Lodgepole pine response to stress treatments

by James Stuart Jacobs

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biological Sciences
Montana State University

Abstract:
Lodgepole pine trees approximately twenty-five years of age were subjected to five stress treatments at three levels (0, 50 and 100%) and observed in a field experiment for five years. The stresses were applied to three sensitive regions of the trees: the roots by root pruning, the stems by girdling, and the canopy by bud pruning and toxic spray (H^+, Zn^{+2} and Cu^{+2}). Response to stress was measured by height growth, stem radial growth, needle health, and electrical resistance of the phloem (shigometer). Low measurements of electrical resistance of the phloem are believed to indicate high vigor.

Overall there was a significant reduction in growth and phloem electrical resistance in the severe treatments (100%) but no effect of the moderate treatments (50%). (1) Girdling was the most severe stress; it caused loss of vigor, reduction in growth, and death. (2) Root pruning was less stressful but caused loss in vigor and growth. (3) Bud pruning was least stressful and caused only reduction in radial growth which only appeared after three years of treatment. Needle health as indicated by needle retention and chlorophyll content in the bud pruned trees did not differ between controls and pruned trees. (4) Acid reduced growth after it was sprayed on the needles repeatedly for four years. Trees sprayed with pH 1 acid showed an increase in chlorotic spotting and needle abscission, but no reduction in chlorophyll content. (5) There was no effect of copper and zinc sprays. Needles from trees sprayed with metals showed increases of copper on needle surfaces and in needles, while zinc sprayed needles showed increases of zinc on the needle surface only.

LODGEPOLE PINE RESPONSE TO STRESS TREATMENTS

by

James Stuart Jacobs

A thesis submitted in partial fulfillment
of the requirements for the degree

of

Doctor of Philosophy

in

Biological Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

July 1992

APPROVAL

of a thesis submitted by

James Stuart Jacobs

This thesis has been read by each member of the graduate committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

22 July 1992
Date

Chairperson, Graduate Committee

Approved for the Major Department

23 July 1992
Date

Robert E Moore
Head, Major Department

Approved for the College of Graduate Studies

24 July 1992
Date

RL Brown
Graduate Dean

STATEMENT OF PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a doctoral degree at Montana State University, I agree that the Library shall make it available to borrowers under rules of the Library. I further agree that copying of this thesis is allowable only for scholarly purposes, consistent with "fair use" as prescribed in the U.S. Copyright Law. Requests for extensive copying or reproduction of this thesis should be referred to University Microfilms International, 300 North Zeeb Road, Ann Arbor, Michigan 48106, to whom I have granted "the exclusive right to reproduce and distribute copies of the dissertation in and from microfilm and the right to reproduce and distribute by abstract in any format."

Signature James Stuart Jacobs

Date 23 July 1992

ACKNOWLEDGEMENTS

Funding for this study was provided by the U.S.D.A. Forest Service Intermountain Research Station cooperative agreements INT-C-3-INT-66 and INT-89408-RJVA and by the U.S. Environmental Protection Agency Cooperative research agreement #CR-812727. The study site was provided by the U.S.D.A. Forest Service, Gallatin National Forest, Bozeman Ranger District.

I thank the staff at the Forest Service Intermountain Research Station in Bozeman for their help in obtaining funding and for providing facilities and equipment that were helpful in completing the study, in particular, Mike Cole, whose input has been helpful from the conception of the project to the end, and Wyman Schmidt, whose encouragement kept things moving.

I express my gratitude to my reading committee, Dr. Tad Weaver, Mike Cole, Dr. Sharon Eversman, and Dr. James Pickett, whose critical review greatly improved the manuscript.

I am especially grateful to my advisor, Dr. Tad Weaver, for his enthusiastic help in all aspects of the project from experimental design to plucking pine needles for analysis, for his many reviews of various reports and manuscripts, and for the energy he puts into teaching.

I am most appreciative of my wife Mary for her patience, support and enduring love throughout my graduate studies, and to my parents for their support and encouragement throughout my education.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF TABLES--(Continued)

LIST OF FIGURES

ABSTRACT

Lodgepole pine trees approximately twenty-five years of age were subjected to five stress treatments at three levels (0, 50 and 100%) and observed in a field experiment for five years. The stresses were applied to three sensitive regions of the trees: the roots by root pruning, the stems by girdling, and the canopy by bud pruning and toxic spray (H^+, Zn^{+2} and Cu^{+2}). Response to stress was measured by height growth, stem radial growth, needle health, and electrical resistance of the phloem (shigometer). Low measurements of electrical resistance of the phloem are believed to indicate high vigor.

Overall there was a significant reduction in growth and phloem electrical resistance in the severe treatments (100%) but no effect of the moderate treatments (50%). (1) Girdling was the most severe stress; it caused loss of vigor, reduction in growth, and death. (2) Root pruning was less stressful but caused loss in vigor and growth. (3) Bud pruning was least stressful and caused only reduction in radial growth which only appeared after three years of treatment. Needle health as indicated by needle retention and chlorophyll content in the bud pruned trees did not differ between controls and pruned trees. (4) Acid reduced growth after it was sprayed on the needles repeatedly for four years. Trees sprayed with pH 1 acid showed an increase in chlorotic spotting and needle abscission, but no reduction in chlorophyll content. (5) There was no effect of copper and zinc sprays. Needles from trees sprayed with metals showed increases of copper on needle surfaces and in needles, while zinc sprayed needles showed increases of zinc on the needle surface only.

INTRODUCTION

Trees suffer from stress due to lack of energy (carbohydrate), nutrients for chemical reactions, and/or water. Stress reduces productivity of trees and predisposes them to pathogenic attack (Levitt 1980). It is important, therefore, to know how trees respond to stress and how to recognize trees that are stressed so that management decisions can be made to either avoid or alleviate the stress.

There are three objects of this dissertation: (1) to recognize stress in tress, (2) to measure trees' response to stress, and (3) to explain the stress effects. To this end, progressively greater stress treatments were applied to lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) and the response to stress was measured by change in growth, electrical resistance of the phloem, and needle health. Lodgepole pine was chosen for study both because it is important for wildlife habitat and timber and because it has wide geographic and elevational range in the Western United States and Canada (Lotan 1983). While these experiments deal with lodgepole pine, I believe the results can be applied to other species and other regions.

In all experiments, the null hypothesis is that, due to reduction of resources captured or delivered, a linear increase of stress (0-50-100%) would cause a linear reduction in height and radial growth, and that the stress might be recognized first with measurements of electrical resistance in the stem phloem.

METHODS

To determine how lodgepole pine responds to stress five treatments at three levels were applied to healthy saplings in a naturally regenerated, thinned timber stand. The five stress treatments were bud pruning, girdling, root pruning, foliar application of acid spray, and foliar application of metal solutions. In each case the levels were 0%, 50%, and 100% of a severe treatment. Tree response to stress was measured by height growth, stem diameter growth, electrical resistance of the phloem, and, after bud pruning and acid spray, needle health.

