moisture and / or nutrients. These belowground resources may be limiting on a site- and season-specific basis.

4.2.1 Reduced Crown Competition

Plants compete above ground primarily for one resource: light. Only a single leaf can occupy a specific area to intercept light, and the amount of space that leaves can fill to intercept light is finite. Competition in this limited space can be minimized if species can separate themselves to unique niches in the canopy layer. This separation can occur physiologically, physically, or temporally (Table 4.1).

Physiological Separation

Competition for light has resulted in physiological adaptations among plants, conferring a gradient of light use efficiencies among species. Some plant species have lower compensation

points, the point where respiration requirements are met by photosynthesis, than others (Boardman 1977). The lower compensation points of 'shade-tolerant' species result in increased light use efficiency, allowing increased carbon fixation per unit of light (Evens *et al.* 1988). However, shade-tolerant species also have lower maximum photosynthetic rates and photosynthetic light saturation points than shade-intolerant species (Boardman 1977). Differences in compensation point, saturation point, and light use efficiency allow species of different shade tolerances to reduce their competition for light. Shade-tolerant species can exploit the space in lower canopy strata by tolerating low light conditions, resulting in less direct competition in the main canopy. The combination of a shade-intolerant overstory with a shade-tolerant understory would result in less light competition per canopy stratum than a single-species stand of either component species of equivalent density (Kelty 1992).

Spatial Separation

The physiological adaptations associated with shade tolerance are complemented with physical adaptations of the crown. Shade-tolerant species will allocate resources among the stem, leaves, and branches, and orient their leaves and branches, differently than shade-intolerant species (Kelty 1992; Man and Lieffers 1999). Shade-tolerant species allocate more resources to lateral growth than height growth, and have lower juvenile height growth rates than shade-intolerant species (Kelty 1992). Given these growth allocation differences, mixed-species stands of a shade-tolerant and -intolerant species would result in the species occupying different canopy strata. This layered structure will increase stand vertical canopy depth, and increase light use efficiency through a greater volume of canopy space.

Shade-tolerant species are able to support greater leaf areas than shade-intolerant species, because their increased efficiency at lower light levels allows more foliage to survive in deeper crown layers, increasing light capture (Assman 1970; Kelty 1992). Shade-adapted foliage is generally oriented along horizontal planes to maximize light interception, enhancing capture of

diffuse light filtered through higher canopy strata. This physical orientation augments the physiological characteristics of shade tolerant species to capture diffuse light under the canopy of a shade intolerant species. Competition for light is reduced most efficiently in a fine-grained intermixing (i.e., trees must be adjacent to trees of a different species) of shade-tolerant and -intolerant tree species (Kelty 1992).

Temporal Separation

Plant species can reduce their competition for light if they can separate the times when they use the resource. This separation can occur seasonally, through phenological separation, or over longer time scales, through differences in growth strategy and longevity.

Evergreen trees are able to photosynthesize both earlier and later in the growing season than deciduous species. Evergreen species exploit the temporal windows in which deciduous species must overcome bud dormancy and flush new foliage, and then sequester nutrients and shed their foliage. This phenological separation results in a longer effective growing season for the more shade-tolerant conifer species that underlie shade-intolerant deciduous species (Man and Lieffers 1999).

Shade intolerance is usually indicative of an early seral species' successional role. Early seral species quickly occupy and capture disturbed sites, and have rapid height growth rates in their juvenile life-stage (Oliver and Larson 1996). Late seral species usually establish themselves after a site has been occupied by species of earlier successional roles, and have the physiological and physical attributes characteristic of shade tolerance. Late seral species usually also have increased longevity relative to early seral species, assuming dominance in late seral stages of stand development (Oliver and Larson 1996; Man and Lieffers 1999).

Incidence of Reduced Crown Competition in Hemlock-Redcedar Stands

Aboveground competitive reduction in hemlock-redcedar stands may occur due to physical canopy separation. Competition for light is reduced most efficiently in a mixture of species with the highest degree of niche separation for the light resource, typically that of a shade-tolerant and -intolerant species. Hemlock and redcedar are both shade-tolerant species, although there have been arguments that hemlock is slightly more shade-tolerant than redcedar (Minore 1979, 1990). More recently, redcedar has been found to be a very shade-tolerant species, as much so as hemlock or Pacific silver fir (*Abies amabilis* (Dougl. Ex Loud.) Dougl. ex J. Forbes) (Wang *et al.* 1994). However, hemlock has a different height growth pattern than redcedar, overtopping redcedar by age 15 (Gashwiler 1970; Curran and Dunsworth 1988). Therefore, even-aged hemlock-redcedar stands in the earlier stages of stand development are likely to be mixtures in which the crowns of each species are vertically separated. This may reduce competition for light between hemlock and redcedar relative to what either species would experience in equally dense single-species stands.

Wherever vertical canopy separation occurs in the hemlock-redcedar study stands, it may be augmented by the relative performance of hemlock and redcedar with respect to climate. On intermediate sites the mean site index of redcedar has been observed to decrease by 5 m with progression in elevation from the Dry Maritime Coastal Western Hemlock (CWHdm) subzone to the Very Wet Maritime CWH (CWHvm) subzone (Green and Klinka 1994; Kayahara *et al.* 1997). Given these findings, the location of all study stands within the CWHvm subzone would give dominant hemlock a 5 m height growth advantage over redcedar, enhancing canopy stratification in even-aged, hemlock-redcedar mixtures. However, in addition to redcedar's site index decreasing with progression from the CWHdm to the CWHvm zone, hemlock's site index has also been observed to decrease by the same amount (Site Productivity Working Group 1997), resulting in no net change in site index differential between the two species. Both studies

suggest the site index of dominant hemlock, on intermediate sites in the CWHvm, is 4 m greater than that of redcedar. This supports the assertion that these species will have vertically separated canopies in the mixed-species study stands. Despite the species' similar shade tolerances, competition among hemlock and redcedar may be reduced in these mixtures. The degree to which this stratification is combined with a random spatial pattern of trees will be assessed in Chapter 6, but a random pattern is assumed to further reduce competition for light among hemlock and redcedar in these stands.

Redcedar shoots have a longer growth period than any associated conifer species (Minore 1990), suggesting a longer photosynthetically active period than its associates. This longer photosynthetically active period could give redcedar a longer growing season relative to hemlock, but the relative difference in growth periods between the two species may be small enough to make redcedar's advantage negligible. Considering that hemlock and redcedar are both very shade-tolerant species (Minore 1990; Packee 1990), suggesting similar specific leaf area capacities (Kayahara *et al.* 1997), phenological separation of these species is unlikely.

Both hemlock and redcedar are able to occupy different successional roles. Both species can act as early seral species, but their shade tolerance, longevity, and regeneration characteristics allow them to act as climax species. However, the lifespan for hemlock is 400 to 500 years (Packee 1990), whereas lifespan for redcedar is 800 to over 1000 years (Minore 1990). This difference in longevity between hemlock and redcedar suggests that temporal separation between the species' canopies occurs on a time scale of centuries. Hemlock will overtop redcedar, assuming no establishment lag, early canopy dominance, and optimal growth rates. Redcedar has the physiological mechanisms to persist beneath and within the hemlock canopy for the first 300-500 years. Dominant and co-dominant hemlock will then be replaced by redcedar, which will assume dominance and co-dominance for the next 3-5 centuries. Thus, by intermixing hemlock, which dominates light resources relatively earlier, with redcedar, which

dominates light resources relatively later, the light competition each species experiences over 800-1000 years would be less than each would experience if grown in similar density single-species stands. This type of temporal stratification is impossible to assess in the study stands, given the brief amount of time since establishment.

4.2.2 Reduced Root Competition

Soil moisture and nutrients are the belowground resources that may limit plant growth, and thus are the resources for which competition may be reduced. The extents to which these resources are limiting are site and species specific, and depend on such factors as climate, topography, soils, and the species in question. Potential mechanisms for belowground competitive reduction can be grouped similarly to those for aboveground competition: physiologically, spatially, and temporally (Table 4.1).

Physiological Separation

Species growing in mixture can reduce competition for nutrients by preferentially using different forms of those nutrients through physiological adaptations (Keltz 1992). Nitrogen, often the most often limiting nutrient in north temperate forests, is available to plants in both nitrate and ammonium forms. Certain species take up different proportions of these nitrogen forms (Waring and Schlesinger 1985). If a mixture is made up of two species that are adapted to uptake nitrogen of different forms, those species are physiologically separated. In such a physiologically separated mixture, the nitrogen competition each species experiences would be less than each would experience in a single-species stand of similar density.

Spatial Separation

Water and nutrients can also be partitioned between competing species, if those species occupy different rooting depths, and/or have different rooting structures (Man and Lieffers

1999). Species with deeper rooting habits have access to moisture and nutrients that shallow-rooted species do not have. A mixture of species with similar rooting habit will pack all roots into the same strata, resulting in intense competition. Mixing shallow- and deep-rooting species will distribute the same root mass over a greater depth, and thus into a larger volume of soil. A larger volume of soil is likely to have greater moisture and nutrient pools available for growth. Thus, root stratification not only pulls the roots of different species apart, reducing direct competition, but also may provide the mixture with more moisture and nutrients due to increased soil volume, providing these resources exist in the lower soil layer. These beneficial effects of root stratification are likely to be enhanced by a fine-grained distribution of trees of the component species (Kelty 1992).

Temporal Separation

Species that separate their individual growth into different time frames, reduce belowground and aboveground competition simultaneously. Evergreen species exploit the temporal windows in which deciduous species are not photosynthesizing. Deciduous species must overcome bud dormancy and flush new foliage in spring, and then sequester nutrients and shed their foliage in autumn. These windows of opportunity allow evergreen species to uptake soil moisture and nutrients with less competition from deciduous species than would be encountered in the middle of the growing season (Kelty 1992). Species with similar phenologies will compete directly for moisture and nutrients over the same time frame. Species with different phenologies reduce the overlap of direct competition, and spread moisture and nutrient demands over a longer portion of the growing season. This will result in less nutrient demand per unit time in a mixture of two species than either species would experience in single-species stands of the same density. The beneficial effects of phenological separation may be enhanced by canopy stratification in mixtures of shade-tolerant and -intolerant species (Kelty 1989; 1992).

The physiological differences between early and late seral species may be associated with different soil moisture and nutrient demands. Early seral species generally have high evapotranspiration and nutrient cycling rates, a relatively short lifespan, and establish themselves at the onset of stand development. Typically, late seral species have relatively lower evapotranspiration and nutrient cycling rates, and relatively longer lifespans.

Each site has a finite resource pool, capable of supporting a maximum density of a species. If that species is early seral, full utilization of the limiting resource is likely to be rapid and of short duration. Alternately, a late seral species is likely to take longer to maximize utilization of the limiting resource, and maintain the utilization for a longer time. Species of similar successional roles will experience high levels of competition due to similar growth patterns and longevities. If early and late seral species are mixed, resources will be fully utilized more rapidly and for a longer duration than could be realized in monocultures of each component species. Early and late seral species reduce competition by maximizing the demand for limiting resources at different times.

Early seral species are commonly deciduous and shade-intolerant, while late seral species are typically evergreen and shade-tolerant. The associated differences in physiology, structure, and phenology may further reduce competition in mixtures of species with different successional roles.

Incidence of Reduced Root Competition in Hemlock-Redcedar Stands

Redcedar is known to uptake high concentrations of nitrate relative to hemlock (Pharis *et al.* 1964; Krajina *et al.* 1973). Hemlock tolerates high soil concentrations of ammonium better than redcedar, does not have high biomass nitrate concentrations, and tends not to nitrify ammonium, even in conditions with sufficient ammonium and phosphorus (Turner and Franz 1985). These findings suggest that redcedar preferentially uptakes nitrate, while hemlock preferentially uptakes ammonium. This physiological separation reduces competition for

nitrogen, commonly the most limiting nutrient for growth in the Pacific Northwest (Weetman 1962; Heilman 1979; Pritchett and Fisher 1987), among hemlock and redcedar. These findings suggest that this mechanism of competitive reduction may be acting in the hemlock-redcedar study stands.

Hemlock is a shallow-rooted species, with a concentration of fine roots very near the surface (Packee 1990). Redcedar is a deeper-rooted species that has an extensive root system, with a poorly defined taproots and a dense root network of fine roots near the surface (Minore 1979, 1990). In two stands of redcedar, western white pine (*Pinus monticola* Dougl. ex D. Don), western larch (*Larix occidentalis* Nutt.), and Douglas fir in northern Idaho, redcedar contributed only 17% of basal area, but accounted for 82% of total root length contribution (Leaphart and Grismere 1974). However, differences in rooting habit between hemlock and redcedar may be site specific, as no significant differences between the species' root area, length or depth could be found when grown on substrates with similar physical characteristics (Eis 1973, 1987).

Since redcedar and hemlock are shade-tolerant species, and both retain considerable amounts of foliage through winter, phenological separation of below ground competition is unlikely. Differences in the lifespan of the species indicate that competition may be reduced due to successional separation. Although this mechanism of competitive reduction may occur in hemlock-redcedar mixtures of the appropriate age, the age of the study stands dictates that this mechanism does not contribute to positive plant interactions in these stands.

