THE INFLUENCE OF NUTRITION AND DENSITY ON REPRESSED LODGEPOLE PINE

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ABSTRACT

Repression in lodgepole pine is a condition of slow growth in very high-density stands of natural regeneration resulting after wildfire. A factorial thinning and fertilization experiment (two levels of thinning, none and thinned, and two levels of fertilization, none and complete mix) was established on the Chilcotin Plateau in central British Columbia in a 36-year-old repressed lodgepole pine stand. The objectives of this study were to 1) examine the effects of thinning and nutrient addition and their interaction on repressed lodgepole pine tree and stand growth, foliage biomass per hectare, and growth efficiency, and 2) examine these same treatment effects on crown response of foliage and branches at the whole-tree level and by whorl, cohort, and branch order within the crown.

Although repression has been considered an irreversible physiological dysfunction, the large increases in growth reported in this study and others indicate that growth of repressed stands was limited primarily by nutrient deficiencies similar to those found in non-repressed lodgepole pine. This suggests that any observed physiological dysfunctions in repressed lodgepole pine are a symptom of repression rather than a cause. Volume growth was increased from 2 to 7 m^3/ha/year with nutrient additions on non-thinned plots and to 5 m^3/ha/year when fertilizer was applied to thinned plots. Thinning produced a tree-level growth response by allocating limited nutrients to fewer trees resulting in increased tree-level foliage biomass and increased growth efficiency. Additions of nitrogen, sulfur, and boron improved both tree-level growth and stand growth through increases in stand-level foliage biomass and growth efficiency. The additive effects of fertilization and thinning on growth indicate that both treatments are needed to achieve the maximum effect.

Increased nutrition and growing space resulted in increases in tree-level foliage biomass, but the mechanisms of these increases differed by treatment. Increased number of fascicles contributed more than increased fascicle weight to the foliage biomass response for all treatments. Increases in the number of foliated branches was more important than increases in the amount of foliage on a branch when fertilizer was applied but these mechanisms were almost equally important to the increase in foliage biomass due to thinning. The lack of treatment effects on foliage biomass at the bottom of the live crown, the position of the bottom of the live crown, and the reduction in the number of cohorts toward the base of the live crown, all suggest that greater foliage biomass response is possible.

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CHAPTER 1

REPRESSED LODGEPOLE PINE

1.1 Introduction

Lodgepole pine (*Pinus contorta*) is a pioneer species of widespread distribution in western North America that succeeds in a variety of environments that challenge other tree species (Lotan and Critchfield 1990). Although it is very intolerant of shade, it is tolerant of poor soils. The coastal variety (*Pinus contorta* var. *contorta*) is the dominant tree species in raised peat bogs and rocky outcrops and the inland variety (*Pinus contorta* var. *latifolia*) naturally occurs in extensive, often nutrient deficient (Brockley 2001a) even-aged stands originating after wildfire. Because it has serotinous cones, lodgepole pine sometimes has extremely dense regeneration after fire (Lotan 1975, Bassman 1985, Lotan and Critchfield 1990, Tinker and Romme 1994). Tree densities as high as 800,000 stems per hectare have been observed in young stands (Mitchell and Goudie 1980) while older stands have been observed with up to 100,000 stems per hectare (Keane 1985). These dense stands sometimes grow and self-thin at very slow rates and are said to be in a "repressed" or "stagnant" condition. Sometimes these two terms are used interchangeably, however, stagnation usually refers to the most severely repressed stands.

Lodgepole pine stands in this condition occupy significant portions of the landscape. The condition is particularly prevalent in the interior of British Columbia, especially in the SBPS biogeoclimatic zone and the MSxv subzone on the Fraser Plateau west of the Fraser River (Newsome and Perry 2003). Over 130,000 hectares of repressed lodgepole pine have been estimated for the Cariboo Forest Region of British Columbia (1.6% of the Cariboo Forest Region, Newsome and Perry 2003).

1.2 Explanations for Stands in a Repressed Condition

Repression has been described as reduced height growth, below that of the site potential, with increasing levels of repression associated with increasing levels of establishment density (Farnden 2001). Mitchell and Goudie (1980) described the strong inverse relationship between height and initial density at eighteen years in natural fire-origin stands (Figure 1A) and suggested

that the reduction in height was due to high density. Carlson and Johnstone (1984) planted lodgepole pine at densities ranging from 2,500 to 160,000 trees per hectare, and found that dominant height at age 14 was less at densities above 15,000 trees per hectare (Figure 1B). Slow growing high-density stands have also been reported for other species such as ponderosa pine (Oliver 1967), jack pine (Rudolph and Laidly 1990), black spruce (Viereck and Johnston 1990), loblolly pine (Baker and Langdon 1990), and Douglas-fir (Kimmins 2004). These species are all fire origin pioneers that typically occur on poor sites.

The negative correlations between height and density have been interpreted to mean stand growth (growth per area) is also lower (Keane and Weetman 1987). Although height (and site index) is correlated with stand volume growth under a range of stocking conditions the utility of using site index as a surrogate for stand growth potential breaks down at very high densities (Carmean 1975, Oliver and Larson 1996). Keane's measurements showed the same strong relationship between height and density that was observed by Mitchell and Goudie (1980) (Figure 2A) but he also reported a much weaker relationship between above-ground biomass and density (Figure 2B).