Site Description

The study site is located at approximately 45°30′ north latitude and 110°57′ west longitude, and 30 km south of Bozeman, Montana, in the Hyalite drainage of the Gallatin Mountain Range. The site is typical of good sites for mid elevation lodgepole pine. It has an average slope of 10% and is uniform in habitat and soil types. The habitat type is *Abies lasiocarpa*/*Vaccinium scoparium* h.t. (Pfister *et al*. 1977). While *Pinus contorta* dominates the overstory, a few *Abies lasiocarpa* and *Picea engelmannii* are interspersed. The soil type is a loamy, skeletal, mixed Typic Cryochrept. It was formed in glacial till and over moderately deep weathered volcanic rock, which is well drained with medium runoff and moderate to moderately slow permeability (Veseth and Montagne 1980). The elevation is 2200 M. Average annual precipitation is 76 cm, average maximum and minimum temperatures for January are 4.3 and -13.1°C and for July are 25.7 and 2.8°C (U.S.D.A. Snow Survey, Lick Creek weather station). The seasonal regime is similar to that described for other subalpine fir forests (Weaver 1979). The lodgepole pine site index (expected tree growth) is 40 feet (12.2 meters) on a 50 year base (Gilgan 1984).

The experimental site was previously occupied by a stand of decadent lodgepole pine with subalpine fir succeeding in the canopy. This stand was clearcut in 1962. After logging the slash was piled and burned and the site was dozer scarified. Natural regeneration of lodgepole pine was good, so the stand was thinned in 1979 to 3 m^2/tree or 600 trees per acre (U.S.D.A. Forest Service, Gallatin National Forest, Bozeman Ranger District). Tree heights at the time of the experiment ranged from 2.6 to 7.8 meters and the age ranged from 15 to 25 years.

Experimental Design

Stress treatments were applied to trees in a block design (Figure 1) that included 12 replications. The plots were adjacent to a forest service road for easy access. To avoid edge effects that might bias tree response, trees next to the road were omitted and used as a buffer. Since the root pruning treatment involved ditching around the trees and might have affected water movement below the treatment, it was placed below the other trees and just above the road border trees. The next three rows contained the bud prune, blue stain girdle, annual H_2SO_4 and HNO_3 acid sprays, and annual $ZnCl_2$ and $CuCl_2$ sprays. These treatments were rotated within the plot, from plot to plot, so the same treatments

C	G_{2A}	girdle	G_{2A}	C	G_{3A}	girdle	G_{3B}	C
C	M_{1A}	zinc	M_{1B}	C	M_{2A}	copper	M_{2B}	C
C	A_{1A}	H_2SO_4	A_{1B}	C	A_{2A}	HNO_3	A_{2B}	C
C	B_{1A}	bud	B_{1B}	C	G_{1A}	girdle	G_{1B}	C
C	RA_{1A}	H_2SO_4	RA_{1B}	C	D_{1A}	root	D_{1B}	C

Figure 1. Layout of a typical plot. Treatments include two acids ($A_1 = H_2SO_4$ and A2 = HNO_3), two metals (M_1 = Zn and M_2 = Cu), girdling (G_1 = blue stain, G2 = blue stain control, and G3 = conventional), ditching (D_1), bud prune (B_1) and a repeated H_2SO_4 (RA_1). Positions of RA_1, D_1, G_2, and G_3 are constant; the other treatments rotate to prevent confounding of any interactions. A and B subscripts represent light and heavy applications. The tallest tree in each treatment was alternated between light and heavy in each plot to ensure that not all the tallest trees were assigned to one level. Wherever two plots are immediately adjacent, the same controls along a common edge are used for both plots. There are 12 plots in the study site.

were not always adjacent, eliminating possible treatment interactions. This rotation was completed twice in the 12 plots. The upper-most row in the plots had the mechanical girdle and the control treatment for the blue stain infection treatment. These trees were not included in the treatment rotation. The original experimental design had only a mechanical girdle. Because infection by blue stain fungus is believed to cause the tree mortality in a bark beetle infestation, I inoculated some trees with this fungus and added an appropriate control treatment (Strobel 1986). Blue stain infection was not successful and is not discussed in this paper. Also added to the experimental design was a repeated (fortnightly) H_2SO_4 spray that was applied to trees next to the root pruned trees in the first row.

Trees in the plots were treated in triplets (control, moderate, and heavy, Figure 1). Each triplet had a geographically central control tree and two treatment trees; the taller treatment tree received the heavy (or moderate) treatment in alternating blocks. Each triplet was bordered on each side by a control tree. Since the stand was regenerated naturally, and not planted in rows, the "rows" of trees were not linear, and spacing was not even. Also, since it is common for trees to reseed naturally in clumps with open space between, plots were not always next to each other. When they were, adjacent plots shared the outside control trees. Where the plots were bordered by an opening, a row of trees was left untreated on the edge as a buffer.

Treatments

Root Pruning

Roots were pruned by ditching around the stem of the tree. Control trees were not ditched, moderate treatment trees were ditched at a radius twice the dripline, and heavy treatment trees were ditched at the dripline. The dripline was assumed to be directly below the tips of the branches reaching furthest from the bole. Ditches were made to a depth of 50 centimeters and all roots were cut with a shovel. The ditches were refilled with soil after the roots were pruned. Roots were re-pruned annually for four years.

Bud Pruning

The bud pruning treatment was applied by removing no buds from control trees, alternate buds (50%) on moderate treatment trees with destruction of the terminal bud on alternate branches, or all buds from heavy treatment trees. The terminal leader bud was left on all trees to allow regular height growth measurement. Removal was done with hand shears. The shearing was done in early summer before the needles completed elongation in 1984, 1985, 1986, 1988 and in August 1987 after needles were fully elongated.

Girdling

In the girdling treatment, trees were girdled by cutting bands 3 to 5 cm wide through the cambium layer with a knife and removing bark from 50% (moderate treatment) or 100% (heavy treatment) of the circumference of the bole. The 50% girdle was divided into 3 or 4 segments (depending on the circumference of the bole) and spaced equally around the stem. Girdles were applied once, in mid-August of 1984.

Acid Spray

Acid treatments included two H_2SO_4 treatments -- one applied annually and one applied fortnightly during the growing season -- and one annual HNO_3 treatment. Each treatment was applied at three concentrations (no acid, pH 3.0 and pH 1.0). In each group the control tree was sprayed with distilled water and its neighbors were given the pH 1 (heavy) and pH 3 (moderate) treatments.

Acid solutions were composed of deionized water with sufficient pure reagent (H_2SO_4 or HNO_3) added to produce the treatment acidities. The solutions were applied with a plastic 10 L pump sprayer. Approximately 0.8 liter was applied to each tree, enough to leave all needles dripping wet. Dates of application are listed in Table 1.

Metal Spray

The metals applied were zinc and copper, as the chlorides. Foliage of control trees were sprayed with approximately 0.8 liters of deionized water, moderate treatment trees were sprayed with approximately 0.8 liters of 0.001 molar solution of $ZnCl_2$ or $CuCl_2$, and heavy treatment trees were sprayed with approximately 0.08 liters of 0.01 molar solution of $ZnCl_2$ or $CuCl_2$. Metals were applied once annually for five years. All spraying was done with a plastic 10 liter pump sprayer. Acid and metal applications were made on different days, and the sprayer was rinsed with an acid solution and deionized water between treatments. All waste was disposed of through the MSU waste disposal system.

Table 1. Dates of acid and metal application.

