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The growth of western hemlock during the first four years of seedling establishment was examined in a competitive environment in which seedlings were exposed to various types of animal damage and salmonberry and/or alder competition. The study utilized an existing Nelder/replacement series experiment which focused on the competitive effects among western hemlock, red alder, and salmonberry. Vegetative competition was evaluated in terms of overtopping and encroaching cover within a one meter radius of each seedling. Animal damage observed in the study included browsing, (feeding injury of deer and elk), racking (antler rubbing from deer and elk), clipping and girdling (feeding injury from rabbits and hares.) Hemlock growth in terms of total height, height growth , and total volume, was compared between damaged and undamaged seedlings through multiple regression analysis. Sites used in this study were located in the central Coast Range of Oregon on three separate clearcut units.

Growth reductions for hemlock seedlings were mainly due to vegetative competition. The best predictors of hemlock growth were overtopping by salmonberry and overtopping by alder. Hemlock seedlings experienced greater growth reductions due to vegetative competition than from the presence of animal damage. This held true for all animal damage, except clipping by lagomorphs. The clipped seedlings showed significant reductions in growth due to the clipping damage. Results suggest the importance of managing competing vegetation to reduce conifer losses and minimize dense shrub habitat which foster rabbit and hare populations.

Animal Damage, Vegetative Competition and Growth of Western Hemlock Seedlings in the Coast Range of Oregon

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Animal Damage, Vegetative Competition and Growth of Western Hemlock Seedlings in the Coast Range of Oregon

INTRODUCTION

The Oregon Coast Range contains highly productive forest ecosystems, which support a wide array of vegetation and animals. Unfortunately, an appreciable proportion of reforestation efforts in the Coast Range are unsuccessful and result in plantation failures (Walstad,et.al. 1987; Dimock et.al. 1976; Knapp et.al. 1984; Newton and Preest, 1988; Stewart, 1978) due to the seedlings' interaction with their immediate biotic environment. Two of the most important factors which conifers encounter in young plantations are the impacts of animal damage and the severe vegetative competition for resources (Black et. al., 1969). The compounding effects of animal damage and competition from surrounding vegetation can have a strong influence on reforestation success.

Managers dealing with reforestation in the Coast Range are faced with various problems associated with seedling establishment. To ensure successful regeneration it is important to minimize the effects of negative environmental influences. This can be done by using vigorous planting stock (Long, 1976), and controlling competing vegetation either mechanically or chemically in the first few years of plantation establishment.

Mechanical and chemical tools were used to establish the present study and provide two adjacent study areas at three different sites. At each site, one area was chemically weeded to provide weed free conditions for the entire length of the study; thus demonstrating the growth potential of western hemlock (Tsuga heterophylla) as affected by other hemlock and/or red alder (Alnus rubra), with no interference by herbs or other woody species. The second area was left unweeded after initial mechanical cleaning to demonstrate the growth potential of hemlock growing in an area dominated by salmonberry (Rubus spectabilis) with virtually no vegetation control. The competing vegetation and animals within the both weeded and unweeded habitats are the focus of this paper.

Historically, Douglas-fir (Pseudotsuga menziesii) has been the species favored for management in the central Coast Range, yet within areas dominated by salmonberry and red alder, it has performed poorly, partly due to its intolerance of shade. To avoid plantation failures within habitats dominated by salmonberry and alder, managers are looking for silvicultural methods in which seedlings are less vulnerable. Where Douglas-fir plantations have failed, the shade tolerant western hemlock is postulated to be a more successful species for reforestation. The major benefit of western hemlock over Douglas-fir is its presumed higher shade tolerance. Western hemlock is considered to be a tolerant species (Minore, 1979), and it may be able to survive in the shade of surrounding vegetation and ultimately exhibit its dominance over competing vegetation. The vigor of coastal vegetation is sufficient to provide a rigorous test of this assumption.

Reforestation with western hemlock instead of Douglas-fir has been tried only on a small scale. Until now, there has been a lack of quantitative information concerning the growth of western hemlock under high salmonberry and alder competition in the presence of animal damage. The physiological attribute of shade tolerance which hemlock possesses may not be enough to guarantee seedling success in environments dominated by salmonberry and alder. In areas where animals play a major role in shaping the seedling environment, damage from animals further reduces the conifers' ability to escape the shrub cover. This study was conducted to examine the growth of western hemlock in environments in which seedlings were exposed to various types of animal damage in the presence of variable levels of salmonberry and alder competition.

CURRENT UNDERSTANDING

Foresters are acutely aware of the role which animals play in the process of reforestation. This role is often expressed by damage to the seedlings, resulting in delayed establishment or total failure of the plantation (Newton et.al.,1992 in press; Crouch, 1969; Hooven, 1973; Black et.al., 1979; Evans, 1981). As defined by Dimock and Black (1968), animal damage is any animal activity which reduces or delays the total forest yield. Animal damage in the early years of plantation establishment can act as an impediment to conifer seedling growth and survival.

Animal damage research

As efforts to reforest with conifers in the Pacific Northwest have intensified, so has the awareness of animal damage upon seedlings. Early studies were initiated in response to high seedling mortality within plantations due to animal damage. The majority of the research has dealt with the occurrence and control of animal damage and generally ignored the compounding effects of vegetative competition. In western Oregon and Washington, emphasis has been focused on Douglas-fir.

Although the history of animal damage research on forest crops has been relatively short, the problem is not new. The first large scale survey in the Pacific Northwest (Crouch, 1969) found that approximately twenty-five percent of all the reforestation work needed to be replanted. Animal damage ranked highest in economic impact, ahead of all other causes including fire and vegetative competition (Black, 1974). In a separate study, it was estimated that animal damage accounted for several million dollars of damage each year. Due to an increased effort to reclaim brushfields, the frequency of observed damage has increased from historic levels (Black et.al., 1979).

A 1988 National Forest survey showed that control measures for animal damage were used on 208,000 acres within the United states. Sixty-two percent of the total acreage treated (128,000 acres) at a cost of $4.3 million occurred in Washington and Oregon (Borrecco and Black, 1990). Thirty-three percent of the National Forests reported animal damage as increasing, six percent reported it as decreasing, and the remainder sixty-one percent reported animal damage levels which remain stable. Studies in the hardwood forests on the Allegheny have shown that as much as a fifty percent reduction in timber production can result from severe deer browsing (Marquis and Brenneman, 1981). These findings indicate the serious impact of animal damage upon reforestation efforts.

Several types of animal damage occur throughout the life of a stand. The majority of this damage occurs in young plantations, during seedling establishment (Black et.al., 1979). Animals responsible for the majority of the damage in the Coast Range of Oregon include blacktail deer (Odocoileus hemionus), elk (Cervus elaphus), mountain beaver (Aplodontia rufa), snowshoe hare (Lepus americanus), brush rabbit (Sylvilagus bachmani), and beaver (Castor canadensis). Each of these animals inflicts a particular type of injury upon the seedlings, which are categorized as follows: browsing (deer and elk), clipping (rabbits, hare, mountain beaver), cutting (beaver), racking (antlers of deer and elk), and girdling (rabbits, hare, mountain beaver). Table 1 gives explanations of the injuries observed in this study. Examples of animal damage observed in this study are shown in figures 1a-1d.

Table 1: Definitions of animal damage (Lawrence et. al., 1961)

TYPE OF DAMAGE	DEFINITION OF ANIMAL DAMAGE
BROWSING -	feeding damage by deer or elk on the foliage and woody parts of the hemlock seedling. The feeding injury leaves a ragged edge when a portion of the stem has been removed.
CLIPPING -	feeding damage by lagomorphs (snowshoe hare or brush rabbit) on the stem of hemlock seedlings. Clipping damage from either animal is indistinguishable. The result is a smooth oblique cut at the site of feeding. The seedlings are usually no larger than 1/4 inch in diameter and the injury is no higher on the seedling than 20 inches.
RACKING -	injury is the result of antler polishing by deer or elk. The damage incurred by the seedling is removal of bark and/or broken branches, and occasionally loss of top.
GIRDLING -	feeding damage by rabbits or hares to the base of the seedling. The injury is the result of gnawing of the bark near the base of the seedling. The feeding can occasionally result in total girdling of the seedling and subsequently seedling mortality.(Seedlings which were completely girdled were excluded from the analyses.)

Figure 1a : Deer or elk browsing damage on the terminal and lateral branches of a hemlock seedling.

Figure 1b : Clipping damage by lagomorphs on the stem of a hemlock seedling.

Figure 1c : Girdling damage by lagomorphs at the base of a hemlock seedling.

Figure 1d : Racking damage by deer or elk on the stem of a hemlock seedling.

Damage to seedlings is generally evaluated in terms of the reduction in seedling growth, frequency of injury, or mortality. One of the first large scale studies in the Pacific Northwest to quantify the growth losses to animal damaged seedlings was done on Douglas-fir and ponderosa pine (Pinus ponderosa). Black et.al. (1979) determined that 30% of the Douglas-fir seedlings measured experienced some animal damage annually. Damaged seedlings lost approximately 1.5 years equivalent of height growth within the first 5 years. The most common type of damage was browsing by deer and elk. However, the most detrimental damage for individual trees was clipping by mountain beaver. Height growth reductions of fifty percent were exhibited by surviving three-year-old seedlings clipped by mountain beaver. Seedlings damaged by hares exhibited a twenty-five percent reduction in height growth, and those seedlings browsed by deer or elk had a ten percent decrease in height growth during the first three years of growth (Anderson, 1987).

The size of planting stock has been shown to be a key determinant in the growth and survival of animal-damaged Douglas-fir seedlings (Allen, 1969; Hartwell and Johnson; 1983). Hartwell and Johnson (1983) found that 3-0 seedlings (approximately 36 inches tall) were able to recover from deer browsing and rabbit clipping significantly better than 2-0 (approximately 12 inches tall) seedlings, although seedlings of all sizes exhibited poor recovery following mountain beaver damage. By increasing the initial height and diameter of seedlings, overall growth was more rapid. Recovery from growth losses as a result of animal damage can be improved and absolute losses decreased. Allen (1969) determined that Douglas-fir seedlings should be 30 inches or taller to avoid rabbit damage in areas of severe salmonberry competition. Initial height was identified as the most important factor in seedling growth (Newton, 1978), but cover was also highly important. Animals were implicated in the failure of small seedlings to perform well in brush competition (Newton, pers. comm. 1991).

Although the bulk of animal damage research in the Pacific Northwest has focused on Douglas-fir, there has been some research on western hemlock. Newton (1978) observed western hemlock in the Coast Range of Oregon which experienced damage similar to that seen on Douglas-fir, by deer, rabbits and mountain beaver. The majority of the deer browsing occurred on hemlock in open areas during the first year after planting (93% of seedlings in the open experienced browsing pressure), although some browsing did occur in brushy habitat (13% of seedlings in brush were browsed). Clipping from rabbits and mountain beaver occurred only in brushy areas (31% of seedlings in brush), whereas racking from deer and elk occurred only in open areas. Generally browsing by deer has not been reported as a serious problem for western hemlock (Emmingham et. al.,1989; Evans, 1976);

whereas clipping by hare, rabbits and mountain beaver is frequent and considerably more damaging to hemlock seedlings than other types of damage (Evans, 1976).

Vegetative competition

Vegetative competition has been quantified and acknowledged as an important variable in plant communities (Wagner et.al., 1989; Cole, 1984; Harrington and Tappeiner, 1990). Surrounding vegetation and overtopping vegetation have been found to be detrimental to the growth of Douglas-fir (Cole and Newton, 1987; Howard and Newton, 1984; Wagner, et. al. 1989) and western hemlock (Cole and Newton, 1990). The impacts of competing vegetation on the growth of animal-damaged conifers have only recently been studied. Gourley et.al (1990) determined that the recovery and growth of animal-damaged Douglas-fir was significantly greater in weeded areas (competing vegetation controlled with herbicides) then in unweeded areas (competing vegetation allowed to grow). This indicates that animal damage increases the seedlings' vulnerability to surrounding vegetative competition, or conversely, that weeding enhances ability to repair damage. Gourley et.al. (1990) found that the success of the large transplant conifers was significantly improved by weeding but not by the use of a variety of physical and chemical animal damage control methods.

The interactions among seedling growth, surrounding vegetation, and animal damage are not entirely understood.

It has been shown that there is a positive relationship between certain vegetation and certain animals (Allen, 1969; Crouch, 1969). Allen (1969) found that Douglas-fir seedlings growing in or near abundant salmonberry cover were frequently damaged by rabbits, and that damage increased with increasing salmonberry cover. Sites with high levels of shrub and slash enhance lagomorph and mountain beaver habitat (Giusti et. al., 1991). Habitats with abundant palatable vegetation and low levels of slash tend to encourage deer and elk use (Crouch, 1969). The presence of favorable habitat leads to increased numbers of animals within an area and subsequently the potential for increased rates of animal damage.

