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.

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APPROVAL

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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
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Date 23 July 1992

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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):

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

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

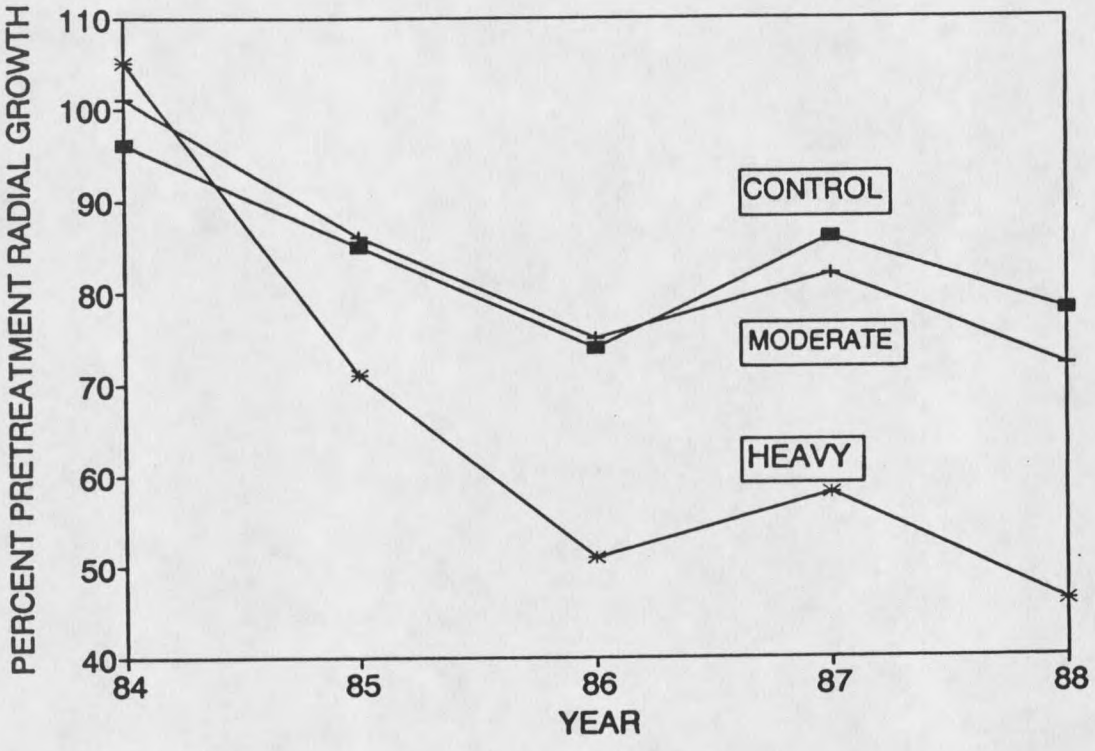

Figure 2. Lodgepole pine stem radial growth rate (percent of the mean of the three pretreatment years) during five years of root pruning at the dripline (severe treatment), twice the dripline (moderate treatment), and control (no pruning).

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.

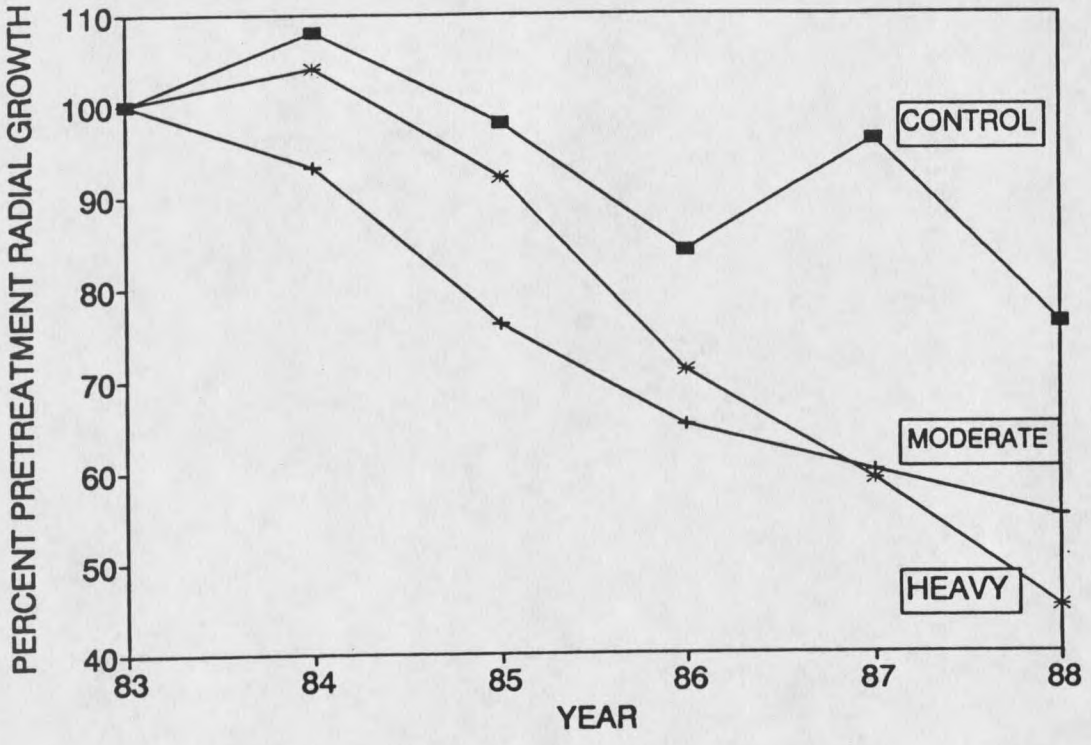

Figure 3. Lodgepole pine stem radial growth rate (percent of the mean of the three pretreatment years) during five years of bud pruning at three levels: all buds pruned (severe treatment), half the buds pruned (moderate treatment), and control (no buds pruned).

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).