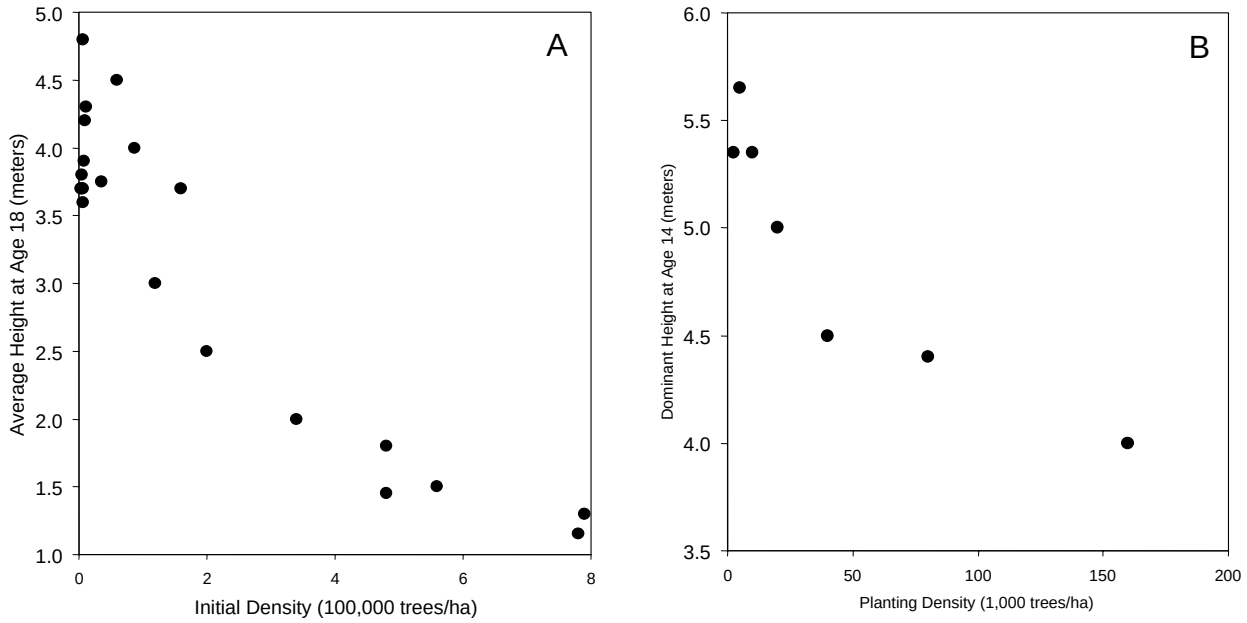

Figure 1. Relationship between lodgepole pine height and initial density from (A) Mitchell and Goudie (1980) and (B) Carlson and Johnstone (1984).

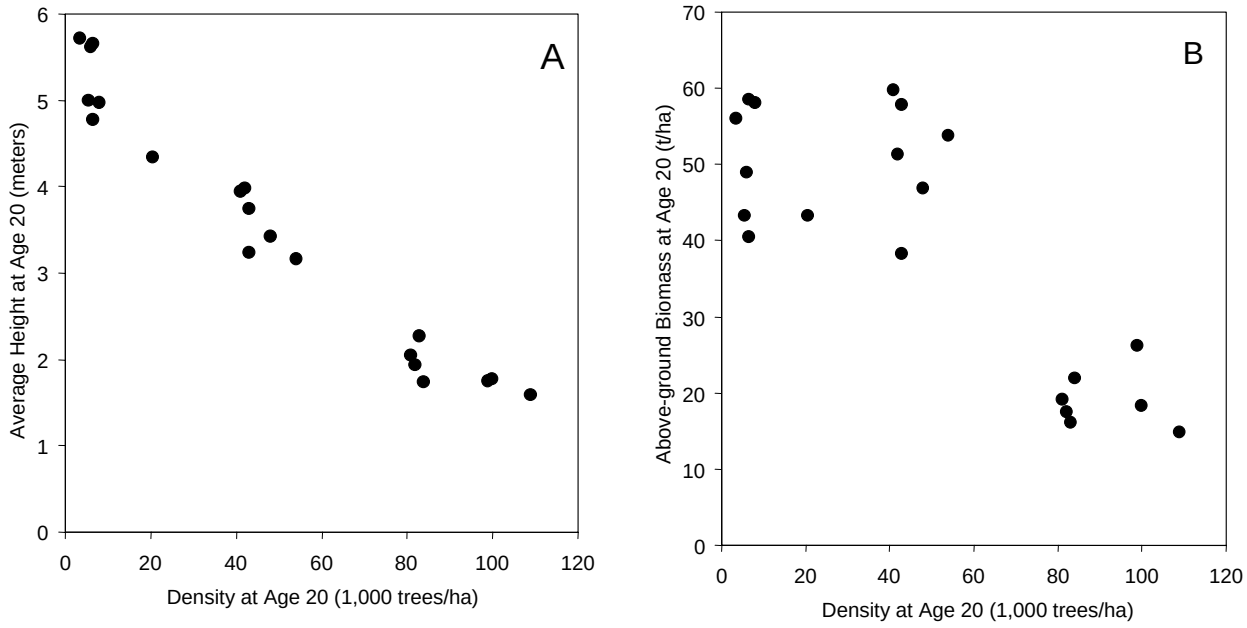

Figure 2. Relationship between lodgepole pine (A) density and height and (B) density and above-ground biomass from Keane 1985.

Unfortunately, Keane's (1985) study was confounded by slope position. All the high-density plots were at the top of a slope, the middle density plots were on a side slope, and the lowest density plots were at the bottom of a slope. The gradient in height would be expected, with greater height on lower slope positions. It is not possible to tell whether the high density is the cause of slow growth or whether slope position caused both the slower growth and the higher density. The confounding of slope position with height and density seems the most likely case since the soils at the top of slopes are typically drier and more nutrient poor with resultant slower tree growth and slower rates of self-thinning.

Another key feature of repressed stands is their apparent lack of response to thinning unless treated early (Cole 1975, Lotan and Critchfield 1990). Bassman (1985) suggested that because thinning does not improve growth, the possibility exists that physiological adaptations allow for the persistence of repressed growth. Several possible physiological explanations have been proposed to explain repression. A common assumption has been that repression occurs due to high density resulting in both slower tree and stand growth and slower rates of self-thinning. Physiological explanations have included changes in carbon allocation, elevated respiration rate, lower photosynthesis, reduced hydraulic conductivity, and changes in growth regulators

(Mitchell and Goudie 1980, Goudie 1980, Keane 1985, Worrall *et al.* 1985, Keane and Weetman 1987, Worrall 1995, Reid *et al.* 2003). Generally, most workers have suggested that high density creates a physiological dysfunction within the trees that reduces or stops height and stand growth and consequently the process of natural self-thinning. It has also been implied that this dysfunction is not reversible (Cole 1975, Bassman 1985, Lotan and Critchfield 1990).