Annual Acid and Metal Application	Fortnightly application
July 20-21 1984	
July 16-17 1985	July 16 1985 August 2 1985 August 25 1985
July 12-13 1986	July 12 1986 July 27 1986 August 7 1986 August 25 1986 September 7 1986 September 24 1986
August 4-5 1987	August 4 1987 August 18 1987 September 10 1987 September 24 1987 October 8 1987
June 1988	June 1988

Response Measurements

Because of the variety of the treatments applied, tree response measurements varied among treatments. For all treatments annual height growth, stem radial growth, and the electrical resistance of the phloem were measured. For the bud pruning, H_2SO_4 and metal spray treatments measurements of needle health were added.

Height Growth

Height growth measurements were made in the autumns of 1986 and 1988. The total height of each experimental tree was measured from the ground to the tip of the terminal leader. Annual height growth was measured as the length in centimeters of each of the eight most recent main stem internodes, and included three pretreatment years and 5 treatment years (1981-1988). Though tested for, no significant correlation between annual height growth and total height was found.

Radial Growth

Radial growth rates were measured in the same annual increments as height growth (1981-1988) in the fall of 1988. Total diameter was also measured. Radial increments were measured on radial cores taken at breast height (1.5 M from the ground). To facilitate the measurement of annual rings, the core samples were sanded smooth and ring widths were measured to the nearest 0.01 mm using a dendrochronometer and microscope with a measurement scale. No significant correlation was found between annual increment growth and total diameter.

Band dendrometers were fitted to trees in six of the 12 blocks to record seasonal diameter growth. The dendrometers were installed in the spring of 1985. Aluminum bands and stainless steel springs were fitted, as described by Liming (1957), at the center of an internode approximately 75 cm. from the ground, and the growth of the tree was recorded as this belt expanded. In the girdle treatment, dendrometers were installed above and below the girdle in the same internode as the girdle. Dendrometer readings were taken fortnightly in the summers of 1985 and 1986.

Shigometer Measurements

Electrical resistance of stem phloem was measured on the theory that it is an index of quantities of mobile ions (especially potassium) in the phloem and therefore general cambium vigor (Shortle _et_ _al_. 1977). Phloem resistance (Smith _et_ _al_. 1976) was measured fortnightly during the summers of 1984, 1985, 1986 and in August and September of 1987. A Northeast Electronics Corp. 7950 Shigometer was used. Measurements were taken on the north facing half of the bole approximately 1 meter from the ground. The two Shigometer probes were inserted horizontally into the bole to a depth of 5 mm. Probes were fixed at a distance of 1.4 cm apart.

Needle Health

After four years of bud pruning, needle condition was measured both by chlorophyll extraction and by counting the number of needles per internode. Needle condition was also measured after H_2SO_4 spray, both 4 annual and 3 years of fortnightly treatments. Needle health of trees sprayed with H_2SO_4 was examined by measuring their quantity (number and biomass per internode), the weight per needle, the water content per gram of needles, the amount of necrosis, and the chlorophyll content.

Needles for analysis were collected by cutting a branch midway up the crown on the tree's south side. Lateral branches were discarded. The needles were plucked from each of seven annual internodes, counted, weighed wet, dried at 60°C, and weighed dry to allow calculation of the first three parameters (quantity, weight per needle, and water content). To estimate amount of necrosis each needle was classified according to the percent of its surface (0-10,11-30,31-90 or 91-100%) which showed yellow-brown spots, bands, or tips.

Needle chlorophyll content was measured as a (perhaps) more objective way to index chlorosis than the visual measurements (Todd and Arnold 1961). To this end branches were cut half way up the south side of the crown, the lateral branches removed, and chlorophyll was extracted from second-year (1986) needles because chlorophyll content was found to be higher in second-year than either current-year or three- to six-year needles. Since the second year needles were removed from the 100% bud pruned trees, fourth year needles (1984) were used for all trees in the bud pruned treatment. After harvest, branches were stored in a dark refrigerator at 1°C for not more than seven days before analysis. Sampling was done in September 1987.

The chlorophyll extraction procedure used was similar to that of Horwitz (1975). 1.0 gram of fresh tissue was ground with 0.1 gram Na_2CO_3 in 85% acetone using a Sorvol Omni Mixer at medium speed (#5) for 5 minutes. The grindate was vacuum filtered through Whatman No. 5 filter paper. The residue was ground again with mortar and pestle in 85% acetone until no green was left in the tissue, and filtered through Whatman No. 5 filter paper. The two filtrates were combined and refiltered through Whatman No. 42 ashless filter paper and diluted to 100 ml with acetone. Optical density was immediately measured at 750nm with a Baush and Lomb Spectronic 20 spectrophotometer. If O.D. at 750nm was greater than 0.01 (Wilkinson 1983) the sample was centrifuged for 10 minutes to spin down any residue that passed through the filter. If O.D. at 750nm was greater than 0.01 after centrifugation the extract was discarded and another sample was prepared. If O.D. at 750nm was less than 0.01, the extract was considered clean and measurements were made at

660nm (Chlorophyll a) and 642.5nm (Chlorophyll b). Total chlorophyll was calculated by the formula (Horwitz 1975, pg. 51):

$$\text{Total chlorophyll} = 7.12\ A_{660} + 16.8\ A_{642.5} \qquad (1)$$

Needle Metal Content

Needles of trees sprayed with metals were analyzed for metal content to determine whether the metals were absorbed into the needles. Needles for analysis were collected by cutting a branch midway up the crown on the tree's south side. Lateral branches were discarded. The needles were plucked from each of seven annual internodes. Total zinc and copper (adsorbed and absorbed) were measured by ashing a subsample of the needles. Total metal concentration was measured using a dry ash digestion where a 1 gram needle sample was ashed in 550°C oven overnight, hydrated in 10 ml 2 N HCL, filtered through #42 Whatman paper, and analyzed either by inductively coupled plasma (ICP) emission spectrophotometry for low levels of metal (all copper and zinc EDTA wash) or atomic adsorption flame spectrophotometry (AAS, zinc dry ash digestion). Adsorbed metals were measured by measuring the metal content of a 10 ml, 1 mM EDTA solution in which a 1 gram sample of whole needles was washed for 30 minutes and the solution was filtered through #42 Whatman paper (Armstrong personal communication 1992). Absorbed metal was calculated by subtracting adsorbed metal from total metal.

Phloem Thickness

Phloem thickness of 50% girdled trees was measured to determine if trees with phloem area reduced by girdling compensated by growing thicker phloem. Bark samples were taken in May of 1992 (Cole and Jensen 1980). Squares of bark approximately 4 cm x 4 cm were cut through the cambium and peeled off the xylem from the intact area between the girdled patches, and two internodes above the girdle as a comparison. Samples were taken from all twelve blocks and measured using 0.7 magnification and a caliper by an impartial volunteer (Mellmann, personal communication 1992). The phloem thickness measured extended from the light colored cambium cells closest to the xylem to the dark colored periderm. Since this area varied in thickness, three measurements were made in areas of the phloem that were void of resin glands and the average was taken. Total bark thickness was also measured.

Statistical Analysis

Analysis of variance (ANOVA) was used across all measures to determine whether variance was associated with treatments or might have been due to other factors.

Data supporting this dissertation and related work are deposited in Jacobs and Weaver (1992).