The relation between the supply of available food and the tendency for animals to concentrate and use conifers as forage has been argued as a reason to favor or to oppose weed control and/or forage seeding. If forage for rodents, such as pocket gophers and mountain beavers, is reduced when trees are present, there is some evidence that there is a temporary increase in damage to trees during the interval of poor food supplies before populations decline. If forage levels are low and vegetative competition is low, there is also evidence that the tree vigor is enhanced (Hooven, Black, and Newton. 1974. Unpublished data.).

The void in the scientific literature regarding the interactions of cover, competition, and animal damage effects on tree vigor has prompted the need for this particular study. The deficiency of integrative literature on this topic exposes a general lack of insight into the interrelationships between seedlings, the competitive environment and the animals present within this environment. As the process of reforestation gains in ecological perspective, the importance of managing this interaction becomes more apparent. Data to facilitate such management are the focus of this thesis.

OBJECTIVES

This study focuses on two aspects of the seedlings' operational environment, herbivory and vegetative competition. The primary question addressed in this study asks whether the damage incurred on hemlock during the first four years after planting significantly inhibits the growth of surviving seedlings in an environment dominated by salmonberry and alder. A secondary topic considers the occurrence of damage in relation to the surrounding salmonberry and alder cover. The study's specific objectives are as follows:

1. To determine the reduction in height and volume experienced by surviving western hemlock seedlings damaged by animals in various ways (deer and elk browsing, deer and elk racking, rabbit and hare clipping, rabbit and hare girdling), as vegetative competition by salmonberry and alder vary during the first four years after planting.

2. To explore the relationship between the frequency of animal damage and the amount of competing salmonberry or alder present.

STUDY SITES AND EXPERIMENTAL DESIGN

Sites included in this study are located in the Tsuga heterophylla zone (Franklin and Dyrness, 1973) in the Coast Range of Oregon. The zone has a mild, maritime climate. The average precipitation ranges between 2000 and 2500 millimeters a year on the study sites, and occurs mainly during the winter months. The summers (mid June - mid September) account for between six and nine percent of the rainfall (Johnsgard, 1963). The abundance of stored soil water and occasional summer rains create highly favorable conditions for hemlock as well as other woody species. The major forest types are referred to as subclimax Douglas-fir and climax western hemlock and Thuja plicata (western redcedar) (Franklin and Dyrness, 1973). The study plots are located on soils derived from colluvium from the Tyee Sandstone formation (Corliss, 1973). The three sites used in this study are located in the central Coast Range of Oregon on three separate clearcut units (Figure 2a). One of the sites, Missouri Bend, is located eight miles west of Alsea (T14S. R9W. Sec. 24), the second site, Sam's Creek, is located near Siletz (T10S. R9W. Sec 6), and the third site, Big Elk Creek, is located 6 miles west of Harlan (T12S. R9W. Sec. 3). All units are in areas which have recently been converted from hardwood/shrub to a conifer dominated forest. Prior to harvest and planting, the sites were occupied largely by alder and salmonberry. All units supported mature conifer stands prior to 1950.

The study reported in this manuscript was part of a larger competition study. The large competition study design combines features of a Nelder type la design (Nelder, 1962) and replacement series design (de Wit, 1960). The large competition experiment investigates various mixtures of alder and hemlock in an array of densities. The overall objective of that study is to examine competitive interactions between western hemlock and red alder over a variety of density and ratio levels, in the presence and absence of salmonberry (Newton et.al., 1986). The original study design of the large competition study did not include the effects of animal damage as part of its objectives.

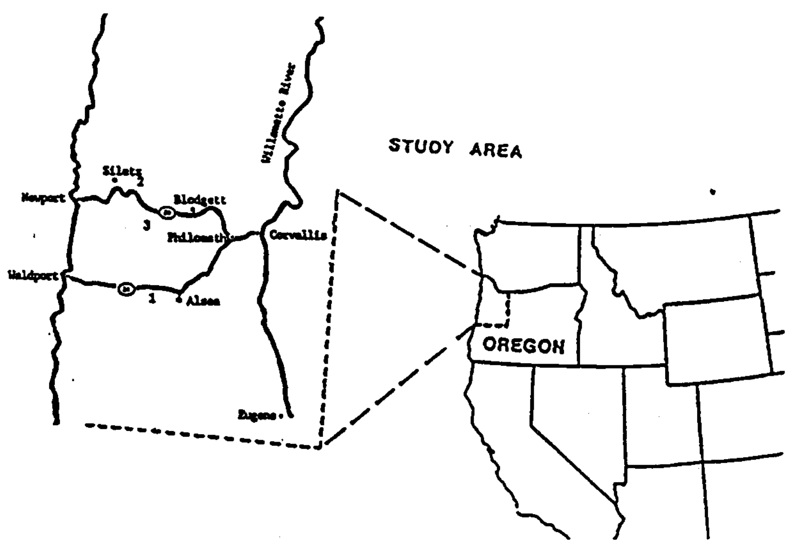

Figure 2a : Location of three experimental units in the central Oregon Coast Range (taken from Kelly, 1991). 1=Missouri Bend Unit / 2=Sam's Creek Unit / 3=Big Elk Creek Unit.

To install the original large study, the following steps were taken. Each site (approximately 4.0 hectares) was cleared of above-ground woody vegetation in the fall of 1986, after one half of each site had been broadcast sprayed with glyphosate. At each site, a complete set of mixed hemlock/alder plots was established on weeded and unweeded areas. The unweeded plots were established in the areas which had not been broadcast sprayed. In these plots shrubs and herbs were allowed to resprout or seed in and grow. The weeded plots were established in the areas that had received the initial glyphosate broadcast spray treatment. In the weeded plots, all shrubs and herbs other than hemlock and alder were controlled periodically through directed spray applications of glyphosate. Within each area, five nelder plots were established, with varying ratios of hemlock and alder; 100:0, 75:25, 50:50, 25:75, 0:100, respectively. An additional nelder plot was established at each site with a ratio of 50:50 western hemlock and Douglas-fir. The hemlock/Douglas-fir plot was then weeded during the length of the study and included in the weeded analyses.

The unweeded and weeded plots supported very different vegetative habitats. In the unweeded plots, a variety of species were allowed to grow, these included herbs, grasses, ferns, and shrubs; all in addition to the planted hemlock and alder. Since all vegetation was allowed to grow in these plots, there were no hemlock seedlings within the unweeded plots which grew free of competing vegetation. The most prominent competing vegetation was salmonberry. The cover of salmonberry ranged from 0% to 100% throughout the plots. For a hemlock seedling with 0% salmonberry cover, there was always some other competing vegetation taking the place of salmonberry.

In contrast, the weeded plots supported some hemlock seedlings which had 0% cover of any competing vegetation. In the weeded plots, all vegetation was controlled except the planted hemlock, alder and Douglas-fir seedlings. The most prominent competing vegetation for the hemlock on the weeded plots was alder. The surrounding vegetative environment for a hemlock in the weeded plots would range from 0% cover of alder, hemlock or Douglas-fir to 100% of alder, hemlock or Douglas-fir. Due to the differences between the weeded and unweeded plots, the data from the two areas were analyzed separately.

Within each plot, density varies systematically, from 10 to 0.1 trees per square meter, with a thirty percent decrease in density at each arc, from the center of the plot outward. There are a total of 342 trees in each plot, and eighteen density levels are represented by the arcs (Figure 2b).

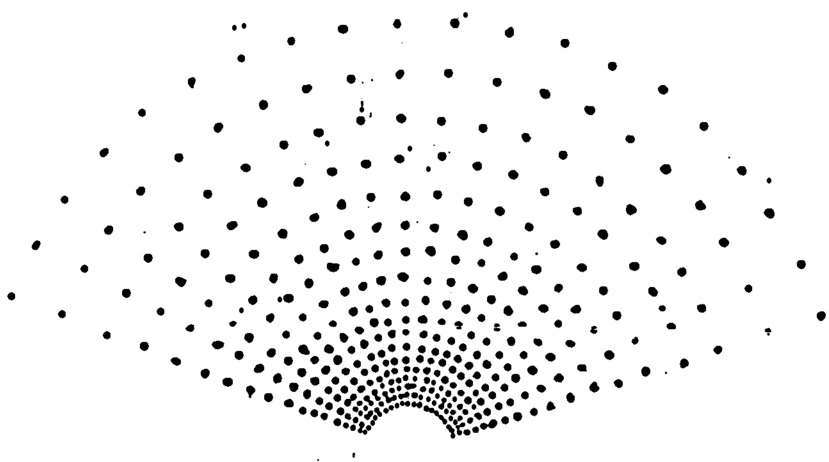

Figure 2b : Diagram of a Nelder plot with a 30% increase in area per plant per arc.

The portions of the competition study which this thesis utilized were 27 plots that include hemlock as a component. This amounted to 9 plots per site. The planting stock used was plug-1 western hemlock, from the Weyerhauser Rochester nursery. The alder seedlings were planted either as 1-0 container seedlings or as 1-0 wildlings of slightly larger size. Seedlings were planted in the winter of 1987.

The experiment looking at animal damage was designed two years after the start of the large competition experiment, thus certain limitations were unavoidable. For the large competition study all seedlings that died during the study were to be excluded from the final analyses. To maintain seedlings densities all the mortality was transplanted as soon as possible. Although mortality was recorded during the first two years, it was not a priority to distinguish between mortality caused by animals and other environmental influences. This made it impossible to analysis the mortality data along with the surviving seedlings. General observations of the mortality data will be reported in the results section.

DATA COLLECTION

Animal damage data and growth data were collected for the first four year after planting. Animal damage was measured twice a year, in the winter and Fall, to avoid misreading winter damage as previous year damage. Damage was identified by the type of injury experienced, browsing, clipping, racking or girdling; and the animal responsible (Lawrence et.al., 1961) (Table 1). Data were collected for deer, elk, rabbit, hare, mountain beaver, and beaver damage. Surviving seedlings damaged once by deer, elk, rabbit, or hare were used in the analysis, along with the undamaged seedlings.

In the third and fourth years of the large competition study (the period involved in the thesis), an effort was made to quantify the severity of animal damage from light to severe using a number scale. All seedlings which experienced lethal animal damage were excluded from the seedling groups and analyses, due to incomplete mortality data. Damage inflicted on the lateral or terminal branches was identified separately. Seedlings were measured at the end of each growing season for total height of the terminal (to the nearest centimeter), height at the beginning of the growing season, basal diameter (to the nearest millimeter, 15 cm above ground), and diameter at breast height (to the nearest millimeter, at 137 cm). To assess competing vegetation, ocular estimates were taken for percent overtopping cover and percent encroaching cover within a one meter radius of each seedling. Percent overtopping of salmonberry, hemlock, alder, Douglas-fir and other vegetation was recorded for each seedling. Overtopping was determined using the cone occlusion method (Howard and Newton, 1984). Within a one meter radius of each seedling ocular estimates were taken for percent encroaching cover of salmonberry, hemlock, alder, Douglas-fir, other shrubs, herbaceous vegetation, and ferns.

STATISTICAL ANALYSES

Fourth-year results were analyzed using correlation analysis, T-Test, multiple stepwise regression and giant-sized regression. All statistical analyses were accomplished using the Statistical Analysis System for microcomputers (SAS 1985). The parameters used to compare seedling growth were total height (measured at the end of the fourth growing season), height growth (calculated by subtracting the height at the beginning of the fourth growing season (HT3) from the total height at the end of growing season (HT4)), and total volume calculated using the following equations:

$$VOL4=0.33*HT4*BA4;$$
$$BA4=0.7854*(BD4/10)^2$$

VOL4=total volume cm^3 in year four, HT4=total height cm year four, BA4= basal area cm^2 year four, BD4=basal diameter mm year four

There were no obvious site differences between the three units used in the study. The average fourth year height for undamaged seedlings at each of the three sites was well within the standard deviation of the other two sites, (e.g. Undamaged seedlings in the weeded plots : Big Elk Creek HT4=240 S.D.=73; Sam's Creek HT4=236 S.D.=73; Missouri Bend HT=234 S.D.=73) (e.g. Undamaged seedlings in the unweeded plots : Big Elk Creek HT4=189cm S.D.=65; Sam's Creek HT4=193 S.D.=66; Missouri Bend HT4=181 S.D.=61). Therefore the three sites were combined for the analyses. Hemlock seedlings within weeded and unweeded plots were analyzed separately.