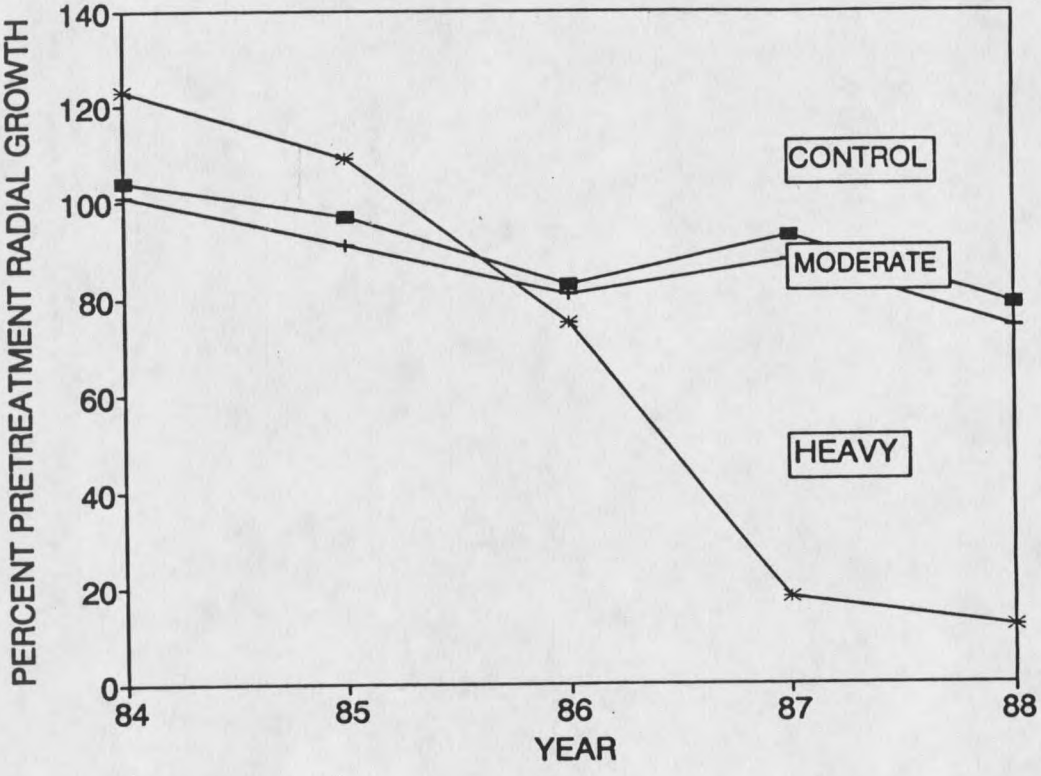

Figure 4. Lodgepole pine stem radial growth rate (percent of the mean of the three pretreatment years) during five years of girdling at three levels: complete girdle (severe treatment), half girdle (moderate treatment), and control (no girdle).

It was expected that the 50% girdle would reduce growth of trees. That this did not happen suggests the tree either does not need the amount of phloem that it produces, or that it compensated for reduced phloem in the region of the girdle by doubling the phloem thickness in the ungirdled area. Comparison of phloem thicknesses showed phloem in the area between the girdles was significantly thicker than in the undisturbed internode (mean 1.99 mm compared to 1.75 mm, $P = .038$). The bark was significantly thicker (means 4.28 mm compared to 3.83 mm, $P = .031$) in the girdled than in the ungirdled internode of the tree. Such differences are from accumulation of past phloem and cork and are coarse measurements because of the variation in roughness and smoothness of lodgepole pine bark. I conclude that while trees do have excess phloem capacity, some compensatory phloem growth does occur. Compensation is only partial because while phloem area was reduced by 50%, phloem thickness was only increased by 13%. One might also expect compensatory increases in xylem thickness between the girdled patches since xylem is not produced in the area of the girdle where the cambium was cut away and such growth might compensate for decreased xylem production in girdled areas. Increased growth in ungirdled areas might be supported by increased flows of sugar through adjacent overly developed phloem (though there is no more area of contact).

In conclusion, while the 100% girdle killed the trees as expected, it took 1 to 5 years with an average of 2-3 years. Death of the canopy promptly followed root death. I speculate that roots were able to survive on stored reserves approximately two years, but with some lasting as long as 5 years. Girdling caused an increase in radial growth above

the girdle due to accumulation of basipetally transported nutrients and perhaps growth regulators and a shrinking of the stem below the girdle due to drying of the stem. The 50% girdle did not affect growth because of excess initial capacity, greater flow rates, and/or compensatory phloem growth between girdled patches. There is probably some point between 50% and 100% girdle where growth is reduced. Partial girdling could open trees to infection though none was seen in this experiment. Abnormal stem growth caused by removal of the cambium was observed, and could weaken the stem making it susceptible to breakage from wind or snow loading.

Acid Spray

Acid deposition from anthropogenic sources is suspected as a cause of the forest decline occurring in eastern Canada (Zoheir and Baschak 1987), northeastern United States (Siccama et al. 1982, Vogelmann 1982), and Europe (Blank 1985). That the acid deposition is causal is, however, under dispute (Woodman and Cowling 1987). Experiments using conifer seedlings in controlled environments have shown that highly acid (pH 1-3) simulated rains cause reduction in germination and early growth, leaching of nutrients, chlorosis, necrosis, erosion of cuticular waxes of foliage, and death (McColl and Johnson 1983, Maurice and Crang 1986, and others). Needle spotting, needle loss, cuticle erosion, and nutrient leaching have also been measured in forest trees exposed to pollution (Armentano and Menges 1987, Karhu and Huttunen 1986, Rice et al. 1986, and Zech et al. 1984). If field studies are confounded by uncontrolled environmental factors, however, they provide no conclusive evidence that acid

deposition affects forest productivity (Woodman and Cowling 1987). My experiment examines the effects of simulated acid precipitation on the foliage and wood production of healthy forest trees growing in natural forest stands without the non-acid pollutants (metals and ozone) confounding field work done in the Northeast.

Leaf Response

Because acid rain is deposited on leaves evidence of its impact on three indices of needle function were examined. 1) Lowered chlorophyll content, usually a good indicator of stress (Treshow 1970, Todd and Arnold 1961), did not appear even under very acid conditions (Table 15). Similarly, in an experiment using flow cytometry, Sigal et al. (1988) found no effect of acid (pH 5 to pH 3.5) on chlorophyll autofluorescence intensities of isolated loblolly pine needle protoplasts. 2) Needle weight (needle size, also an indicator of stress) which might have been decreased by nutrient leaching (Maurice and Crang 1986) or lowered

Table 15. Effect of stress treatments on chlorophyll content (mg/g) of 2 year old needles. Means of twelve replications with letters indicating no significant differences in means within rows using Newman-Kuels comparison of means.

