AN ABSTRACT OF THE THESIS OF

Brian Edward Roth for the degree of Master of Science in Forest Science presented on April 29, 1994.

Title: Interaction of Seed Source, Competition and Fertility on Planted Douglas-fir (*Pseudotstuga menziesii* [Mirb.] Franco).

Signature redacted for privacy.

Abstract Approved: ______________________

Michael Newton

The main objective of this study was to evaluate the interaction between herbaceous competition, fertility, and seed source on Douglas-fir survival and growth. A secondary objective was to evaluate the effect of these various factors on the production of lammas shoots and the selectivity of deer browse. Finally, the role of lammas growth in the recovery from deer browsing was examined. Lammas growth, commonly referred to as second flushing, is the precocious flush of growth from the newly formed terminal bud in mid-summer.

Weed control was the dominant factor influencing seedling survival and growth, accounting for 49 percent of the explained variation in seedling volume after two years. Weed control significantly conserved soil moisture and resulted in an increased number of seedlings exhibiting a second flush of growth. Fertilization through the addition of nitrogen had no effect when used in conjunction with weed control and had a negative effect when used without the benefit of weed control. Seedlings from the seed orchard source were significantly

larger in diameter than the wild type source after two growing seasons, but were of similar height.

Of the seedlings which were browsed twice by deer those with the benefit of weed control had over twice the stem volume of those without the benefit of weed control. Lammas growth contributed to the stem volume response to weed control by additional height growth, thus allowing the seedlings to recover from and escape the effects of deer browse.

Interaction of Seed Source, Competition and Fertility on Planted Douglas-fir (*Pseudotstuga menziesii* [Mirb.] Franco).

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Finally Professor Michael Newton deserves credit. Mike's vision and trust brought me to Oregon, and his unending encouragement and support made my experience here truly memorable. Mike allowed me the freedom to choose this thesis topic, design the study, and see it to completion on my own, which resulted in a greater degree of learning than otherwise would have been possible. Thank you for getting me started Mike.

A person may plan as much as he wants to, but nothing of consequence is likely to come of it until the magician *circumstance* steps in and takes the matter off his hands... A circumstance that will coerce one man will have no effect upon a man of a different temperament.

Mark Twain

What is man and other essays

Harper & Brothers, New York, 1906

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INTRODUCTION

Douglas-fir growth and survival are influenced by associated vegetation which deplete resources such as water, nutrients, and light. Availability of these resources may be influenced by controlling competing vegetation, fertilization, and selection of seed sources which will effectively utilize these available resources. These factors can be expected to interact and have varying levels of effect when applied in combination. Numerous studies have examined the effects of individual treatments, while some have studied two in combination. Only one study has examined effects of the three treatments in the same study. The studies presented in this thesis have the general goal of evaluating the relative contributions and interactions of these three treatments on planted Douglas-fir.

Obviously a study of this scope is limitless in the number of different formulations of these three treatments. Weed control, for example, can be accomplished in many ways, each having its own level of efficacy in a given situation. The amount and form of the associated vegetation has varying levels of impact on young Douglas-fir growth, with overtopping shrubs affecting survival and growth in a different manner than herbaceous competition. These relationships are more crucial than is the methodology for shaping them. Seedling fertilization consists of three main components, which can all be manipulated independently of one another: type of element(s) supplied, the form (source) of the nutrient(s), and the method of application. Seed source can be chosen from a range of provenances (elevation, latitude) and races representing various levels of genetic improvement in growth and form. Seed lots from these sources can be out-planted in either mixed or pure form.

The treatments chosen for this study represent those which are commonly used in intensive forest management in western Oregon today. This study was limited in scope to newly planted units with exclusively herbaceous cover. Complete weed control each season was achieved through a single application of Velpar L® at an operational rate, a chemical registered for forestry and widely used. Additional spot treatments were necessary only to reduce variation in the efficacy of the first treatment. Nitrogen in the form of urea was chosen as the element to be tested in the fertilization treatment. This was broadcast twice, once in the spring of each of the two years, at a rate of 100 lbs/ac. of nitrogen. A seed orchard source was chosen to test against a wild type source from the same seed zone. This seed orchard source was developed by the Burnt Woods Tree Improvement Cooperative at the J.E. Schroeder seed orchard, near St. Paul, Oregon and has been utilized operationally since the late 1980's by members of this cooperative. In addition to these treatments, the study was replicated across three sites representing a range of productivity in the central Oregon Coast Range.

The primary purpose of this study was to identify quantitatively the effects and interactions of these treatments on survival, growth and potential tree form, and to identify their relative importance. The resulting range of weed control and nutrient availability also provided an opportunity to examine the growth responses over a wide range of competitive factors.

A secondary objective was to examine the occurrence of lammas growth as affected by the treatments. Browsing by local populations of deer provided the opportunity to study the selectivity of the deer to the various treatments and individual seedlings. In addition, the role of lammas growth in the recovery of the seedlings from deer browse was examined.

CHAPTER 1: Survival and Growth of Douglas-fir Relating to Weeding, Fertilization and Seed Source.

Introduction

Douglas-fir survival and growth in western Oregon is limited by the competitive effects of associated vegetation (Wagner 1989; Zedaker 1981). Competition for limited site resources such as water, nutrients, and light reduces the survival and growth of seedlings, and can be compounded by the pressures of deer browse (Hartwell 1973). To increase seedling growth and survival, silviculturists can manipulate the availability of site resources through vegetation control and fertilization. These treatments interact and have varying levels of efficacy when applied in combination. As well, seedling response is related to the planting stock selected (Newton *et al.* 1993). This paper describes experiments which evaluate these factors interactively on several sites in the Oregon Coast Range.

Numerous studies have examined the effects of individual treatments, while some have studied two in combination. Only one has examined effects of the three treatments in the same study. White and Newton (1990) and White *et al.* (1986), determined a positive interaction of nitrogen and simazine, and an additive effect of nitrogen and hexazinone respectively, on the efficacy of weed control, while, Blackmore and Corns (1979), Waring (1972), and Squire (1977) demonstrated a positive interaction of weed control and fertilization on conifer growth. Smith *et al.* (1966a) determined an almost equal positive influence of seedbed fertilization and seed source on juvenile growth and survival of Douglas-fir but did not examine the interaction between the two. Bell *et al.* (1979) examined a family X fertilizer interaction in one-year-old Douglas-fir in which some families performed well at one level of nitrogen while others performed well at all levels. Jahromi *et al.* (1976) showed a similar family X fertilizer interaction in slash pine. Shiver and Rheney (1992) found a positive interaction between the level of genetic improvement and vegetation control in southern pines, while Duba *et al.* (1985) determined that the expression of genetic potential in loblolly pine was dependent upon the presence or absence of competition. Joly *et al.* (1989) found little evidence for an irrigation X seed source interaction between mesic and dry site sources of Coastal Douglas-fir. Finally, Brown (1970) demonstrated a three way interaction in *Pinus sylvestris* L. seedlings between seed provenance, fertility and moisture level, with the latter contributing the most to growth.

The primary objective of this study was to quantify the effects and relative importance of weed control, nitrogen fertilization, and seed source, including any interactions, on the survival and growth of Douglas-fir outplants over a wide range of competitive factors and site conditions. Specific objectives were:

1. Test for differences in Douglas-fir survival, growth and vigor on plots with complete weed control compared to those without weed control.
2. Test for differences in Douglas-fir survival, growth and vigor on plots with nitrogen addition compared to those without nitrogen addition.
3. Test for differences in Douglas-fir survival, growth and vigor on plots containing seedlings from a seed orchard source compared to plots with seedlings from a woods run source.
4. Determine whether the response due to the influence of one factor influences the response to another (i.e. interaction).
5. Determine the relationships between the survival and growth of Douglas-fir seedlings and various competition indices, moisture stress, foliar nutrient composition and initial seedling size.

Site description

The study was undertaken in the central Oregon Coast Range west of Corvallis, Oregon in Benton county (44°N, 123°W). The three study sites represent much of the range of Douglas-fir production in this area: (*i*) a relatively droughty Willamette Valley site on abandoned state nursery beds in Oregon State University's McDonald Research Forest, (*ii*) a moderately productive forest site in the Willamette Valley foothills of Oregon State University's Paul M. Dunn Research Forest, and (*iii*) a highly productive site in the mid-Coast Range on Starker Forests, Inc. property, near the community of Summit. Table 1.1 provides a general description of these sites. The Dunn Forest and Summit sites were on newly harvested units that had recently supported stands of Douglas-fir. The old state nursery beds were fully occupied with a combination of exotic and native grasses and herbs, plus patches of blackberries (*Rubus procerus* Muell.). Herbs, grasses and ferns were the main form of associated vegetation on all the sites (Table 1.2). The climate of the study

Table 1.1 General site description.

Site	Elevation	Annual Precipitation (Johnsgard 1963)	% Soil N	% Soil P	Douglas-fir SI_{100} (U.S.D.A.1975)
McDonald Forest	120 m	945 mm	.137	.095	42 m
Dunn Forest	185 m	1270 mm	.202	.083	48 m
Summit	365 m	1905 mm	.290	.111	55 m

area is characterized by warm winters with heavy precipitation and warm dry summers during which the moisture deficit often exceeds 325 mm on the McDonald and Dunn sites (Johnsgard 1963). The soils are all silty clay loams but vary among the sites by series. The McDonald Forest soil is of the Bellpine series, derived from Spencer sandstone, and covered with 20 cm of offsite loam. The Dunn Forest soil is of the Price-Ritner complex, derived from Siletz River basalts. The Summit soil is associated with the Apt series, derived from Tyee sandstone/siltstone (U.S.D.A. 1975).

Table 1.2 Common plant species associated with the three sites[1].

