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Forest Canopies and Their Influence on Understory Vegetation in Early-Seral Stands on West Vancouver Island

Abstract

The abundance of shrubs, salal and salmonberry in particular, is a characteristic feature of the understory in old-growth, west coast forest stands. We analyzed relationships between forest canopy cover and the cover of the shrub layer, salal, salmonberry, herb layer, and moss layer using data from 157 early-seral (35 year-old) stands from west Vancouver Island having variable canopy cover, canopy species, and site quality. The analysis indicated that (i) canopy cover was influenced by canopy species and site quality, (ii) canopy cover had a strong influence on the cover of shrubs but no influence on the cover of herb and moss layers, and (iii) site quality had a moderately strong influence on the cover of salal and salmonberry and a weak influence on the cover of shrub, herb, and moss layers. As the canopy cover decreased from 95 to 5%, the shrub cover consistently increased from about 5 to 95%. The canopy cover alone was a good predictor of the cover of shrubs ($R^2 = 0.83$), salal ($R^2 = 0.72$), and salmonberry ($R^2 = 0.73$), providing the stands were stratified into poor and rich soil nutrient strata. The quantified relationships between canopy cover and the cover of shrubs, salal, and salmonberry provide a simple tool for foresters to manipulate canopy cover of early-seral stands in perhumid cool mesothermal climates for creating suitable wildlife habitats.

Introduction

Stand structure describes the characteristics of canopy (tree layer) as well as understory vegetation (shrub, herb, and moss layers) and, thus, it describes habitat suitability for animal communities (e.g., Daniel et al. 1979, Kimmins 1987, Smith 1986). The structure of a forest stand depends on a number of factors, such as, site quality (climate, soil water, and soil nutrient conditions), history of disturbance, canopy species, stand density, and stand developmental stage.

Poorly developed understory vegetation is the natural characteristic of early-seral or stem exclusion stages of stand development (Oliver 1981). When timber production is the sole management objective, there is little impetus to change the structure of early-seral stands except to control stand density while maintaining high canopy cover: thus, the stem exclusion stage may extend over a long period of time. Manipulations of both stand density and canopy cover are tools which can enable foresters to modify stand structure and to promote the development of understory vegetation. Foresters, therefore, need to know the impact of canopy manipulations on the development of understory vegetation in early-seral stands, i.e., how understory

vegetation will respond to different light conditions imparted by a change in canopy cover. This knowledge may be useful in fine-tuning canopy manipulations to increase biodiversity or animal population in situations where the management goal is to maintain or improve wildlife habitats, in addition to producing wood.

The objectives of this study were (1) to characterize the forest canopy cover of seven tree species in relation to site quality and (2) to examine the possible influence of canopy cover and site quality on the cover of shrub layer, in particular salal (*Gaultheria shallon* Pursh) and salmonberry (*Rubus spectabilis* Pursh), herb layer, and moss layer by comparing estimated cover value data from 157 early-seral, west coast stands. Considering that salal (on poorer sites) and salmonberry (on richer sites) are (i) nearly absolute dominants in the shrub layer of late-seral west coast stands and (ii) important for wildlife in coastal British Columbia, our study focused on these two shrub species.

Materials and Methods

The 157 study stands were all plantations and included two B.C. Forest Service experimental

projects established in 7 locations over a wide range of sites on south-western Vancouver Island (Omule 1987, Omule and Krumlik 1987). The experimental design was a randomized complete block with 7 tree species replicated seven times in one location and with 4 tree species replicated five times in 6 locations. Twelve stands were rejected from a total of 169 stands as they were heterogeneous in soil moisture and nutrient conditions. A replicate (stand) consisted of 81 trees planted at square spacing of 3.5 m. All stands had a similar management history the cutting of old-growth stands, slashburning, and planting one of the following: Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), Pacific silver fir (*Abies amabilis* Dougl. ex Forbes), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn ex D. Don), or Port-Orford-cedar (*Chamaecyparis lawsoniana* (A. Murr.) Parl). The study stands, each approximately 0.01 ha square and containing one of the 7 study species, were 35 years-old and had a wide range in canopy cover.

