AN ABSTRACT OF THE THESIS OF

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Title: THE INTER-RELATIONSHIP OF SALMONBERRY AND DOUGLAS-FIR IN CUTOVER AREAS

Abstract approved:
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The inter-relationship of salmonberry and Douglas-fir on cutover areas was investigated in the Coast Range of western Oregon. Animal influences affecting the survival of Douglas-fir in a salmonberry habitat were also investigated. The autecology of salmonberry was considered first by formulating a mathematical model to characterize the lateral encroachment of the shrub on an opening containing a Douglas-fir seedling or sapling. The height response of Douglas-fir along with its general physiological condition were examined under different degrees of competition imposed by salmonberry. The response of salmonberry's growth to the development of Douglas-fir was also generally described.

Data were obtained in cutover and burned areas containing several age-classes of salmonberry that had Douglas-fir seedlings or saplings interspersed within the shrubs. For the purpose of

characterizing the lateral encroachment of salmonberry by a model, origins of the shrub stems and the shrubs' area of occupancy around an opening were mapped. A ratio of the area of an initial opening before brush encroachment and the area after brush encroachment was used to give a relative size of opening value. This ratio served as the dependent variable in the model. Average maximum heights of the shrubs, the initial size of the opening, time or age of salmonberry, and the number of stem origins or clumps of salmonberry were used as the independent variables. The data were analyzed with the aid of a multiple regression program. Height increments that had accrued in 1968 on Douglas-fir seedlings were examined under conditions ranging from total suppression by salmonberry to no suppression. Data were obtained from 1,950 two-year-old nursery seedlings (Douglas-fir) that gave an index of animal damage with respect to succession.

The findings indicate that the mathematical model formulated is deficient in its prediction ability although it is useful in that it gives a first approximation to the growth characteristics of salmonberry. The growth in height of the shrubs and the initial size of the opening are especially important variables in determination of encroachment.

Suppression by salmonberry substantially reduces the growth of Douglas-fir. Moreover, seedlings dominated by salmonberry or even in close proximity to the shrub are frequently damaged by rabbits. Results reveal that the succession of salmonberry on cutover areas causes an increased frequency of damage to Douglas-fir seedlings. Seedlings that are planted early will have a much better chance of avoiding suppression by the brush and will be less likely to be severely damaged by rabbits, at least during the first year. The inter-relationship of salmonberry and biotic influences are formidable to the establishment of Douglas-fir, both because of salmonberry's fast growth and the increasing rabbit damage to seedlings with increasing age of the shrub.

The Inter-Relationship of Salmonberry and Douglas-fir in Cutover Areas

by

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INTRODUCTION

Shrub competition is an important element in the field of forest ecology. The understanding of the inter-relationships of shrubs and desirable tree species is fundamental in the establishment or re-establishment of forest stands.

Some of the more important forest plant species imposing problems in the Coastal Mountains of the Pacific Northwest are: salmonberry (Rubus spectabilis Pursh), thimbleberry (Rubus parviflorus Nutt), vine maple (Acer circinatum Pursh), and red alder (Alnus rubra Bong.). All of these species sprout vigorously and are noted for their rapid, early growth (Ruth, 1956). This growth capability causes extreme competition between the above species and Douglas-fir (Pseudotsuga menziesii (Mirb) Franco).

Salmonberry, especially, has caused major difficulty in the regeneration of Douglas-fir. Its prolific sprouting coupled with its fast growth give a substantial, early advantage over both natural and planted Douglas-fir. As a consequence, most of the research that has been done on the shrub has been in the area of basal and foliage herbicide controls (Krygier and Ruth, 1961); ecological studies of this species have been neglected.

The primary purpose of this thesis is to describe the research involved in formulating a growth model to characterize the growth of salmonberry and its close associates. The growth of salmonberry is characterized with respect to its lateral encroachment upon an open area containing primarily herbs and a Douglas-fir seedling or sapling. The shrubs' height, distribution of clumps, and the shape and size of the open area are intrinsic to the model and will also be described. The factors in the growth model of salmonberry will be discussed as they affect competition with Douglas-fir and other desirable tree species.

A general description of the response by Douglas-fir to salmonberry's competitive encroachment is also considered in this thesis. Height increment and the general physiological condition of Douglas-fir are functions of the degree of competition imposed by salmonberry. The above responses by Douglas-fir are described within the contents of this paper.

It has been known for some time that animals are a factor in the growth of vegetation. Within a salmonberry habitat, there are many animals that affect the establishment of desired species such as Douglas-fir. This paper gives empirical observations concerning the biotic influences affecting Douglas-fir as they condition the ability of this conifer to tolerate competition from salmonberry.

REVIEW OF LITERATURE

Salmonberry

Salmonberry is an important shrub of economic importance in the Pacific Northwest because of its influence in the regeneration of coniferous seedlings. Ruth (1956) lists salmonberry as the most competitive shrub in association with planted seedlings on an area near Florence, Oregon. Several other workers including Krygier (1961), and Madison and Freed (1962) have reported that salmonberry provides severe competition to conifer seedlings.

Little is known about the ecology of salmonberry even though it presents such a threat to conifer reproduction. Some ecological features and morphological characteristics have been observed although there has been a lack of formal investigation. The plant is described as being a perennial shrub having an erect or curved-spreading stem. The stem is stout with short and straight prickles, making it extremely difficult to work among the shrubs (Peck, 1961). The species ranges from Alaska to northern California along the coast and inland to northern Idaho and western Montana. Salmonberry reaches its maximum size in wet creek bottoms in the coastal forest. It invades cutover or burned-over areas in the coastal forest by propagating from suckers and seed. Even long-delayed germination is apparently stimulated by soil disturbance and increased sunlight (Krygier and Ruth, 1961).

<u>Shrub and Weed Competition with Desirable Tree Species</u>

Competition between shrub-weed plants and desirable tree species has been a subject of investigation for a long time, traditionally on a qualitative basis. With development of modern computer and related technology, more quantification in studies of competition is now possible. One main means of quantifying competition has been to formulate mathematical models to describe growth relationships between plants.

A study of the relationship between one weed species, red alder, and Douglas-fir is described by the following linear model:

$$\Delta H = \alpha + \beta_1 \text{ Ln } H + \beta_2 (\text{Ln} H)^2 + \varepsilon$$

where ΔH = annual height increment

α, β_1, β_2 = constant terms

H = total height

ε = error term

The above model predicts the growth patterns and the difference between actual and predicted height for red alder and Douglas-fir (El-Hassan, 1967).

Jameson (1967) also uses a mathematical model to describe the competition between trees and understory vegetation. In this model, the measurement of the trees is taken as the independent variable and the measurement of herbage as the dependent variable.

Mathematical models are not the only means of quantifying or describing competition between desirable trees and weed species. Some investigators merely measure the rate of weed invasion, the number of weeds or shrubs, the height of their crowns, and the characteristics of individual specie groups. They also record the reaction of the competing tree species in response to different control measures. A study of the above type has been conducted by Brender and Nelson (1954) in a cutover Piedmont pine stand. In this study, they discuss the amount of shade increase, and the increase in density of shrub cover after various treatments. Another similar study in the upper Coastal Plain shows that the removal of the overstory stimulates the growth of pre-existing understory vegetation. In this study, it was noted that a tall, dense shrub thicket often develops and many years elapse before trees penetrate it (Phillips, 1962). Baskerville (1961) shows the response of young balsam fir and white spruce to release from shrub competition on a one-acre plot at Green River, New Brunswick. He reports that if a young fir or spruce is given a moderate amount of release it will not only increase its rate of height growth but maintain the increased rate even after the shrubs have closed in again.

Biotic Influences in Shrub Habitat

The virgin coastal forest of the Pacific Northwest apparently supported few animals. As timber has been cleared and opening created, however, more small mammals plus deer and elk have found suitable habitat (Mitchell, 1950). Hooven (1969) notes that with logging and resultant burning on clear-cuts, there is a marked recovery of vegetation. He points out that with the development of more cover and the addition of increased food from weed seeds and insects, the small mammals continue to increase until the populations equilibrate with the supply of food and cover.