4.3 Facilitation

Facilitation in mixed-species stands implies that: (1) one species requires the other to establish or grow, or (2) a synergy exists between the component species. In either case, facilitation in a mixture results in greater productivity than could be realized by each component species in monoculture. Callaway (1995) provides a comprehensive review on positive

interactions among plants, and his categorization of facilitative mechanisms has been adapted to provide the framework for the following discussion.

4.3.1 Resource Modification

Through its establishment and growth, a plant interacts constantly with the environment. Part of this interaction involves some modification of the environment by the plant. Resource modification by a benefactor species may: (1) facilitate growth of a beneficiary species, where the environment may not have been initially suitable for the beneficiary, or (2) may improve the growth of a beneficiary beyond that which it could achieve in monoculture (Callaway 1995).

Light and Temperature

The presence of an overstory canopy will impact the amount and quality of light available to plants in lower strata. Plants perform better as the amount of available light increases. However, shade can have many beneficial effects on plants. Shade reduces water loss, photoinhibition during stomatal closure, and temperature extremes, even though it also reduces the energy available for photosynthesis (Callaway 1995). Those plants adapted to the low energy environment in the shade, especially those in arid climates, may be facilitated by the ancillary benefits associated with shade.

Trees on high-elevation sites modify the microclimate around them, often to the benefit of understory species in close proximity. Larger stems absorb short- and longwave electromagnetic radiation, and then re-radiate this energy in their immediate vicinity (Oke 1987). This phenomenon creates snow craters, in which understory species are facilitated due to a longer effective growing season (Brooke *et al.* 1970).

Soil Moisture

Plants species commonly compete for soil moisture, however there are ways in which one species can improve moisture conditions for another. Soil improvement through organic matter contributions and hydraulic lift, are mechanisms in which benefactor plants may improve soil moisture conditions for beneficiaries. Those benefactor plants able to establish on mineral soil, and their organic inputs to that soil, would facilitate species favoring organic seedbeds. Organic matter accumulations are known to improve soil structure, and increase porosity, improving the soil's moisture holding capacity over time (Brady and Weil 1996).

Plants with a deep rooting habit create water potential at depth, hydraulically lifting tapped water through their root systems into shallower soil layers, improving water relations for shallow-rooted species (Caldwell and Richards 1989; Dawson 1993).

Trees on high-elevation sites tend to grow in irregularly grouped cohorts, and so modify soil moisture conditions by creating 'tree islands' or 'ribbon forests'. The modified microclimate around tree stems creates snow craters (Brooke *et al.* 1970). Drifting of snow in the lee of these trees then creates store of soil moisture enhancing the growth of the species established in the craters (Billings 1969). This sequence allows the gradual establishment of tree species in a ribbon of ameliorated conditions in the lee of the benefactor tree.

Soil Nutrients

Benefactor species may improve soil nutrient availability for other plants through soil organic matter contributions, canopy drip, and symbiotic organisms. Some of the nutrients that plants extract from the soil are incorporated into leaf tissues for maintenance and growth. Varying amounts of these leaf-stored nutrients are sequestered in the plant at senescence, but the remaining nutrients are returned to the forest floor in litter. Soil nutrient capital can be increased, given appropriate amounts and composition of litter. Sub-canopy nutrient enrichment, often with subsequent species changes and increased productivity, has been widely reported, especially in

savanna habitats (Callaway 1995). Hardwood-softwood mixtures have exhibited increased nutrient cycling rates, relative to softwood stands, due to the relatively higher nutrient content and lower levels of compounds which inhibit decomposition in hardwood litter (Gordon 1983; Kelty and Cameron 1995).

Leaves can have concentrations of minerals and nutrients on their surfaces, from the leaves themselves or from airborne particles intercepted by the leaves. Precipitation washes these minerals and nutrients into solution, and returns them to the soil as canopy drip and stem flow. Nutrient-rich canopy drip is more common among deciduous hardwoods. For example, bigleaf maple (*Acer macrophyllum* Pursh) leaves contain high concentrations of potassium, calcium, and other nutrients (Tarrant *et al.* 1951), and the species improves the nutrient status of the sites on which it grows (Minore and Zasada 1990).

Plant symbioses with nitrogen-fixing organisms often result in soil enrichment, as these species shed leaves with high nitrogen concentrations. These symbioses act as natural fertilizers, extracting and dispersing atmospheric N₂ onto the soil in readily mineralizable forms. Soil nitrogen content has been observed to increase tenfold with the introduction of a nitrogen fixer to a bare soil (Lawrence *et al.* 1977), and facilitative effects of nitrogen fixers on secondary species have been observed (Walker and Chapin 1986).

It is common for particular plant species to be associated with particular mycorrhizal and bacterial communities that enhance nutrient uptake. Beneficiary species can indirectly profit from benefactor symbioses by reaping the benefits of the benefactor's nutrient-rich litter. Beneficiary species can directly profit from the mycorrhizal and bacterial symbioses of a benefactor, where the beneficiary is able to exploit direct symbioses with the fungi and/or bacteria introduced by the benefactor. Such linkages have been observed to allow bi-directional, inter-species transfers of water, nutrients, and photosynthate among trees (Simard *et al.* 1997). Studies have also been conducted which suggest the possibility of inter- and intra-specific root

grafting, resulting in the inter-tree passage of water, nutrients and photosynthate (Bormann and Graham 1959; Bormann 1966).

When hydraulic lift occurs in a mixture, 'nutrient pumping' often occurs as a corollary mechanism, whereby deeply-rooted species uptake nutrients and make them available to shallow-rooted species via litterfall and canopy drip (Richards and Caldwell 1987).

Incidence of Resource Modification in Hemlock-Redcedar Stands

Hemlock and redcedar are similar in shade tolerance, and neither species thrives in conditions of high insolation and temperature (Minore 1990; Packee 1990). Neither species is better suited than the other to act as a shade-providing benefactor where shade protection is required. Therefore, light modification is an unlikely facilitator between these species.

Hemlock and redcedar are both able to regenerate on mineral and organic seedbeds (Morris 1970; Parker 1986; Minore 1990; Packee 1990; Feller and Klinka 1998). Since both species are able to regenerate on mineral soil, and under their own canopy, neither hemlock nor redcedar regeneration is facilitated by organic contributions of the other species.

Studies have suggested that redcedar has a deeper rooting habit than hemlock (Minore 1979). However, these differences may be influenced more by differences in rooting substrate than by genetic expression (Eis 1973, 1987), eliminating hydraulic lift as a facilitative mechanism among hemlock and redcedar.

Since hemlock and redcedar presence decreases with increasing elevation, and neither species is commonly found in the subalpine parkland (Minore 1990; Packee 1990), the mechanisms of facilitation associated with areas of heavy, persistent snowpack would not occur in hemlock-redcedar mixtures.

The chemical composition of hemlock litterfall is distinctly different from that of redcedar, resulting in different forest floor and mineral soil nutrient properties beneath each species (Alban 1967; 1969). Forest floors influenced by redcedar litter have higher pH, base

saturation, and exchangeable calcium, than forest floors influenced by hemlock litter (Daubenmire 1953; Ovington and Madgewick 1957; Alban 1967, 1969; Turner and Franz 1985; Weetman *et al.* 1988, Collins *et al.* in review). Hemlock litterfall acidifies underlying forest floor and mineral soil, promoting the development of fungal populations over bacterial populations (Turner and Franz 1985). The increases in pH, soil microbial communities, and exchangeable base cations in forest floors influenced by redcedar litter, suggest that redcedar may facilitate hemlock by creating improved nutrient conditions. This assumption is uncertain, given that hemlock grows best where nutrients are supplied in small quantities, and tolerates any nutrient deficiency better than other conifers (Klinka *et al.* 2000). Additionally, redcedar does lower forest floor N concentrations due to a high nitrogen resorption rate and nitrogen use efficiency (Keenan *et al.* 1995), and its seedlings have been observed to survive and grow better than most competitors on nitrogen poor sites, promoting further decreases in soil nitrogen content. These findings suggest that redcedar's influence on forest floor nutrient properties is linked to a competitive advantage for its progeny (Tilman 1988; Weetman *et al.* 1990; Messier 1993; Keenan *et al.* 1995). However, hemlock also establishes and grows well on nitrogen poor sites, making hemlock uniquely suited, relative to other conifers, to grow on sites where redcedar has depleted the nitrogen capital. Given the uncertainty as to whether or not hemlock growth may be facilitated by redcedar increasing forest floor pH, microbial populations, and base cation concentrations, this type of facilitation cannot be proven.

Neither hemlock nor redcedar share symbioses with nitrogen-fixing organisms, however both species do benefit from mycorrhizae. Hemlock is associated with ectomycorrhiza, while redcedar is associated with endomycorrhiza (Rygiewicz *et al.* 1984a and b). Since hemlock and redcedar profit from different mycorrhizal associations, interspecies linkages and resource exchanges through mycorrhizae are unlikely.

4.3.2 Substrate Modification

Plants and soils continually affect each other, within a feedback mechanism governed by factors like climate, topography, and disturbance regime. The physical presence of a plant, and its influence on the soil, may be able to modify the substrate enough to facilitate the growth of beneficiary plant species.

Aeration/Soil Oxygenation

Contribution of organic materials to the soil, from litterfall, ephemeral roots, and root exudates, enhances the suitability of the soil for plant growth. Organic matter contributions decrease soil bulk density, improve soil structure, and increase soil porosity and aeration, resulting in the colonization and growth of new species (Callaway *et al.* 1991; Joffre and Rambal 1993). Evapotranspiration may also reduce soil moisture levels and increase soil oxygenation near the ground surface, allowing the colonization and growth of beneficiary species (Berendse and Aerts 1984).

Substrate Supply and Stabilization

Plants can serve as substrate traps and stabilizers in exposed environments, decreasing wind (and water) velocities and thus promoting the deposition of substrate in the lee of the plant (Oke 1987). The shelter and additional substrate deposited may then allow the colonization and growth of plants that could not have done so without the contributions of the benefactor species (Vasek and Lund 1980).

Epiphytic plants utilize the stems of live trees as a substrate, and exploit light unavailable to plants in the understory. Many epiphytes appear to be obligatorily dependent on their benefactors for access to light (Callaway 1995).

Certain species continue as benefactors after death. Decaying logs provide a favorable substrate for other tree species, allowing seedlings to grow on an elevated platform free from competition for light resources with shrubs and herbs (Harmon and Franklin 1989).

Incidence of Substrate Modification in Hemlock-Redcedar Stands

Since both hemlock and redcedar regenerate on mineral seedbeds (Minore 1990; Packee 1990), neither species requires the other's inputs of organic matter to modify soil aeration for establishment and growth.

In established stands, hemlock and redcedar regenerate on decaying wood (Morris 1970; Parker 1986). Redcedar veglings, from layering, rooting of fallen branches, and branch development on fallen trees, may be more abundant than seedlings in mature stands (Parker 1979). Both species benefit by regenerating on decaying wood, but neither species specifically requires decaying wood of the other for regeneration.

4.3.3 Mortality Agent Attenuation

A benefactor species can reduce the likelihood of mortality for a beneficiary by: (1) acting as a buffer between the beneficiary and its direct, vigorous competitors, (2) shielding the beneficiary from herbivory, and (3) ameliorating environmental extremes.

Competitor Control

Competition among plant species can vary in intensity, depending on the relative competitive strengths and strategies of the species involved. A direct clash of similar competitive strategies will result in the stronger competitor succeeding at the expense of the weaker. A pairing of dissimilar competitive strategies may allow for the growth of both species on a site. These species groupings for which competition is reduced may have an additional, facilitative effect, where the presence of one species inhibits the invasion of a direct, detrimental

competitor. In boreal forests, overstory hardwood species are believed to inhibit the growth of highly competitive understory species, allowing the establishment of more shade-tolerant conifers (Man and Lieffers 1999).

Herbivory Reduction

One plant can directly or indirectly reduce herbivory of another. Benefactor species can provide herbivory protection both chemically and physically (Vandermeer 1989). Palatable species are able to gain chemical protection against herbivory by intermixing, or surrounding themselves, with plants that produce unpalatable secondary compounds (McNaughton 1978; Holmes and Jepson-Innes 1989). The foliage and odours of a benefactor can camouflage beneficiary species, masking the sight and scent of the palatable species to herbivores. Increased complexity and species diversity have been found to decrease herbivore search efficiency, resulting in decreased herbivory. Such visually complex mixtures are known as 'associational plant refuges' (Pfister and Hay 1988). This concept has further been observed with respect to the dilution of host odors by the presence of other, non-host species (May and Ahmad 1983; MacLean 1996). Thorns, spines and prickles are other physical adaptations by which armoured benefactor species can shield palatable plants from attack (Callaway 1995).

Amelioration of Environmental Extremes

Temperature increases associated with increased light levels can be detrimental to plant growth, and the negative effects are most pronounced in hot, arid environments. Seedlings are particularly susceptible to the temperature regime of the ground surface. The shade provided by a benefactor species can reduce temperature and exposure levels to those tolerated by the beneficiary (Callaway 1995). Blue oak (*Quercus douglasii* Hook. & Arn.) survivorship of 35% has been observed in the shade, compared to 0% in the open, after one year (Callaway 1992). In

certain environments, shading can also result in decreased soil salinity, due to less evaporative soil moisture losses (Callaway 1994).