Common name	Scientific name	Site[2]
Woody species		
Bigleaf maple	*Acer macrophyllum* Pursh	2
Himalaya blackberry	*Rubus procerus* Muell.	1
Salal	*Gaultheria shallon* Pursh	3
Snow-berry	*Symphoricarpos albus* (L.) Blake	3
Ocean spray	*Holodiscus discolor* (Pursh) Maxim	3
Western hazel	*Corylus cornuta* Marsh	2 3
Wild blackberry	*Rubus ursinus* Cham. & Schlecht	2
Herbs		
Bedstraw	*Galium* sp.	2 3
Bull thistle	*Cirsium vulgare* (Savi) Tenore	1 2 3
Canada thistle	*Cirsium arvense* (L.) Scop.	1 2 3
Clover	*Trifolium* sp.	2
Common daisy	*Erigeron* sp.	2
Dove's foot geranium	*Geranium molle* L.	3
False spikenard	*Smilacina racemosa* (L.) Desf.	3
Woodland groundsel	*Senecio sylvaticus* L.	3
Groundsel	*Senecio vulgaris* L.	2
Lotus	*Lotus* sp.	3
Pathfinder	*Adenocaulon bicolor* Hook.	3
Purple iris	*Iris tenax* Dougl.	2 3
Sheperd's purse	*Capsella bursa-pastoris* (L.) Moench	2
Sow-thistle	*Sonchus oleraceus* L.	2
Star-flower	*Trientalis latifolia* Hook.	3
Sweet colt's foot	*Petasites frigidus* (L.) Fries	2
Tansy ragwort	*Senecio jacobaea* L.	3
Vari-leaved collomia	*Collomia heterophylla* Hook.	3
Wild carrot	*Daucus carota* L.	1 2
Wild ginger	*Asarum caudatum* Lindl.	3
Wild pea	*Vicia americana* Muhl.	2
Wind-flower	*Anemone* sp.	3
Wood nemophila	*Nemophila parviflora* Dougl.	2
Yarrow	*Achillea millefolium* L.	1
Ferns		
Sword-fern	*Polystichum munitum* (Kaulf.) Presl	2 3
Western bracken	*Pteridium aquilinum* (L.) Kuhn	3
Grasses		
Reed's canary grass	*Phalaris arundinacen* L.	1
Ripgut grass	*Bromus rigidus* Roth	1
Velvet grass	*Holcus lanatus* L.	1 2 3

[1] Nomenclature after Gilkey and Dennis (1980), Hitchcock (1971).
[2] Site: 1 = McDonald Forest, 2 = Dunn Forest, 3 = Summit.

Materials and methods

Experimental design

The experimental design was a 2^3 factorial, randomized complete block, with three replicates, split across three sites for a total of 72 plots. The factorial design created eight treatments which were randomly assigned to 3.6 m × 11.0 m plots within blocks, with a minimum of a two-metre untreated buffer between adjacent plots (Figure 1.1). Blocking was achieved by grouping the plots according to position on slope, with each having eight plots in an approximate two by four arrangement. On steep slopes where there was likely to be an environmental gradient the blocks were oriented perpendicular to the slope and parallel to each other. This was done in order to minimize plot to plot site variation within each block while maximizing variation among blocks (Steel and Torrie, 1980).

Figure 1.1 Overview of the McDonald Forest site showing weeded plot in foreground.

The three factors in the experiment were herbaceous competition level, nitrogen fertility level, and seed source. Each factor had two levels: complete weed control W_1 vs. none W_0, nitrogen fertilization F_1 vs. none F_0, and seed orchard seed source S_1 vs. woods-run seed source S_0. The experimental unit was the mean of 28 seedlings on each plot.

Plant material

Two seed sources of Douglas-fir plug-1 transplants were used. A genetically improved seed orchard source was developed by the Burnt Woods Tree Improvement Cooperative at the J.E. Schroeder seed orchard, near St. Paul, Oregon. The seed orchard seed was derived from open pollinated crosses between progeny of 161 superior trees chosen from across the same seed zone (252) as the woods run source. A more detailed explanation of the "progressive" tree improvement program, of which the Burnt Woods Tree Improvement Cooperative is a member, is outlined by Silen and Wheat (1979). The seed orchard stock was grown at the IFA nursery at Toledo, Washington as plug-1 transplants. The wild type seedlings were grown from a general collection of seed from within the local seed zone (252) and does not represent any level of genetic selection. Unfortunately, nursery stock from this seed source was not available from the IFA nursery in Toledo and plug-1 transplant stock of this source was obtained at the D.L. Phipps State Nursery, near Elkton, Oregon. Hence, there was some confounding between genetics and nursery regime. However, the seedlings were of approximately the same size ranges.

Treatments

All seedlings were planted within one week of each other in February, 1992 at a 0.5 m $\times$ 1.0 m spacing. Each block was completely planted before starting a new one as were the three sites. Complete weed control was accomplished by an application of 1.37 kg/ha of hexazinone (Velpar L®) herbicide using a hand-held 3.6 m boom, powered by a pressurized backpack sprayer at a rate of 92 ℓ/ha. Re-invading herbs were controlled where necessary later, by directed spot applications. The nitrogen treatment was established through the addition of 220 kg/ha of urea prill (46-0-0) broadcast with a hand-held rotary dispenser in a 3.6 m swath. Fertilizer and weeding treatments were performed on March 18th, 1992; fertilizer and maintenance weeding were repeated on March 25, 1993. On each site, an electrically charged 18 gauge wire, suspended one metre above the ground by fiberglass poles, was systematically wound between all plots in an attempt to discourage deer browsing. Each wire was electrified during May and June of each year with a 12 volt car battery, regulated by a Jolt electric fence controller (model 4000B, IAAB U.S.A., Inc. Bellveue, WA). Vegetation under the wire was controlled with a single directed application of glyphosate in the spring of each year to prevent short circuiting. Care was taken to avoid treating unweeded plot vegetation in this process.

Measurements

Douglas-fir and cover measurements

Seedling size was measured shortly after planting (Spring 1992), and at the end of each growing season (Fall 1992, 1993). Individual tree measurements were made on seedling height (nearest centimeter), diameter at 15 centimeters (nearest millimeter), and overall vigor. Vigor, as a qualitative measure, was quantified on a five point scale (1 = Vigorous, 5 = Dead) based on seedling color and general appearance. Concurrent measurements taken in the fall included the occurrence of deer browse, lammas growth, or herbicide damage. Volume, diameter and height increment were calculated from yearly differences in seedling dimensions. From the height and diameter measurements (@ 15 cm), stem volume was estimated using the formula for a cone:

$$\text{Volume} = \pi \times d^2 \times h/12$$

Where d = diameter at 15 cm
h = total height

Percent cover by herbaceous forbs and grasses was estimated on a half-meter radius around each seedling in the fall of 1992 and as a percentage of total plot area in the fall of 1993 due to the relative homogeneity of the vegetation within the plots. Percent overtopping was based on the cone occlusion method as described by Howard and Newton (1984).

Xylem water potential and soil moisture

Predawn and midday xylem water potentials were estimated from current year shoots of three randomly selected seedlings per plot for a total of 432 measurements per year. These measurements were made in mid-July 1992, and mid-August 1993, using a Scholander pressure chamber (Waring and Cleary 1967; Ritchie and Hinckley 1975). These dates were chosen for contrasting water regimes in weeded vs unweeded treatments. Soil moisture content was estimated gravimetrically at the time of the xylem water potential measurements in mid-July of 1992. Soil moisture measurements were not taken in 1993 due to an abnormally wet summer. A composite of two soil samples were collected from the seedling rooting depth (0-30cm) on each plot. The samples were placed in bulk density cans, weighed, dried at 70°C for 72 h, and then reweighed. The difference in weights was used to calculate the percent soil moisture.

Nutrient analysis

A baseline analysis of mineral soil nitrogen and phosphorous was done on each site at the time of planting in February of 1992. A composite of six subsamples from the top 30 cm of mineral soil was bulked per site for a total of three samples. Foliage samples were taken from the current year's growth of an upper whorl lateral, excluding any lammas shoots, on the southeast side of each surviving seedling in October of 1993. These samples were bulked by treatment across blocks on each site for a total of 24 samples. Total N and P were determined by a standard micro-kjeldahl digestion method, with nutrient concentrations calculated on a dry weight basis (Lavender 1970).

Analysis

Diameter response and vigor were transformed using natural logarithms to approximate normality and constant variance. Some additional variables, based on probability, were transformed by the arcsine square root (Sabin and Stafford 1990). Analysis was carried out using plot averages weighted by the number of surviving seedlings in each plot. Differences in response were analyzed with analysis of covariance (ANCOVA) for main and interaction effects according to the following model (Steel and Torrie 1980):

$$Y_{ijklm} = \mu + L_i + B(L)_{ij} + W_k + F_l + WF_{kl} + S_m + WS_{km} + FS_{lm} + WFS_{klm} + LW_{ik} + LF_{il} + LWF_{ikl} + LS_{im} + LWS_{ikm} + LFS_{ilm} + \beta(X_{ijklm} - \chi_{..}) + LWFS_{iklm}$$

where

L = site (i = 1,2,3)
B = block (j = 1,2,3)
B(L) = error a (blocks within sites)
W = weed control (k = 0,1)
F = fertilizer (l = 0,1)
S = seed source (m = 0,1)
$\beta(X_{ijklm} - \chi_{..})$ = covariate denoted by X
and LWFS = error (b).

Site terms were tested against error (a) and all remaining terms tested against error (b). Where a significant covariate was not found, the covariate term was left out of the model. Significant differences between means were determined using Bonferroni's protected Least Significant Difference (LSD) procedure (Milliken and Johnson 1984). Foliar nutrient contents were bulked by treatment across blocks and analyzed using ANOVA with the following model:

$$Y_{ijkl} = \mu + L_i + W_j + F_k + WF_{jk} + S_l + WS_{jl} + FS_{kl} + WFS_{jkl} + LWFS_{iklm}$$

where

L = site (i = 1,2,3)
W = weed control (k = 0,1)
F = fertilizer (l = 0,1)
S = seed source (m = 0,1)
and LWFS = error (a).

All terms in the model were tested against error (a).

Multiple linear regression models were developed, on an individual seedling basis, to relate seedling survival, size, growth and vigor to the various levels of competition, fertility, and initial seedling traits developed by the various treatments. The models explaining the most variance were chosen using the stepwise selection procedure as described by Neter *et al.* (1989). Several seedlings on two sites showed signs of herbicide damage in the second season and were eliminated from the analysis. As a result second year survival is only reported for the McDonald site.

Results

Weed control was the dominant factor influencing every variable measured for survival, growth, vigor, and xylem water potential. To demonstrate the relative effect of the weed control treatment over the other treatments, a table of means for the main effects is presented in Table 1.4.

Weed Control

The results show an overwhelming amount of variation between weed control treatments, with a highly significant difference ($p<0.001$) for survival, growth, vigor and xylem water potentials, and with differences between sites. By the second year, plots with the benefit of weed control had significantly higher survival and growth rates, and lower predawn and midday xylem water potentials. Weed control resulted in the greatest absolute volume increment increases on the best site (Figure 1.2), but the greatest improvement in survival on the poorest site (Table 1.3). Weeding alone accounted for 49 percent of all explained variation in seedling volume at age two, and a similar percentage of variation in other growth parameters.

Table 1.3 First year survival by site and weed control [3].

	Weed Control	
	Complete	**None**
McDonald Forest	96.8 a	58.7 b
Dunn Forest	95.3 a	60.9 b
Summit	96.6 a	92.3 a

[3] Means with the same letter are not significantly different at the 95% confidence level using Bonferroni's adjusted LSD.

Controlling the associated vegetation significantly conserved soil moisture ($p < .0001$).