Vegetative cover was chosen to represent vegetative competition instead of seedling density, because density did not accurately reflect the vegetative environment surrounding each seedling. The eighteen density levels were therefore combined for analyses. The cover measurements took into account the size differences and any mortality of neighboring seedlings, which density would not take into account. The effects of surrounding herb, shrub, and seedling vegetative competition were evaluated for hemlock seedlings by comparing the growth of seedlings throughout a range of percent vegetative cover (0 to 100%). The effects of animal damage were determined on the basis of deviations from the trend demonstrated by undamaged seedlings. The experimental unit was the individual hemlock seedling. A total of 3,801 hemlock seedlings were included in the analyses. Data gathered from 1987 to 1990 were used in these analyses, reflecting the first four years of stand and habitat development.

Prior to comparing damaged and undamaged seedlings through giant-sized regression analyses, it was necessary to determine whether seedlings experiencing similar damage but which were damaged in different years exhibited similar growth in the fourth year and responded similarly to fourth year cover variables. Through the use of giant-sized regression it was determined that all browsed seedlings regardless of year damaged or the damage severity rating, exhibited similar fourth year growth for their size, and were therefore grouped together. The same analysis was done for the clipped, racked and girdled seedlings, and it was determined that the year of damage or severity rating were inconsequential. Thus seedling groups were established for each type of damage.

The hemlock seedling groups in the unweeded plots which were documented through four years of growth include undamaged (1093 seedlings), browsed (427 seedlings), clipped (106 seedlings) and girdled (78 seedlings). The seedling groups in the weeded plots included, undamaged (1451 seedlings), browsed (568 seedlings), and racked (78 seedlings).

Hemlock growth demonstrated a logarithmic relationship to vegetative competition, subsequently the data were transformed for all analyses. A natural logarithmic transformation was found to produce the best residual plots in terms of residual randomness and independence and reduction of variance. It was necessary to add a value of 1 to all variables to make them all greater than zero in order to perform the log transformation. Multiple stepwise regression was used to develop regression equations for each seedling group (Table 2a and 2b).

Table 2a: Regression equations for fourth year hemlock growth in unweeded plots (all three sites are combined).

UNDAMAGED (n=1093)

LHT4 = 3.648 - 0.143[LOG(ORUSP4 + 1)] + 0.467[(LOG(HT0 + 1)] $R^2 = 0.44$

LHTG4 = -0.283 - 0.121[LOG(ORUSP4 + 1)] + 0.872[LOG(HT3 + 1)] $R^2 = 0.47$

LVOL4 = 4.155 - 0.407[LOG(ORUSP4 + 1)] + 0.908[LOG(VOL1 + 1)] $R^2 = 0.55$

BROWSED (n=427)

LHT4 = 3.854 - 0.157[LOG(ORUSP4 + 1)] + 0.377[LOG(HT0 + 1)] $R^2 = 0.38$

LHTG4 = 0.311 - 0.120[LOG(ORUSP4 + 1)] + 0.790[LOG(HT3 + 1)] $R^2 = 0.44$

LVOL4 = 4.197 - 0.434[LOG(ORUSP4 + 1)] + 0.718[LOG(VOL1 +1)] $R^2 = 0.47$

CLIPPED (n=106)

LHT4 = 4.488 - 0.275[LOG(ORUSP4 + 1)] + 0.148[LOG(HT0 + 1)] $R^2 = 0.43$

LHTG4 = 1.563 - 0.249[LOG(ORUSP4 + 1)] + 0.500[LOG(HT3 + 1)] $R^2 = 0.48$

LVOL4 = 3.866 - 0.605[LOG(ORUSP4 + 1)] + 0.505[LOG(VOL1 +1)] $R^2 = 0.46$

GIRDLED (n=78)

LHT4 = 3.716 - 0.120[LOG(ORUSP3 + 1)] + 0.489[(LOG(HT0 + 1)] $R^2 = 0.43$

LHTG4 = -2.491 + 0.137[LOG(ORUSP3 + 1)] + 1.216[LOG(HT3 + 1)] $R^2 = 0.51$

LVOL4 = 4.682 - 0.375[LOG(ORUSP3 + 1)] + 0.796[LOG(VOL1 + 1)] $R^2 = 0.57$

LHT4=LOGARITHMIC TRANSFORMATION OF TOTAL HEIGHT IN YEAR FOUR

LHTG4=LOGARITHMIC TRANSFORMATION OF HEIGHT GROWTH IN YEAR FOUR

LVOL4=LOGARITHMIC TRANSFORMATION OF TOTAL VOLUME IN YEAR FOUR

ORUSP4=OVERTOPPING BY SALMONBERRY IN YEAR FOUR

HT3=TOTAL HEIGHT AT THE BEGINNING OF THE FOURTH YEAR

HT0=INITIAL HEIGHT

VOL1=VOLUME IN YEAR ONE

ORUSP3=OVERTOPPING BY SALMONBERRY IN YEAR THREE

TSHE3=ENCROACHING COVER OF HEMLOCK IN YEAR THREE

Table 2b: Regression equations for fourth year hemlock growth in weeded plots (all three sites are combined).

UNDAMAGED (n=1451)

LHT4 = 4.355 - 0.097[LOG(OALRU3 + 1)] + 0.337[(LOG(HT0 + 1)] $R^2 = 0.31$

LHTG4 = 1.065 - 0.227[LOG(OALRU3 + 1)] + 0.671[LOG(HT3 + 1)] $R^2 = 0.59$

LVOL4 = 5.702 - 0.386[LOG(OALRU3 + 1)] + 0.702[LOG(VOL1 + 1)] $R^2 = 0.44$

BROWSED (n=568)

LHT4 = 4.532 - 0.083[LOG(OALRU3 + 1)] + 0.266[LOG(HT0 + 1)] $R^2 = 0.24$

LHTG4 = 1.913 - 0.214[LOG(OALRU3 + 1)] + 0.529[LOG(HT3 + 1)] $R^2 = 0.59$

LVOL4 = 5.857 - 0.331[LOG(OALRU3 + 1)] + 0.583[LOG(VOL1 +1)] $R^2 = 0.35$

RACKED (n=78)

LHT4 = 4.487 - 0.104[LOG(TSHE4 + 1)] + 0.274[LOG(HT0 + 1)] $R^2 = 0.11$

LHTG4 = 2.635 - 0.154[LOG(TSHE4 + 1)] + 0.373[LOG(HT3 + 1)] $R^2 = 0.40$

LVOL4 = 6.257 - 0.421[LOG(TSHE4 + 1)] + 0.388[LOG(VOL1 + 1)] $R^2 = 0.17$

LHT4=LOGARITHMIC TRANSFORMATION OF TOTAL HEIGHT IN YEAR FOUR

LHTG4=LOGARITHMIC TRANSFORMATION OF HEIGHT GROWTH IN YEAR FOUR

LVOL4=LOGARITHMIC TRANSFORMATION OF TOTAL VOLUME IN YEAR FOUR

OALRU3=OVERTOPPING BY ALDER IN YEAR FOUR

HT3=TOTAL HEIGHT AT THE BEGINNING OF THE FOURTH YEAR

HT0=INITIAL HEIGHT

VOL1=VOLUME IN YEAR ONE

TSHE4=HEMLOCK ENCROACHING COVER IN YEAR FOUR

Through stepwise regression, variables which explained the greatest variation in hemlock growth were chosen. Within the multiple stepwise regression program a default of p>=0.15 was used to delete variables from the model. Vegetative cover variables which had a p-value of 0.15 or greater were dropped from the model. The regression equations in tables 2a and 2b are in the log transformed status. The equations were then back-transformed to develop figures and compare the seedling groups. All figures depicting hemlock growth give the data in the back-transformed status. The overall means of the growth of each seedling group are given in Table 3.

Table 3 : Seedling growth means and standard errors for undamaged and damaged seedling groups (all three study sites combined). HT0=initial height cm, HT4=height year 4 cm, HTG4=height growth year 4 cm;VOL1=volume year 1 cm^3, VOL4=volume year 4 cm^3.

GROUP	HT0	HT4	HTG4	VOL1	VOL4
			UNWEEDED PLOTS		
UNDAMAGED	35 ± 0.3	185 ± 1.9	52 ± 0.8	2.8 ± 0.1	211 ± 7.0
BROWSED	35 ± 0.4	169 ± 2.8	57 ± 1.2	2.7 ± 0.1	172 ± 7.9
CLIPPED	31 ± 0.8	83 ± 6.1	22 ± 2.1	2.0 ± 0.2	58 ± 15.5
GIRDLED	36 ± 0.9	204 ± 7.9	53 ± 3.3	3.6 ± 0.4	427 ± 88.0
			WEEDED PLOTS		
UNDAMAGED	35 ± 0.2	234 ± 1.9	71 ± 0.9	4.6 ± 0.1	827 ± 24
BROWSED	34 ± 0.4	228 ± 2.6	83 ± 1.3	3.6 ± 0.1	823 ± 28
RACKED	35 ± 1.1	235 ± 6.8	87 ± 2.7	4.7 ± 0.5	1125 ± 88

Giant-sized regression was found to be the most appropriate method to statistically compare the growth of the damaged and undamaged seedling groups. Giant-sized regression is basically a method used to compare regression lines. This analysis enabled us to compare slopes and intercepts of regression lines, and therefore determine if the equations were different. To perform giant-sized regression, the independent variables within the different regression equations needed to be the same. This meant that the girdled seedlings could not be compared with the undamaged in the unweeded plots using giant-sized regression, since the variables which best explained the variation in each of the seedling groups were not the same. The racked seedlings could not be compared with the undamaged seedlings in the weeded plots using giant size regression, for the same reason. These groups were compared using T-Tests.

Total height of hemlock seedlings in year four

For the analyses of total height in both unweeded and weeded plots, initial height (HT0) was used to take into account the initial size of the seedlings. The independent variable which best described the variation in fourth year seedling height in the unweeded plots was determined to be overtopping by salmonberry in year four (ORUSP4) For hemlock seedlings in the weeded plots, the variables used to described the variation in total height were overtopping by alder in year three (OALRU3) and initial height (HT0). Giant-sized regression was then used to compare the regression equations between undamaged, browsed and clipped groups within unweeded and a second giant-sized regression was used to compare undamaged and browsed groups within weeded plots.

Height growth of hemlock seedlings in year four

For hemlock seedlings in the unweeded plots, the variables that best described the variation in seedling height growth in the fourth year were overtopping by salmonberry in year four (ORUSP4) and the height at the beginning of the fourth growing season (HT3). The variables used for hemlock in the weeded plots were overtopping by alder in the third year (OALRU3) and height at the beginning of the growing season (HT3). Giant-sized regression was used to compare regression equations between undamaged, browsed, and clipped groups within unweeded plots and a second giant-sized regression was used to compare undamaged and browsed groups within weeded plots.

Total volume of hemlock seedlings in year four

The independent variables used in the regression equations for total volume of hemlock seedlings in the unweeded plots were overtopping by salmonberry in year four (ORUSP4) and total volume in the first year (VOL1). The variation in total volume of the hemlock seedlings in the weeded plots was best explained by overtopping by alder in the previous year (OALRU3) and total volume in the first year (VOL1). Total volume in the first year was used as a measure of initial size. Giant-sized regression was used to compare the undamaged, browsed and clipped seedling groups in the unweeded plots, and a second giant-sized regression was to compare the undamaged and browsed groups in the weeded plots.

The racked or girdled seedlings were not analyzed in the giant-sized regression with the browsed and clipped groups, due to differences in regression equation independent variables. The independent variable which best explained the variation in growth for racked seedlings was percent cover of hemlock and not overtopping cover of alder. A T-Test was performed between the racked and undamaged groups, adjusting for site differences. The independent variable which best explained the variation in growth for girdled seedlings was overtopping by salmonberry in the third year, not overtopping in the fourth year. A T-Test instead of giant-sized regression was performed for girdled and undamaged seedlings in the unweeded plots. Site was adjusted for in the t-test for these two groups because the sample sizes for the girdled seedling group and the racked seedling group was much smaller than the undamaged groups and the damaged did not occur evenly over the three sites.

<u>Variables deleted from analyses</u>

A number of cover variables were eliminated through the process of stepwise regression because they provided a minimal amount of information, encroaching cover of fern, herbs, and other shrubs, all explained very little of the variation in growth ($p>0.15$). Certain variables were deleted because they were highly correlated with other variables, such as encroaching cover of salmonberry, and alder. Encroaching cover of salmonberry was highly correlated with overtopping cover of salmonberry. Multiple regression analysis determined that overtopping of salmonberry explained more of the variation than encroaching cover. This same relationship was found for encroaching cover of alder and overtopping cover of alder. All seedlings which were interplants during the four years of the study were excluded from the analyses. Due to incomplete mortality data, all seedlings which experienced damage that resulted in seedling mortality during the study were excluded from the growth analyses. General observations of mortality will be reported in the results section.