Treatment	Number of Sprays	Control	Moderate	Heavy
Annual HNO_3	5	11.96 A	12.37 A	12.93 A
Annual H_2SO_{O4}	5	12.87 A	12.48 A	13.25 A
Repeated H_SO_4	14	12.09 A	12.20 A	11.67 A

photosynthesis, were not affected even by the most rigorous treatment (Table 16). 3) Acid treatment might reduce the water content of needles increasing water loss through either erosion of the cuticle or causing stomatal dysfunction (Tamm and Cowling 1977, Zech et al.). I observed no difference in the water content of control needles and those sprayed with either dilute acid of ph 3 or more concentrated acid of pH 1 (Table 17).

Acid stress might also cause chlorosis or abscission of needles (basal injury, Rice et al.). Visual examination (Todd and Arnold 1961) showed low levels of foliar injury, so despite high variability, it can be concluded that the pH 1 (though not pH 3) treatment increased chlorosis relative to the control (Table 18), though it was not great enough to affect chlorophyll measurements (above). This damage is least in current year needles, perhaps because they have been treated fewer times, but does not vary much among needles of older age classes.

Since heavily damaged needles are abscised (Table 19) one might expect needle numbers (and weights) to be smaller on treated than untreated trees. No such effect of pH 3 was seen. While stronger acid (pH 1) apparently has no effect on retention of young needles (1-4 years) it did cause a reduction in older (5-7 year old) photosynthetic surface (Tables 19 and 16, Figures 5 and 6).

One may speculate that older needles suffered greater damage because cracked and eroded cuticles allowed more acid to enter and/or made needles accessible to attacking insects (Karhu and Huttunen 1986). Rice et al. (1986) attributed basal injury to needles of ponderosa pine growing in areas of high sulfur emissions in Billings and Colstrip, Montana to concentration of acid at the point of needle attachment in the

Table 16. Effect of acid treatments on biomass per needle (grams). Means of twelve replications with letters indicating no significant differences in means within rows using Newman-Kuels comparison of means.

Needle Age	Number of Spray	Control	Moderate	Heavy
		Repeated H_2SO_4 Treatment		
yr1	4	0.017 A	0.018 A	0.022 A
yr2	10	0.020 A	0.019 A	0.022 A
yr3	13	0.019 A	0.020 A	0.021 A
yr4	13	0.017 A	0.019 A	0.015 A
yr5	13	0.020 A	0.021 A	0.017 A
yr6	13	0.022 A	0.023 A	0.021 A
yr7	13	0.024 A	0.028 A	0.019 A
		Annual H_2SO_4 Treatment		
yr1	1	0.017 A	0.018 A	0.018 A
yr2	2	0.020 A	0.020 A	0.017 A
yr3	3	0.019 A	0.020 A	0.021 A
yr4	4	0.020 A	0.021 A	0.020 A
yr5	4	0.022 A	0.022 A	0.022 A
yr6	4	0.022 A	0.020 A	0.021 A
yr7	4	0.023 A	0.026 A	0.020 A

Table 17. Effects of acid treatments on needle water content (g water/ g needle). Means of twelve replications with letters indicating no significant differences in means within rows using Newman-Kuels comparison of means.

Needle Age	Number of Spray	Control	Moderate	Heavy
		Annual H_2SO_4 Treatment		
yr1	1	1.196 A	1.206 A	1.234 A
yr2	2	1.134 A	1.125 A	1.121 A
yr3	3	1.055 A	1.058 A	1.078 A
yr4	4	0.897 A	0.896 A	0.876 A
yr5	4	0.993 A	0.989 A	1.001 A
yr6	4	1.000 A	0.976 A	1.005 A
yr7	4	1.084 A	0.981 A	0.832 A
		Repeated H_2SO_4 Treatment		
yr1	4	1.060 A	1.188 A	1.184 A
yr2	10	1.009 A	1.094 A	1.072 A
yr3	13	0.947 A	1.029 A	0.985 A
yr4	13	0.824 A	0.822 A	0.557 A
yr5	13	0.887 A	0.983 A	0.668 A
yr6	13	0.807 A	0.981 A	0.801 A
yr7	13	0.780 A	0.986 A	0.750 A

Table 18. Effects of acid treatments on needle damage (chlorosis, % needles >10% damaged). Means of twelve replications with letters indicating significant differences in means within rows using Newman-Kuels comparison of means.

Needle Age	Number of Spray		Control	Moderate	Heavy
		Repeated H_2SO_4 Treatment			
yr1	1		2.175 A	1.567 A	1.317 A
yr2	2		1.917 A	2.792 A	4.300 A
yr3	3	*	2.375 A	3.950 A	9.733 B
yr4	4		1.236 A	3.381 A	3.936 A
yr5	4	*	4.733 A	1.658 A	30.22 B
yr6	4		9.583 A	1.175 A	18.34 A
yr7	4		8.992 A	1.958 A	25.07 A
		Annual H_2SO_4 Treatment			
yr1	4		4.067 A	2.992 A	2.892 A
yr2	10	*	1.908 A	2.492 A	10.18 B
yr3	13		2.633 A	4.117 A	5.600 A
yr4	13		16.18 A	17.47 A	8.392 A
yr5	13		3.883 A	2.450 A	6.817 A
yr6	13	*	1.917 A	1.633 A	4.600 B
yr7	13		1.233 A	1.208 A	1.450 A

* Rows with significant differences at the 5% level.

Table 19. Effects of acid spray on needle number per internode. Means of twelve replications with letters indicating significant differences in means within rows using Newman-Kuels comparison of means.

Needle Age	Number of Spray		Control	Moderate	Heavy
		Annual H_2SO_4 Treatment			
yr1	1		197.9 A	158.0 A	175.8 A
yr2	2		190.4 A	180.0 A	175.0 A
yr3	3		150.3 A	146.2 A	172.5 A
yr4	4		59.6 A	39.1 A	33.8 A
yr5	4		172.5 A	160.3 A	143.7 A
yr6	4	**	168.8 AB	205.3 B	119.8 A
yr7	4	*	160.4 B	178.7 B	89.4 A
		Repeated H_2SO_4 Treatment			
yr1	4		166.9 A	169.3 A	170.4 A
yr2	10		163.4 A	144.3 A	162.4 A
yr3	13		175.6 A	139.3 A	137.5 A
yr4	13		73.4 A	52.3 A	27.3 A
yr5	13	**	141.9 B	174.3 B	55.3 A
yr6	13	**	159.1 B	196.7 B	28.5 A
yr7	13	**	111.9 B	162.3 B	22.4 A

