

Above- and below-ground vegetation recovery in recently clearcut and burned sites dominated by *Gaultheria shallon* in coastal British Columbia

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ABSTRACT

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Above- and below-ground vegetation recovery was assessed 2, 4 and 8 years after logging and burning on an age sequence of sites dominated by salal (*Gaultheria shallon* Pursh) on northern Vancouver Island, British Columbia. The total above-ground vegetation biomass quadrupled from 1372 kg ha⁻¹ on the 2-year-old sites to 5574 kg ha⁻¹ on the 8-year-old sites. These are low values for post-logging above-ground biomass when compared with many other forest ecosystems. Salal was the dominant species on these sites, representing 77%, 87% and 73% of the total above-ground biomass on the 2-, 4- and 8-year-old sites, respectively. Leaf area index increased from 0.67 to 2.31 between the 2- and 4-year-old sites, but was only 2.53 on the 8-year-old sites. The total below-ground biomass increased six times from 1908 kg ha⁻¹ on the 2-year-old sites to 11 415 kg ha⁻¹ on the 8-year-old sites. The proportion of fine-roots to total roots declined with increasing site age as new rhizomes were produced. The upper 15 cm of the forest floor was found to contain 56% and 74% of the live fine-roots and 64% and 49% of the new rhizomes of the *Gaultheria-Vaccinium* and *Epilobium-Cornus* species groups, respectively. The ratio of below-ground to above-ground biomass varied from 1.4 on the 2-year-old sites to 2.5 on the 8-year-old sites.

The post-disturbance dominance of salal on these sites after logging and burning appears to be due to its ability to recoupy the site rapidly and completely both above-ground and below-ground from rhizomes present before disturbance, and to resist invasion by other species by pre-empting resources (nutrients in this case). A conceptual model of the leaf and fine-root biomass of salal over a period of 60 years is presented.

INTRODUCTION

Regrowth of minor vegetation has been shown to be a very important factor in the recovery of forest ecosystems from severe disturbance (Likens et al., 1970). However, abundant regrowth of competing vegetation has also been shown to interfere with the early establishment of conifer trees (Stewart et al., 1984), and thereby to slow down the process of secondary succession. The

positive or negative impact of the competing vegetation depends largely on the rapidity with which it establishes itself after disturbance. This varies according to the intensity of the disturbance (Dyrness, 1973; Halpern, 1988), the fertility of the site (Boring et al., 1981; Gholz et al., 1985; Hamilton and Yearsley, 1988), the type of understory vegetation present in the forest before disturbance (Halpern, 1988), and the amount, availability and establishment success of off-site seeds (Hamilton and Yearsley, 1988). In some cases, the recovery of the vegetation is extremely rapid. Marks (1974) estimated the time needed for pin cherry (*Prunus pensylvanica* L.) to occupy fully both the above- and below-ground environment of a site after clearcutting in a hardwood forest in the northeastern USA to be approximately 4 years. Raich (1980), working in a tropical forest in Costa Rica, reported fine-root biomass to be fully recovered to pre-disturbance levels 1 year after clearcutting.

Recent studies have indicated that maximum fine-root biomass occurs during the first 10–15 years after clearcutting. Vogt et al. (1987), comparing the fine-root biomass of 11- and 150-year-old Douglas fir (*Pseudotsuga menziesii*) stands in coastal Washington (USA), found the highest amount to be in 11- and 12-year-old plantations dominated by competing vegetation. Similarly, Yin et al. (1989) found a greater amount of fine-roots in a 6-year-old clearcut dominated by ferns than in an adjacent undisturbed northern red oak (*Quercus rubra* L.) forest. The potential for competing vegetation to occupy quickly and abundantly the below-ground environment can confer erosion protection on steep sites, but may also retard forest re-establishment. Vegetation management may be required if occupancy of the below-ground environment by competing species prevents or reduces the growth of the associated conifer species.

Although an understanding of the recovery of competing vegetation after forest removal has very important implications for forest regeneration, very few studies have examined the below-ground recovery during the first 10 years. Marks (1974) studied the early above- and below-ground recovery of pin cherry in a northern hardwood forest ecosystem using a chronosequence of 1-, 4-, 6- and 14-year-old sites, but did not describe the depth of root sampling, the size of the roots sampled, and whether the roots were alive or dead. Berish (1982) sampled root biomass in a chronosequence of 1-, 8-, and 70-year-old sites in a tropical forest in Costa Rica, but she did not distinguish between dead and live roots. Raich (1980) reported on the fine-root biomass 1 year after clearcutting in a tropical forest in Costa Rica, and Yin et al. (1989) compared the live fine-root biomass of a 6-year-old clearcut and an undisturbed hardwood forest in Wisconsin. Other studies of the early recovery of both the above- and below-ground biomass include those of Boring and Swank (1984), Uhl and Jordan (1984), and Auclair (1985), but none of these studies provided detailed information on the below-ground biomass.