The study area was within the Submontane (10 to 500 m in elevation) Very Wet Maritime Coastal Western Hemlock (CWHvm1) biogeoclimatic variant, influenced by a perhumid cool mesothermal climate (Klinka et al. 1991). Site association, which is comparable to habitat type (Pfister and Arno 1980), of biogeoclimatic ecosystem classification (Pojar et al. 1987) was used as a qualitative categorical measure of site quality. Within the CWHvm1 variant, site associations were determined by identifying soil moisture regime and soil nutrient regime for each study stand, and by using the site classification for coastal British Columbia (Green and Klinka 1994). The stratification of study stands according to site associations and tree species indicated (i) the presence of site quality gradient from slightly dry to very moist sites and from very poor to very rich sites, represented by 5 site associations, (ii) occurrence of all study stands on blueberry (*Vaccinium* spp.) (SA2) sites, and (iii) occurrence of only Douglas-fir, Sitka spruce, western hemlock, and western redcedar stands on all sites (SA1 through SA5) (Table 1).

The cover of forest canopy, shrub layer, salal, salmonberry, herb layer (including ferns and herbs), and moss layer (including mosses and liverworts) in each study stand was estimated visually from

TABLE 1. Stratification of the study stands according to tree species and site associations identified in the study area.

Tree species	Site association				
	SA1 ¹	SA2 ²	SA3 ³	SA4 ⁴	SA5 ⁵
Pacific silver fir	1	5	0	0	1
Grand fir	0	6	0	0	1
Western redcedar	2	15	2	5	9
Douglas-fir	2	15	3	5	10
Western hemlock	5	14	3	4	7
Port-Orford-cedar	0	7	0	0	0
Sitka spruce	3	15	4	5	8

¹SA1: CwHwSalal; slightly dry and very poor, poor, and medium sites.

²SA2: HwBaBlueberry (*Vaccinium alaskense*, *V. ovalifolium*, and *V. parvifolium*); fresh and very poor, poor, and medium sites.

³SA3: BaCwFoamflower (*Tiarella trifoliata* and *T. laciniata*); fresh and rich and very rich sites.

⁴SA4: HwBaDeer fern (*Blechnum spicant*); moist and very moist and very poor, poor, and medium sites.

⁵SA5: BaCwSalmonberry; moist and very moist and rich and very rich sites.

Dry to very moist soil moisture regimes are defined by actual evapotranspiration (Et):potential evapotranspiration (Emax) ratio plus depth to water table (after Klinka et al. 1989a). Soil nutrient regimes are defined by mean mineral soil (0 - 30 cm) mineralizable-N (after Varga and Klinka, unpublished data).

4 observation points using percent cover (the vertical crown or shoot-area projection in the stand) (Mueller-Dombois and Ellenberg 1974). Soil moisture and nutrient regimes were identified in the field using a combination of topographic and soil morphological properties and the procedure described by Green and Klinka (1994).

Homogeneity of variance in cover data was tested using Bartlett's procedure (Zar 1984). All variables were assessed for normality using probability plots (Chambers et al. 1983). The linear model (Wilkinson et al. 1992) used for testing the effect of canopy species, site association, and their interaction with canopy cover was:

[1] $A = m + SPECIES + SA + SPECIES*SA + e$
 where A is canopy cover, m is the overall mean, $SPECIES$ is canopy species, SA is site association, $SPECIES*SA$ is the interaction term, and e is the error term. This test included only Douglas-fir, Sitka spruce, western hemlock, and western redcedar stands ($N = 136$) because they occurred on all sites (Table 1).

The linear model used for testing the effect of canopy cover, canopy species, and their interaction with the cover of understory vegetation was:

$$[2] Y = m + A + SPECIES + A * SPECIES + e$$

where Y is the cover of shrub layer, salal, salmonberry, herb layer, or moss layer; m is the overall mean; A is canopy cover; $SPECIES$ is tree species; $A * SPECIES$ is the interaction term; and e is the error term of the model. This test included only stands on blueberry sites (SA2) ($N = 77$) because all study tree species occurred on these sites (Table 1).

One-way ANOVA and Tukey's test (Zar 1984) were conducted to detect differences in the cover of forest canopy, shrub layer, salal, salmonberry, herb layer, and moss layers between study stands grouped according to site associations or tree species. Regression analyses (Draper and Smith 1966, Chatterjee and Price 1977) were used to examine relations of canopy cover and site quality to the cover shrub, layer, salal, salmonberry, herb layer, and moss layer.

Results

ANOVA by model [1] indicated that (i) the forest canopy cover varied with canopy species ($p < 0.001$) and site quality ($p < 0.001$) and (ii) there was interaction between canopy tree species and site quality ($p < 0.001$). Each canopy tree species had the lowest cover on salal (SA1, slightly dry and poor) sites and the highest cover on foamflower (*Tiarella* spp.) (SA3, fresh and rich) sites (Figure 1). On foamflower sites canopy cover decreased in order from Sitka spruce to Douglas-fir to western hemlock to western redcedar.