1.3 Current Management Strategies for Ameliorating Repression

Current management of repressed lodgepole pine stands generally consists of two options based on the severity of repression. In young stands not yet exhibiting the symptoms of repression a precommercial spacing treatment is applied to reduce density and increase stand growth while in older severely repressed stands a rehabilitation treatment is used to restore productivity by establishing a new stand of healthy trees. It is commonly believed that early thinning in repressed stands offers the greatest opportunity for increasing stand-level productivity (Cole 1975, Lotan and Critchfield 1990). However, most thinning treatments in non-repressed lodgepole pine have either little or no effect on height growth (Alexander 1960, Alexander 1965, Lotan 1967, Dahms 1971, Johnstone 1981a and b) and it is generally accepted for non-repressed stands that thinning increases diameter growth on crop trees at the expense of stand volume growth (Brix 1983, O'Hara 1990). The hypothesized increase in stand-level growth from thinning repressed stands is based on the idea that reducing the density soon enough can increase tree and stand growth by avoiding the unknown physiological problem caused by high density.

For stands that are considered to be severely repressed (stagnant) it is believed that the trees are not capable of responding to thinning (Lotan and Critchfield 1990). For these stands a ‘rehabilitation’ treatment establishing a new stand at a lower density is prescribed (Newsome and Perry 2003). There are no published results on the effectiveness of rehabilitation in restoring productivity but there are several studies currently underway designed to address this issue (Newsome and Perry 2003).

The belief that severely repressed stands are not capable of responding to thinning comes from thinning trials in high-density lodgepole pine stands that have produced either little or no growth response (Smithers 1957, Johnstone 1982 and 2002, Lotan and Critchfield 1990, J.S. Thrower and Associates 1993, Worrall 1995). What little response has been observed was found in

younger stands, leading to the hypothesis that the ability of a repressed stand to respond to thinning declines with age.

1.4 Ecophysiological Basis for Forest Production

Interestingly, a link between site quality and repression has been suggested for ponderosa pine (Oliver 1967), jack pine (Rudolph and Laidly 1990) and other species (Kimmins 2004). The results of Keane (1985) also suggest that site quality may play a role in lodgepole pine repression once the confounding with slope position is recognized (Figure 2). Perhaps it was not possible for Keane to establish plots covering a range of heights and densities without confounding site quality because these factors are so commonly confounded on the landscape.

Over the last couple of decades there have been considerable advances in our understanding of the ecophysiological basis for forest production (Linder 1987, Cannell 1989, Allen 2001). Wood production has been shown to be limited by low leaf area for many species in many areas of the world (Axelsson and Axelsson 1986, Linder 1987, Linder *et al.* 1987, Vose and Allen 1988, Colbert *et al.* 1990, Benson *et al.* 1992, Snowdon and Benson 1992, Albaugh *et al.* 1998, and Bergh *et al.* 1998, Jokela and Martin 2000). Foresters have historically considered light to be a major limitation to tree growth, especially in stands where trees are crowded and there are few gaps between crowns. It was generally thought that trees respond to thinning because of increases in the availability of light. It is now recognized that trees respond to thinning of closed-crown, low leaf area stands because of increases in soil resource availability per tree, not just light (Gillespie *et al.* 1994, Smith et al. 1997). In these stands, the limit to productivity is not light but the ability of the forest canopy to intercept light (Gillespie *et al.* 1994). The traditional concept of stocking as expressed in stand density management diagrams may not always provide an adequate understanding of the potential growth or site occupancy of a stand (Vose and Allen 1988). Stocking is typically expressed relative to a reference stand growing on a site with similar productive potential (Davis and Johnson 1987), so stocking in repressed stands is difficult to assess without knowledge of what the site's potential productivity is. Repressed stands are said to be overstocked because of the large number of trees per hectare. However, repressed stands may actually be under stocked with respect to their ability to intercept light. Low leaf area has

been reported for repressed stands (Bassman 1985, Keane and Weetman 1987) and low leaf area has been shown to result from low nutrient availability (Linder 1987, Vose and Allen 1988, Colbert *et al.* 1990, Vose *et al.* 1994, Binkley *et al.* 1995, Albaugh *et al.* 1998) and other resource limitations such as water availability (Benson *et al.* 1992, Pereira *et al.* 1994). Stands growing at very high density may capture the growth potential of a site more quickly than lower density stands and might, therefore, more rapidly exhaust the limited resource supply of a site. This could accelerate the disparity between potential resource use and supply and hasten growth reduction.

Measures of the amount of foliage, such as foliage biomass or leaf area, are strongly related to current growth (Jarvis and Leverenz 1983, Waring 1983, Linder 1987, Vose and Allen 1988, Cannell 1989, Gower *et al.* 1994, Landsberg and Gower 1997, Allen 2001). The amount of foliage per area represents an integrative measure of tree size, stand density, and site resource supply and is directly related to how much light a stand can intercept for photosynthesis. Vose and Allen (1988) proposed that maximum site occupancy (or full stocking) could be defined as the maximum sustainable amount of foliage given fixed site resources. Fixed site resources are those resources that cannot be manipulated silviculturally. Vose and Allen (1988) proposed a method for applying this technique to predicting the magnitude and duration of response to silvicultural treatments, based on the difference between the stands current and maximum potential amount of foliage. By defining the relationship between the amount of foliage and the current growth it is possible to gain insight into how much more growth a stand could produce if the difference between its current and maximum potential foliage biomass could be achieved. This method is now used operationally to estimate response to nutrient additions in the southeastern United States (Allen *et al.* 2001).

Another mechanism for increasing growth can be expressed as the slope of the relationship between growth and leaf area (called growth efficiency or foliage efficiency). More efficient foliage produces more growth than the same amount of less efficient foliage. Within an individual site, changes in growth efficiency generally do not contribute as much to the variability in productivity as to changes in leaf area (Linder 1987, Albaugh *et al.* 2004). Growth efficiency can vary due to differences in photosynthetic efficiency, respiration, and partitioning to various biomass components (Cannell 1989). Improved nutrient and water availability has

been shown to increase photosynthetic efficiency (Linder 1987, Murthy *et al.* 1996), and the proportion of above-ground productivity (Gower et al. 1992, Haynes and Gower 1995, Albaugh *et al.* 1998).

How well do these ecophysiological concepts apply to stands in a repressed condition? Replicated manipulative experiments (Hurlbert 1984) are needed in repressed stands to determine the effects of increasing nutrient availability per tree and per area on the amount of foliage, growth efficiency, and tree and stand growth. Such studies could be used to answer the following key questions. Will improved nutrition and reduced density result in increased growth in a repressed stand? Will thinning produce a tree-level growth response by allocating limited nutrients to fewer trees? Will growth efficiency improve at the tree and stand level with thinning alone? Will fertilization improve both individual growth and stand growth through increases in foliage biomass and growth efficiency?