RESULTS

Results indicate that animal damage to hemlock seedlings from big game and lagomorphs takes place through a range of different vegetative environments. The majority of browsing by deer and elk occurred in areas of little salmonberry cover. Figure 3a shows that in the unweeded plots 54% of all browsing damage in year three occurred on hemlock overtopped by 10% or less salmonberry. The majority of the clipping and girdling damage inflicted on hemlock by rabbits and hares occurred in areas with abundant salmonberry cover. In year three 75% of the clipping damage occurred on hemlock seedlings overtopped by 30% or more salmonberry cover (Figure 3a). All of the racking damage was found on hemlock in the weeded plots with little or no alder cover (Figure 3b). The majority of girdling was found in the unweeded plots, with salmonberry cover of 40% or greater (Figure 3c).

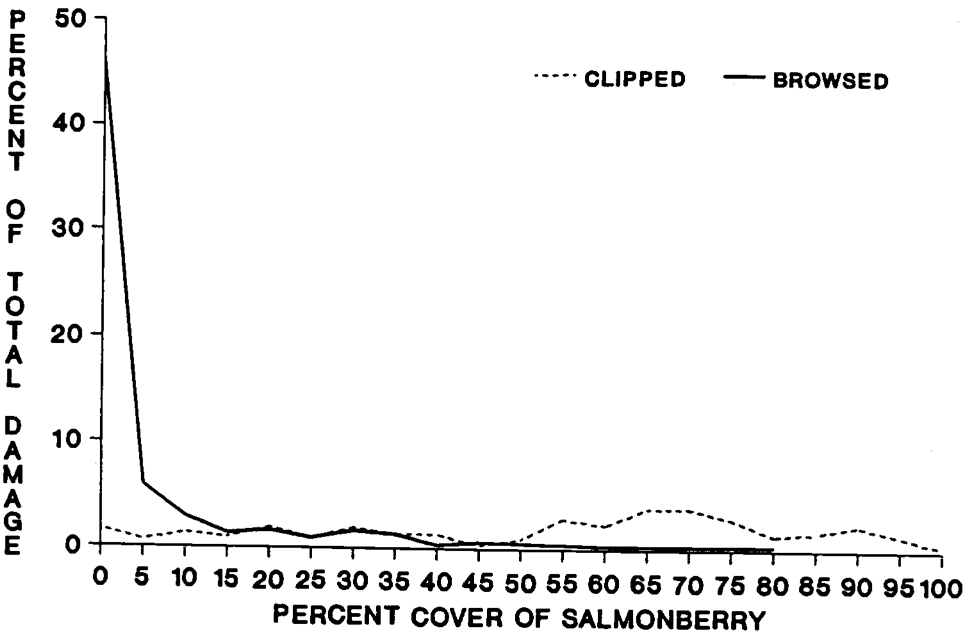

Figure 3a: Hemlock seedlings which were browsed or clipped in the third year compared to salmonberry cover in the third year as a percentage of all seedlings damaged in the third year. (There were at least 20 seedlings in each cover class which were available to be damaged).

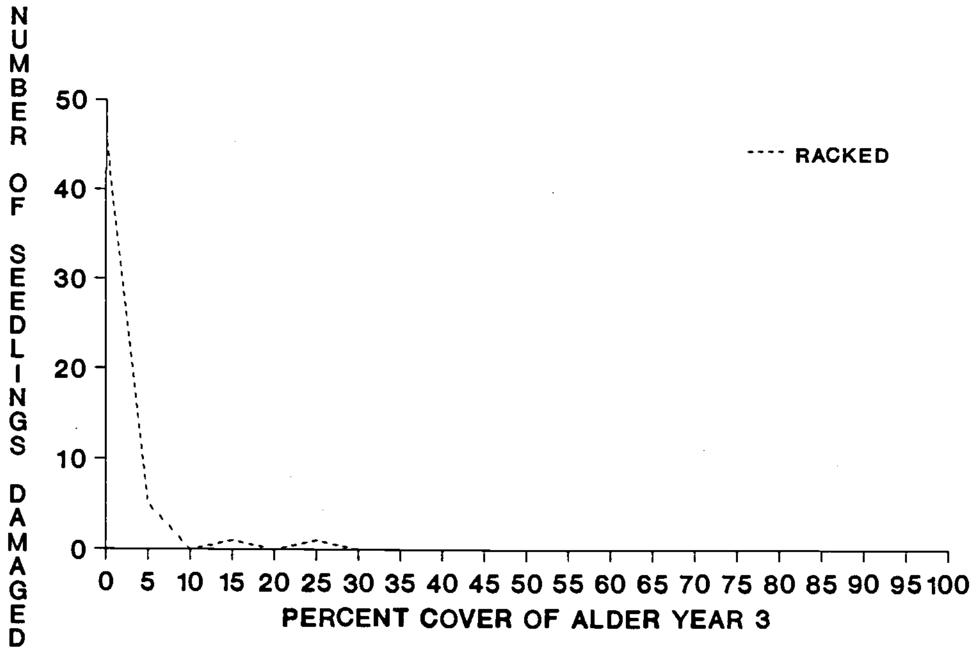

Figure 3b: The number of racked seedlings in the weeded plots in year three by alder cover in year three. (There were at least 20 seedlings in each cover class which were available to be damaged).

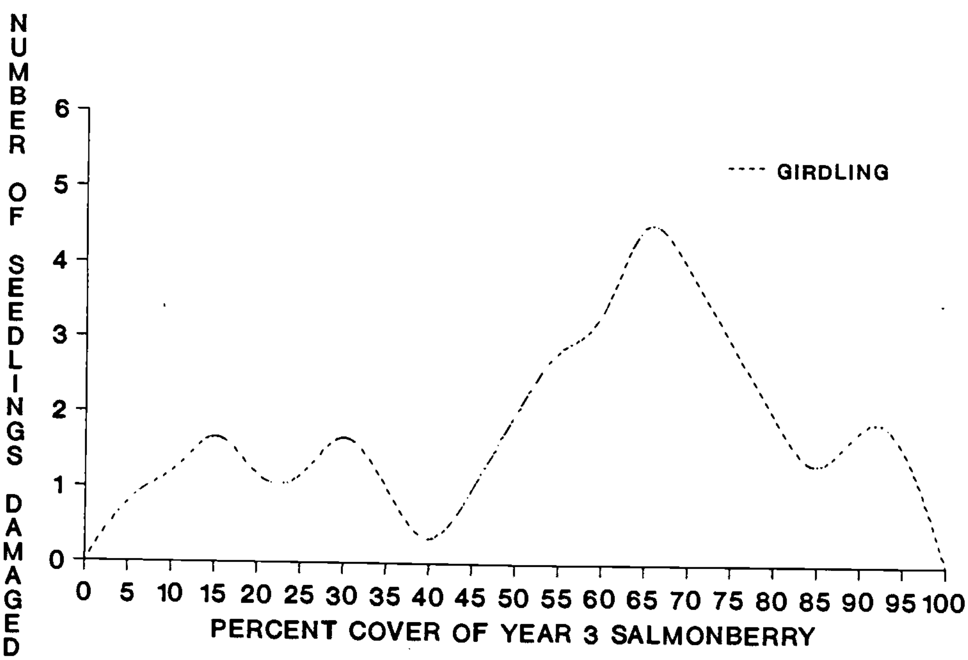

Figure 3c: The number of girdled seedlings in the unweeded plots in year three by salmonberry cover in year three. (There were at least 20 seedlings in each cover class which were available to be damaged).

During the four years of the large competition study, the majority of the deer and elk browsing was concentrated in the second and third years, and the racking damage occurred in the third year with some in the second year. Lagomorph clipping occurred in the second and third years, and the bulk of the girdling took place in the third year. Of the 3,801 hemlock seedlings followed during the study, 26% were browsed (995 seedlings), 3% were clipped (106 seedlings), 2% were racked (78 seedlings), and another 2% were girdled (78 seedlings). The browsing, clipping and girdling damage occurred during the winter months. The racking took place during the Fall (Sept-Dec). Very little damage occurred in the summer months.

Perhaps the most surprising result was that, in general, surviving hemlock seedlings experienced greater growth reductions due to the vegetative competition from salmonberry and alder than from the presence of animal damage. This was true for all animal damage, except clipping by lagomorphs. Clipped seedlings showed significant reductions in growth due to the damage in addition to reductions in growth due to competing vegetation.

Total height of hemlock seedlings in year four

The total height of the hemlock in unweeded plots was negatively correlated with overtopping by salmonberry. Figures 4a, 4b and 4c demonstrate the inverse relationship between total height and overtopping by salmonberry as initial height is held constant. The growth potential of hemlock seedlings can be seen by looking at the undamaged group. The results of the giant size regression indicate that the growth of undamaged and browsed seedlings was not significantly different. Their responses to overtopping by salmonberry (p=0.320) and to initial height (p=0.208) were similar. The clipped seedlings were found to be significantly smaller than the browsed and undamaged seedlings for a given degree of overtopping by salmonberry (p=5.96 x E-11) and initial height (p=0.016). The clipped group exhibited a greater sensitivity to overtopping by salmonberry than either the undamaged or browsed groups. The height of the clipped seedlings decreased more rapidly with additional salmonberry cover than the height of the undamaged and browsed groups. Initial height was not as important a factor in determining the total height for clipped seedlings as it was for undamaged and browsed. This is demonstrated in the regression equation coefficients for initial height, for the clipped group B=0.148, undamaged group B=0.467 and browsed group B=0.377 (Table 2a). The coefficients show that initial height had three times more influence on total height for undamaged and browsed groups than it did for the clipped group.

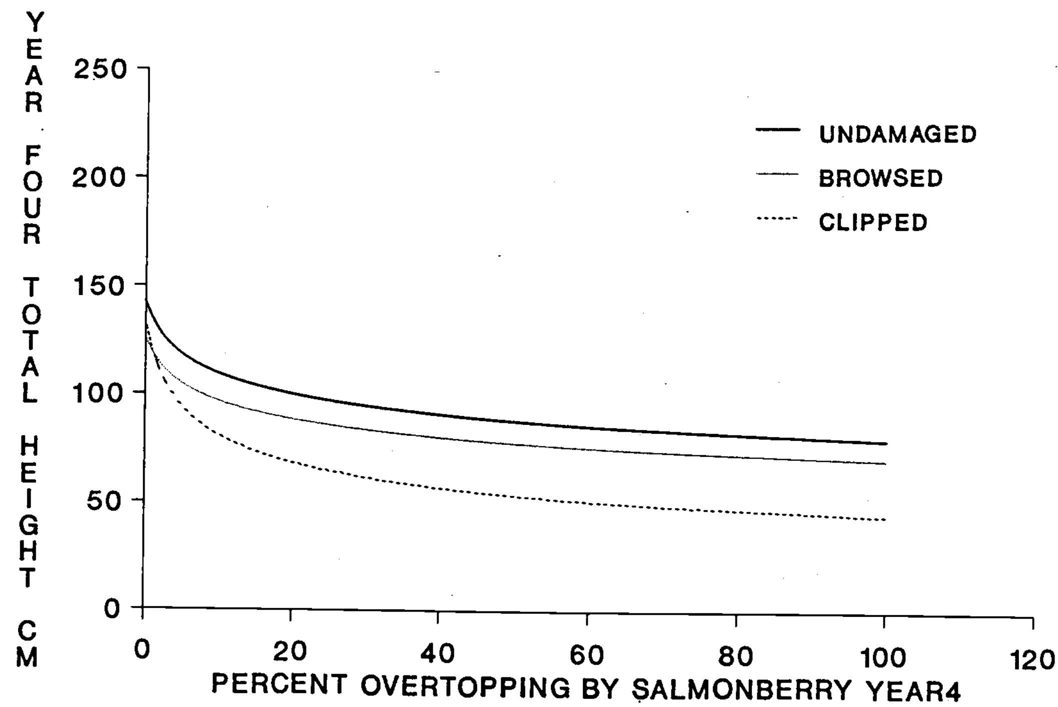

Figure 4a: Fourth year total height of hemlock in the unweeded plots by salmonberry overtopping cover in the fourth year, as initial height (HT0) is held constant (HT0 = 15cm). The curves were derived from the regression equations in Table 2a. Three separate seedlings groups are shown in each figure, undamaged, browsed and clipped.