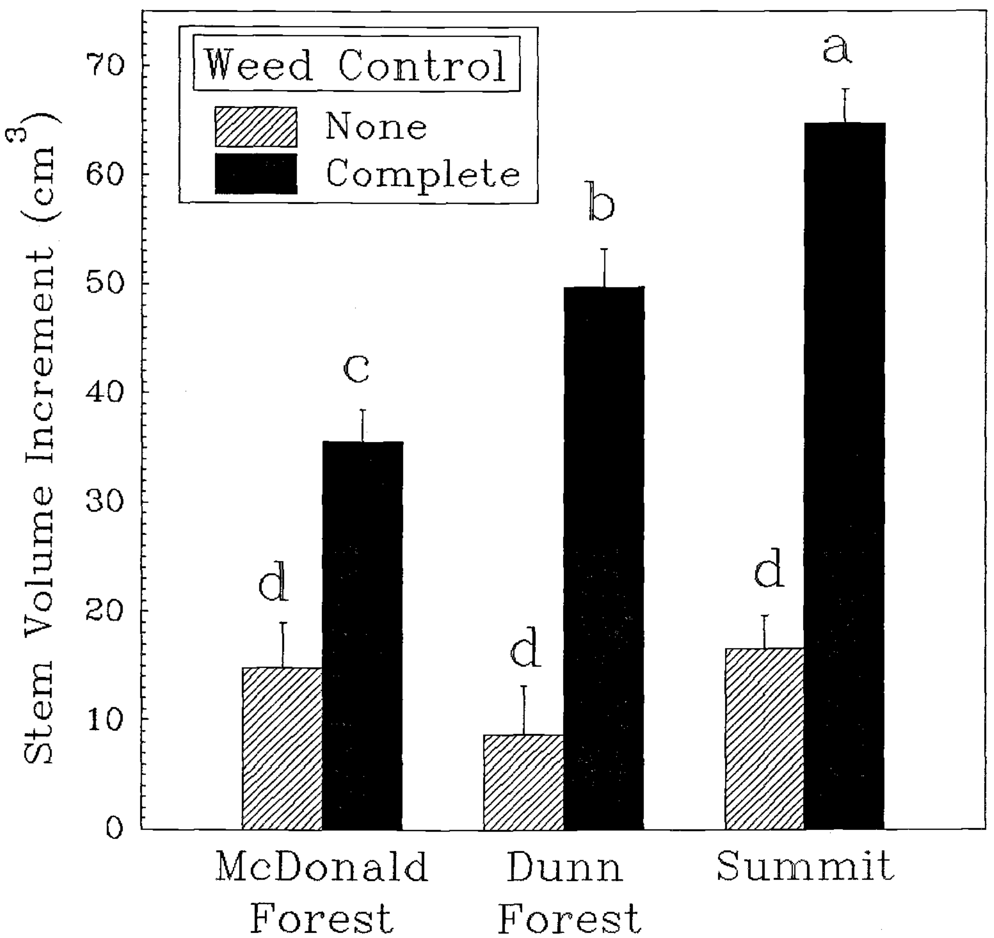
Table 1.4 Table of means for 1993 data by main effect.

	Weed Control			Fertilization			Seed Source		
	W_1	W_0	% Diff	F_1	F_0	% Diff	S_1	S_0	% Diff
Height† (cm)	82.5	68.9	16.5 ***	74.1	77.3	-4.1 *	77.0	74.4	3.4
Height Increment (cm)	27.9	16.1	42.2 ***	20.5	23.5	-12.8 *	23.2	20.8	10.4
Diameter (mm)	15.9	10.7	33.2 ***	13.1	13.5	-2.5	14.1	12.5	11.3 ***
Diameter Increment (mm)	7.0	2.7	61.1 ***	4.6	5.1	-9.3	5.1	4.5	11.5 *
Height:Diameter	5.3	6.7	-20.5 ***	6.0	6.0	0.0	5.8	6.1	-5.2 **
Volume‡ (cm^3)	49.5	18.6	62.4 ***	28.7	32.1	-10.6	35.5	25.9	27.4 ***
Volume Increment (mm^3)	50.1	13.4	73.2 ***	30.3	33.2	-8.9	36.6	26.9	26.4 ***

* $p<0.05$, ** $p<0.01$, *** $p<0.001$
† Adjusted for initial seedling height.
‡ Back transformed from the natural log.

Fertilization

Fertilization significantly increased the average foliar nitrogen concentration in both years, but had the effect of reducing predawn xylem water potentials and percentage survival in the first year, especially on unweeded plots. Height and height growth were significantly reduced in the second year, a pattern also most pronounced on weeded plots. Second year



* Bars represent one standard error.
Bars with the same letter are not signifficantly different at the 95% level of confidence using Bonferroni's LSD.

Figure 1.2 Site by weed control interaction for stem volume increment after two growing seasons *.

diameter growth of fertilized seedlings tended to be less than unfertilized seedlings on sites with high soil nitrogen (Figure 1.3).

Phosphorous concentrations were not significantly affected by the fertilization treatment. Fertilization interacted with weed control to reduce first year vigor,

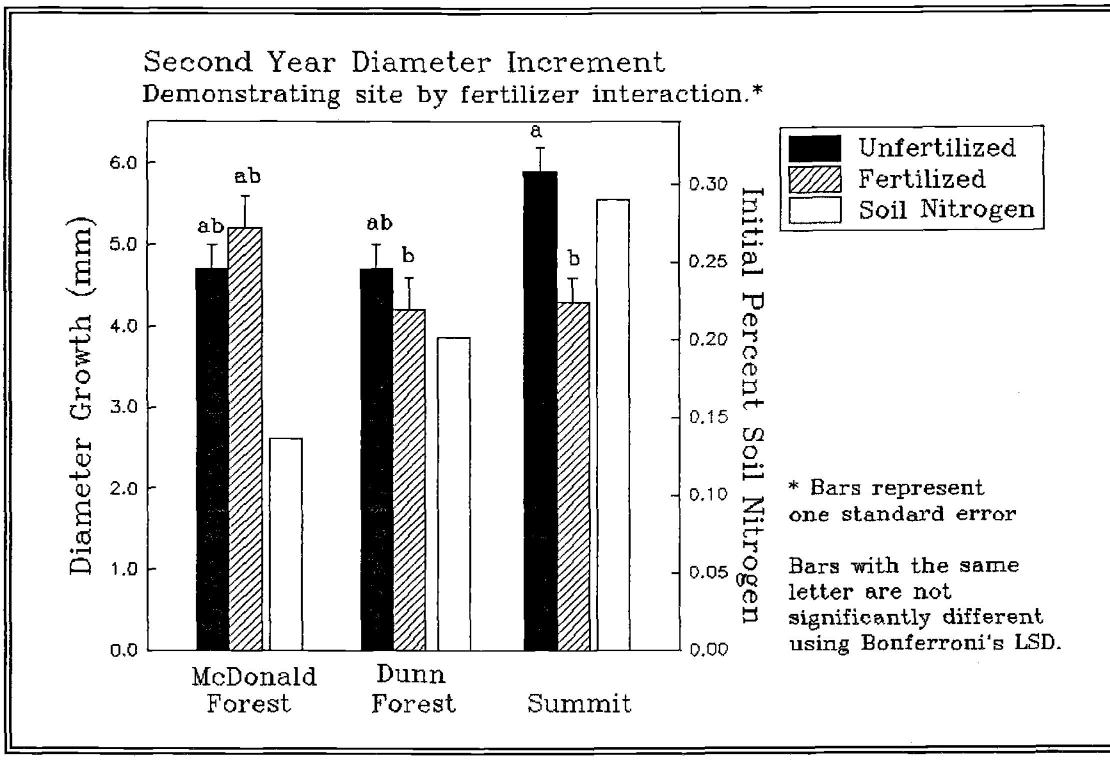


Figure 1.3 Second year diameter increment demonstrating site by fertilizer interaction *.

diameter and volume growth in unweeded fertilized plots. The height to diameter ratio was also significantly higher for the unweeded fertilized seedlings than for the unweeded unfertilized seedlings. The weed control by fertilization interaction was evident where fertilization stimulated herbaceous vegetation, thus reducing first year survival on the unweeded fertilized plots (Figure 1.4). Second year predawn xylem water potentials and vigor were also reduced for all sites in the unweeded fertilized plots.

Seed source

First year seedling diameter and volume were significantly larger for the seed orchard seed source after accounting for initial diameter and volume. By the second year the seed orchard seedlings were slightly, but significantly,

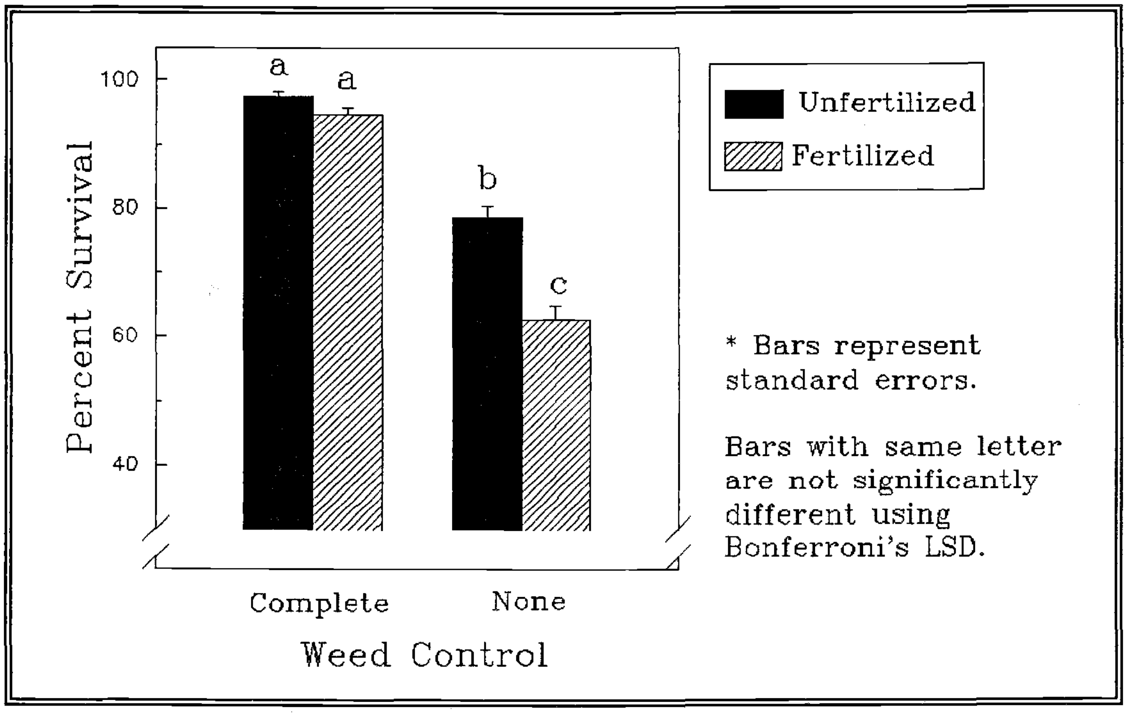


Figure 1.4 First year survival demonstrating the weed control by fertilization interaction *.

larger and growing faster in diameter and volume. Height was not responsive to the seed source. The seed orchard source also had a lower height to diameter ratio than the wild type after accounting for the initial height-to-diameter ratio. Seedlings from the seed orchard source seemed to be more vigorous in general appearance and color. There was no interaction with weed control or fertilization, indicating that the gains from the seed orchard source were additive.