Several thousand hectares of poorly growing coniferous plantations on

northern Vancouver Island, British Columbia, are completely dominated by an ericaceous species, salal (*Gaultheria shallon* Pursh). It has been shown that salal is at least partially responsible for this poor growth during the first 15 years after plantation establishment, either by competing directly for nutrients (Germain, 1985; Messier and Kimmins, 1991a,b) or by inhibiting nutrient availability to trees (Germain, 1985; Weetman et al., 1990). On these sites, salal re-establishes itself quickly after disturbance, mainly by resprouting from old rhizomes already present in the undisturbed old-growth forest of western red cedar (*Thuja plicata* Donn) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). Salal is an erect to nearly prostrate ericaceous shrub growing up to 2.5 m tall. It has an extensive, shallow root system with spreading rhizome-like structures. Salal occurs all along the Pacific coast of North America in lowland coniferous forest. Its distribution suggests that it requires a humid to perhumid coastal climate with mild temperatures, little snow, and unfrozen soils in winter. A few studies have documented the above-ground biomass (Sabhasri, 1961; Stanek et al., 1979; Vales, 1986) and below-ground biomass of salal (Sabhasri, 1961; Vogt et al., 1987) growing in a forest understorey, but none has investigated both the above- and below-ground recovery of salal and associated species on recently disturbed sites.

The objective of this study was to document the patterns of above- and below-ground biomass recovery of the competing vegetation in an age sequence of salal-dominated plantations from 2 to 10 years after logging and burning. A greater understanding of both above- and below-ground successional patterns during early ecosystem recovery is necessary to prescribe effective silvicultural treatments to enhance forest regeneration. This study was part of a larger project which investigated the below-ground factors that limit the growth of conifer seedlings after the logging and burning of old-growth western red cedar and western hemlock forests on northern Vancouver Island.

MATERIALS AND METHODS

Research sites

The study area is located between Port McNeill and Port Hardy in the CWHb_{vm} biogeoclimatic windward submontane maritime wetter variant (Green et al., 1984) on northern Vancouver Island (50°60'N, 127°35'W). The study area receives approximately 1700 mm of rain annually, with 65% of the precipitation occurring between October and February. Although the summer months experience less rainfall than the winter months, rainfall during the growing season is thought to be sufficient to prevent any soil moisture deficit (Lewis, 1982). Mean daily temperature ranges from a low of 3.0°C in January/February to a high of 13.7°C in July/August. All weather data were

obtained from the Port Hardy Airport weather station, located within 15 km of the study area.

All the research sites are in what Lewis (1982) called the *Thuja plicata*-*Tsuga heterophylla*-*Abies amabilis*-*Gaultheria shallon*-*Rhytidadelphus loreus* 'salal-moss' ecosystem association (S1). This ecosystem is the climatic climax association for the CWHb_{vm} variant and covers approximately 60% of Block 4 of Tree Farm Licence No. 25. Lewis (1982) further divided this S1 ecosystem association into two phases: (1) the undisturbed old-growth western red cedar-western hemlock phase (CH-phase), and (2) the windthrown western hemlock-amabilis fir phase (HA-phase). The area is characterized as having a gently undulating topography which rarely exceeds 300 m in elevation. The surface material consists of deep (more than 1 m in many places) unconsolidated morainal and fluvial outwash material. Within each phase, there is little variability in site features.

According to Lewis (1982), the CH-phase represents the climatic climax community and consists of an open western red cedar-western hemlock stand. This phase is thought to have remained relatively undisturbed for several thousand years. The open canopy allows light to penetrate the tree cover, which promotes the growth of a dense understory of salal and *Vaccinium* spp. Only sparse herbs (*Blechnum spicant*, (L.) Roth) and mosses (*Hylocomium splendens*, (Hedw.) B.S.C. and *Rhytidadelphus loreus* (Hedw.) Warnst.) are found under the *Gaultheria*-*Vaccinium* cover (Germain, 1985). This forest ecosystem has a thick (20-60 cm, but mostly over 45 cm) compacted lignohumic (Klinka et al., 1981) humus layer overlying a moderately well to somewhat imperfectly drained ferro-humic podzol. Germain (1985) described the Bf horizon as being of firm consistency, lying above a highly cemented till layer 40-50 cm below the surface. Western hemlock and western red cedar germinants are sparse, occurring mainly on rotten logs, and the stand structure suggests that few of these survive more than a few years. After logging or burning, the CH-phase is quickly reinvaded by salal. Natural regeneration of conifers after disturbance is slow and sparse, and consists mainly of western red cedar and western hemlock seedlings.

Field studies were initiated in summer 1987 on an age sequence of mesic CH-phase sites planted with western red cedar. Two ages of sites were chosen for this study: 2 and 8 years post-logging and burning. No suitable sites of intermediate age were found, so that the 2 years post-logging and burning sites were remeasured in summer 1989 to provide data 4 years after logging and burning. The measurement data were collected in different areas of the sites, so the 2- and 4-year-old observations were independent of each other within the sites. For each site age, two different cutovers (8-12 ha in size and 2-5 km apart) were selected. All four cutovers were selected based on their homogeneity: similar slope position, aspect, surface material, forest floor thickness, soil characteristics, intensity of burn as determined by Western

Forest Product's files and foresters in charge of the burning, and tree species composition before disturbance as determined by the stumps.

This kind of age sequence research assumes that all the cutovers had similar ecological attributes before disturbance and share a similar post-disturbance stand history (Cole and Van Miegroet, 1989). The assumption is believed to be realistic for this study because of the characteristic uniformity of the CH-phase ecosystem in the area of northern Vancouver Island where the study was conducted, and the care taken in the selection of the study sites. Four pits were dug on each cutover and the soil horizons were described. Only the cutovers that had very similar soil profile characteristics were selected. The four cutovers selected were considered to be very representative of the CH-phase ecosystem described by Lewis (1982). However, to test further the assumption that they were representative of the population of cutovers in the area, and that the temporal patterns revealed by the intensively studied cutovers were mainly a function of time since disturbance, a visual survey was conducted of per cent cover of salal in 11 other rather similar cutovers representative of the CH-phase ecosystem, and varying in ages from 1 to 15 years after logging and burning.