RESULTS AND DISCUSSION

Root Pruning

Roots are stressed by being consumed by soil fauna such as nematodes and arthropods; by being mechanically and chemically damaged by human activities like logging and pollution; or by soil conditions including porosity, bulk density, water and nutrient content (Waisel et al. 1991). Although comparatively little attention is given to root pathogens, studies of below ground herbivores indicate they may consume more plant material than above ground herbivores (Detling et al. 1980). Root stress can reduce either the area or function of the roots, and since the shoot is dependent on the root system for water, mineral nutrients and certain plant growth regulators, reduction in root area is expected to be accompanied by proportional reduction in shoot function.

Horizontal and vertical root distribution in pines has been documented. In scots pine, the largest volume of fine roots was found in the first 1.5 meters from the stem and that there was a significant decrease in fine roots beyond this distance (Persson 1980). Also 98% of fine roots were found in the upper 30 centimeters of the mineral soil (Persson 1980, Moir and Bachelard 1969). By pruning the roots of lodgepole pine at the dripline (approximately 1 meter) and twice the dripline (approximately 2 meters), fine root mass (and area by extrapolation) was reduced by approximately 70%-80% and 10%-20% respectively, and by ditching to a depth of 50 centimeters 98%-100% of the fine roots important for water and mineral absorption in these areas became unavailable to the shoot (Weaver and Jacobs manuscript).

In the moderate treatment, where roots were pruned at a distance of twice the dripline from the stem, there was a small and statistically insignificant ($p > .05$) reduction in annual radial growth of the stem during the five years the treatment was applied (Table 2). The radial growth rate after 5 years was 72% of the average of the 3 pretreatment years compared to 78% in the control trees. The graph of radial growth (Figure 2) shows little difference in radial growth rate between moderately root pruned trees and controls, but the difference does increase with time. Thus there may be a small effect of moderate root pruning on shoot growth which, if the treatment were continued might become significant. Radial growth rate of the moderately root stressed trees was 85% of the controls after 5 years of root pruning compared to 92% for the same trees during the average of the 3 pretreatment years.

The severe root stress had a greater effect on stem radial growth causing a statistically significant reduction the second year of treatment ($p = .05$, Table 2). After five years of treatment, radial growth declined to 43% of the average growth rate of the 3 pretreatment years, and was 49% of the control trees growth rate (Table 2). The greatest decrease in growth rate relative to pretreatment growth occurred during the first three years of treatment, leveling off in the last two years (Figure 2). This suggests that if the treatment were continued the trees might survive at a reduced growth rate.

Because height growth rates varied more from year to year it was a less sensitive indicator of treatment stress. Moderately root stressed

Table 2. Radial growth of root pruned trees 1981-1988. (A) Values are expressed as means of twelve replications (mm/year) with letters indicating significant differences in means within rows using Newman-Kuels comparison of means. (B) Values are expressed as the percent of controls or pretreatment means.

(A)

Year		Control	Moderate	Heavy
Pretreatment				
1981		3.81 A	3.39 A	2.90 A
1982		3.29 A	3.06 A	2.78 A
1983		3.75 A	3.60 A	3.46 A
Treatment Years				
1984		3.47 A	3.39 A	3.21 A
1985	*	3.07 B	2.89 B	2.18 A
1986	*	2.67 B	2.50 B	1.57 A
1987	*	3.12 B	2.75 B	1.77 A
1988	*	2.82 B	2.40 B	1.39 A

* Rows with significant differences at the 5% level.

(B)

Year	Control	Moderate		Heavy	
	% of Pretreat.	% of Control	% of Pretreat.	% of Control	% of Pretreat.
81-83		92		84	
1984	96	98	101	93	105
1985	85	94	86	71	71
1986	74	94	75	59	51
1987	86	88	82	57	58
1988	78	85	72	49	46

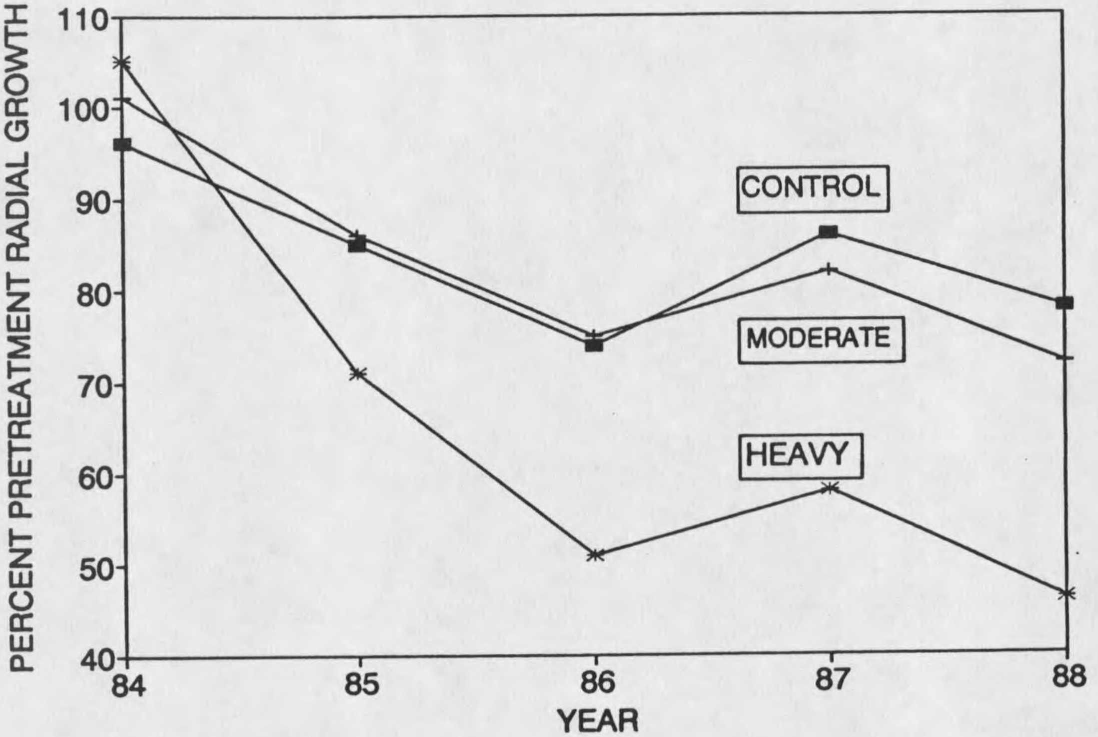

Figure 2. Lodgepole pine stem radial growth rate (percent of the mean of the three pretreatment years) during five years of root pruning at the dripline (severe treatment), twice the dripline (moderate treatment), and control (no pruning).

trees showed no difference from the controls in height growth. Severely root stressed trees never showed a significant reduction in height growth rate compared to controls until the fourth year (p = .01) and fifth year of treatment (p = .05, Table 3). Because of the high fluctuation in height growth from year to year, it is difficult to compare height growth in pre- and post-treatment years; this is especially so because height growth in the fifth year of treatment was so much greater than pretreatment years.

Table 3. Height growth (cm/year) of root pruned trees 1981 to 1988. Means of twelve replications with letters indicating significant differences in means within rows using Newman-Kuels comparison of means.

