


AN ABSTRACT OF THE THESIS OF

David W. Huffman for the degree of Master of Science in
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Title: Regeneration of Salal: Seedling Establishment and the
Effects of Overstory Stand Density on Clonal Morphology and
Expansion

Signature redacted for privacy.

Abstract approved by:  John C. Tappeiner II

Regeneration of salal (Gaultheria shallon Pursh.) in the Coast Range of western Oregon was examined over two growing seasons in a three part study consisting of seedling establishment, clone excavation, and population sampling experiments. The effects of study site location, overstory stand density, and substrate on seedling emergence and survival were tested. Additionally, the effects of overstory stand density on clonal morphology and expansion, and on stem and rhizome population productivity were tested.

Results of the seedling establishment experiment showed that emergence, survival and seedling:seed ratios were significantly affected by study site location, overstory stand density, and substrate ($p < 0.05$). Establishment was found to

be highest at Cascade Head, in thinned stands, and on rotten logs and stumps. First-year survival on logs was found to be significantly correlated with percent sky ($p < 0.0001$, $r = 0.516$). Overall, just 1.4 percent (± 1.4 SE) of the seeds sown became established. Second-year seedling heights averaged 2.4 cm (± 0.16 SE) but ranged up to 20 cm.

The clone excavation experiment allowed description of clonal architecture and identification of three clone types termed "invader", "senescent", and "remnant". Results showed that vegetative expansion and clone size were negatively correlated with overstory density. Clones up to 218 m in total rhizome length were found in low density stands. Invader clones expanded rhizome systems 16.2 percent per year on average. Clones in dense stands were small and did not expand. Significance of regressions of clone characteristics on overstory density indices ranged from 0.001 to 0.94. Correlation coefficients ranged from 0.027 to 0.894.

Productivity of stem and rhizome populations were found to be negatively correlated with overstory density. Correlation coefficients for regressions of stem density, aboveground biomass, rhizome density and rhizome biomass on overstory density indices ranged from 0.584 to 0.944. Trends were consistent with previous findings for salal, as well as other species. Dynamics of salal regeneration with respect to forest succession were discussed.

Regeneration of Salal: Seedling
Establishment and the Effects of Overstory Stand
Density on Clonal Morphology and Expansion

by

David W Huffman

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Signature redacted for privacy.

Professor of Forest Science in charge of major

Signature redacted for privacy.

Head of department of Forest Science

Signature redacted for privacy.

Dean of Graduate School

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Typed by David W Huffman for David W Huffman

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REGENERATION OF SALAL: SEEDLING ESTABLISHMENT
AND THE EFFECT OF OVERSTORY STAND DENSITY ON
CLONAL MORPHOLOGY AND EXPANSION

INTRODUCTION

Salal (Gaultheria shallon Pursh.) is an important understory shrub in the coastal Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) and western hemlock (Tsuga heterophylla (Raf.) Sarg.) forests of the Pacific Northwest. An ubiquitous component of these forests, salal often forms extensive patches that compete with commercial tree species for moisture and possibly nutrients (Price et al. 1986; Black et al. 1980; Weetman et al. 1990; and Vihnanek and Ballard 1988). Salal leaves and fruits are beneficial to wildlife and are used by many animals including black-tailed deer, mountain beaver, and black bear (Van Dersal 1938; Cowan 1945; and Martin 1971). Its leaves are valued as greenery by florists (Dimock et al. 1974) and salal is often propagated for urban landscaping purposes. Further, the rhizomatous growth of salal makes it suitable for coastal dune stabilization (Brown and Hafenrichter 1962).

Although salal is a major component of coastal forests in the Pacific Northwest, little is known about its' reproductive ecology or natural history. A small number of studies have addressed the ecology of salal (Sabhasri 1961; Vales 1981;

Bunnell 1990; Smith 1991; and Messier et al 1989), however, most have examined populations of stems or leaves located within fixed plots. None have attempted to describe the architecture, morphology or development of individual clones. Further, the recruitment of new genotypes (ie. seedlings) of salal into local populations is little understood. Seedling recruitment patterns have profound effects on life history evolution (Eriksson 1989). Salal seedlings have been rarely observed in the field and seedling survival has been reported as low relative to other understory species (Sabhasri 1961; and Tappeiner and Zasada 1992). Field observations and a pilot study for this research indicated that coarse woody debris was important for seedling establishment. Other species in the Pacific northwest have been found to rely heavily on rotten logs and stumps for regeneration (Harmon 1987; and Christy and Mack 1984). Examination of salal's clonal architecture and seedling recruitment requirements is crucial to an understanding of the ecology and life history of the species.

This paper details a pilot study and a 2-year study that examined salal seedling establishment, a 1-year study of salal's clonal morphology, architecture and expansion, and a 1-year study of salal stem and rhizome populations. The objectives of these studies were: (1) to determine if salal seedling establishment is affected by substrate and overstory density, (2) to describe salal's clonal architecture and

development and, (3) to examine clonal and population expansion rates and morphology under various overstory densities.

To meet the above objectives, I examined the emergence and survival of experimentally sown salal seeds in clearcuts, thinned stands and unthinned stands at three study sites located in the Tsuga heterophylla vegetation zone of the Oregon coast range (Franklin and Dyrness 1973). The seeds were sown on coarse woody debris (ie. rotten logs and stumps), mineral soil, and the undisturbed forest floor. I also examined the effects of overstory stand density on clonal morphology and relative expansion rates. To do this I excavated 51 entire clones in nine various stand densities at one of the three coast range study sites. These excavations allowed me to describe the clonal architecture of salal. Further, I used 1 m² fixed plots at this site to examine overstory effects on populations of stems and rhizomes. I hypothesized that salal seedlings would establish most frequently on rotten logs in thinned stands. I also hypothesized that overstory density would affect clonal morphology and vegetative expansion rates.

LITERATURE REVIEW

Botanical Description

Salal (Gautheria shallon Pursh.) is an evergreen shrub in the Heath (Ericaceae) family. Stems are rigid and sometimes decumbent commonly growing from 0.5 to 1 m in length. Salal has alternate leaves that are dark green above and pale below. The leaves are ovate, from 2.5 to 5 cm long, and have serrate margins. Flowers, 5 to 15 per inflorescence, are borne on glandular racemes. They are light pink to white and are urn-shaped. Salal fruit is a capsule from 6 to 12 mm in diameter. Fruits appear berry-like as they are purple and fleshy. Salal ranges from southeast Alaska, south along the Pacific coast to central California (Martin et al. 1951; Gilkey and Dennis 1980).

Seedling Establishment

Plant breeding systems, seed dispersal, and germination are all processes which, together with seedling survival, determine seedling establishment. These processes can be mutually exclusive in their requirements and responses to environmental stimuli. Grubb (1977) developed the concept of the "regeneration niche". The regeneration niche is, "an expression of the requirements for a high chance of success in

the replacement of one mature individual by a new individual of the next generation", (Grubb 1977). For any particular species, this niche is not only a function of plant processes such as those mentioned above, but also of the physical characteristics of the site, predators, pathogens, competition and amensalistic interactions.

The regeneration niche of salal is not thoroughly understood. Bunnell (1990) found salal flowering to be age-dependent. No shoots under 4 years-old were found with flowers. Additionally, flowering was effected by overstory density. Shoots under sparse canopies had more flowers than those under dense canopies. Flowering dates are generally March through July (Dimock et al. 1974). The primary pollinators of salal are not known. It is reported that wintergreen (Gaultheria procumbens L.) may be autogamous (Mirick and Quinn 1981). Field observations of salal indicate that bees and hummingbirds may be important pollinators.

Fruits of salal ripen from August through October (Dimock et al. 1974). Seed dispersal agents of salal are not known, however, many species of animals ingest the fruits including black bear, grouse and band-tailed pigeon (Dimock et al. 1974; and Martin et al. 1951). Field observations indicate that birds and small rodents may be important dispersal agents. I observed salal seedlings growing in a dense mass that appeared

to be a former seed cache. Additionally, salal plants are often observed growing on top of tall snags. This suggests seed deposition by rodents or birds.

Requirements for salal seedling emergence and survival are partially known. Dimock et al (1974) found that salal seeds had no significant cold stratification requirement and that germination rates were greater on sand or soil than on filter paper. The highest germination rates were found to be 76.0 %. Sabhasri (1961) attempted an experiment in which he sowed salal seeds in the field. Unfortunately, frost killed all of these seedlings during the first growing season. Tappeiner et al. (1992) sowed salal seeds on caged and uncaged mineral soil and undisturbed forest floor plots. These plots were located in thinned stands, unthinned stands, and clearcuts. Their results showed that salal seedling emergence and survival was greatest in thinned stands on mineral soil. There was no significant difference in the emergence of seedlings due to protection from macro-fauna.

Architecture of Clonal Plants

Salal is a clonal plant. Clonal plants are those which produce subsequent individuals of identical genotypes through vegetative growth (Cook 1983). Individuals produced vegetatively are termed ramets. Ramets are shoots with

associated roots having the potential for independent survival (Cook 1979). Ramets may be produced below ground by roots, rhizomes, or buds. They may be also produced above ground by layering, tillering, rooting of surface runners, or by the formation of bulbils or plantlets. Salal produces ramets from rhizomes, horizontal stems which grow underground. All genetically identical ramets produced from a single zygote make up the genet (Cook 1983).

The development of rhizomatous plants follows basic principles of modular tree growth proposed by Hallé et al. in 1978 (Bell and Tomlinson 1980). Modular units are produced sequentially by plant meristems following a genetically controlled primary model (Fisher 1986). Reiteration of the basic morphological units during growth determines the architectural structure of the plant (Harper and Bell 1979). Bell and Tomlinson (1980) suggest that the basic architectural patterns of rhizomatous plants have three components. These components are linearity, divergence from linearity, and the spacing of modular units. These components are, in turn, influenced by meristem position, the timing of meristem activity, and meristem potential. Harper and Bell (1979) point out that meristem "fate" or demography also influence the geometric form of a plant. Although plants are thought to follow a genetic "blueprint", the reiterations of modules during growth are effected by environmental factors (White

1979). Meristems responding to environmental conditions give rise to various organs of diverse shapes and sizes in an "open-ended pattern of development" (Silvertown 1982).

Little is known of the clonal architecture of salal. In fact, no study to date has attempted to describe salal in terms of its architecture. A number of studies have addressed isolated morphological characteristics (Smith 1991; Dimock et al. 1974; Chou 1952; Vales 1986; Bunnell 1990; and Sabhasri 1961). However, all previous research of salal morphology has followed plot sampling methodologies. No study has excavated entire clones in order to describe them in terms of their architecture. Bunnell (1990) excavated clones which were located within sample plots, however, their architecture was not described.

The Effects of Overstory Tree Density on Understory Environments

Plant overstories such as those of forests affect the micro-environment of the understory in many ways and measurements of overstory density may be indicative of a complex array of effects (Anderson et al. 1969). Of the effects, the most significant include the modification of light and temperature, and the interception of precipitation. Competition and amensalistic interactions are also important, however, these are beyond the scope of this review.

The attenuation of light beneath forest overstories is obvious. In 1948, Wellner attempted to predict the light intensity transmitted to an understory using simple stand density measurements such summation of tree diameters per acre and basal area per acre. Wellner found what appeared to be an exponential attenuation curve for light transmittance with increases in stand density. Similar results were found by Jackson and Harper (1955). Monsi and Saeki, in 1953, developed their adaptation of Beer's light attenuation law. This demonstrated that the relative light intensity beneath a forest canopy decreases exponentially with increasing leaf area index (total leaf area per unit area of ground). Their equation is as follows:

$$I = I_0 e^{(-kF)}$$

where I is the transmitted light intensity, I_0 is the intensity of light in the open, k is an extinction coefficient, and F is the leaf area index (LAI) of the canopy. The specifics of this equation have been analyzed and refined (Anderson 1966). However, the simple relationship between relative light intensity and leaf area still remains. In the Douglas-fir forests of the Pacific northwest, LAI values of the overstory may reach as high as $12 \text{ m}^2/\text{m}^2$ (Waring and Schlesinger 1985). Using the above equation and an extinction coefficient of -0.5 , we find that at this extreme LAI less

than 1 percent of the solar radiation is transmitted to the forest floor.

A direct correlation between tree diameter and leaf area has been found for many species including trees in the northwest (Gholz et al 1979). This suggests that simple stand density indices that incorporate tree diameters or leaf area estimations may be good predictors of transmitted light intensity. Vézina and Péch (1964) found an exponential relationship between crown closure and net solar radiation while Vales and Bunnell (1988) found that Reineke's stand density index (Reineke 1933), summation of diameters and mean crown completeness were strongly related to transmitted light.

Light quality, or the relative flux density of specific wavelengths of radiation, is also affected by forest canopies (Smith 1982; and Holmes and Smith 1977a). As light passes through the parenchyma tissue and chloroplasts of leaves, it is reflected and absorbed to a great degree (Ruechardt 1958). In general, blue and red wavelengths (0.45 to 0.50 μm and 0.66 to 0.70 μm respectively) are absorbed while green wavelengths (0.50 to 0.575 μm) are reflected and far-red (0.70 to 0.80 μm) are reflected and transmitted. As canopy density increases, the amount of red and blue light reaching the forest understory decreases while far-red light is not affected

significantly. Thus the ratio of red:far-red light decreases (Smith 1982).

The interception of precipitation by the crowns of forest trees additionally effects the environment of the understory. A significant amount of intercepted precipitation maybe "lost" by direct evaporation from the canopy back into the atmosphere (Kittredge 1948). In Douglas-fir forests, annual interception loss may be up to 34 % (Kittredge 1948). However, the relationship of interception to overstory density is not clear. Kimmins (unpublished data) found that interception loss in a Douglas-fir plantation decreased with increasing stand density. The measurement of density used in this study was the number of trees per hectare. Kimmins attributed the results to larger crowns and storage capacity of more widely spaced trees. Others have found that forest canopies can increase gross precipitation (Harr 1982). Wind-driven clouds may condense on plant surfaces and subsequent fog drip to the forest understory may occur.