Below-ground biomass

The vertical distribution and biomass of live salal, *Vaccinium* spp., fireweed, and bunchberry (*Cornus canadensis* L.) roots were measured on the 2, 4, and 8 years post-logging and burning sites by taking 12 root cores (7.4 cm in diameter) at the beginning of June 1987 on each of the 2 and 8 years post-logging and burning sites, and at the beginning of June 1989 on the sites that had been 2 years old in 1987, and were 4 years old at the time of resampling. Six cores were taken on each of the two cutovers for each site age. In 1989, the below-ground biomass on the 4 years post-logging and burning sites was assessed by taking a root core in the center of 12 1-m² quadrats that were also used to assess the above-ground biomass (see below). Pre-sampling indicated that very few roots were present below 45 cm. Therefore, the cores were taken from depths 0–15 cm, 15–30 cm, and 30–45 cm, providing 108 root-core samples. Because the depth of the forest floor was greater than 45 cm in most places, most cores were composed mostly of organic matter. The non-root organic matter contained in each core was carefully washed through a 2 mm sieve, and the roots and rhizomes were separated and sorted by hand into different sizes (0–1, 1–2, 2–5, and more than 5 mm) and species groups. *Gaultheria shallon* and *Vaccinium* spp. were combined in a single group, and *Cornus canadensis* and *Epilobium angustifolium* in another group, because of the difficulty in distinguishing between fine-roots of individual species within these groups. Distinction of fine-roots between the two species groups was possible because of the differences in root morphology, resilience when bent,

and colour. Roots were visually separated into live and dead categories: living roots were resilient, slightly translucent and light brown (*Gaultheria-Vaccinium*) or translucent and white (*Epilobium-Cornus*); dead roots fragmented easily, were dull and were darker in colour. After sorting, the roots were dried at 70°C for 24 h and weighed to determine the oven-dry biomass per hectare. Each 645 cm³ core required an average of 20 person-hours of work.

Above-ground biomass, percentage cover and leaf area

The above-ground biomass, percentage cover and leaf area were assessed on the same sites as for the below-ground biomass. Twelve 1-m² quadrats were clipped at the end of July on each cutover to assess the above-ground biomass. The biomass collected from each 1-m² quadrat was separated by species and then further divided into leaf and stem + fruit components. The biomass was dried at 70°C for 48 h and weighed to determine the oven-dry mass for each species and plant component. The percentage cover of each species was assessed visually at the beginning of April and at the end of July in 1987, 1988 and 1989 in four permanent 1-m² quadrats within each plot. Total leaf area for each species was determined by calculating a conversion factor between oven-dry weight and leaf area; correlation coefficients between leaf area and mass were all more than 0.88, based on 20 subsamples for each species.

Soil temperature

Eighteen soil temperature measurements were made using dial soil thermometers intermittently at depths of 3, 10 and 25 cm on each site between 11:00 h and 13:00 h from June to September in 1987 and 1988.

Soil nutrient status

Eighteen forest floor cores were taken from depths of 0–8 and 8–20 cm in 1988 on each of the two cutovers for each of the 2 and 8 years post-logging and burning sites. The fresh samples were stored at 3°C for less than 1 week before being passed through a 2 mm sieve before analysis. A subsample was oven-dried at 70°C for 24 h to determine the moisture content. All the results are reported on an oven-dry basis.

Forest floor pH was determined in distilled water with a glass electrode using a soil–water ratio of 1:4 (w:v). Total N and P were measured by digesting 0.2 g (oven-dry weight) of forest floor material overnight with a mixture of potassium sulfate, sulfuric acid and selenium in a block digester. Extractable N was determined by extracting and shaking 5 g (fresh weight) of forest floor material with 100 ml of 2 M KCl solution for 1 h. Available P was

determined by extracting and shaking 5 g (fresh weight) of forest floor material with 100 ml of 0.01 M HCl solution for 5 min. Mineralizable N was determined by extracting 5 g (fresh weight) of forest floor material with 100 ml of 2 M KCl solution after incubation in 25 ml of distilled water at 30°C for 7 days. The digest solutions were then analyzed for N and P using a Technicon AutoAnalyser II (Technicon Instrument Corp., Tarrytown, NY). Soil organic matter was determined by loss on ignition (24 h at 500°C), and carbon content was calculated by dividing the organic matter content by 1.723 (Armson, 1979).

Statistical analyses

The experiment did not use any particular design, but consisted of sampling two cutovers for each site age selected. For the analysis of variance, the cutovers were nested within site ages (3 site ages \times 2 cutovers per site age for vegetation biomass and 2 site ages \times 2 cutovers per site age for soil data). The Tukey HSD multiple comparison test was used to compare the treatment means. Log- or square-root-transformed values were used when the variances were not homogeneous based on Bartlett's test. In this paper, only untransformed means are presented, but the statistics of some of the means were performed on transformed means.

RESULTS AND DISCUSSION

Above-ground biomass, percentage cover and leaf area index

Figure 1 shows the per cent cover of salal in six intensively studied cutovers plus 11 other cutovers representative of the population of cutovers in the region. This figure illustrates that the six intensively studied cutovers are indeed representative of the population of cutovers found in the region.

