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The Structure of Single- and Mixed-species, Second-growth Stands of Western Hemlock and Western Redcedar

Introduction

The structure of a forest stand is characterized by: (a) species composition, (b) age, (c) size (diameter and height), and (d) spatial (horizontal and vertical) arrangement of the trees. Depending on the species, site, and disturbance history, the stand structure varies with time, thus providing a snapshot of a particular development stage.

Research on growth and stand structure has shown that the spatial distribution of trees is one of the key determinants of stand productivity. Forest inventories and ecological surveys carried out in British Columbia (BC) have shown that the structure of naturally established, unmanaged stands varies from simple (single-species, single-storied, and even-aged) to complex (multi-species, multi-storied, and uneven-aged). Only a few studies have quantitatively characterized this range of structural complexity, with nearly all studies focusing on old-growth stands.

BC forest policy requires that harvested areas be regenerated with a mixture of tree species whenever a mixture is suited to the site. This policy is based upon the assumption that under appropriate conditions, increases in stand productivity, reliability, and/or biodiversity can be attained in mixed-species stands. This assumption has not yet been tested for forest ecosystems. One mechanism by which different tree species can reduce crown competition for light is through vertical separation (the development of multiple canopy strata). Canopy stratification is not easily recognized in mixed-species stands, particularly when species have similar shade tolerance and height growth patterns, and no quantitative methods have been developed to detect stratification.

The diameter frequency distribution of two-storied stands have been characterized by inverted J-shaped as well as modal curves. Although it would be more appropriate to characterize stand structure by height frequency distributions, these distributions have not been developed. We suggest that (i) a stand is stratified if there are distinct, quantitatifiable modes in the size distribution; either diameter, height, or crown height, and (ii) height or crown height distributions will be the most sensitive measures.

To characterize the structure of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (Hw) and western redcedar (*Thuja plicata* Donn ex D. Don in Lamb.) (Cw) second-growth stands, and to investigate its influence on tree growth, we (1) described and compared size (diameter, height, and crown height) frequency distributions in single- and mixed-species stands, (2) determined whether mixed-species stands develop a stratified canopy, and (3) examined whether interactions between hemlock and redcedar affect tree growth.

Study Stands and Methods

Study stands were located in the Capilano River valley (Capilano), University of British Columbia, Malcolm Knapp Research Forest east of Vancouver (Knapp), and Mission Tree Farm License No. 26 (Mission). A total of 18 stands were selected for the study: 7 hemlock, 4 redcedar, and 7 hemlock-redcedar mixtures. The stands were naturally regenerated, unmanaged, closed-canopied, and even-aged (53 to 65 years @ bh), and represented the end of the stem exclusion stage of stand development. All stands were within the Submontane Very Wet Maritime Coastal Western Hemlock (CWHvm1) variant, and were located on fresh, nutrient-medium sites. Regardless of stand type, all had very similar understory vegetation, indicating climatic and edaphic similarity of the study stands.

Soil moisture regime was fresh (no growing-season water deficit or surplus) and soil nutrient regime was medium. Although the stands varied physically, they were considered equivalent in growing conditions. Diameter at breast height (dbh) and height were measured. Each live tree was assigned into one of four crown classes: dominant, codominant, intermediate, or suppressed. Species, dbh, total height, and crown height (distance from the ground to the lowest live branch) were recorded for all trees taller than 1.3 m. The breast height ages of three dominant trees of each species per plot were determined from increment cores. Site indices of Cw and Hw were estimated using standard equations.

To quantitatively characterize diameter, height, and crown height distributions, we used descriptive statistics and standardized cumulative frequency distributions. We compared variances (using Bartlett's test) and means of diameter, height, and crown height. If the variances were not significantly different, means were compared using one-way analysis of variance. The non-parametric Kruskal-Wallis test was used to compare means when the variances were significantly different. Comparisons were made (i) for each species between plots within the same stand type, (ii) for each species between single- and mixed-species stands, and (iii) between species within mixed-species stands. To compare the shape of distributions, we used the Kolmogorov-Smirnov test.

Results and Discussion

Frequency distributions for all variables were modal, but varied in shape. In single-species stands, the spread of the distributions varied but were more or less symmetric. The principal difference between diameter, height, and crown height distributions was in skewness: many plots had skewed distributions for crown height. The diameter distributions were predominantly skewed to right, while the majority of height and crown height distributions skewed to left (Figure 1).

In the mixed-species stands, each species was distributed across a similarly wide range of diameter, height, and crown height values as in the single-species stands. Hw was more frequent in the upper classes and Cw in the lower classes indicating their prevalence in the upper and lower canopy strata. The distributions of both species in mixed-species stands reflected their distributions in single-species stands, except for the diameter distributions, which are almost identical. However, the combined distributions were unimodal (Figure 1). Neither the diameter, height, nor the crown height frequency distribution gave any indication that mixed stands are stratified. All results indicated a single canopy layer with bell-shaped frequency distribution. The relationship between diameter and height showed that either variable could be used to detect modes in the size distributions.