Year	Control	Moderate	% of Control	Heavy	% of Control
1981	33.5 A	34.1 A		25.3 A	
1982	30.8 A	32.0 A		24.0 A	
1983	30.5 A	34.2 A		33.0 A	
81-83	31.6	33.4	106	27.4	87
1984	29.8 A	30.1 A	101	31.7 A	106
1985	31.3 A	25.7 A	82	26.6 A	85
1986	29.4 A	27.0 A	92	27.3 A	93
1987 **	37.1 B	35.2 B	95	25.6 A	69
1988 *	41.7 B	40.2 B	96	32.7 A	78

* Rows with significant differences at the 5% level.
** Rows with significant differences at the 1% level.

Electrical resistance in the phloem (shigometer readings) increased in treated trees relative to controls suggesting a reduction in ions and vigor (Shortle et al. 1977, Smith et al. 1976). The difference is statistically significant (p = .05) only in the spring and late summer, and only under heavy pruning. Trees with roots pruned at the dripline showed a 16% and 17% increase in shigometer readings in June one and two years after treatment was begun, and a 13% and 19% increase in August of the same years (Table 4). The difference in June could be the result of greater spring moisture increasing the vigor of unpruned trees while pruned trees are unable to absorb water because of lost root area. Also

Table 4. Effect of root pruning on shigometer readings. Means of twelve replications with letters indicating significant differences in means within rows using Newman-Kuels comparison of means.

Date	Control	Moderate	Heavy
11 July 84	6.71 A	6.58 A	6.73 A
20 Aug. 84	10.28 A	10.43 A	11.38 A
18 Sept 84	11.58 A	12.76 A	11.74 A
29 June 85 *	6.08 A	6.57 AB	7.07 B
14 July 85	7.54 A	7.81 A	8.21 A
2 Aug. 85	10.42 A	10.47 A	10.92 A
24 Aug. 85 *	8.08 A	8.73 AB	9.17 B
11 Sept 85	12.00 A	11.97 A	12.50 A
14 June 86 *	6.30 A	6.58 AB	7.43 B
12 July 86	7.73 A	8.29 A	9.10 A
27 July 86	8.86 A	10.16 A	10.13 A
8 Aug. 86 *	9.13 A	9.59 AB	10.88 B
25 Aug. 86	10.62 A	10.74 A	11.23 A
7 Sept 86	10.85 A	11.50 A	12.34 A
24 Sept 86	14.80 A	14.52 A	14.70 A

* Rows with significant differences at the 5% level.

because of lost root area, heavily pruned trees may be more susceptible to lost vigor during periods of water stress in August.

From the whole tree perspective it is helpful to review these results in terms of the root/shoot ratio. The amount of shoot that a unit of root can supply with water and nutrients (and conversely the amount of root area the crown can supply with energy) is constant, and therefore, the growth of the crown is inextricably linked to root growth (Ledig et al. 1970). In this case, radial growth, the most sensitive measurement, was reduced by half when 80% of the root area was removed, but was unaffected when 20% of the roots were removed. In terms of fine root biomass, lodgepole can apparently afford to loose approximately one quarter of its roots before shoot growth is affected, and is only stressed when pathogens remove over half of its roots.

In the moderate treatment, the roots are confined to an area that becomes proportionally smaller relative to the normally growing crown, and at some point (possibly when the crown perimeter is equal to the root perimeter), shoot growth will begin to suffer. Root area at the start of treatment does not saturate all of the soil inside the treatment diameter so fine root growth in the ditched area supports crown growth. As long as the tree can maintain its root/shoot ratio in the limited soil area, the shoot should grow at a rate comparable to unpruned controls.

Conifer trees may allocate at least 65% of their carbon budget to below ground biomass (Grier et al. 1981), and up to 30% to root respiration alone (Lambers et al. 1991). Whereas the trees loose invested energy through pruning root biomass, they also may reduce energy demand for root respiration or maintenance. Factor compensation may, thus, explain why an 80% reduction in root area only caused a 50% reduction of stem diameter growth and even less reduction of height growth.

Another factor not to be overlooked is the effect root pruning has on the amount of growth regulators produced in the roots and transported to the shoot. It is believed that 70% of the cytokinin in plants is synthesized in the roots (Itai and Birnbaum 1991). Cytokinin is important in cell division and therefore important in growth. Also, abscisic acid produced in roots is important in stomatal regulation during drought (Zhang et al. 1987).

Root pruning has also been shown to reduce photosynthesis (Detling et al. 1980, Giesler and Ferree 1984). In beans, excision of 70-80% of the roots reduced photosynthesis even with water and mineral supplementation and CO_2 saturation (Carmi and Kaller 1978). This could be a cytokinin influence on regulation of chlorophyll or enzymes (RuBP carboxylase) important in carbon fixation (Caers et al. 1985).

Although root pruning at the level applied in this experiment did not kill trees, it did cause reduction in growth of the crown. With lodgepole pine, where intraspecific competition is the norm, root attack would likely put individuals at a lethal disadvantage. These results show that if resources supplied by the roots become limiting, height growth suffers after radial growth, indicating the terminal bud is the stronger nutrient sink than the lateral cambium.

Bud Pruning

Of the stress treatments applied in the experiment, bud pruning had the greatest visual impact on the trees; there was a striking loss of leaf area, especially when all buds were pruned. Heavily pruned trees maintained their height growth and thus produced tall spindly stems similar to lodgepole pine growing in a dense stand. Lateral buds were pruned from the terminal leader and there were no branches in the upper part of the crown (1.5 M average). Lower branches established before treatment were short and stubby. Since only 5 year old and older needles remained on the trees, the trees did not have the normal bright green color characteristic of younger needles. Trees with 50 % of their buds removed appeared similar to the controls, with only secondary branching patterns obviously different. Branches with the terminal bud removed had a dichotomous branching pattern compared to the decurrent form with whorls of secondary branches seen on the controls.

For comparison between bud pruning treatments and with other stress treatments such as acid spray (needle drop) and root pruning (reduced root area), leaf areas were estimated from the needle counts made in 1987, after four years of treatment (Table 5). The average of twelve replications for each branch internode for the seven years collected was summed to calculate total needle numbers for each bud pruning level. Since leaf area is proportional to needle size and number, and since needle size is consistent (Table 6), needle numbers expressed as a percent of controls gives a fair estimation of relative needle loss by bud pruning. Leaf area relative to controls was reduced by 36% in the

Table 5. Effects of bud pruning on needle number (needles/internode). Means of twelve replications with letters indicating significant differences in means within rows using Newman-Kuels comparison of means.

Year		Control	Moderate	Heavy
yr1	**	220.3 C	96.8 B	0.0 A
yr2	**	206.7 C	87.8 B	0.0 A
yr3	**	199.1 C	60.8 B	0.0 A
yr4	**	88.7 B	50.3 AB	0.0 A
yr5		170.8 A	147.9 A	172.9 A
yr6		168.8 A	154.6 A	190.3 A
yr7		148.9 A	164.7 A	169.9 A

** Rows with significant differences at the 1% level.

Table 6. Biomass per needle (grams) of a sample of control trees.

Needle Age	Control
yr1	0.017 A
yr2	0.020 A
yr3	0.019 A
yr4	0.020 A
yr5	0.022 A
yr6	0.022 A
yr7	0.023 A

moderate treatment and by 56% in the severe treatment. Since the leaf area of the treated trees relative to the controls decreases with each annual pruning, this estimate is accurate for the fourth year of treatment (1987) when the branches were collected. Reduction in leaf area would be less in years before 1987, and could be as much as 54% (moderate pruning) and 71% (severe pruning) in the fifth year. This is in contrast to root pruning where root area likely increases within the ditched radius so the initial ditching might cause the greatest reduction in root area. My leaf area calculation underestimates the loss of photosynthetic capacity because it does not take into consideration the photosynthetic efficiency of different age needles, that is, the youngest most productive leaves (O'Neil 1962) are removed by the pruning treatments. Conversely, the estimate is low due to omission of the leaves produced by the unpruned terminal leader, and a possible 13% increase in needle size of older needles (calculated from Table 6).