The presence of a plant species can also improve the microclimate in cold environments. Plants decrease wind velocities, creating an insulating, laminar boundary layer of air above the plant (Oke 1987). Plants also increase the amounts of short and long wave energy absorbed and emitted (Oke 1987), increasing temperatures and reducing snowpack duration in the immediate vicinity of the plant. Therefore, benefactor species tolerant of extreme cold and desiccation can modify the microenvironment sufficiently to allow the establishment and growth of beneficiary species.

A deeper or more extensively rooted plant can serve to trap and stabilize the substrate for a less stable associate. Substrate stabilization can reduce mortality where wind velocities are sufficient to cause windthrow (Kerr *et al.* 1992). Root grafts among species of different rooting habit have been observed to be more common in wetland than upland areas, suggesting stabilization benefits in wetland soils (Keeley 1988). Gusting winds can cause abrasion damage of tree crowns. Mixtures with a stratified canopy, like those of shade-tolerant and shade-intolerant species, serve to separate tree crowns and may be able to reduce crown abrasion (Man and Lieffers 1999).

Incidence of Mortality Agent Attenuation in Hemlock-Redcedar Stands

It is unlikely that hemlock and redcedar in mixture displace more vigorous competitors for each other, facilitating growth. With similar shade tolerances (Minore 1990; Packee 1990; Klinka *et al.* 2000), and initial growth rates less than those of most shrub-hazard species (Curran and Dunsworth 1988), neither hemlock nor redcedar would be better suited than the other at competing with understory vegetation. Thus neither species would preferentially adopt the role of benefactor, displacing competing species and providing a favourable environment for regeneration.

Insect pests commonly attack hemlock and most of these pests are defoliators, such as the western blackheaded budworm (*Acleris gloverana*), western hemlock looper (*Lambdina fiscellaria lugubrosa*), and the hemlock sawfly (*Neodiprion tsugae*) (Packee 1990). Hemlock is browsed to a lesser extent by elk, deer and hares. Alternately, redcedar suffers little damage from insects (Minore 1990), but seedlings and saplings are so often severely browsed by elk, deer and rodents that browse damage may be the most important stand establishment problem (Curran and Dunsworth 1988). Since the pests that attack hemlock and redcedar are different, herbivory reduction may be possible when the species are intermixed. The benefits of mutual camouflage and decreased herbivore/insect search efficiencies are those most likely to occur in hemlock-redcedar mixtures, as neither species produces armor or secondary compounds to combat herbivory. Unfortunately, no evidence of this exists in the study stands, as stands were selected to be free from disease or obvious herbivory damage.

High temperatures and drought can damage both hemlock and redcedar seedlings, and redcedar seedlings are more susceptible to high and low temperatures than most of its common associates (Minore 1990). In areas of high insolation, seedlings of both species would benefit from shade, and are protection-requiring in this lifestage. However, neither hemlock nor redcedar is better adapted than the other to grow in environments with high temperature extremes (Minore 1990; Packee 1990). Thus neither species is suited to act as a regular benefactor to the other in these environments.

Absolute minimum temperatures tolerated by hemlock are -39°C for the coast and -48°C for the interior (Packee 1990), while those tolerated by redcedar are -30°C and -47°C respectively (Krajina 1969). Both species tolerate similar cold extremes, leaving no clear role separation between benefactor and beneficiary, making this type of facilitation in hemlock – redcedar mixtures unlikely.

Hemlock and redcedar are not known to form root grafts with each other, and evidence is weak that redcedar has a deeper rooting habit. Hemlock is subject to severe windthrow on many exposed sites, while redcedar is relatively windfirm except on wet sites (Minore 1990; Packee 1990; Klinka *et al.* 2000). This suggests that on sites with a high windthrow hazard, redcedar may protect hemlock from windthrow. Therefore a hemlock-redcedar mixture may facilitate hemlock growth on sites subject to wind disturbance. No support for this mechanism of facilitation can be established in the study stands, since the stands were selected to be free from damage such as that caused by windthrow.

Redcedar is commonly overtopped by hemlock and then grows slowly in the understory (Minore 1990). This tends to stratify hemlock and redcedar into separate canopy positions, and increases the distance between tree crowns in each canopy layer. Such an arrangement could decrease canopy abrasion in windy conditions, facilitating both species in hemlock-redcedar stands. However, no evidence of this was found in the hemlock-redcedar study stands.

4.3.4 Additional Effects

Pollination and Propagule Concentration

Certain plants are relatively more attractive to pollinators than others, due to adaptations in flowering, coloration, and pheromone production. Greater pollination rates have been observed for less attractive species, when intermixed with attractive, co-flowering species (Dafni 1984). These benefactor plants are known as 'magnet species' (Lavery 1992).

When plants concentrate the propagules of others, the result may simply be altered spatial distribution patterns. Propagule concentration can also have a facilitative effect, where the propagules are prevented from being lost to the system or destroyed (Callaway 1995). This phenomenon may act in concert with other facilitating mechanisms. Seeds concentrated at the

base of a benefactor species may receive the additional benefits of resource and substrate modification, and decreased impacts of mortality agents.

Incidence of Additional Facilitating Effects in Hemlock-Redcedar Stands

Hemlock and redcedar rely upon wind for pollination, and pollination is not subject to preferential visitation by insect vectors. Both species are prolific seed producers, with hemlock producing 19.8 million seeds per hectare from a 100 year-old coastal stand in a good year (Packee 1990), and redcedar producing 2.47 million seeds per hectare in coastal stands (Minore 1990). It is unlikely that either species is facilitated by having their seeds concentrated by the other, given the massive quantities of seeds produced.

4.4 The Dynamics and Implications of Positive Interactions among Plants

Identifying competitive reduction as a driver for enhanced productivity in mixtures implies that competition occurs simultaneously with positive plant interactions. Therefore, the overall effect of one species upon another is likely the cumulative effect of multiple, complex interactions (Callaway 1995), involving the balance of positive plant interactions and competitive interactions. Ellison and Houston (1958) demonstrated this balance in a study of understory herbs. The growth of open-grown herbs was compared that in a stand of aspen, and that in a stand of aspen in which aspen root competition was reduced by trenching. The herbs in the untrenched aspen stands grew the least, the open-grown herbs had intermediate growth, and the herbs in the trenched aspen stands grew the most.

The two most prominent factors affecting the balance between facilitation and competition appear to be the life stage of the interacting species, and the severity of environmental extremes the species are subjected to (Callaway 1995). Facilitation commonly occurs in mixtures where the species are in different life stages, such as seedling establishment in the shade of a mature tree. Those benefactor species that enable the colonization and growth of a

beneficiary are often later overtopped and outlived by the species being nursed (Archer and Rykiel 1994). The balance shifts from facilitation to competition, with the shift in each species' life stage dynamics, often resulting in succession of the beneficiary.

As abiotic stress and consumer pressure increase, facilitation may become more important in plant communities, while competition gains importance as physical stress and consumer pressure decrease (Bertness and Callaway 1994). Callaway and Bertness (1994) examined relationships between whitebark pine (*Pinus albicaulis* Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) in sheltered, low-stress habitats, and in exposed, high-stress habitats. In low-stress habitats, fir was randomly distributed with respect to pine, and fir growth improved as pine died. In high-stress habitats, fir was clumped around the pine, and fir growth decreased as the pine died. Facilitation appeared to be more important in the high-stress areas, while competition seemed to dominate in the low-stress areas. Similar relationships were found among marsh species, where increasing salinity was the stressor promoting facilitation (Bertness and Yeh 1994).

Positive interactions may partly determine community spatial patterns, permit coexistence, enhance species and structural diversity, enhance productivity, and drive community dynamics (Callaway 1995). Benefactor plants may also provide regeneration niches for beneficiary species (Grubb 1977), allowing the beneficiary to incrementally creep into previously uncolonized areas. Therefore, the boundaries between plant communities may shift across the landscape, suggesting that facilitative processes drive dynamic change in the absence of large-scale disturbance (Callaway 1995). The early stages of primary and post-glacial succession are environmentally extreme, causing stressful conditions for plants. Facilitative mechanisms may then be more important during these successional stages than during secondary succession (Connell and Slatyer 1977; Chapin *et al.* 1994).

4.5 Methods of comparing productivity of single- and mixed-species stands

Productivity studies of mixed-species stands have been based upon either additive or substitutive experimental designs (Harper 1977). Additive experiments compare multiple plots that contain a single species at a fixed density, and incrementally increasing densities of a second species. Substitutive, or replacement series, experiments keep total density the same for all plots, but alter the proportion of constituent species. Substitutive designs are more common than the additive experiments, as they allow yield comparisons among each species in mixture with its yield in monoculture (Harper 1977; Vandermeer 1989). These comparisons detect if two species are relatively more or less productive in mixture than in single-species stands, supporting arguments for positive or negative interactions among those species. If both species use resources in mixture identically to that in monoculture, the RY of each should be 0.5 and the RYT should be 1.0. Where competition is reduced or species are facilitated, RYT values greater than 1.0 are expected. Where the species compete, RYT values of less than 1.0 are expected.

However, it is necessary to compare absolute, and not relative, yield to identify the highest yielding stand type in these experiments (Kelty 1992). If one of the component species is much more productive than the other in monoculture, the RYT of the mixture can be greater than 1.0, but not exceed the absolute yield of the more productive species in monoculture. The less productive species effectively dilutes the productivity potential of the more productive species (Figure 4.1). This characteristic of RY comparisons means that both relative yields and absolute yields are necessary for meaningful productivity comparisons (Kelty 1992).

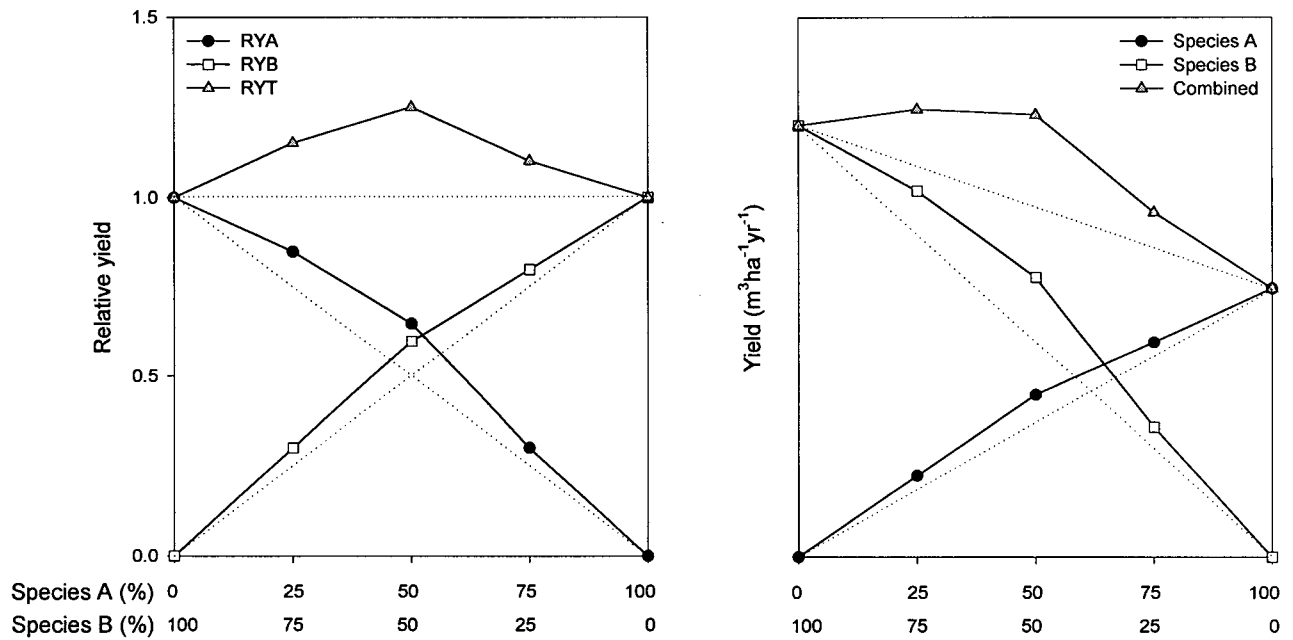


Figure 4.1 (From Kelty 1992) Results from hypothetical replacement series experiment, expressed as relative and absolute yield. Dashed lines represent expected yield if intra- and inter-specific interactions were equivalent. Solid lines represent experimental yields.

Comparisons based on relative land output (RLO) also compare yields based on replacement series experiments, but involve equal populations and equal areas allocated to mixture and monocultures (Jolliffe 1997) (Figure 4.1).