In general, temperature extremes tend to be dampened by forest canopies (Kimmins 1987). Although more total incoming solar radiation is absorbed by a forest canopy than by a clearing, less radiation reaches the soil beneath a canopy. A proportion of the radiation that reaches the soil may be conducted downward, raising the temperature. Additionally, the

sensible heat flow from dry bare soil may be as much as 70 % of the net radiation while that from a forest canopy may be just 30 % (Kimmins 1987). Therefore, summer daytime temperatures may be much higher, and nighttime temperatures much lower, in clearings than beneath a forest canopy. However, it is unclear how stand densities between these two extremes influence temperature.

Response of Salal Productivity to Changes in Overstory Density

Besides its competitive effects on commercial tree species, the response of salal productivity to changes in overstory density is one of the most researched aspects of the species. Sabhasri (1961) first called salal a "sun-loving species". Although his research did not measure productivity, he found that the photosynthetic rate of salal under a stand of Douglas-fir was 15.6 % of that for salal plants in full sunlight.

Long and Turner (1975) found that as the basal area of an age sequence of Douglas-fir stands increased, the aboveground biomass of salal in the understory decreased. They attributed these results to salal's shade intolerance. Vales (1986) found similar results when he examined salal shoot biomass, foliar biomass and percent cover over a range of stand densities. Results from Vales's study showed that the stand density

indices, summation of tree diameters and Reineke's stand density index, were good predictors of salal percent cover and total shoot biomass/m². Overstory cover, as measured by mean crown completeness, was also a good predictor; however, basal area and number of trees per hectare were relatively poor predictors of salal abundance. Vales attributed reductions in salal biomass to overstory attenuation of transmitted radiation and competition for soil moisture and nutrients .

Bunnell (1990), also measured salal growing in various stand densities. Although he excavated portions of just 10 clones, his results showed that the total interconnecting rhizome length observed in stands of 30 percent mean crown completeness was nearly twice that found in stands of 78 to 90 percent mean crown completeness. Additionally, there were more interconnected shoots per clone under sparse canopies than under dense canopies.

Smith (1991), found that salal leaf biomass peaked at Curtis's metric relative density of 5.9. These results showed the dry weight of leaves (g/m²) to be greatest under partial shade where salal forms both sun and shade leaves in equal abundance. A relative density value of 5.9 corresponds to a availability of 15 % of global photosynthetically active radiation (PAR).

Messier et al. (1989) found 1.2 to 3.3 % global PAR to be the minimum light requirement for salal survival. These conclusions were based on decreases in salal percent cover, leaf biomass, leaf area, specific leaf weight, and leaf thickness with increases in overstory percent cover. Messier et al. postulated that an overstory canopy cover of 80 % or greater would be sufficient to eliminate salal from their study sites.

Morphological Response of Salal to Changes in Overstory Density

Morphological changes associated with differential light intensity have been observed for many plant species. Responses include changes in clonal structure and size, leaf morphology, stem heights, internode lengths, and ramet size (Tucker and Emmingham 1977; Slade and Hutchings 1987; Antlfinger et al. 1985; Pitelka et al. 1980; and Morgan and Smith 1981). However, many of these responses are believed to be phytochrome related and thus are functions of light quality (ie. red:far-red light ratios) rather than light quantity (Holmes and Smith 1977b; Vince-Prue 1977; and Smith 1982). It may be reasonable to presume that both light quality and light quantity effect changes observed in plant morphologies.

The morphological responses of salal to changes in overstory density are less clear than its' productivity

responses. Sabhasri (1961), in a greenhouse study, found that salal plants grown in high light intensities produced longer shoots with more leaves per shoot than those grown under low light intensities. Unfortunately, the highest light intensity used in this study, 400 foot-candles, was only around 4% of normal daylight intensities. Sabhasri also found that light quality, observed using colored filters on artificial lights, effected shoot elongation and the number of leaves per shoot.

Smith (1991) found that salal leaf morphology was effected by overstory density. Salal shoots growing in full sunlight developed relatively narrow leaves with low specific areas as compared to leaves produced by shaded shoots. These results were similar to those found by Messier (1989).

Bunnell (1990) concluded that, "salal plants under sparse canopies tended to consolidate site occupancy", while plants under dense canopies, "invested more in rhizome extension". He found that there was a tendency for young ramets to be located closer to older ramets under sparse canopies. Intershoot rhizome lengths were significantly longer under the dense overstories ($p < 0.05$). Thus, salal clones may take on a "guerilla" form under dense canopies and a "phalanx" form under sparse canopies (eg. Lovett-Doust 1981). Guerilla forms are those that have relatively small ramet densities and long rhizome lengths. Phalanx forms are those that have high ramet

densities and short rhizome lengths. Bunnell's conclusions, however, were based on the excavation of just 10 clones.

CHAPTER I. SEEDLING ESTABLISHMENT EXPERIMENT

It had been noted in field observation that seedlings of salal are most often found on coarse woody debris. Tappeiner and Zasada (1992) found that seedlings became established most successfully in thinned stands. The seedling establishment experiment was conducted to determine the effects of substrate and overstory density on seedling establishment. Seedling emergence and survival on coarse woody debris, mineral soil, and the undisturbed forest floor was observed for two growing seasons in clearcuts, thinned stands, and unthinned stands. Differences in establishment due to substrate and overstory density were tested. For seedlings growing under forest canopies, correlations between percent sky and first year survival were tested.

METHODS

Study Sites

Three study areas in the Tsuga heterophylla vegetation zone (Franklin and Dyrness 1973) of the central Oregon coast range were selected for this experiment. Two sites, Cape Creek and Cascade Head, were on the western side of the range near the Pacific coast while the third site, Randall Saddle, was more interior. The Cape Creek site was located within the

Siuslaw National Forest near the town of Florence, Oregon. The Cascade Head site was located within the Cascade Head Experimental forest and the Siuslaw National Forest near the town of Lincoln City, Oregon. The Randall Saddle site was located within the Siuslaw National Forest near the town of Harlan, Oregon. The three sites were selected to represent growing conditions in the central Oregon coast range favorable to salal. Mean annual precipitation in this region ranges from 100 to 230 cm, the majority of which falls in the winter as rain. Mean summer temperatures range from 15 to 17 °C while mean winter temperatures range from 5 to 9 °C. Soils are generally silty clay loams generated from parent material of the Tyee sandstone formation (Franklin and Dyrness 1973). Forest overstories at the coastal sites were dominated by western hemlock while forests at the Randall Saddle site were dominated by Douglas-fir. Table I-1 provides a description of each study site.

At both Cape Creek and Cascade Head, 1 clearcut, 1 thinned stand, and 1 unthinned stand were selected. Stands at these sites were comprised of trees ranging from 50 to 80 years old. At Randall Saddle, 1 clearcut, 1 thinned stand, and 3 unthinned stands were selected. All stands at Randall Saddle except one were comprised of trees ranging from 50 to 80 years old (table I-1). The total number of stands used for this experiment was 11.

Table I-1. Description of seedling study sites and stands.

Randall Saddle						Cape Creek			Cascade Head		
Latitude	44 25' N					44 05' N			45 03' N		
Longitude	123 50' W					123 57' W			123 59' W		
Elevation	150-350 m					100-300 m			100-300 m		
Annual Precipitation	178 cm					178 cm			251 cm		
Average Summer Temperature	17 C					15 C			15 C		
Average Winter Temperature	5 C					9 C			5 C		
Soils	Moderately-well drained; Clay loam					Moderately-well drained; Silty-clay loam; acidic			Moderately-well drained; Silty-clay loam; acidic		
Dominant Overstory Species	<i>Pseudotsuga menziesii</i>					<i>Pseudotsuga menziesii</i> - <i>Tsuga heterophylla</i>			<i>Pseudotsuga menziesii</i> - <i>Tsuga heterophylla</i>		
Dominant Understory Species	<i>Gaultheria shallon</i> <i>Rubus</i> spp. <i>Vaccinium</i> spp. <i>Sambucus callicarpa</i> <i>Polystichum munitum</i>					<i>Gaultheria shallon</i> <i>Acer circinatum</i> <i>Rubus</i> spp. <i>Polystichum munitum</i>			<i>Gaultheria shallon</i> <i>Vaccinium</i> spp. <i>Rubus</i> spp. <i>Acer circinatum</i> <i>Sambucus caerulea</i>		
Stand #	1	2	3	4	5	1	2	3	1	2	3
Descript.	Clear-cut	Un-thinned	Un-thinned	Thinned	Un-thinned	Clear-cut	Thinned	Un-thinned	Clear-cut	Thinned	Un-thinned
Trees per ha	750-875	250-375	550-750	75-150	250-375	750-875	100-150	300-425	750-875	75-150	300-425
Average Diameter (cm)	1-3	55-65	15-20	50-65	50-65	3-7	50-60	45-55	2-5	50-60	45-55
Age (yrs)	2-5	60-80	30-50	60-80	60-80	5-8	50-70	50-65	3-6	50-65	50-65

Seed Collection

During November of 1990, I collected salal fruits from plants found near Cascade Head and near the Oregon State University campus in Corvallis, Oregon. These fruits were allowed to dry on wire screens for 2 weeks. The dry fruits were then carefully ground using a mortar and pestle and the seeds were separated from the fruit material using a fine sieve. I next tested the seeds for germination potential. This was done using 10 petri-dishes, lined with filter paper, sowed with 100 seeds each. The petri-dishes were kept at approximately 10 °C with diurnal exposure to florescent light. The filter paper was kept moist. The seeds were observed for 4 weeks and germinated seeds were noted and removed from the petri-dishes. At the end of this period, approximately 25% of the seeds had germinated.

Establishment of Plots and Seedling Monitoring

In the stands selected at the 3 study sites, plots were established on which to sow salal seeds. Circular plots, each plot approximately 0.5 m in diameter, were created randomly on rotten logs and stumps, exposed mineral soil, and the undisturbed forest floor. Logs that were selected for plot establishment were of decay class III or IV (Sollins 1982). Plots were replicated 10 times per substrate making a total of

30 plots per stand. Approximately 400 seeds were sown per plot. This number was selected as a result of the germination test. I wanted to have at least 100 seeds germinate per plot. The seeds were sown using a small spoon to scatter them on top of the substrate. None of the seeds were buried.

The seedling plots were monitored beginning in March 1991 and ending in August 1992. Plots at the Randall Saddle site were checked at approximately 2-week intervals during the first growing season while plots at both the Cape Creek and Cascade Head sites were monitored once per month. The first growing season was defined as the period from March through October, 1991. During the second growing season, plots at all 3 sites were examined twice, once in June and once in August, 1992. Monitoring consisted of seedling counts, and noting signs of disturbance and seedling mortality. At the end of the first growing season, the largest of the seedlings were measured for height. The heights of up to 50 seedlings per stand were randomly measured at the end of the second growing season.

Measurement of Percent Sky and Substrate Moisture Content

"Percent sky" was measured on cloudless and overcast days in June, 1992. This was done using a pair of Licor 2000 Canopy Analyzers. Percent sky is an estimate of the relative amount

of sky not obscured by a forest overstory. In this experiment, percent sky was used as an indirect measurement of relative light availability. To measure percent sky, three canopy analyzer readings were taken over each seedling plot at a height of approximately 1 meter. These readings were compared with simultaneous readings taken in the open and an average percent sky was calculated for each plot.

The moisture content of logs and mineral soil was measured at Randall Saddle throughout the summer in 1991. Approximately 2 square centimeters of substrate was collected each month from 5 to 10 seedling plots per stand. The samples were collected from a depth of 1 to 5 cm which was assumed to be the depth of the seedling's roots. The moisture content was determined gravimetrically by oven-drying at 70 °C for 48 hours. The moisture content of the undisturbed plots was not measured.

Pilot Study

The pilot study, conducted at the Cascade Head site, followed similar methods. In 1987 and 1988, approximately 850 viable seeds were sown on mineral soil, litter, and coarse woody debris plots in a clearcut, a thinned stand, and an unthinned stand. Five plots per stand were sown. The

emergent seedlings were monitored from the spring of 1987 until the spring of 1991.

Data Analysis

Peak emergence was defined as the maximum number of seedlings counted in a plot during the first growing season:

(1) Peak Emergence = maximum # of seedlings counted in a plot

Percent survival was defined as the number of seedlings surviving at the end of the first, or second growing season divided by the number at peak emergence:

(3) Percent Survival = $\frac{\text{number of surviving seedlings}}{\text{Peak Emergence}}$

Seedling:seed ratio, a measure of the ecological importance of a site, was defined as the number of seeds counted divided by the number of seeds sown:

(4) Seedling:seed ratio = $\frac{\text{\# of seedlings counted}}{\text{\# of seedlings sown}}$

This variable was used for seedling counts at the end of the two growing seasons.

The data were treated as a randomized block design using study site, stand density, and substrate as blocking factors.

Multifactor analysis of variance (ANOVA) was used to analyze emergence, survival, percent survival, and seedling:seed ratios for significant effects due the blocking factors. The data was normalized when necessary using the square-root transformation. The least significant difference (LSD) test was used to compare differences within the factor groups. The significance level used in the multi-range tests was 95 %.

One-way ANOVA was used to test for differences in percent survival and seedling:seed means due to substrate within stands. The data were square-root transformed when necessary to normalize the distributions. LSD multi-range tests were used to test for differences between substrates. For these tests, a 95 % significance level was used.

Two sample t-tests were used to test for differences in percent survival and seedling:seed ratio due to stand density within study sites. The data were square-root transformed when necessary and a 95 % significance level was used. When these data could not be transformed satisfactorily, a Wilcoxon rank-sum test was used to compare the groups.

Simple linear regression was used to test correlations between percent survival in thinned and unthinned stands and percent sky measurements. Residuals were examined and the data were square-root transformed when necessary.

