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Relations Between Site Index, Salal, Plant Communities, and Sites in Coastal Douglas-fir Ecosystems

Abstract

Salal is often considered an undesirable forest plant in coastal British Columbia and is thought to have adverse effects on tree growth. To assess the relationship between salal cover and tree growth in southwestern British Columbia, vegetation data from 101 sample plots in disturbed immature Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] plantations were analyzed. This analysis indicated that the plots could be placed into one of five vegetation units. To eliminate non-plant influences on Douglas-fir growth, plots with the same climatic, soil moisture, and soil nutrient regimes in two vegetation units where salal was most and least abundant, were selected for detailed analysis. This analysis indicated that there were no significant differences between the two sets of plots in Douglas-fir foliar nutrients despite the fact that one set had high cover and the other low cover of salal. Furthermore, regression analyses indicated a poor relationship between site index and salal cover suggesting that salal cover had no major adverse effect on Douglas-fir height growth. When data from all the study plots were analyzed, it was found that variables representing the soil moisture or nutrient regimes were better predictors of site index than were various vegetation variables, not involving salal cover. Salal cover was a poorer predictor of site index than any of these variables. It is concluded that salal may not necessarily significantly influence tree growth in the ecosystems studied.

Introduction

Classification of forest lands according to ecological site quality is recognized as being essential for sound forest management. Recent efforts have attempted to (a) identify ecological variables controlling forest productivity and (b) use these variables to estimate potential productivity of crop trees on different sites. This study examines relationships of vegetation and sites to site index in coastal Douglas-fir ecosystems by applying the methods of biogeoclimatic ecosystem classification (Pojar *et al.* 1987), with particular attention to salal (*Gaultheria shallon* Pursh).

The influence of salal on tree growth has attracted considerable research attention in coastal British Columbia resulting in the development of the Salal-Cedar-Hemlock Integrated Research Program (W. W. Bourgeois, pers. comm.). Field observations, surveys, and studies in the Wet or Very Wet, Hypermaritime or Maritime Coastal Western Hemlock subzones have indicated that the growth performance of crop tree species in salal-dominated plantations, and immature and old-growth stands is very poor (e.g., Lewis pers. comm., Germain 1985, Weetman *et al.* pers. comm.). Where sites have been burned and planted, tree growth has improved; similarly, dense, naturally regenerated, immature stands that developed after disturbance by wind or harvesting feature rapid growth rates and a nearly complete absence of salal.

An ecological parallel between the growth stagnation in salal-dominated and other ericaceous species-dominated ecosystems, e.g., *Calluna*-ecosystems in Britain (Malcolm 1987) and *Kalmia*-ecosystems in eastern Canada (Damman 1971), has been suggested by G. F. Weetman (pers. comm.). As there is some evidence of an adverse, direct or indirect, influence of ericaceous plants on forest productivity, foresters in coastal British Columbia consider the presence of salal undesirable and expect treatments that eradicate the species are likely to improve forest growth.

This study examines (1) the possible effect of salal on the stand and soil nutrient status and site index and (2) the relations between site index, salal, plant communities, and sites in disturbed, immature, coastal Douglas-fir ecosystems. These objectives are accomplished by comparing vegetation and environmental characteristics of 101 ecosystems and through the use of analysis of variance and regression analysis. Differences in foliar and soil nutrient characteristics and site index between stands with high and low salal cover are examined on a population of 30 biologically-equivalent ecosystems with the same climatic, soil moisture, and soil nutrient regimes. The authors recognize that, when stands of different vegetation are compared on similar sites, the question always remains whether differences in productivity are due to differences in vegetation changes, or manifest original differences in site quality.