CHAPTER 2

EFFECTS OF THINNING AND FERTILIZATION ON REPRESSED LODGEPOLE PINE GROWTH, FOLIAGE BIOMASS, AND GROWTH EFFICIENCY

2.1 Introduction

Many trials have examined the effects of nutrient additions on lodgepole pine growth (Weetman *et al.* 1988, Cochran 1989, Brockley 1990 and 2001b, Marshall *et al.* 1991, Kishchuk and Brockley 2002, Kishchuk *et al.* 2002). However, few replicated experiments have examined fertilization in repressed stands. The Fish Lake trial (Farnden and Herring 2002) is a replicated thinning and nitrogen fertilization trial in an 18-year-old repressed lodgepole pine stand. Nineteen years after treatment, the best responses in height growth were observed when both growing space was increased and nitrogen was added (Farnden and Herring 2002). These results support the idea that increasing the availability of resources will produce a tree-level growth response even in a repressed stand. However, interpretations from this trial are somewhat limited because stocking on fertilized plots was reduced by hares. This makes it difficult to distinguish thinning from fertilization effects. In addition, only nitrogen was applied and it may not be the only limiting nutrient. Farnden and Herring (2002) discussed the potential of their results for improving the management of repressed lodgepole pine but cautioned extrapolation of these results until more trials could be established. They also called for a better understanding of the causal mechanisms of the observed response. An improved understanding of the causal mechanisms of how repressed stands respond to more resources per hectare and per tree will improve the portability of the results (e.g. Allen 2001).

Evidence from lodgepole pine fertilizer trials in non-repressed stands in the region indicates that nitrogen is not the only nutrient in short supply. Evidence for sulfur and boron deficiency has been reported (Brockley 2000 and 2001b, Kishchuk and Brockley 2002, Kishchuk *et al.* 2002) and other elements as yet untested might also increase growth if added. To test the hypothesis that nutrient availability is limiting tree and stand growth in repressed stands, a nutrient

amendment should comprise a complete blend of all the elements that could conceivably limit growth. To better understand the effects of thinning and fertilization and their interactions, this fertilizer treatments needs to be applied in factorial combination with thinning.

2.2 Objectives

The objectives of this study are to examine the effects of thinning and nutrient addition and their interaction on the growth, foliage biomass, growth efficiency and stand development of a repressed lodgepole pine stand. Based on the visibly low leaf area (personal observation) suggesting the possibility of poor nutrition, and high density, indicating too many stems sharing too few resources, it is hypothesized that:

1) thinning will increase individual tree growth by allocating limited nutrients to fewer trees and
2) nutrient amendments will improve individual tree and stand productivity through increases in leaf area and growth efficiency,
3) the combined treatment where greater nutrient resources are provided to fewer stems will result in the best individual tree growth, due to increasing leaf area and growth efficiency.

2.3 Methods

2.3.1 Site Description

A trial was established to test the effects of thinning, fertility and rehabilitation (replanting at a lower density) on repressed lodgepole pine in the interior of British Columbia (Newsome and Perry 2003). The site is located on the Chilcotin Plateau in the SBPSdc (Sub-Boreal Pine Spruce-dry, cold) biogeoclimatic subzone about 96km west of Williams Lake near Rosita Lake. The combined cold and dryness of this zone makes it one of the climatically harshest relative to other forested biogeoclimatic zones in British Columbia. The soils are predominantly Luvisols (Soil Classification Working Group 1998), with fine textures ranging from silt loams to clay loams. The location was selected because it was considered typical of repressed stands common throughout the area.

The Rosita fire was a natural wildfire that burned approximately 900 hectares in the summer of 1961, killing the previous stand of lodgepole pine and providing conditions for dense natural regeneration. Thirty-six years after the fire (1997) the area was covered with dense, even-aged, lodgepole pine forests ranging from around 4,000 to more than 30,000 trees per hectare (Newsome and Perry 2003). This variability was minimized in the study to improve treatment comparisons by locating plots in the most homogenous areas with the smallest trees and highest density. The study plots exhibited stronger repression symptoms than in Keane's (1985) study (Figure 2A). The trees in this study were only 3.6 meters tall on average with an average density of over 22,000 trees per hectare (Table 1). This places this study below the height-density relationship described by Keane (1985) despite being thirteen years older. Interestingly, there has been significant size differentiation within the stand. Crop trees (the largest 400 well spaced dominant and codominant trees/ha) averaged one meter taller and 1.4 cm larger in diameter at breast height (DBH) than the stand average for all trees. Although crop trees represent only 1.8% of the total trees on non-thinned plots, they contributed 3.6% of the stand volume and 2.4% of the foliage biomass.

Table 1. Stand description for all trees for thinned and non-thinned plots and for a subset of crop trees at trial establishment.

	Height	DBH	Density	Basal Area	Volume	Foliage
	m	*cm*	*trees/ha*	*m^2/ha*	*m^3/ha*	*kg/ha*
non-thinned	3.6	3.0	22,558	16.4	74.9	4,468
thinned	4.4	4.2	2,472	3.7	15.8	638
crop trees	4.6	4.4	400	0.6	2.7	105

The very low foliage biomass (Table 1) and low foliar nutrient concentrations (Table 2) indicated that response to fertilization was a strong possibility (Allen 2001). Foliar nitrogen, sulfur, and boron were all below critical values (Table 2).

Table 2. Initial foliar nutrient concentrations (Newsome and Perry 2003) and critical values (Brockley 2001b).

	N	P	K	Ca	Mg	S	B
	---------- % ----------						*ppm*
Foliar Concentration	0.92	0.14	0.40	0.19	0.09	0.08	5
Critical Value	1.35	0.10	0.40	0.10	0.08	0.10	15

2.3.2 Experimental Design

The larger study consists of ten treatments including a non-treated control, six rehabilitation treatments, and three treatments applied to the existing stand. This analysis focuses on the three treatments applied to the existing stand and the control. These four treatments provided two levels of thinning (none and thinned) and two levels of fertilization (none and fertilized) resulting in four treatment combinations (control, thinned, fertilized, and both thinned and fertilized). Plots were blocked based on initial height, and one replication of each treatment was assigned randomly to each of three blocks.