RESULTS AND DISCUSSION

Emergence

Emergence of the experimentally sown salal seedlings was first observed in early April. Seedlings in clearcuts were noticed a few weeks before those in other stand densities. Peak emergence, the maximum number of seedlings counted in a plot during the season, followed this same pattern. For all study sites, seedling emergence peaked earlier in the clearcuts than either the thinned or unthinned stands. Among study sites, peak emergence was observed earlier at the Randall Saddle site. Peak emergence occurred in Randall Saddle clearcuts from late April to mid May, while the highest total counts in Cape Creek and Cascade Head clearcuts were in late May. Emergence in thinned stands and unthinned stands at Randall Saddle peaked during mid June. Emergence in thinned and unthinned stands at both coastal sites peaked from early to mid July. There was no apparent differences in the timing of peak emergence due to substrate at any site.

Study site location affected peak emergence. The total emergence was lower at Randall Saddle ($p < 0.05$) than either Cape Creek or Cascade Head. The latter two sites were statistically similar in numbers of emerged seedlings. Mean emergence values with respect to study site location were

89.23 (± 6.66 SE), 70.27 (± 6.66 SE), and 25.75 (± 5.25 SE) seedlings per plot for Cascade Head, Cape Creek, and Randall Saddle respectively (table I-2).

Stand density also had a significant effect on the number of seedlings that emerged (table I-2). At all sites, clearcuts (50.5 ± 6.53 SE) had significantly lower emergence values than either thinned stands or unthinned stands ($p < 0.05$). Overall, there were no significant differences in emergence between thinned stands (74.65 ± 6.22 SE) and unthinned stands (60.11 ± 5.76 SE). At the Randall Saddle site, however, unthinned stands had greater emergence values than thinned stands ($p < 0.05$).

Results showed that the magnitude of peak emergence was significantly affected by substrate (table I-2). At all three study sites, emergence was significantly greater on coarse woody debris (102 ± 5.66 SE) than on either mineral soil (35.25 ± 5.66 SE) or the forest floor (47.81 ± 7.16 SE) ($p < 0.05$). At Cape creek and Cascade Head, there was no significant difference between mineral soil or the forest floor in emergence yet, at Randall saddle, emergence was greater on mineral soil than on the forest floor plots ($p < .05$).

The above results suggest that differences in local and

Table I-2. Least squares means for peak emergence*.

Level	Mean Number of Emerged Seedlings	Standard Error
Grand Mean	61.75	3.63
Substrate:		
Logs	102.19a	5.66
Mineral Soil	35.25b	5.66
Undisturbed Floor	47.81b	7.16
Stand Density:		
Thinned	74.65a	6.22
Unthinned	60.11a	5.76
Clearcut	50.5b	6.53
Study Site:		
Randall Saddle	25.75a	5.25
Cape Creek	70.27b	6.66
Cascade Head	89.23b	6.66

* Like letters read within a group denote statistically similar means at a 95% confidence level.

microsite environments effect salal seedling emergence. These factors appear to include precipitation and temperature. For example, the Cascade Head site receives nearly 100 cm more precipitation annually than the other 2 study sites. Additionally, mean winter temperatures at the coastal sites are warmer than those of Randall Saddle.

The mean emergence rate (peak emergence divided by the number of seeds sown) of thinned stands, 18.5 %, was greater than that of clearcuts by nearly one-third. Diurnal temperature extremes experienced in clearcuts (Kimmins 1987) may explain their low emergence values. These results are consistent with those of the pilot study. Both cohorts, 1987 and 1988, had higher mean emergence in the thinned stand than the unthinned stand. Mean emergence in the thinned stand ranged from 92 (± 22 SE) to 18 (± 8 SE) seedlings per plot, while emergence in the unthinned stand and clearcut ranged from 66 (± 16 SE) to 9.6 (± 6 SE) and from 37 (± 14 SE) to 8 (± 8) seedlings per plot respectively.

The seedling emergence results also suggest that coarse woody debris provides "safe sites" (Harper et al. 1961) for salal seeds. During this experiment, soil pedestals were noted on many mineral soil plots. These pedestals indicated significant erosion of the plots. Thus, exposed seeds may have been transported off the plots during heavy rains. These seeds

may have moved to sites beneath forest litter or moss. Further, mineral soil had significantly lower moisture content throughout the year (figure I-1). The micro-fissures of course woody debris may hold seeds and protect them from being washed beneath litter and vegetation. These fissures may also protect seeds from water loss. Harper et al (1965) found that these kinds of micro-topological features have significant effects on seed germination. Seeds sown on undisturbed forest floor plots may have also become buried in the moss and litter. These buried seeds may have germinated but not emerged. These results were also consistent with those from the pilot study. Maximum emergence was 92 (\pm 22 SE) seedlings on logs while minimum was 9.6 (\pm 6 SE) seedlings on mineral soil.

First Year Survival

From mid July through August of the first growing season, substantial seedling mortality was observed. This was particularly true for the clearcut plots and plots on the undisturbed forest floor. Seedlings in thinned stands, especially those on logs, survived well relative to seedlings in other stands. Some surviving seedlings appeared vigorous. These were measured up to 4.4 cm in height by October of 1991.

Study site location, stand density, and substrate all had significant effects on salal seedling survival. Over all

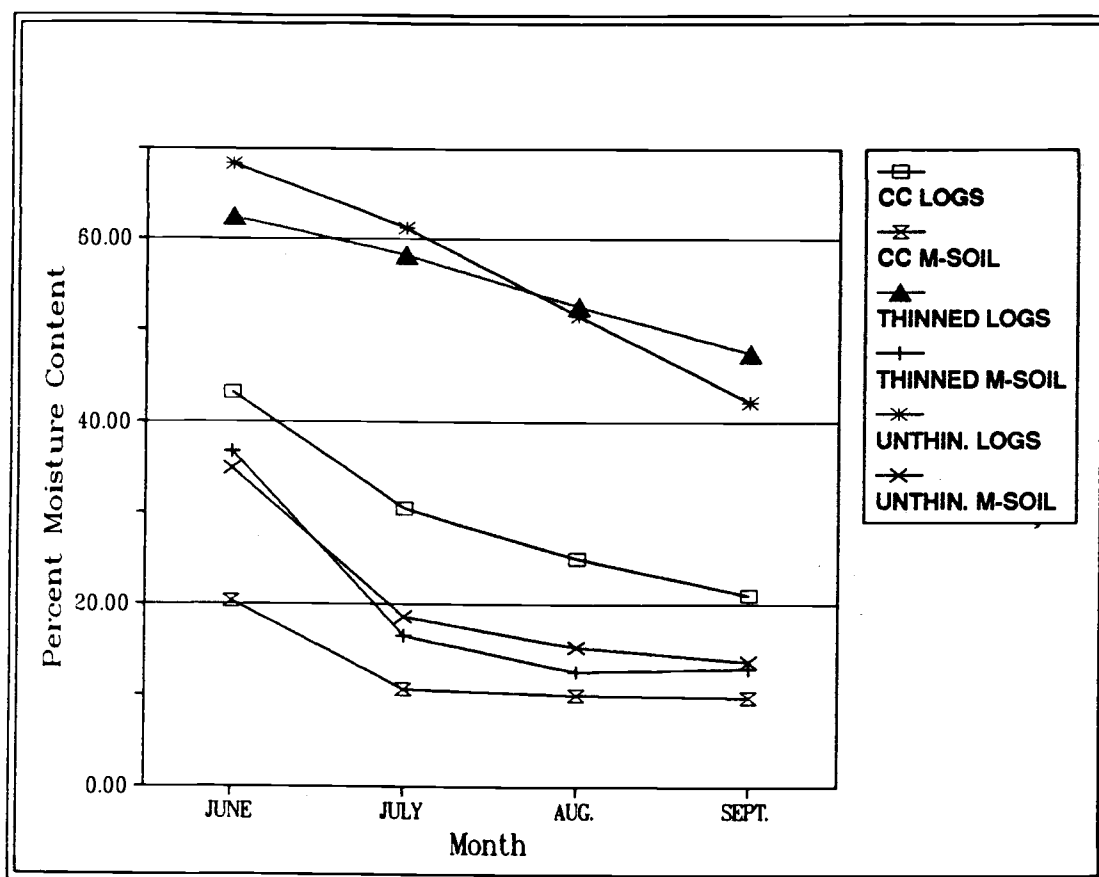


Figure I-1. Moisture content, in percent by weight, of logs and mineral soil (M-SOIL) in clearcuts (CC), thinned stands, and unthinned stands (UNTHIN.) during the 1991 growing season.

sites, Cascade Head significantly higher survival than Randall Saddle and Cape Creek (table I-3) ($p < 0.05$). At Cascade Head, 23.6 percent (± 2.2 SE) of emerged seedlings survived through the first growing season while at Cape Creek and Randall Saddle just 8.1 (± 2.2 SE) and 10.5 (± 1.7 SE) percent survived respectively. Survival at the latter 2 sites was not statistically different.

Of the three stand densities, seedling survival was greatest in the thinned stands (table I-3) ($p < 0.05$). Over all sites, thinned stands averaged 30.1 (± 2.1 SE) percent survival while unthinned stands and clearcuts averaged 8.0 (± 1.7 SE), and 4.3 (± 2.4 SE) percent respectively. Unthinned stands had significantly higher survival than clearcuts ($p < 0.05$). No seedlings survived in the clearcut at Cape Creek.

Logs and stumps had significantly higher survival than either mineral soil or undisturbed forest floor plots ($p < 0.05$) (table I-3). On average, 25.4 (± 1.83 SE) percent of the seedlings that emerged on woody debris survived to the end of the first growing season while 14.3 (± 1.85 SE) and 2.6 (± 2.5 SE) percent survived on mineral soil and undisturbed forest floor plots respectively.

Figure I-2 shows percent survival of seedlings at each study site and within each stand (except unthinned stand #3 at

Table I-3. Least squares means for first year percent seedling survival*.

Level	Mean Percent Survival	Standard Error
Grand Mean	14.1	1.2
Substrate:		
Logs	25.4a	1.8
Mineral Soil	14.3b	1.8
Undisturbed Floor	2.6c	2.5
Stand Density:		
Thinned	30.1a	2.1
Unthinned	8.0b	1.7
Clearcut	4.3c	2.4
Study Site:		
Randall Saddle	10.5a	1.7
Cape Creek	8.1a	2.2
Cascade Head	23.6b	2.2

* Like letters read within a group denote statistically similar means at a 95% confidence level.

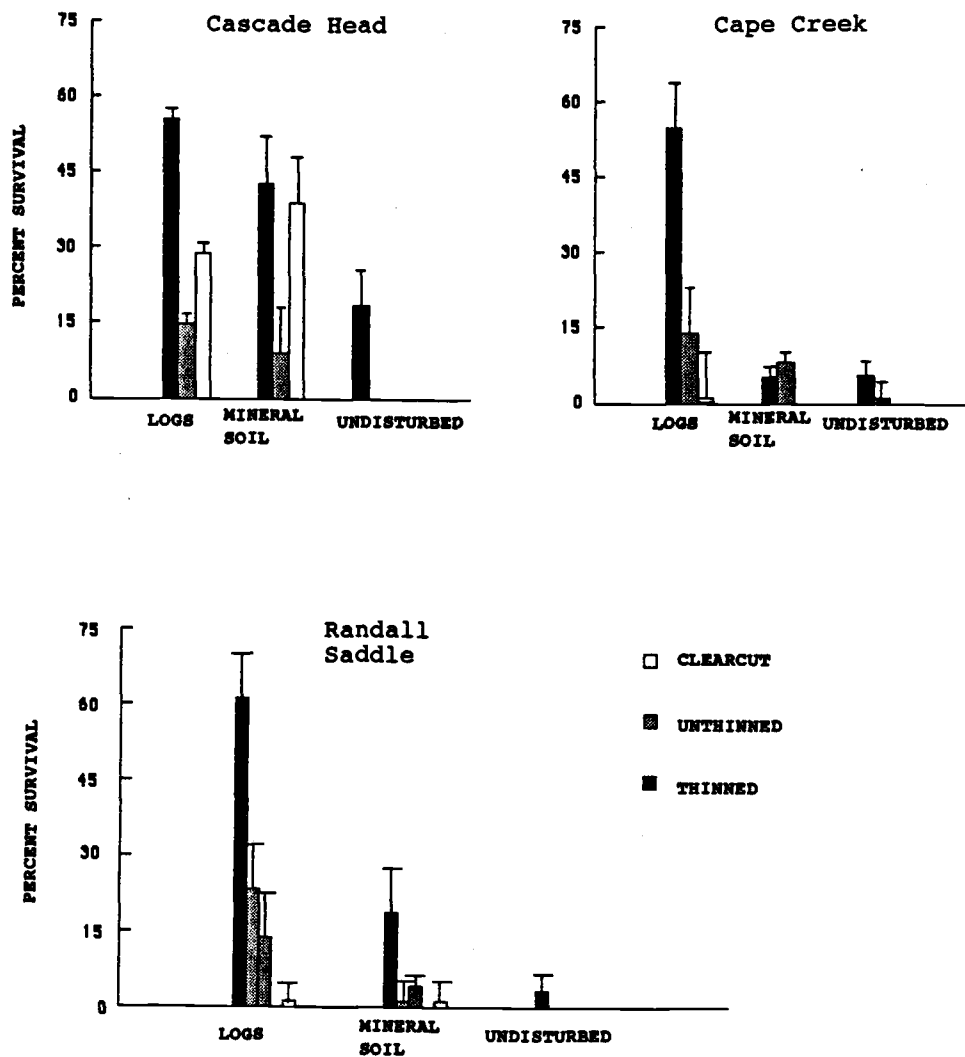


Figure I-2. Percent survival of seedlings at Cascade Head, Cape Creek, and Randall Saddle, by substrate and overstory density.

Randall Saddle which had no surviving seedlings). These values are reported in table I-4. Note that at each study site percent survival follows the reported overall pattern. Thinned stands had consistently higher survival than unthinned stands and clearcuts while logs had consistently higher survival than mineral soil and the undisturbed forest floor.