The two principal species occurring on brushy, cutover lands of western Oregon are: the snowshoe hare (Lepus americanus) and the brush rabbit (Sylvilagus bachmani) (Lawrence, Kverno, and Hartwell, 1961). Abundance of rabbits and hares is limited to the early stages of forest succession including stabilized brush fields. Both species inhabit brushy patches of vine maple, willow, rhododendron, or other shrubs. Both rabbits and hares prefer the edge effect of brush and open areas, but the snowshoe hare will travel long distances when feeding (Hooven, 1969). Mitchell (1950) reports that the snowshoe hare is the principal source of clipping damage in tree plantations but notes that the brush rabbit causes some trouble with new plantings along the coast area. One worker writes that in conifer plantations with much shrub competition, rabbits that live in the brush could destroy the few trees that survive the competition (Jemison, 1962).

Another small mammal of concern in shrub habitats is the mountain beaver (Aplodontia rufa). Dalquest (1948) relates that the principal habitat of the mountain beaver is clearings. Mountain beaver is also said to occupy habitats where seepage slopes and streamside thickets of alder form. The animal is limited to moist areas, partly by its inability to form a concentrated urine (Hooven, 1969). Several workers say that mountain beaver is very significant in the damage it causes to conifer plantations. Black and Vladimiroff (1963) write that mountain beaver accounted for most of the wildlife-caused damage in a study on the grazing effects of Douglas-fir in southwestern Oregon. The animal caused about nine-tenths of all the "very heavy" damage which was localized. King (1958), reporting on a ten-year study of damage to planted Douglas-fir and naturally seeded conifers stated that most of the damage was attributed to wildlife. He writes that the greatest single component of damage was incurred by the mountain beaver, which destroyed about 40 percent of the planted trees and eight percent of the natural seedlings. Mitchell (1950) points out, however, while mountain beaver's damage to plantations is positive and severe in localized areas, it is not serious over the Pacific Northwest as a whole.

Larger animals such as deer and elk roam the coastal forests. Mitchell (1950) writes that maximum game forage is produced in three to five years on areas that are clear-cut and burned. Deer and elk take advantage of the abundant and nutritious growth according to Mitchell. The diet of these animals includes browse from woody plants, conifers, and some variety of herbaceous plants eaten during the spring and summer months (Lawrence, Kverno, and Hartwell, 1961). Douglas-fir, however, ranks high enough on a deer food preference list that some degree of browsing can be expected despite apparent abundance of other forage (Crouch, 1966).

It is worth mentioning that animal populations can be manipulated or controlled by alteration of the vegetational pattern. Lawrence (1967) says,

> with the ability to shape vegetative patterns, tailoring them to certain specifications, with herbicides alone or in combination with other land management techniques (fire, scarification, drainage, etc.) land managers have the potential to and in fact do control local distribution and abundance of wildlife.

In summary, then, reports of the animal component of shrub communities are much more abundant than those of the autecology of the shrubs themselves. Since the interaction of cover with animal behavior in the above types must also be lacking, this thesis will strive first to consider the autecology of salmonberry communities, then attempt to consider animals as a part of this ecosystem.

THE STUDY AREA

Location

This research was conducted on the Siuslaw National Forest in the Coast Range of western Oregon. Eleven clear-cuts or tree plantations containing plots lie within the Waldport District. One plantation lies within the boundaries of the Alsea District. All of the plots are located within a radius of 11 miles from Waldport, Oregon. (See Figure 1 on page 10.)

Climate and Soil

The study area has a marine climate with moderate temperatues. These temperatures are usually above 32 degrees and below 80 degrees with a mean temperature of 50 degrees. July temperatures average about 60 degrees and January temperatures are near 40 degrees. The annual precipitation is about 90 inches with approximately 20 inches occurring between April and September. The soil parent materials are usually marine shales, coastal plain sediments, Pleistocene dunes, and some basalt. The soils developed may be classified into the following Great Soil Groups: Lithosol, Sol Brun Acides, Ando, and Reddish Brown Lateritic (Corliss, Dyrness, 1963). The soils appear deep, porous, and medium textured (Ruth, 1964).

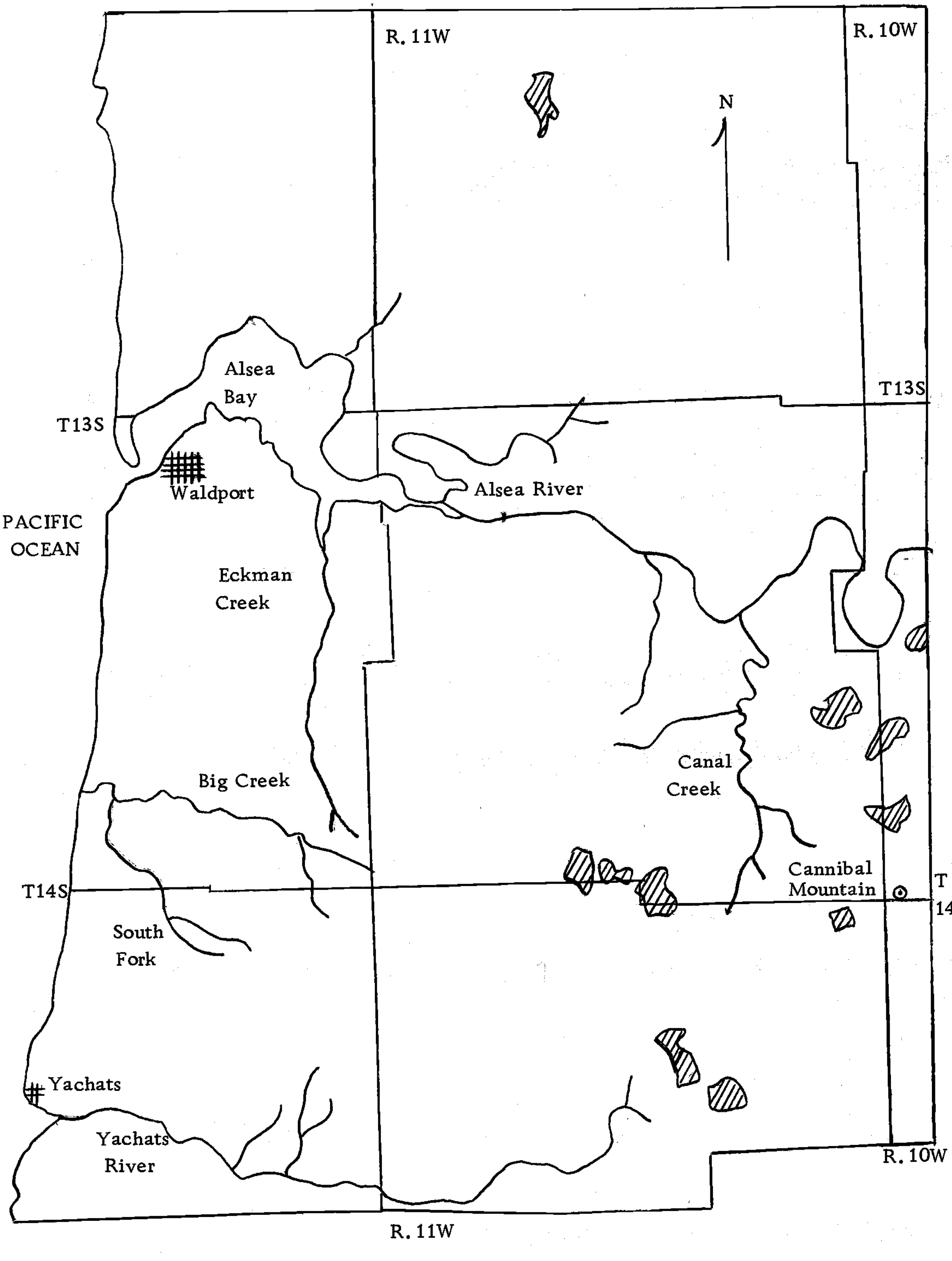

Figure 1. Map of study area showing the clear-cut units containing the sample plots, Siuslaw National Forest, Oregon.

The above climatic and soil characteristics make this area one of the most productive forest areas in North America.