2.3.3 Treatments

Treatment plots were 50 x 50 meters with an additional 10 meters of untreated buffer surrounding all sides. The thinning treatment was applied from September to October 1997 with a target density of 2,000 to 3,000 trees per hectare, which is at the high end of the normal stocking range specified by Cole (1975), with an emphasis on leaving larger trees. The thinning treatment removed 89% of the trees but, because smaller trees were favored for removal (Appendix A), the resulting volume reduction was 79% (Table 1). Thinning also left the stand with trees that averaged 0.8 meters taller and 1.2 centimeters larger in DBH (Table 1).

Fertilizer was a custom blend (Table 3) broadcast applied by hand from October 13 to 17, 1998, the year after thinning. The fertilizer prescription was developed in consultation with Rob Brockley of the B.C. Ministry of Forests to address the deficiencies indicated in the foliar analysis (Table 2).

Table 3. Type and amount of blended fertilizer.

Source	*kg/ha*	Element	*kg/ha*
Urea	328	Nitrogen	200
Monoammonium phosphate	446	Phosphorus	100
Sulphate potassium magnesia	357	Potassium	100
Muriate of potash	75	Sulfur	75
Borate granular	21	Magnesium	36
		Boron	3

2.3.4 Sampling and Measurements

Measurement plots were located within a 30 x 30 meter area centered within the treatment plot. Two different subsets of trees were sampled within this area representing “all trees” and “crop trees” (400 well spaced dominant and codominant trees/ha).

All trees were sampled using a different regime for non-thinned and thinned plots. Measurement plot size varied on non-thinned plots depending on stand density. Four sub-plots were used to assess tree growth on non-thinned areas due to the high density. The radii of these circular sub-plots plots ranged from 1.78 meters to 3 meters and were of a size sufficient to result in approximately 25 trees per subplot (100 measurement trees in each treatment plot). All trees on thinned plots were measured within a circular 12.64 meter fixed radius plot centered inside the measurement plot.

Crop trees were a subset of all trees on both thinned and non-thinned plots. Thirty-six well spaced dominant and codominant trees were selected on a square grid within each 30 x 30 meter measurement plot (representing 400 trees/ha). Height and DBH was measured on the live trees within the measurement plots prior to treatment in 1997 (year 0) and again in 2000 (year 3) and 2001 (year 4). Thinned plots were also measured immediately after thinning in 1997. Additional details of the study design, layout, and measurements can be found in Newsome and Perry (2003).

Thirty-six trees were destructively sampled to develop site-specific stem volume and foliage biomass equations. One small, one medium, and one large tree was harvested from within each of the treated plots but outside the measurement plots in August, 2001. The stem and live crown of each tree was returned to the lab for more detailed data collection.

2.3.5 Calculations

A volume equation was developed for this site based on ten disks cut from each of the 36 sample trees. Volume was calculated for each section of stem assuming linear change in diameter between disks and then all the sections were summed to calculate total outside bark volume for

each tree. Linear regression was used to create a volume equation based on height and DBH (Equation 1).

Equation 1 $V = 0.00028852\ D^2 + 0.00019352\ H$

where:
V = Outside Bark Volume (m^3/tree)
D = DBH(cm)
H = Height(m)

The relationship between volume, height, and DBH had a coefficient of determination of 0.99 and was not affected by treatment so this equation was used for all trees. Individual tree volumes were summed for each plot and divided by a plot size factor to calculate volume on an area basis.

All foliage from each of the 36 destructively sampled trees was oven dried and weighed. Regression analysis was used to develop an equation to estimate summer foliage dry weight per tree from DBH (Appendix B). There was a single strong exponential relationship ($R^2 = 0.91$) for treated plots but the relationship on control plots was weakly linear ($R^2 = 0.32$), therefore one equation was used for control plots (Equation 2) and a separate equation was used for treated plots (Equation 3). Although the R^2 for the control equation was weak it provided a slightly better estimate than the alternative of assuming a constant amount of foliage biomass for all control trees.

Equation 2 $F_{control} = 4.0065\ D + 89.154$

Equation 3 $F_{treated} = 0.2384\ D^{2.0649}$

where:
F = Oven Dry Summer Foliage Biomass (g/tree)
D = Diameter at Breast Height (mm)

These equations were applied to the individual tree diameter data to estimate the foliage biomass for each tree. The estimated foliage biomass for each tree was summed then divided by a plot size factor to calculate the total foliage biomass per hectare. Estimates of foliage biomass prior to treatment (1997) were calculated using Equation 2 developed from control plots. DBH data from 2001 were used to estimate year 4 post treatment foliage biomass. Growth efficiency was calculated for each plot by dividing year 4 volume growth by year 4 foliage biomass.

2.3.6 Statistical Analysis

A randomized complete block analysis of variance (2 x 2 factorial with three replications) was used to examine the effects of thinning and fertilization on growth, foliage biomass, and growth efficiency (Table 4). An alpha of 0.05 was used for the purpose of discussing significant main effects and interactions.

Table 4. Design of the analysis of variance for all tree and crop tree height, DBH, and volume growth, and for foliage biomass, and growth efficiency.

Source of variation	Degrees of freedom
block	2
thinning (t)	1
fertilization (f)	1
interaction (t x f)	1
error	6
total	11

Several measures of growth were used. Current annual growth for the four years of the study (*e.g.* 2001 height –1997 height) and current annual increment for the fourth year since treatment (third year since fertilization) (*e.g.* 2001 height –2000 height). Average height growth, average DBH growth, and stand volume growth were calculated for each period and for the two different subsets of trees (all trees and crop trees). Analysis of thinning effects on crop tree height and DBH growth is more meaningful than analyzing all-trees because the thinning treatment favored larger, faster growing trees. Part of the total thinning response for height growth and DBH growth for all trees is an effect of removing slower growing trees in thinned plots. Foliage biomass and growth efficiency were calculated for the fourth year since treatment for both subsets of trees.

Growth rather than yield variables were used as dependent variables for these analyses due to the relatively short response time compared to stand age. Any changes in yield over the four-year treatment period would be a combination of pre-treatment yield and growth over the treatment period, and since pre-treatment yield is unrelated to treatment, its effects would obscure the most recent four-year growth effects.