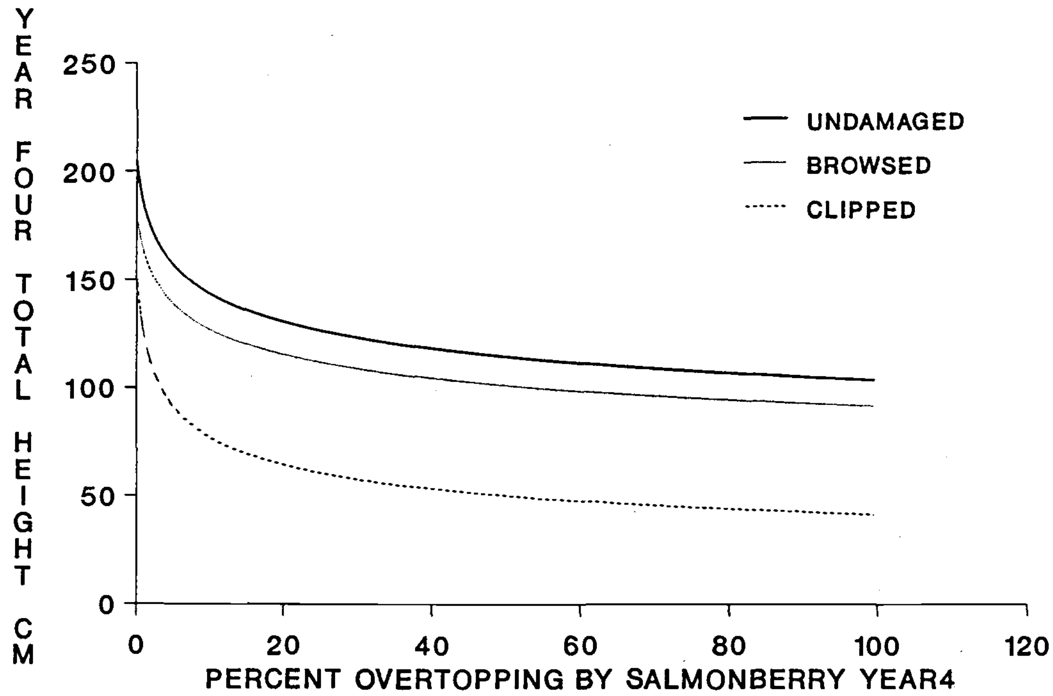

Figure 4b: Fourth year total height of hemlock in the unweeded plots by salmonberry overtopping cover in the fourth year, as initial height (HT0) is held constant (HT0 = 35cm). The curves were derived from the regression equations in Table 2a. Three separate seedlings groups are shown in each figure, undamaged, browsed and clipped.

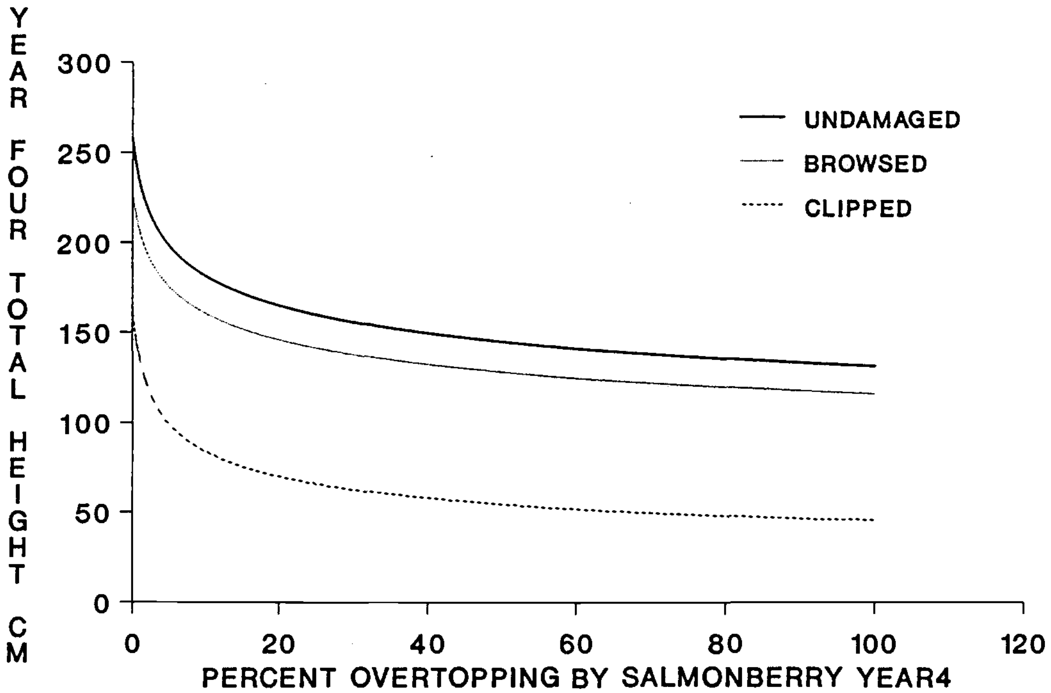

Figure 4c: Fourth year total height of hemlock in the unweeded plots by salmonberry overtopping cover in the fourth year, as initial height (HT0) is held constant (HT0 = 60cm). The curves were derived from the regression equations in Table 2a. Three separate seedlings groups are shown in each figure, undamaged, browsed and clipped.

In the weeded plots, the regression equations indicated a negative relationship between hemlock total height and overtopping by alder, as initial height is held constant, for both undamaged and browsed seedlings (Figure 5). The undamaged and browsed groups responded similarly to initial height ($p=0.15$). They did however exhibit some difference in their response to overtopping by alder ($p=0.089$). The undamaged seedlings appear to be somewhat more sensitive to alder overtopping. This difference may be due to the fact that a large proportion of the undamaged seedling group occurred in areas of dense alder overtopping, and a small proportion of the browsed group occurred in dense alder overtopping cover.

Height growth of hemlock seedlings in year four

Height growth of hemlock seedlings in the unweeded plots was negatively correlated with overtopping by salmonberry. There was no significant difference in height growth between undamaged and browsed seedlings throughout the range of salmonberry cover ($p=0.999$ Figure 6a) or in their response to previous year height ($p=0.133$). It appears to be vegetative competition, not the presence of animal damage which determined the seedlings' growth. The clipped group was found to be more sensitive to salmonberry overtopping than both the undamaged and browsed groups ($p=0.001$) and less responsive to previous years height ($p<0.001$).

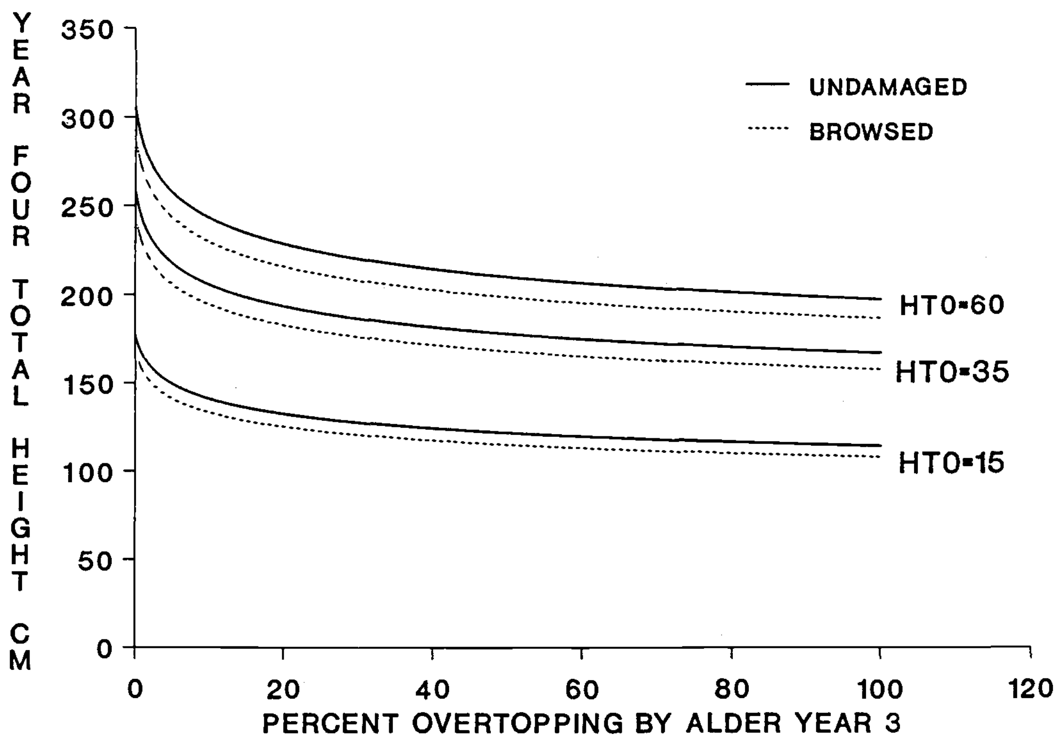

Figure 5: Fourth year total height of hemlock in weeded plots by alder overtopping cover in the third year, as initial height is held constant at 15cm, 35cm, and 60cm. The curves were derived from regression equations in Table 2b. Two seedling groups, undamaged and browsed, are shown in the figure.

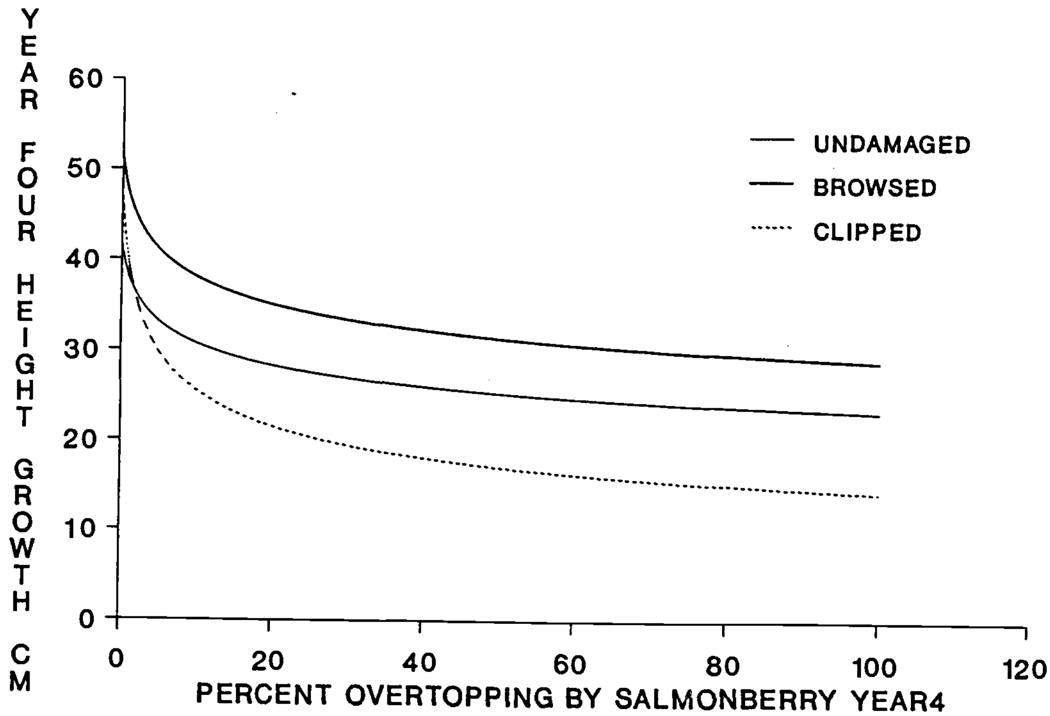

Figure 6a: Fourth year height growth of hemlock in the unweeded plots by salmonberry overtopping cover in the fourth year, as previous year height (HT3) is held constant (HT3 = 100cm). The curves were derived from the regression equations in Table 2a. Three separate seedlings groups are shown in each figure, undamaged, browsed and clipped.