Vegetation

The common shrubs associated with salmonberry in the Coast Range are: thimbleberry, elderberry (Sambucus callicarpa Greene), trailing blackberry or western dewberry (Rubus vitifolius C. and S.), Oregon grape (Berberis aquifolium Pursh), salal (Gaultheria shallon Pursh), and red huckleberry (Vaccinium parvifolium J. E. Sm.). The above shrubs, with the exception of salal, are best adapted to quite mesic sites such as along creeks or in the drainages. Elderberry along with red huckleberry grow well in damp woods providing they have sufficient light. Salal grows well on moist, but moderately drained slopes. These shrubs together comprise a vegetation complex that competes strongly with juvenile Douglas-fir and other conifers.

Some of the deciduous tree species associated with Douglas-fir and salmonberry are: red alder, big-leaf maple (Acer macrophyllum, Pursh.), vine maple, and bitter cherry (Prunus emarginata (Dougl.) Walp.). All of these species require moist areas for growth. Sitka spruce (Picea sitchensis Carr), western hemlock (Tsuga heterophylla Raf.), and western red cedar (Thuja plicata D. Don) are the chief coniferous tree species associated with Douglas-fir and salmonberry.

Several non-woody plants also occur in the area. Some of the more prominent ones include: sword fern (*Polystichum munitum* Kaulf.), bracken fern (*Pteridium aquilinum* Kuhn.), *Senecio* species, and *Lupinus* species. Several grasses also occur in the area; the most common of these is velvet grass (*Holcus lanatus* L.).

Corliss and Dyrness (1963) described several understory species that occur with salmonberry. They considered the dominant plant species in the understory to be salal, vine maple, salmonberry, and sword fern.

History of the Area

Before logging, most of the clear-cuts that were sampled consisted of even-aged Douglas-fir stands. These stands resulted primarily because of a catastrophic fire in 1847 and smaller localized fires in successive years. Due to these fires, the harvested stands of timber were 110 years or less in age. The average volume of these stands ranged from about 60,000 to 100,000 board feet per acre. Another ubiquitous species that occurred with Douglas-fir as a result of fire was red alder. Almost all of the cutover areas sampled contained red alder in the original stand. Salmonberry was a six to ten feet tall, vigorous plant in the mature forest overstory, especially where red alder was present in the stands among the Douglas-fir. Tree species of secondary importance associated with Douglas-fir were western hemlock and western red cedar; they occurred in scattered remnants of the old stands which escaped the fires.

Much of the land containing the cutover units had incised drainages and steep slopes. Cable logging methods, primarily high-lead, were employed for harvesting because of this topography. Tractor logging was possible on gentle slopes, but high soil moisture made it impractical much of the time.

Regeneration was attempted by planting rather than natural seeding. Trees were difficult to establish in the stands of brush on the clear-cuts. Several areas had to be replanted two or three times. Planting stock consisted of two-year-old Douglas-fir seedlings from the nursery; one clear-cut was planted with a mixture of Sitka spruce and Douglas-fir, but Douglas-fir was the primary species planted.

METHODS AND MATERIALS

Sampling Technique

It was known prior to sampling that certain criteria would have to be established before stands of salmonberry could be selected. Several age-classes of unsprayed salmonberry were necessary to describe its growth over a period of time. Continuous, homogeneous stands of salmonberry were needed containing Douglas-fir seedlings or saplings within them. Douglas-fir trees from two to eight years were sought to relate their response to salmonberry at different times in their life-cycle. Burned, cutover areas were necessary so that the probable age of salmonberry could be determined.

After the criteria were established for the selection of salmonberry stands, extensive field reconnaissance was accomplished with the aid of the files of the U. S. Forest Service. These records facilitated the selection of clear-cut areas with the right age-classes of shrubs and trees. They also helped to alleviate the problem of distinguishing sprayed from unsprayed units. Even though the files of the U. S. Forest Service were utilized, additional time was spent searching for areas with adequate densities of salmonberry that had Douglas-fir trees interspersed within the brush. It was impossible to select randomly among cutover areas because of the restrictions of the study design.

The establishment of plots within the salmonberry stands was systematic with a random start. Transect lines were chosen along an azimuth corresponding to the major growing area of the salmonberry and plots were located on each transect line. There was a total of 300 plots established on 12 clear-cut units. A plot consisted of: a Douglas-fir tree; an opening around the tree, if any; and the shrub stems around the opening. Plots were chosen by this procedure:

1. The transects were broken into segments of six paces.
2. At every sixth pace, the nearest Douglas-fir seedling or sapling within a radius of ten feet was selected as the reference point of the plot. The plots overlapped to some extent, but samples were taken without replacement so that no tree was sampled twice.
3. A Douglas-fir tree was sought at the end of the next six-pace segment if none was found at the end of the preceding segment.

In addition to the plots mentioned above, 39 plots containing 50, two-year-old nursery, Douglas-fir seedlings were located in ten of the same 12 clear-cuts. These plots were established for the purpose of obtaining an index of animal damage. They were placed anywhere in the stand of salmonberry that would allow a 5 x 10 grid of seedlings planted about one foot apart. The place of occurrence within the stand of salmonberry was therefore non-random since it was dictated by the amount of space available for planting a plot of that size.

Data Collection

The first task of data collection was to measure the encroachment of salmonberry and its associate species upon the Douglas-fir tree and the opening in which the tree had been planted, if any. It was necessary to measure the initial size of the opening and the residual size of the opening to obtain a percentage of closure. The initial size of the opening, designated A_0, consisted of the original area between the salmonberry stem origins. The subscript "0" refers to the age of salmonberry when the stems of the shrubs were just sprouting; the age of salmonberry was considered to be zero at this time. The residual size of the opening, designated A_t, consisted of the area circumscribed by the maximum growth of the shrubs (see Figure 2). The subscript "t" refers to the age of salmonberry when the residual size of the opening was recorded, (t=2-8). Salmonberry's age was based on the number of years since the occurrence of burning.

Accomplishment of the first task above was instrumented by a pantograph and a planimeter. The pantograph is shown in

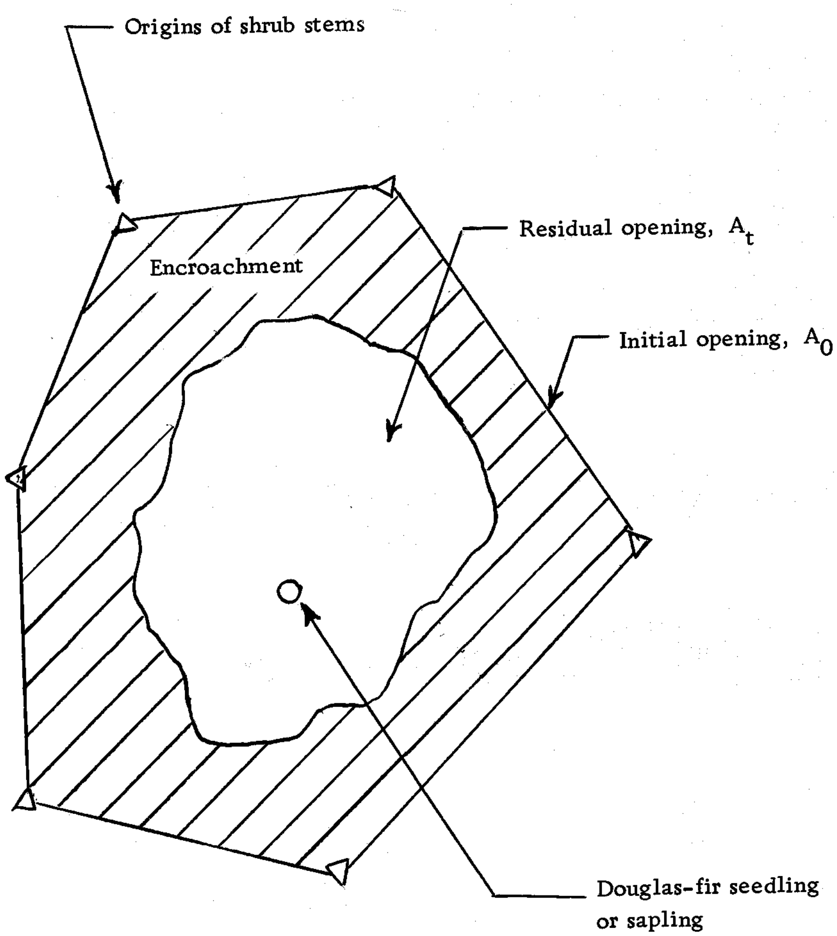

Figure 2. Sketch illustrating a field plot.