Graphical analysis was used to explore the relationship between volume growth and foliage biomass and to explore whether this relationship was affected by treatment. Graphical analysis was also used to explore the relationships between height growth and volume growth with stand density and whether this relationship was affected by treatment.

A subset of the foliar nutrient data and statistical analyses reported by Newsome and Perry (1993) were re-summarized using the same format as the growth analyses. These data are presented again here because they are important for interpreting the growth, foliage biomass, and growth efficiency results.

2.4 Results

Both thinning and fertilization had strong effects on all measures of tree growth, stand growth, foliage biomass, and growth efficiency (Table 5). Very few interactions were observed, indicating that the effects of thinning and fertilization are additive. Consequently, main effect treatment means were used to describe the effects of thinning and fertilization (Table 6).

2.4.1 Effects of Thinning on Growth

Thinning had varying effects on height growth over the four-year period (Table 5). For all trees during the fourth year, height growth and diameter growth were increased by 41% and 40% respectively but there was no significant volume growth response (Table 6). Thinning did not increase height growth for crop trees in the fourth year but there was an 132% increase in DBH growth and 138% increase in volume growth due to thinning.

Thinning resulted in a small but significant reduction in height growth for crop trees for the four-year period; however, this negative effect had diminished so it was not significant for year 4 growth. Thinning increased height growth for all trees with a statistically significant effect during year four. Thinning increased diameter growth, and the response was strongest in the fourth year. The response to thinning was less for crop trees than for all trees probably because crop trees in non-thinned plots were already in dominant positions and growing well.

Table 5. Treatment means and analysis of variance for all tree and crop tree growth annualized over the four-year treatment period and for year four growth as well as foliage biomass and growth efficiency (GE) in year four.

	----- 1-4 Year Growth ------			------- Year 4 Growth -------			Year 4	Year 4
	Height *cm/yr*	DBH *cm/yr*	Volume *m^3/ha/yr*	Height *cm/yr*	DBH *cm/yr*	Volume *m^3/ha/yr*	Foliage *kg/ha*	GE *m^3/1000kg*
ALL TREES								
	---------- Treatment Means ----------							
Control	5.42	0.06	2.76	4.39	0.04	2.01	4,518	0.46
Thinned	8.01	0.25	1.50	8.26	0.31	2.01	1,886	1.15
Fertilized	12.51	0.13	6.23	17.59	0.13	7.01	8,433	0.83
Both	14.32	0.39	3.27	22.80	0.54	4.94	3,073	1.62
	---------- Pr. > F ----------							
Block	0.378	0.276	0.166	0.367	0.480	0.370	0.779	0.107
Thinned	0.064	**<0.001**	**0.003**	**0.039**	**<0.001**	0.114	**<0.001**	**0.001**
Fertilized	**<0.001**	**0.003**	**0.001**	**<0.001**	**0.008**	**<0.001**	**<0.001**	**0.017**
Interaction	0.702	0.164	0.090	0.710	0.150	0.114	**0.013**	0.694
CROP TREES								
	---------- Treatment Means ----------							
Control	8.42	0.11	0.13	6.44	0.10	0.11	113	0.99
Thinned	7.72	0.24	0.27	7.24	0.31	0.36	336	1.08
Fertilized	19.91	0.26	0.32	26.65	0.27	0.37	386	0.95
Both	14.55	0.42	0.54	23.52	0.55	0.78	509	1.54
	---------- Pr. > F ----------							
Block	0.906	**0.030**	0.818	0.977	0.086	0.594	**0.024**	**0.007**
Thinned	**0.017**	**<0.001**	**0.001**	0.453	**<0.001**	**0.001**	**0.001**	**0.008**
Fertilized	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.001**	**0.001**	**<0.001**	0.108
Interaction	**0.047**	0.566	0.235	0.225	0.402	0.183	0.150	**0.058**

Table 6. Thinning and fertilizer growth response* for all tree and crop tree growth annualized over the four-year treatment period and for year four growth as well as foliage biomass and growth efficiency (GE) in year four.

	1-4 Year Growth Response			Year 4 Growth Response			Year 4 Foliage	Year 4 GE
	Height *cm/yr*	DBH *cm/yr*	Volume *m^3/ha/yr*	Height *cm/yr*	DBH *cm/yr*	Volume *m^3/ha/yr*	Response *kg/ha*	Response *m^3/1000kg*
ALL TREES								
Thinned	-none-	0.22	-2.11	4.54	0.34	-none-	-2632 | -5360	0.74
Fertilized	6.7	0.10	2.62	13.87	0.16	3.96	3915 | 1187	0.42
CROP TREES								
Thinned	-0.70 | -5.36	0.14	0.18	-none-	0.24	0.33	173	0.34
Fertilized	11.49 | 6.83	0.16	0.23	18.24	0.20	0.36	223	-0.04 | 0.46

** Growth response was calculated as the difference between the main effect means (e.g. thinning effect for height growth = ((mean height growth on thinned plots + mean height growth on thinned and fertilized plots)/2)-((mean height growth on control plots + mean height growth on fertilized plots)/2); responses not statistically significant at α = .05 are listed as "-none–"; responses with significant interactions are listed with the untreated comparison first (i.e. non-fertilized | fertilized responses for thinning growth responses and non-thinned | thinned responses for fertilizer growth responses).*

As would be expected, thinning reduced volume growth per hectare over the four-year period when all trees were considered, but this growth reduction was no longer statistically significant during the fourth year. Crop tree volume growth per hectare was increased, in contrast, with the greatest response in the fourth year.

Thinning significantly reduced year four foliage biomass for all trees but increased foliage biomass for crop trees. Thinning for both all and crop trees increased foliage growth efficiency with a greater response for all trees.

2.4.2 Effects of Fertilization on Growth

Fertilization had a significant positive effect on all measures of tree and stand growth (Table 5) and response was strongest in the fourth year (Table 6). For all trees during the fourth year (3rd year after fertilization) height growth, diameter growth, and volume growth were increased by 219%, 91%, and 197%, respectively. For crop trees these responses were 267%, 100%, and 155%, respectively. For height growth and volume growth the effects of fertilization were much greater than thinning.

During year four current annual volume increment on fertilized only plots averaged 7 m^3/ha/year as compared to 2 m^3/ha/year on control plots, a 250% response (350% increase in growth). Fertilization dramatically increased foliage biomass and for all trees the magnitude of the response differed by thinning levels (significant fertilizer x thinning interaction, Table 5). Fertilizer response was 86% on non-thinned plots and 63% on thinned plots. The main effect of fertilization was a 99% increase without a significant interaction.