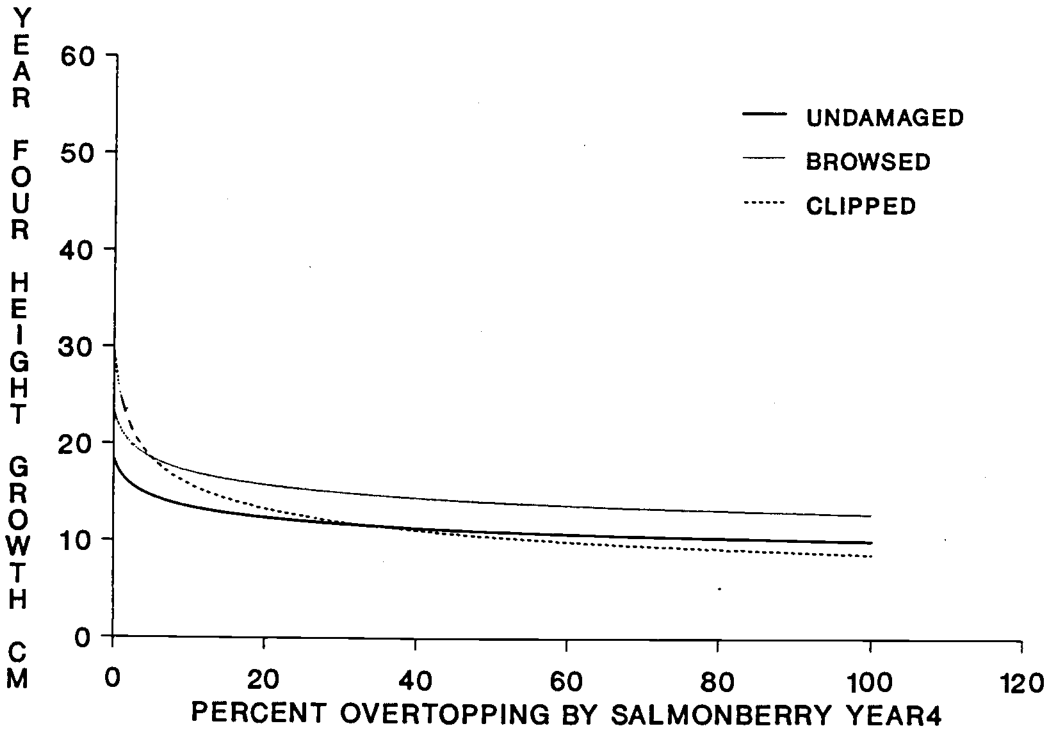

Figure 6b: Fourth year height growth of hemlock in the unweeded plots by salmonberry overtopping cover in the fourth year, as previous year height (HT3) is held constant (HT3 = 40cm). The curves were derived from the regression equations in Table 2a. Three separate seedlings groups are shown in each figure, undamaged, browsed and clipped.

Figures 6a and 6b show the relationship between height growth and overtopping by salmonberry when HT3 was held constant.

The height growth of undamaged and browsed groups in the weeded plots was negatively affected by alder overtopping (Figure 7). The giant size regression comparing the undamaged and browsed seedling groups indicted major differences between the two groups (p=3.59 x E-13). Both groups responded the same to alder overtopping (p=0.297), but they responded differently to previous years height (p=0.0235). The coefficient of the undamaged group showed a steeper slope for height growth in relation to HT3, thus an increase in HT3 saw a greater increase in fourth year height growth for the undamaged group than it did for the browsed group. The previous years height (HT3) for the browsed seedlings was taken from either a stub left from feeding injury, or a dominant lateral. The HT3 of an undamaged seedling was a terminal shoot. Thus an increase in HT3 for a browsed seedling was not the same as a increase in HT3 for an undamaged seedling.

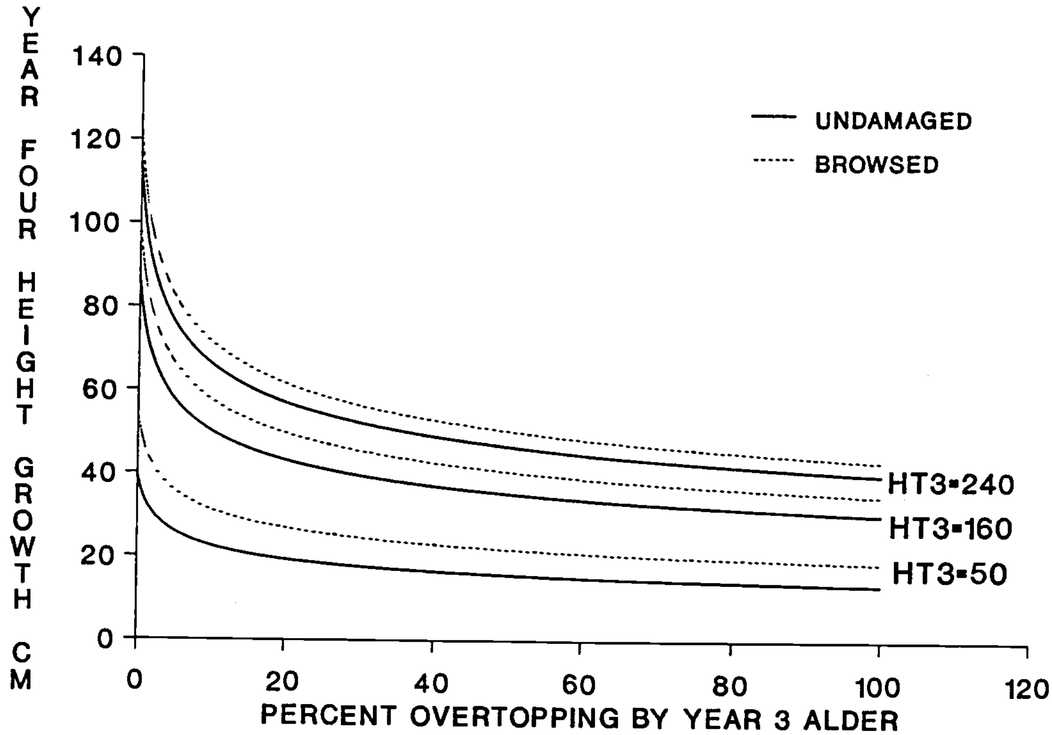

Figure 7: Fourth year height growth of hemlock in the weeded plots by alder overtopping cover in the third year, as height at the beginning of the growing season (HT3) is held constant at 50cm, 160cm, and 240cm. Two seedling groups, the undamaged and browsed, are represented in the figure. The curves were derived from regression equations in Table 2b.

Total volume of hemlock seedlings in year four

In the unweeded plots, Figures 8a, 8b and 8c illustrate the negative relationship between total volume and overtopping by salmonberry as initial volume is held constant. The volume of all seedling groups tends to decrease as salmonberry overtopping increases. The browsed and undamaged groups responded similarly to overtopping by salmonberry ($p=0.465$); yet the initial volume of seedlings had a more positive effect on the fourth year volumes of undamaged than the browsed seedlings ($p=0.028$). Looking at the coefficients for initial volume for undamaged (0.908) and browsed (0.718)in Table 2a, it is evident that initial volume had more influence on undamaged fourth year volume than initial volume had on browsed volume in year four. The clipped seedlings exhibited reduced volume, with growth significantly different from that in the undamaged and browsed groups, in terms of salmonberry ($p<0.001$) and initial volume ($p=0.009$) effects on growth.

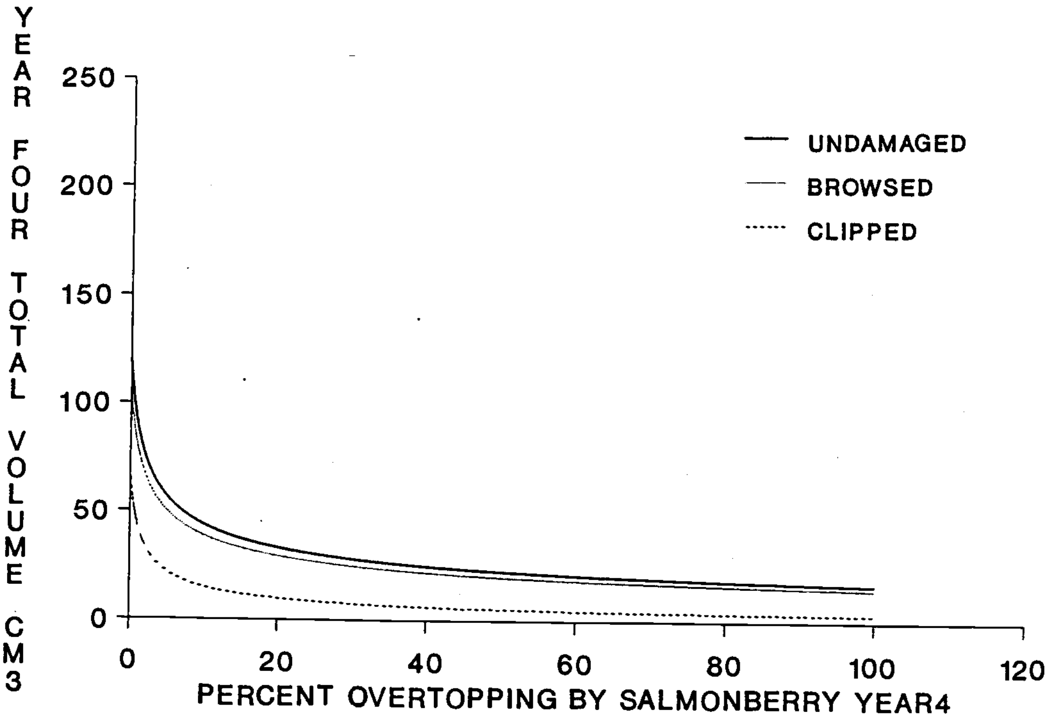

Figure 8a: Fourth year total volume of hemlock in the unweeded plots by salmonberry overtopping cover in the fourth year as volume in the first year (VOL1) is held constant ($VOL1=1cm^3$). The curves were derived from the regression equations in Table 2a. Three separate seedlings groups are shown in each figure, undamaged, browsed and clipped.

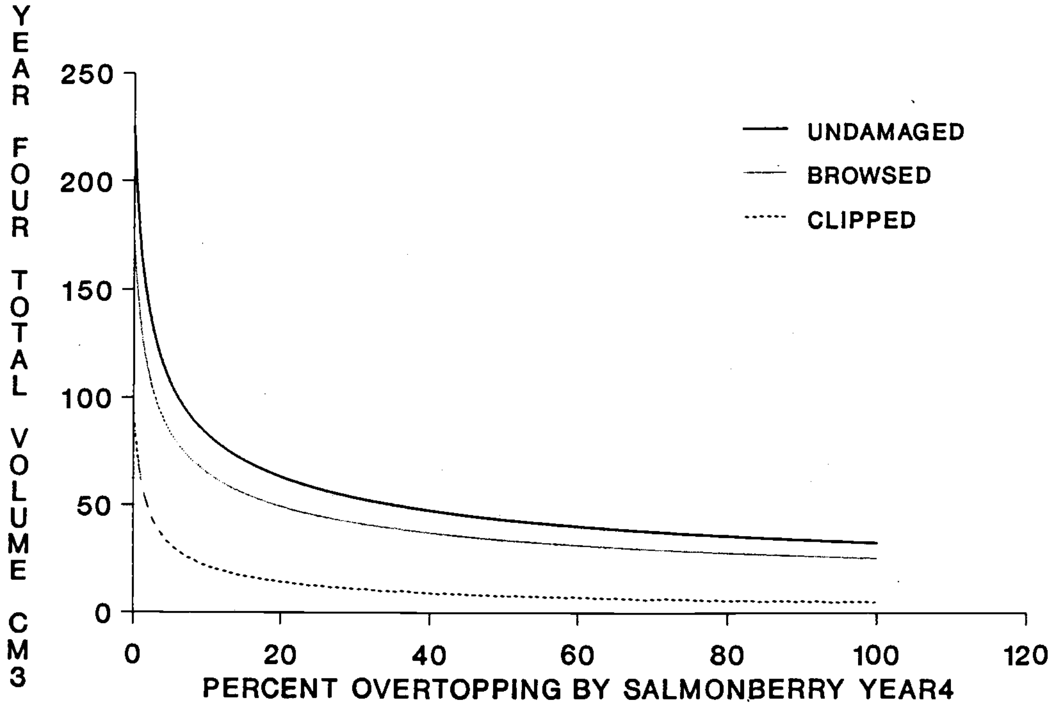

Figure 8b: Fourth year total volume of hemlock in the unweeded plots by salmonberry overtopping cover in the fourth year as volume in the first year (VOL1) is held constant ($VOL1=3cm^3$). The curves were derived from the regression equations in Table 2a. Three separate seedlings groups are shown in each figure, undamaged, browsed and clipped.