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

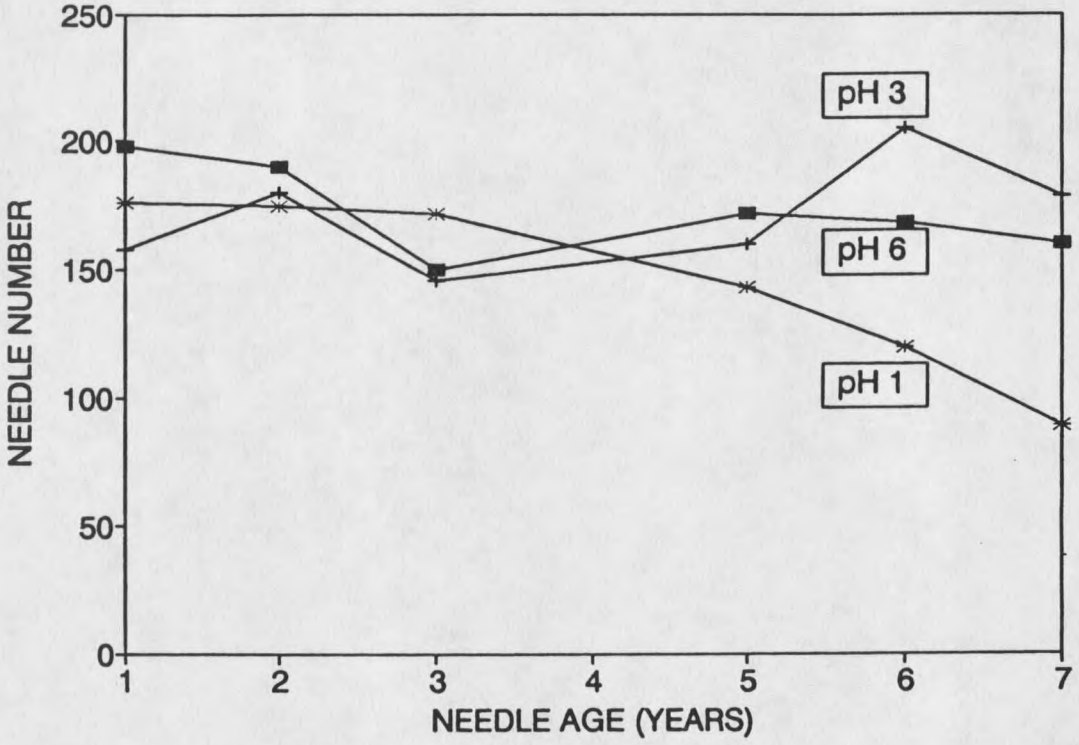

Figure 5. Lodgepole pine needle number per internode (7 years) on branches of trees sprayed annually for five years with three concentrations of H_2SO_4: pH 1 (severe treatment), pH 3 (moderate treatment), and pH 6 (control).

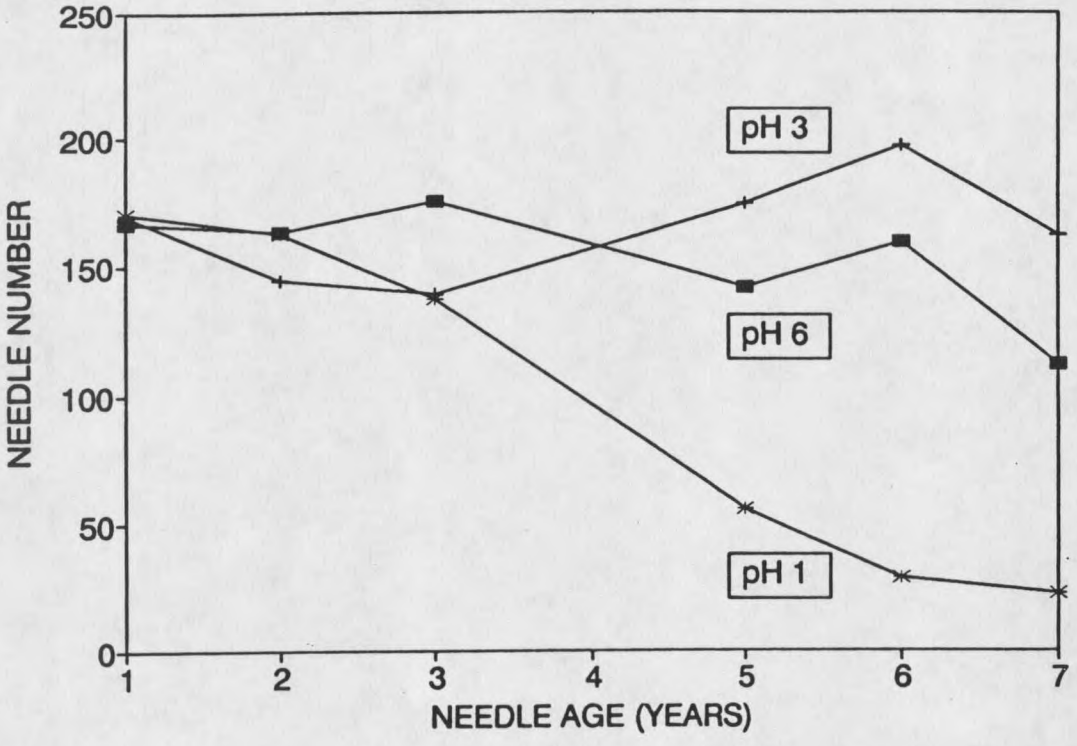

Figure 6. Lodgepole pine needle number per internode (7 years) on branches of trees sprayed fortnightly for four growing seasons with three concentrations of H_2SO_4: pH 1 (severe treatment), pH 3 (moderate treatment), and pH 6 (control).

fascicle. Though not statistically significant, my pH 3 acid treatment appears to increase needle retention suggesting a beneficial effect of acid to conifer needles. Repeated applications of dilute H_2SO_4 or HNO_3 solutions (pH 2.3-5.6) stimulated conifer (Pinus, Pseudotsuga and Juniperus) growth perhaps due to sulfur and nitrogen fertilization (Lee and Weber 1979, Wood and Borman 1971), or increased levels of phosphorous as in loblolly pine needles exposed to pH 3 acid rain (Lee et al. 1990). Increases in photosynthesis have also been reported in red spruce (Kohut et al. 1990) and loblolly pine (Lee et al. 1990) treated with acid rain pH 3.