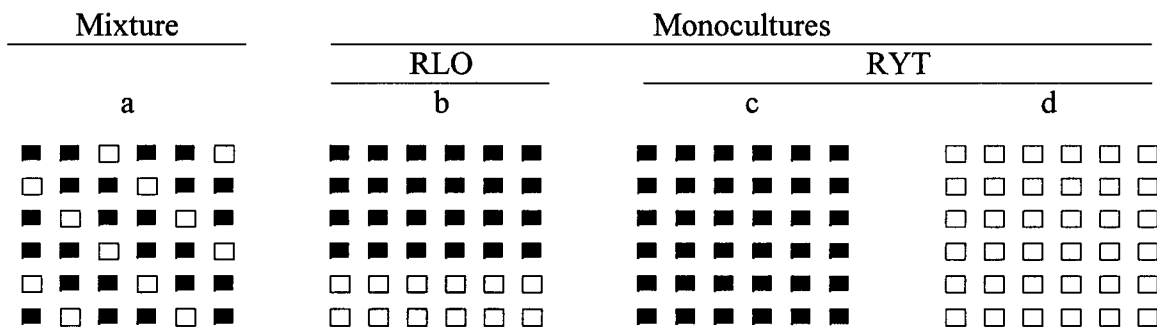


Figure 4.2 (From Jolliffe 1997) Example plots in which the same area is planted in a (a) 2:1 mixture of two species, (b) 2:1 ratio of pure sub-plots, (c) pure stand of species 1, and (d) pure stand of species 2.

Higher yields may not necessarily be realized in mixed-species stands where competitive reduction and facilitation are expected to occur. Positive interactions can be muted by inappropriate species proportions, densities, spatial arrangement of individual trees, or site conditions where resource limitations are not reduced by the species chosen (Kelty 1992; Man and Lieffers 1999). A review of yield studies suggests that it is uncommon to find mixtures significantly more productive than the highest yielding constituent species in monoculture (Trenbath 1974). However, further analysis of these studies revealed that species in the mixtures were not necessarily chosen for their niche separation (Harper 1977). A recent review of yield studies using RLO comparisons, found the average productivity of mixtures to be 12% higher than that of monocultures based on 202 direct observations, and 13% higher than that of monocultures based on 604 yield – density relationships (Jolliffe 1997).

Comparisons in replacement series experiments require a fixed planting density, site quality, and time frame (Kelty 1992), requiring controlled plantations. Such plantation experiments are limited by the number of species combinations possible, and the time span required (the lifespan of the species involved). Therefore, it is useful to augment plantation experiments with empirical studies involving existing single-and mixed-species stands. However, natural variation in sites (climate and soils) and stands makes the empirical studies challenging, but not impossible. There are opportunities among some species to locate an adequate number of acceptable study stands on ecologically-equivalent sites, given the biogeoclimatic ecosystem classification in BC, and the variety of existing, naturally regenerated, unmanaged, second growth stands on a variety of sites. This study is an example of such an opportunity.

4.6 Summary and Conclusions

Positive plant interactions are those where competition between species is reduced, and/or the presence of one species facilitates the growth of another. Competition between species can be reduced both above- and below-ground, where the species exploit relative differences in physiology, physical attributes, phenology, or successional roles. A plant species can facilitate the growth of another by creating favourable substrate and nutrient conditions, decreasing exposure to mortality agents, and increasing visitations by pollinators.

Theory on the mechanisms of competitive reduction and facilitation suggest that hemlock and redcedar in mixture may experience positive plant interactions through: (1) vertical canopy separation and a random spatial pattern of trees, (2) longevity differences, which spread and separate resource demands in time, (3) preferential uptake of different forms of nitrogen, (4) reducing herbivore search efficiencies, and (5) increased windfirmness. Based on stand selection criteria from the hemlock-redcedar study stands, evidence of longevity differences, herbivory reduction, and increased windfirmness is unexpected in the study stands. However, both species in the study stands may experience positive interactions through: (1) vertical canopy separation and a random spatial pattern of trees, and (2) preferential uptake of different nitrogen forms.

5. THE PRODUCTIVITY OF SINGLE- AND MIXED-SPECIES STANDS OF HEMLOCK AND REDCEDAR

Abstract

I compared the productivity of western hemlock and western redcedar growing in even-aged, unmanaged, second-growth, single- and mixed-species stands on intermediate (fresh and nutrient-medium) sites, within the perhumid mesothermal climate of southern coastal British Columbia. The relative yield of hemlock and redcedar was lower in mixture, as compared to single-species stands, due to the effects of competition with each other and non-study species. Mean annual increment and wood volume production increased with increasing presence of hemlock. Basal area increased with increasing presence of redcedar, and the redcedar stand type was also the densest. Redcedar trees in the redcedar stand type were similar in height, diameter, and mean annual increment, relative to those in the hemlock-redcedar stand type. Hemlock trees in the hemlock stand type were taller, had larger diameters, and had higher mean annual increments, than those in the hemlock-redcedar stand type. These differences in hemlock and redcedar growth in each stand type are thought to be responsible for the differences in mean productivity detected among stand types.

5.1 Introduction

Theory on positive plant interactions suggests that a mixture of two species can be more productive than either species in monoculture, if those two species have high ecological combining ability (Harper 1977; Kelty 1992). Hemlock and redcedar may have high ecological combining ability, due, in part, to vertical canopy separation, spatial randomness in their distribution patterns, and uptake of different nitrogen forms. The first step in assessing whether

or not hemlock and redcedar interact positively in mixture is to compare productivity between mixed- and single-species stands of these species.

The objective of this study was to determine whether there are differences in productivity between single- and mixed-species stands of hemlock and redcedar, with the mixed-species stands containing approximately an equal proportion of each species, on a basal area basis. Productivity was measured by mean annual increment. Similar comparisons were also made with stand volume, and basal area. Specifically, this study addressed two questions: (1) Is there a difference in the relative yield of hemlock and redcedar in mixture, or in mean annual increment between mixed- and single-species stands? (2) What are the possible causal factors for any differences observed?

5.2 Results

Uncorrected mean annual increment and quadratic mean diameter increased with increasing presence of hemlock, while the opposite trend was found for mean stems per hectare (Table 5.1), suggesting greater annual volume per tree in the hemlock stands. The highest mean basal area was also found in hemlock stands, although this may be misleading considering the influence of stand H7, which appears substantially higher in basal area than the other hemlock stands. Without the contribution of H7, the mean basal area of the hemlock stands was intermediary ($\bar{x} = 80.0 \text{ m}^2 \text{ ha}^{-1}$, $s_{\bar{x}} = 5.5 \text{ m}^2 \text{ ha}^{-1}$) between the hemlock-redcedar and redcedar stands. Stand H7 had a higher mean annual increment than the other hemlock stands, likely due to its relatively higher age, site index, and density values (Table 5.1), but these values were not found to be outliers.

Mean dominant tree height, site index, volume, and mean annual increment decreased with increasing presence of redcedar (Table 5.1). However, increasing presence of redcedar was also associated with higher mean basal area (excluding the influence of H7) and stems per

hectare. These findings suggest that redcedar stands have relatively higher numbers of shorter, more tapered stems, relative to the other stand types.

Table 5.1 Selected characteristics of study stands, stratified according to stand type; where: \bar{x} is the stand type mean, $s_{\bar{x}}$ is the standard error of the stand type mean, and mixed-species stand values separated by a slash represent those for each of redcedar / hemlock.

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)	Mean annual increment (m ³ ha ⁻¹ yr ⁻¹)
C1	26.4	58	23.6	1100	29.7	19.6	76.0	699.9	12.1
C2	27.7	55	26.3	1478	27.4	23.1	87.0	796.3	14.5
C3	27.5	55	26.3	767	39.6	21.7	94.7	762.6	13.9
C4	30.7	57	28.5	967	33.1	20.5	83.2	786.5	13.8
\bar{x}	28.1	56	26.2	1078	32.5	21.2	85.2	761.3	13.6
$s_{\bar{x}}$	(1.8)	(2)	(2.0)	(300)	(5.4)	(1.5)	(7.8)	(43.3)	(1.0)
M1	30.3 / 34.8	60	26.6 / 31.1	978	32.2	19.9	79.6	850.7	14.2
M2	26.9 / 32.7	51	24.6 / 28.9	944	35.0	21.9	90.8	935.0	15.5
M3	26.1 / 33.5	55	24.4 / 31.0	1356	26.5	20.1	74.5	830.1	15.1
M4	30.1 / 31.7	50	30.0 / 32.0	822	34.3	18.5	76.1	730.1	14.6
M5	28.3 / 33.3	51	27.6 / 32.6	989	29.7	17.6	68.4	680.8	13.4
M6	30.0 / 31.9	58	27.2 / 29.0	1000	32.7	20.8	84.0	935.3	16.1
M7	28.7 / 33.3	58	26.3 / 29.9	944	30.8	17.9	70.5	713.6	12.3
\bar{x}	28.6 / 33.0	56	26.7 / 30.6	1005	31.6	19.5	77.7	810.8	14.4
$s_{\bar{x}}$	(1.6 / 1.1)	(4)	(1.9 / 1.4)	(166)	(2.9)	(1.6)	(7.8)	(104.7)	(1.3)
H1	34.5	65	29.5	1000	32.0	20.1	80.6	999.8	15.4
H2	31.1	57	28.4	989	33.2	21.0	85.4	1002.6	17.6
H3	35.7	61	31.7	767	37.4	19.7	84.0	1061.0	17.4
H4	41.2	65	35.0	744	35.3	17.5	72.7	1044.0	16.1
H5	37.8	66	31.9	1033	30.1	18.9	73.8	1037.4	15.7
H6	38.7	61	34.5	822	36.0	20.0	83.8	1105.4	18.1
H7	47.4	70	38.8	500	63.5	30.1	158.3	1619.0	23.1
\bar{x}	38.1	64	33.0	837	38.2	21.1	91.2	1121.2	17.6
$s_{\bar{x}}$	(5.2)	(4)	(3.9)	(190)	(11.4)	(4.1)	(30.0)	(221.1)	(2.6)

5.2.1 Productivity Comparisons – Relative Yield

The total relative yield of the hemlock-redcedar stands, when the effects of non-study species have been removed, was greater than 1.0 (Equations [3.1-3.2]) (Table 5.2). This suggests that the mixtures are more productive than single-species stands of either species. Hemlock and redcedar both had RY values greater than 0.5, implying that they benefit from each other's presence (Table 5.2).

Table 5.2 Relative yield (RY) and total relative yield (RYT) values comparing volume of hemlock and redcedar stands with stands of hemlock-redcedar mixtures, with and without the volume contributions of non-study species.

Contribution of non-study species	RY_{Redcedar}	RY_{Hemlock}	RYT
No	0.63	0.61	1.24
Yes	0.40	0.50	0.90

However, yields of hemlock and redcedar in mixture were relatively lower than those in monoculture when the volume contributions of non-study species were accounted for. Although hemlock still achieves the same yield in mixture with redcedar relative to what it would in a single-species stand, redcedar achieves lower yield in mixture with hemlock relative to what it would in a single-species stand. Both species appear to suffer from competitive interactions with the non-study species, but the yield of redcedar is more severely impacted. This impact on redcedar yield decreases total relative yield in hemlock-redcedar mixtures below 1.0, indicating that the mixtures are experiencing competitive inter-species interactions. Although plantation studies have never had to account for the impacts of non-study species, these impacts in existing, unmanaged mixtures cannot be ignored.

Non-study species were present in all stands, although their presence did vary slightly among stand types. Non-study species contributed most to the basal area of hemlock stands, and least to the redcedar stands, while the mixtures had intermediate contributions (Table 5.3).

Table 5.3 Mean basal areas, standard errors (in parentheses), and percent contribution of hemlock, redcedar, and non-study species to total stand basal area, stratified according to stand type.

Stand type	Hemlock		Redcedar		Non-study species		Total	
	Basal area (m ² ha ⁻¹)	(%)	Basal area (m ² ha ⁻¹)	(%)	Basal area (m ² ha ⁻¹)	(%)	Basal area (m ² ha ⁻¹)	(%)
Hemlock n = 7	78.5 (32.4)	85.1	5.8 (4.8)	7.2	6.9 (4.6)	7.7	91.2 (30.0)	100.0
Hemlock- redcedar n = 7	36.9 (4.2)	47.8	36.6 (7.3)	46.9	4.2 (3.2)	5.3	77.8 (7.7)	100.0
Redcedar n = 4	21.8 (7.2)	25.2	60.4 (4.7)	71.0	3.1 (3.4)	3.8	85.1 (7.8)	100.0

5.2.2 Productivity Comparisons – Absolute Yield

Analysis of variance revealed that mean annual increment did not significantly differ among the locations (Table 5.4). This model indicates that non-significant differences among replicates exist. These differences were corrected for in analyses of covariance among stand types.

Table 5.4 Analysis of variance summary for mean annual increment ($\text{m}^3\text{ha}^{-1}\text{yr}^{-1}$), where: hemlock, hemlock-redcedar, and redcedar are stand types; Capilano, Malcolm Knapp, and Mission are locations.

Source	Sum of squares	Degrees of freedom	Mean square	F value	$P > F$
Stand type	54.7	2	27.3	9.037	0.007
Location	5.7	2	2.8	0.939	0.426
Stand type by location interaction	22.2	4	5.5	1.833	0.207
Error	27.2	9	3.0		
Total	109.8	17			

Increasing hemlock presence was associated with increasing mean annual increment (Table 5.5) (equation 3.7). Increasing amounts of variation in mean annual increment were explained as the complexity of the density covariate increased, allowing more sensitive testing for significant differences among the stand types. When density was expressed in the ANCOVA model as stems per hectare, a non-significant, increasing trend of productivity with hemlock presence was observed. Quadratic mean diameter explained more variation than stems per hectare, allowing the hemlock stand type to be found significantly more productive than the redcedar stand type. 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 hemlock.