Fertilizer increased growth efficiency for all trees and increased crop tree growth efficiency on thinned plots. Volume growth was positively related to foliage biomass among fertilized plots but there was no relationship among non-fertilized plots (Figure 3).

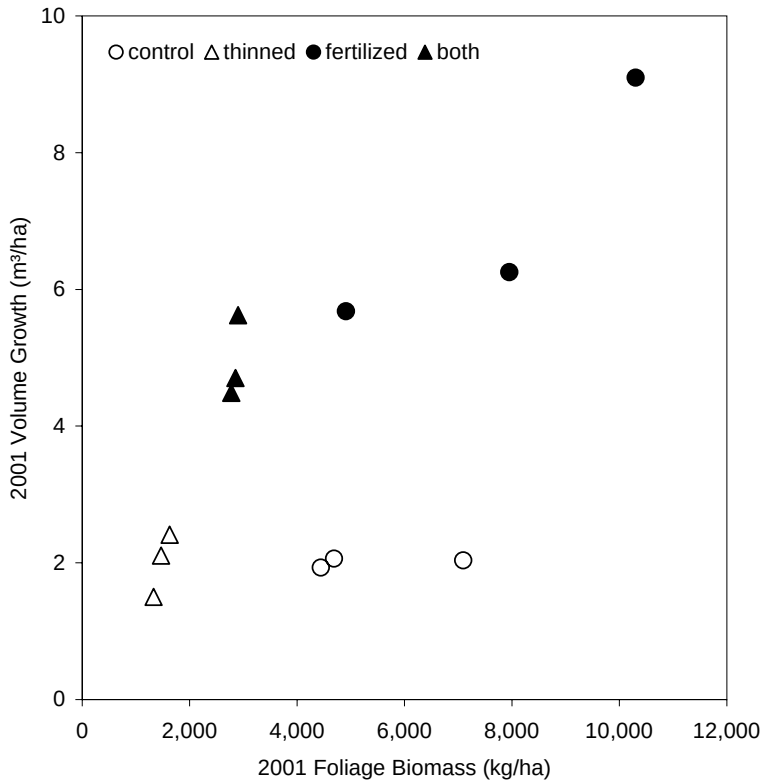

Figure 3. Relationship between year four all tree annual volume growth and stand foliage biomass for each plot in year 4 (four years after thinning but three years after fertilization).

2.4.3 Foliar Nutrient Concentration Response

Newsome and Perry (2003) reported treatment means and analysis of variance for foliar nutrient concentrations (Table 7) from the present study site. Based on the magnitude of response to nutrient additions and foliar critical values, it appears that boron was in shortest supply followed by sulfur and nitrogen. Boron foliar concentration was increased by fertilization by 24 ppm (276% increase) in the first year following fertilization, and remained elevated by 14 ppm (165%) in year four despite dilution by increased foliage biomass. Thinning also had a smaller but highly significant effect on boron concentration in the fourth year suggesting that the felled trees may have contributed a small amount of boron. Although thinning increased boron concentration by only 4 ppm this amounts to a 30% increase over non-thinned plots. The increase in boron concentration due to thinning was not enough to bring the foliar concentration above the critical value but the fertilization treatment resulted in foliar boron well above the critical value.

Table 7. Foliar nutrient concentration treatment means and analysis of variance (probability of a greater F) summarized from Newsome and Perry (2003) and foliar critical values from Brockley (2001a).

	N	P	K	Ca	Mg	S	B
Year 2 (1st year after fertilization)							
	---------- Treatment Means (%) ----------						*ppm*
Control	0.81	0.13	0.42	0.20	0.08	0.07	8
Thinned	0.89	0.14	0.43	0.18	0.09	0.07	9
Fertilized	1.22	0.15	0.50	0.18	0.09	0.10	31
Both	1.31	0.14	0.51	0.23	0.08	0.11	33
	---------- Pr. > F ----------						
Thinned	**0.010**	0.880	0.440	0.180	**0.017**	0.240	0.560
Fertilized	**< 0.001**	**0.052**	**<0.001**	0.059	0.500	**<0.001**	**<0.001**
Interaction	0.860	**0.052**	0.640	**0.001**	**0.003**	0.880	0.900
Year 4 (3rd year after fertilization)							
	---------- Treatment Means (%) ----------						*ppm*
Control	0.88	0.12	0.41	0.16	0.09	0.07	7
Thinned	0.92	0.13	0.44	0.18	0.09	0.07	10
Fertilized	0.97	0.14	0.44	0.14	0.08	0.08	20
Both	0.92	0.14	0.47	0.17	0.09	0.08	25
	---------- Pr. > F ----------						
Thinned	0.950	0.400	**0.032**	**0.028**	0.190	0.930	**<0.001**
Fertilized	0.140	**0.004**	**0.055**	0.340	0.240	**0.006**	**<0.001**
Interaction	0.150	0.400	0.890	0.560	0.820	0.410	0.200
Critical Values							
	---------- % ----------						*ppm*
Lodgepole Pine	1.35	0.10	0.40	0.10	0.08	0.10	15

There were no thinning effects on foliar sulfur concentration but there were strong effects of fertilization. Foliar sulfur concentration was increased by 50% the first year after fertilization and remained elevated 10% above non-fertilized plots in the fourth year. The fertilizer treatment resulted in foliar sulfur concentrations at the critical level on fertilized plots and 0.01 above critical for plots that were thinned and fertilized. Fertilization increased foliar nitrogen concentration by 0.42 (49%) the first year after fertilization but by year four this effect was lost due to, at least in part, dilution caused by the increase in foliage biomass. Thinning also had a small effect on foliar nitrogen the first year following fertilization (8%) but this effect was also lost by year four. Foliar nitrogen remained below the critical value for all treatments and years.

2.4.4 Relationship between growth and density

The inverse relationships between height and density and volume and density are the primary symptoms of repression (Figures 1 and 2), but these relationships were small when compared to the growth response to fertilization (Figure 4). There was an inverse relationship between height growth and density for non-fertilized plots but the range in height growth was small compared with the growth of fertilized plots (Figure 4A). However, there was no relationship between stand volume growth and density unless fertilizer was applied and then volume growth was greater at higher density (Figure 4B).