Regression analysis

The response models regressing seedling xylem water potential against estimated cover and overtopping associate increasing seedling stress with increasing levels of herbaceous competition (Table 1.5). The models describing

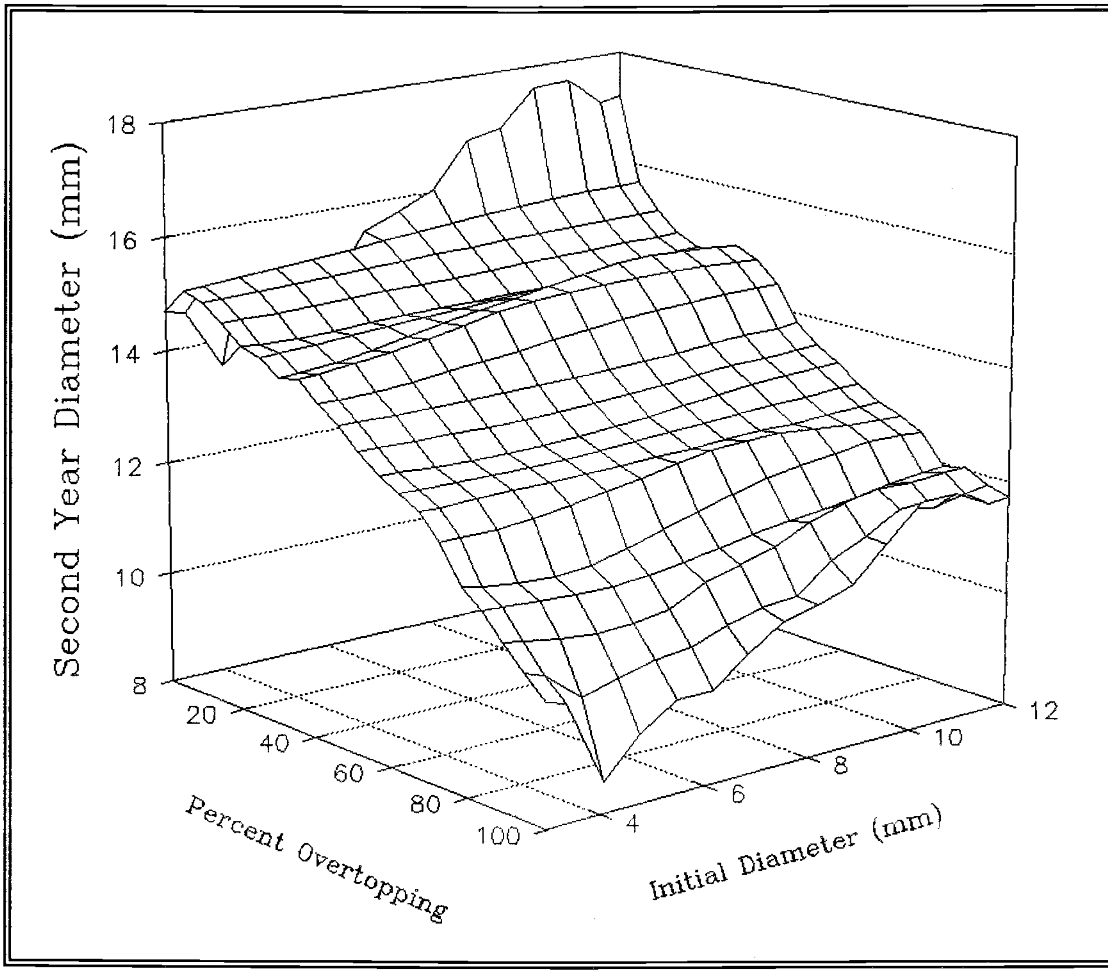


Figure 1.5 Response surface for second year stem diameter vs. percent overtopping and initial diameter.

second year seedling height and diameter support the findings that initial seedling dimensions influence seedling size over time (Table 1.7). Volume was associated with initial seedling diameter, but much more by overtopping vegetation, which was also found to reduce seedling diameter growth while increasing seedling height to diameter ratios. Average predawn moisture stress explained most of the variation for the other growth variables. Second year height was negatively affected by the occurrence of deer browse which occurred in the second year. First year seedling height growth was dependent upon an interaction between browse and lammas growth. This forms the basis for a second paper (Chapter 2).

Table 1.5 Response models for seedling xylem water potential (Ψ = -MPa) after two years.

MODEL (Standard errors in parentheses)	p-value	r^2
Ln(PREDAWN Ψ) = -0.18552(0.00364) - 0.0006(0.00006)OV	0.0001	0.31
MIDDAY Ψ = - 1.9460(0.0898) - 0.0020(0.0004)COV + 0.0366(0.0131)IHD	0.0001	0.15

Table 1.6 Response and independent variables used in regression models.

RESPONSE VARIABLES	INDEPENDENT VARIABLES
HT = Total height (cm). **HGRTH** = Height increment (cm). **DIAM** = Total diameter (mm). **DGRTH** = Diameter increment (mm). **H:D** = Height to diameter ratio. **VOL** = Stem volume (cm^3). **VGRTH** = Volume increment (cm^3). **PREDAWN Ψ** = Predawn xylem water potential (-MPa). **MIDDAY Ψ** = Midday xylem water potential (-MPa).	**COV†** = Percent cover. **OV†** = Percent overtopping. **PRE‡** = Predawn xylem water potential (-MPa). **MOIST§ = Soil moisture.** **BRSE** = Occurrence of browse. **IHT** = Initial height. **IDIAM** = Initial diameter. **IHD** = Initial height:diameter. **IVOL** = Initial volume.

† Second year cover and overtopping was based on a plot average.
‡ Based on a plot average of three random seedlings.
§ First year soil moisture on a plot basis.

Table 1.7 Response models for seedling size and growth after two growing seasons.

MODEL (Standard errors in parentheses)	p-value	r^2
Ln(HT) = 3.985(0.029) + 0.013(0.001)IHT - 0.121(0.011)BRSE + 0.278(0.016)PRE	0.0001	0.41
HGRTH = 39.6(1.1) + 19.4(1.2)PRE	0.0001	0.15
DIAM = 9.431(0.330) - 0.057(0.002)OV + 0.885(0.041)IDIAM	0.0001	0.45
DGRTH = 7.213(0.102) - 0.049(0.002)OV	0.0001	0.35
H:D = 2.730(0.145) + 0.020(0.001)OV + 0.349(0.021)IHD	0.0001	0.44
Ln(VOL+0.5)† = 3.199(0.074) - 1.289(0.050)PRE + 0.189(0.008)IDIAM	0.0001	0.45
Ln(VGRTH+0.5)† = 3.60(0.11) - 1.93(0.08)PRE + 0.14(0.01)IDIAM	0.0001	0.34

† As some values of volume growth were zero, 0.5 was added before the transformation.

Table 1.8 Response models for seedling size and growth after first growing season.

MODEL (Standard errors in parentheses)	p-value	r^2
HT = 12.59(0.55) + 0.91(0.01)IHT - 4.14(0.22)BRSE	0.0001	0.82
HGRTH† = 8.27(0.13) - 4.48(0.18)BRSE	0.0001	0.29
HGRTH‡ = 15.52(1.11) - 9.15(1.16)BRSE	0.0001	0.22
Ln(DIAM) = 1.332(0.016) - 0.107(0.002)IDIAM - 0.002(0.0002)COV	0.0001	0.62
Ln(DGRTH) = -1.875(0.127) + 0.045(0.004)MOIST + 0.153(0.013)IHD	0.0001	0.14
H:D = 2.534(0.137) + 0.009(0.001)COV + 0.585(0.020)IHD	0.0001	0.35
VOL = -4.14(0.57) + 1.08(0.02)IVOL + 0.29(0.02)MOIST	0.0001	0.66
Ln(VGRTH+0.5) = - 0.91(0.13) + 0.017(0.001)IHT + 0.054(0.004)MOIST	0.0001	0.15

† For seedlings without lammas growth.
‡ For seedlings with lammas growth.

Discussion

This experiment applied three silvicultural treatments, weed control, nitrogen fertilization, and seed source, in a factorial design. Weed control (i.e. competing cover) proved to be the dominant factor influencing every component of seedling survival and growth measured. The other factors were of a much lesser importance. This is consistent with other similar factorial experiments in which one factor proves to be dominant over the others (Brand and Janus 1988; Magnussen 1983; Reed *et al.* 1983).

Weed control

Weed control had the effect of reducing the amount of associated vegetation, thereby conserving soil moisture, thus increasing seedling survival and growth rates. This supports the work of Cole and Newton (1986 and 1987), Newton and Preest (1988), Preest (1977), Sands and Nambiar (1984), Nambiar and Zed (1980). Seedling diameter was most sensitive to overtopping vegetation. Seedling height and volume responses were most responsive to predawn xylem water potential (ψ), which was related to weeding. This is supported by Eissenstat and Mitchell (1983) and Chan (1984) who found that Douglas-fir seedling diameter was a sensitive indicator of competition, especially overtopping. Newton and Preest (1988), showed xylem water potential to be related to all seedling growth parameters. Gains in absolute stem volume growth were the greatest on the best sites and where the weeds were controlled. It follows that in order to capture the site potential early in the life of a plantation, vegetation control is necessary. Waring (1972), Brand and Janus (1988) and Sutton (1975) speculated that the positive effect of vegetation control on foliar nitrogen was related to the uptake of nutrients not utilized by the vegetation (i.e. removal of a dominant sink).

Fertilization

Nitrogen fertilization had no effect when used in conjunction with weed control and increased weed density, with a negative effect on seedling survival, vigor and growth when applied without the benefit of weed control. Others have seen similar responses to fertilization with soluble fertilizers on seedling survival and growth (Smith *et al.* 1966, Walters *et al.* 1966, Brockley 1988). The effect of fertilization depends upon the degree to which vegetation is controlled (Waring 1972). Associated vegetation can be stimulated by fertilization leading to rapid depletion of available soil moisture (Waring 1972, Squire 1977). Although the seedlings in this study had elevated foliar nitrogen concentrations in the fertilized unweeded treatment, there was a lack of growth response possibly due to the low xylem water potentials and overtopping vegetation.