Table 5.5 Least squares means and standard errors (in parentheses) of mean annual increment (MAI), volume, and basal area (BA) of 18 study stands, stratified according to density covariate and stand type. Values in the same row with the same superscript are not significantly different ($\alpha = 0.05$).

Productivity measure	Density covariate	Stand productivity according to stand type		
		Hemlock n = 7	Hemlock- redcedar n = 7	Redcedar n = 4
Stand MAI ($\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$)	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 ($\text{m}^3 \text{ha}^{-1}$)	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)
Stand BA ($\text{m}^2 \text{ha}^{-1}$)	Stems per hectare	70.4 ^a (8.2)	87.5 ^a (6.7)	97.8 ^a (8.4)
	Quadratic mean diameter	78.7 ^a (4.5)	85.9 ^a (3.5)	90.6 ^a (4.5)
	Relative density	85.0 ^a (3.2)	85.1 ^a (2.3)	83.3 ^a (3.2)

Wood volume production also increased with increasing presence of hemlock (Table 5.5). The analysis of covariance model for volume performed similarly with the addition of different density covariates as the model used for mean annual increment. Increasing amounts of variation in volume were explained as the complexity of the density covariate increased, although significant differences among stand types were only found using relative density. In

this model each stand type was found to be significantly different, with an increasing trend in volume with progression from the redcedar to the hemlock-redcedar to the hemlock stand types.

Basal area was not found to significantly differ among stand types (Table 5.5). Like the models for mean annual increment and volume, the analysis of covariance model for basal area explained increasing variation with increasing complexity of the density covariate. However, this was also associated with increasingly similar predictions of basal area among stand types.

The redcedar trees in the single-species stands were similar in most respects to those in the mixed-species stands (Table 5.6). No significant differences in mean diameter at breast height, tree height, height to live crown, and mean annual increment were found in the redcedar trees of either stand type. The mean height to live crown of redcedar in the hemlock-redcedar stands was significantly greater than that in the redcedar stands. No differences were found among the cumulative distribution functions of redcedar in each of the tree characteristics compared.

In the single-species stands the hemlock trees had greater mean annual increment, and significantly greater mean diameter, height, and height to live crown, than the hemlock in mixed-species stands (Table 5.6). No differences were found among the cumulative distribution functions of hemlock in each of the tree characteristics compared.

Table 5.6 Individual mean tree characteristics, and standard errors of the means (in parentheses), of each species in single- and mixed-species stands. Redcedar tree values in the same row with the same lowercase superscript are not significantly different, and hemlock tree values in the same row with the same uppercase superscript are not significantly different ($\alpha = 0.05$).

Tree characteristic	Redcedar Trees		Hemlock trees	
	Redcedar stand type	Hemlock-redcedar stand type	Hemlock stand type	Hemlock-redcedar stand type
Diameter at breast height (cm)	28.4 ^a (14.1)	28.1 ^a (11.6)	33.3 ^A (11.5)	29.4 ^B (10.9)
Total height (m)	22.2 ^a (5.7)	22.8 ^a (5.3)	31.0 ^A (6.6)	26.6 ^B (6.5)
Height to live crown (m)	13.0 ^a (3.4)	14.4 ^b (3.5)	18.1 ^A (4.1)	15.3 ^B (4.5)
Mean annual increment (m ³ ha ⁻¹ yr ⁻¹)	0.012 ^a (0.013)	0.011 ^a (0.011)	0.022 ^A (.017)	0.017 ^A (0.013)

5.3 Discussion

5.3.1 Productivity Comparisons – Relative Yield

Relative yield comparisons in existing mixed-species stands are more difficult to interpret than those in plantation studies. Non-study species can influence the results and interpretation of relative yield (Table 5.2). Since most existing single or mixed-species stands commonly contain inclusions of other species, this influence on the study species cannot be ignored. In the single- and mixed-species stands of hemlock and redcedar, total relative yield changed from 1.24, indicating positive interactions, to 0.90, indicating competitive interactions, when the yield contributions of non-study species were factored into calculations. Comparing relative yield calculations with and without non-study species may indicate the degree to which non-study species compete, or positively interact, with the study species.

If non-study species compete with study species, the relative yield of the mixture being studied will decrease. More competitive study species may decrease the negative impact the non-study species have on total relative yield. If non-study species interact positively with the study species, then total relative yield of the study mixture should be higher than would be observed in a plantation study. Although this increased yield may be desirable in economic terms, the effects of non-study species make it difficult to compare findings among other studies in existing, unmanaged mixtures.

Hemlock and redcedar both appear to compete with non-study species. Redcedar's relative yield decreases below 0.5 with the influence of non-study species (Table 5.2), suggesting that redcedar competes with these species, and that this competition mutes the benefits of any positive interactions redcedar experiences with hemlock. It should be noted that redcedar stands are uncommon, and locating such stands was difficult. The result was redcedar stands averaging 25.2% basal area contribution by hemlock, and 3.8% by non-study species (Table 5.3). Conversely, relatively pure hemlock stands were much easier to locate, and these stands averaged only 7.2% and 7.7% basal area contributions by redcedar and non-study species respectively. Thus hemlock stands contained 15% inclusions and redcedar stands contained 29% inclusions, providing evidence of relatively greater competition in the redcedar stands. Overall, the competition between hemlock and redcedar with non-study species resulted in a net decrease in the yield of mixed- versus single-species stands.

Although hemlock's relative yield decreases under the influence of non-study species, it still remains at 0.5 (Table 5.2). Hemlock appears to achieve the same productivity it would in a single-species stand while contending with non-study species.

However, the relative yields of hemlock and redcedar in mixture must be interpreted with caution. Although the basal area contributions of hemlock and redcedar in the mixed-species stands were roughly equal, each of these contributions was not exactly half of the basal area of

each species in single-species stands. In fact, the basal area contribution of hemlock in hemlock-redcedar stands was 56% of the contribution of hemlock in hemlock stands. The basal area contribution of redcedar in hemlock-redcedar stands was 66% of the contribution of redcedar in redcedar stands. Based on these percentages, the relative yields of hemlock and redcedar are biased toward higher values, and their true relative yields are lower than those calculated with the equations for relative yield for plantation experiments. This suggests that the relative yields greater than 0.5 calculated without non-study species are inaccurate, and that the true relative yields for each species are lower. Since including non-study species in calculations further decreases relative yield, it must be concluded that the mixed-species stands are dominated by competition among hemlock, redcedar, and the non-study species.

5.3.2 Productivity Comparisons – Absolute Yield

Mean annual increment was found to be similar among study locations (Table 5.4). Both mean annual increment and volume increased from redcedar, to hemlock-redcedar, to hemlock stands (Table 5.5). The mean annual increment model was more sensitive than the model detecting differences in volume. Mean annual increment eliminates the need for age correction, and may have resulted in a more sensitive analysis of variance model. The models for mean annual increment and volume became more sensitive with increasing complexity of the density covariates used in each model. Since relative density incorporates more stand information, including quadratic mean diameter and basal area, this density measure was expected to explain more variance in productivity among stand types than the density measures containing relatively less stand information. Analyses of covariance for each of mean annual increment and stand volume reveal that hemlock stands produce relatively higher wood volumes, and mean annual increments, than hemlock-redcedar stands or redcedar stands of equivalent age, site, and density.

A trend of decreasing basal area with increasing hemlock presence was detected when density was represented by stems per hectare in analysis of covariance (Table 5.5). The trend was more weakly expressed when quadratic mean diameter was used in the model, and disappeared when relative density was used. Like the models for mean annual increment and volume, the basal area model explained more variation and had lower error when the complexity of the density measure increased. However, the best predictor of basal area among stand types is probably the basal area model employing stems per hectare. Stems per hectare does not incorporate measures of stand basal area, as do quadratic mean diameter (equation [3.8]) and relative density (equation [3.9]). Using quadratic mean diameter and relative density, forced these models, that were designed to detect differences in basal area, to reflect stand types of equivalent basal area. Other observations support the output of the model employing stems per hectare, where increasing basal area is associated with increasing redcedar presence. The redcedar stands had similar quadratic mean diameters as the other stand types, but had higher stems per hectare (Table 5.1). Given roughly equal tree diameters in each stand type, redcedar stands simply seem to contain more trees than hemlock-redcedar or hemlock stands.

Based on the observations of stand characteristics (Table 5.1), relative yield calculations (Table 5.2), and analyses of covariance (Tables 5.3-5.5), it can be concluded that the hemlock stands produce higher wood volume and mean annual increment, on less basal area, than the hemlock-redcedar or redcedar stands. Although hemlock stands have fewer stems, they appear to achieve superior productivity through much taller trees than the other stand types, and higher quadratic mean hemlock diameters than those in mixture. This suggests that, within the single-species stands, hemlock trees are taller and of better form than redcedar trees.

Hemlock trees are less productive in mixed-species stands, while redcedar trees are equally productive, compared to their growth in single-species stands. The reductions in diameter at breast height, tree height, height to live crown, volume, and mean annual increment

that hemlock trees exhibit in mixture with redcedar support the hypotheses, based on relative yield, that hemlock experiences a decrease in productivity in mixture with redcedar. However, redcedar in hemlock-redcedar stands suffers no appreciable decrease in diameter, height, height to live crown, or mean annual increment, compared to that in redcedar stands. In fact, the increased height to live crown redcedar exhibits in mixture may improve stem form factor. These characteristics of redcedar in mixture contradict the hypotheses from relative yield calculations that the relative yield redcedar suffers due to competition. The intermediate productivity of the hemlock-redcedar stands appears to be due to relative decreases in the height and diameter growth of hemlock trees, as a result of competition with redcedar and non-study species. This competition appears to more than offset any potential yield increases due to positive interactions among hemlock and redcedar in mixture.

When grown in single-species stands, hemlock seems to have stronger capacity to self-thin than redcedar. The result is hemlock of higher diameter growing in stands of lower density. Hemlock also exhibits superior height growth, at the age of trees sampled, resulting in higher productivity stands. Redcedar in these stands tends to grow at higher density, and, when mixed with hemlock, mutes hemlock's tendency to self-thin. In mixture, hemlock experiences the effects of higher density, enhancing the negative effects of competition on tree growth. This combination of factors results in increases in productivity with increasing hemlock presence. Where maximum wood volume production is desired, single-species stands of hemlock should be established on sites similar to those studied.

5.4 Conclusions

In mixtures of hemlock and redcedar, the relative yields of each species in single- versus mixed-species stands appear to suffer from competitive interactions. The natural occurrence of other species in existing stands further decreases the relative yields of hemlock and redcedar in

mixture. Mean annual increment and wood volume production increased with increasing presence of hemlock, while basal area increased with increasing presence of redcedar. The hemlock stand type was most productive because hemlock's height growth was greater than that of redcedar, and its height and diameter growth were greater in single-species stands. This greater diameter growth may be due to hemlock's superior ability to self-thin on these sites. The redcedar stand type was the least productive due to redcedar growing in high numbers of short, small diameter stems. Although hemlock was shorter and of smaller diameter in mixed-species stands, redcedar grew equally well in mixed- and single-species stands. Maximum wood volume production on similar sites would be achieved by establishing hemlock stands with a minimal component of other species.

6. ARE INCREASING CANOPY SEPARATION AND SPATIAL RANDOMNESS ASSOCIATED WITH INCREASED PRODUCTIVITY IN MIXED-SPECIES STANDS OF HEMLOCK AND REDCEDAR?

Abstract

I examined mixed-species stands of western hemlock and western redcedar to determine if increasing mean annual increment was associated with increasing canopy separation, or increasing spatial randomness in the arrangement, of the two species. The second-growth stands were located in southern coastal British Columbia on intermediate sites, and were unmanaged, and even-aged, with approximately equal proportions of hemlock and redcedar on a basal area basis. Increasing stand productivity was associated with increasing vertical separation of hemlock and redcedar canopies, where the area of hemlock canopy overtopping that of redcedar, and crown depths of both species, were maximized. Increased productivity was not associated with increasing levels of randomness in stand spatial tree patterns, but was associated with decreasing stand density, and a tendency towards regularity in the stand spatial tree patterns. Maximum productivity in fully stocked hemlock-redcedar mixtures can be attained with low density stands in which hemlock does not experience an establishment lag.

6.1 Introduction

Aboveground competitive reduction can be logically subdivided into physiological, spatial, and temporal components. Whatever the mechanism of aboveground competitive reduction, the manifestation is a stand canopy vertically separated into clearly defined layers of each species, spatially arranged to maximize the benefits of this separation.

The objective of this chapter was to determine whether aboveground competitive reduction is associated with a gradient of increasing productivity in hemlock-redcedar stands. Specifically, this chapter sought to address the following question: Is increasing mean annual

increment (MAI) in hemlock-redcedar stands associated with (1) increasing vertical separation of hemlock and redcedar canopies, and/or (2) increasing randomness in tree spatial patterns?

Previous studies suggest that increased canopy stratification is associated with increased stand productivity (Kelty 1992), and that clustering of two species indicates facilitation, while regularity in the pattern of two species indicates competition (Moeur 1993). Where this competition is reduced among the species, a random pattern intermediate between regularity and clustering is expected, and so spatial randomness will be presumed to indicate a reduction in competition between the species.

6.2 Results

6.2.1 Canopy stratification

Significant differences in mean annual increment per tree were detected among the hemlock-redcedar stands (Table 6.1). When corrected for age, site, and density, the average mean annual increment was greatest for trees in stand M2, and lowest in stand M3.