These results, like those of emergence, may be explained by the local and micro-site environmental differences. Relative precipitation and temperature of the study sites and stands may have affected seedling survival since the lowest survival was at Randall Saddle, the most interior site. These results are consistent with those of Haeussler (1987). She found lower survival of red alder (Alnus rubra Bong.) and lower soil moisture at interior sites as compared with coastal sites.

The relative light availability of thinned stands and unthinned stands was also apparently important. These results are consistent with the findings of Tappeiner et al (1992). Light conditions in dense stands appear to be below the light compensation points of salal seedlings. Additionally, important amensalistic interactions were observed. Burial by litter-fall, especially in stand 3 at Randall Saddle, appeared to be a factor in seedling mortality. In clearcuts, high evaporative demand and competition with ruderal herbs and

Table I-4. First year percent survival values of seedlings at Cascade Head, Cape Creek, and Randall Saddle study sites. Table presents means and standard errors for all tested substrates and stand densities*.

Percent Survival and (Standard Errors)				
Study Site	Stand Density	Substrate		
		Logs	Mineral Soil	Undisturbed
Cascade Head	Thinned	55.2 (2.2)ai	42.8 (9.2)ai	18.5 (7.0)bi
	Unthinned	14.8 (6.1)aii	8.8 (2.7)abii	0.0 (0.0)bi
	Clearcut	28.7 (8.0)aii	38.8 (10.7)ai	NA
Cape Creek	Thinned	54.6 (9.2)ai	5.2 (2.2)bi	5.5 (3.2)bi
	Unthinned	13.9 (5.5)aii	8.1 (3.8)abi	1.0 (0.5)bi
	Clearcut	0.0 (0.0)aiii	0.0 (0.0)aii	NA
Randall Saddle	Thinned	61.1 (8.7)ai	18.8 (8.8)bi	3.4 (3.4)bi
	Unthinned	23.2 (6.6)aii	1.4 (0.8)bi	0.0 (0.0)bi
	Unthinned	13.8 (4.5)aii	4.0 (1.6)bi	0.0 (0.0)bi
	Unthinned	0.0 (0.0)aiii	0.0 (0.0)ai	0.0 (0.0)ai
	Clearcut	1.2 (0.9)aiii	1.3 (1.0)ai	NA
	Clearcut	0.3 (0.3)aiii	0.0 (0.0)ai	NA

* Like letters read across rows within study site groups denote statistically similar means at a 95% confidence level.
 ** Like numbers of (i)s read down columns within study site groups denote statistically similar means at a 95% confidence level.

grasses may have contributed to seedling mortality. unthinned stands buried some seedlings.

The relative moisture content of course woody debris may have contributed to higher seedling survival. Logs, as reported, contained more moisture by weight throughout the growing season than did mineral soil. Additionally, seedlings on logs were removed from competition with forest floor vegetation (Harmon 1986). This was particularly true in thinned stands and in clearcuts. This may have improved survival in thinned stands while log seedlings in clearcuts were exposed to the lethal effects of extreme temperatures and full sunlight. Pathogens and predation may have contributed to seedling mortality on undisturbed forest floor plots. However, Tappeiner and Zasada (1992) found no substantial evidence of predation of salal seed. Findings of Haeussler (1987) indicate that forest floor pathogens were important in red alder establishment. Additionally, many seedlings appeared to be perched within the litter layer, hindering the penetration of seedling radicles into the soil substrate.

Relationship of First Year Survival to Percent Sky

For all sites, percent sky, the variable used to indicate light availability, was found to be significantly and positively correlated to first year survival of seedlings on

course woody debris ($p < 0.05$). There was no significant correlation found between percent sky and percent survival for seedlings on mineral soil or the undisturbed forest floor at Cape Creek ($p > 0.05$). At Randall Saddle, a significant relationship was found for undisturbed forest floor plots ($p < 0.05$). There were significant relationships between survival and percent sky for all substrates at Cascade Head ($p < 0.05$).

The relationship between survival and percent sky was most pronounced for seedlings on logs at the Randall Saddle study site ($r = 0.77$) (table I-5). Results showed that percent sky explained 60 percent of the variability survival for these data. Percent sky was least important to seedling survival on mineral soil at Randall Saddle ($r = -0.1363$). For these data, percent sky explained just 1.86 percent of the variability in seedling survival. Similar results were found for Cape Creek seedlings. There was a significant and positive relationship between survival and percent sky on logs but no such relationship was found for seedlings on mineral soil or the forest floor. Seedling survival on logs at Cascade Head was intermediately correlated with percent sky relative to the other sites ($r = 0.60$). Percent sky explained just 36.6 percent of the variability in seedling survival on logs at this site. Cascade Head was the only site to show significant relationships between survival and percent sky on mineral soil and the undisturbed forest floor.

Table I-5. Correlation coefficients, (R-squared values), and p-values for regressions of first year seedling survival on percent sky.

Study Site	Correlation Coefficient; (R-Squared); P-value			
	Substrate			
	Logs	Mineral Soil	Undisturbed	
Overall	0.516 (0.2663) 0.00001	-0.129 (0.0168) 0.375	0.192 (0.0367) 0.236	
N	66	48	39	
Cascade Head	0.605 (0.3664) 0.0078	0.57 (0.3255) 0.011	0.487 (0.2368) 0.035	
N	18	18	18	
Cape Creek	0.5799 (0.3364) 0.0092	-0.2672 (0.0714) 0.2546	-0.0324 (0.0010) 0.902	
N	19	20	17	
Randall Saddle	0.774 (0.5993) < 0.00000	-0.1363 (0.0186) 0.9987	0.467 (0.2179) 0.02474	
N	29	29	23	

These results indicate that light availability is important to seedling survival. However, other factors such as competition, pathogens, and moisture stress may also have significant effects. Further, factors other than light availability appear to be most important in effecting survival on the forest floor. This seems to concur with the above reported findings and with findings of other studies (Haeussler 1987; and Harmon 1987). Light availability may be more important to seedlings on logs due to seedling position above competition, reduced moisture stress, and an absence of pathogens or predators.

Second Year Percent Survival

By September 1992, relatively few seedlings remained. Survival in the second season, like the first, was affected by study site location, overstory density, and substrate.

Over all sites, Cascade Head had significantly higher survival than Randall Saddle or Cape Creek ($p < 0.05$) (table I-6). Mean survival at Cascade Head was 7.17 (± 1.17 SE) percent while just 3.8 (± 0.89 SE) and 2.4 (± 1.16 SE) percent of the emergent seedlings survived at and Randall Saddle and Cape Creek respectively. Survival means at the latter two sites were not statistically different ($p > 0.05$).

Table I-6. Least squares means for second year percent seedling survival*.

Level	Mean Percent Survival	Standard Error
Grand Mean	4.47	0.64
Substrate:		
Logs	10.81a	0.96
Mineral Soil	2.60b	0.97
Undisturbed Floor	0.0c	1.30
Stand Density:		
Thinned	10.16a	1.08
Unthinned	1.71b	0.92
Clearcut	1.52b	1.26
Study Site:		
Randall Saddle	3.80a	0.89
Cape Creek	2.40b	1.17
Cascade Head	7.17a	1.17

* Like letters read within a group denote statistically similar means at a 95% confidence level.

Thinned stands had significantly higher survival than unthinned stands or clearcuts ($p < 0.05$) (table I-6). No seedlings survived in clearcuts except at Cascade Head. Mean percentages of seedlings to survive in thinned stands, unthinned stands, and clearcuts were 10.16 (± 1.08 SE), 1.71 (± 0.92), and 1.52 (± 1.26 SE) percent respectively. Percent survival means in unthinned stands and clearcuts were not statistically different ($p > 0.05$)

All substrates showed significant differences in percent survival ($p < 0.05$) (table I-6). Seedlings on logs and stumps had the greatest survival while seedlings in the undisturbed plots survived only in the thinned stand at Cascade Head. On logs, 10.81 (± 0.96) percent of the emergent seedlings survived. Mean survival values in mineral soil and undisturbed plots were 2.6 (± 0.97 SE) and 0.0 (± 1.30 SE) percent, respectively.

Stands at the individual study sites followed these same patterns. Logs and thinned stands had consistently greater survival after the second growing season than the other substrates and stand densities. Table I-7 shows percent survival at each study site.

Table I-7. Second year percent survival values of seedlings at Cascade Head, Cape Creek, and Randall Saddle study sites. Table presents means and standard errors for all tested substrates and stand densities*.

Percent Survival and (Standard Errors)				
Study Site	Stand Density	Substrate		
		Logs	Mineral Soil	Undisturbed
Cascade Head	Thinned	23.6 (4.8)ai	5.4 (2.2)ai	2.9 (2.1)bi
	Unthinned	3.4 (2.0)aii	0.0 (0.0)bii	0.0 (0.0)bi
	Clearcut	19.3 (8.0)ai,ii	9.14 (4.6)bi	NA
Cape Creek	Thinned	25.13 (5.6)ai	0.0 (0.0)bi	0.0 (0.0)bi
	Unthinned	1.2 (0.77)aii	0.0 (0.0)bi	0.0 (0.0)bi
	Clearcut	0.0 (0.0)aii	0.0 (0.0)ai	NA
Randall Saddle	Thinned	27.6 (6.7)ai	5.8 (3.5)bi	0.0 (0.0)bi
	Unthinned	6.1 (3.2)aii	0.92 (0.64)bi	0.0 (0.0)bi
	Unthinned	9.4 (3.7)aii	0.0 (0.0)bi	0.0 (0.0)bi
	Unthinned	0.0 (0.0)aiii	0.0 (0.0)ai	0.0 (0.0)ai
	Clearcut	0.0 (0.0)aiii	0.0 (0.0)ai	NA
	Clearcut	0.0 (0.0)aiii	0.0 (0.0)ai	NA

* Like letters read across rows within study site groups denote statistically similar means at a 95% confidence level.

** Like numbers of (i)s read down columns within study site groups denote statistically similar means at a 95% confidence level.

Seedling:Seed Ratios

Seedling:seed ratios generally followed the same pattern as second year survival. Seedling:seed ratios were affected by study site location, stand density, and substrate. Table I-8 shows the least squares estimates of seedling:seed means and standard errors over all sites. Overall, the mean percentage of seeds to become established was just 1.4 (± 0.003 SE).

The Cascade Head study site did not have seedling:seed which were significantly greater than Randall Saddle and Cape Creek ($p > 0.05$) (table I-8). However, the latter two sites did have statistically dissimilar means ($p < 0.05$). Mean seedling:seed ratios for the three study site locations were 0.023 (± 0.005 SE), 0.013 (± 0.005 SE), and 0.006 (± 0.004 SE) at Cascade Head, Cape Creek, and Randall Saddle respectively.

Thinned stands had significantly greater ratios than unthinned stands and clearcuts ($p < 0.05$) (table I-8). The latter two stand densities did not have statistically different means. Seedling:seed ratios for the three stand densities were 0.037 (± 0.004 SE), 0.007 (± 0.004 SE), and 0.003 (± 0.005 SE) in thinned, unthinned, and clearcuts respectively.

Significantly greater percentages of seeds become

Table I-8. Least squares means for second year seedling:seed ratios*.

Level	Mean Seedling: Seed Ratio	Standard Error
Grand Mean	0.014	0.014
Substrate:		
Logs	0.038a	0.004
Mineral Soil	0.005b	0.004
Undisturbed Floor	0.00b	0.005
Stand Density:		
Thinned	0.037a	0.004
Unthinned	0.007b	0.004
Clearcut	0.003b	0.005
Study Site:		
Randall Saddle	0.006a	0.004
Cape Creek	0.013ab	0.005
Cascade Head	0.023b	0.005

* Like letters read within a group denote statistically similar means at a 95% confidence level.

established on logs and stumps by the end of the second growing season than mineral soil or the undisturbed forest floor ($p < 0.05$) (table I-8). The latter two substrates did not have statistically different means. Seedling:seed ratios for the 3 substrates were 0.038 (± 0.004 SE), 0.005 (± 0.004 SE), and 0.0 (± 0.005 SE) in log, mineral soil, and undisturbed plots respectively.

Seedling:seed ratios within individual stands followed this same pattern. Thinned stands and logs had consistently greater ratios than other stand densities and substrates.

Seedling Heights

Due to low seedling survival in stand densities other than thinned stands and on substrates other than coarse woody debris, seedling height sample sizes were extremely uneven. This made statistical comparison difficult. Over all stand densities and substrates, seedling heights averaged just 2.4 cm (± 0.16 SE) after the second growing season. However, seedlings as large as 20 cm were measured in the thinned stand at Randall Saddle. Additionally, large seedlings (10.4 cm) were observed in the mineral soil plots at Cascade Head. The smallest seedlings (0.2 cm) were measured on logs in the unthinned stand at Cape Creek.

Discussion of Second Year Results

The results of second year survival and seedling:seed analyses were consistent with those following the first growing season. Logs and stumps in thinned stands appear to be important to salal seedling recruitment. However, seedling:seed ratios indicate that seedling recruitment is low. These results are similar to those found in the pilot study. In 1991, numbers of surviving seedlings were significantly greater on logs and in thinned stands ($p < 0.05$). Table I-9 shows the least squares estimates of mean numbers of seedlings for the pilot study. Seedling:seed ratios calculated using the estimates of the overall means were 0.021 and 0.016 for the 1987 and 1988 cohorts respectively.

Seedling mortality was apparently higher during the first growing season than the second. On average, 86% of the emergent seedlings died during the first year. Of the survivors, 68% died during the second year. This agrees with studies showing increases in the probability of survival with seedling age and size (Cook 1980; and Antliffinger et al. 1985). Thus, the small size of seedlings in the unthinned stands suggests that these seedlings may not survive in the coming years. Conversely, the large seedlings found may survive and begin to expand vegetatively as was observed in 1991 of seedlings from the 1987 cohort.