The lack of response or slightly negative response by seedlings to fertilization on the weeded plots was unexpected. Even though foliar nitrogen concentrations were increased by fertilization the absolute growth rates were reduced. As foliar nitrogen concentrations increased phosphorous concentrations decreased. Van den Driessche (1980) found a similar pattern in a nursery trial with Douglas-fir. Gill and Lavender (1983) found a poor growth response of urea-fertilized western hemlock in the Coast Range of Oregon; although foliar nitrogen content was significantly increased, the concentrations of P, Ca, Mg, Mn, Fe, Al, and B were reduced. However, in the present study, nitrogen and phosphorous concentrations were within the range considered adequate for seedling growth (Landis 1985). Therefore the absence of response to the nitrogen treatment may be due to a change in the soil chemistry due to the pH effects of the fertilizer, thus influencing the form of nitrogen or availability of other nutrients in the soil (Otchere-Boateng and Ballard 1978). The NH_4^+ form of nitrogen is rapidly accumulated in seedlings and is toxic at higher concentrations, possibly resulting in reduced growth or death (Shaedle 1991). Gill (1981) found that the addition of urea to western hemlock stands altered the soil pH thus damaging the mycorrhizal roots. This resulted in increased NH_4^+ and NO_3^- concentrations and decreased amounts of Ca, Mg and K.

Seed source

The seed orchard seed source diameter and volume increments responded in an additive manner to competition control and fertilization. There was no synergistic effect with competition control as was found in southern pines (Duba *et al.* 1985, Shiver and Rheney 1992). The seed orchard source had a greater influence on diameter and volume growth than on height growth. Due to the effects of planting shock, the response in height growth is usually not expected until the third year after outplanting. In this study the true genetic effect could not be quantified due to confounding between the seed sources and the different nurseries where they were grown.

Initial seedling size

The relative importance of initial seedling size on the size of these seedlings after two growing seasons is notable. Even though these seedlings were subjected to a wide range of herbaceous competition levels, the effect of initial seedling size was evident for all treatments. In various experiments initial seedling size was positively related to long term growth of Douglas-fir over a range of site conditions and competition levels (Long and Carrier 1993; Newton *et al.* 1993). Initial seedling height helps the seedling to escape the effects of deer browse and overtopping vegetation. Initial seedling diameter is related to the ability to generate root volume, which helps the seedling compete for scarce soil moisture in the presence of herbaceous vegetation. Long and Carrier (1993) found that increasing root mass was positively associated with seedling survival under environmental stress, while Rose *et al.* (1991) showed that root volume was a significant factor in the survival and growth of three different seed sources of Douglas-fir over two seasons. Height-to-diameter ratios were the most stable of the size parameters, with the ratio increasing only in the most dense competition.

The results of this study indicate that the early control of herbaceous competition in conjunction with large planting stock are the silvicultural treatments which contribute the most to Douglas-fir growth. Tree improvement shows promise at this early stage but does not offer the consistency or magnitude of influence of weed control. Nitrogen fertilization should be approached cautiously as the response may be negligible or negative if the soil chemistry or seedling nutrient balance is upset during initial establishment. Where appropriate, nitrogen fertilization treatments should be done in conjunction with herbaceous weed control where conifers are the dominant beneficiaries.

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CHAPTER 2: Role of Lammas Growth in Recovery of Douglas-fir Seedlings Deer Browse, as Influenced by Herbaceous Competition, Fertility, and Seed Source.

Introduction

Reforestation in the Coast Range of Oregon is hampered by intense competition from associated vegetation, often in combination with browsing by the coastal blacktail deer (*Odocoileus hemionus columbianus* Richardson) (Hartwell 1973). Browsing results in a loss of annual height growth, leaving the seedlings susceptible to further browsing or overtopping by associated vegetation if not controlled (Ruth 1956, Mitchell 1964, Crouch 1969, Dimock 1970, Gourley *et al.* 1990). Lammas growth, commonly referred to as second flushing, can increase height increment and is believed to play a role in allowing Douglas-fir seedlings to recover from and escape the reach of browsing deer (Gourley *et al.* 1990). Silvical treatments such as weed control, fertilization and selection of fast growing genetic stock are thought to influence the occurrence of lammas growth and may affect the probability of deer browsing. This paper reviews the existing literature relevant to the role of lammas growth in the over-all responses of trees, primarily coniferous, to browsing as affected by herbaceous competition, fertility and seed source. It then relates these data to controlled experiments in Douglas-fir where each of these factors is manipulated in the field.

Review of lammas growth

Lammas growth is the precocious flush of height growth from the newly formed terminal bud in mid-summer. It is termed after the Lammas day harvest festival in England during the period when this type of growth occurs (Rudolph 1962). Lammas growth has been observed as early as the times of

Theophrastus (Hort 1916) and has been reported in many northern conifers (Table 2.1). Lammas growth is a form of "free growth" which, as defined by Jablanczy (1971), is the simultaneous initiation and extension of stem units without interruption following "fixed" or predetermined growth. In this paper, lammas growth refers only to free growth occurring after the cessation of predetermined growth, identified by a temporary halt in shoot extension with the formation of bud scales. Lammas growth should not be confused with syllepsis which is defined by Späth (1912) as the development of a lateral shoot from components not contained previously in a resting bud. Lammas growth is influenced by environmental conditions (Carvell 1956; Sokolov and Artyushenko 1957; Rudolph 1958, Newton and Preest 1988, Hallgren and Helms 1992; Büsgen and Münch 1929; Walters and Soos 1961; Smith and Allen 1962; Walters and Kozak 1967; Coutts and Philipson 1976), genetic variation (Thümmler 1958; Wood and Lines 1959; Rudolph 1961; Walters and Soos 1961; Hallgren and Helms 1988), and tree size, age and vigor (Walters and Soos 1961; Jablanczy 1971; Pollard *et al.* 1975).

Soil moisture

Büsgen and Münch (1929) and Carvell (1956) associate summer rainfall with increased lammas shoot formation. Likewise, under favorable soil moisture conditions, Hallgren and Helms (1992), demonstrated an increased frequency of lammas shoot production in California red and white fir. Newton and Preest (1988) found that lammas growth in Douglas-fir seedlings was stimulated by soil water conservation through chemical control of grass competition. While Büsgen and Münch (1929) observed that poor growth conditions did not always suppress the formation of lammas shoots, Späth (1912) maintains that the length of these lammas shoots is controlled by available soil water.

Table 2.1 Literature referencing multiple flushing in northern conifer species.

Abies concolor (Gord. and Glend.) Lindl.	Hallgren and Helms 1992; Phillips 1911; Walters and Soos 1961.
A. grandis (Dougl.) Lindl.	Walters and Soos 1961.
A. magnifica A. Murr.	Hallgren and Helms 1992.
Picea abies (L.) Karst.	Walters and Soos 1961; Wülisch and Muhs 1986.
P. glauca (Moench) Voss.	Nienstaedt 1966; Watt and McGregor 1963.
P. mariana (Mill.) B.S.P.	Pollard and Logan 1974, 1976; Watt and McGregor 1963.
P. pungens Englm.	Young and Hanover 1978.
P. sitchensis (Bong.) Carr.	Cannell and Johnstone 1978; Coutts and Phillipson 1976; Millard and Proe 1992; Walters and Soos 1961; Wood and Lines 1958.
Pinus banksiana Lamb.	Honey 1944; Rudolph 1964; Sokolev and Artyushenko 1957; Thomas 1958.
P. contorta Dougl.	Thompson 1976; Tümmler 1958.
P. monticola Dougl.	Walters and Soos 1961.
P. resinosa Ait.	Carvell 1956; Honey 1944; Jump 1938a, 1938b; Kienholz 1933, 1941; Littlefield 1956; MaCabe and Labisky 1959; Thomas 1958; Watt 1961; Watt and McGregor 1963.
P. strobus L.	Friesner 1943; Honey 1944; McCabe and Labisky 1959; Owston 1968; Paul 1957; Santamour 1960; Watt 1961; Watt and McGregor 1963.
P. sylvestris L.	Aldén 1971; Downs and Borthwick 1956; Kovalenko 1960; Sokolev and Artyushenko 1957; Szczerbinski and Szymanski 1957, Wright and Bull 1963.
Pseudotsuga menziesii (Mirb.) Franco	Büsgen and Münch 1929; Carlson and Preisig 1981; Gourley *et al.* 1990; Lavender and Cleary 1974; Marcet 1975; Newton and Preest 1988; Smith and Allen 1962; Walters and Kozak 1967; Walters and Soos 1961.
Tsuga heterophylla (Raf.) Sarg.	Mitchell 1965; Walters and Soos 1961.

Fertility

Soil fertility has long been associated with lammas growth as has fertilization with nitrogen containing fertilizers. Sokolov and Artyushenko (1957) attributed lammas growth in jack pine and Scotch pine to an application of inorganic fertilizer, and Smith and Allen (1962) found a positive relationship between the rate of fertilization and lammas growth in 2-year-old Douglas-fir seedlings. Coutts and Philipson (1976) demonstrated that nitrogen fertilization stimulated lammas growth in Sitka spruce which resulting in real height gains. In addition, Büsgen and Münch (1929) found that heavy manuring stimulated lammas growth and Walters and Kozak (1967) showed that out of seven fertilizer treatments, all but the two non-N fertilizers influenced lammas shoot production. In general the most productive sites have the highest occurrence of lammas growth for any given species (Carvell 1956; Walters and Soos 1961).

Mechanical damage

In addition to surplus resources, lammas growth may also be stimulated by mechanical processes. Büsgen and Münch (1929) state that any mutilation causing a proportionally greater root to shoot ratio in young plants can stimulate lammas growth. Huxley (1945) and Baker (1945) observed lammas growth on horse-chestnut trees following bomb blasts, and Schrenk (1898) describes the recovery of trees damaged in the 1898 St. Louis tornado through lammas growth. Duryea and Omi (1987) contend that lammas growth is a common occurrence in nurseries following top pruning of seedlings. Büsgen and Münch (1929) note that defoliation by insects and animals can cause lammas growth.

Genetic variation

The propensity for trees to exhibit lammas growth can vary between species, provenances, populations and within populations (Thümmler 1958; Walters and Soos 1961; Rudolph 1961; Kaya *et al.* 1989). Generally in conifers, provenances of southern latitudes tend exhibit a greater propensity to second flush over northern ones (Jump 1938b; Wood and Lines 1959; Santamour 1960; Rudolph 1961; Wright and Bull 1962, 1963; Logan and Pollard 1975; Pollard and Logan 1974, 1976; Cannell and Johnstone 1978) as well as lower elevation provenances over higher ones (Jump 1938b; Moulalis 1975). Hallgren and Helms (1988) noted that irrigation induced lammas growth in 80% of low-elevation white fir seedlings compared to 40% of red fir and high-elevation white fir seedlings.