ANOVA by model [2] indicated that on blueberry (SA2, fresh and poor to medium) sites (i) the cover of shrub layer and salmonberry was significantly related to canopy cover but not to canopy species, (ii) salal cover significantly interacted with canopy cover and canopy species, and (iii) the cover of herb and moss layers was not significantly related to the canopy cover or canopy species (Table 2).

Stratification of 157 study stands according to site associations (Table 3) and canopy species (Table 4) indicated that the mean cover of forest canopy and understory vegetation layers had a great variability within site association and canopy species. Comparisons among site associations showed that the mean canopy cover was the low-

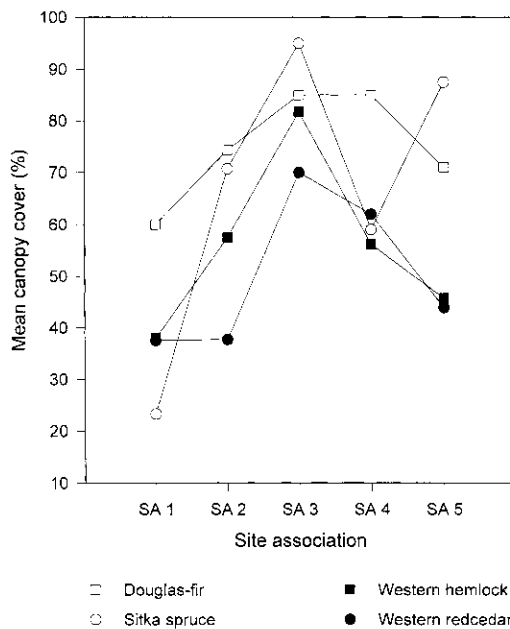


Figure 1. Mean canopy cover of early-seral Douglas-fir, Sitka spruce, western hemlock, and western redcedar stands according to site quality. Number of stands for each species and site association and abbreviations for site associations are given in Table 1.

TABLE 2. Results (p values) of ANOVA of canopy cover (A), tree species (SPECIES), and their interaction (A*SPECIES) on the cover of shrub layer, salal, salmonberry, herb layer, and moss layer, using linear model [2].

Source	Shrub layer	Salal	Salmonberry	Herb layer	Moss layer
A	0.000	0.636	0.049	0.440	0.143
SPECIES	0.475	0.022	0.154	0.610	0.069
A*SPECIES	0.351	0.015	0.247	0.643	0.109

est and the shrub layer was the highest on salal sites, while the opposite was determined for foamflower sites (Table 3). The salal cover was the highest on salal sites and the lowest on foamflower and salmonberry (SA5, moist and very moist, rich and very rich) sites. The salal cover decreased and the salmonberry cover increased from poor to rich sites, but this trend appeared to be confounded with the variation in canopy cover. The cover of herb and moss layers was low, in general $< 20\%$, and without any apparent relationship to site quality.

TABLE 3. Mean, minimum, and maximum values (%) of the cover of forest canopy, shrub layer, salal, salmonberry, herb layer, and moss layer in the study stands stratified according to site associations. Abbreviations for site associations as in Table 1. Values in the same row with the same superscript are not significantly different ($p < 0.05$, Tukey's test).

Character	Site association				
	SA1 n=13	SA2 n=77	SA3 n=12	SA4 n=19	SA5 n=36
Forest canopy	37.7 ^c 5-65	59.7 ^b 25-95	85.0 ^a 65-95	66.1 ^{a,b} 25-95	61.5 ^b 20-95
Shrub layer	80.8 ^c 35-95	51.8 ^{a,b} 1-95	6.5 ^c 1-35	43.6 ^b 1-95	44.9 ^{a,b} 1-95
Salal	61.5 ^a 25-80	23.2 ^b 0-85	4.5 ^c 0-25	29.2 ^b 1-90	7.6 ^c 0-25
Salmonberry	3.1 ^a 0-10	18.1 ^{a,c} 0-75	1.2 ^c 0-5	10.3 ^b 0-65	35.6 ^a 0-90
Herb layer	10.7 ^b 3-45	17.8 ^{a,c} 1-30	11.3 ^b 1-40	10.2 ^b 1-40	23.8 ^a 3-70
Moss layer	9.7 ^{a,b} 0-50	20.2 ^a 0-60	3.7 ^b 1-15	9.8 ^c 1-40	20.1 ^a 2-40