In general, the means and variances of the measurements of both species were significantly different within ($\alpha = 0.05$) but not between stand types. Comparison of single- to mixed-species stands showed that crown height of Cw was significantly higher in the mixed-species than single-species stands, while diameter and height values were the same. For Hw, all size measures were significantly higher in the Hw stands than mixed stands. When comparing Hw and Cw in mixed stands, diameter was the same, but Hw had significantly higher mean and crown heights than Cw (Table 1). The similarity of distribution was confirmed by the Kolmogorov-Smirnov test.

Comparison of the distribution of crown classes between Hw and Cw in single- and mixed-species stands showed between-species and between-stand type differences (Figure 2). Hw had a higher percentage of dominants and codominants, and Cw had relatively more intermediate and suppressed trees. Hw generally assumed the dominant position relegating dominant Cw to codominance. Although the percentage of codominant Cw increased from single- to mixed-species stands, that of codominant Hw decreased. For intermediate trees, there was a decrease from single- to mixed-species stands for Hw, and an increase for Cw; the percentage of suppressed trees showed no effects, as did mean height for each crown class. These results agree with the differences in mean and crown height between both species in mixed stands. Since the percentage of suppressed Hw did not change from single- to mixed-species stands, the reduction in mean and crown height in mixed-species stands is not due to an increase of suppressed trees. The change in the percentage and mean height of dominant Hw and Cw indicates that at this stage of stand development the faster growing dominant Hw trees overtop the dominant Cw trees.

Regression analysis showed that diameter, height, and crown height growth of Hw is inversely related to the presence of Cw while Cw growth was unaffected by the increasing presence of Cw. We concluded that mixtures of shade-tolerant Hw and Cw (i) do not develop a stratified canopy in the stem exclusion stage on the study site, despite differences in early height growth, and (ii) do not show evidence of enhanced growth resulting from competitive reduction or facilitation.