There was no statistical difference ($P > 0.1$) between cutovers within each site age for most above-ground variables measured. Therefore, the above-ground biomass values from the two cutovers within each site age were combined, and are reported in Table 1. Two years after logging and burning, salal and fireweed accounted for 77% and 17% of the total above-ground biomass, respectively. The few clumps of *Vaccinium* spp. and conifers present represented only 2–3% of the total above-ground biomass. Bunchberry and other species were extremely sparse at this age, making up less than 1% of the total above-ground biomass.

From 2 to 4 years after logging and burning, salal, *Vaccinium* spp., bunchberry and conifers more than doubled in biomass, whereas fireweed increased only slightly (Table 1). The increase was significant ($P < 0.05$) only for salal. Salal leaf biomass increased dramatically during this 2 year period, going from

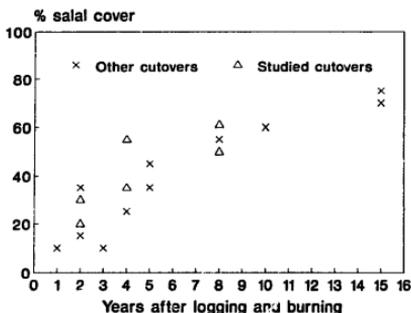


Fig. 1. Per cent cover of salal on the 2-, 4- and 8-year-old intensively studied sites, and on 11 other cutovers representative of the population of cutovers found in the CH-phase ecosystem type on northern Vancouver Island.

596 to 2462 kg ha⁻¹, a four-fold increase. By 4 years after logging and burning, salal had increased its dominance of the site and represented 87% of the total above-ground vegetation biomass. Hendrickson (1988) and Boring et al. (1981) also found that sprouting species dominated their sites rapidly after clearcutting.

Between the 4- and 8-year-old sites, *Vaccinium* spp., bunchberry, conifers and other species all increased their above-ground biomass substantially, whereas salal increased only slightly, and fireweed decreased slightly (Table 1). Of all these changes between the 4- and 8-year-old sites, only the increases in *Vaccinium* spp. and bunchberry biomass were significant ($P < 0.05$). The increase in salal biomass was entirely the result of an increase in the stem and fruit component; no increase in leaf biomass was measured. On the 8 years post-logging and burning sites, the above-ground dominance of salal was reduced to 73% of the total above-ground biomass. The range in above-ground biomass values among individual quadrats was substantial in this study, as indicated by the high standard deviations (Table 1).

Weetman and Fournier (1986), working on similar sites, found slightly smaller salal above-ground biomass values on 2 and 4 years post-logging and burning sites and slightly higher values on an 8-year-old site. The total above-ground biomass values found on our sites at 2, 4 and 8 years were substantially lower than those reported by Marks (1974) for a northern hardwood forest ecosystem (17 573 and 32 556 kg ha⁻¹ at 4 and 6 years after clearcutting, respectively), by Boring and Swank (1984) for a southern Appalachian hardwood forest ecosystem (21 993 kg ha⁻¹ at 4 years after clearcutting), by Hendrickson (1988) for a northern mixed conifer-hardwood forest ecosystem (7878 kg ha⁻¹ at 4 years after clearcutting), by Uhl and Jordan (1984)

TABLE 1

Mean above-ground biomass (kg ha^{-1}) and leaf area index (projected $\text{m}^2 \text{m}^{-2}$) of the vegetation on the intensively studied 2-, 4- and 8-year-old site ages

Plant species and components	Biomass (kg ha^{-1}) and leaf area ($\text{m}^2 \text{m}^{-2}$) at specified site age		
	2 years	4 years	8 years
<i>Gaultheria shallon</i>			
Leaf	596 ^a (141)	2462 ^b (366)	2219 ^b (246)
Stem + fruit	462 ^a (129)	1164 ^b (185)	1858 ^c (227)
Total	1058 ^a (267)	3626 ^b (519)	4078 ^b (454)
<i>Epilobium angustifolium</i>			
Leaf	126 ^a (56)	131 ^a (26)	66 ^a (26)
Stem + fruit	110 ^a (52)	162 ^a (35)	103 ^a (44)
Total	236 ^a (107)	293 ^a (58)	169 ^a (70)
<i>Vaccinium</i> spp.			
Leaf	10 ^a (6)	14 ^a (11)	85 ^a (39)
Stem + fruit	18 ^a (15)	40 ^a (32)	290 ^b (121)
Total	28 ^a (22)	54 ^a (43)	375 ^b (148)
<i>Cornus canadensis</i>			
Total	1 ^a (1)	26 ^a (14)	406 ^b (79)
<i>Conifers</i>			
Total	43 ^a (16)	163 ^{ab} (78)	446 ^b (159)
<i>Other species</i>			
Total	6 ^a (2)	6 ^a (5)	101 ^a (52)
<i>Grand total</i>			
Leaf	757	2705	2846
Stem + fruit	615	1464	2728
Total	1372	4169	5574
Leaf area index	0.67	2.31	2.53

Numbers in rows followed by the same superscript letter are not significantly different ($P > 0.05$) between sites.