Figure 3.[1] It was used to sketch the origins of the shrub stems and the shrubs' frontal edge of encroachment upon the residual opening, A_t. The area occupied by the shrubs (encroachment) and the residual opening containing the Douglas-fir tree were reduced onto a paper mounted on the drawing table of the instrument. This paper sketch was one-fourteenth the scale of the actual field plot.

The planimeter was used to measure the reduced sketches of the original plot that were made by the pantograph. It was used to measure both the initial opening, A_0, and the residual opening, A_t, of the plot.

The area constriction of the initial opening, as determined by the planimeter, was recorded as a decimal percentage of opening size left after encroachment, A_t/A_0. When this percentage was recorded for plots of seven different age-classes of salmonberry, it was considered to give an estimate of the complement of encroachment. One minus this percentage multiplied by 100 estimated the actual percent of encroachment by salmonberry relative to the size and shape of the initial opening, i.e., $100(1-A_t/A_0)$ = percentage encroachment.

There were 247 plots measured by the planimeter. An additional 53 plots were recorded that did not avail themselves to this

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[1] The use of the pantograph as an instrument to map vegetation was developed at Oregon State University by Dr. Michael Newton.

Figure 3. A pantograph used to sketch the field plot containing: the Douglas-fir seedling or sapling; the opening around the Douglas-fir, if any; the origins of salmonberry; and salmonberry's encroachment toward the opening.

type of measuring procedure or analysis.

Additional information was recorded concurrently with the sketching of the shrubs by the pantograph. This information included the height of the various shrub stems, Douglas-fir's growth condition on the plot, a description of the canopy in relation to the seedling, animal damage to both salmonberry and Douglas-fir on the plot, and associated plant species.

An examination of height increment of Douglas-fir seedlings during 1968 was the second requirement of data collection. The seedlings were those occurring in each plot already defined. The measurements were accomplished in October, 1968, to permit the full season of elongation. This measurement permitted an examination of current growth under various conditions of competition.

The third requirement of data collection was to obtain an estimate of animal damage on newly planted Douglas-fir seedlings in the seven different age-classes of salmonberry. This was done in the latter part of February, 1969, to permit adequate exposure of Douglas-fir to animals.

Three types of animal damage were recorded. These consisted of rabbit, deer or elk, and mountain beaver. The types of damage were distinguished from each other by each animal's particular way of feeding (Lawrence, Kverno, and Hartwell, 1961). Brush rabbits and snowshoe hares were listed under one category, that of rabbits, since their damage was difficult to delineate.

The procedure used to record animal damage to the 50 trees in a plot was as follows:

1. The total numbers of trees that could be found were recorded.

2. The trees that could be found were inspected for the major types of animal damage mentioned above. The damaged trees were recorded under the appropriate column of animal damage.

3. Percentages of total animal damage and damage of each animal group were computed. Percentages were recorded for each cutover unit and for each age-class of salmonberry. They were calculated by dividing the number of trees damaged in each case by the total number of trees found and multiplying by 100.

Only damage occurring on terminal shoots, affecting growth of the seedling, was recorded as damage. Minor damage occurring on the lateral branches of seedlings below the terminal was considered negligible.

FORMULATION OF A GROWTH MODEL FOR SALMONBERRY

The initial stage of formulating a growth model for salmonberry was to obtain an indication of what model would best characterize its growth. This was done by plotting the mean-decimal percentage of the opening size left after encroachment against age-class of salmonberry. The resulting curve had approximately an exponential form. The initial opening, represented by this kind of model, would constrict very rapidly at first and gradually decrease in constriction until it approached a limit or a plateau. This limit would result because salmonberry's growth would be curtailed by either competition offered by the Douglas-fir seedling or by competition imposed by other salmonberry plants. This type of model is:

$$y = e^{(\beta_0 + \beta_1 x_1 + \varepsilon)} \quad (1)$$

where y = decimal percentage of opening size, A_t/A_0

β_0 = constant,

β_1 = regression coefficient,

x_1 = time or age-class of salmonberry,

ε = error term.

A stepwise, multiple-linear regression program was used to fit equation (1) to the data. Linearization was achieved by letting "ln y" be the dependent variable. The coefficient of multiple determination, or R^2, due to its low value, indicated that the postulated model given above would need to be elaborated. More variables other than time would need to be added to explain the variation in the dependent variable.

It was then theorized that three other independent variables could be used as covariates to account for the unexplained variation in "y." The three other proposed variables in addition to age were: x_2, the initial size of the opening; x_3, the number of shrub origins or clumps; and x_4, the mean maximum heights of the shrubs on each plot.

A model was then postulated which contained the above three additional variables. The resulting exponential model was:

$$y = e^{(\beta_0+\beta_1 x_1+\beta_2 x_2+\beta_3 x_3+\beta_4 x_4+\varepsilon)} \tag{2}$$

where: y = decimal percentage of opening size, A_t/A_0,

β_0 = constant,

$\beta_1, \beta_2, \beta_3, \beta_4$ = regression coefficients,

x_1 = time or age-class of salmonberry,

x_2 = initial size of the opening,

x_3 = number of shrub origins or clumps,

x_4 = the mean maximum height of the shrubs for each plot,

ε = error term.

The above model was transformed to the linear form which appeared as:

$$\ln y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_4 + \varepsilon \qquad (3)$$

The data were fitted to this model and was analyzed again with a multiple, linear regression program. This time, the value of the coefficient of multiple determination increased considerably, but was still too low for adequate predictions.

Residuals or deviations of the model were plotted against each independent variable to determine if additional variables such as quadratic terms or cross-product terms were needed in the model. The graphs gave no indication that additional terms for which data were available should have been introduced.

The next stage of approaching a final model was to perform a sequential F-test on each variable in the model to test for its significance. The analysis of variance tables for each variable are given in Table 1. Three variables provided F-values greater than the five percent level of significance and were: (in order of significance) x_4, the mean maximum height of the shrubs on each plot; x_2, the initial size of the opening; and x_3, the number of shrub origins or clumps. The confidence level for these tests was 95 and 99 percent which allowed very little reason to doubt the importance of these variables.

The final model was obtained after the above tests had been performed. It was apparently the best model that could be formulated under the existing study design and method of analysis. The final model will be discussed under the "Results" section of the thesis.

Table 1. Analysis of variance of the effects of the variables in the model. Sequential F-tests

Source	D.F.	S.S.	M.S.	F
Full model	242	303.63	1.16	
Deleting b_1, b_4	244	352.61		
Deleting b_4	243	348.57		
Due to $b_1 \mid b_2, b_3$	1	4.04	4.04	3.48
Deleting b_2	243	321.59		
Due to $b_2 \mid b_1, b_3, b_4$	1	17.96	17.96	15.48**
Deleting b_3	243	310.30		
Due to $b_3 \mid b_1, b_2, b_4$	1	6.67	6.67	5.75*
Deleting b_4	243	348.57		
Due to $b_4 \mid b_1, b_2, b_3$	1	44.94	44.94	38.74**

5% significance level: $F(1, 242) = 3.84$

1% significance level: $F(1, 242) = 6.63$

RESULTS

The Derived Growth Model of Salmonberry

The final model that could best characterize the percent of encroachment of salmonberry is:

$$\ln y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_4 + \varepsilon \tag{4}$$

$$\ln y = -1.2535 - .0146 x_1 + .0005 x_2 + .0881 x_3 - .3718 x_4 + \varepsilon$$

Time or the age-class of salmonberry, x_1, proved to be statistically insignificant, but obviously must remain in the model. Height of salmonberry is a variable responsive to time or age of salmonberry and therefore is not completely independent of time. The contribution of time to the model is therefore largely embodied in the height variable, with which it is confounded. It is clear that as the shrubs become older, their height will increase with their general development. Together, time and site quality constitute the components of height; since time and height were recorded in the field, the model was restricted to these parameters.