Comparisons according to canopy species in 157 study stands indicated that the mean canopy cover was highest and that of the shrub layer was lowest in Port-Orford-cedar, Douglas-fir, and Sitka spruce stands, while the opposite was found for grand fir, Pacific silver fir, western hemlock, and

western redcedar stands which had nearly consistently open canopy (canopy cover <50%) (Table 4). Regardless of species, the cover of salal and salmonberry appeared to be related to canopy cover, i.e., it was always higher in open-canopy stands and lower in closed-canopy stands. The cover of herb layer had no relationship to canopy species, but the cover of moss layer showed a weak relationship to canopy cover both being the highest in the open-canopy stands of Pacific silver fir and grand fir.

To examine relationships of canopy cover and site quality (independent variable) to the cover of shrub layer, salal, and salmonberry (dependent variables), multiple regressions were developed (Table 5). Canopy cover was a better predictor of the cover of understory vegetation than site association. The performance of the models decreased in order from the shrub to salal to salmonberry model. Canopy cover accounted for the largest proportion of the variation in the shrub cover of all models tested ($R^2 = 0.83$, Table 5, Figure 2). Multiple regressions using canopy cover and site associations as dummy variables resulted in improved performance for predicting the cover of salal (model [4]) and salmonberry (model [5]).

The models using canopy cover and site association as predictors, accounted for 58% and 43% of the variation in the cover of salal and salmonberry, respectively (Table 5). Considering the strong

TABLE 4. Mean, minimum, and maximum values (%) of the cover of forest canopy, shrub layer, salal, salmonberry, herb layer, and moss layer in the study stands stratified according to tree species. Values in the same row with the same superscript are not significantly different ($p < 0.05$, Tukey's test).

Character	Tree species						
	Pacific silver fir n=7	Grand fir n=7	Western redcedar n=33	Douglas- fir n=35	Western hemlock n=33	Port-Orford- cedar n=7	Sitka spruce n=35
Forest canopy	44.3 ^b 35-60	42.1 ^b 30-55	45.0 ^b 20-85	75.0 ^a 50-95	54.1 ^b 15-85	80.7 ^a 65-95	71.6 ^a 5-95
Shrub layer	65.7 ^a 40-80	77.1 ^a 55-95	72.0 ^a 10-95	23.1 ^b 1-60	61.5 ^a 1-95	17.1 ^b 5-35	35.1 ^{a,c} 1-95
Salal	23.6 ^{a,b} 5-70	20.7 ^{a,b} 5-35	30.7 ^a 1-80	9.6 ^{a,b} 0-50	31.9 ^a 2-85	10.3 ^{a,b} 2-20	19.5 ^{a,b} 0-90
Salmonberry	37.9 ^a 5-60	46.4 ^a 40-60	29.6 ^a 0-90	10.7 ^b 0-50	19.6 ^{a,b} 0-85	4.6 ^c 2-5	8.7 ^b 0-45
Herb layer	18.6 ^a 10-60	21.4 ^a 10-30	22.0 ^a 4-50	17.0 ^a 2-70	17.5 ^a 1-40	11.4 ^c 5-20	12.4 ^c 1-35
Moss layer	37.9 ^a 20-60	35.7 ^a 10-50	15.2 ^b 0-40	14.7 ^c 2-40	14.8 ^b 0-50	17.6 ^{a,b} 10-30	13.9 ^b 0-60

TABLE 5. Selected models for the regression of the cover of shrub layer, salal, salmonberry, herb layer, and moss layer on forest canopy cover (A) and site association (SA). All model are significant at $p < 0.05$. Abbreviations for site associations as in TABLE 1. SA1 through SA5 are dummy variables designating SAs with unit value 0 or 1. N = 157.