Study Area

All study ecosystems were located within the Very Dry Maritime CWH (CWHxm) subzone on eastern Vancouver Island and the Dry Maritime CWH (CWHdm) subzone on the adjacent mainland (Carter and Klinka 1988). This area is characterized by a very dry (CWHxm subzone) to dry (CWHdm subzone) maritime cool mesothermal climate and it is underlain by volcanic rocks (Vancouver Island) or granitic rocks (coastal mainland). Glacial till is the most common landform, although fluvial or marine deposits are frequently encountered. Soils are typically coarse-textured (loamy-sand to sandy-loam) Humo-Ferric Podzols (Canada Soil Survey Committee 1978). Most soils have a high content of coarse fragments and are acidic with acidity decreasing with depth.

Old growth forests are usually dominated by western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] and Douglas-fir with significant amounts of western redcedar (*Thuja plicata* Donn *ex* D. Don *in* Lamb.). Second growth forests are usually dominated by naturally regenerated or planted Douglas-fir. A high cover of ericaeous species (e.g., *Gaultheria shallon* Pursh and *Vaccinium parvifolium* Sm. *in* Rees) and acidiphilous mosses [e.g., *Hylocomium splendens* (Hedw.) B.S.G., *Kindbergia oregana* (Sull.) Ochyra, *Plagiothecium undulatum*, (Hedw.) B.S.G., and *Rhytidiadelphus loreus* (Hedw.) Warnst.] are the characteristic floristic features of zonal ecosystems. A more complete description of the study area is given by Carter and Klinka (1988).

Materials and Methods

The study stands were all plantations and part of a larger fertilization study (Carter and Klinka 1988). The stands were dominated by Douglas-fir, even-aged with a relatively narrow range in age (18 to 43 years), stocking (400 to 880 stems/ha), and free of disease and insect problems. All study stands had a similar management history following the harvest of old growth stands: slashburning, planting to Douglas-fir of various coastal seed sources, and spacing treatment.

Sample plots within these stands were chosen to represent the major segments of the soil moisture and soil nutrient gradients present in the CWHxm and CWHdm subzones. In each stand a 20 × 20 m plot (0.04 ha) was selected to represent an individual ecosystem relatively uniform in understory vegetation and soils.

Vegetation, topography, and soils of each plot were described using a simplified version of the standard procedure employed by Ecological Program Staff of the B.C. Forest Service (Walmsley *et al.* 1980). The cover of all species present in the shrub, herb, and moss layers was estimated visually using the species significance scale (Mueller-Dombois and Ellenberg 1974). Species growing exclusively as epiphytes, on decaying wood, and/or coarse fragments/rocks were not included in the analysis. Soil moisture and nutrient regimes were identified in the field using the methods described by Klinka *et al.* (1984) and Carter and Klinka (1988). Forest floors and soils were described and identified according to Klinka *et al.* (1981) and Canada Soil Survey Committee (1978) respectively. Site index was calculated using Bruce (1981) with measurements of age and height for not less than 30 dominant and codominant trees per stand.

Sample plots were classified using the methods and system of biogeoclimatic ecosystem classification as described by Pojar *et al.* (1987). The classification was based on plant species present in the understory stratum, using tabular comparisons (Westhoff and van der Maarel 1980), diagnostic criteria (Pojar *et al.* 1987), and VTAB tabling program (Emanuel pers. comm.). To examine consistency of groupings obtained from the tabular comparisons, multivariate analysis of vegetation was conducted using principal components analysis (Fox and Guire 1976), and the ORDIFLEX program of Gauch (1977). PCA was performed on a correlation matrix (Noy-Meir and Whittaker 1977), using only those species included in the diagnostic table.

On each plot the current year's foliage from the upper crown of 15 dominant or codominant trees was sampled in October, and analyzed for total N, P, K, S, SO_4-S, Ca, Mg, "active" Fe, Mn, Cu, Zn, and B following the guidelines and procedure given by Ballard and Carter (1986). The same guidelines were used to evaluate forest stand nutrient status using concentrations (dry-mass basis) and total content (milligrams per 100 needles).