Variable x_2 and x_3 were included to define better the initial opening of the plot and account for variation in the encroachment due to the size of the opening. It was evident that the larger the initial size of the opening, the longer it would take for the encroachment to cover the plot, thus affecting the growth ratio for any given growth rate. There was also a confounding effect between opening size and the number of origins (x_2 and x_3). The smaller initial opening sizes had fewer stem origins or clumps than the larger openings. Under the conditions of this experiment, the initial openings of three origins took less time to be completely constricted for a given growth rate than those of six origins, largely because of their smaller size.

Height, x_4, was also considered in the explanation of the encroachment. The growth rate increased relative to the increase of the height of the shrubs. The shrubs leaned over more into the opening with increased age, contributing to encroachment. (See Figure 4.) Even though the shrubs generally increased in height and encroachment with age, younger plants, because of a better site, occasionally were taller and had encroached further than plants a few years older.

The final model, even though it is inadequate, presents certain trends in the growth of salmonberry on an opening. (See Table 2.) The growth of salmonberry progresses most with a change in height of the shrubs. For example, in a 7.73 square feet initial opening with three shrub origins that are two-years-old, salmonberry with an average maximum height of two feet occupies 79 percent of the opening, while six feet salmonberry theoretically of the same age occupies 95.3 percent, which is roughly the upper

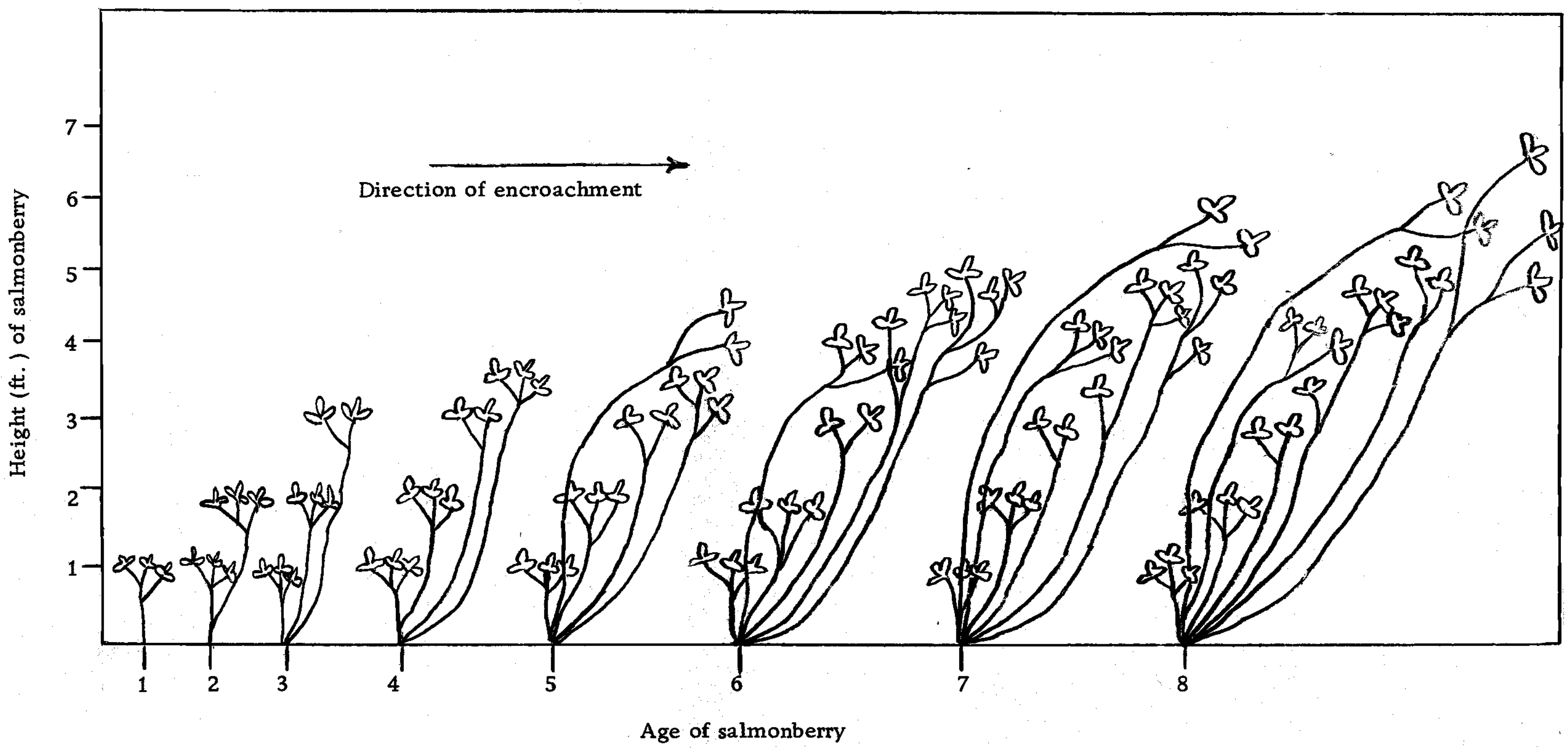

Figure 4. Schematic drawing showing curved-spreading stem development of salmonberry with age. Encroachment increases with height.

Table 2. Percentage of encroachment by salmonberry as given by various values of variables in the model.

x_1 Time or age-class of salmonberry	x_2 Initial size of opening (sq. ft.)	x_3 No. of origins	x_4 Ave. maximum ht. of shrubs on each plot (feet)	(1-y) x 100 Amount of encroachment (Percent)
2	7.73	3	2	79
2	7.73	3	6	95.3
2	25.76	3	2	74.4
2	25.76	3	6	94.2
2	7.73	8	2	67.4
2	7.73	8	6	92.5
2	25.76	8	2	60.2
2	25.76	8	6	90.9
8	7.73	3	2	80.8
8	7.73	3	6	95.7
8	25.76	3	2	76.5
8	25.76	3	6	94.7
8	7.73	8	2	70.1
8	7.73	8	6	93.3
8	25.76	8	2	63.6
8	25.76	8	6	91.9

asymptote.

The variable ranking second in significance is the initial size of the opening, x_2. The relative encroachment of shrubs is directly proportional to the decrease in size of the initial opening. Three origins of two-year-old salmonberry with an average maximum height of two feet growing on an initial opening of 7.73 square feet encroaches 79 percent; salmonberry of the same age and height growing on 25.76 square feet encroaches 74.4 percent.

The number of origins or clumps of salmonberry, x_3, ranks third in significance and accounts for some change in the encroachment of the shrubs. An increase in origins slightly decreases the amount of encroachment on an opening. In an initial opening of 25.76 square feet with an average maximum height of six feet for eight-year-old salmonberry with three and eight origins respectively, salmonberry encroachment decreases from 94.7 percent to 91.9 percent.

Table 2 illustrates that encroachment on plots with older salmonberry, a small initial opening, few clumps of salmonberry, and a large average maximum height of shrubs will be much greater than on plots of the opposite extremes. According to the model, one could expect 95.7 percent encroachment by eight-year-old salmonberry on a 7.73 square feet initial opening with three origins averaging a maximum height of six feet. The opposite extreme is an encroachment of 60.2 percent by two-year-old salmonberry on an initial opening of 25.76 square foot surrounded by eight origins of shrubs averaging a maximum height of two feet.

Douglas-fir Response to Encroachment by Salmonberry

The growth of Douglas-fir was studied with respect to competition by salmonberry. Analyses were made on Douglas-fir seedlings exposed to different degrees of competition. These degrees were "full overtop" of the seedling by salmonberry, "partial overtop," and "no overtop" where the terminal of the seedling was in the open. The condition of salmonberry completely closing over the seedling and the initial opening was "full overtop." If the seedling was obtaining lateral light and the salmonberry was over only part of the initial opening, the condition was "partial overtop." The Douglas-fir was considered to have "no overtop" if it was in the open and obtaining sunlight directly overhead.