Growth Parameters

In the long term wood production is the best economic (and physiologic) indicator of acid stress effects. After three years of treatment there was no significant effect of annual acid precipitation (either pH 3 or pH 1) on either height growth (Tables 20-22) or radial growth (Tables 23-25) of Pinus contorta. Fortnightly dousings at pH 1, but not pH 3, caused a significant decrease in radial growth in the third year of treatment (Table 23, Figure 7), and a significant decrease in height growth five years after treatment was started (14 sprays) (Table 22). One might expect to see height growth affected after radial growth because, while current year conditions determine radial growth, previous year conditions determine bud elongation. Delayed response to acid stress has also been seen in other response parameters. Sigal et al. (1988) demonstrated that pollution stress can have biochemical effects on the following year's needle crop.

Table 20. Height growth (cm/year) of annual H_2SO_4 sprayed trees 1981 to 1988 (5 sprays). 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	39.0 A	40.0 A	37.9 A
1982	37.0 A	41.4 A	37.9 A
1983	37.0 A	36.8 A	35.3 A
81-83 Mean	37.66	39.4	37.0
1984	32.8 A	36.7 A	34.8 A
1985	32.8 A	32.5 A	29.5 A
1986	31.7 A	32.0 A	32.0 A
1987	43.7 A	41.6 A	37.9 A
1988	45.4 A	45.7 A	42.1 A

Table 21. Height growth (cm/year) of annual HNO_3 sprayed trees 1981 to 1988 (5 sprays). Means of twelve replications with letters indicating significant differences in means within rows using Newman-Kuels comparison of means.

Year		Control	Moderate	Heavy
1981		34.2 A	39.6 A	41.8 A
1982		36.2 A	40.7 A	42.0 A
1983	*	35.8 A	37.8 AB	43.1 B
81-83 Mean		35.4	39.4	42.3
1984		34.8 A	36.7 A	40.2 A
1985		31.1 A	31.3 A	36.2 A
1986		29.6 A	30.5 A	34.4 A
1987		40.87 A	40.8 A	44.9 A
1988		43.9 A	41.1 A	43.7 A

* Rows with significant differences at the 5% level.

Table 22. Height growth (cm/year) of repeated H_2SO_4 sprayed trees 1981 to 1988 (14 sprays). Means of twelve replications with letters indicating significant differences in means within rows using Newman-Kuels comparison of means.

Year		Control	Moderate	Heavy
1981	*	34.9 AB	40.5 B	32.3 A
1982		38.0 A	39.3 A	36.2 A
1983		32.2 A	38.8 A	35.9 A
81-83 Mean		35.0	39.5	34.8
1984		32.6 A	38.7 A	33.25 A
1985		31.7 A	39.2 A	33.4 A
1986		29.4 A	36.16 A	30.4 A
1987		37.8 A	43.0 A	34.0 A
1988	*	42.9 B	42.8 B	30.3 A

* Rows with significant differences at the 5% level.

Table 23. Radial growth of repeated H_2SO_4 sprayed trees 1981-1988 (14 sprays). (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	3.10 A	3.71 A	4.17 A
1982	3.05 A	3.45 A	3.33 A
1983	3.58 A	3.87 A	3.95 A
1984	3.52 A	3.92 A	3.91 A
Mean	3.81	3.74	3.84
Treatment Years			
1985	3.14 A	3.51 A	3.18 A
1986	2.89 A	3.09 A	2.82 A
1987 *	2.92 B	3.30 B	2.17 A
Post treatment			
1988	2.63 A	2.68 A	2.29 A

(B)

Year	Control	Moderate		Heavy	
	% of Pretreat.	% of Control	% of Pretreat.	% of Control	% of Pretreat.
81-84		98		101	
1985	82	111	93	101	83
1986	75	107	82	98	73
1987	77	113	88	74	57
1988	69	102	72	87	60

* Rows with significant differences at the 5% level.

Table 24. Radial growth of annual H_2SO_4 sprayed trees 1981-1988 (5 sprays). (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	NO DATA		
1982	3.31 A	3.30 A	3.27 A
1983	3.84 A	3.77 A	4.01 A
Mean	3.58	3.54	3.64
Treatment years			
1984	3.66 A	3.58 A	3.78 A
1985	3.50 A	3.24 A	3.30 A
1986	3.01 A	2.87 A	2.76 A
1987	3.37 A	3.43 A	3.18 A
1988	2.83 A	2.65 A	2.85 A

(B)

Year	Control	Moderate		Heavy	
	% of Pretreat.	% of Control	% of Pretreat.	% of Control	% of Pretreat.
81-83		99		102	
1984	102	97	101	103	104
1985	98	108	92	94	91
1986	84	95	81	92	76
1987	94	102	97	94	87
1988	79	94	75	101	78

Table 25. Radial growth of annual HNO_3 sprayed trees 1981-1988 (5 sprays). (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	3.37 A	3.75 A	4.09 A
1982	3.38 A	3.53 A	3.44 A
1983	4.16 A	4.19 A	4.18 A
Mean	3.64	3.82	3.90
Treatment years			
1984	4.19 A	4.09 A	4.04 A
1985	3.77 A	3.62 A	3.66 A
1986	3.17 A	3.29 A	3.26 A
1987	3.45 A	3.64 A	3.47 A
1988	3.10 A	3.13 A	3.16 A

(B)

Year	Control	Moderate		Heavy	
	% of Pretreat.	% of Control	% of Pretreat.	% of Control	% of Pretreat.
81-83		105		107	
1984	115	98	107	96	103
1985	103	96	95	97	94
1986	87	104	86	103	84
1987	95	106	95	101	89
1988	85	101	82	102	81