On the 56 sample plots forest floor and mineral soil physical and chemical properties were examined and sampled separately at five random sampling points in each of these plots. Composite samples of forest floor and composite bulk samples of 0-30 cm mineral soil were taken from three points of an equilateral triangle (2 m on a side), located over each point. Bulk density was measured near the point from which each soil sample was collected by cutting out a core, measuring its volume, and measuring its mass after oven-drying at 105°C to constant mass. All soil samples were air-dried to constant mass; forest floor samples were then ground in a Wiley mill to pass a 2-mm sieve, while mineral soil samples were sieved through a 2-mm sieve to separate coarse fragments. Soil pH was measured with a pH meter and glass plus reference electrodes using a 1:1 suspension in water for the mineral soil and a 1:5 suspension for forest floor material. Total C was determined using a Leco Induction Furnace (Bremner and Tabatabai 1971). Total N was determined by semimicro-kjeldahl digestion followed by estimation of NH_4 using a Technicon Autoanalyzer (Anonymous 1976).

Mineralizable-N was determined by an anaerobic incubation procedure modified from Waring and Bremner (1964). Released NH_4 was determined colorimetrically using a Technicon Autoanalyzer.

Mineralizable-N was expressed as concentrations on a dry mass basis and, where applicable, on a mass per unit area basis. The mass per unit area calculation used bulk density corrected for coarse fragment content for both forest floor and mineral soil and the results represent mass per hectare in the forest floor and surface 30 cm of the mineral soil.

Actual evapotranspiration (E_t) and components of the annual water balance were calculated using a slight modification of the Energy-Soil Limited water balance model of Spittlehouse and Black (1981) and 30-year normals for precipitation and temperature (Anonymous 1982). This model is driven by solar radiation, temperature, and precipitation using soil rooting depth and texture data to calculate available water storage capacity. Growing-season water deficit (WD) was calculated as the sum of daily potential evapotranspiration (E_{max}) minus E_t, for each day of the growing season (April-September). E_t was calculated as monthly totals during the growing season and as a growing season total.

Homogeneity of variance in vegetation cover and nutrient data was tested using Bartlett's procedure (Zar 1974). One-way analysis of variance (ANOVA) and T-tests (Zar 1974) were conducted to detect differences between vegetation units and site index, salal cover, foliar nutrients, soil chemical properties, and components of the annual water balance. Multiple comparisons were carried out on sample means using Scheffe's allowances (Zar 1974). Simple and multiple regression analyses were employed to examine relationships between site index, salal cover, vegetation units, and soil moisture and nutrient regimes (Chatterjee and Price 1977).

Results and Discussion

Plant Community Classification and Delineation of Biologically-equivalent Sites with High and Low Salal Cover

All the sample plots were classified into a hierarchy of vegetation units (associations and subassociations) representing early stages of secondary succession on different sites. For two of the three plant associations, two subassociations were delineated, making a total of five basic vegetation units (one plant associations and four subassociations) (Table 1). The associations and subassociations were delineated according to the floristic differences between the groups of plots (diagnostic combinations of species) which are summarized in Table 2. These vegetation units were named by the generic names of diagnostic or dominant understory species, as Douglas-fir was the dominant tree species in all units. The specific names were used to prevent ambiguities.

TABLE 1. The vegetation units distinguished in the study plots.

Plant association Plant subassociation
Gaultheria—Mahonia
Gaultheria—Mahonia—Polytrichum (juniperinum) (1)[1]
Gaultheria—Mahonia—Rhytidiadelphus (2)
Mahonia—Kindbergia (3)
Polystichum—Mycelis
Polystichum—Mycelis—Mahonia (4)
Polystichum—Mycelis—Rubus (spectabilis) (5)

[1] A numerical symbol for a vegetation unit.

TABLE 2. Diagnostic combination of species for the plant associations (a.) and subassociations (sa.) distinguished in the study plots.