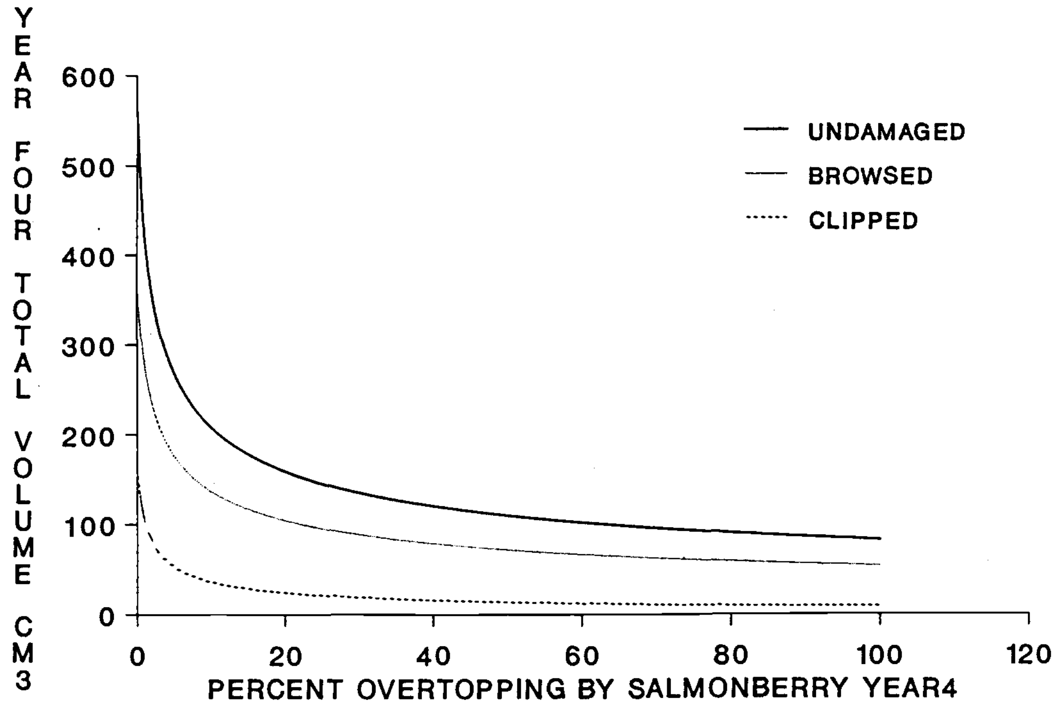

Figure 8c: Fourth year total volume of hemlock in the unweeded plots by salmonberry overtopping cover in the fourth year as volume in the first year (VOL1) is held constant ($VOL1=10cm^3$). The curves were derived from the regression equations in Table 2a. Three separate seedlings groups are shown in each figure, undamaged, browsed and clipped.

In the weeded plots, Figure 9 illustrates the relationship between total volume and overtopping by alder as initial volume remains constant. The results of the giant size regression show that the undamaged and browsed groups are marginally different in terms of initial volume (p=0.100), and in their response to overtopping of alder (p=0.049). The coefficients indicate that the undamaged seedlings (-0.386) exhibited greater decreases in growth with an increase of alder overtopping, then the browsed seedlings (-0.333). The undamaged seedlings showed greater increases in volume growth as initial volume (VOL1) increased (0.702), as compared to the browsed seedlings (0.673).

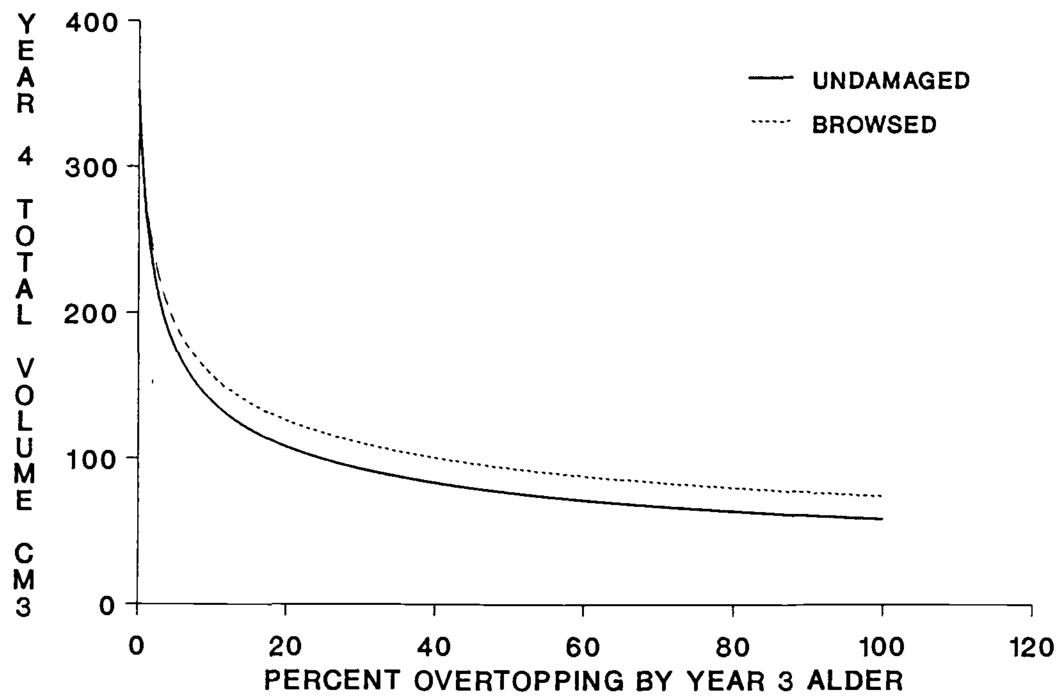

Figure 9: Fourth year volume of hemlock in the weeded plots by alder overtopping cover in the third growing season, as volume in the first year (VOL1) is held constant at 5cm^3. Two seedling groups, the undamaged and browsed, are represented in the figure. The curves were derived from regression equations in Table 2b.

Racked and undamaged seedlings in weeded plots

The damage by deer and elk which is classified as racking occurred almost solely in the weeded plots. The racking damage occurred in areas of low seedling density (the outer seven arcs of the plots). A subsample of the undamaged group was taken from the outer seven arcs of the plots in which the racking had occurred, and compared to the racked group through T-Test analysis, adjusting for site. The results of this test showed that the groups were not significantly different in height growth (p=0.109), total height (p=0.163), or total volume year four (p=0.329). The means in Table 3 show that the racked seedlings are larger than the undamaged seedlings. These are the overall means of the undamaged group, not the subsample which was used in the T-Test comparing undamaged and racked seedling growth.

Partially Girdled and Undamaged seedlings in unweeded plots

Non-lethal girdling damage by rabbits and hares occurred mostly on the unweeded plots. A T-Test was conducted and determined that the growth of the girdled and undamaged groups was similar, in terms of height growth (p=0.821), total height (p=0.739) and total volume (p=0.274).

Seedling Mortality

Mortality data reported in this thesis are data gathered in the third and fourth years of the large competition study. Recording the damage in both the first and second years was not a priority, and therefore the conditions which led to seedling mortality are not consistently clear. Seedling mortality in the third and fourth years of the study showed differences between the weeded and unweeded plots. Using the same categories which were used in the analysis of the surviving seedlings, undamaged, browsed, clipped, racked, and girdled, the results indicate higher mortality rates in the unweeded plots (Figure 10) than in the weeded plots (Figure 11). The mortality rates for undamaged seedlings was 8.29%, and 4.73% in the unweeded and the weeded plots, respectively. The mortality rates for all damaged seedlings in the unweeded plots was 13.94%, and in the weeded plots the mortality rate was only 5.00%. The following are mortality rates for the various groups of damaged seedlings: 44.21% of the clipped seedlings, 3.70% of the girdled seedlings, 1.27% of the racked seedlings, 2.45% of the browsed seedlings (2.06% of the browsed seedlings in the unweeded plots and 2.74% of the browsed seedlings in the weeded plots). The mortality rates for browsed, racked, and girdled seedlings were far below the rates for undamaged seedlings in both weeded and unweeded plots. The mortality rate for the clipped seedlings was far greater than the rate for undamaged seedlings.

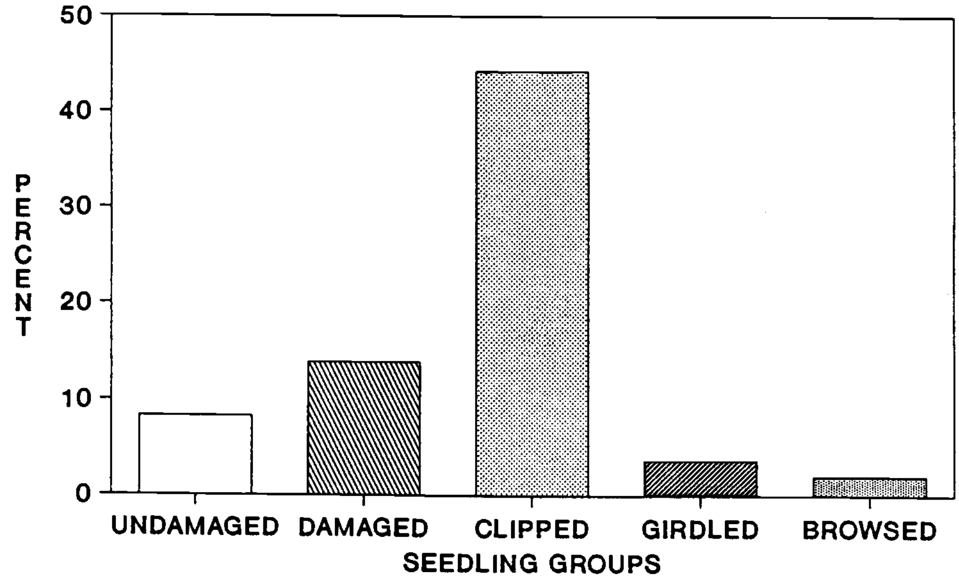

Figure 10: Fourth year seedling mortality rates in the unweeded plots. The figure shows the percentage of each seedling group which died in the third and fourth years of the study.

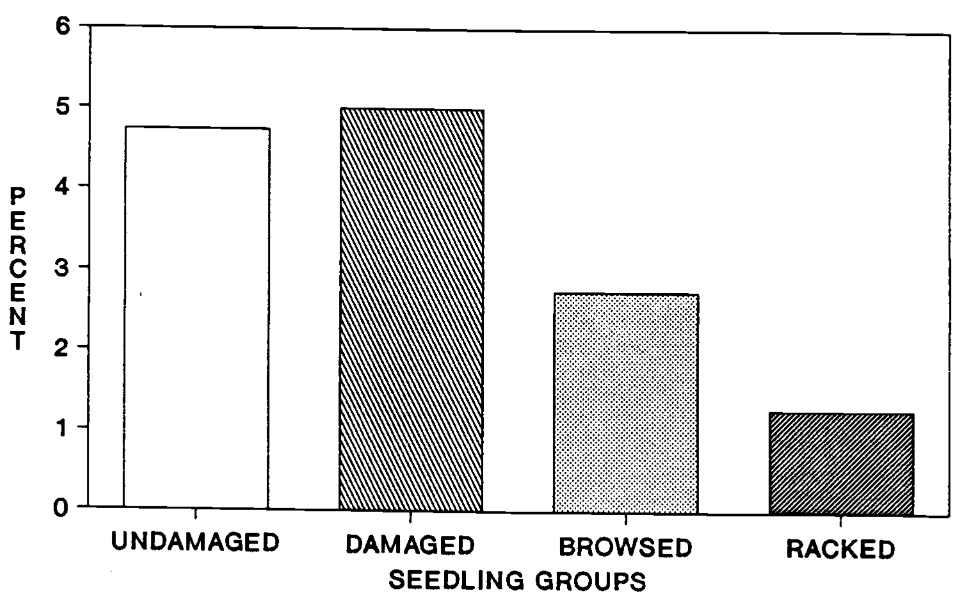

Figure 11: Fourth year seedling mortality rates in the weeded plots. The figure shows the percentage of each seedling group which died in the third and fourth years of the study.

DISCUSSION

Animal damage to western hemlock appears to be less of a deterrent for growth than the pressure of vegetative competition. This study showed that in most situations the impact of competition was greater than the impact of animal damage, and that all types of animal damage except clipping, did not compound losses from vegetation competition. The figures illustrate that the growth of all hemlock seedlings was inversely related to vegetative competition, measured as overtopping cover by salmonberry or alder. Undamaged hemlock overtopped by 30-40% salmonberry were 100cm shorter in height by the fourth year, and had 300cm^3 less volume, than seedlings with no overtopping, a difference of 40 percent. Seedlings overtopped by 20% alder cover were 50cm shorter in total height than those with no overtopping, after four years of growth, and 200cm^3 was lost in volume. These figures illustrate the effects of vegetative competition.

Vegetative competition has been recognized as a major influence on conifer growth (Cole and Newton, 1987; Howard and Newton, 1984; Wagner et.al.,1989; Chan, 1984; Stewart, 1978; Cole and Newton, 1990). Howard and Newton (1984) reported that Douglas-fir seedlings overtopped for seven years exhibited significantly less growth than seedlings influenced by encroaching vegetation. In their study, the vegetation in year five was found to be a better predictor of the growth in year seven than the vegetation in year seven. This was referred to as an "environmental memory effect". In the present study, overtopping vegetation in the fourth year was found to be a better predictor than encroaching vegetation for the growth of the four-year-old seedlings. In the weeded plots overtopping by alder in the third year was a better predictor of seedling growth than fourth year overtopping, this seems to support the idea of an "environmental memory effect". The surrounding vegetation clearly has a lasting effect on future growth of hemlock seedlings, especially if it overtops the conifer.