Table I-9. Least squares means for numbers of surviving seedlings from the pilot study*.

	Mean Seedling: Number	Standard Error
Grand Mean:		
1987 Cohort	17.8	4.42
1988 Cohort	13.3	3.48
Substrate:		
1987 Cohort		
Logs	31.1a	5.89
Mineral Soil	4.5b	6.58
1988 Cohort		
Logs	21.9a	4.78
Mineral Soil	4.7b	5.06
Stand Density:		
1987 Cohort		
Thinned	30.4a	6.22
Unthinned	5.2b	6.22
1988 Cohort		
Thinned	23.5a	5.06
Unthinned	3.1b	4.78

* Like letters read within a group denote statistically similar means at a 95% confidence level.

CHAPTER II. EFFECTS OF OVERSTORY DENSITY ON CLONAL MORPHOLOGY AND EXPANSION

Little is known about the clonal structure of salal. No previous research has attempted to excavate and describe entire clones. Additionally, little is known about how salal clonal morphology is affected by overstory density. It has been suggested that clone form may be plastic and affected by light availability (Bunnell 1990). These conclusions were, however, based on a plot sampling methodology and from limited data of individual clones. Previous studies found salal productivity to be positively correlated with light availability (Sabhasri 1961; Long and Turner 1975; Bunnell 1990; and Vales 1986). However, no research has yet measured the individual growth of salal clones in the field. This research, conducted during the summer of 1991, was designed to describe salal's clonal morphology, architecture, and vegetative expansion rates. Further, I wanted to test the conclusions of previous research with respect to clonal responses to overstory density.

METHODS

Study Site

The Randall Saddle study site, used in the seedling establishment experiment (chapter I), was also used for salal

clone excavation. Nine stands of various overstory densities were systematically selected for sampling. The stands were selected on the basis of salal cover, and overstory density. I selected stands in which salal was a dominant member of the understory and which represented a gradient of overstory densities. I did not sample clearcuts. Table II-1 provides a description of the stands selected for salal clone excavation.

Data Collection

Four overstory density indices were determined for the stands sampled. These indices were Curtis's metric relative density (RD) (Curtis 1972), Reineke's stand density index (SDI) (Reineke 1933), basal area in square meters/hectare, and percent sky. Curtis' relative density equation is as follows:

$$RD = \frac{BA}{(Dq)^{1/2}}$$

where BA is basal area in square meters per hectare, and Dq is the quadratic mean diameter of the sampled trees in centimeters.

Reineke's stand density index is as follows:

$$SDI = [(Dq/10)^{1.605}] * TPA * 10$$

where Dq is the quadratic mean of the trees sampled in inches and TPA is the number of trees per acre. This index was not

Table II-1. Description of stands sampled for clone excavations. Stands 2, 5, and 9 were heavily stocked young stands. Stands 7 and 8 were thinned stands. Stands 1, 3, 4 and 7 were unthinned stands.

Stand #	1	2	3	4	5	6	7	8	9
Trees/ha	250	1400	383	437	1925	92	362	162	1975
Stand Age	70	40	70	80	40	60	70	60	40
Average Diameter (cm)	57	19.5	41	42	15.6	56	51	51.5	16.2
Basal Area (m ² /ha)	63.3	41.5	50.2	60.1	36.5	22.5	73.4	33.5	40.4
Relative Density	8.4	9.3	7.8	9.3	9.2	3	10.3	4.7	10
Stand Density Index	274	371	293	392	361	142	372	248	398
Percent Sky	12.6	1.2	12.8	9.8	1.3	27.3	8.4	30	1.7

converted to metric units. The three indices, RD, SDI, and BA were determined using a systematic sampling design and fixed plots of 1/25 hectare (1/10 acre) in area. One to four plots per stand were systematically placed to measure the overstories near the excavated clones. All trees in the plots were counted and measured for diameter at 1.4 m above ground level (dbh). Percent sky was measured in the nine stands using a pair of Licor 2000 Canopy Analyzers (chapter I). Twenty measurements, taken at a height of approximately 1.4 m, were collected in each stand. These readings were taken directly above the sites of the excavated clones. The 20 readings per stand were averaged to determine percent sky values.

From three to nine salal clones per stand were excavated and measured. A clone was defined as the aggregate of all interconnected aerial stems and rhizomes. Clones were selected for excavation systematically by stem age. The age classes used for clone selection were 1 to 2 year-old stems, and 7 to 25 year-old stems. Stems within these age classes were randomly chosen from the populations within the stands. Entire clones were excavated by beginning at a selected stem and excavating all connected rhizomes and aerial stems. A total of 51 clones were excavated using hand trowels and small picks. Care was taken to excavate entire clones.

The following measurements of the excavated clones were

collected; (1) extension lengths of current season rhizomes, (2) previous season's rhizome extension lengths, (3) ramet number per clone, (4) numbers of aerial stems per ramet, (5) ramet lengths, and (6) stem ages. Current season rhizomes were defined as rhizomes that were pink to white in color and that still retained bud scales. Rhizomes produced in previous seasons were light brown to black. The older rhizomes lacked bud scales. Rhizome extensions were defined as the rhizome growth modules of the clone. These were the unbranched rhizome lengths apparently produced by one meristem. Ramets were defined as any number of aerial stems originating from a common rhizome within approximately 2 cm of each other. Ramet lengths were measured from the base to the tip of the longest aerial stem. Stem age was estimated by counting aerial growth modules. As will be described, the branching pattern of the stems made age estimation possible. Age estimates were intermittently checked against xylem ring counts. The ages of the oldest and youngest stems of the ramets were recorded.

The measurements conducted on the excavated clones helped in forming an overall description of clonal architecture and morphology. Additionally, 13 of the 51 clones were mapped. Maps were constructed of 9 clones in stand 1 and 4 clones in stand 2. These maps recorded the length, relative spatial position, and density of a clone's ramets, rhizome extensions, and roots.

The rhizomatous connections of 24 ramets were severed to test for independence. Twelve ramets in a clearcut and 12 beneath a Douglas-fir overstory were separated from their clonal system during the winter of 1991. Care was taken to disturb the substrate as little as possible. These ramets were marked with a flag and examined during the winter of 1992. At this time, the ramets were classified as dead or alive.

Data Analysis

Total rhizome length, and indicator of clone size, was defined as the sum length of all rhizome extensions measured on an excavated clone:

$$(1) \quad \text{Total rhizome length} = \text{sum length of all rhizome extensions}$$

The number of ramets per clone, another size indicator, was defined as the sum number of all interconnected ramets associated with an excavated clone:

$$(2) \quad \text{Number of Ramets/clone} = \text{sum number of all interconnected ramets}$$

Current season rhizome length was used to estimate vegetative expansion rates. This was defined as the sum length of all current season rhizome extensions measured on a clone:

$$(3) \quad \text{Current season rhizome length} = \text{sum length of all current season rhizome extensions}$$

Annual growth percent, an estimator vegetative expansion relative to clone size, was defined as current season rhizome length divided by the difference of total rhizome length and current season rhizome length:

$$(4) \text{ Annual growth percent} = \frac{\text{current season rhizome length}}{\text{Total rhizome length} - \text{current season rhizome length}}$$

Ramet density (MPR) was used to describe morphological characteristics of the clones. This was defined as the number of ramets divided by total rhizome length:

$$(5) \quad \text{MPR} = \frac{\text{number of ramets}}{\text{total rhizome length}}$$

Average rhizome extension length (ARL) was also used to describe clonal morphology. This parameter was defined as total rhizome length divided by the number of extensions measured on a clone:

$$(6) \quad \text{ARL} = \frac{\text{total rhizome length}}{\text{Number of rhizome extensions}}$$

Stems per ramet (SPR) was a third parameter used to describe morphological characteristics of the clones. This was defined as the sum number of stems divided by the number of ramets counted on an excavated clone:

$$(7) \quad \text{SPR} = \frac{\text{sum number of stems}}{\text{number of ramets}}$$

The data collected for the clone excavation research was

treated as if from a randomized sample. Stand densities functioned as treatments and clone measurement values were averaged within stands. Simple linear regression was used to test correlations between these variables and the four stand density indices. The data were normalized when necessary using the natural log and square-root transformations. The relationships were considered statistically significant if the probability of a Type I error in a two-sided test was less than 0.05.

One-way ANOVA was used to test for difference in clone variables by clone type. The data were natural log or square-root transformed when appropriate. LSD multi-range tests were used to determine differences between means. The significance level used for these tests was 95 %.

RESULTS AND DISCUSSION

General Description of Salal Clones

Salal is an ericaceous shrub that often dominates the understories of the coastal forests in the Pacific northwest (Long 1977). Salal, through vegetative expansion, often forms large continuous patches. These patches can comprise up to 65 % of the groundcover in understory plant communities (Long 1977). Judging from stem xylem counts, individuals may live up to 25 years. Additionally, patches of salal appear to persist over multiple cycles of overstory stand succession. Stem replacement through vegetative expansion appears to facilitate the persistence of these patches in the forest understory.

Clonal Development

Once past the seedling stage, salal begins to increase in size through vegetative expansion. This involves the production rhizomes, modified stems that grow horizontally within the soil or rotting logs. Seedlings examined in the field were estimated to be 3 to 4 years-old before they produced their first rhizome extension. In an optimal environment, this may occur as early as the second year (Zasada personal comm.). Generally, salal rhizomes grow just

below the humus layer but often they grow into the mineral soil. Rhizome extensions eventually turn upward to become aerial stems termed "ramets" (figure II-1). Ramets are aerial stems with the potential for independent growth (Cook 1983). Since I defined ramets as groups of stems originating within 2 cm of each other on a common rhizome, the term ramet here is used liberally. The average length of first year stems was 22.25 cm (± 0.75 cm SE) and ranged up to 65 cm.

Sympodial formation of ramets from rhizomes may take just one season. However, the longest current season rhizome extension measured was 94 cm while previous season's extensions often exceeded 1 meter. It is therefore apparent that rhizomes may grow for 2 or more years before turning upward and producing a ramet. If a rhizome is injured such that it's apical meristem is nonfunctional, buds just proximal to the injury become activated to produce rhizomes and/or aerial shoots. In the field, 50 % of the stems severed from rhizome connections survived. This indicates that injury to salal rhizome systems due to management activities may increase rhizome and ramet density. Once a ramet is established, an additional 1-6 aerial stems and/or "daughter" rhizomes are often produced near its base. Shoots and rhizomes may then be produced filling in along rhizomes connecting ramets.

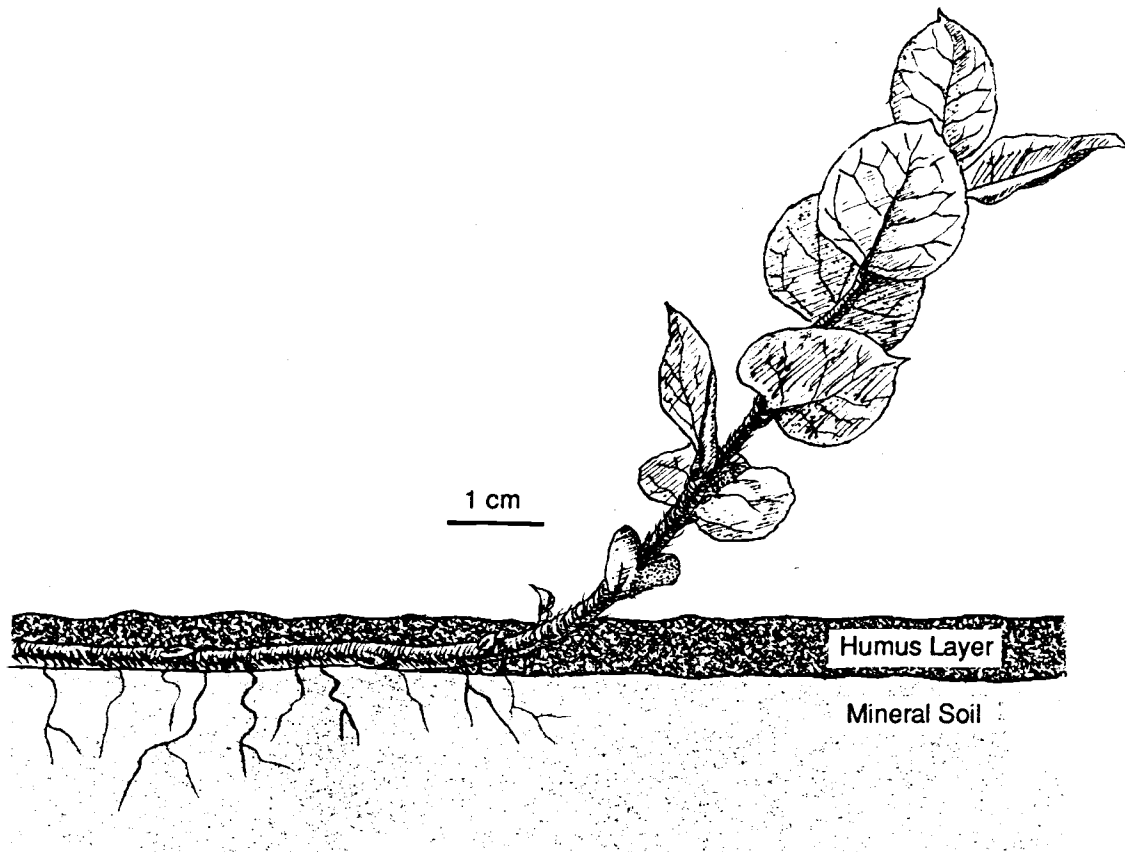


Figure II-1. Illustration of rhizome turning upward to become an aerial shoot, or ramet.

As described, salal plants develop into clones, groups of ramets connected by a network of rhizomes (figure II-2). Figure II-2 shows a clone excavated in stand 1. This clone was vigorous and larger than most with 78 m total of rhizome length and 78 ramets. The average clone excavated was comprised of 20.25 (± 6.28 SE) ramets, connected by 19.60 m (± 4.88 m SE) of rhizome. The largest clone measured was comprised of 293 ramets connected by 218 m of rhizome and covered an area of approximately 28.9 square meters.