Number of plots		13		26		26		30		6	
Vegetation units and species	Diagnostic value[1]	Presence class[2] and mean species significance[3]									
Gaultheria—Mahonia a.											
Gaultheria shallon	(dd)	V	9	V	8	V	5	IV	4	I	1
Pinus monticola	(d)	III	1	II	1	I	+	I	+	I	1
Rosa gymnocarpa	(d)	III	1	III	1	I	+	I	+		
Gaultheria—Mahonia—Polytrichum (juniperinum) sa.											
Polytrichum juniperinum	(d)	III	1	I	+	I	+	I	+	I	+
Gaultheria—Mahonia—Rhytidiadelphus sa.											
Achlys triphylla	(d)	II	+	IV	4	IV	3	V	4	III	4
Rhytidiadelphus loreus	(d)	I	+	III	1	II	+	III	1	II	+
Mahonia—Kindbergia a.											
Polystichum—Mycelis a.											
Galium triflorum	(d)	I	+	I	+	II	+	IV	1	V	2
Polystichum—Mycelis—Mahonia sa.											
Achlys triphylla	(d,c)	II	+	IV	4	IV	3	V	4	III	4
Gaultheria shallon	(d)	V	9	V	8	V	5	IV	4	I	1
Hylocomium splendens	(d)	III	1	III	2	IV	2	IV	4	II	+
Mahonia nervosa	(d)	V	3	V	3	IV	4	IV	3	I	1
Rubus ursinus	(d,c)	V	1	V	2	V	2	V	2	III	1
Polystichum—Mycelis—Rubus (spectabilis) sa.											
Athyrium filix-femina	(d,c)			I	+	I	+	I	+	V	4
Bromus vulgaris	(d)	II	+	II	+	II	+	II	1	IV	2
Dicentra formosa	(d)									III	2
Gymnocarpium dryopteris	(d)					I	+	I	+	IV	4
Petasites palmatus	(d)									III	2
Rubus spectabilis	(d,cd)	I	+	I	+	III	2	III	3	V	6
Sambucus racemosa	(d)					I	+	I	+	IV	3

[1] Species diagnostic values: d—differential, dd—dominant differential, cd—constant dominant, c—constant (Pojar *et al.* 1987).

[2] Presence classes as percent of frequency: I = 1-20, II = 21-40, III = 41-60, IV = 61-80, V = 81-100.

[3] Species significance class midpoint percent cover and range: + = 0.2 (0.1-0.3), 1 = 0.7 (0.4-1.0), 2 = 1.6 (1.1-2.1), 3 = 3.6 (2.2-5.0), 4 = 7.5 (5.1-10.0), 5 = 15.0 (10.1-20.0), 6 = 26.5 (20.1-33.0), 7 = 41.5 (33.1-50.0), 8 = 60.0 (50.1-70.0), 9 = 85.0 (70.1-100).

In order to examine the possible effect of salal on the stand and soil nutrient status and site index, it was necessary to consider only a group of plots with the same climatic, soil moisture, and soil nutrient regimes in order to eliminate variation due to non-plant influences on tree growth.

Based on a comparison of the site characteristics for each of the vegetation units (Table 3) and an assessment of where salal was most abundant (in the *Gaultheria—Mahonia* association), it was decided to use plots from the *Gaultheria—Mahonia—Rhytidiadelphus* and *Mahonia—Kindbergia* units. These two vegetation units have similar soil properties as indicated by the data in Table 4. T-tests indicated that the only significant differences between the two units ($p < 0.05$) were in forest floor pH and total N. The quantitative soil parameters given in Table 4

TABLE 3. Average values of selected site characteristics of the distinguished vegetation units.