Figure 5a, 5b, and 5c show three seedlings of the same age exposed to different conditions of competition. None of these seedlings are damaged by animals. Notice that the seedlings in Figures 5a and 5b have grown much less than the seedling in 5c with its terminal in the opening. Although the current growth of these seedlings appeared to be satisfactory, much of it was predetermined by the conditions of the previous 1967 growth season. The competition offered by the salmonberry during the previous

Figure 5a. Two-year-old Douglas-fir seedling completely "overtopped." The last yearly increment was eight inches.

Figure 5b. Two-year-old Douglas-fir seedling partially "overtopped." The last yearly increment was seven inches.

Figure 5c. Two-year-old Douglas-fir seedling with its terminal in the open. The last yearly increment was 27 inches.

growth season may have been much less causing the seedling to maintain growth during the 1968 season. Salmonberry has, however, gained in dominance over the seedling during the 1968 growth season so that the seedling may actually have been losing the race of dominance. Seedlings such as the one in Figure 6 will probably survive and eventually gain in dominance if salmonberry is not above it more than three feet. The seedling in Figure 6 has grown 11 inches, almost one-third of its total height, but most of this growth was probably a function of the previous year's competition. The seedling was probably taller than the salmonberry during the previous 1967 season.

Seedlings which are under partial or full overtop by the shrubs have a weak and spindly appearance even though their height appears to be satisfactory. Table 3 and Figure 7 illustrate that the best growth occurs when the terminal of the Douglas-fir is in the open and obtaining light. The table and graph indicate that growth is reduced considerably when the tree is fully or partially overtopped. Almost as much growth occurs when the tree is fully overtopped as it does when it is partially overtopped and in some cases more, but this is probably due to the sample size. One would expect much less growth under complete overtop than partial overtop.

Figure 6. Four-year-old seedling which is fully "overtopped." The last yearly increment was 11 inches.

Table 3. Response of Douglas-fir seedlings to various degrees of competition imposed by salmonberry.

No. of stems measured	Average last year height increment (inches): seedling fully overtopped	seedling partially overtopped	seedling with no overtop
a. Response of two-year-old seedlings			
7	10.3 ± 7.8 [1]		
13		9.61 ± 5.25	
21			13.71 ± 8.98
b. Response of three-year-old seedlings			
2	11.0		
6		14.17 ± 3.97	
23			25.61 ± 4.36
c. Response of four-year-old seedlings			
9	12.33 ± 5.78		
2		12.0	
31			30.52 ± 6.598

[1] Inches plus or minus one standard deviation.

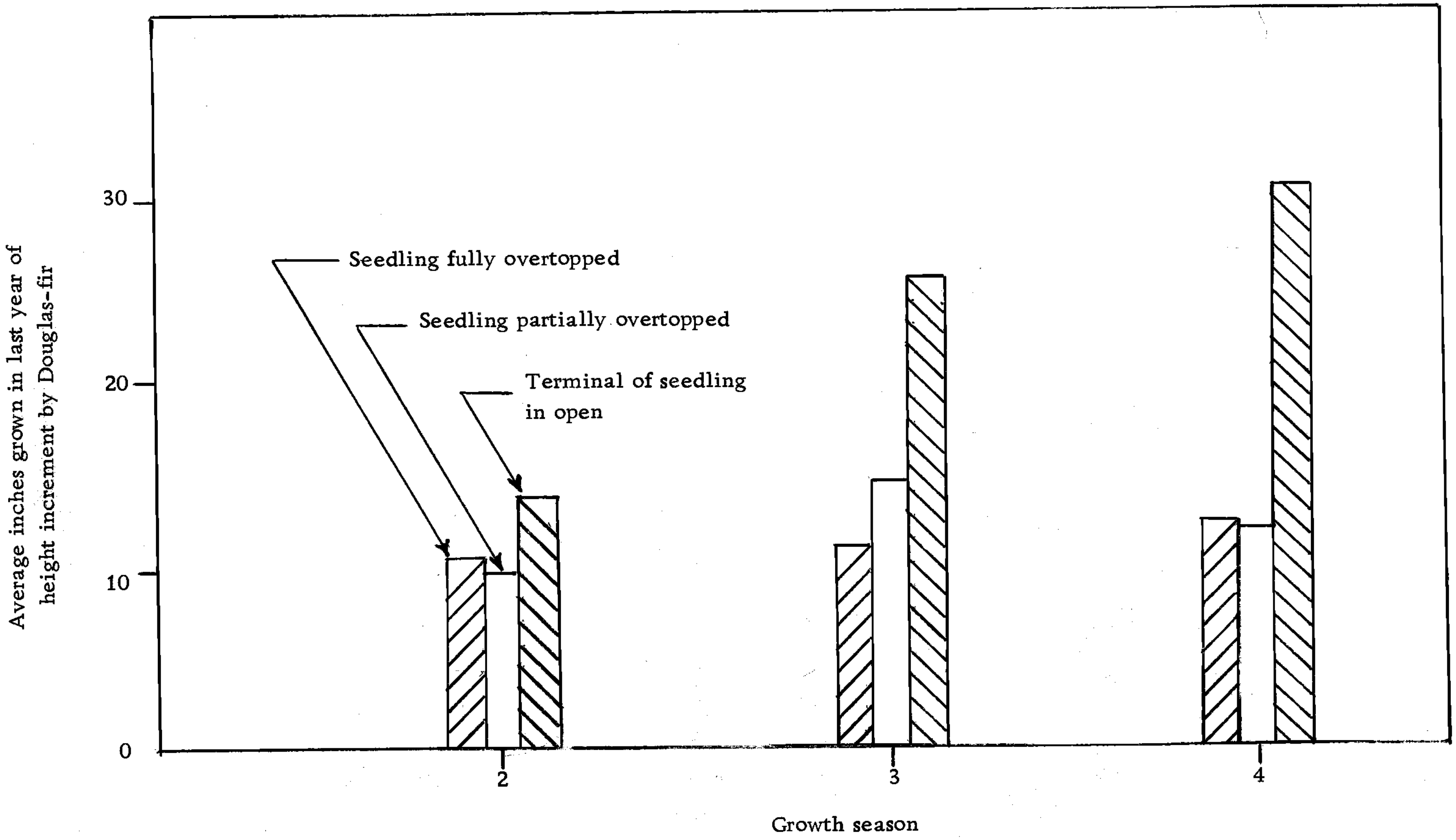

Figure 7. Douglas-fir response to salmonberry competition.

The results only give an indication of the growth of seedlings under competition. They are based on a small sample size due to the sampling method; the sampling method dictates that the first tree found nearest to the transect point is the sample tree. This may be one which is fully overtopped, partially overtopped, or in the open. The disadvantage is that many trees fully or partially overtopped were not found and only the residual trees could have been examined. It could not be determined what trees or how many prospective trees had been killed previously by suppression because of competition.

Biotic Influences Affecting Douglas-fir in a Salmonberry Habitat

Douglas-fir seedlings grow well when exposed to moderate competition by salmonberry. Moderate competition is defined as that of which Douglas-fir is not completely or partially overtopped but which is in close proximity to salmonberry. A major problem that complicates the establishment of the tree under this situation is that rabbits, mountain beaver, deer and elk tend to feed upon Douglas-fir. This removes net growth and consequently reduces chances for survival under increasing competition.

Findings show that a significant number of trees have been damaged when they are located within the proximity of salmonberry and associate shrubs. Table 4 points out that from the 300 trees observed in the Douglas-fir-salmonberry plots, 114 of them were damaged by animals. This damage is 38.91 percent of all the trees observed from two through eight-years old. Most of the damage, as can be seen, has been incurred by rabbits and deer. Mountain beaver damage is small in comparison; it has occurred only in localized areas.

Table 4. Animal damage on Douglas-fir seedlings located at each transect point. The ages of the seedlings range from two through eight years. All of the seedlings are in the proximity of salmonberry.