Values in parentheses represent one standard error of the mean. $n = 24$ for each cell.

for an Amazonian forest ecosystem (28 880 kg ha^{-1} at 4 years after clearcutting), and by Outcalt and White (1981) for an *Abies balsamea*-*Betula papyrifera* forest ecosystem in northern Minnesota (4181 kg ha^{-1} and 2604 kg ha^{-1} at 2 years after clearcutting for whole-tree and tree-length logged and burned sites, respectively). They are higher, however, than the values reported by Auclair (1985) for a boreal forest ecosystem in northern Quebec (1369 and 3015 kg ha^{-1} at 4 and 7 years after wildfire, respectively), and similar to those reported by Gholz et al. (1985) for a Douglas fir forest ecosystem in Oregon (1633 kg ha^{-1} at 2 years after clearcutting).

Leaf area index (LAI) increased rapidly between the 2- and 4-year-old sites, but increased only slightly between the 4- and 8-year-old sites (Table 1).

Salal was always the dominant species on all site ages, and reached its maximum cover of about 60% 4 years after logging and burning. Bunchberry was the second most abundant species on the initially older site age (i.e. 8-year-old sites), and reached its maximum cover of about 30% 9 years after logging and burning. The planted and naturally regenerated conifer species increased slowly in cover over time, reaching 23% by year 10 on the initially older site age. The small change in percentage cover of salal between 4 and 10 years suggests that salal has reached its maximum cover by 4 years. There was virtually no change in the percentage cover of fireweed from 2 to 10 years after logging and burning. Weetman and Fournier (1986) estimated the percentage cover of salal at 55% on a similar 8 years post-logging and burning site. The high percentage cover of salal found at 4 years (58%) indicates that salal can reach these high cover levels very rapidly.

Below-ground biomass and distribution

There was no statistical difference ($P > 0.1$) between cutovers within each site age for all of the below-ground variables measured. Therefore, the below-ground biomass values from the two cutovers within each site age were combined, and are shown in Table 2. The total below-ground biomass on 2, 4, and 8 years post-logging and burning CH-phase sites averaged 1908, 4110, and 11 415 kg ha⁻¹, respectively. The *Gaultheria-Vaccinium* group (of which salal was by far the dominant species) comprised 95%, 90%, and 75% of the total live fine-root (0–2 mm) biomass on the 2-, 4-, and 8-year-old sites, respectively. The proportion of live fine-roots (0–2 mm) to total live roots was greatest (88%) on the 2 years post-logging and burning sites and smallest (47%) on the 8 years post-logging and burning sites.

Although the above-ground vegetation was very sporadic on the 2-year-old sites, live fine-roots were found in all core samples at all depths. From the 2- to 4-year-old sites, fine-roots increased only marginally, whereas rhizomes (roots of over 2 mm) increased from 169 to 1542 kg ha⁻¹. Most of the *Gaultheria-Vaccinium* live fine-roots were found in the 1 mm diameter category (Table 2). The amount of live fine-roots found in the 8-year-old sites (5311 kg ha⁻¹) is similar to that found by Vogt et al. (1987) in a low-productivity open 11-year-old Douglas-fir stand dominated by a dense understory of salal (5780 kg ha⁻¹). It is, however, significantly less than the 12 910 kg ha⁻¹ found in an 8-year-old tropical clearcut in Costa Rica (Berish, 1982), and the 9800 kg ha⁻¹ found in a 6-year-old northern hardwood clearcut in Wisconsin (Yin et al., 1989).

Figure 2 compares the distribution of *Gaultheria-Vaccinium* and *Epilobium-Cornus* fine-roots and rhizomes between the three sampling depths. The *Gaultheria-Vaccinium* species group concentrated 57% of its fine-roots in the top 15 cm, whereas the proportion was 74% for the *Epilobium-*

TABLE 2

Vertical and diameter class distribution of below-ground biomass (kg ha^{-1}) of the *Gaultheria-Vaccinium* and *Epilobium-Cornus* species groups on the intensively studied 2-, 4- and 8-year-old site ages

Site age (years)	Depth (cm)	Biomass							
		<i>Gaultheria-Vaccinium</i>				<i>Epilobium-Cornus</i>			
		0-1 mm	1-2 mm	2-5 mm	>5 mm	0-1 mm	1-2 mm	2-5 mm	>5 mm
2	0-15	805 (149)	48 (37)	89 (62)	39 (30)	39 (9)	32 (23)	48 (48)	00 (0)
	15-30	395 (135)	32 (29)	41 (38)	00 (00)	5 (2)	0 (0)	00 (0)	70 (68)
	30-45	248 (60)	13 (9)	00 (0)	00 (0)	4 (2)	0 (0)	00 (0)	00 (0)
4	0-15	843 (121)	102 (50)	264 (206)	950 (610)	55 (28)	9 (8)	50 (50)	28 (30)
	15-30	659 (173)	105 (40)	139 (103)	189 (193)	27 (14)	0 (0)	25 (26)	330 (316)
	30-45	253 (57)	57 (25)	000 (00)	000 (00)	9 (3)	0 (0)	16 (16)	000 (00)
8	0-15	2189 (238)	309 (85)	1007 (369)	2666 (485)	625 (209)	373 (138)	14 (10)	00 (0)
	15-30	748 (197)	68 (24)	202 (134)	1318 (658)	125 (39)	22 (21)	2 (2)	00 (0)
	30-45	557 (77)	120 (42)	275 (227)	620 (635)	100 (35)	75 (51)	00 (0)	00 (0)

Values between parentheses represent one standard error of the mean. Twelve root cores were taken on each site for each depth.