[3]	Shrub layer (%) = $113.68 - 0.625A(\%) - 0.007A^2(\%)$ Adjusted $R^2 = 0.83$ SEE = 13.9%
[4]	Salal (%) = $43.102 - 0.579A(\%) + 40.245(SA1) + 14.646(SA2) + 10.578(SA3) + 24.326(SA4)$ Adjusted $R^2 = 0.58$ SEE = 15.6%
[5]	Salmonberry (%) = $72.825 - 0.607A(\%) - 46.856(SA1) - 18.466(SA2) - 19.971(SA3) - 22.461(SA4)$ Adjusted $R^2 = 0.43$ SEE = 18.2%

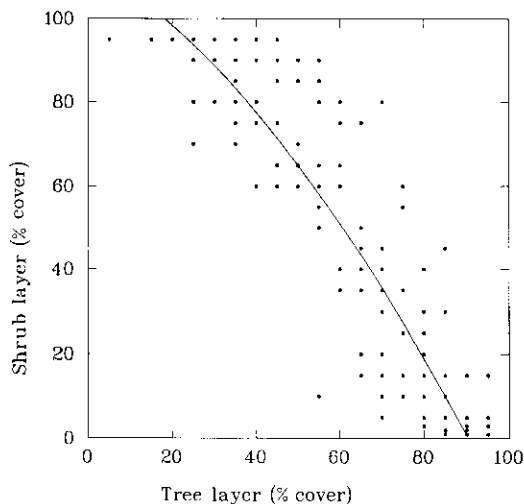


Figure 2. Scattergram and fitted regression line of shrub cover on forest canopy cover using model [3] (Table 5).

relationship between the canopy and shrub covers, a limited success of these models was not expected. Therefore, we examined the relationship between the cover of salal and salmonberry. Visual examination of the resulting scattergram suggested that these species occupy different edaphic niches. In the stands with the cover of salal $>40\%$, salmonberry had $<20\%$ cover and was confined to special microsites, usually disturbed soils or shallow depressions. Similarly, when the cover of salmonberry was $>20\%$, salal had $<35\%$ cover and was confined to special microsites, usually thick forest floors. The stands with a high

salal cover ($>40\%$) were those with open canopy and located typically on very poor and poor sites, less often on medium sites. The stands with a high salmonberry cover ($>20\%$) were also those with open canopy but located typically on rich and very rich sites, less often on medium sites.

Considering a consistently low cover of salal on rich and very rich sites (SA3 and SA5), and a consistently low cover of salmonberry on very poor and poor sites (SA1, SA2, and SA4), stronger relationships between forest canopy cover and the cover of each species may be expected by deleting from the complete data set the stands on rich and very rich sites for regressing salal cover on canopy cover ($n = 115$), and the stands on very poor and poor sites for regressing salmonberry cover on canopy cover ($n = 121$). Using only canopy cover as the predictor, models [6] and [7]), each based on a presumed nutrient niche, explained $>70\%$ of the variation in the cover of salal and salmonberry (Table 6).

TABLE 6. The models for regression of salal and salmonberry on forest canopy cover (A) using for each species the data set based on its a presumed nutrient niche. Both models are significant at $p < 0.05$.

[6]	Salal (%) = $94.295 - 1.038A(\%)$ Adjusted $R^2 = 0.72$ SEE = 14.3% $n = 115$
[7]	Salmonberry (%) = $96.215 - 1.088A(\%)$ Adjusted $R^2 = 0.73$ SEE = 13.5% $n = 121$

Discussion

Our study of the 35 year-old, early-seral, west coast stands endorses the well-known fact that forest canopy cover, controlling below-canopy light conditions, strongly affects the cover of understory vegetation; other factors, such as site quality, pre-disturbance vegetation, and the type of disturbance, have a greater influence on the composition of understory vegetation (Daubenmire 1974, Kimmins 1987).

In the study stands, the canopy cover itself was influenced by canopy species and site quality, i.e., its influence was canopy species- and site-specific. Omule (1987), and Omule and Krumlik (1987) attributed the variation in the canopy cover to between-stand differences in site quality and between-species differences in initial mortality

and growth rates. Thus, on the nitrogen-poor, salal sites, which had the lowest canopy cover, salal must have re-established very shortly after disturbance, assumed dominance in the shrub layer, and interfered with the survival and growth of planted seedlings, especially those with a slow initial growth, as observed also by Messier and Kimmins (1990). On the nitrogen-rich, foamflower sites, early-seral vegetation was likely herbaceous and did not interfere with the survival and growth of planted seedlings, especially those with a fast initial growth.

Many authors (cited by Haeussler et al. 1990) have reported an inverse relationship between canopy cover and salal or salmonberry cover. The cover and vigour of both species in the study stands increased with decreasing canopy cover, and both species were shaded out when the canopy cover was approximately > 85%. The salal cover estimated by model [6] (Table 5) agrees with the predictions given for several canopy cover values by Messier and Kimmins (1990).