As well as attaining great size, salal clones can also be long lived. The oldest aerial stem measured was at least 25 years old based on a count of xylem rings. Stems of this age were greater than 1 meter long and often prostrate. The distal ends of rhizomes connected to older ramets were often found to be dead. Apparently, older clones may disintegrate. This disintegration appears to occur in old parts of a clone where larger ramets compete with each other. These clone fragments often included connections to young ramets and vigorously growing rhizome systems. This developmental pattern may lead to virtual immortality for some genotypes.

Below-Ground Architecture

The below-ground architecture of salal is influenced by rhizome branching angle, rhizome density and length, and root

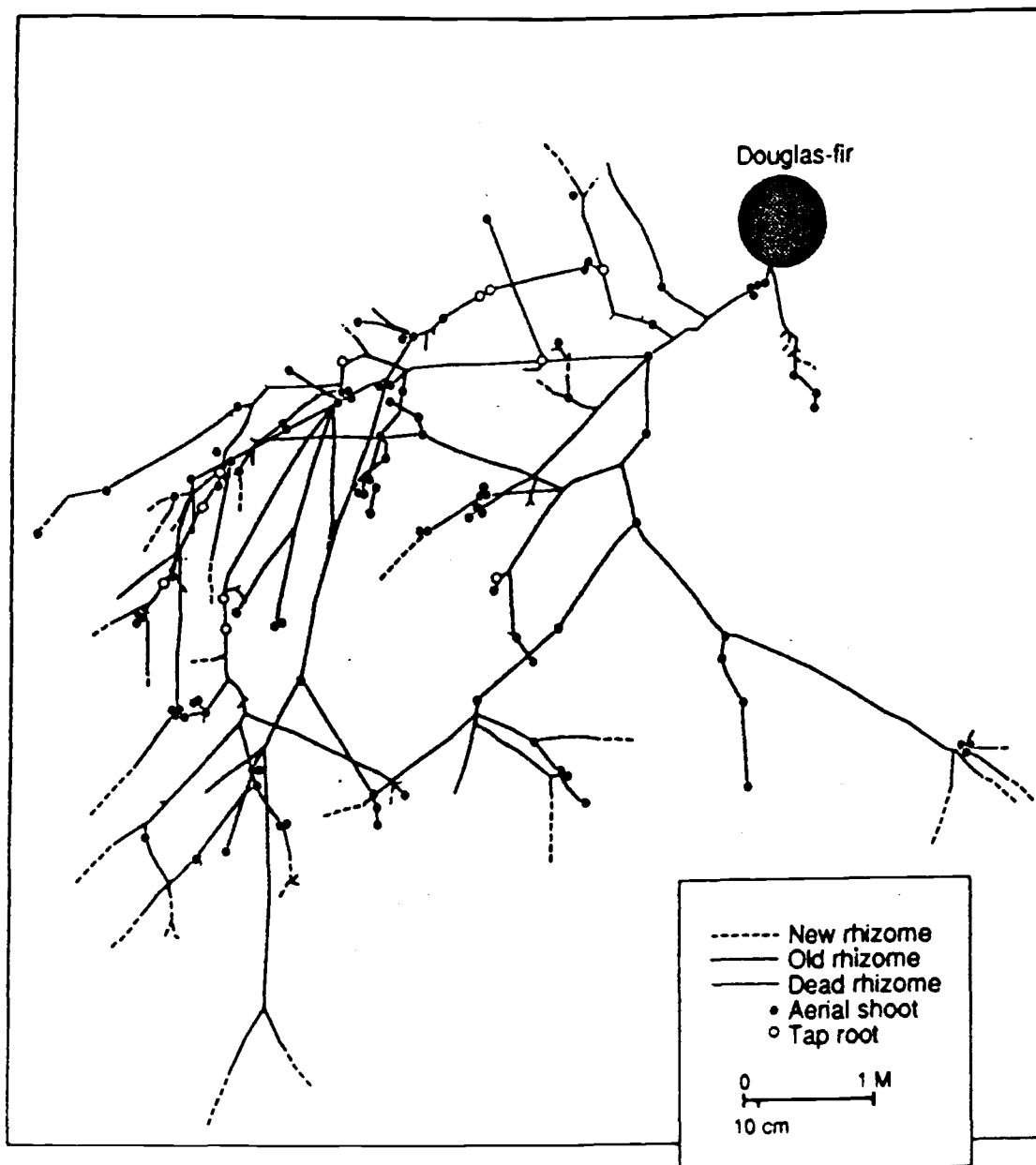


Figure II-2. Map of excavated clone. This clone, excavated in stand 1, was comprised of 78 ramets and 91.44 m of rhizome.

characteristics. I found that the branching angles of salal rhizomes are generally acute relative to the direction of growth of the parent rhizome. Daughter rhizomes typically form a 45 degree angle to the parent rhizome. Although rhizome networks doubled back on themselves through repeated branching, rarely did I find rhizomes that appeared to be growing back toward their parent rhizome. One clone, growing entirely within a rotten log, showed this characteristic.

As described, ramets are often located at what I term "centers" of bud activity. These centers typically produce 1 to 6 rhizomes and/or ramets. Approximately, 75 % of the rhizomes produced at these locations were excavated within 10 cm of the soil surface. However, rhizomes were also found growing down to 50 cm below the soil surface. Depths of rhizomes exceeded 50 cm when they were found growing in tree root channels or animal tunnels.

In general, the distribution of rhizome extension lengths on any one clone appears to be skewed towards smaller lengths with a "tail" of longer lengths. Figure II-3 shows the length distribution of all rhizome extensions measured. The average length of these was 36.71 cm (± 0.71 SE). Seventy-six percent of all extensions were under 50 cm, six percent of the rhizome extensions were found to exceed 1 m, and 11 extensions

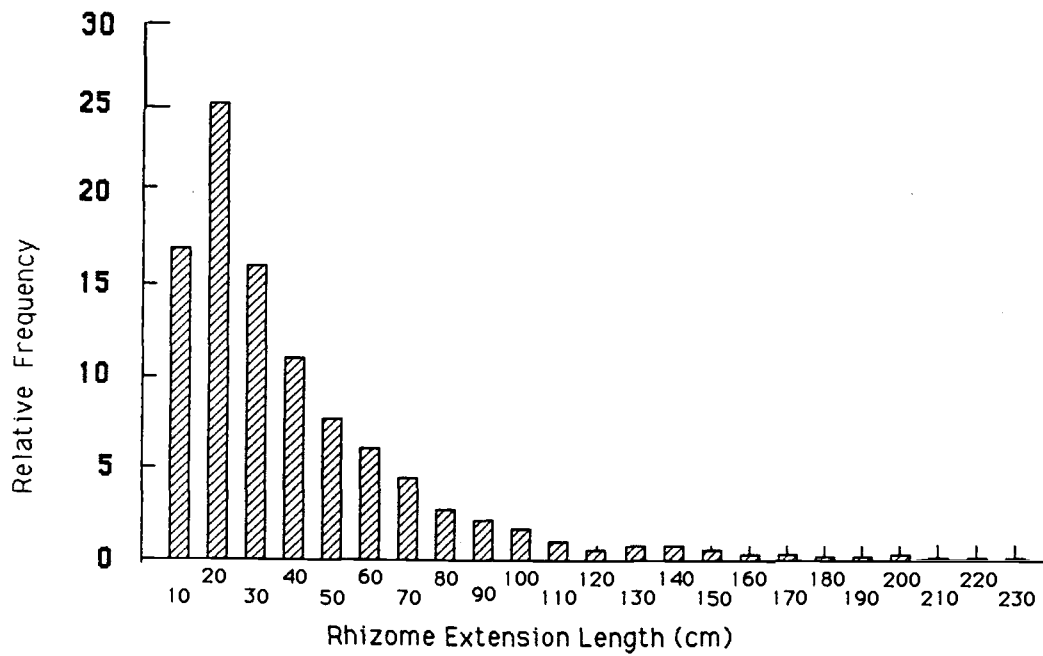


Figure II-3. Relative frequency of rhizome extension lengths for all clones measured. The longest rhizome extension measured was 282 cm.

measured were longer than 2 meters. The longest rhizome extension on any clone was 2.82 m.

The root system of salal consists of fine roots and tap roots. The fine roots occur in dense mats on young rhizomes near the soil surface. Fine roots appear to comprise the majority of the root biomass of clones. Tap roots appear to be located most often beneath ramets. These roots are narrow in diameter but extend deep into the substrate. Tap roots of clones are observed less than fine roots. They may serve to anchor the clone in addition to supplying moisture.

Above-Ground Architecture

The above-ground architecture of salal was not examined as intensively as the below-ground architecture. However, branching patterns, number of stems per ramet, stem ages, and stem heights were measured. The branching pattern of salal is influenced by the seasonal abortion of the stem's apical meristems. The abortion of these buds results in lateral shoots contributing to the seasonal elongation of the branch (figure II-4a). This process leads to a zig-zag branching pattern and allows for approximations to be made of stem age (figure II-4b).



Figure II-4a. Illustration showing aborted apical meristem. Seasonal abortion of these buds results in a zig-zag branching pattern.

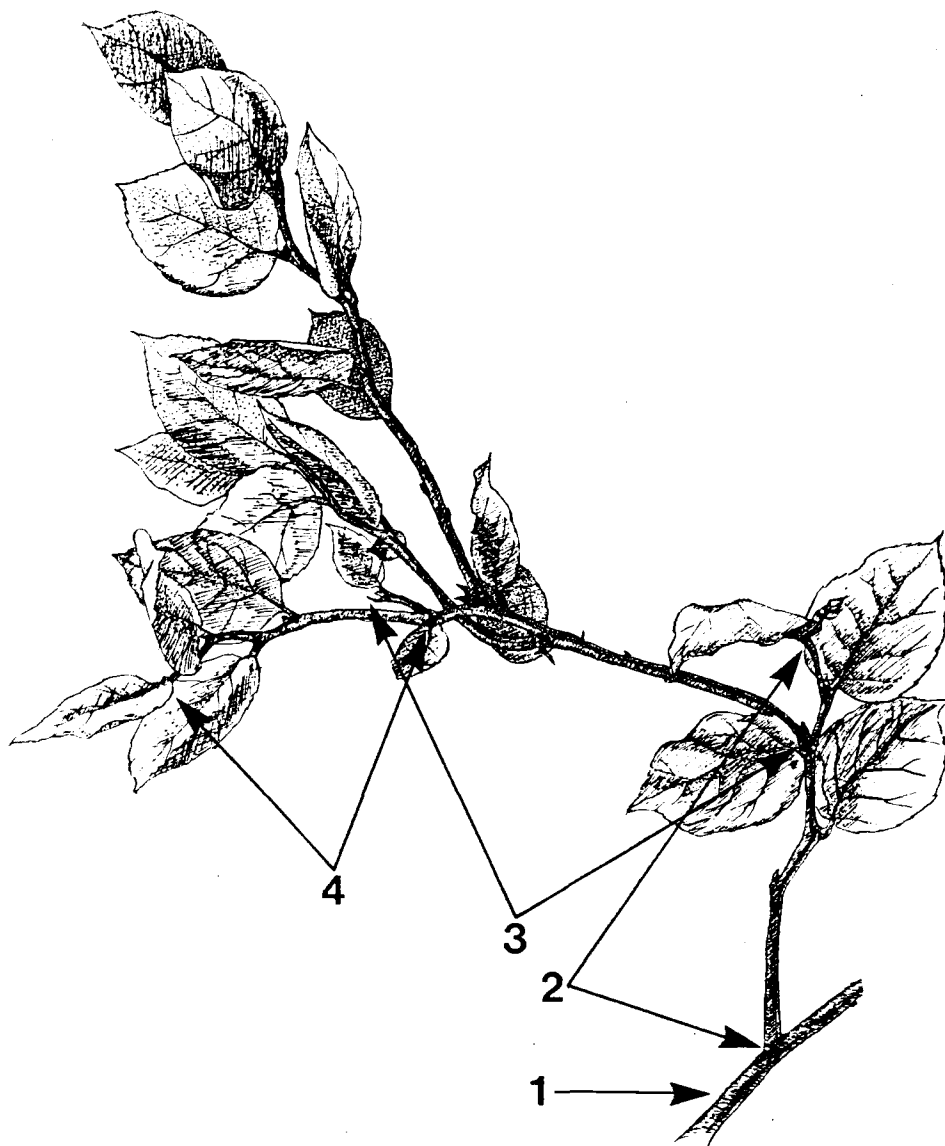


Figure II-4b. Illustration showing the branching pattern of aerial stems. Numbers represent previous seasonal growth.

The number of aerial stems comprising ramets ranged from 1 to 6 stems. Ramets with six stems, however, were rare. Fifty-eight percent of the ramets sampled were comprised of just one stem. Eighty-three percent had from 1 to 2 stems per ramet. The average was 1.65 stems per ramet (± 0.03 SE).

The age of the aerial stems ranged from 1 to 25. A plot of the distribution of stem ages shows that salal clones tend to have uneven-aged stem populations. Figure II-5 shows the relative frequency of stem ages for all clones. Over fifty percent of all stems measured were from 1 to 2 years old. Stem heights were found to have a similar distribution.