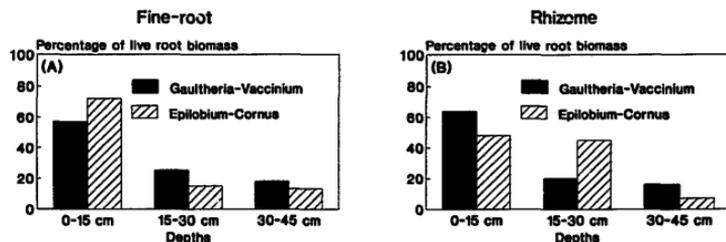


Fig. 2. Comparison of the vertical distribution of (A) fine-root (0-2 mm) and (B) new rhizome (more than 2 mm) biomass of *Gaultheria-Vaccinium* and *Epilobium-Cornus* species groups within the upper 45 cm of the forest floor. Each value represents an average from the three site ages. The distribution is expressed as the percentage of the total fine-roots or total rhizomes in the upper 45 cm found at each of the three depths.

Cornus species group. Many studies have found the roots of herbs and shrubs to be concentrated in the upper soil horizons (Kummerow et al., 1977; Ruark and Bockheim, 1987; Aerts et al., 1989; Yin et al., 1989), especially in the forest floor (Kimmins and Hawkes, 1978; Persson, 1980). Persson (1980) found that 89% and 98% of the live fine-roots of *Calluna vulgaris* and *Vaccinium vitis-idaea*, respectively, were in the upper 10 cm in a 15–20-year-old Scots pine (*Pinus sylvestris*) stand in Sweden. Aerts et al. (1989), working in a wet heathland in the Netherlands, reported that 95% of the roots of *Calluna erica* were in the upper 20 cm of the soil. Most of the studies cited above were done on sites with relatively thin forest floor layers (less than 15 cm), whereas the forest floor on our study sites was more than 45 cm in most places. Kimmins and Hawkes (1978) reported that the shallow rooting habit of the vegetation on their study site could have been explained by the low nutrient status of the mineral soil underlying the forest floor.

The thick forest floor found on our study sites could explain why we found somewhat less of a concentration of fine-roots in the uppermost soil layer compared with other studies dealing with similar species but thinner forest floor layers. The observed degree of concentrations of roots in the top 15 cm of the forest floor found in our study correlated with a better nutrient status found for the 0–8 cm layer compared with the 8–25 cm layer (Table 3), and to the higher soil temperature measured during the growing season at 3 and 10 cm (19 and 17°C, respectively) as compared with 25 cm (14°C). Mois-

TABLE 3

Comparison of some soil properties in 1988 for depths of 0–8 and 8–25 cm and ANOVA *P* values between the 2- and 8-year-old intensively studied site ages

Property	Means (standard error)				ANOVA <i>P</i> values	
	2 year		8 year		Ages	Depth
	0–8 cm	8–25 cm	0–8 cm	8–25 cm		
pH	4.47 (0.10)	4.03 (0.07)	4.33 (0.04)	3.91 (0.03)	0.156	0.000
C/N ratio	45.2 (1.7)	60.7 (2.5)	58.3 (5.4)	68.5 (3.4)	0.024	0.000
Total N (%)	1.25 (0.05)	0.95 (0.03)	1.10 (0.06)	0.84 (0.03)	0.010	0.000
Total P (%)	0.068 (0.017)	0.045 (0.013)	0.063 (0.017)	0.042 (0.012)	0.082	0.000
Extractable NH ₄ ⁺ (ppm)	0.14 (0.01)	0.13 (0.02)	0.05 (0.01)	0.05 (0.01)	0.000	0.560
Mineralizable NH ₄ ⁺ (ppm)	0.37 (0.03)	0.24 (0.02)	0.28 (0.02)	0.17 (0.01)	0.006	0.000
Available PO ₄ ⁻ (ppm)	0.220 (0.056)	0.043 (0.016)	0.005 (0.000)	0.001 (0.000)	0.000	0.000

ture was not a major factor on our study sites because of the frequent rainfall and heavy fog present throughout the growing season.

There was no statistical difference ($P > 0.1$), for any of the soil properties measured, between the two cutovers within each site age. Therefore, the soil data from the two cutovers within each site age were combined (Table 3). Many of the soil properties indicative of site fertility measured in this study were found to be statistically ($P < 0.05$) lower on the older site age (Table 3). These results suggest that the overall fertility of these sites declines over time (Messier and Kimmins, 1991b). Similar results were obtained by Weetman et al. (1990) on comparable sites.

Growth allocation strategy during the period of vegetation recovery after logging and burning

Figure 3 compares the pattern of above- and below-ground biomass accumulation of the two main species groups (*Gaultheria-Vaccinium* and *Epilobium-Cornus*) after the logging and burning of old-growth western red cedar and western hemlock forests. During the first 2 years, few new rhizomes were produced by the *Gaultheria-Vaccinium* species group, the new growth being concentrated in the fine-roots and leaves. The strategy of these species for the first 2 years thus appears to be to produce leaves and fine-roots with which to explore the newly unoccupied above- and below-ground environment created by logging and burning. Once salal has produced enough shoots and roots from its old rhizomes to occupy its immediate territory fully, new rhizomes and shoots are produced. Between years 2 and 4, the amount of rhizomes had increased by almost 10 times (Table 2), the leaves by more than four times (Table 1), and the fine-roots by only approximately 25% (Table 2). Between the 4- and 8-year-old sites, however, the increase in salal biomass came mainly from fine-roots (a two times increase) and rhizomes (a four times increase).