The distribution of damaged seedlings was generally as we expected. The greatest number of browsed seedlings were found in areas where vegetative competition was low to moderate. It has been documented that deer tend to avoid slashy areas (Crouch, 1974; Grisez, 1960). The occurrence of browsing damage showed an obvious relationship to encroaching salmonberry cover, with 75% of all browsing occurring in areas of 10% or less salmonberry cover. The racking damage occurred almost exclusively on the weeded plots and at wider spacings, which indicates the preference of big game for the open areas while polishing antlers. The fact that all racking was found at wide spacing complicates the relationship between damage and growth. The extra space resulted in reduced vegetative competition and therefore had a positive effect on growth, which was not overcome by the presence of damage. To some extent this was also true for browsed seedlings.

The lack of lagomorph clipping in the weeded plots was understandable considering the habits of lagomorphs. Snowshoe hare and brush rabbit both require dense vegetative cover to avoid predation, and have relatively small home ranges, (less than 0.5 kilometers radius (Evans, 1981)). They appeared to nest exclusively in areas with dense shrub cover (such as the unweeded plots) hence clipping damage was found almost solely on the unweeded plots, even though there were weeded plots within 100m of where the clipping damage was concentrated. Newton (1978) reported that clipping of hemlock by rabbits and mountain beaver occurred only in brushy areas (31% of seedlings in brush clipped). Similar findings were reported by Allen (1969) on Douglas-fir seedlings growing in salmonberry. Allen (1969) found that rodent clipping showed a marked increase as salmonberry developed. He reported the damage observed on Douglas-fir seedlings planted in 2-year-old salmonberry (17% of the seedlings were clipped) and 8-year-old salmonberry (98% of the seedlings experienced clipping damage). Although the majority of clipping in the present study occurred in areas of thirty percent and greater salmonberry cover, there were still a fair number of clipped seedlings in areas of reduced salmonberry cover, within the unweeded plots. Hartwell and Johnson (1983) found that hare clipping was most likely to occur in areas with dense vegetation, yet some clipping was noted in open areas near dense vegetation. They concluded that the animals may reside in the dense areas and feed in both areas. Lagomorph damage occurred throughout the entire range of salmonberry cover in the present study; this indicates that the mosaic of open and brushy habitat within the unweeded plots was on a scale entirely within the use-range of animals whose primary cover was dense brush.

The most important influence on hemlock seedling growth was vegetative competition. The majority of the non-lethal damage observed during the study did not significantly reduce the growth of hemlock seedlings in the first four years, with the exception of clipping damage. The growth potential of hemlock seedlings was demonstrated by the undamaged seedlings. Due to the log transformations used in the analyses, the potential growth of hemlock in areas of zero to moderate overtopping was conservatively depicted. This was partly due to the nature of log transformations and how the data were portrayed in the log form. Comparing overall means of the undamaged hemlock groups in the weeded plots and in the unweeded plots, it appears that on the average the weeded hemlock are 75% larger in terms of volume, after four years of growth. Yet after analyzing the data through log transformations and backtransforming the data, the curves of the regression lines depict the weeded hemlock as only 36% larger in total volume than the unweeded hemlock. The reason for this discrepancy is due to both the use of log transformations and the regression models, and their inherent weaknesses in determination of intercepts. The regression models are general approximations and show trends in the population.

An effort was made to simplify the regression equations by using only two independent variables, unfortunately there was a good deal of variation within the population which was unexplained. For example in the weeded plots zero percent overtopping of salmonberry does not mean zero competition. In areas where there was no salmonberry overtopping, it was possible to have overtopping or encroaching competition by other shrubs or herbs. The total volume of undamaged hemlock in the fourth year at 0% salmonberry cover ranged from $2cm^3$ to $2861cm^3$, with a mean of $211cm^3$. In the case of the weeded plots, at zero percent overtopping by alder there was a large group of hemlock seedlings from the plots without the alder component, which may have had overtopping or encroaching competition from other hemlock or Douglas-fir seedlings. Although regression analysis found that overtopping by alder explained the greatest amount of variation in growth for hemlock in weeded plots, there was still a large amount of unexplained variation. Undamaged hemlock volume in the fourth year at 0% alder overtopping ranged from $2cm^3$ to $6872cm^3$, with a mean at $872cm^3$. Although there is a great deal of variation in seedling growth, because of the large number of observations the means are well defined. It is extremely important to recognize the limitations of the model, since it does not characterize all sources of variation. In addition to the variation in overtopping, there were other very important variables associated with hemlock growth which were not considered in this study. Those include soil nutrients, soil moisture, genetics, microclimate, nitrogen fixation, and other environmental parameters.

The browsed and undamaged seedling groups in both weeded and unweeded treatments exhibited similar growth reductions throughout a range of vegetative competition. In the presence of salmonberry or alder competition and a moderate amount of browsing pressure, the growth of browsed hemlock seedlings was comparable to that of undamaged seedlings. Gourley et.al. (1991) found that competing vegetation was a greater inhibiter of Douglas-fir seedling growth than moderate levels of deer browsing. Gourley et. al. (1991) found that conifer growth was enhanced more by weeding, and thereby reducing competition from surrounding vegetation, than by the use of physical devices or chemicals to protect the seedlings against browsing. This thesis suggests that hemlock follows a pattern similar to that of Douglas-fir.

There are several factors which may explain the recovery of hemlock seedlings from browsing damage. The hemlock growth habit, in terms of leader and bud growth, may play a role in the resilient nature of hemlock. The leader of a hemlock grows much differently from that of most other conifers; a hemlock leader droops, and in many case there is little distinction between leaders and dominant laterals. Another important aspect of hemlock growth is the large number of lateral buds throughout the length of its terminal. A hemlock seedling is well adapted to recover from the loss of a leader (Hibbs, 1981). Due to the large number of lateral buds and the drooping leader of a hemlock, a lateral can take over from wherever truncation has occurred and become dominant with little net growth loss, unless late in the growing season. The loss of the terminal leader is not as traumatic an event for a hemlock seedling as it can be for a Douglas-fir. Also, the timing of damage may play a role in the quick recovery of hemlock from browsing. The majority of browsing in this study occurred in the winter months, thus the hemlock seedlings were able to recover the loss of growth. Whereas browsing damage on Douglas-fir generally takes place in the spring and summer during shoot elongation (Hartwell and Johnson, 1983; Crouch, 1968), therefore Douglas-fir does not have the same opportunity to recover the growth loss as hemlock seedlings. In addition to the hemlock physiology itself, it should be noted that the level of browsing damage on all plots was low to moderate. The resident population of deer at all study sites was considered average (3.1 deer/mile; Hostick, pers. comm. 1991), this would explain the lack of severe browsing pressure. Browsing by deer has been reported as a minor problem for western hemlock (Emmingham et. al.,1987; Evans, 1976); whereas clipping is considerably more damaging to hemlock seedlings (Evans,1976).

The growth of hemlock seedlings clipped by lagomorphs was much less than the growth of all other groups of hemlock seedlings growing under similar vegetative competition. Although clipped and undamaged seedling groups were both negatively related to vegetative competition, the clipped seedlings were affected more severely. Anderson (1987) found that three year old Douglas-fir seedlings experienced a 25% reduction in height growth after hare clipping. The present study found that the total height of clipped hemlock seedlings was 45% shorter than the total height of undamaged seedlings, the height growth was 42% less, and volume was 27% less in the fourth year of growth. Clipping damage was the most detrimental damage observed in this study. Currently, the clipped seedlings are 2 years behind the undamaged and browsed seedlings in terms of size, and are in a very inferior competitive position. Severe vegetative competition will probably keep the seedlings in a zone vulnerable to further animal damage; additional animal damage would make the seedlings more sensitive to competition, in an increasing spiral most likely ending in additional mortality. Since the combination of clipping and vegetative competition was responsible for killing almost 50% of the clipped seedlings, any future damage or competition may very likely be responsible for the mortality of all clipped seedlings.

It was surprising to find that the growth of racked seedlings was statistically equivalent to that of undamaged seedlings. This may be partly due to the location of racked seedlings. The majority of racked seedlings occurred on the outer edges of the weeded plots. These seedlings had the added benefit of little vegetative competition, and subsequently were large bushy seedlings. The healthier seedlings seemed to have been chosen by the big game. It should be noted that the sample of racked seedlings was very small as compared to the undamaged.

The growth of girdled seedlings was statistically comparable to that of undamaged seedlings. The average height of girdled seedlings was 19cm taller than the undamaged seedlings. Although these differences are not statically different, it is an interesting trend. Reasons for these differences are not entirely clear. Perhaps the effects of the girdling damage had been expressed by the fourth year. Most of the girdling occurred in the third year. It should also be noted that seedlings chosen to be girdled were large healthy seedlings prior to the damage.

Mortality data for the third and fourth years were used to show general trends in seedling mortality. The animal damage which was most detrimental to young seedlings was lagomorph clipping, with a 45% mortality rate. The other forms of damage observed in this study, browsing, girdling, and racking were associated with mortality rates lower than those for undamaged seedlings. Mortality rates were higher in the unweeded plots than in the weeded plots. This would suggest that in addition to reducing the growth of hemlock seedlings, vegetation competition can determine to seedling survivorship.

The vigor of coastal vegetation provided a rigorous test of western hemlocks' shade tolerance. It was suggested earlier that the attributes of western hemlock, namely its high shade tolerance, may allow it to succeed in habitats where Douglas-fir had failed. The higher mortality rates and decreased growth in the unweeded plots versus the weeded plots indicated that western hemlock is not entirely tolerant of overtopping vegetation. To determine the extent of hemlocks' tolerance it would be necessary to follow the growth of the hemlock seedlings for a number of years. Although hemlock appears to be very sensitive to lagomorph clipping, the effects of deer and elk browsing and racking are negligible. Hemlock may be more tolerant than other conifer species of certain types of animal damage, consequently hemlock may be the species of choice in coastal habitats where animals play a major role in shaping the vegetative environment. Further studies would be needed to determine the tolerance of hemlock to animal damage in comparison to other conifer species.

CONCLUSIONS

As increased pressure is placed upon managers to improve reforestation, especially in efforts to reclaim brushfields, understanding seedlings' interaction with their surroundings is of utmost importance. To fully capitalize on the improvements made in nurseries toward more vigorous planting stock, obstacles within the environment in which the seedlings are planted must be considered. Managers need to determine the expected levels of growth a plantation should be capable of and take steps to see these expectations are met. To maximize seedling growth, competing vegetation must be kept from severely overtopping western hemlock. By reducing competing vegetation, managers will also reduce the impacts of damage from certain animals, and also improve the seedlings ability to overcome damage. Although the importance of improved larger seedling stock should not be overlooked, the environment in which the seedlings are placed will determine success or failure. This study dealt with two of the obstacles which seedlings encounter in their immediate environment, vegetative competition and animal damage. The study found that although larger seedlings can grow faster than small seedlings, efforts to use vigorous seedling stock will be wasted if the seedlings are overtopped by salmonberry within the first few years of growth and subsequently vulnerable to lagomorph damage.

Maximum growth potential of hemlock occurs where there is negligible competition. If competition is reduced for several years, negative impacts of most animals will also be reduced. If managers allow shrubs such as salmonberry and alder to grow unchecked, the seedlings will experience reduced growth and/or mortality due to vigorous competition and seedlings will be most vulnerable to animals whose preferred habitat is dense shrub cover. Severe vegetative competition results in smaller seedlings, these seedlings are more vulnerable to clipping damage from lagomorphs. The longer the seedlings are suppressed by surrounding vegetation, the greater the chance of clipping damage from small animals, and the more serious the impact. Specific findings of the study are listed.

1. Reductions in the growth of surviving western hemlock seedlings during the first four years of seedling establishment are associated with severe vegetative competition and clipping by lagomorphs.
2. Moderate browsing does not significantly reduce the growth of western hemlock seedlings in the first four years of growth.
3. Racking damage to hemlock seedlings by deer and elk does not appear to cause significant reductions in growth.
4. Browsing and racking damage to hemlock seedlings was more abundant in areas where shrubs were absent or sparse.

5. Western hemlock seedlings that were partially girdled by lagomorphs exhibited height and volume comparable to that of undamaged seedlings.

6. Clipping damage on western hemlock seedlings by lagomorphs produced significant growth reductions within the first four years of seedling establishment.

7. Lagomorph clipping or girdling occurred only in areas within or near dense salmonberry cover.

8. Clipping damage increased seedling susceptibility to surrounding vegetative competition.

9. Mortality rates were higher in the unweeded plots than in the weeded plots, and lagomorph damage contributed to this difference.

10. Lagomorph clipping was the only animal damage which produced a higher mortality rate than the rate experienced by undamaged seedlings.

Direct application of these findings in land management involves the recognition of competition as the primary cause of reduced conifer growth. This study indicates that reforestation efforts should concentrate upon reducing vegetative competition, and in doing so will minimize animal damage impacts. For the types of animal damage analyzed in this study, direct animal control is not suggested.

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