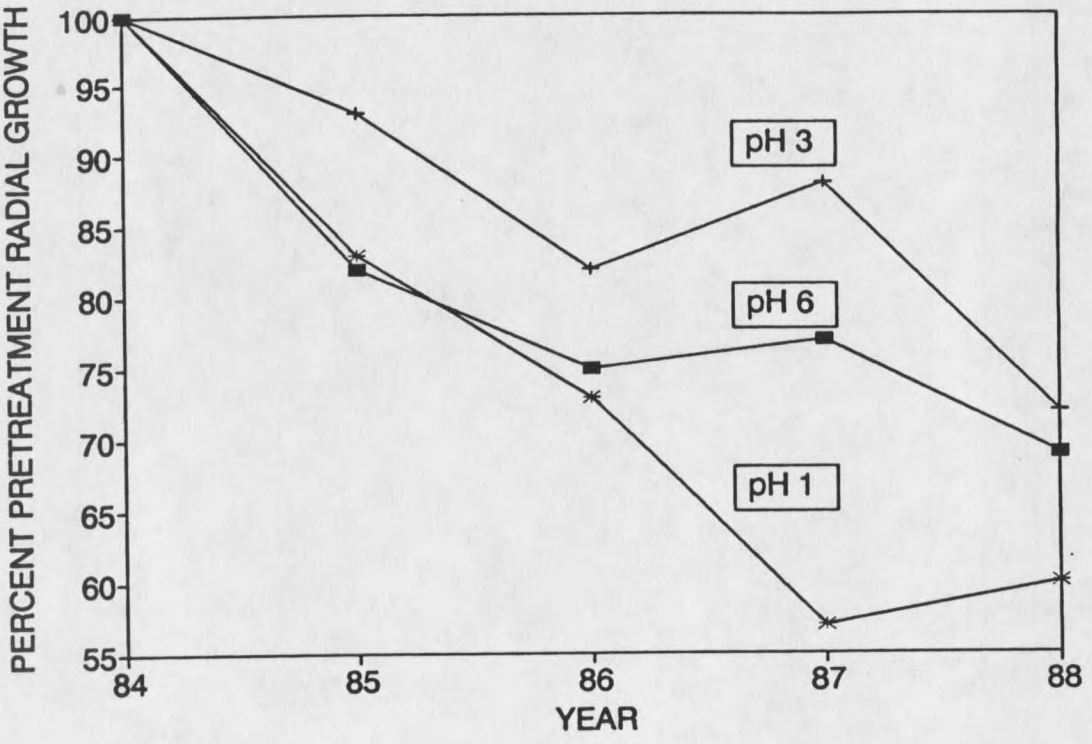

Figure 7. Lodgepole pine stem radial growth rate (percent of the mean of the three pretreatment years) during four growing seasons of fortnightly H_2SO_4 spray at three concentrations: pH 1 (severe treatment), pH 3 (moderate treatment), and pH 6 (control).

From this data one might conclude that lodgepole pine is insensitive to acid deposition at any likely level and therefore is not a reliable indicator of acid pollution. Greenhouse studies (Jacobs et al. 1992) support this conclusion; seedlings after dipped once in solutions with concentrations up to pH 2, an extremely acid rain, showed no increase in chlorosis or needle death. More mature saplings studied here showed growth reduction only after repeated applications at pH 1, a concentration far greater than acid rain (Marsh 1983, Knapp et al. 1988). Similarly, Pinus strobus needle damage appeared only when pH fell to the 0.5-1 range (Haines et al. 1980). It is conceivable that acid this strong could occur as water from acid rain evaporates from foliage.

For three reasons acid rain might affect pines in spite of these negative results. 1) Dilute acid rain may increase in concentration to pH 1 or more as water evaporates. 2) The fortnightly application of acid may underestimate rainfall frequency in the northern rocky mountains (Weaver 1980) and certainly does in the northeast U.S. where pollution problems are evident. Results of the fortnightly application show acid event frequency is related to the amount of damage. 3) Species that were not affected by acid in controlled experiments have been damaged in natural environments. For example, Haines et al. (1980) showed white pine unaffected by acid as low as pH 2, whereas Armentano and Menges (1987) showed white pine in Michigan sand dunes sensitive to acid deposition. Environmental conditions such as water and nutrient availability, competition and pollution synergisms may affect a trees sensitivity to acid rain.

I conclude that the reduction in growth of the trees treated fortnightly with pH 1 H_2SO_4 was caused by the loss of older needles because loss occurred (Table 19) and there was no indication of other damage. There was no evidence of disruption of the cuticle (water loss, Table 17), reduced photosynthetic surface of expanding needles during treatment (needle size, Table 16), or reduction of chlorophyll (except chlorotic older needles, Tables 15 and 18). While it is believed that the bulk of energy needed for the growing tree is produced by young fully expanded leaves (O'Neil 1962), my data show the importance of older conifer needles in a photosynthetic capacity as well as storage of resources. However, abscission of older needles before younger needles which were treated an equal number of times, suggests a selection by the tree to preserve younger leaves.

In my bud pruning experiment, where the buds and young needles were removed from lodgepole pine trees for 5 years, the remaining old needles were important in maintaining radial growth for three years. A comparison of needle areas shows that the trees sprayed with pH 1 acid had a 39% (fortnightly treatment) and 33% (annual treatment) reduction in leaf area (old needles) similar to the leaf area (young needles) lost in the moderate pruning treatment (31%). Comparing reduction in radial growth -- relative to pretreatment rates -- shows that the trees from which half the needles were removed (moderate bud pruning) had a greater reduction in radial growth than the trees sprayed with pH 1 acid. This shows that trees that lost less leaf area (31%) from young leaves had greater growth reduction than trees that lost more leaf area from older leaves.

The comparison of leaf area between annual and fortnightly sprayed trees (pH 1) shows a small difference in reduction of leaf area (estimated by needle numbers, Table 19), only 6%. The reduction in radial growth is 18% (Table 23) in the fortnightly sprayed trees and shows that chlorophyll loss indicated by the chlorosis observed (Table 18) reduces growth potential. The fortnightly treated trees had a higher percentage of needles with greater than 10 % surface area necrotic than the annually treated trees in all years except the second (Table 18). The reduction in height growth on the trees sprayed fortnightly also suggests damage to the needles and bud of the terminal leader (see bud discussion) although needle analysis showed no needle drop or chlorosis on first year needles.

My experiment suggests that acid deposition from anthropomorphic sources in concentrations that have been measured in rain (above pH 3) and at frequencies tested (fortnightly) will not cause directly observable damage to foliage of the conifer tested. The data does show that repeated exposure to more concentrated acid increases damage to foliage (pH 1) and that the concentration of acid is an important factor. Conifer and angiosperm species associated with environments where forest decline has been reported may be more susceptible to acid deposition (Armentano and Menges 1987). This experiment does not address the effect of acid precipitation on the soil\root system where it is a problem (Wellburn 1988, Cizkova 1990, Jentschke et al. 1991-1, Jentschke et al. 1991-2), or synergistic effects of acid and associated industrial waste such as ozone (Aitken 1984, Berry 1974, Patton et al. 1991) or toxic

toxic metals (Armentano and Menges 1987, Siccama et al. 1982, and Vogelmann 1982).