Vegetation unit	1	2	3	4	5
Number of plots	13	26	26	30	6
Biogeoclimatic unit[1]	CWHxm - dm				
Elevation (m)	270	230	250	230	210
Slope gradient (%)	16	17	16	19	8
Actual SMR[2]	VD	MD-SD	MD-F	SD-F	M
Actual SNR[3]	VP-P	VP-M	VP-M	P-R	R-VR
Humus form[4]	MR-MD	MR-MD	MR-MD	MR-MD	MD
Forest floor depth (cm)	3	4	3	4	4
Soil particle size[5]	S-L	S-L	S-L	S-L	L
Coarse fragments (%)	58	56	57	44	21
Rooting depth (cm)	60	60	60	70	90
Ground cover (%)					
—forest floor	75	82	69	70	82
—decaying wood	13	11	18	22	7
—mineral soil	3	<1	3	3	10
—coarse fragments	9	6	10	5	<1
Site index—mean	21	28	28	33	34
(m/50 yrs)—std. dev.	2.3	3.3	3.5	2.3	2.9

[1] CWHxm—Very Dry Maritime CWH subzone, CWHdm—Dry Maritime CWH subzone.

[2] SMR (soil moisture regime): VD—very dry, MD—moderately dry, SD—slightly dry, F—fresh, M—moist.

[3] SNR (soil nutrient regime): VP—very poor, P—poor, M—medium, R—rich, VR—very rich.

[4] MR—Mor, MD—Moder.

[5] L—loamy, S—sandy.

TABLE 4. Means and standard deviations (in parentheses) of some physical and chemical characteristics of the soils in the *Gaultheria—Mahonia—Rhytidiadelphus* and *Mahonia—Kindbergia* vegetation units.

Vegetation unit	*Gaultheria—Mahonia—Rhytidiadelphus*	*Mahonia—Kindbergia*
Number of plots	10	8
Actual evapotranspiration (mm/year)	236 (23)	221 (27)
Water deficit (mm/year)	43 (27)	65 (48)
Forest floor thickness (cm)	4.0 (2.4)	3.6 (2.2)
Forest floor pH	4.8 (0.3)	5.1 (0.2)
Forest floor C (%)	37.8 (4.0)	39.7 (3.8)
Forest floor N (%)	1.04 (0.12)	0.89 (0.11)
Forest floor C/N ratio	36 (5)	45 (4)
Forest floor mineralizable-N (ppm)	390 (138)	228 (188)
Mineral soil mineralizable-N (kg/ha)	14.1 (5.7)	16.5 (4.1)

are those which have been found to be the most important for characterizing soil moisture (Major 1963; Giles 1983; Carter and Klinka pers. comm.) and soil nutrient regimes (Carter and Klinka pers. comm.; Kabzems and Klinka 1987a,b; Courtin *et al.* in press). Accordingly 15 plots could be selected from each of the two vegetation units such that each plot had the same regional climate (the same biogeoclimatic subzone—CWHxm) and the same soil moisture (moderately dry) and nutrient (poor) regime. All these 30 plots are considered to have similar site quality and to develop in the climax *Pseudotsuga—Gaultheria—Mahonia* plant association (Kojima and Krajina 1975).

The major difference between the two sets of selected plots is in the cover of salal which ranged from a mean of 60 percent (5 to 100 percent range) for the 15 plots belonging to the *Gaultheria—Mahonia—Rhytidiadelphus* unit to a mean of 15 percent (0 to 33 percent range) for the 15 plots belonging to the *Mahonia—Kindbergia* unit. This difference in salal cover was significant at $p < 0.01$. Data from these 30 plots were then used to test two hypotheses; firstly that salal competes successfully against Douglas-fir for both available soil water and nutrients; and secondly, that there is a strong relationship between the cover of salal and Douglas-fir site index on these moderately dry, nutrient-poor sites.

Reasons for the difference in salal cover between the 30 biologically-equivalent plots cannot be determined with certainty. There is no information on understory vegetation in the original old-growth stands prior to their harvest. However, high salal cover (absolutely dominating) on very to moderately dry and nutrient-poor sites in the drier maritime CWH subzones has been documented and is generally associated with the presence of acid forest floors (Mor humus forms) and the absence of dense tree or high-brush layers (Spilsbury and Smith 1947; McMinn 1957; Mueller-Dombois 1959; Orloci 1961, 1964; Krajina 1969; Kojima and Krajina 1975; Beese 1981; Klinka and Krajina 1986).