Despite the striking loss of young photosynthetic surface area (lost needles), bud pruned trees maintained height growth comparable to unpruned controls (Table 7). This is consistent with observations made on *Pinus resinosa* (Kozlowski and Winget 1964). When the sugar source from the lower portion of *P. resinosa* was cut off from the terminal leader by girdling, terminal leaders elongated normally as long as

Table 7. Height growth (cm/year) of bud pruned trees 1981 to 1988. Means of twelve replications with letters indicating no significant differences in means within rows using Newman-Kuels comparison of means.

Year	Control	Moderate	Heavy
1981	41.2 A	36.8 A	30.3 A
1982	40.2 A	38.3 A	31.3 A
1983	37.3 A	36.6 A	25.7 A
1981-1983 X	39.6	37.2	29.1
1984	38.0 A	36.5 A	23.5 A
1985	37.3 A	32.7 A	20.3 A
1986	34.8 A	29.2 A	18.9 A
1987	45.3 A	49.7 A	48.6 A
1988	43.8 A	45.5 A	46.9 A

needles on the leader remained intact. Therefore, removal of the buds below the terminal leader does not immediately affect leader elongation, and the terminal bud and the needles on the leader supply enough energy and growth regulators for that growth (Kozlowski and Winget 1964). If these data are projected into the future, there is no indication that continued treatment would decrease height growth even when all buds, except the terminal bud, are removed.

Unlike height growth, diameter growth of bud pruned trees does decline relative to controls (Table 8). Moderately bud pruned trees declined from a growth rate of 118% of controls for the three pretreatment years to an average of 84% of controls in the fifth year of pruning (not significant, $P > .05$). This compares to a decrease from 107% of control tree growth rate to 63% in the severe treatment ($P < .05$, Table 4). Decreased radial growth rate is more pronounced when compared to pretreatment growth rate (Figure 3). After five years of treatment, relative growth rate of moderately stressed trees decreased to 55% of pretreatment growth and severely stressed trees 45%, compared to 76% in controls.

The reduction of radial growth in the bud pruned trees can be explained by the loss of photosynthesis and perhaps auxin as well. First, diameter growth requires an energy source either from photosynthesis or stored reserves. Bud pruning effectively reduced the photosynthetic area available to the growing tree, and eliminated the young, most photosynthetically active leaves (O'Neil 1962), and thus reduced sugar supplies. Second, diameter growth requires a source of auxin which must be supplied by the buds (Denne and Wilson 1977), and

Table 8. Radial growth of bud pruned trees 1981-1988. (A) Values are expressed as means of twelve replications (mm/year) with letters indicating significant differences in means within rows using Newman-Kuels comparison of means. (B) Values are expressed as the percent of controls or pretreatment means.

(A)

Year		Control	Moderate	Heavy
Pretreatment years				
1981		3.57 A	4.26 A	3.71 A
1982		3.56 A	4.03 A	3.66 A
1983		3.86 A	4.60 A	4.41 A
81-83 mean		3.66	4.30	3.93
Treatment years				
1984		3.96 A	3.99 A	4.10 A
1985		3.60 A	3.25 A	3.60 A
1986		3.07 A	2.80 A	2.79 A
1987	*	3.52 B	2.57 B	2.32 A
1988	*	2.79 B	2.35 B	1.75 A

(B)

Year	Control	Moderate		Heavy	
	% of Pretreat.	% of Control	% of Pretreat.	% of Control	% of Pretreat.
81-83		118		107	
1984	108	101	93	104	104
1985	98	90	76	100	92
1986	84	91	65	91	71
1987	96	73	60	66	59
1988	76	84	55	63	45

* Rows with significant differences at the 5% level.

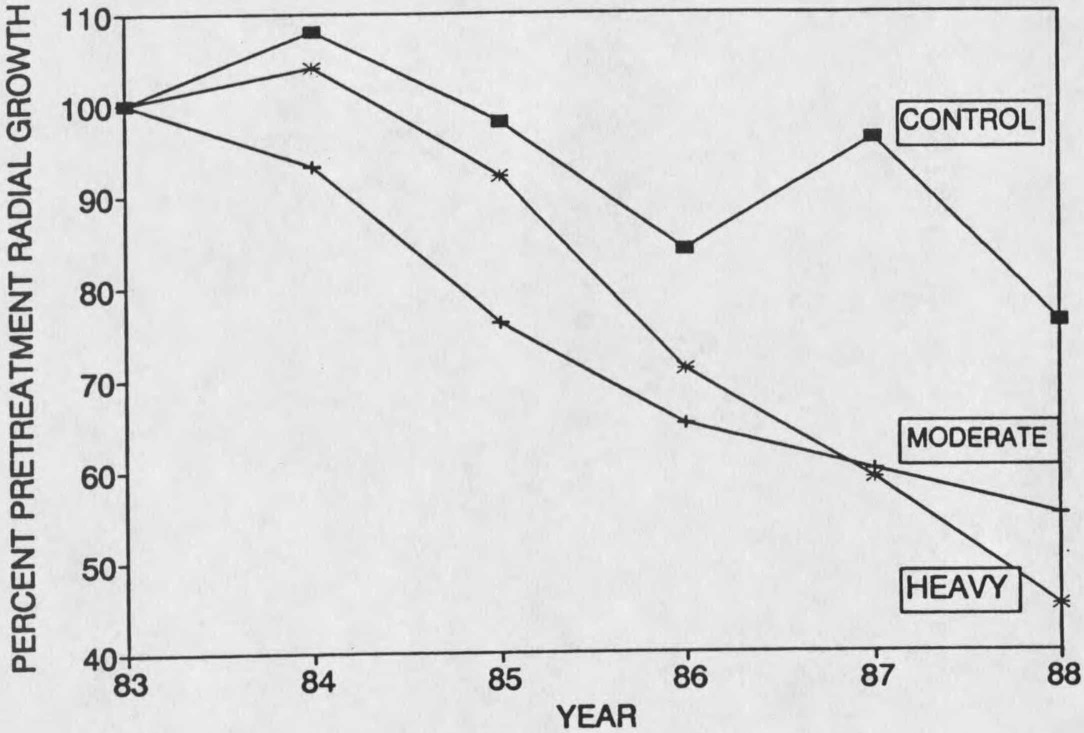

Figure 3. Lodgepole pine stem radial growth rate (percent of the mean of the three pretreatment years) during five years of bud pruning at three levels: all buds pruned (severe treatment), half the buds pruned (moderate treatment), and control (no buds pruned).

possibly the young leaves (Wareing 1982). Removal of all buds with needles effectively cuts off much of the auxin except that supplied by the terminal leader. With the normal growth of the terminal leader, this source of auxin became more remote. Also, auxin activity in xylem formation has been shown to be reduced by low sucrose concentration (Zajaczkowski, 1973).