Metal Spray

Damage to terrestrial ecosystems from airborne toxins, including metals, has been a concern for many years (Legge and Krupa 1986, Hogan and Wotton 1984, Kreutzer et al. 1983). Most of the attention of pollution research has been given to acid deposition or toxic metals absorbed by roots (Patterson and Olson 1983, Hobbs and Streit 1986, Godbold and Hüttermann 1985) and I have found no reports of the impact of metals applied to conifer foliage, though it is recognized to be a path of entry (Hogan and Wotton 1984). In angiosperms, metals enter the free spaces of the leaves where they have local metabolic effects or from which they can be translocated to other susceptible parts of the plant (Huges et al. 1980). Also, copper absorbed by Pinus radiata roots and transported to leaves inhibited electron transport in photosystems 1 and 2, and chlorophyll synthesis (Gorgé et al. 1985).

Since no information on the effects of metal pollution on foliage of major trees of the Rocky Mountains is available, simulated metal deposition was applied to Pinus contorta and Pseudotsuga menziesii seedlings in a greenhouse experiment (Jacobs et al. 1992), and concentrations toxic to the seedlings in the greenhouse were sprayed on trees in the field.

Metals sprayed on P. contorta foliage in the field had little effect on the parameters measured. Table 26 shows no significant decrease in the height growth occurred during the study when zinc was applied, and a

Table 26. Height (cm/year) growth annual zinc sprayed trees 1981-1988. 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	30.2 A	40.5 A	40.5 A
1982	31.8 A	40.8 A	44.0 A
1983	30.1 A	37.9 A	38.2 A
81-83 Mean	30.7	39.7	40.9
1984	28.2 A	35.8 A	36.0 A
1985	24.1 A	32.7 A	35.0 A
1986	23.9 A	34.5 A	34.9 A
1987	37.1 A	42.6 A	44.3 A
1988	44.9 A	44.7 A	46.4 A

Table 27. Height growth (cm/year) for annual copper sprayed trees 1981-1988. Means of twelve replications with letters indicating significant differences in means within rows using Newman-Kuels comparison of means.

Year	Control	Moderate	Heavy
1981	39.6 A	40.0 A	37.9 A
1982	39.9 A	41.0 A	37.7 A
1983	38.6 A	36.3 A	38.1 A
81-83 Mean	39.4	39.2	37.9
1984	39.9 A	35.1 A	38.3 A
1985	35.0 A	31.5 A	34.3 A
1986 *	35.7 B	33.0 AB	28.2 A
1987	43.8 A	40.4 A	42.3 A
1988	46.0 A	47.25 A	49.0 A

* Rows with significant differences at the 5% level.

significant decrease in height growth of trees treated with Copper appeared in 1986 only (Table 27). There were no significant effects of zinc or copper on radial growth (Tables 28 and 29). Table 30 shows a significant increase in phloem resistance (decrease vigor) for both treatments on the same date (2 August, 1985), but since there was no effect on any other date and because in the copper treatment the moderate level had a greater effect than the heavy level, I doubt that the differences are significant. As explained below, there could actually be copper deficiency in the trees.

Metals are absorbed by the roots of plants including crop herbs (corn, sunflower, beans, and rice; Bazzaz et al. 1974, Carlson et al. 1975, Chino 1981) and trees (eg Picea abies, Schlegel et al. 1987) and at high levels may reduce rates of photosynthesis, transpiration, growth, and possibly respiration (Van Assche and Clijsters 1983, Schlegel et al. 1987). Electron micrography suggests that chloroplasts especially sensitive to metal damage (Guderian 1986).

One time applications of 0.01 molar $ZnCl_2$ and $CuCl_2$ damaged seedlings in greenhouse experiments (Jacobs et al. 1992) but applications at the same concentrations had no effect on trees in the field when applied annually over five years. There are at least three possible explanations for the difference in greenhouse and field response. First, the field application was not as severe due to the rinsing effects of natural rainfall. This effect seems minimal since review of data from a nearby S.C.S. snow survey weather station shows that a rinsing rain within 24 hours of application occurred only once. Second, it is possible that the seedlings in the greenhouse have more permeable cuticles than field grown

Table 28. Radial growth (mm/year) of annual zinc sprayed trees 1981-1988. Means of twelve replications with letters indicating no significant differences in means within rows using Newman-Kuels comparison of means.

Year	Control	Moderate	Heavy
Pretreatment years			
1981	3.71 A	4.09 A	3.64 A
1982	3.65 A	3.96 A	3.51 A
1983	4.24 A	3.96 A	3.58 A
Treatment years			
1984	3.76 A	3.55 A	3.66 A
1985	3.55 A	3.42 A	3.36 A
1986	3.03 A	3.05 A	2.80 A
1987	3.52 A	3.58 A	3.16 A
1988	3.11 A	2.80 A	2.86 A

Table 29. Radial growth (mm/year) of annual copper sprayed trees 1981-1988. Means of twelve replications with letters indicating significant differences in means within rows using Newman-Kuels comparison of means.

Year	Control	Moderate	Heavy
Pretreatment years			
1981	3.69 A	4.11 A	4.00 A
1982	3.33 A	3.75 A	3.41 A
1983	4.03 A	4.28 A	3.92 A
Treatment years			
1984	3.90 A	3.97 A	3.84 A
1985	3.41 A	3.80 A	3.69 A
1986 *	2.78 A	3.46 B	3.23 AB
1987	3.41 A	3.75 A	3.68 A
1988	2.99 A	3.14 A	3.09 A

* Rows with significant differences at the 5% level.

Table 30. Effect of metal application 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 (0.001M)	Heavy (0.01M)
		Zinc		
11 July 84		6.61 A	6.49 A	6.71 A
20 Aug. 84		10.52 A	9.55 A	10.37 A
18 sept 84		12.45 A	12.09 A	11.74 A
29 June 85		6.13 A	6.13 A	6.15 A
14 July 85		7.66 A	8.28 A	7.75 A
2 Aug. 85	*	9.30 A	10.22 AB	11.04 B
24 Aug. 85		8.43 A	9.18 A	9.03 A
11 Sept 85		12.06 A	11.89 A	13.32 A
14 June 86		6.49 A	6.42 A	6.42 A
12 July 86		7.46 A	7.83 A	7.89 A
27 July 86		8.12 A	9.27 A	8.31 A
8 Aug. 86		9.02 A	9.44 A	8.90 A
25 Aug. 86		9.82 A	10.91 A	10.31 A
7 Sept 86		10.43 A	11.42 A	11.14 A
24 Sept 86		14.28 A	15.14 A	14.04 A
		Copper		
11 July 84		6.93 A	6.66 A	6.68 A
20 Aug. 84		9.44 A	9.75 A	10.25 A
18 Sept 84		11.00 A	12.09 A	11.51 A
29 June 85		5.71 A	6.33 A	6.28 A
14 July 85		6.66 A	7.38 A	7.15 A
2 Aug. 85	*	8.86 A	10.43 B	9.67 AB
24 Aug. 85		7.45 A	8.24 A	8.03 A
11 Sept 85		11.27 A	11.80 A	12.16 A
14 June 86		6.08 A	6.38 A	6.10 A
12 July 86		6.68 A	7.38 A	7.39 A
27 July 86		7.58 A	7.46 A	8.38 A
8 Aug. 86		7.86 A	8.95 A	8.65 A
25 Aug. 86		9.08 A	10.13 A	9.50 A
7 Sept 86		9.84 A	10.52 A	10.56 A
24 sept 86		13.59 A	14.24 A	14.67 A

* Rows with significant differences at the 5% level.

trees (Schriner 1986) and are thus less able to exclude the metals. Simulated metal pollution on seedlings in the field would test this, and shows the importance of further field study of pollution effects on plants.