Size, age and vigor

Carvell (1956) found that in a 6-year-old red pine plantation, lammas shoots were on the largest and most vigorous trees. Smith and Allen 1962 found that the occurrence of lammas growth increased with average seedling height. The phenomenon of lammas growth is limited to juvenile growth in northern conifers (Büsgen and Münch 1929; Walters and Soos 1961; Jablanczy 1971; Pollard *et al.* 1975), although it has been observed in Douglas-fir on good sites at ages up to 20 years and heights to 18 meters (Newton 1994, pers. comm. OSU Coll. of Forestry).

There has been much speculation as to the influence of lammas growth on the following season's predetermined growth. Since there is less time available during the growing season for a lammas shoot to set bud it is possible that a reduction in the number of predetermined needle primorida would result. However, Rudolph (1961) did not see a reduction in growth of jack pine with lammas shoots the following season while Hallgren and Helms (1988) found that California white and red fir seedlings had 26% more needle primordia in the winter bud of seedlings with previous lammas growth than those without. Weber (1983), in an observational study, noted no difference in heights between Douglas-fir saplings with lammas shoots and those without over a nine year period.

Review of selectivity of browsing

Crouch (1969) states that management practices such as planting, weed control with herbicides, and fertilizing all greatly influence browsing by deer. Newton (1978) observed deer browsing on western hemlock to be more common in areas cleared of brush (93%) than in uncleared areas (13%), with Hyatt (1992) confirming this trend. Borrecco *et al.* (1972) found that although deer usage was greatest in areas where herbaceous vegetation was removed, browsing of Douglas-fir seedlings was not significantly increased. Mitchell (1964) showed that exposed seedlings were more likely to be browsed by deer than seedlings protected by vegetation or logging slash. Oh *et al.* (1970) and Crouch and Radwan (1980) demonstrated that nitrogen fertilization of Douglas-fir in field trials increased growth rates as well as the occurrence of deer browse. However, Radwan *et al.* (1974) showed that the source of nitrogen from nursery fertilization had no effect on deer preference upon outplanting.

Dimock *et al.* (1976) demonstrated substantial differences in deer preference among superior phenotypes within a local race of Douglas-fir. Hahn and Smith (1983) noted a selectivity of deer browsing toward larger bare-root Douglas-fir stock which was preferred two to one over smaller containerized stock, but failed to mention that the smaller seedlings would eventually pass through the larger phase. Likewise, under controlled conditions, Dimock (1971) found that, within the range of 10.5 to 22.5 cm, taller Douglas-fir seedlings were browsed more readily than shorter ones.

However, Newton and Black (1965) found that within the range of 10 to 115 cm, the chance of deer browse was inversely related to seedling height and that the larger seedlings outperformed the smaller ones. The purpose of this study was to examine the occurrence of lammas growth as affected by various silvicultural treatments. Browsing by local populations of deer provided the opportunity to study the selectivity of the deer to the various treatments and individual seedlings. A secondary objective was developed to determine the role of lammas growth in the recovery of the seedlings from deer browse and to note any differences in stem form. Specific objectives were:

1. Test for differences in lammas shoot production and deer browse between fertilization, competition, and seed source in all combinations.
2. Determine what environmental variables are associated with lammas growth and deer browse.
3. Determine the relationships between seedling size, vigor, lammas growth and deer browse.
4. Determine the relationship between the occurrence of lammas growth and subsequent growth.

Materials and methods

The experimental design and setting are presented in chapter one, dealing with seedling survival and growth as related to various silvicultural treatments. Methods will only be covered here in enough detail to support the current interpretive needs.

Experimental design

The experimental design was a 2^3 factorial, randomized complete block, with three replicates per site, split across three sites for a total of 72 plots. The three factors in the experiment were herbaceous competition level, nitrogen fertility level, and seed source. Each factor had two levels: complete weed control W_1 vs. none W_0, nitrogen fertilization F_1 vs. none F_0, and seed orchard seed source S_1 vs. woods run seed source S_0. The experimental unit was a percentage of the surviving seedlings on each plot.

The two seed sources of Douglas-fir transplants used were a genetically improved seed orchard source, developed by the Burnt Woods Tree Improvement Cooperative, and a wild type source from within the same local seed zone (252).

Treatments

All seedlings were planted within one week of each other in February, 1992 at a 0.5 m × 1.0 m spacing. Complete weed control was accomplished by an application of 1.37 kg/ha of hexazinone (Velpar L®) herbicide using a hand-held 3.6 m boom, powered by a pressurized backpack sprayer at a rate of 92 ℓ/ha. The nitrogen treatment was established through the addition of 220 kg/ha of urea prill (46-0-0) broadcast with a hand-held rotary dispenser in a 3.6 m swath. Fertilizer and weeding treatments were installed on March 18th, 1992 and were repeated on March 25, 1993. In an effort to moderate the occurrence of deer browse an electrically charged 18 gauge wire, suspended one metre above the ground by fiberglass poles, was systematically wound between all plots on each site. The random plot layout within replications insured that the level of deer browse among treatments was not influenced by the electric fence. Each wire was charged during May and June of each year with a 12 volt car battery, regulated by a Jolt electric fence controller (model 4000B, IAAB U.S.A., Inc. Bellveue, WA). Vegetation under the wire was controlled, to prevent short-circuits, with a single directed application of glyphosate in the spring of each year. Care was taken to avoid treating unweeded plot vegetation in this process.

Measurements

Douglas-fir and cover measurements

Seedling size was measured shortly after planting (Spring 1992), and at the end of each growing season (Fall 1992, 1993). Individual tree measurements were made on seedling height (nearest centimeter), length of lammas shoot, diameter at 15 centimeters (nearest millimeter), and overall vigor. Vigor, as a qualitative measure, was quantified as five point scale (1 = Vigorous, 5 = Dead) based on seedling color and general appearance. Concurrent measurements taken in the fall included the occurrence of deer browse, lammas growth, or herbicide damage. From the height and diameter measurements, relative stem volume was calculated with the formula for a cone:

$$\text{Volume} = \pi \times d^2 \times h/12$$

Where d = diameter at 15 centimeters
h = total height

Percent cover by herbaceous forbs and grasses was estimated on a half-metre radius around each seedling in the fall of 1992 and as a percentage of total plot area in the fall of 1993 due to the relative homogeneity of the vegetation within the plots. Percent overtopping was based on the cone occlusion method as described by Howard and Newton (1984).

Xylem water potential and soil moisture

Predawn and midday xylem water potentials were estimated from current-year shoots of three randomly selected seedlings per plot for a total of 432 measurements per year. These measurements were made in mid-July 1992, and mid-August 1993, using a Scholander pressure chamber (Waring and Cleary 1967; Ritchie and Hinckley 1975). These dates were chosen for contrasting water regimes in weeded vs unweeded treatments.

Nutrient analysis

Foliage samples were taken from the current year's growth of an upper whorl lateral, excluding any lammas shoots, on the southeast side of each surviving seedling in October of 1993. These samples were bulked by treatment across blocks on each site for a total of 24 samples. Total N and P were determined by a standard micro-kjeldahl digestion method, with nutrient concentrations calculated on a dry weight basis (Lavender 1970).

Analysis

Differences in lammas growth response and level of deer browse were detected by analysis of covariance (ANCOVA) for main and interaction effects according to the model on the following page based on plot averages weighted by the number of surviving seedlings in each plot (Steel and Torrie 1980). Site terms were tested against error a and all remaining terms tested against error (b). Covariates tested included initial seedling size and surrounding cover. Where a significant covariate was not found the covariate term was left out of the model.

$$Y_{ijklm} = \mu + L_i + B(L)_{ij} + W_k + F_l + WF_{kl} + S_m + WS_{km} + FS_{lm} + WFS_{klm} + LW_{ik}$$

$$+ LF_{il} + LWF_{ikl} + LS_{im} + LWS_{ikm} + LFS_{ilm} + \beta(X_{ijklm} - \chi_{\cdot\cdot}) + LWFS_{iklm}$$

where

L = site (i = 1,2,3)
B = block (j = 1,2,3)
B(L) = error a (blocks within sites)
W = weed control (k = 0,1)
F = fertilizer (l = 0,1)
S = seed source (m = 0,1)
$\beta(X_{ijklm} - \chi_{\cdot\cdot})$ = covariate denoted by X
and LWFS = error (b).

Several seedlings on two sites showed signs of herbicide damage in the second season and were eliminated from the analysis. Browsing and lammas growth variables based on probability, were transformed by the arcsine square root transformation where necessary (Sabin and Stafford 1990). Significant differences between means were determined using Bonferroni's protected Least Significant Difference (LSD) procedure (Milliken and Johnson 1984). Multiple linear regression models were developed, based on weighted means from individual plots, to relate lammas shoot production and probability of deer browse to the various levels of competition, fertility, and initial seedling traits as developed by the various treatments. The models explaining the most variance were chosen using the stepwise selection procedure (Neter *et al.* 1989).

Results

Lammas growth

Weed control significantly increased lammas shoot growth ($p<.0001$), presumably through conservation of soil moisture (Table 2.3). Weeding alone accounted for about two thirds of all explained variation. Fertilization with urea significantly reduced lammas growth on all sites ($P<0.0018$) and interacted with weed control in reducing the occurrence of lammas growth on unweeded fertilized plots (Figure 2.1). Seed source had little effect on lammas shoot production in this study. The frequency of lammas growth over the first two growing seasons contributed to the stem volume response to weed control (Figure 2.3).

Table 2.2 Stem volume of surviving seedlings by weed control and number of years lammas growth occurred, averaging across seed source and fertilization.

	Complete Weed Control		No Weed Control	
Lammas Flush	**Number** *	**Average Volume (cm^3)**	**Number** *	**Average Volume (cm^3)**
None	146 (10.1)	44.1 c	270 (18.7)	20.0 e
One Year	534 (37.1)	64.0 b	334 (23.2)	29.1 d
Two Years	135 (9.4)	74.2 a	21 (1.5)	26.5 de

* Based on 1440 surviving seedlings (percentage of total). Values with the same letter are not significantly different by Bonferonni's adjusted LSD.

Regression analysis was done on second year plot averages, weighted by the number of surviving seedlings. Lammas growth the second year was negatively related to the current season's predawn xylem tension and positively related to the previous year's vigor.

Table 2.3 ANOVA Table for second season terminal lammas shoot length *.

Source	DF	Mean Square	P-value
Site (L)	2	3294.9	0.0001
Block (Site)	6	499.4	0.0007
Weed Control (W)	1	15981.7	0.0001
Fertilization (F)	1	1126.2	0.0018
W x F	1	230.3	0.1395
Seed Source (S)	1	119.3	0.2845
W x S	1	24.6	0.6248
F x S	1	6.3	0.8051
W x F x S	1	7.9	0.7815
L x W	2	1081.7	0.0002
L x F	2	289.1	0.0692
L x W x F	2	107.4	0.3562
L x S	2	52.7	0.5987
L x W x S	2	302.7	0.0615
L x F x S	2	51.7	0.6045
L x W x F x S	2	44.0	0.6509
Error	42	101.5	

* based on plot means weighted by the number of surviving seedlings.