Table 6.1 Least squares means and standard errors (in parentheses) of mean annual increment per tree, stratified according to hemlock-redcedar stand. Values in the same row with the same superscript are not significantly different ($\alpha = 0.05$).

Productivity measure	Stand Identification						
	M2	M6	M4	M7	M1	M5	M3
Mean annual increment per tree (m^3yr^{-1})	0.01646 ^a (0.00133)	0.01623 ^{ab} (0.00127)	0.01618 ^{ab} (0.00156)	0.01360 ^{abc} (0.00133)	0.01303 ^{abc} (0.00134)	0.01274 ^{bc} (0.00109)	0.01208 ^c (0.00127)

Hemlock had larger quadratic mean diameters than redcedar in all but one of the hemlock-redcedar stands (Table 6.2). Hemlock was significantly taller than redcedar in all hemlock-redcedar stands. The height to the live crown of hemlock was significantly greater than that of

redcedar in all but 2 of the mixed-species stands. Ratios of hemlock and redcedar crown overlap (Equation [3.15]) ranged from 31 to 92% (Table 6.2). No significant differences in cumulative distribution functions of tree height, or height to live crown, were found among hemlock and redcedar.

Table 6.2. Percentage of basal area contribution (%BA), quadratic mean diameter, mean tree height, mean height to live crown, and crown overlap ratio (COR), of hemlock and redcedar in each of the hemlock-redcedar stands. Stands are arranged in order of decreasing productivity. Standard errors of means appear in parentheses. Tree height values in the same row with the same lowercase superscript are not significantly different, and height to live crown values in the same row with the same uppercase superscript are not significantly different ($\alpha = 0.05$).

Stand	%BA		Quadratic mean diameter (cm)		Tree height (m)		Height to live crown (m)		COR
	Cw	Hw	Cw	Hw	Cw	Hw	Cw	Hw	
M2	52	40	32.3	35.8	21.6 ^a (5.8)	26.5 ^b (5.2)	13.4 ^A (2.9)	14.7 ^B (2.3)	0.319
M1	55	39	31.1	32.5	22.9 ^a (5.0)	26.5 ^b (8.0)	12.5 ^A (2.4)	12.8 ^A (3.6)	0.472
M6	40	51	27.8	29.6	23.6 ^a (4.6)	28.3 ^b (4.4)	15.7 ^A (2.3)	17.9 ^B (2.8)	0.314
M7	39	52	27.9	29.5	22.0 ^a (5.0)	26.0 ^b (6.6)	15.2 ^A (2.8)	16.7 ^B (3.7)	0.428
M4	48	52	40.3	31.9	22.1 ^a (7.4)	21.7 ^a (9.1)	8.6 ^A (3.2)	7.8 ^A (3.0)	0.916
M5	42	58	31.1	33.9	22.6 ^a (5.1)	28.1 ^b (5.3)	15.2 ^A (2.7)	18.8 ^B (2.4)	0.369
M3	52	43	26.0	27.0	23.9 ^a (4.6)	27.7 ^b (4.8)	16.7 ^A (2.3)	17.6 ^B (2.2)	0.477

The hemlock in the most productive mixed-species stand (M2) had a larger quadratic mean diameter, and significantly lower height to live crown, than those in the least productive mixture (M3) (Table 6.3). Hemlock was shorter in stand M2 than in stand M3, but not significantly so. The redcedar in stand M2 had larger quadratic mean diameters, and had

significantly lower mean tree height and mean height to live crown, than the redcedar in stand M3 (Table 6.3).

Table 6.3. Percentage of basal area contribution (%BA), quadratic mean diameter, mean tree height, and mean height to live crown, of hemlock and redcedar in the most (M2) and least (M3) productive hemlock-redcedar stands. Standard errors of means appear in parentheses. Tree height values in the same row with the same lowercase superscript are not significantly different, and height to live crown values in the same row with the same uppercase superscript are not significantly different ($\alpha = 0.05$).

Species	%BA		Quadratic mean diameter (cm)		Tree height (m)		Height to live crown (m)	
	M2	M3	M2	M3	M2	M3	M2	M3
Hemlock	40	43	35.8	27.0	26.5 ^a (5.2)	27.7 ^a (4.8)	14.7 ^A (2.3)	17.6 ^B (2.2)
Redcedar	52	52	32.3	26.0	21.6 ^a (5.8)	23.9 ^b (4.6)	13.4 ^A (2.9)	16.7 ^B (2.3)

6.2.2 Spatial randomness

Refined nearest neighbour analysis

Figure 6.1 shows how empirical nearest neighbour distance changes as a function of distance, for the most (M2) and least (M3) productive hemlock-redcedar stands. The nearest neighbour function of stand M2 showed the highest degree of regularity in the distribution function of nearest neighbour distances of any hemlock-redcedar stand. This regularity reaches a maximum approximately 0.7 m from trees in stand M2 (Figure 6.1). At distances greater than 4.4 m from trees in stand M2, nearest neighbouring trees were found at the same distance as would be found in a stand of randomly arranged trees.

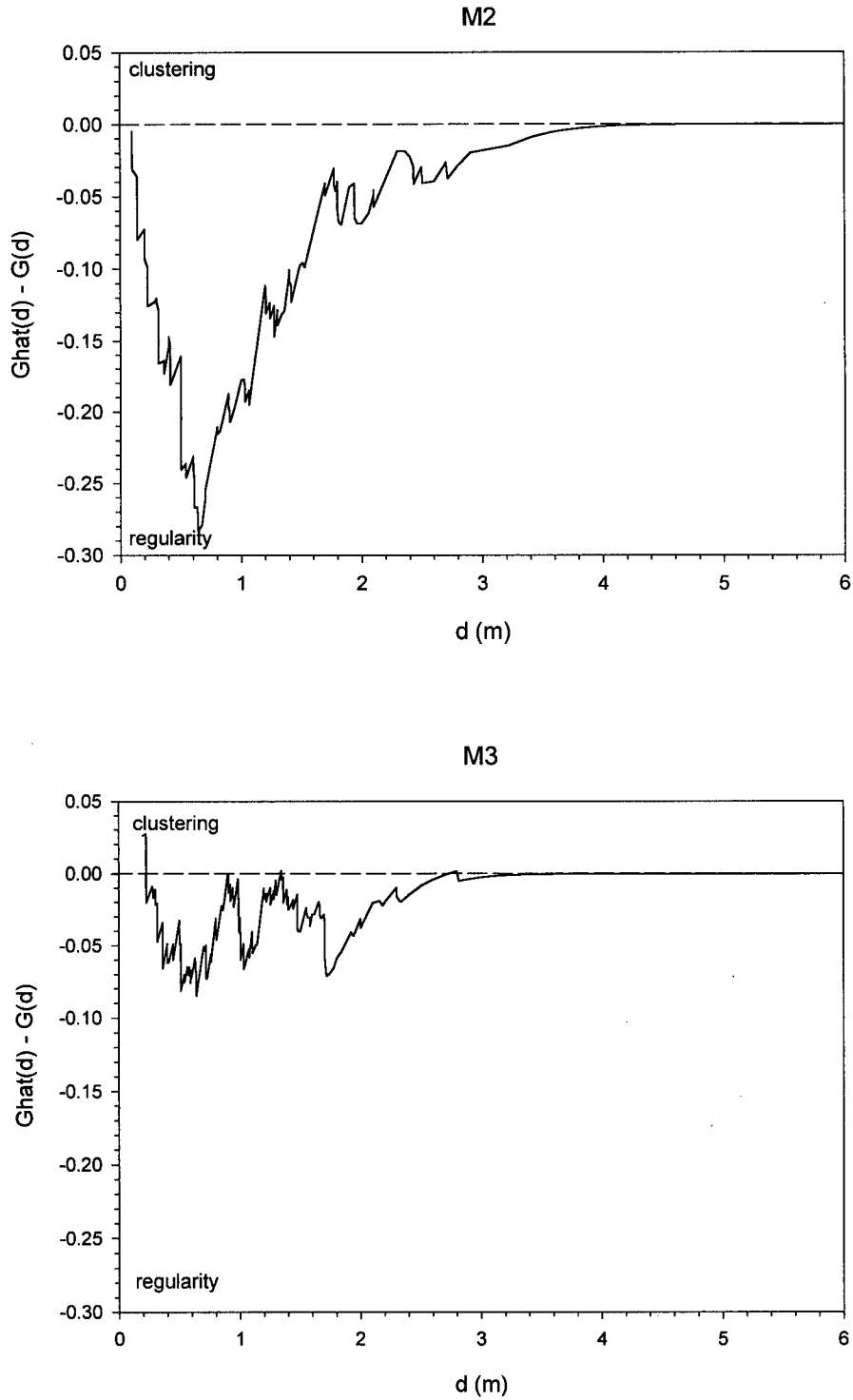


Figure 6.1. Output of refined nearest neighbour analysis for the most (M2) and least (M3) productive hemlock-redcedar stands, in terms of mean annual increment ($\text{m}^3\text{ha}^{-1}\text{yr}^{-1}$). The horizontal line with Y intercept = 0 represents the expected nearest neighbour function for a Poisson forest [$G(d) = 1 - e^{-\lambda \pi d_i^2}$].

The nearest neighbour function of stand M3 spiked toward a clustered pattern at a distance of approximately 0.3 m. This clustering was followed by a rapid trend toward regularity, but the regularity was less strongly expressed than in stand M2 (Figure 6.1). This regularity was most strongly expressed at distances of 0.7 m , 1.0 m, and 1.7 m from trees in stand M3. At distances greater than 3.6 m from trees in stand M3, nearest neighbouring trees found at the same distance as would be found in a stand of randomly arranged trees.

Combined count and distance analysis

In the most productive stand (M2) inter-tree distances deviated significantly from those expected from completely random tree spatial patterns (Figure 6.2A-C). Significant clustering was detected in the stand at distances less than 1 m from any tree (Figure 6.2A). At inter-tree distances in the stand between 1.5 m and 7 m, the trees closely follow a random spatial pattern. Significant regularity in inter-tree distances was found between 9 m and 11 m. Beyond 11 m inter-tree distances were considered random, but displayed a persistent tendency toward regularity. Redcedar in stand M2 were highly clustered at distances less than 1 m (Figure 6.2B). The redcedar then closely follow a random pattern to a distance of 9 m, and remain random with a regular tendency to 15 m, beyond which they remain significantly regular. The hemlocks in stand M2 were also clustered within a 1 m inter-tree distance (Figure 6.2C). Between 1 m and 4 m the arrangement of hemlocks closely follows a random pattern. Beyond 4 m, hemlock tends toward regularity, and beyond 7 m hemlock maintains a random inter-tree distance with a tendency towards regularity.

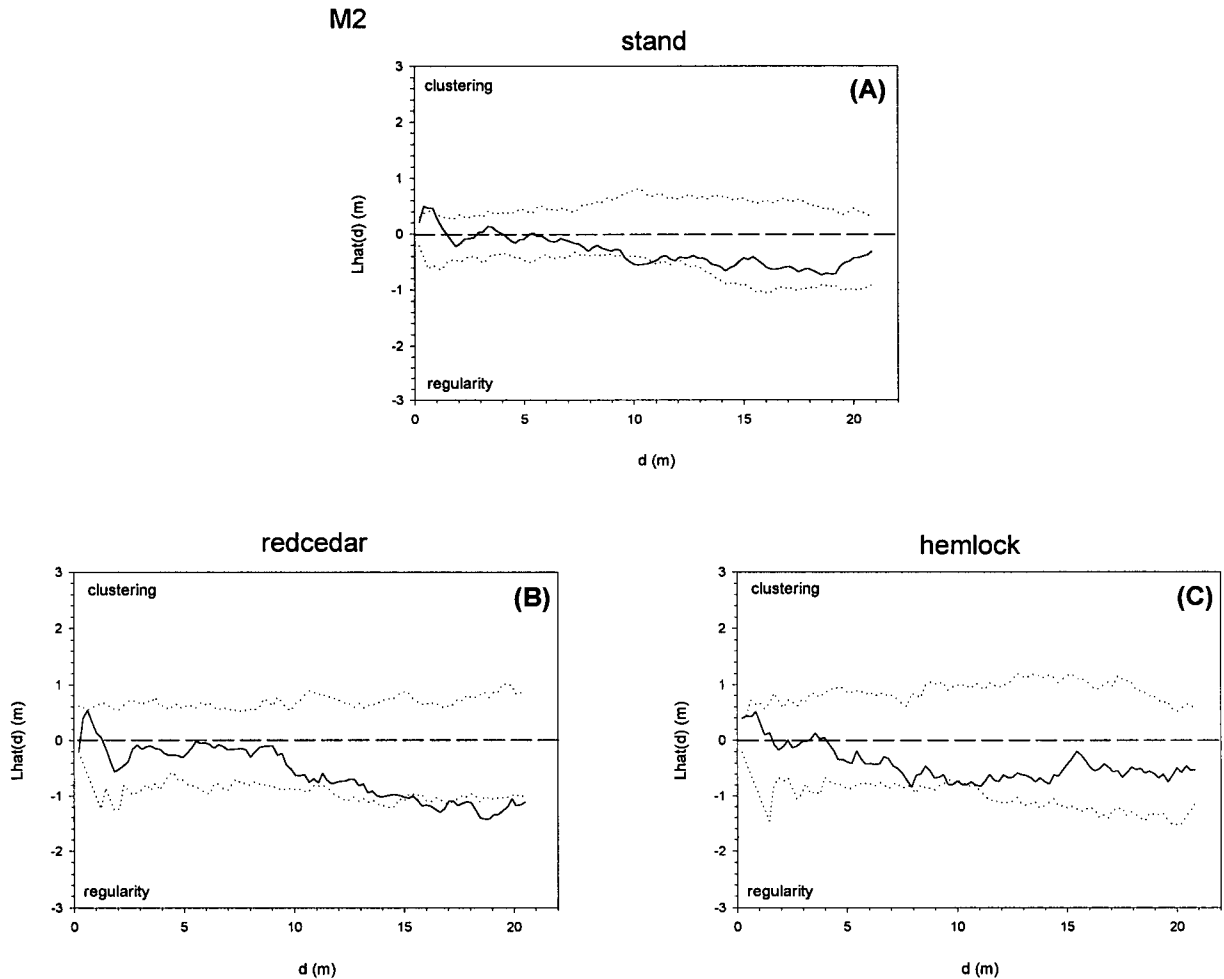


Figure 6.2 Ripley's $\hat{L}_{12}(d)$ results for composite (stand - A), and individual (redcedar - B; hemlock - C), spatial point patterns for the most productive hemlock-redcedar stand (M2). The horizontal line with Y intercept = 0 represents the expected value [$L_{12}(d) = 0$] of a random spatial point pattern, and the dotted lines represent the upper and lower pointwise 95% confidence envelope boundaries.