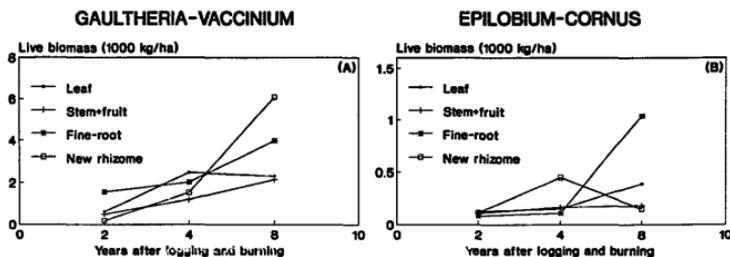


Fig. 3. Above- and below-ground vegetation biomass patterns for the *Gaultheria-Vaccinium* (A) and *Epilobium-Cornus* (B) species group on 2-, 4- and 8-year-old intensively studied sites. (Note that the scale of the y-axis for A is different from that for B.)

The large increase in *Epilobium-Cornus* leaf and fine-root biomass between the 4- and 8-year-old sites was entirely due to bunchberry (Table 1). Moreover, the large increase in the 1–2 mm *Epilobium-Cornus* root category between the 4- and 8-year-old sites came mainly from small bunchberry rhizomes.

It is important to remember that the comparisons between 4 and 8 years are based on different sites, whereas the comparisons between 2 and 4 years are based on the same sites, but sampled at a 2 year interval. We feel strongly, however, that all the sites were similar enough to warrant the conclusion that the differences between 4 and 8 years were mainly due to time, and not to any major difference in stand history and/or ecological attributes of the sites.

The pattern of above- and below-ground recovery found at the Port McNeill study sites differed somewhat from those in other regions. In northeastern (Marks, 1974) and southeastern (Boring and Swank, 1984) USA hardwood forests, the below-ground to above-ground biomass ratio has been shown to decrease gradually after the revegetation of the sites. Uhl and Jordan (1984) showed that the roots in a tropical forest in Amazonia remained a fairly constant percentage of total plant biomass throughout the first 5 years of succession after clearcutting. In contrast, we found that the below-ground to above-ground biomass ratio increased from 1.4 in the 2-year-old sites to 2.5 in the 8-year old sites. However, the low ratios found in years 2 and 4 would have been greater if we had included in the calculations the old rhizomes produced before disturbance, but still present after the disturbance. Sabhasri (1961) found a below-ground to above-ground ratio of 2.4 for salal growing under a 120-year-old Douglas fir stand in Washington. He reported that most of the above-ground biomass of salal was in the stem, but did not make any distinction between fine-roots and rhizomes for the below-ground biomass component. The high below-ground to above-ground biomass ratios found in our study resemble those found on other sites dominated by shrub and perennial herb communities (e.g. Whittaker and Marks, 1975; Yin et al., 1989).

In 1989, the below-ground biomass on the 4 years post-logging and burning sites was assessed by taking a root core in the center of 12 1-m² quadrats that were also used to assess the above-ground biomass. A correlation analysis was done between the different components of the above- and below-ground biomass to see if any useful relationships existed. Although both above- and below-ground biomass components varied greatly between the 12 quadrats, no significant ($P > 0.1$) correlation ($0.18 > r > -0.38$) was found between any of the above- and below-ground biomass components. It appears that the amount of above-ground vegetation present on a particular microsite in these post-harvest disturbance communities does not indicate how much below-ground biomass is present in the soil. The rhizomatous nature of the main species, salal, may explain this lack of correlation, reflecting comparative in-

dependence of local shoot and root production. Salal may produce its shoots in areas which are not necessarily good for the production of fine-roots (e.g. old decaying logs), and vice versa.

Ecological and silvicultural implications

One of the most striking features of recently logged and burned sites on northern Vancouver Island is the strong above- and below-ground dominance by salal. Hendrickson (1988) stated that the rapid occupancy of clearcut areas by aspen and maple sprouts in Ontario, Canada, probably prevented the growth of non-woody species on his study sites. On our study sites, however, salal does not occupy a significant proportion of both the above- and below-ground environment until 3–4 years after logging and burning. This delay should give enough time for any potential invaders (e.g. fireweed, red alder (*Alnus rubra*) and salmonberry (*Rubus spectabilis*)) to become established. However, of all the potential invaders, only fireweed colonized a significant fraction of the site (around 12% at 4 years). Fireweed appears to prefer small depressions on these sites, although no edaphic explanation for such preference has been established (Messier and Kimmins, 1991c).

One possible hypothesis to explain the failure of early successional species to become firmly established on our study sites is that the thick, wet and recalcitrant forest floor of mainly decaying wood was not disturbed enough by logging and burning to allow for the growth of early seral species such as fireweed, salmonberry and red alder, all of which require a certain amount of disturbance to become established (Kimmins, 1987). Salal may be able to re-establish itself and dominate these nutrient-poor sites because of its ability to survive logging and burning, to resprout vigorously from rhizomes, to occupy the site quickly, and to resist invasion by other species. Resistance to invasion may be achieved by making nutrients unavailable and/or by inhibiting the germination and growth of other species by direct or indirect allelochemical mechanisms (Kimmins, 1987). Messier and Kimmins (1991b) estimated that 30–45% of the potentially available N is tied up in living tissue of salal annually on these sites during the first 8 years.