	Total stems observed	Rabbit damage	Deer damage	Mountain beaver	Unknown damage	Total percent
Actual percent of damage	300	15.66	14.91	5.66	2.66	38.91
Relative percent of damage	300	41.23	36.84	14.92	7.01	100.00

Much damage has also occurred in the Douglas-fir plots containing the 50, two-year-old nursery trees located among salmonberry. Results from Table 5 reveal there was 47.47 percent animal damage inflicted on a total of 1664 seedlings that could be found. It is interesting to note that 93.79 percent of all this damage was that of rabbit. This seems to indicate that trees of different ages in salmonberry habitat receive different amounts of certain damage. Young trees of a height less than or equal to about 30 inches, such

Table 5. Animal damage within plots containing 50, two-year-old nursery seedlings.

Age of salmonberry	Total no. planted	No. of stems found	Total no. of stems damaged	Actual % of rabbit damage	Actual % of deer damage	Actual % mountain beaver damage	% of all animal damage
2	200	174	16	6.3	1.7	.06	9.2
3	500	440	110	24.5	.04	0.0	25.0
4	550	432	240	47.4	3.0	4.6	55.6
5	100	94	41	39.4	3.8	0.0	43.6
6	200	170	91	53.5	0.0	0.0	53.5
7	250	209	171	75.6	3.8	0.0	75.6
8	150	145	131	90.34	0.0	0.0	90.34
Total	1950	1664	790	33.44	1.68	1.26	47.47[1]
Relative percent of animal damage				93.79	3.54	2.66	

[1]Rabbit, deer, and mountain beaver damage do not total the 47.47% total animal damage because there was some damage that could not be distinguished.

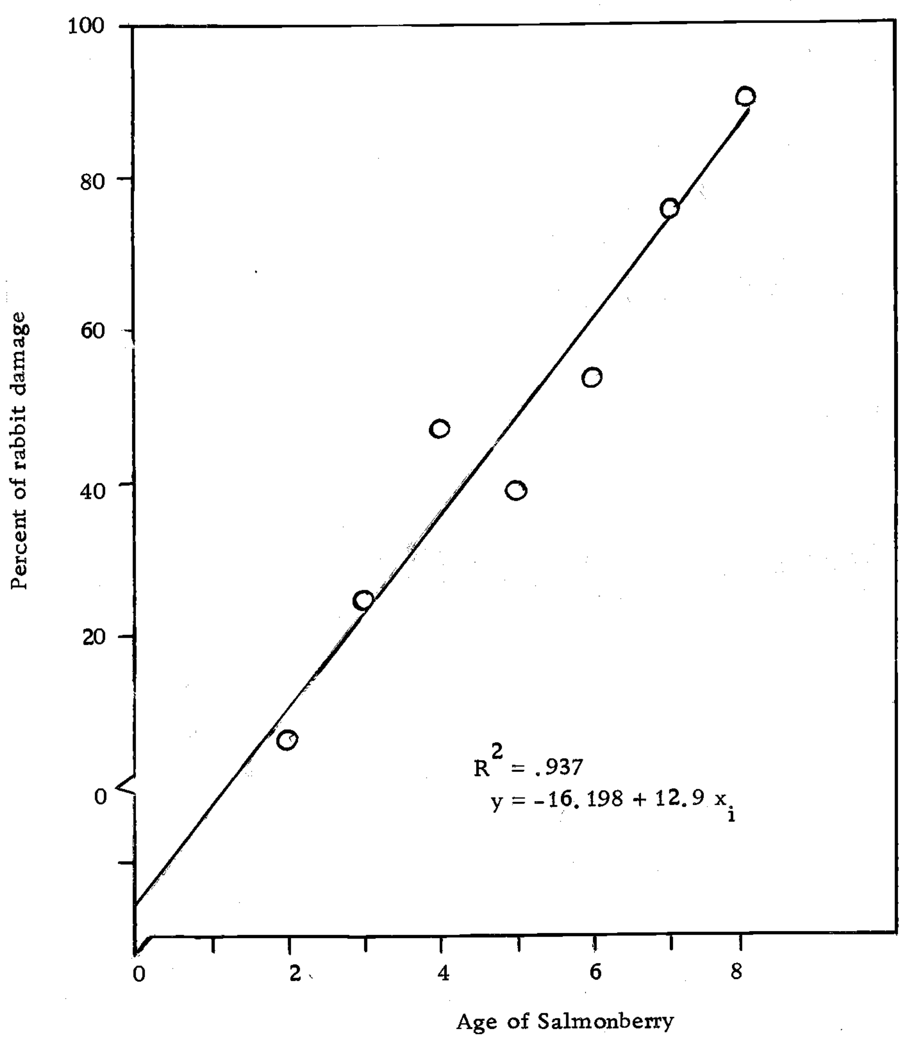

Figure 8. Rabbit damage on 2-0 Douglas-fir seedlings in a salmonberry habitat.

as the trees in these plots, receive a preponderance of rabbit damage when they are under or near salmonberry. Trees above that height are affected more by deer or elk simply because the rabbits cannot reach the terminal.

One should note from Table 5 that there is a linear increase in the amount of rabbit damage as the salmonberry stands become older. Figure 8 illustrates this trend graphically. The extreme of 90 percent rabbit damage occurs in an eight-year-old salmonberry stand, the oldest age class under investigation.

Some of the plots containing the two-year-old nursery seedlings were located in more open areas than were others. Some of the plots were partially in the open and partially under salmonberry. More damage occurred under salmonberry than in the open where the seedlings were fully exposed.

It was found that even trees damaged once and under considerable competition managed net height increment with a lateral branch. The terminal of one particular two-year-old seedling which was partially overtopped was clipped by a rabbit; the lateral branch of that seedling grew 12 inches, two inches more than the average undamaged tree under the same conditions. Trees which were damaged continually and exposed to extensive competition were in poor condition. The undesirable situation was that wholly or partially overtopped trees were the ones most frequently clipped. (See Figure 9.)

Figure 9. A three-year-old seedling completely "overtopped" that has been damaged by rabbits at least twice.

Snowshoe hare damage was recorded under the category of general rabbit damage because its damage was often indistinguishable from that of the brush rabbit. Encountered, however, were many cases of fecal matter distributed by the snowshoe hare over the various plots. Many stems too large for the brush rabbit to have damaged were clipped almost to the ground. This type of damage was devastating to newly planted Douglas-fir seedlings. An example of this damage is shown in Figure 10.

Damage by brush rabbits tended to be restricted to clipping of the new growth on the terminals and the laterals of young seedlings. This damage was enough to retard growth. When this damage occurred repeatedly on Douglas-fir in close proximity to salmonberry, its chance of survival was remote.

The damage inflicted by mountain beaver, even though it was infrequent and occurred only in localized areas, was usually fatal to the seedling. The animal nearly always clipped the main stem near the ground. (See Figure 11.)

Damage by deer or elk was noticed more in openings in the brush or on seedlings directly adjacent to the brush exposed to browsing from one side. This type of damage retarded the growth of Douglas-fir, which allowed the shrubs to gain in dominance and become more competitive for space and light. (See Figure 12.)

Figure 10. Snowshoe hare damage in a Douglas-fir plot of 50, two-year-old nursery seedlings.

Figure 11. Mountain beaver damage on a Douglas-fir seedling. (The twig rising up is a lateral originating below the clipping.) The stem was 3/8 inch in diameter and one inch above the ground.

Figure 12. Damage by deer or elk on a Douglas-fir. This occurred on a terminal directly above the white flagging. A lateral proceeded to function as the terminal.

DISCUSSION AND CONCLUSIONS

This study has attempted to characterize the lateral encroachment of salmonberry on openings containing Douglas-fir by the use of a mathematical model. The response of Douglas-fir to salmonberry encroachment has also been generally described. The study has shown that animals have affected the response of Douglas-fir and influenced succession on a cutover area. It has also shown that succession of a clear-cut can determine the frequency of animal damage on Douglas-fir seedlings. This study is the first of its kind to describe growth of salmonberry by the use of a mathematical model. It is also a preliminary approximation at quantifying the growth of a plant in an ecosystem as it is affected both by animals and competitive plants.

Although the growth model presented is deficient in its prediction ability, it is useful in that it gives a first approximation to the growth characteristics of salmonberry. It also presents important variables to consider in a model of this type containing a ratio of opening size, A_t/A_0, which is a complement of encroachment by salmonberry. This ratio is expressed as the dependent variable.