The forest floor in old-growth stands of the *Pseudotsuga—Gaultheria—Mahonia* association was reported to have a mean of 4.4 cm and 3 to 12 cm range in thickness (compared to the mean of 3.5 cm and 1 to 12 cm range in this study), with a mean pH of 4.8 (range 4.2 to 5.5), and a mean C/N ratio of 37 (range 18 to 62) (Kojima and Krajina 1975). These data are characteristic of less-acidic Mors and Mormoders (Klinka *et al.* 1981, Klinka and Nuszdorfer 1988). In contrast, salal-dominated sites that feature forest growth stagnation generally have thick (usually over 10 cm) forest floors largely composed of residues which are resistant to decomposition and/or decaying coniferous wood (lignic and residuic Mors), are strongly acid (mean pH 3.8, range 3.1 to 4.3), and have a high C/N ratio (mean 54, range 34 to 79) (Klinka and Nuszdorfer 1988).

On nutrient-rich to -very rich sites with Moder or Mull humus forms, salal may be present but it is restricted to acid organic microsites, such as decaying coniferous wood (Kojima and Krajina 1975, Klinka and Krajina 1986). It is probable that high salal cover sites were not burned or burned only lightly with sufficient forest floor materials left for resprouting of rhizomes and re-establishment of salal during the treeless stages of succession, and that the understory light conditions during the life of the stands have provided for salal growth under the tree canopy (Long and Turner 1975, Stanek *et al.* 1979). Low salal cover sites might have a similar history of disturbance but the presence of dense tree or shrub layers restricted the development of semi-tolerant salal in the understory. Forest floor materials may also have been destroyed by fire with no suitable substrate left for salal establishment. Observations indicate that salal is absent in immature Douglas-fir stands with a dense western redcedar understory, probably due to poor light conditions and/or the effect of western redcedar on forest floor quality, or under the canopy of scattered bigleaf maple (*Acer macrophyllum* Pursh), likely due to the presence of Mull humus forms.

Relations Between Salal Cover, Foliar Nutrients, and Site Index on Biologically-equivalent Sites

In the absence of significant differences in soil moisture and soil nutrient characteristics, it might be expected that there were no significant differences between high and low salal cover sites in the foliar nutrient levels in the Douglas-fir trees. This was, in fact, found when the foliar nutrient levels were compared ($p < 0.05$; Table 5). There were also no significant differences ($p < 0.05$) between the sites in Douglas-fir site index. When the results of all comparisons between the high and low salal cover sites are

TABLE 5. Mean foliar nutrient concentrations (dry-mass basis) of the Douglas-fir trees in the 15 biologically-equivalent plots in each of the *Gaultheria—Mahonia—Rhytidiadelphus* and *Mahonia—Kindbergia* vegetation units. Standard deviations are given in parenthesis.

Nutrient element	*Gaultheria—Mahonia—Rhytidiadelphus*	*Mahonia—Kindbergia*
Mass of 100 needles (mg)	472 (79)	492 (71)
Nitrogen (%)	1.17 (0.078)	1.17 (0.116)
Phosphorus (%)	0.209 (0.036)	0.199 (0.042)
Calcium (%)	0.397 (0.067)	0.414 (0.047)
Magnesium (%)	0.130 (0.022)	0.129 (0.014)
Potassium (%)	0.689 (0.080)	0.687 (0.070)
Sulphur (%)	0.131 (0.023)	0.128 (0.018)
Sulphate-sulphur (ppm)	325 (135)	312 (133)
Copper (ppm)	3.9 (0.52)	3.7 (0.59)
Zinc (ppm)	19.4 (3.87)	20.5 (2.47)
Manganese (ppm)	547 (327)	499 (257)
Boron (ppm)	19.5 (8.82)	21.9 (5.87)
Active-iron (ppm)	42 (11.5)	39 (12.9)

taken into account, it appears that, on apparently biologically-equivalent sites, high salal cover did not adversely affect the height growth of Douglas-fir in the ecosystems studied.