Deer browse

Deer browse was mostly limited to the first flush of growth, with most occurring within three weeks of bud break. Browsing by deer was highly variable between seasons, treatments and sites studied. Second year browsing was negatively related to the amount of surrounding herbaceous cover and positively related to the occurrence of browsing the previous year (table 2.4).

No relationship was found for any seedling characteristics such as size, within the range of 15 to 155 cm, when examined on a plot mean basis.

Table 2.4 Response models for second year percent browse and lammas growth†.

MODEL (Standard errors in parentheses)	p-value	r^2
BRSE2 = 0.089(0.070) - 0.003(0.0005)COV2 + 0.759(0.092)BRSE1	0.0001	0.64
LAMMAS2 = 1.294(0.067) - 0.137(0.034)VIG1 - 0.295(0.070)PRE Ψ	0.0001	0.61

† based on a plot average weighted by the number of surviving seedlings.
Ψ = -Mpa.

Table 2.5 Response and independent variables used in regression models.

RESPONSE VARIABLES	INDEPENDENT VARIABLES
BRSE2 = Percent browsed seedlings, year two. **LAMMAS2** = Percent seedings with lammas growth, year two.	**COV2†** = Percent cover, year two. **PRE2‡** = Predawn xylem water potential (-MPa), year two. **BRSE1** = Percentage browsed, year one. **VIG1** = Vigor, year one.

† Second year percent cover was based on a plot average.
‡ Based on a plot average of three random seedlings.

Frequency of browsing by deer influenced stem volume by reducing height increment. Of the surviving seedlings that were browsed twice, those with the benefit of weed control were twice as large as those without. Among seedlings browsed only once, weeded trees were close to three times the size of the unweeded (Table 2.6).

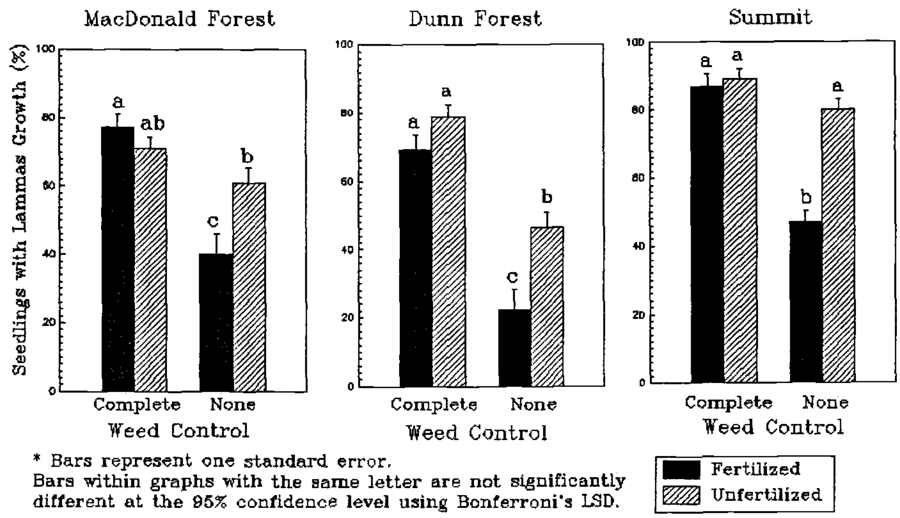


Figure 2.1 The interaction between weed control and fertilization on the occurrence of lammas shoots on three sites*.

Table 2.6 Stem volume of surviving seedlings in year two by weed control and number of years browsed, averaging across seed source and fertilization.

	Complete Weed Control		**No Weed Control**	
Browsed	**Number***	**Average Volume (cm^3)**	**Number***	**Average Volume (cm^3)**
None	231 (16.0)	74.0 a	237 (16.5)	27.2 c
One Year	263 (18.3)	68.1 a	241 (16.7)	23.2 c
Two Years	321 (22.3)	48.7 b	147 (10.2)	24.7 c

* Based on 1440 surviving seedlings after two years out of a total of 2016 outplanted (percentage browsed in brackets). Values with the same letter(s) are not significantly different using Bonferonni's adjusted LSD.

Although there is confounding between browse, lammas growth and seedling size and vigor which cannot be separated in this study, several trends were apparent. Deer preferentially browsed wild type seedlings on the Dunn

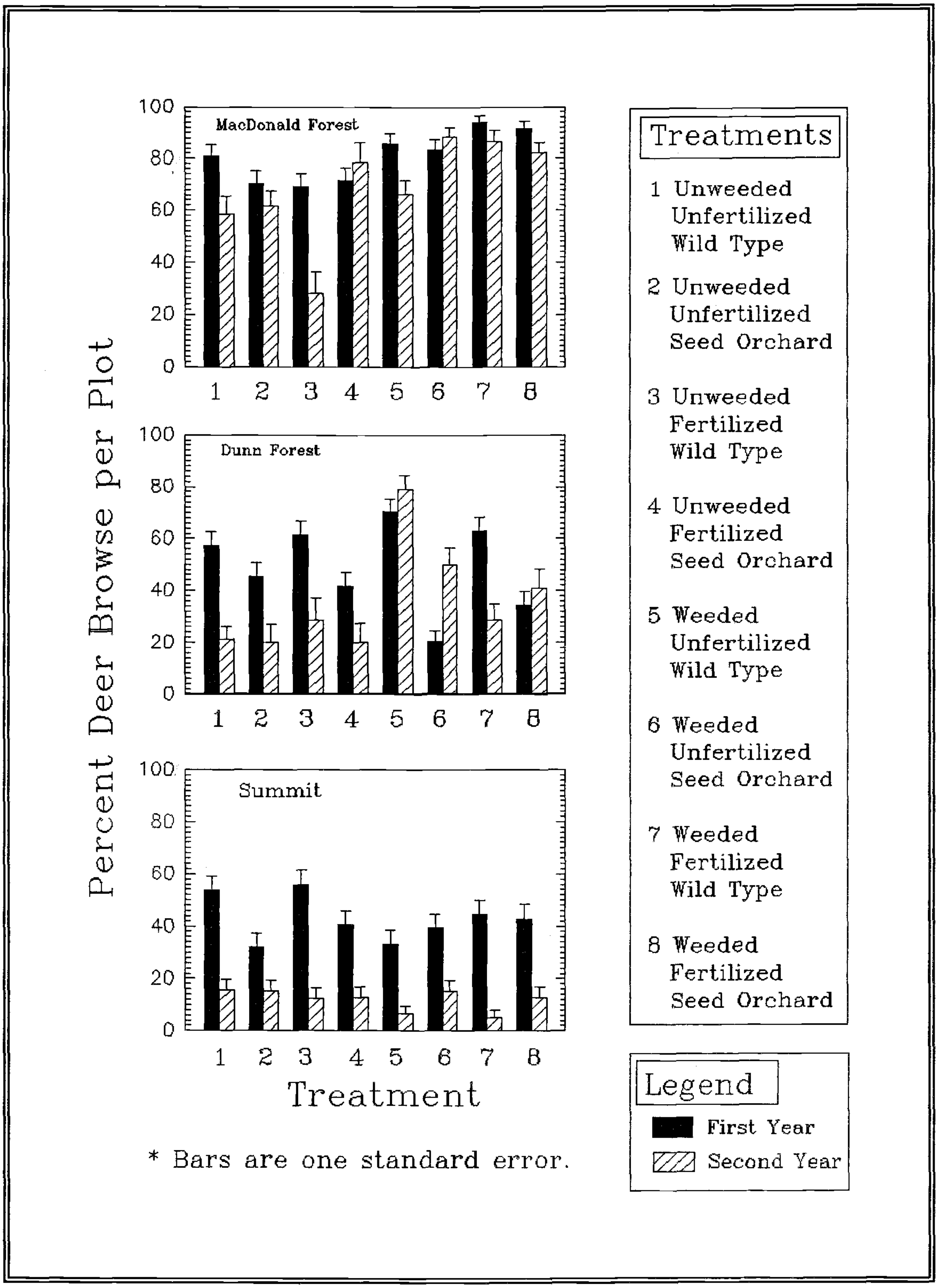


Figure 2.2 Percentage deer browse over two years by silvicultural treatment*.

Forest site ($p < .0001$) during the first growing season but the pattern was not repeated for other sites or in other years (Figure 2.2). There is a significant interaction between deer browse and lammas growth. During the first season of growth, with few exceptions, only vigorous seedlings that were browsed showed a propensity for lammas growth (Figure 2.3). For seedlings with the benefit of weed control lammas growth following browse made up for lost height growth due to the browsing to the extent that browsed seedlings were as large as unbrowsed at year's end (Figure 2.4).

Lammas growth in the previous year did not significantly reduce the amount of growth the following season for any of the sites (Figure 2.5). In order to eliminate confounding due to repeated browsing, only browsed seedlings with lammas growth in the first season were examined. Seedlings browsed in the second year were also excluded. No difference was found in this relationship between weeded and unweeded seedlings.