The findings reveal that the growth in height of the shrubs and the initial size of the opening are especially important variables in determination of encroachment. Moreover, as the shrubs become taller, they lean into the opening, which improves their encroaching capability. Also, the relative encroachment will be faster for a given growth rate on a smaller opening.

The number of origins or clumps of salmonberry proves to be statistically important in the model. The model indicates that more encroachment by salmonberry occurred in openings surrounded by fewer origins. It could be conjectured that the vigor of fewer clumps of salmonberry sparsely surrounding an opening was greater than the vigor of many clumps surrounding the opening.

It is not surprising that the first variable, time or age of salmonberry, proved to be statistically insignificant, in view of variations in growth rate. It is biologically important to the model, however, and is included. The fact that height, x_4, is responsive to time confounds the importance of time to the model. More variation in the dependent variable would also have to be explained before the importance of time would increase. Refinement in the field measurements could have possibly revealed curvilinearity in the model rather than simple linearity, permitting a better fit to biological parameters.

The model points out the need to plant Douglas-fir when the salmonberry is small or young. It indicates, also, that Douglas-fir seedlings should be planted in the largest possible openings, which would allow them to evade immediate suppression from salmonberry.

The present model gives a first approximation of the growth of salmonberry; however, it should be improved for reliable prediction. It is now believed that a site quality index (salmonberry) of some kind for each plot sampled would have helped to explain the variation in the rate of encroachment. For example, salmonberry that was four years was occasionally no further along in development than two-year-old salmonberry simply because of the latter's better site quality. A site-quality parameter is needed in the model to account for variation in growth of shrubs on different areas, to be used with appropriate proportional height increment curves.

Animals affect the development of salmonberry as well as that of Douglas-fir. It is possible that a parameter could have been used in the model to account for this growth reduction in salmonberry.

All of the clear-cut areas were examined both by reference to the U. S. Forest Service files and by field reconnaissance to check for any spray damage to the salmonberry. Although precautions were taken, it is known that some spray damage occurred anyway, thus affecting the growth of salmonberry. In the future, it would be advisable to avoid areas completely if any spray damage was evident whatsoever.

The age of salmonberry was determined by the number of years since it was burned. It would seem reasonable that the season of burning, whether it was fall or spring, would have been important to determine the uniformity of the stands. Perhaps an index of burning response could have also characterized the uniformity of the stands, as well as growth responses to catastrophe at varying stages in carbohydrate balance.

More research is needed to formulate an adequate growth model of salmonberry. A sophisticated model could predict not only the growth of salmonberry but could help in the prescription of Douglas-fir planting to alleviate severe competition from the brush.

The interrelationships of salmonberry, Douglas-fir, and animals are important in a biological system of succession. Figure 7 illustrates that much growth is lost by Douglas-fir dominated by salmonberry. Moreover, Figure 8 points out the potential animal damage that can occur to a Douglas-fir seedling in a salmonberry habitat. It is obvious that the succession of salmonberry on a cut-over area causes an increased frequency of damage to Douglas-fir seedlings. Seedlings that are planted early will have a much better chance of avoiding suppression by the brush and will be less likely to be severely damaged by rabbits, at least during the first year. Many seedlings in the proximity of salmonberry would become established if the rabbits would leave them alone. If planting a clear-cut must be delayed, it would be advantageous to plant older and taller growing stock to avoid severe rabbit damage. Trees should be 30 inches or taller. Such a tree would also have a better chance of competing with the existing brush.

Animals also feed upon salmonberry, but damage to salmonberry is not as critical to its survival as damage is to the survival of Douglas-fir. Salmonberry has more branches and sprouts easily, whereas Douglas-fir is dependent upon one terminal for most of its growth. If the terminal is clipped repeatedly, the tree is greatly reduced in growth ability.

Eventually, a three-dimensional model can and should be derived to predict chances of survival and establishment for conifers in cut-over areas with a potential for salmonberry domination. Douglas-fir's growth probably is a function of the site potential, time since burning, the index of rabbit damage, and the degree of encroachment from the shrubs. Salmonberry's growth is believed to be primarily a function of the site potential, time since burning, and animal damage. The above model can be based on both the encroachment equations and the animal index generated in this thesis.

BIBLIOGRAPHY

Baskerville, G. L. 1961. Response of young fir and spruce to release from shrub competition. Ottawa, Ontario. 14 p. (Canada. Dept. of Forestry. Forest Research Division. Technical Note no. 98)

Black, H. C. and B. T. Vladimiroff. 1963. Effect of grazing on regeneration of Douglas-fir in southwestern Oregon. Proceedings of the Society of American Foresters, 1964, p. 69-76.

Brander, E. V. and T. C. Nelson. 1954. Behavior and control of understory hardwoods after clear cutting a Piedmont pine stand. Ashville, North Carolina. 17 p. (U. S. Southeastern Forest Experiment Station. Station Paper no. 44)

Corliss, J. F. and C. T. Dyrness. 1963. A detailed soil-vegetation survey of the Alsea area in the Oregon Coast Range. In: Forest-soil relationships in North America, ed. by Chester T. Youngberg. Corvallis, Oregon, Oregon State University. p. 457-483.

Crouch, Glenn L. 1966. Preferences of black-tailed deer for native forage and Douglas-fir seedlings. Journal of Wildlife Management 30:471-475.

Dalquest, Walter W. 1948. Mammals of Washington. Lawrence. 444 p. (Kansas. University. Museum of Natural History. Publications Vol. 2)

Draper, Norman and Harry Smith. 1966. Applied regression analysis. 3d ed. New York, John Wiley and Sons. 407 p.

El-Hassan, Babiker. 1967. Juvenile development of Douglas-fir, red alder and snowbrush associations in western Oregon. Master's thesis. Corvallis, Oregon State University. 52 numb. leaves.

Hooven, Edward F. 1969. Unpublished research on the influence of forest succession on small animal populations in western Oregon. Corvallis, Oregon, Forest Research Laboratory, Dept. of Forest Management.

Jameson, Donald A. 1967. The relationship of tree overstory and understory vegetation. The Journal of Range Management 20: 247-249.

Jemison, G. M. 1961. Regeneration in summer-drought forests of the western United States. In: Proceedings of the Thirteenth Congress of the International Union of Forest Research Organizations, Vienna, 1961. Vol. 1, part 2, sec. 23-25. Vienna, 1962. n. p.

King, James E. 1958. Development of a stand of coniferous reproduction and interplanted Douglas-fir. Northwest Science 32:1-8.

Krygier, James T. and Robert H. Ruth. 1961. Effect of herbicides on salmonberry and on sitka spruce and western hemlock seedlings. Weeds 9:416-422.

Lawrence, W. H. 1961. Guide to wildlife feeding injuries on conifers in the Pacific Northwest. Portland, Western Forestry and Conservation Association. 44 p.

Lawrence, W. H., Nelson B. Kverno and Harry D. Hartwell. 1967. Effects of vegetation management on wildlife. In: Symposium proceedings: Herbicides and vegetation management in forests, ranges, and noncrop lands, ed. by Michael Newton. Corvallis, Oregon State University, School of Forestry. p. 88-93.

Madison, Robert W. and Virgil H. Freed. 1962. Basal treatments for control of salmonberry. Weeds 10:247-248.

Mitchell, Glenn E. 1950. Wildlife-forest relationships in the Pacific Northwest Region. Journal of Forestry 48:26-30.

Peck, Morton Eaton. 1961. A manual of the higher plants of Oregon. 2d ed. Portland, Binfords and Mort. 936 p.

Phillips, J. J. 1962. Some effects of competition on the survival of yellow-poplar seedlings. Upper Darby, Pennsylvania. 4 p. (U. S. Northeastern Forest Experiment Station. Forest Research Note no. 134)

Ruth, Robert H. 1956. Plantation survival and growth in two brush-threat areas in coastal Oregon. Portland, Oregon. 14 p. (U. S. Pacific Northwest Forest and Range Experiment Station. Research Paper no. 17)

Ruth, Robert H. 1964. Silviculture of the coastal sitka spruce-western hemlock type. Proceedings of the Society of American Foresters. p. 32-36.