Relationship of Clone Type to Stand Conditions

Three types of clones were identified: "invader", "senescent", and "remnant" clones. Each type was associated with particular overstory conditions, and was distinguished by aerial stem density and age, and clone vigor. Invaders were found in the stands of Douglas-fir of moderate to low density and did not in high density stands. Invaders were composed mostly of younger ramets up to 7 years-old and vigorously growing rhizome networks and were not often found associated with patches of older ramets. Invader clones were rapidly expanding and had relatively high annual growth percents averaging 16.24 % (± 1.66 SE). This expansion rate facilitated

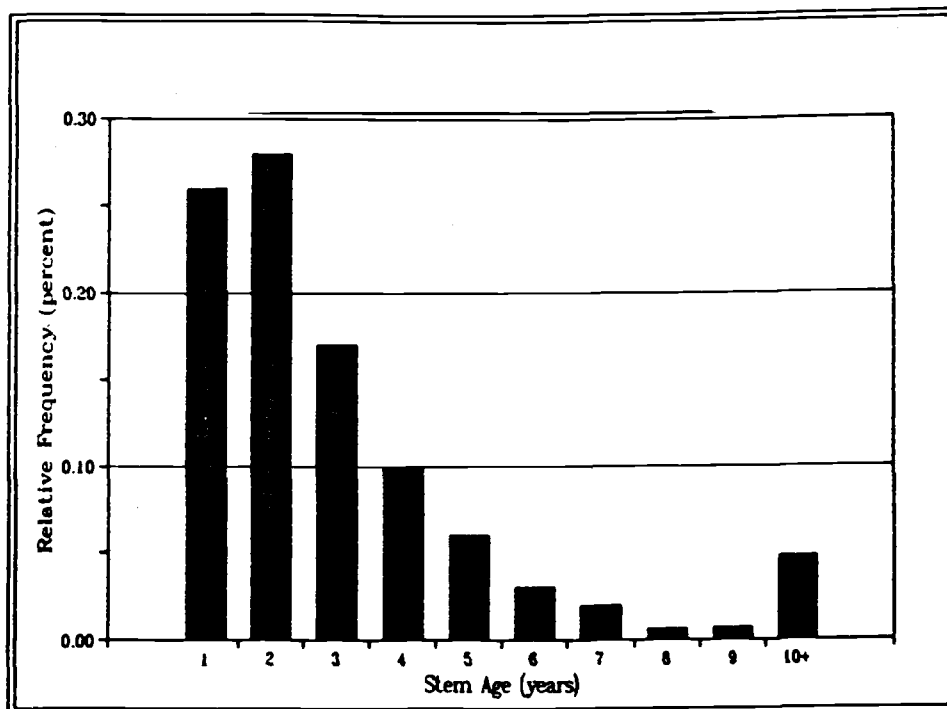


Figure II-5. Relative frequency of stem ages from 51 sampled clones.

the development of large clones. Invader clones had rhizome systems up to 218 m in total length.

Senescent clones were found growing within stands of moderately dense overstories. They were not found in stands of high or low density. Senescent clones were comprised mostly of older ramets that ranged up to 25 years-old and 3 m in length. These clones were generally found growing in patches where salal cover was near 100%. Often, the stems in these patches were prostrate and laid over on top of one another. Senescent clones were typically observed to be fragments of a genet. This was evidenced by dead and rotted rhizome tissue attached to older ramets. These ramets were sometimes found connected to vigorously expanding rhizome networks. On average, however, these clones had a relatively low annual growth percent of 5.26 % (± 1.08 SE).

Remnant clones were found in the stands of high density. These clones were assumed to be the remnants of clones growing beneath the overstory before crown closure. The extreme shade created by young Douglas-fir overstories at crown closure had apparently reduced clones to small fragments. The total rhizome length of remnant clones was found to range from just 0.09 m to 8.39 m. The average total rhizome length was 1.57 m (± 0.56 SE). Numbers of ramets per clone ranged from 1 to 2 and the age of the aerial stems never exceeded 2 years. No

current season rhizome was found on remnant clones. They were, apparently, little more than subsisting in the understory.

Analysis showed invader clones and senescent clones to be similar in total rhizome length and number of ramets per clone. Both types were found to have larger clonal systems than remnant clones ($p < 0.05$) (table II-2). Although there was no statistical difference between invader and senescent clone total rhizome length, a plot of the distribution of total rhizome lengths reveals that relatively more large invaders were excavated than were large senescent clones (figure II-6).

Invaders were found to have a significantly larger annual growth percent and total length of current season rhizome than senescent clones ($p < 0.05$). This suggests that younger modules of salal clones are more vigorous than older modules. The metabolic costs of maintaining large aerial stems beneath a forest overstory may come at a sacrifice to vigorous vegetative expansion as well as maintaining rhizomatous connections. As reported, remnant clones had no current season rhizome (table II-2).

No significant difference was found between the three clone types with respect to ramet density (MPR) or stems per ramet (SPR). The average rhizome extension length (ARL) of

Table II-2. Mean values of morphological characteristics for invader, senescent, and remnant clone types*.

Clone Type	Mean (Standard Error)						
	Total Rhizome Length (m)	Number of Ramets/Clone	Current Season Rhizome Length (m)	Annual Growth Percent	Average Rhizome Ext. Length (cm)	Ramet Density (meters of rhizome/ramet)	Stems/Ramet
Invader	30.55a (9.49)	35.0a (15.1)	4.44a (1.25)	16.24a (1.66)	34.2a (0.73)	0.95a (0.08)	1.69a (0.04)
Senescent	17.81a (5.87)	16.11a (5.72)	0.87b (0.32)	5.26b (1.08)	48.33b (2.18)	1.4a (0.3)	1.46a (0.08)
Remnant	1.57b (0.56)	1.09b (0.09)	0.0c (0.0)	0.0c (0.0)	34.89a (4.9)	1.03a (0.19)	1.45a (0.21)

* Like letters read within columns denote statistically similar means at a 95% confidence level.

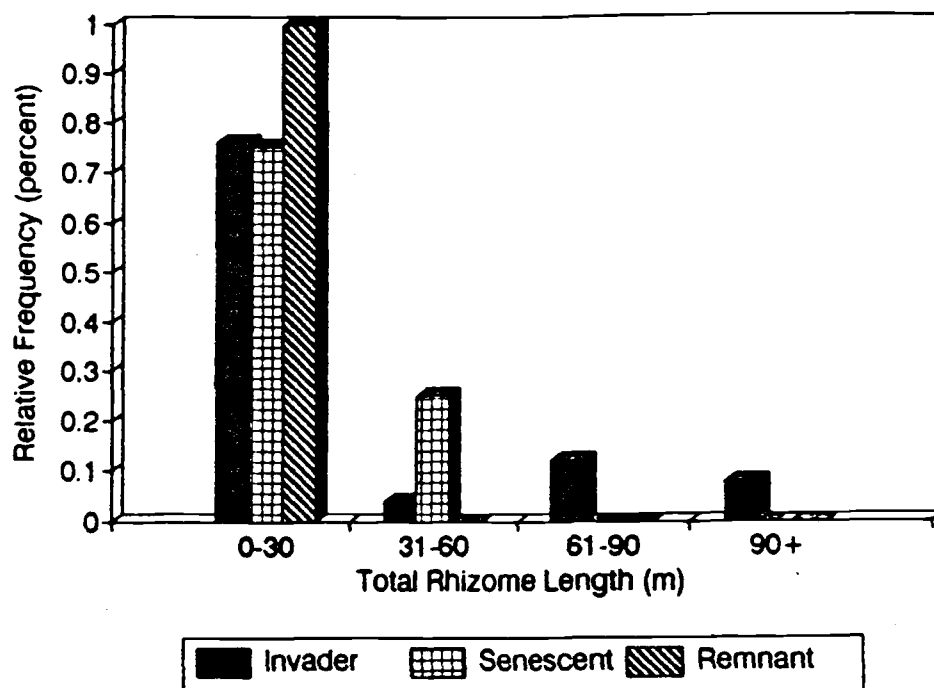


Figure II-6. Relative frequency of total rhizome lengths for invader, senescent, and remnant clones. Lengths are divided into 30 m classes. Frequency represents the percent of the total number of each clone type excavated.

senescent clones (48 cm) was found to be significantly greater than those of invader clones (34.2 cm) and remnant clones (34.9 cm) ($p < 0.05$). The latter two were not statistically different in ARL (table II-2). This suggests that relatively long rhizome extensions persist as senescent clones disintegrate. These long extensions may allow physiological integration of the clone with vigorous ramets growing away from interclonal competition.

Correlations Between Stand Density and Clone Growth

Size of salal clones was significantly related to overstory density ($p < 0.05$). Total rhizome length and number of ramets per clone were found to be negatively correlated with the density indices RD, SDI and percent sky (table II-3). The size variables were not found to be significantly correlated with BA.

Expansion rates were also effected by overstory density ($p < 0.05$). Annual growth percent and current season rhizome length were found to be negatively correlated with the density index RD (table II-3). Current season rhizome length was also significantly correlated with SDI. Annual growth percent was also correlated with this variable at the 90 % significance level.

Table II-3. Correlation coefficients, (p-values), and R-squared values for regressions of average clone characteristics on overstory density indices (N = 9).

Characteristic	Stand Density Index			
	Basal Area	Stand Density Index	Relative Density	Percent Sky
Total Rhizome Length per Clone	-0.43 (0.250) 0.1825	-0.868 (0.002) 0.7532	-0.823 (0.006) 0.6780	0.818 (0.007) 0.6693
Number of Ramets per Clone	-0.46 (0.21) 0.2136	-0.875 (0.002) 0.7655	-0.796 (0.01) 0.6349	0.814 (0.007) 0.6628
Current Rhizome Length	-0.171 (0.66) 0.0294	-0.854 (0.003) 0.7301	-0.820 (0.006) 0.6726	0.840 (0.005) 0.7060
Annual Growth Percent	0.027 (0.94) 0.0007	-0.6413 (0.06) 0.4113	-0.692 (0.039) 0.6726	0.894 (0.001) 0.8001
Ramet Density	0.0317 (0.93) 0.001	-0.05 (0.89) 0.0025	-0.224 (0.56) 0.0502	0.385 (0.30) 0.1487
Average Rhizome Extension Length	0.335 (0.37) 0.1126	0.237 (0.54) 0.0562	0.398 (0.29) 0.1585	-0.337 (0.37) 0.1138
Stems per Ramet	-0.35 (0.39) 0.1225	-0.638 (0.089) 0.4071	-0.761 (0.028) 0.5792	0.822 (0.012) 0.6764

No relationship was found between the variable ARL and any of the stand density indices. As reported, the average rhizome extension length was 36.70. Further, no relationship was found between the variable MPR and any of the stand density indices. Clones had, on average, 1.2 meters of rhizome per ramet (± 0.09 SE). However, the number of shoots per ramet was significantly correlated with overstory density ($p < 0.05$). The variable SPR was found to be negatively correlated with RD and percent sky (table II-3). At a 90% significance level, this variable was also correlated with SDI.

Discussion

The findings of the clone excavation experiment indicate that clonal architecture of salal is similar over most stand densities. Branching angles, directional growth, and characteristics of apical dominance did not appear effected by light availability. Clones were generally compact with a small number of long rhizome extensions. My results suggest that salal clones do not respond to overstory density with changes in clonal ramet density. No evidence of guerilla-phalanx transitions (Lovett-Doust 1981) were found.

Long, continuous extensions that grow for more than one season may be an adaptation which facilitates the exploration of new environments without the risks associated with seedling

establishment (see chapter I). One-year old ramets connected to clonal systems reach heights of up to 50 cm, an obvious advantage in resource capture over 4 cm seedlings. These long extensions may additionally remove ramets from both intra- and interspecific competition.

Although the effect of overstory density on rhizome depth was not tested, it is apparent that downward growth of rhizomes is an important aspect of salal's clonal architecture. Rhizomes deep within the soil may be protected from fire or other disturbances. Thus, protected regenerative buds may allow the re-establishment of salal populations. Additionally, downward growth may facilitate the colonization of snags. From field observations, and from the findings of this research, it is apparent that seedlings do become established on snags (see chapter I). Rhizomes that grow downward may give the plant an advantage over other species that colonize the log after that snag falls (Harmon 1987; and Christy and Mack 1984).

Clone morphology and relative expansion rates varied considerably among stand densities. Results indicate that salal clones grow more vigorously and thus become larger in open stands than in dense stands. Clones in very dense stands appear to disintegrate into what I describe as remnant clones. These results are similar to those found for salmonberry

(Rubus spectabilis Pursh), another rhizomatous shrub of the coast range (Tappeiner et al. 1991). However, important differences between these species are apparent. The average annual growth percent, 16.24 %, found for salal invader clones was considerably less than 27 % which was found for salmonberry in clearcuts. However, salal appears to form much larger clones than salmonberry. The largest salmonberry clone found by Tappeiner et al. (1991) was just over 20 m in total rhizome length while my excavations revealed a clone of 218 m.

The positive relationship between the number of stems per ramet and light availability suggests that, as stands become more open, more buds on stems and rhizomes are activated. This may be thought of an additional measure of clone vigor.

CHAPTER III. EXAMINATION OF STEM AND RHIZOME POPULATIONS

Previous studies have concluded that the productivity of salal is positively correlated with light availability (Long and Turner 1975; Vales 1986; and Smith 1991). I wanted to test these findings by comparing rhizome and stem biomass and density across a gradient of overstory stand densities. Additionally, I wanted to test whether resource allocation to aboveground stems versus below-ground rhizomes was affected by overstory stand density. Biomass has been reported to be a good indicator of resource allocation (Hickman and Pitelka 1975). To do this I used a plot sampling method to examine stem and rhizome populations. This research was conducted in the summer of 1991 at the Randall Saddle study site.

METHODS

Study Site

Ten stands of various overstory densities were selected in the Randall Saddle study area (table III-1). Six of these were stands used in the clone excavation experiment. Three clearcuts and one moderately dense stand were additionally selected. Clearcuts were 4 to 8 years-old and had not been burned or treated with herbicide.