Stanek *et al.* (1979) reported increases in the biomass and nitrogen content of salal following thinning and nitrogen fertilization in immature stands on sites similar to those used in the present study (i.e., the *Gaultheria—Mahonia* association), but concluded, in agreement with other workers (Gessel *et al.* 1973, Björkman *et al.* 1967, Mead and Pritchett 1975), that the amount of nitrogen tied up by salal was relatively small and not likely to be critical for tree growth except on nutrient-very poor sites (Miller *et al.* 1976).

Brix and Mitchell (1986), in a study of the same ecosystems examined by Stanek *et al.* (1979), suggested that removal of the salal understory in thinned and fertilized stands did not affect the soil or predawn shoot water potential. However, the studies of Black and coworkers (Spittlehouse and Black 1981, Tan *et al.* 1977, Kelliher and Black 1986, Price *et al.* 1986) showed that the salal understory can account for a large fraction of stand water consumption, especially toward the latter part of the dry period in late July and early August. Because Douglas-fir develops terminal buds approximately at the onset of the dry period, subsequent soil water deficits, possibly exacerbated by salal water consumption, are not likely to have a significant influence in height growth, vis-a-vis site index. This could explain the failure of this study to find significant differences in Douglas-fir site index between the high and low salal cover sites. The studies by Black and coworkers also showed that the removal of salal slightly improved basal area increment by 0.5 to 2.3 percent.

Relations Between Site Index, Salal Cover, Vegetation Units, and Site Variables

The frequency and mean cover of salal decreased from 100 percent and 73 percent in the *Gaultheria—Mahonia—Polytrichum (juniperinum)* unit to 16 percent and 0.6 percent in the *Polystichum—Mycelis—Rubus (spectabilis)* unit, respectively. If salal exerted a profound influence on forest productivity, then a reasonable relationship might be expected between its cover and stand growth performance. For this purpose, the relationship between site index and salal cover (estimated as midpoint percent cover of the species significance scale) was examined across all 101 study sites. A simple linear regression of SI (m/50 yr) as a function of salal cover produced the following equation:

$$[1]\quad SI = 32.44 - 0.71\ (\text{midpoint percent salal cover})$$
$$R^2 = 0.23 \qquad F = 30.17 \qquad SE = 4.45\ \text{m}$$

Although significant ($p < 0.01$), the equation explained only a small amount of the variation in Douglas-fir site index across a wide range of sites. This regression appears to reflect the relationship between salal and humus form quality, in that salal cover generally decreased as the humus form changed from Mor to Moder or Mull. This humus form change occurred progressively from vegetation unit 1 through 5 (Table 2). The respective means of the midpoint percent cover values for salal are 73, 60, 15, 7.5, and 0.6 percent, in vegetation units 1 through 5, respectively.

Regressions of site index (m/50 yr) on component scores extracted from the first two PCA axes based on all understory diagnostic species and vegetation units were also examined. These resulted in the following equations:

$$[2]\ \mathrm{SI} = 30.55 + 0.70\,(\mathrm{PCA1}) + 0.32\,(\mathrm{PCA2})$$

$$R^2 = 0.36 \qquad F = 28.00 \qquad SE = 4.15\ \mathrm{m}$$

where PCA1 and PCA2 refer to scores for axis 1 and 2, respectively; and,

$$[3]\ \mathrm{SI} = 34.3 - 13.2\,\mathrm{U1} - 5.8\,\mathrm{U2} - 6.45\,\mathrm{U3} - 0.87\,\mathrm{U4}$$

$$R^2 = 0.67 \qquad F = 49.70 \qquad SE = 2.94\ \mathrm{m}$$

where U1-U4 are dummy variables with unit value, for the *Gaultheria—Mahonia—Polytrichum (juniperinum), Gaultheria—Mahonia—Rhytidiadelphus, Mahonia—Kindbergia,* and *Polystichum—Mycelis—Mahonia* units, respectively.