Bud pruning might also affect growth in other areas of the tree. Gordon and Larson (1968) found young needles were important in supplying energy for growth of stems and roots. Hodgkinson and Bass Becking (1977) found reduced root growth in defoliated perennial plants; if this occurs in pines it could lead to water-nutrient deficiencies. This is consistent with the discussion of root/shoot ratios in the root stress section. Thus not only would we expect reduced diameter growth, but also a reduction in root growth, leaving bud pruned trees at a competitive disadvantage with their neighbors at the soil level.

During the first three years of bud pruning, there was no significant decrease in height or diameter growth even in the most severe treatment and this led to the hypothesis that the trees were maintaining growth levels by retaining old leaves longer, maintaining chlorophyll in the older leaves, and/or metabolizing stored energy reserves. Such adaptation is shown in tomato and tobacco plants when buds are removed; there was an increase in cytokinin in xylem sap, maintenance of chloroplast integrity, and a delay in leaf senescence (Colbert and Beever 1981). To determine whether such adaptations might explain maintenance of diameter growth in pruned trees, the health of needles in control and debudded branches was compared with respect to needle persistence and chlorophyll content after four years of treatment.

Consider needle persistence first. Control trees suggest a continuous decline (P > .05) in needle number per branch internode with age (Table 5). In the treatment years (yr 0-4), bud pruning eliminated all needles from fully debudded branches and half the needles from half-debudded branches. There was no significant difference (P > .05) in numbers of needles on the pre-treatment branch segments (years 4 through 6) of bud pruned trees compared to unpruned controls (Table 5). I conclude therefore, that trees loosing young needles to pruning did not compensate by holding on to older needles longer.

Second, the effect of debudding on the physiological condition of pre-treatment needles was indexed by comparing chlorophyll contents between needles from the fourth internodes of control and debudded trees. The chlorophyll content of four year old needles on debudded trees was not significantly higher (P > .05) than those of control trees (Table 9).

Table 9. Effect of bud pruning on chlorophyll content (mg/g). Means of twelve replications with letters indicating significant differences in means within rows using Newman-Kuels comparison of means.

4 yr Control	Moderate	Heavy
11.63 AB	12.39 B	12.85 B

* 2 yr control--9.45 A significant at p = .05.

I conclude that diameter growth of the bole of bud pruned trees was maintained by older needles and/or reserves, and as photosynthetic surface area decreased with needle drop and reserves were spent, diameter growth decreased.

If 100% bud pruning were continued, one could predict a continued reduction in diameter growth, that when combined with the continued height growth seen above, would leave a tall tree with a narrow stem low in timber value and susceptible to breaking from wind or snow loading. This tree form is typical of lodgepole pine growing in dense un-managed stands, for example stands regenerating after a forest fire. Pruning 50% of the buds had no effect when compared to unpruned controls (Table 8), but comparison to pretreatment growth shows even the moderate canopy stress could reduce radial growth if the treatment were continued (Figure 3).

No significant effect of debudding was seen on shigometer measurements and I therefore conclude that the shigometer was not effective in detecting stress that would lead to reduced diameter growth due to bud pruning stress (Table 10).

Bud pruning treatments simulated leaf/bud pathogen impacts on radial growth well since these pathogens will most likely consume the more susceptible immature foliage and nutrient rich buds reducing photosynthetic area and perhaps production of auxin. My results show that only an intense and persistent pathogenic attack on the buds and foliage of lodgepole pine will cause a reduction in wood production. Conversely, impacts on height growth are less well simulated since leaf/bud pathogens commonly attack the terminal leader also reducing

Table 10. Effect of bud pruning on shigometer readings. Means of twelve replications with letters indicating no significant differences in means within rows using Newman-Kuels comparison of means.

Date	Control	Moderate	Heavy
11 July 84	6.28 A	6.99 A	7.15 A
20 Aug. 84	9.55 A	9.83 A	8.73 A
18 Sept 84	11.94 A	11.06 A	11.07 A
29 June 85	6.80 A	6.30 A	6.16 A
14 July 85	7.17 A	7.74 A	7.01 A
2 Aug. 85	9.05 A	9.63 A	9.03 A
24 Aug. 85	8.14 A	8.00 A	7.90 A
11 Sept 85	11.22 A	11.61 A	11.33 A
14 June 86	6.33 A	6.58 A	6.06 A
12 July 86	6.90 A	7.84 A	6.88 A
27 July 86	8.30 A	8.60 A	7.98 A
8 Aug. 86	8.68 A	9.08 A	8.14 A
25 Aug. 86	10.17 A	10.35 A	10.03 A
7 Sept 86	10.07 A	10.70 A	10.42 A
24 Sept 86	14.32 A	15.02 A	15.02 A

height growth. Because a major response variable was height growth, I never pruned terminal buds and height growth was never significantly inhibited. Thus, the heavy bud pruning treatment is more characteristic of lodgepole pine in a dense forest occurring after fire.

Girdling

Stress caused by leaf and root grazers may reduce growth in lodgepole pine, and this stress appears to be elastic, that is, if the stress is taken away, growth would return to normal. On the other hand, pathogens that feed on the phloem are more destructive, and when they successfully attack a tree, they kill by girdling it. Such a pathogen, Mountain Pine Beetle (Dendroctonus ponderosae Hopkins,) is the largest source of insect caused mortality of lodgepole pine, and along with fire is important in giving a seral tree a persistent role in forest succession (Peterman 1978).

The effects of tree girdling are well studied and the method has been long used in the study of phloem transport (Noel 1970). What makes experimental girdling interesting is that it disrupts the flow of transported solutes including sugars and growth regulators from the canopy to the roots, yet the transport of root absorbed water and mineral nutrients in the xylem to the canopy is undisturbed. This allows for conclusions to be drawn on the longevity of roots when they are dependent only on stored reserves for growth and maintenance. Also transport of solutes can be studied.

I expected the 100% mechanical girdle to cause tree mortality. Trees generally die one to two years after girdling but can survive for up to 10 years (Noel 1970, Starker 1942). In this case, the first tree died (as indicated by brown needles and high shigometer resistance, Table 11) in June of 1986, one full growing season after the treatment was applied. By the end of the second growing season, half of the 100% girdled trees had died. Five years after girdling, two trees remained alive, but with a much reduced growth rate (1.06 mm/year radial growth, 8.25 cm/year height growth).

The difference in the response above and below the girdle was seen in the shigometer readings and radial growth measurements (Tables 12 and 11). In September 1984, one month after the trees were girdled, phloem vigor significantly increased (relative to controls) above the girdle

Table 11. Effect of conventional girdle on shigometer readings (K-Ohms). Means of twelve replications with letters indicating significant differences in means within rows using Newman-Kuels comparison of means.