Connell and Slatyer (1977) described three models of species replacement during secondary succession: the facilitation model, the tolerance model, and the inhibition model. Based on the results of this study and of other studies done in the same area, it would appear that succession on these salal-dominated sites more or less follows the tolerance model in which slower-growing, more tolerant, western red cedar and western hemlock seedlings invade and grow in the presence of salal immediately after disturbance, but are adversely affected by the presence of salal. Eventually, however, the conifer trees will grow above salal and shade it out (Messier et al., 1989). Because it can take as many as 40 years for the conifers to shade out salal (Messier et al., 1989), and because salal has been shown to interfere effectively with the growth of

conifer trees (Messier and Kimmins, 1991a,b), there is some evidence that salal may also exhibit some of the attributes of the inhibition model. Salal produces large amounts of fine-roots of less than 1 mm that can effectively pre-empt site resources. Moreover, salal is believed to inhibit the growth of other species by direct or indirect allelochemical mechanisms (Germain, 1985; Weetman et al., 1990). Salal may also play an important role in nutrient conservation (compare *Prunus pensylvanica*; Marks, 1974), as no other species seems able to colonize these sites quickly after the removal of the forest canopy.

Our study provides a basis for predicting patterns after logging and burning of salal above- and below-ground biomass accumulation on similar sites in the CWHb_{vm} biogeoclimatic variant in coastal British Columbia. A hypothetical successional pattern of the live fine-root and leaf biomass of salal over a 60 year period involves three stages in salal development: (1) a rapid increase in salal fine-root and leaf biomass occurring during the first 8–15 years; followed by (2) a rapid decline in salal fine-root biomass and a more gradual decrease in leaf biomass occurring after tree canopy closure; and (3) the virtually complete elimination of salal as the overstory tree canopy increases above 80% cover (Fig. 4).

The first stage in the successional pattern of salal is based on data from this study. The second stage is based on above-ground biomass data from Vales (1986), fine-root data from Vogt et al. (1987), and above- and below-ground biomass data from a pot experiment conducted at Port McNeill (Messier and Kimmins, 1991a). Vogt et al.'s (1987) study showed that the understory angiosperm fine-root biomass, predominantly of salal, on low-productivity Douglas-fir stands decreased from between 5500 and 7000 kg ha⁻¹ at 11 and

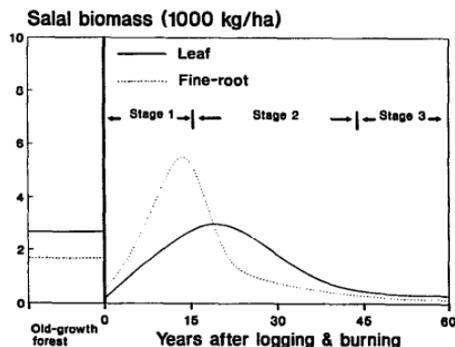


Fig. 4. Conceptual model of the pattern of live fine-root and leaf biomass of salal over a 60 year period after the logging and burning of old-growth forests of western red cedar and western hemlock on Vancouver Island.

12 years in relatively open stands to between 400 and 700 kg ha⁻¹ at 33 and 69 years in relatively closed stands, yet the per cent cover of the understory salal remained unchanged at 25–50%. Their study appears to indicate that salal shifts a major portion of its carbon allocation from fine-root to leaf tissues as it experiences lower light availability caused by the closing of the overstory canopy. Similar results were obtained in a pot experiment in which salal was grown under declining light intensities (Messier and Kimmins, 1991a). Such a shift in carbon allocation agrees with Chapin et al. (1987), who stated that plants short of carbon compensate by producing proportionately more shoot than root materials. Vales (1986) examined the relationship between salal above-ground biomass and overstory tree cover and resultant level of solar radiation. His data showed that salal maintains a more or less constant amount of above-ground biomass under tree covers up 65–75%. The third stage is based on the data of Messier et al. (1989) and Vales (1986), who found salal's above-ground biomass to be almost completely eliminated under tree canopy covers greater than 80%.

The conceptual model presented in Fig. 4 suggests that the net immobilization of nutrients by salal will stop between 10 and 20 years after logging and burning as salal stops expanding its biomass. Between 20 and 45 years, salal biomass will decline, especially the fine-root biomass, so that below-ground competition by salal may be less than that suggested by the magnitude of the above-ground biomass. After approximately 45 years the salal understory almost completely disappears as the tree canopy reaches 80% cover or more. This scenario is plausible on our nutrient-poor study sites only if a fairly dense stand of more than 4000 trees ha⁻¹ is maintained (Messier et al., 1989). On nutrient-rich sites, however, this scenario may be achieved at somewhat lower tree densities or at similar densities but at an earlier age.

Salal's survival strategy appears to be to build a large biomass of rhizomes in the clearcut to store carbohydrates which will permit it to survive under very dense stand covers for many years. This strategy allows salal to 'wait' until stand self-thinning occurs and the canopy opens up, whereas other species without such below-ground storage would be eliminated.

After the logging and burning of old-growth western red cedar and western hemlock forests, *Gaultheria shallon*, *Epilobium angustifolium*, *Vaccinium* spp., *Cornus canadensis*, and a variety of other minor species colonized our study sites. Eight years after forest removal, all of the vascular plant species that were present in the old-growth forest were represented in the cutovers, suggesting that clearcut logging and burning of these ecosystems does not result in any loss of vascular plant species diversity.

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