In the least productive stand (M3) inter-tree distances closely approximated those expected of a completely random spatial pattern of trees (Figure 6.3A-C). The combined spatial pattern of hemlock and redcedar trees is somewhat regular between distances of 2 m to 4 m, beyond which the pattern maintains a random pattern with a slight tendency toward regularity (Figure 6.3A). The pattern of redcedar in stand M3 spiked toward regularity twice at distances less than 1.5 m (Figure 6.2B). The redcedar then approach and closely follow a random pattern.

The hemlock in stand M3 are highly regular between 1 m and 5 m, then are arranged approximately randomly at all distances beyond 5 m (Figure 6.3C).

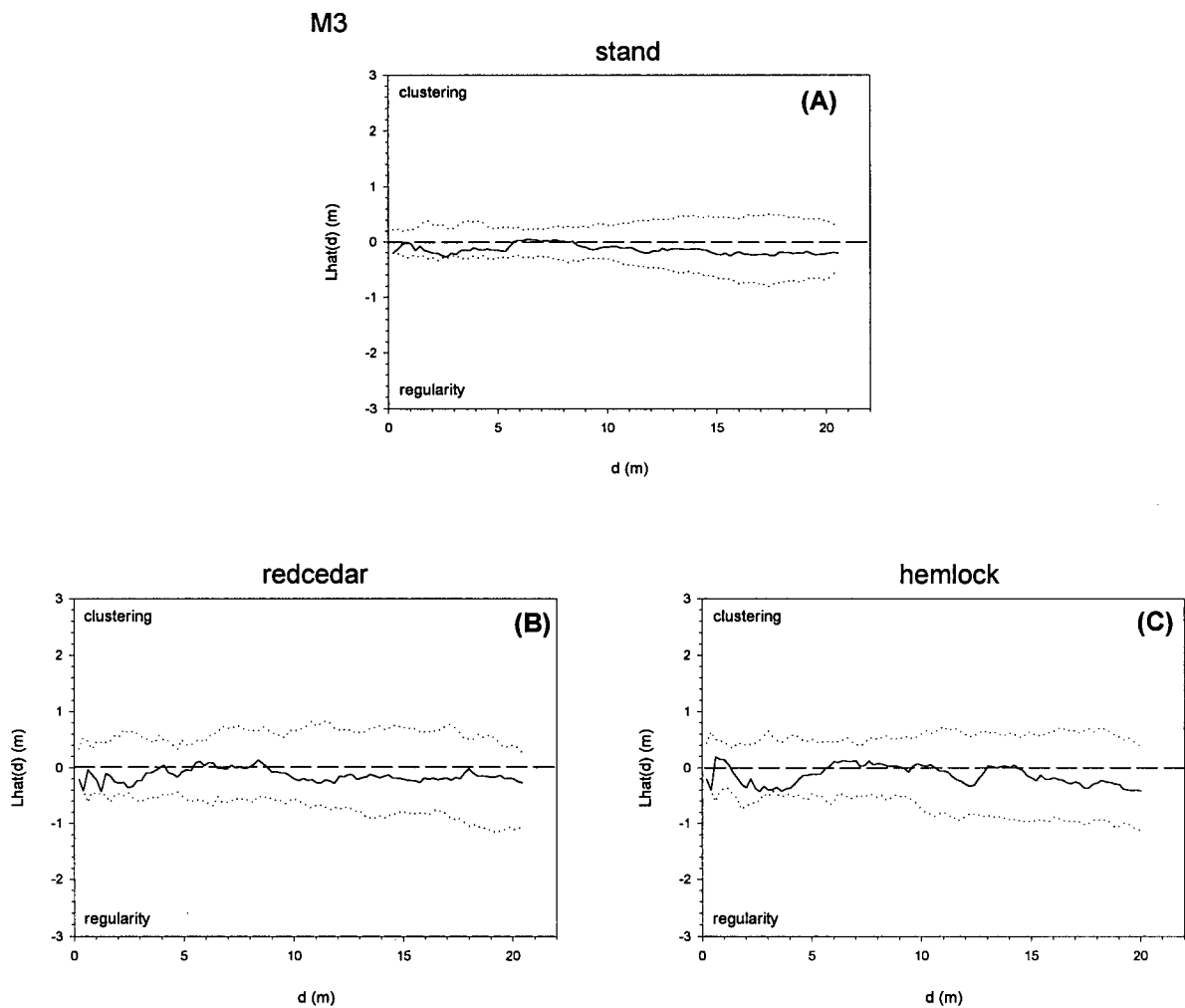


Figure 6.3 Ripley's $\hat{L}_{12}(d)$ results for composite (stand - A), and individual (redcedar - B; hemlock - C), spatial point patterns for the least productive hemlock-redcedar stand (M3). The horizontal line with Y intercept = 0 represents the expected value [$L_{12}(d) = 0$] of a random spatial point pattern, and the dotted lines represent the upper and lower pointwise 95% confidence envelope boundaries.

6.3 Discussion

6.3.1 Canopy stratification

The trend of increasing productivity in the hemlock-redcedar stands was not associated with an increase in the percentage of basal area contribution by hemlock (Table 6.2). Although hemlock stands were more productive than hemlock-redcedar and redcedar stands, and this productivity was due to hemlock's superior height and diameter growth, increasing productivity in hemlock-redcedar stands was not simply due to increasing hemlock content. This suggests that hemlock and redcedar do exert influences on each other in mixture, and that these influences have a direct bearing on the productivity of these mixtures. Where the influences that hemlock and redcedar have on each other are competitive, separating each species spatially can reduce this competition. Within the hemlock redcedar stands, increasing separation of hemlock and redcedar canopies appeared to be associated with increased productivity in hemlock redcedar mixtures.

The characteristics of hemlock and redcedar in the most (M2) and least (M3) productive stands indicate that differences between these stands exist in canopy architecture. Both hemlock and redcedar in stand M2 have greater mean crown depths than those in stand M3. In addition to the deeper crowns in stand M2, there is a greater difference in height between hemlock and redcedar, relative to that in stand M3. The hemlock is 4.9 m taller than redcedar in stand M2, while hemlock is only 3.8 m taller than redcedar in stand M3. Therefore, the hemlock in stand M2 has a greater crown area free from competition with redcedar than the hemlock in stand M3. The crown overlap ratios of each stand support these findings, confirming that the crown of redcedar overlaps that of hemlock approximately 15% more in stand M3 than in stand M2 (Table 6.2). However, no clear trend between increasing productivity and crown overlap ratio was evident in the hemlock-redcedar stands (Table 6.2). This implies that either crown overlap

among redcedar and hemlock is not a strong indicator of competition, or that above ground competition is not sufficiently explained by crown overlap ratio alone, or that the crown overlap equation does not accurately explain crown overlap. It seems likely that some other factors act in concert with crown overlap to affect the productivity of hemlock-redcedar mixtures.

In addition to lower crown overlap, the hemlock and redcedar in stand M2 have a greater leaf area than the hemlock and redcedar in stand M3. Although the hemlock and redcedar are taller in stand M3, the heights to their live crowns were also greater than in stand M2. The greater leaf areas of hemlock and redcedar in stand M2 explain the greater quadratic mean diameters in this stand, and these greater diameters may partially explain the greater productivity of this stand.

Wood volume production was calculated as a function of both diameter and height (equations [3.3-3.6]). Although the hemlock and redcedar in stand M2 were shorter than those in stand M3, stand M2 still had higher wood volume and mean annual increment. It appears that the greater quadratic mean diameters of hemlock and redcedar in stand M2 more than offset their lower mean heights, resulting in trees of greater volume than in stand M3.

The deeper crowns of hemlock and redcedar in stand M2 indicates that the trees in this stand are more widely spaced than in stand M3. In fact, at 944 stems per hectare, stand M2 is more widely spaced than stand M3, which has 1356 stems per hectare (Table 5.1). However, stand M2 is of higher relative density than stand M3 (Table 5.1). These findings suggest that the wider spacing of stand M2 produces wood volume more efficiently than the narrower spacing of stand M3.

Therefore, the productivity of hemlock-redcedar stands appears to be a function of stand density and crown overlap between the two species. Given a fully stocked stand, decreasing stems per hectare results in a higher quadratic mean diameter, without a major impact on mean height growth (Davis and Johnson 1987). Where hemlock does not experience an establishment

lag, it will overtop redcedar and reduce crown overlap. The result is a stand that produces wood volume more efficiently per unit basal area, than a stand of higher stems per hectare and crown overlap.

6.3.2 Spatial randomness

It should be noted that pattern classifications (e.g.: clustered, random, or regular) reflect the level of measurement, or scale used for examination (Chen and Bradshaw 1999). As a result, what appears clustered at one scale may seem regular at another (Upton and Fingleton 1985). However, refined nearest neighbour and Ripley's analyses are powerful tools, as they cover the entire range of scales bounded by the limits restricted by sampling boundaries (Moeur 1993). Interpretations of similar stands can be made to the scale of the study stands.

Refined nearest neighbour analysis

Stand data for nearest neighbour analysis included the point locations of dead stems in each stand. Stand M2 had a total of 345 dead stems per hectare, while stand M3 had 800 dead stems per hectare. It may be that the initial spike of clustering observed in stand M3 at a distance of approximately 0.3 m (Figure 6.1) is caused, in part, by the presence of the dead stems. During stand mapping dead stems appeared clustered around surviving stems, especially in the case of redcedar, and particularly in stand M3, which had a high number of stems per hectare. If the clustering observed in stand M3 represents dead stems, then the minimum nearest neighbour distance (where minimum nearest neighbour distance is defined as the first distance at which $\hat{G}(d) - G(d)$ is positive (Moeur 1993)) observed in this stand would represent the minimum physical distance between clustered trees prior to the understory reinitiation stage of stand development. The minimum physical distance between the stems represents the zone of inhibition between the trees in the cluster (Moeur 1993). However, there is no minimum nearest neighbour distance in the plot for stand M2 (Figure 6.1), and this may demonstrate the weakness

of spatial analyses based only on nearest neighbours. However, the zone of inhibition in stand M2 can likely be inferred from the spike toward regularity between 0.1 m and 1.8 m. The visual evidence of dead stems clustered around live ones, and the nearest neighbour plots, suggests that the zone of inhibition around trees in the cluster increases with stand age, and only the most successful trees in each cluster will survive at the expense of their neighbours. The zone of inhibition also increases, and becomes more strongly expressed, as stand density decreases from stand M3 to stand M2. It seems likely that this phenomenon is the result of a uniquely regular seedling establishment pattern in stand M2, due to the lack of evidence of clustered dead stems in this stand.

Combined count and distance analysis

The significant clustering in stand M2 at distances less than 1 m (Figure 6.2A-C) directly contradicts the output of nearest neighbour analyses for this stand (Figure 6.1). The results of Ripley's analyses are likely to be more accurate due to the increased complexity of spatial pattern information incorporated into these analyses. Based on Ripley's analyses, the hemlock and redcedar in stand M2 both tend to cluster at distances less than 1 m, and this clustering occurs within and among the species (Figures 6.2A-C and 6.4). The combined spatial pattern of hemlock and redcedar, and each of their individual spatial patterns, reflects a random arrangement of stems between approximately 1 m and 7 m, followed by a significant departure toward regularity at 10 m. These findings suggest that hemlock and redcedar in stand M2 are arranged in inter-mixed groups. These groups tend to have smaller stems clustered within a meter of larger stems, but the groups are randomly arranged and are roughly 10 m in radius. Hemlock in this stand is likely to occur randomly outside this 10 m radius, while redcedar is much more likely to be found within each group (Figures 6.2A-C and 6.4). Hemlock tends to arrange itself in a regular pattern as close as 5 m, while redcedar does not do so until 9 m. This suggests that either hemlock competes more vigorously with conspecifics than redcedar, or that

hemlock seedlings originally established themselves according to a more regular pattern than redcedar.