Table III-1. Description of stands used for rhizome and stem population sampling. Stands 2, 5, and 9 were clearcuts, 6, 8 and 10 were thinned stands, and 1, 3, 4, and 7 were unthinned stands.

stand #	1	2	3	4	5	6	7	8	9	10
Trees/ha	250	875	383	437	875	92	362	162	875	137
Stand Age	70	6	70	80	7	60	70	60	6	70
Average Diameter (cm)	57	3	41	42	4	56	51	51.5	3	51.2
Basal Area (m ² /ha)	63.3	1	50.2	60.1	1	22.5	73.4	33.5	1	28.2
Relative Density	8.4	1	7.8	9.3	1	3	10.3	4.7	1	3.9
Stand Density Index	274	1	293	392	1	142	372	248	1	174
Percent Sky	12.6	100	12.8	9.8	100	27.3	8.4	30	100	48

Data Collection

Stand density data was collected in selected stands following the procedures described in chapter II. Overstory density indices determined were RD, SDI, BA, and percent sky. Since there were no overstories in the clearcut stands, a value of 1 was assigned for RD, SDI, and BA. Additionally, 100 % was the value assigned to the variable percent sky for the clearcuts.

A 1 m² sampling frame was used to examine salal rhizome and stem populations. Patches of salal stems within stands were selected for sampling on the basis of relative stem density. Patches with relatively high stem density were selected. The sampling frame was then randomly tossed into the selected patch. All stems originating from within the perimeter of the frame's landing spot were clipped and measured. These stems were measured for length, age, and density (number per m²). The ages of the stems were estimated by counting seasonal branch elongations (chapter II). Seventy-four stems were collected representing the range of heights found in all plots. Necrotic branches and leaves were removed from the stems. The stems were then oven-dried at 70 °C for 48 hours and weighed to determine stem biomass.

Forest litter was removed from the plots after stem

clipping and all rhizomes beneath were excavated. Rhizomes were excavated to a depth of 40 cm. Rhizomes were cleaned of soil and dead material, and fine roots were removed. Current season rhizome extensions were removed and measured for length. Rhizome density, the total length of rhizome per m² plot, was measured and the rhizomes were bundled. Dry weights of the rhizome bundles were determined after oven-drying at 70 °C for 48 hours.

Data Analysis

These data were analyzed similarly to the clone excavation data. They were treated as if collected from a randomized experiment where stand density was a treatment factor. Simple linear regression was used to test correlations between stem and rhizome variables and stand density indices. The data were normalized by the natural-log or square-root transformations when plots of the residuals showed it appropriate. Probability levels less than 0.05 were used to identify significant correlations.

Regression was also used to estimate stem biomass from stem length data. An exponential relationship was fit through the data points. This curve was of the following equation:

$$\text{Stem Biomass} = e^{(0.208 + 0.03 * \text{stem length})}$$

RESULTS AND DISCUSSION

Stem Populations

Stem density and estimates of aboveground biomass were significantly and negatively correlated with overstory density and positively correlated with percent sky ($p < 0.05$). The number of stems/m² was found to be strongly correlated with all the stand density indices. The best correlation was with percent sky ($r = 0.944$) (table III-2). Up to 380 stems/m² were counted in clearcut plots while as few as 6 stems/m² were found in dense stands.

Aboveground biomass was most strongly correlated with the overstory density index RD ($r = -0.835$) (table III-2). Estimates of the dry weight of aerial stems and leaves ranged from 141 g/m² to 2744 g/m². These estimates were calculated using the stem biomass equation (see page 80). Overall, this equation appeared adequate for prediction ($r = 0.88$; R-squared = 77.6 %). However, estimates of biomass for longer stems (200+ cm) appeared to be exaggerated.

The age and height structure of stems sampled followed an uneven age distribution pattern similar to that found for individual clones (chapter II). Although the range of ages were different for the various stands, this pattern of

Table III-2. Correlation coefficients, (p-values), and R-squared values for regressions of salal population variables on overstory density indices (N = 10).

Characteristic	Stand Density Index			
	Basal Area	Stand Density Index	Relative Density	Percent Sky
Rhizome Biomass	-0.887 (0.0006) 0.7875	-0.935 (<0.0001) 0.8742	-0.909 (0.0003) 0.8271	0.920 (0.0002) 0.8473
Rhizome Density (m/m ²)	-0.901 (0.0004) 0.8127	-0.873 (0.001) 0.7619	-0.876 (0.0009) 0.7677	0.944 (<0.0001) 0.8913
Current Rhizome Length	-0.850 (0.002) 0.7228	-0.744 (0.01) 0.5542	-0.845 (0.002) 0.7147	0.759 (0.01) 0.5767
Stem Density	-0.860 (0.001) 0.7396	-0.880 (0.0008) 0.7737	-0.871 (0.001) 0.759	0.918 (0.0002) 0.8437
Aboveground Biomass	-0.794 (0.006) 0.6305	-0.775 (0.008) 0.6012	-0.835 (0.003) 0.6973	0.584 (0.08) 0.3414
Aboveground: Belowground Biomass	0.592 (0.07) 0.3509	0.650 (0.04) 0.4229	0.536 (0.11) 0.2878	-0.825 (0.003) 0.6807

distribution did not appear to be affected by stand density. Figure III-1 shows the relative frequencies of stem ages for plots combined into general classes of stand density. Here, the classification "thinned" refers to stands with overstory densities less than $RD = 5$. "Unthinned" refers to stands with overstory densities greater than $RD = 5$.

Rhizome Populations

Rhizome biomass and density were significantly effected by overstory density ($p < 0.05$). These variables were found to be negatively correlated with stand density and positively correlated with percent sky. The weight of rhizomes excavated from the plots was most strongly correlated with the index SDI (table III-2). Rhizome biomass values ranged from 141 g/m^2 in a dense stand to $1,866 \text{ g/m}^2$ in a clearcut. These differences were most evident during excavation. In clearcuts, rhizomes near the soil surface were so dense that they could be rolled up into cylindrical bundles. In dense stands, although I sampled the densest salal patches, rhizomes needed to be sifted from the soil.

Rhizome density, the sum length of rhizomes excavated from a plot, was most strongly correlated with the index percent sky ($r = 0.944$) (table III-2). This relationship showed rhizome density increasing with light availability.

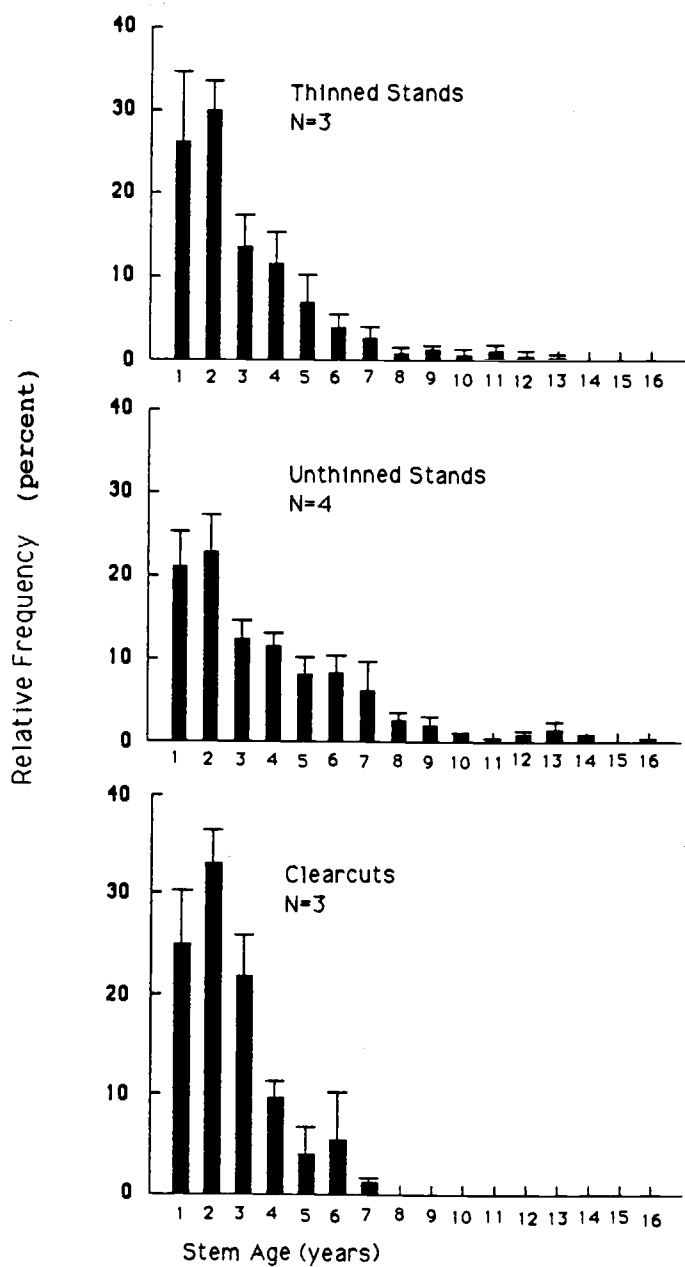


Figure III-1. Mean relative frequencies of stem ages in thinned, unthinned and clearcut stands.

Rhizome densities ranged from 9.7 m/m² in a dense stand to 217 m/m² in a clearcut. Further, the density of current season rhizome showed this same pattern. This relationship was strongest with the index BA (table III-2). Densities of current season rhizome ranged from 12 cm/m² in a dense stand to 7.6 m/m² in a clearcut.

Ratio of Above-Ground:Below-Ground Biomass

The ratio of above-ground:below-ground biomass, an indicator of resource allocation (Hickman and Pitelka 1975), showed a positive correlation with overstory density and a negative relationship with percent sky. This most apparent when tested against percent sky ($r = -0.825$) (table III-2). The relationship of aboveground:below-ground biomass to stand density was only slight. This variable was not statistically correlated at a 95 % significance level with either BA or RD. These results may be due to indirect measurement of aboveground biomass.

Discussion

Results from this study agree with the findings of other research. Aerial stem density and aboveground biomass of salal decreases with increasing stand density. Similar results have

been found for salal as well as other species (Long and Turner 1975; Vales 1986; Tappeiner et al. 1991; and Hughes et al. 1987). Vales (1986) reported stem densities of salal ranged from near 150 to under 5 stems/m² as mean crown completeness increased. Tappeiner et al. (1991) found salmonberry stem densities of up to 52 stems/m² in young clearcuts and as few as 2.3/m² in dense conifer stands.

Long and Turner (1975) reported aboveground salal biomass ranging from 6300.6 to 1010.2 Kg/ha (630.0 to 101.0 g/m²) as overstory stand age increased. Vales (1986) found a similar range (600 to 150 g/m²) of salal stem biomass as canopy completeness increased. Vales' and Long and Turner's studies, however, were based on random samples of understory communities while I sampled dense patches of salal systematically. Tappeiner et al. (1991) reported aboveground biomass of salmonberry patches ranged from 6130 g/m² in clearcuts to 390 g/m² in dense conifer stands. Hughes et al. (1987) examined age sequences of deerbrush (Ceanothus interrimus), varnishleaf (Ceanothus velutinus var. laevigatus) and whiteleaf manzanita (Arctostaphylos viscida) in southwest Oregon. They estimated maximum aboveground biomass to be 1800 g/m², 4000 g/m², and 2000 g/m² for deerbrush, varnishleaf, and whiteleaf manzanita respectively.

Rhizome biomass and density were found to be negatively

related to overstory density. These results are consistent with those found by Tappeiner et al. (1991) for salmonberry. Tappeiner reported rhizome biomass ranged from 2000 g/m² in young clearcuts to less than 100 g/m² in alder stands. Additionally, salmonberry rhizome densities ranged from 18 m/m² to less than 5 m/m².

Direct comparisons between this and the studies of others was difficult. However, it appears that values reported here are within the ranges found by others. It appears that salmonberry stem populations are found at lower densities in clearcuts than those of salal. However, the biomass of these populations appears to be greater than salal. Further, the two species appear to be similar in rhizome biomass in clearcuts. However, rhizome densities of salal appear to be considerably greater than those of salmonberry. These comparisons may provide information on the differential competitive strategies of salmonberry and salal. For example, salmonberry populations appear to dominate a site through large stems and rhizomes. Salal, in turn, appears to dominate a site through high densities of smaller stems and rhizomes.

The age and height structures of the stem populations all appeared to fit a pattern found for an uneven aged stand of trees (Smith 1986). This agrees with the results found for other understory species (Tappeiner et al 1991; Kurmis and

Sucoff 1989). This structure may facilitate the persistence of these populations within the understory.

CONCLUSIONS

Salal appears to have a regenerative niche (Grubb 1977) that requires rotten logs, stumps, or snags and partial shade for seedling establishment. Forest characteristics such as these may be found during the stem reinitiation stage of stand development (eg. Oliver and Larson 1990). During this time self-thinning and localized disturbances create canopy gaps within which seedlings may become established (Spies and Franklin 1989). Salal seeds dispersed to coarse woody debris appear to have a higher probability of survival than those dispersed to forest floor sites. However, this research suggests that seedling recruitment on any substrate is low. This indicates that salal's regenerative "strategy" (eg. Grime 1981) is by vegetative expansion.

The fine-scale disturbances which create canopy gaps may also facilitate the expansion of salal clones. Before disturbance, salal in the understory may be slow growing and clone sizes may be small. After disturbance, clones may invade and dominate the opening through rapid rhizome growth and ramet generation. Salal clones may then persist on the site through long-lived stems, evergreen leaves, and stem replacement. Over time, these clones may disintegrate into separate plants. Plants such as salal that are long-lived, evergreen, and rely on vegetative expansion for regeneration

have been classified by Grime (1981) as stress-tolerators.

After coarse-scale disturbances, such as fire or thinning, salal populations may replace themselves from buds on rhizomes deep within the soil. These populations may have rapid growth rates due to a high availability of light. However, as evidenced by the remnant clones in this experiment, shade-intolerant tree species such as Douglas-fir or alder may over-top salal and effectively constrain its development. As these trees become more dense and reach canopy closure, percent sky may be reduced to as little as 1.2 %. At this stage of stand development, salal clones apparently disintegrate into small fragments. These remnants generally do not produce rhizomes and subsist with just 1 or 2 small aerial stems. As overstory stands develop further, they begin to self-thin and move into the stem reinitiation cycle. Thus, the cycle of expansion and seedling recruitment may be repeated.

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