Third, seedlings may be more susceptible than trees to pollution injury, due to differences in ability to exclude metals from the leaf or at least from metabolic processes in the leaf. If so, pollution would have profound effects on the normal process of succession. Seedlings in the understory would die and would thus be replaced by species with higher tolerances to metal pollution.

Analysis of leaves for metals on leaf surface and within leaves shows whether metals were excluded by leaves in the field. Results show significant increases of copper on the leaf surface and within the needles of trees sprayed with 0.01 molar $CuCl_2$ (Table 31). The leaf cuticle thus excluded some of the copper, but a significant amount did penetrate. Enriched levels within the leaf were apparently non-toxic and, since copper is a micronutrient, the copper may have served as a nutrient. Zinc was also excluded by the leaf cuticle (Table 31). While there was a significant increase in zinc on the leaf surface of trees sprayed with 0.01 molar ZnCl, there was no increase in zinc in the leaf.

Zinc contents of the leaves ranged from 32.55 mg/Kg in the moderate zinc treatment to 50 mg/Kg in the zinc control: and 1.35 mg/Kg copper in the control to 6.58 mg/Kg in the heavy copper treatment (Table 31). Zinc concentrations are similar to those found in lodgepole pine from Southern

Table 31. Metal content of lodgepole pine needles (mg/Kg). Means of twelve replications with letters indicating significant differences in means within rows using Newman-Kuels comparison of means.

		Control	Moderate	Heavy
Copper				
Total Cu	*	1.35 A	1.65 A	6.58 B
Leaf surface	*	0.15 A	0.45 A	2.55 B
Zinc				
Total Zn	*	49.53 B	32.55 A	48.88 B
Leaf surface	*	0.70 A	0.82 A	1.76 B

* Rows with significant differences at the 5% level.

Alberta, whereas copper concentrations in the control and light are comparatively low (Ayer et al. 1986).

Although I find no information on deficiency or toxic levels of copper and zinc for lodgepole pine, comparison of my data with other data suggests no toxic level. Toxic levels of copper and zinc for sitka spruce (Picea sitchensis) in South Wales' forests were 88 mg/Kg and 226 mg/Kg respectively (Burton et al.), 10 times higher than the levels of copper found in the heavy treatment, and five times higher than zinc levels. Deficiency limits of 12 to 20 mg/Kg for zinc in wheat and maize (Sillanapää 1982, Takkar and Mann 1978) suggest no zinc deficiency in the lodgepole pine. Conversely, there may be copper deficiency; douglas fir showed visual symptoms of copper deficiency at foliar levels of 3.1 to 6.2 mg/Kg, and Larix leptolepis showed deficiency symptoms at 1.8 to 3.8 mg/Kg foliar copper (Van Den Berg 1983), levels greater than found in the

control and moderate copper treatments (Table 31). Sillanapää (1982) does warn that deficiency and toxicity limits established for one species may not apply to others. Also, these critical limits depend on parts of the plant tested and the stage of development.

My experiment suggests that mature lodgepole pine trees in the field are not susceptible to damage from metal pollution applied to the foliage because they are well adapted to exclude it (thick cuticle), excrete it, or sequester it. This does not rule out the likelihood (Patterson and Olson 1983, Hobbs and Streit 1986, Godbold and Hüttermann 1985) that mature lodgepole pine trees are susceptible to metal pollution at the root level via the soil.

CONCLUSIONS

Increasing levels of stress do not cause a linear response in trees hypothesized in the introduction. The response to moderate levels of all treatments (50% level) was the same as the control, suggesting that below some critical point there is no damage and, above it, damage is significant. In other words, trees of this size or age have the ability to absorb a certain amount of stress. In this case, the trees were able to grow normally for two to three years even under the most severe stress, a complete girdle. This is true whether the stress was applied to the canopy, stem or roots. The ability to survive a stress is most likely due to the presence of energy reserves stored in the roots and leaves, and the ability to efficiently use resources when they are available (e.g. water absorption in the spring when snow melt makes it plentiful despite reduced root area). It must be kept in mind that the experimental trees were growing in a thinned stand where intraspecific competition was reduced. One might expect more permanent stress to trees growing in dense stands because they are put at a competitive disadvantage due to reduced root growth, weaker stems, or less height growth.

Trees respond to stress differently depending on where the stress is applied, that is, the canopy, stem, or roots. Root stress caused the most immediate loss of vigor and growth, but the tree was able to compensate by growing new roots in the area available. Bud pruned trees

showed reduction of growth and increasing phloem electrical resistance as the treatment progressed and intensified. Girdled trees showed little response until they died. Within the limits tested, canopy and root stress appear to be plastic; stem injury was permanent.

Comparison with the literature shows the responses of lodgepole pine are similar to responses of other plant species and encourages me to cautiously extend these results to other species and other regions. Caution is appropriate here because the trees were of one species and were grown in an optimally thinned plantation. Synergisms of these stresses and others, for example, ozone, should also be considered.

The stresses applied (except the complete girdle) seem to cause a plastic response, that is, vigor and growth are reduced, but if the stress is taken away the tree has the capacity to rebound to previous growth rates. This hypothesis should be tested by remeasuring height and radial growth 5 or 10 years after treatments were ended (1993 or 1998).

This study was originally designed as base data for a project to determine if trees under stress could be recognized from aerial photographs. Near infrared low altitude aerial photographs were taken during the first three years of treatment and are available from the author. Density measurements of the film could be compared to the results reported here to see if the stress effects can be seen from the air. If they can be seen from the air, the indicators would assist foresters in inventorying timber stands for management decisions involving stress.

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