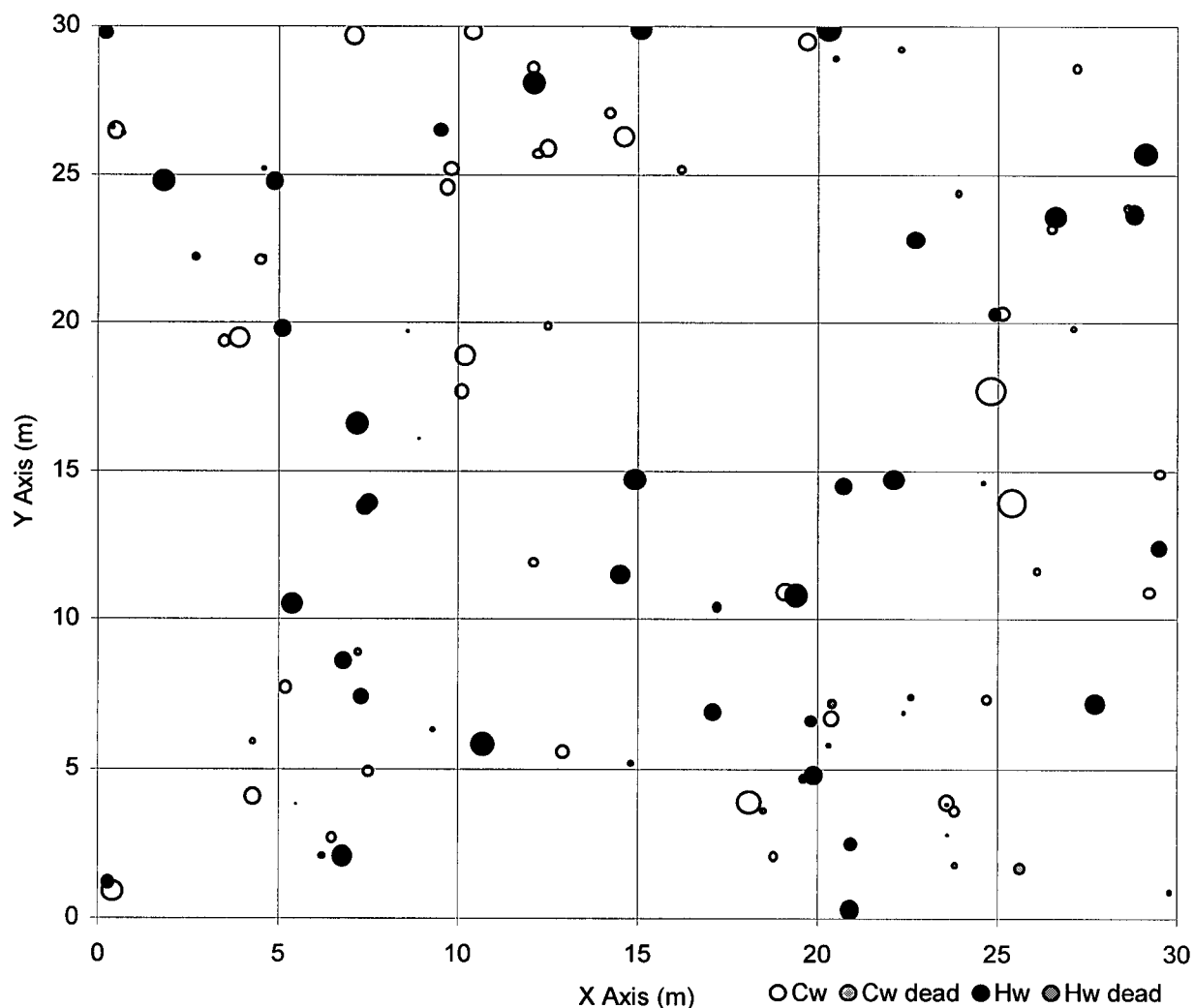


Figure 6.4 Top down view of the most productive hemlock-redcedar stand M2. Each circle represents an individual stem, stratified by colour according to species, and the diameter of each circle is based on the diameter at breast height of each tree.

In stand M3, the clustering detected in nearest neighbour analyses at distances less than 1 m was also detected with Ripley's analyses, but only in the case of the hemlock trees (Figure 6.3C). Since the stand data used for Ripley's $\hat{K}_{12}(d)$ and $\hat{L}_{12}(d)$ analyses did not include the spatial point patterns of dead stems, comparison of $\hat{L}_{12}(d)$ and nearest neighbour plots over distances less than 1 m should reveal the degree to which dead stems contributed to the

clustering at these distances. Therefore, it can be assumed that the trees clustered at distances less than 1 m in stand M3 are either dead stems or live hemlock trees (Figures 6.1, 6.3A-C, and 6.5). The spatial patterns of hemlock, redcedar, and their combined pattern, all approach significant regularity between distances of 2 m and 3 m, beyond which a random, if not slightly regular, pattern is maintained. The trees in stand M3 appear to be arranged in a random pattern of individuals. Where larger hemlock trees are clustered with smaller trees, these trees are likely to be smaller hemlocks or dead trees. Where larger redcedar trees are clustered with smaller trees, these tend to be dead trees only. Live trees tend to be 2 m to 3 m from each other, and the area within this radius delineates each tree's zone of inhibition.

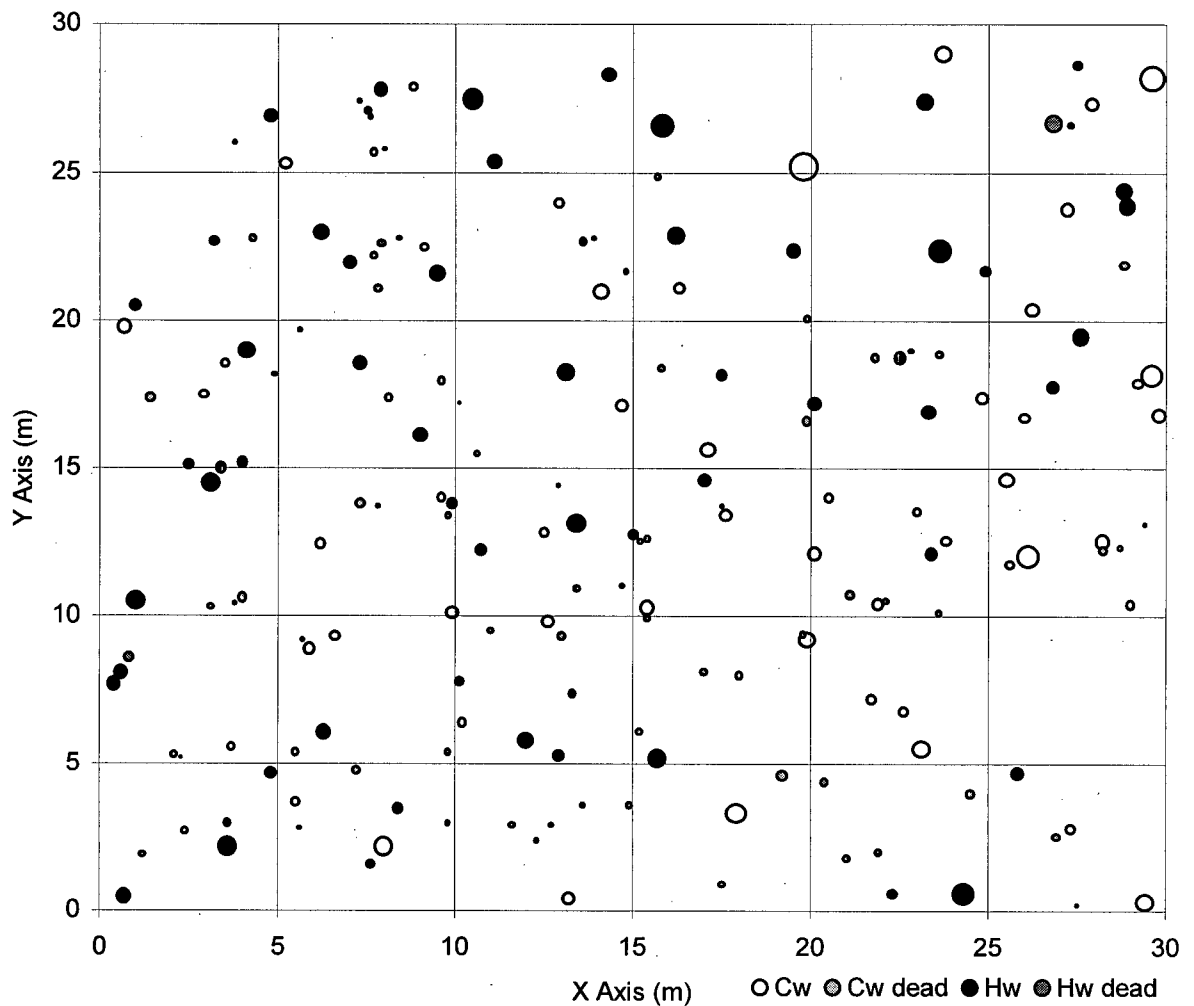


Figure 6.5 Top down view of the least productive hemlock-redcedar stand M3. Each circle represents an individual stem, stratified by colour according to species, and the diameter of each circle is based on the diameter at breast height of each tree.

Moeur (1993) found that competitively inferior trees in a stand tended towards clustering while successful competitors tend toward regularity. Since the most productive stand (M2) is characterized by regularity, and the least productive stand (M3) by randomness, this implies that the trees in the most productive stand are competing more successfully with each other than those in the least productive stand. If the total of dead and live stems in each stand represent the density of each stand before stem exclusion, the least productive stand is still more dense than the most productive stand was at the beginning of stem exclusion. Given the assumption that the least productive stand will self-thin towards the density of the most productive stand, the least

productive stand represents a relatively earlier stage of stand development than the most productive stand, in which inter-tree competition is more intense. It seems likely that stands progress from clustering to regularity as they age due to competition-induced mortality, and that trees primarily compete with their immediate neighbours. These conclusions agree with findings from other studies involving spatial analyses of forest stands (Ford and Diggle 1981; Kenkel 1988; Moeur 1993).

Based on the findings of nearest neighbour and Ripley's analyses, productivity was not observed to increase with increasing spatial randomness in the hemlock-redcedar stand type. A trend of increasing regularity was found from the least to the most productive hemlock-redcedar stand. Thus decreasing density and increasing regularity in spatial pattern are associated with increasing productivity in hemlock-redcedar mixtures.

6.4 Conclusions

Increasing productivity in the hemlock-redcedar stand type was associated with increasing vertical separation of hemlock and redcedar canopies. In particular, productivity appeared to increase with increasing area of hemlock canopy overtopping that of redcedar, and with increasing canopy depths of both species. Increasing spatial randomness in the spatial patterns of hemlock, redcedar, or their combination, was not associated with increasing productivity. However, productivity did increase with increases in the regularity of the spatial patterns of trees in hemlock-redcedar stands. These findings suggest that density plays a key role in the productivity of these stands. Given full stocking and no establishment lag for hemlock, reductions in density will promote slightly shorter trees of higher quadratic mean diameter, and

deeper crowns with reduced overlap, in the stand. These tree and stand characteristics allow more efficient wood volume production per unit basal area. It can be concluded that hemlock and redcedar in mixture may experience some reduction in competition due to vertical canopy separation, but that competition probably dominates the dynamics of how hemlock and redcedar arrange themselves on the ground.

7. GENERAL CONCLUSIONS

Given the silvical characteristics of hemlock and redcedar, theory on positive plant interactions suggests that mixed-species stands might have a higher productivity than single-species stands. Hemlock-redcedar stands may have higher productivity due to canopy separation, longevity differences, preferential uptake of different forms of nitrogen, beneficial modification of soil nutrients, reduced herbivore search efficiencies, and increased windfirmness.

Evidence has been found that suggests hemlock and redcedar may benefit from positive plant interactions. Both species have been shown to uptake different forms of nitrogen, and analyses indicated that increasing differentiation of hemlock and redcedar canopies was associated with increasing productivity.

However, the benefits associated with growing in mixture appear to be offset by competition for growing space, particularly in dense stands. This competition results in hemlock and redcedar producing lower relative yields in mixture compared to single-species stands. In terms of mean annual increment, the hemlock stand type was more productive than the hemlock-redcedar, and redcedar stand types. The increasing trend in productivity with increasing presence of hemlock seemed to be due to hemlock's superior height growth compared to redcedar, and hemlock's superior height and diameter growth in single-species stands compared to mixtures.

Given the choice between single- and mixed-species stands of hemlock and redcedar, hemlock stands should be established if maximum wood production is the management objective. If maintaining a mixture, or improving site nutrient status, is the management objective, then hemlock-redcedar stands should be established. Maximum wood production in a hemlock-redcedar stand will be achieved where stands are fully stocked, but established at low density. These recommendations are for intermediate (zonal, Hw-Ba Blueberry) sites in the

Submontane Very Wet Maritime Coastal Western Hemlock (CWHvm1) variant, for stands less than 80 years old.

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