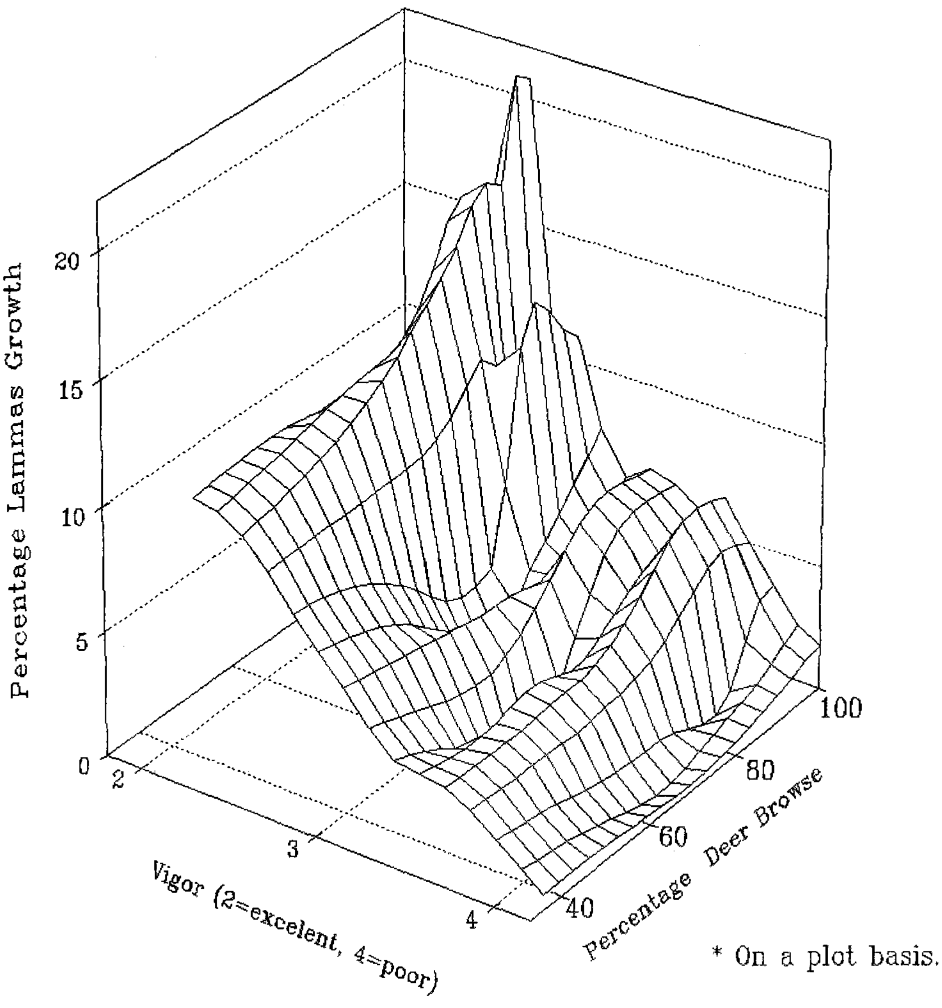
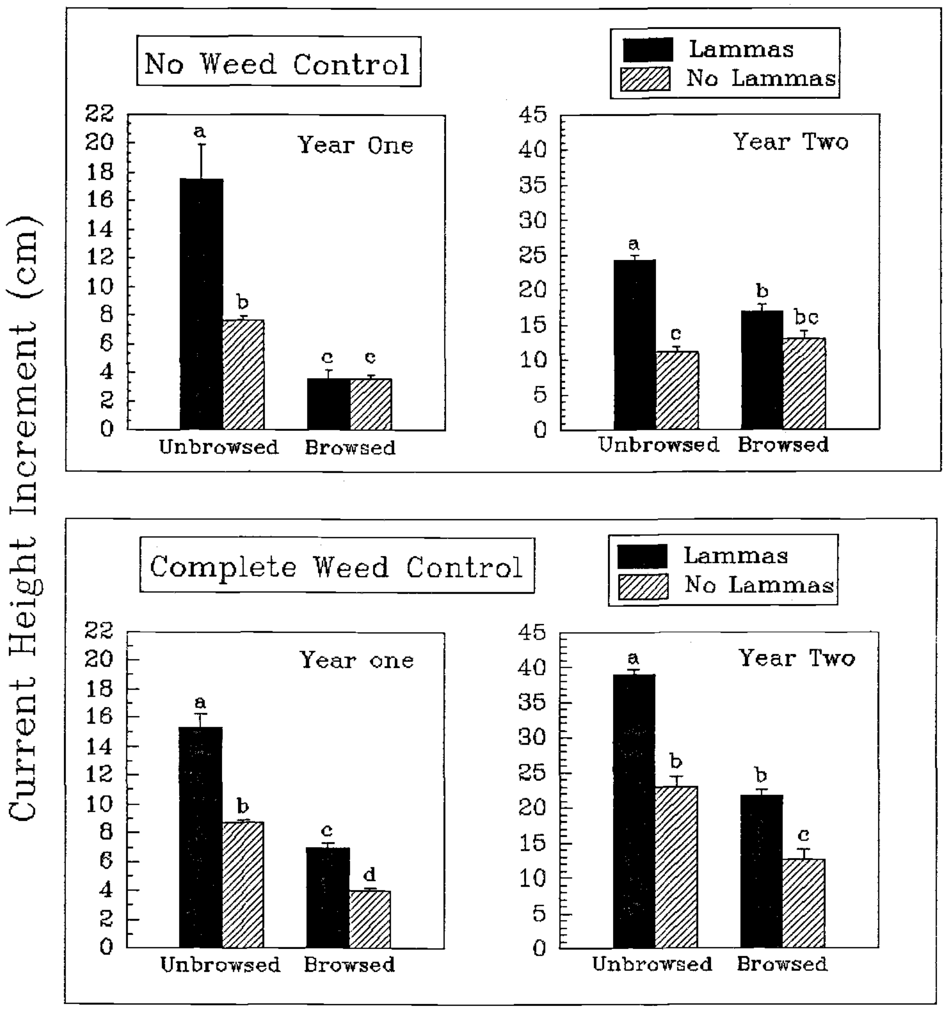


Figure 2.3 Response surface of lammas growth vs. vigor and browse (year one) *.



* Bars represent one standard error.

Bars within graphs with the same letter are not significantly different using Bonferroni's LSD.

Note: The scales are different between year one and year two.

Figure 2.4 Current height growth of browsed and unbrowsed seedlings by year *.

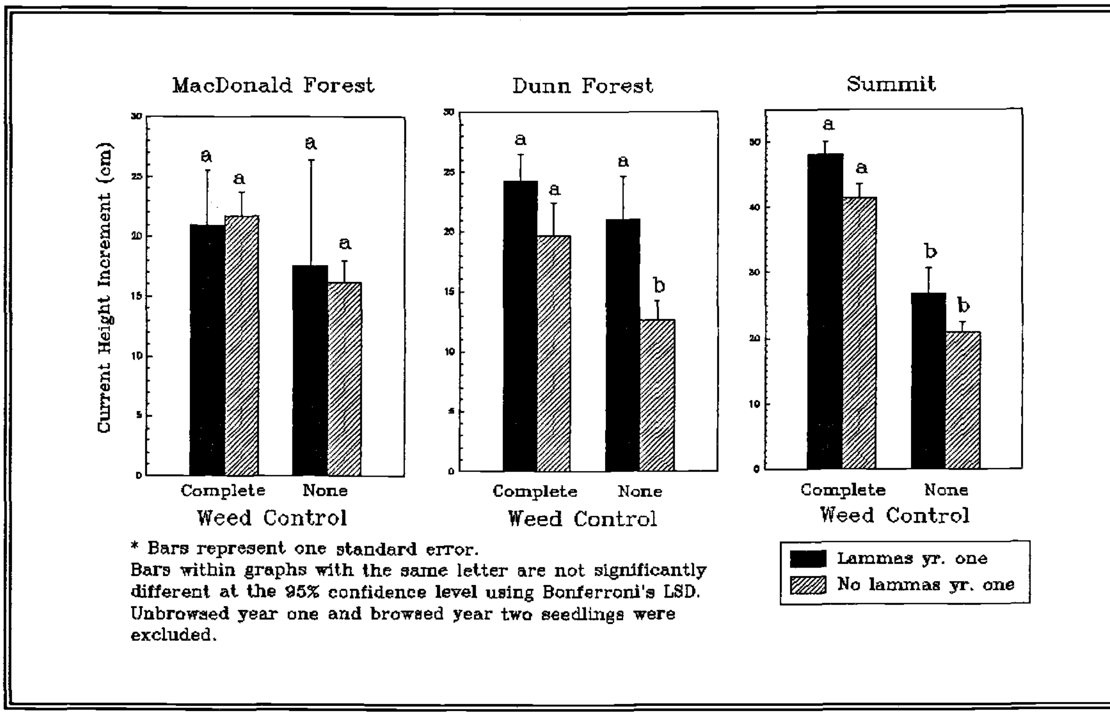


Figure 2.5 The effect of previous year's lammas growth on the current year's height increment *.

Discussion

Weed control

Weed control is the single factor most influencing lammas and total growth, explaining over 10 times the variation contributed by the next most important factor. In western Oregon where there is a summer drought the soil moisture conserved through weed control is enough to trigger lammas growth. Broadcast fertilization with urea does not increase this tendency. These points are important in areas where browsing from deer reduces the annual height increment of seedlings thus retarding early plantation development, leaving it susceptible to overtopping from competing vegetation. While McDonald and Radosevich (1992) state that reducing the amount of competing vegetation may induce browsing by exposing seedlings to animals, vigorous weed free seedlings have a higher propensity for lammas and total growth, thus a greater recovery potential from deer browse. Since lammas shoots are rarely browsed by deer, this mechanism allows seedlings an escape from the reach of browsing deer and overtopping vegetation. The findings of this study support the theory forwarded by Gourley *et al.* (1990) that vigorous seedlings in a weed free environment escape from moderate deer browse through lammas growth.

Fertilization

Application of nitrogen in the form of 200 lbs/ac. of urea was likely ineffective in positively influencing lammas growth because it may not be a limiting nutrient on these sites. The possibility of the additional nitrogen serving to dilute other elements in the foliage is unlikely as the fertilized seedlings were actually smaller than the unfertilized. Where broadcast fertilization is appropriate it should be done in conjunction with weed control.

Seed source

Although the seed orchard seed source was growing significantly faster than the field run seed source it did not have any affect on lammas growth occurrence. For these two populations it appears that environmental conditions play a bigger role than genetics with regard to lammas and total growth in low-elevation Douglas-fir populations.

Since lammas growth in year one did not reduce growth the following season and restored height losses from deer browse in the same season, the ability to second flush may be a desirable trait in juvenile Douglas-fir provided the lammas shoots harden off before fall frosts. Any defects in stem form (i.e. multiple tops) due to lammas growth at this early age in stand development should result in limited losses which would be offset by the increased growth rate of seedlings with the propensity for lammas growth.

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SUMMARY

Reforestation in the Coast Range of Oregon is hampered by intense competition from associated vegetation, often in combination with browsing by the coastal blacktail deer (*Odocoileus hemionus columbianus* Richardson). The first few years following planting are critical in the development of well stocked rapidly growing Douglas-fir plantations. A regeneration forester must choose among various silvicultural treatments necessary to encourage rapid plantation development, while minimizing costs which need to be carried through the length of the rotation. These various silvicultural treatments are: control of associated vegetation, fertilization, and selection of an appropriate seed source and planting stock. This study provided an excellent opportunity to study the relative partial contribution of each of these silvicultural treatments, when combined, on Douglas-fir survival and growth in the central Oregon Coast Range.

Weed control proved to be the dominant factor influencing survival and growth contributing over three times the amount of volume growth contributed by seed source as of year two. Fertilization with urea did not have any effect in this study with the exception of stimulating herbaceous growth on plots without weed control, a result with negative effects on Douglas-fir seedlings. It follows that broadcast fertilization should not by done without concurrently controlling herbaceous vegetation, and then only once the trees have become established on the site. In many cases weed control alone may be enough to make nutrients available which would otherwise be tied up in associated vegetation.

Weed control was also effective in mediating the effects of deer browse. Of the seedlings which were browsed twice, those with the benefit of weed control had over twice the stem volume of those with out weed control. Lammas growth was responsible for the stem volume response to weed control through additional increment. Since lammas growth is associated with vigorously growing seedlings, weed control may be the most beneficial treatment in areas with excessive deer browsing.

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