Site index for units 1 through 4 is equal to the intercept term plus the partial coefficient of the corresponding dummy variable, while the site index for unit 5 [*Polystichum—Mycelis—Rubus (spectabilis)*] is equal to the intercept term (34.3) since the dummy variable for this variable is always equal to zero. Results of ANOVA showed that the variances for site index among vegetation units were homogeneous ($p < 0.05$) and that site index differed significantly ($p < 0.01$; $F = 44.25$) among the vegetation units. The mean site indices of units 2 and 3 and 4 and 5 were not significantly different ($p > 0.05$).

Equation [1] suggests that there is poor correlation between salal cover and Douglas-fir site index across all study plots. However, a significant improvement resulted when the regression was based on either the scores for the first and second axis of the PCA (based on diagnostic species) or the vegetation units rather than salal cover.

Climatic, soil moisture, and soil nutrient regimes are used in the biogeoclimatic ecosystem classification to differentiate among biologically-equivalent sites (Pojar *et al.* 1987). In order to determine whether these variables have a stronger relationship to productivity than the vegetation characteristics of a site, the relationship between site index (m/50 yr), soil moisture regime (SMR) and soil nutrient regime (SNR) was examined. Climatic regime (biogeoclimatic unit) was not included as all study ecosystems were distributed within the very dry maritime cool mesothermal climate (the CWHxm subzone). Multiple linear regression produced the following equation:

$$[4]\ \mathrm{SI} = 35.5 - 7.50\mathrm{VD} - 1.72\mathrm{MD} + 3.33\mathrm{F} - 9.10\mathrm{VP} - 5.03\mathrm{M} - 1.75\mathrm{R}$$

$$R^2 = 0.86 \qquad F = 68.62 \qquad SE = 1.99\ \mathrm{m}$$

where VD (very dry), MD (moderately dry), SD (slightly dry), and F (fresh) are dummy variables, with unit value, designating SMRs; while VP (very poor), P (poor), M (medium), and R (rich) are dummy variables, with unit value, designating SNRs.

Thus, variables representing the SMRs and SNRs were better predictors of site index than vegetation variables. This is to be expected because understory vegetation often has a less pronounced effect on site quality, than humus form and mineral soil fertility factors. Furthermore, the understory vegetation which grows up after a timber harvesting operation may depend more on factors such as site disturbance, stand structural characteristics, time, and chance. This suggests that SMR and SNR—site factors that directly affect plant growth—offer a simple means of characterizing site quality and explaining forest productivity. Although understory vegetation may provide a good indication of site quality and can influence forest floor formation and decomposition rate through above- and below-ground litter production, such vegetation is usually a symptom, rather than a controlling factor, of site quality.

Salal, and other ericaeous plants are known to thrive in, and, hence, indicate the presence of Mor humus forms (e.g., Ellenberg 1974, Klinka *et al.* in press). However, Mor humus forms are often found in the absence of ericaceous plants and, due to their relatively wide ecological amplitude, ericaceous plants are actually found over a wide range of soil nutrient regimes—from nutrient-very poor (characterized by lignic and residuic Mors) to nutrient-poor (characterized by orthic Mors) to nutrient-medium (characterized by friable Mors or Mormoders) (Klinka *et al.* 1981, in press).

Conclusions

There were few significant differences in soil and foliar chemical properties between the high and low salal cover ecosystems having similar climatic, soil moisture, and soil nutrient regimes. Regression analyses showed poor relationships between Douglas-fir site index and salal cover. Much better relationships were obtained using variables representing vegetation units or SMRs and SNRs. These results imply that salal may not significantly influence height growth in immature Douglas-fir stands growing on moderately dry and nutrient-poor sites within very dry, cool mesothermal climates. A different sampling design and further experimental testing would be required to prove this conclusively.

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