Date		Control	Moderate	Heavy	P-Value
Above Girdle					
3 Sept 84		9.83 A	9.73 A	8.96 A	> .05
18 Sept 84	*	11.12 B	11.24 B	9.34 A	.006
30 Sept 84		12.56 A	12.57 A	10.59 A	> .05
29 June 85		5.99 A	5.80 A	5.87 A	> .05
14 July 85		7.18 A	6.77 A	7.26 A	> .05
2 Aug. 85		9.04 A	9.14 A	8.30 A	> .05
24 Aug. 85		7.72 A	7.03 A	6.48 A	> .05
11 Sept 85	*	11.32 B	11.24 B	7.28 A	< .001
14 June 86		6.67 A	6.50 A	50.75 A	> .05
12 July 86		7.45 A	6.83 A	93.28 A	> .05
27 July 86		7.54 A	8.25 A	148.20 A	> .05
8 Aug. 86	*	18.08 A	8.18 A	204.60 B	.02
25 Aug. 86	*	22.26 A	9.01 A	211.70 B	.005
7 Sept 86	*	23.35 A	10.19 A	211.60 B	.005
24 Sept 86	*	27.37 A	14.33 A	213.20 B	.005
27 Aug. 87	*	9.78 A	10.14 A	253.7 B	.0008
15 Sept 87	*	12.72 A	12.77 A	255.2 B	.0008
7 Oct. 87	*	13.66 A	13.74 A	255.1 B	.0008
Below Girdle					
3 Sept 84		9.21 A	9.59 A	8.28 A	> .05
18 Sept 84		11.22 A	11.58 A	10.00 A	> .05
30 Sept 84		13.06 A	13.85 A	12.85 A	> .05
29 June 85	*	5.63 A	6.99 A	15.63 B	< .001
14 July 85	*	6.79 A	8.25 A	22.44 B	< .001
2 Aug. 85		8.42 A	9.56 A	72.13 A	.04
24 Aug. 85		7.61 A	7.93 A	54.33 A	.1
11 Sept 85		10.76 A	12.08 A	75.38 A	.07
14 June 86	*	6.38 A	6.69 A	163.00 B	.002
12 July 86	*	6.52 A	6.56 A	213.30 B	.001
27 July 86	*	8.23 A	8.56 A	212.90 B	.001
8 Aug. 86	*	7.83 A	8.39 A	259.60 B	< .001
25 Aug. 86	*	8.53 A	8.63 A	259.00 B	< .001
7 Sept 86	*	9.48 A	9.70 A	261.10 B	< .001
24 Sept 86	*	12.99 A	12.12 A	271.00 B	< .001
27 Aug. 87	*	9.24 A	9.39 A	268.4 B	< .001
15 Sept 87	*	12.58 A	11.92 A	285.1 B	< .001
7 Oct. 87	*	13.05 A	13.63 A	285.7 B	< .001

* Rows with significant differences at the 5% level.

Table 12. Radial growth of girdled trees 1981-1988. (A) Values are expressed as means of twelve replications (mm/year) with letters indicating significant differences in means within rows using Newman-Kuels comparison of means. (B) Values are expressed as the percent of controls or pretreatment means.

(A)

Year		Control	Moderate	Heavy
Precondition years				
1981		3.86 A	4.38 A	3.63 A
1982		3.59 A	3.76 A	3.69 A
1983		4.53 A	4.53 A	3.85 A
81-83 Mean		3.99	4.22	3.72
Treatment years				
1984		4.16 A	4.25 A	4.56 A
1985		3.88 A	3.84 A	4.07 A
1986		3.32 A	3.40 A	2.79 A
1987	*	3.75 B	3.72 B	0.67 A
1988	*	3.17 A	3.13 B	0.44 A

(B)

Year	Control	Moderate		Heavy	
	% of Pretreat.	% of Control	% of Pretreat.	% of Control	% of Pretreat.
81-83		106		93	
1984	104	102	101	123	110
1985	97	99	91	105	109
1986	83	102	81	84	75
1987	93	99	88	18	18
1988	79	99	74	14	12

* Rows with significant differences at the 5% level.

Table 13. Effect of girdle on diameter growth mm/week (band dendrometers, Liming 1957). Means of six replications with letters indicating significant differences in means within rows using Newman-Kuels comparison of means.

		Treatments	
	Control	Moderate	Heavy
29 June 85 - 11 Sept 85			
Above Girdle	0.06 A	0.13 A	0.15 A
Below Girdle *	0.10 B	0.13 B	-0.01 A
14 June 86 - 24 Sept 86			
Above Girdle	0.30 A	0.30 A	0.12 A
Below Girdle *	0.30 B	0.28 B	0.00 A

* Rows with significant differences at the 5% level.

(P = .006), which was also seen in the fall of 85 (P < .001). This was the result of the build up of photosynthate and perhaps growth regulators at the girdle (Noel 1970). As suggested by the shigometer readings, there was also a corresponding increase in radial growth in this region (Tables 13 and 12). It was not until one full growing season later that the stem above the girdle showed signs of stress (reduction in shigometer readings, P = .02 to .005, Table 12). The stem below the girdle was unaffected the year it was girdled, and first showed signs of stress in the spring following girdling.

The shigometer showed the progression toward death from girdling over the course of the growing season. In 1986, the second growing season after girdling, 4 trees died. This was recognized by the shigometer when no electrical current passed between the probes resulting in the highest reading on the meter (500 K-Ohms). In all cases, death occurred below the girdle first. The below girdle stem cambium and phloem (and presumably roots since this system was still intact and possibly shared reserves) was able to live at a level of conductance 1/2 to 1/3 that of the control trees (Table 11). Death in the stem below the cambium was first apparent with an increase in shigometer readings to 500 K-Ohms over a period of 2-4 weeks. After the lower stem reached readings of 500 the stem above the girdle showed a rapid increase in shigometer readings and was dead within 2-4 weeks. In one case, the stem above the girdle survived for the growing season when the lower stem was dead. From these results we can draw two conclusions. First, the lower stem and roots cut off from energy provided from the crown can survive on reserves for an average of 2 years. Second, once the lower part of the tree dies, the upper stem and canopy dies within one month.

Height growth of girdled trees -- both 50% and 100% -- remained normal relative to controls two years after treatment (1985 and 1986, Table 14). The trees were girdled in August of 1984, and since height growth occurs in the spring, no effect of the girdle was expected in 1984. Height growth of fall girdled trees dropped off dramatically in 1987 and 1988 to a rate of 10.8 (three live trees in 1987) and 7.8 cm/year (two live trees in 1988) compared to 42.3 and 46.7 (the control tree averages for 1987 and 1988). This shows again that the roots were able to survive on the average for two years after the girdle, and where they survived longer their growth and function was much reduced. Height growth of 50% girdled trees was unaffected.

Table 14. Height growth (cm/year) of girdled trees 1981 to 1988. Means of twelve replications with letters indicating significant differences in means within rows using Newman-Kuels comparison of means.

Year		Control	Moderate	Heavy
1981	**	43.0 B	40.1 B	14.4 A
1982		29.3 A	42.2 A	30.7 A
1983		29.3 A	40.0 A	38.3 A
81-83 Mean		33.9	40.8	27.8
1984		26.4 A	36.7 A	35.8 A
1985		24.1 A	36.0 A	32.4 A
1986		21.8 A	33.7 A	32.0 A
1987	**	42.3 B	41.8 B	1.8 A
1988	**	46.7 B	47.9 B	2.2 A

** Rows with significant differences at the 1% level.

Radial growth measured from cores taken above the girdle shows similar results. There was no decrease in growth until two growing seasons after the 100% girdle, and there was never any effect of the 50% girdle (Table 12 and Figure 4). Radial growth above the girdle increased in the 100% girdle treatment the year of treatment and the following year due to the build up of basipetally transported photosynthate (and auxin) at the girdle (Table 12 and Figure 4). This is compared to the shrinking of the stem as it dried out below the girdle (band dendrometers, Table 13).