Salal and salmonberry grow best in perhumid cool mesothermal climates and both species are considered moderately shade-tolerant (e.g., Sabhasri 1961, Klinka et al. 1989a, Haeussler et al. 1990). The understory light conditions imparted by the canopy cover > 85% [corresponding approximately to <5% of above canopy light in mixed western hemlock-western redcedar stands (Messier and Kimmins 1990)] did not support salal growth in climatically comparable conditions on northern Vancouver Island (*op. cit.*). The same study and Sabhasri (1961) demonstrated that with decreasing light, salal responded with the structural changes expected in shade-intolerant species. The growth habit observed in both salal and salmonberry in the closed-canopy stands was strongly erect, loosely branched growth with a very low foliar biomass which is characteristic for shade-intolerant plants (Kimmins 1987). When the canopy cover approached 80%, we observed salal as tall as 4 m and salmonberry as tall as 6 m, which are greater heights than those given in Haeussler et al. (1990).

The difference in soil nutrient niche between salal and salmonberry in the study stands agreed with Sabhasri (1960), Franklin and Dyrness (1973), Klinka et al. (1989a), and Haeussler et al. (1990). It appears that the ecological amplitude of salal in relation to available soil nitrogen (Table 1) is

within very poor, poor, and medium soil nutrient regimes, and that of salmonberry is within medium, rich and very rich soil nutrient regimes. A high salal cover (absolutely dominating) in west coast forest stands has been documented to be associated with the presence of acid Mor humus forms, often with ligneous residues; a high salmonberry cover (absolutely dominating) with the presence of less-acid, friable, Moder and Mull humus forms (Klinka et al. 1989b, 1990; Messier and Kimmins 1990). Salal and other ericaceous plants are known to tolerate acid and nitrogen-poor soils whereas salmonberry grows predominantly in association with nitrophilous species (e.g., Sabhasri 1960, Ellenberg 1974).

A generally low cover of herb and moss layers in the study stands was likely the reason for weak relationships between their cover and forest canopy cover or site quality (Table 2). This suggests that abundance of herbs in the study stands depends on some other factors, possibly shrub cover. Providing adequate light conditions (<80% of canopy cover), shrubs (either salal or salmonberry) always had higher cover than herbs, except on foamflower sites on which forest floors were shallow and friable. Reasons for low abundance of herbs and bryophytes can not be determined with certainty. Depending on site, the predominance of ericaceous species and salmonberry is the characteristic feature of old-growth stands in very wet cool mesothermal climates (Franklin and Dyrness 1973, Meidinger and Pojar 1991). We presume that this feature has been imparted to early-seral stands and that well developed and dense shrub layers have suppressed the development of the lower herb and moss layers.

The quantified relationships between canopy cover and the cover of salal and salmonberry provide a simple tool for foresters to predict how these species will respond to manipulation of the canopy in early-seral, immature stands in perhumid cool mesothermal climates. This prediction can be made by estimating canopy cover of a stand together with the soil nutrient regime of a site, i.e., estimates routinely employed in preparing silvicultural prescriptions in British Columbia. Both salal and salmonberry are important wildlife foods in coastal B.C., particularly for black-tailed deer (e.g., McTaggart-Cowan 1945, Rue 1978, Brown 1961) and black and grizzly bears (Herrero 1985). For example, if the management goal in an area

is to maintain or improve wildlife habitat in addition to producing wood, then canopy of fully stocked stands (>80% canopy cover) on fresh, moist and very moist, and rich and very rich sites (SA4 and SA5) should be opened to provide a higher understory light availability for the development of moderately shade-tolerant salmonberry. Canopy cover need not be significantly and uniformly reduced the canopy cover of 60% would result in approximately 40% salmonberry cover, which could be distributed either more or less uniformly throughout the stand or in randomly or systematically distributed gaps. Once salal or salmonberry are present on a site, further expansion is almost exclusively by vegetative means including layering and sprouting or suckering from roots and stem bases.

Conclusions

The canopy cover of early-seral west coast stands was influenced by canopy species and site quality, had a strong influence on the cover of understory shrubs, and had no influence on the cover

of herb and moss layers. Site quality had a moderate influence on the cover of salal, and salmonberry. Canopy cover alone was a good predictor of shrub cover, as well as the cover of salal and salmonberry, providing stratification of stands into poor and rich soil nutrient strata. These results suggest that (i) the cover of shrub layer can be decreased or increased by increasing or decreasing canopy cover and (ii) both salal and salmonberry are moderately shade-tolerant species, each with different ecological soil nutrient amplitude.

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