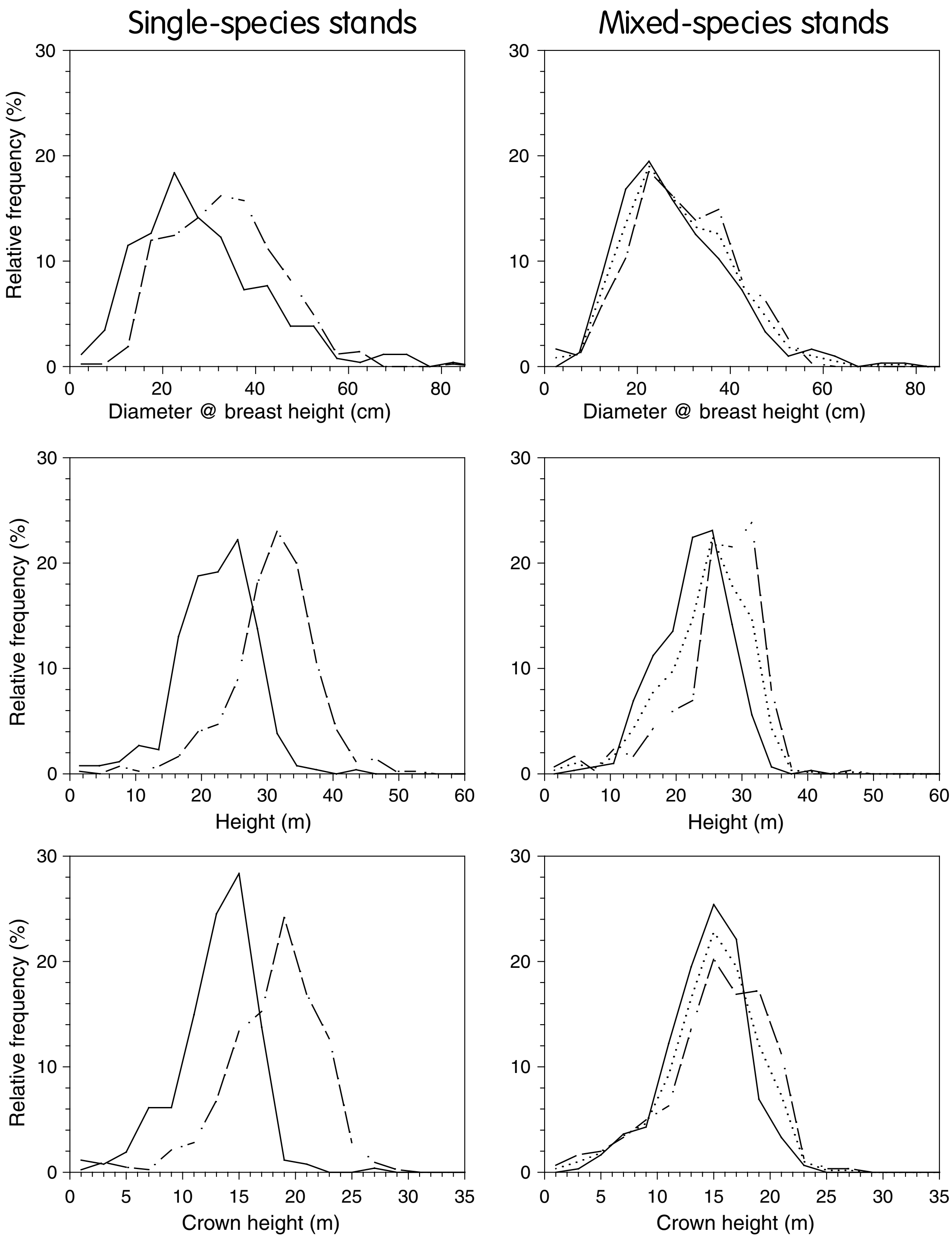

Figure 1. Diameter (@ breast height), height, and crown height frequency distributions of hemlock, redcedar, and both species in single- and mixed-species stands. Hemlock - dashed lines, redcedar - solid lines, both species - dotted lines.

Table 1. Mean and standard deviation (in parentheses) for diameter @ breast height (dbh), height, and crown height of redcedar and hemlock in the three stand types.

	Redcedar				Hemlock			
	n	Dbh (cm)	Height (m)	Crown height (m)	n	Dbh (cm)	Height (m)	Crown height (m)
Cw	261	28.4 (14.04)	22.2 (5.71)	13.0 (3.39)				
Hw-Cw	303	28.2 (11.65)	22.7 (5.29)	14.4 (3.45)	302	29.4 (10.90)	26.5 (6.62)	15.3 (4.46)
Hw					426	33.3 (11.49)	31.0 (6.55)	18.1 (4.11)

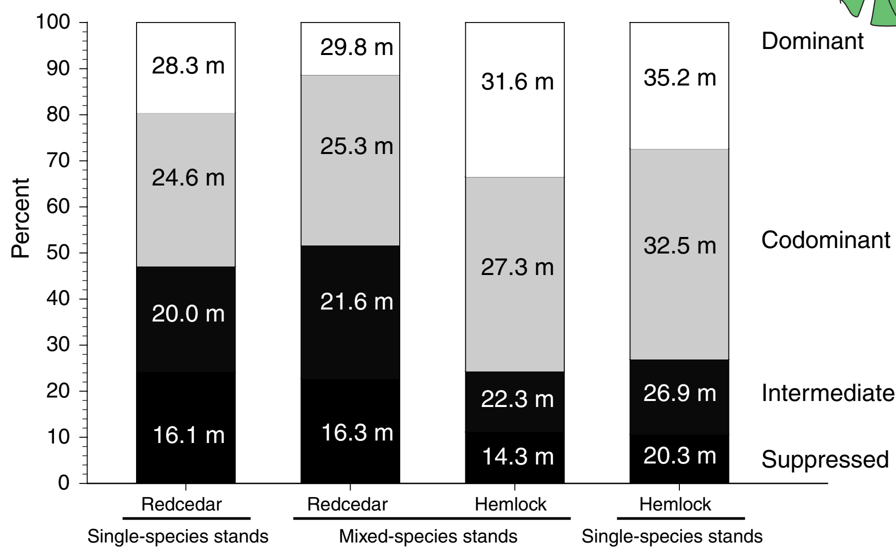

Figure 2. Distribution of crown canopy classes for redcedar and hemlock in single- and mixed-species stands. The numbers indicate the mean height values for the crown class of each species in each stand type.

These results suggest (i) lack of positive interactions, (*i.e.*, competitive reduction and facilitation) between Hw and Cw, and (ii) the possibility of a negative influence of Cw on the growth of Hw. We found no evidence that the mixtures develop stratified canopies. Based on the results at this stage of stand development, we conclude that Hw and Cw do not necessarily have a high combining ability as evidenced by lack of increased growth.

Silvicultural Implications

Foresters need to know how to differentiate between stratified and non-stratified canopies, and whether a mixture of two or more tree species will develop a stratified canopy, as the canopy stratification may influence silvicultural decisions affecting forest productivity, structural diversity, and understory plant diversity. We propose that stratified stands should have size distributions (diameter, height, or crown height) with clearly apparent modes, using either diameter or height frequency distributions as a quantitative measure. Taking into account the lack of canopy stratification in single-cohort, Hw-Cw mixtures, and the improved growth of Hw with decreasing presence of Cw, pure Hw stands appear to be the most productive tree species option.

Reference

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