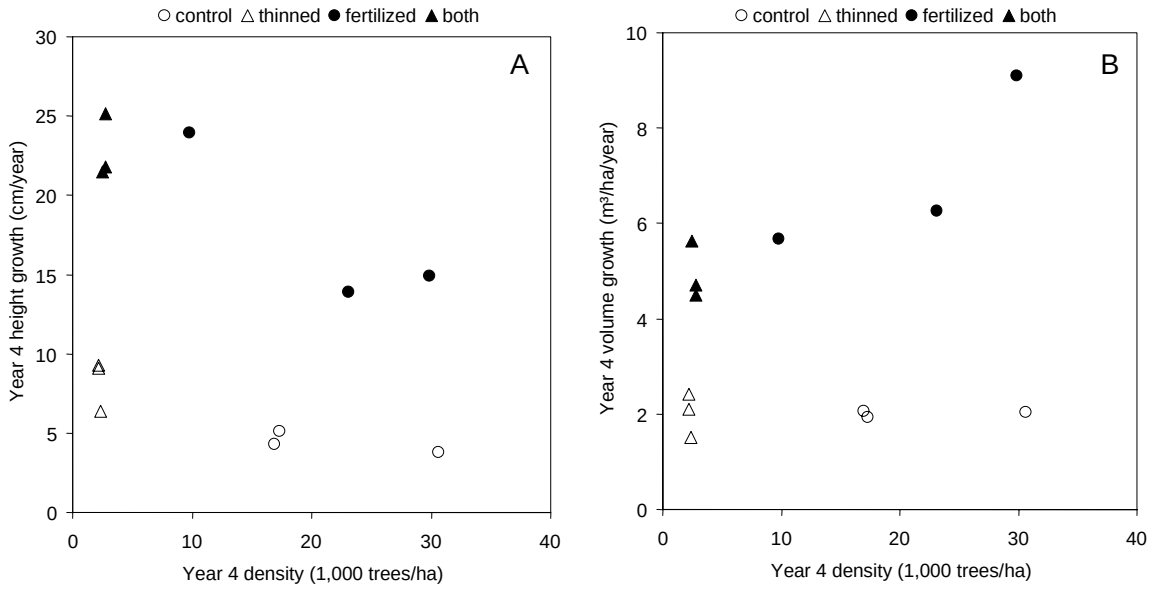

Figure 4. Relationships between height growth and density (A) and volume growth and density (B) in year four (four years after thinning but three years after fertilization).

2.5 Discussion

The combination of fertilization and thinning have clearly overcome repression. The large growth responses to both fertilization and thinning found in this study (Table 6), and the responses reported by Farnden and Herring (2002), indicate that repressed stands can respond immediately when nutrient limitations are ameliorated and density is reduced. Amelioration of nutrient deficiencies overcame the relationships between height and density and volume and density that define the repressed condition (Figure 4).

2.5.1 Growth Response

Not surprisingly, thinning effects on stand volume growth (all trees) were negative immediately following thinning because of the almost 90% reduction in the number of trees per hectare and the almost 80% reductions in basal area and volume (Table 5). However, what was surprising was that during the fourth year following thinning there was no significant reduction on stand volume growth (all tree) indicating that trees on thinned plots have already recaptured the site growth potential despite the significant reduction in density (Table 5). In contrast, crop tree volume growth responded positively (80%) over the four-year treatment period and this response was greater during the fourth year (138%). These crop trees also continued to show increased levels of growth efficiency suggesting that more resources continue to be available to crop trees on thinned plots.

The varying temporal effects of thinning are well documented, typically with a period of reduced height growth followed by a later period of increased growth (Brix 1983, Gillespie 1994). This period of reduced height growth is typically associated with rapid lateral crown development (Brix 1981, Gillespie 1994, Chapter 3). The increased DBH growth observed in year four is also typical of thinning responses.

Fertilizer had very strong positive effects on growth for all measures on all trees and crop trees (Table 6). Fertilizer response was stronger than thinning for height growth and volume growth but weaker for DBH. Apparently, a complete fertilizer (Table 3) was needed to ameliorate nutrient deficiencies based on the low initial foliar nutrient concentrations and foliar response to

fertilization (Table 7). Nitrogen, sulfur, and boron appear to be most limiting.

Boron appears to be the most limiting element on this site based on the foliar nutrient concentration response and initial concentrations well below critical levels (Table 7). Low foliar boron concentrations are common in lodgepole pine stands throughout north-central British Columbia (Brockley 2001a). Boron has been reported to be lost in hot fires (Stone 1990) and may be a common limitation in repressed stands, especially those on volcanic origin soils (Stone 1990).

2.5.2 Comparison With Other Local Studies

Volume growth responses of this study (Rosite Lake) were greater than five non-repressed lodgepole pine fertilizer trials within 150 km (Table 8, Figure 5). The cold dry climate of the Chilcotin Plateau may not be as favorable to tree growth as some other regions within the natural range of lodgepole pine. These trials are in lodgepole pine stands typical for the region with the same experimental design and treatments. They are all in managed lodgepole pine stands around twenty years old with between 1,100 and 1,600 trees per hectare (Table 8). The mean annual increment of these stands ranges from 1.5 to 4.0 m^3/ha/year with the repressed stand in this study (Rosita Lake) near the middle of the range.

Table 8. Stand origin, history, zone, age, density, and mean annual increment (MAI) for nearby fertilizer trials used to compare with this study.

Name[1]	Origin	History	BEC[2]	Treatment Age	Density *trees/ha*	MAI *vol/ha/year*
Rosita Lake	Fire	Repressed	SBPSdc	36	21,000	2.4
Meldrum Creek	Fire	Thinned	IDFdk	19	1,100	2.2
Raven Lake	Harvest	Plantation	SBPSxc	19	1,600	1.5
Longjohn Lake	Harvest	Plantation	SBPSmc	20	1,600	4.0
Pantage Creek	Harvest	Plantation	SBPSmk	23	1,100	1.9
Mons Creek	Harvest	Plantation	SBPSxc	21	1,100	1.5

[1] *The present study (Rosita Lake) and five other fertilizer trials within 150km (Brockley, unpublished data).*
[2] *BEC = Biogeoclimatic Classification*

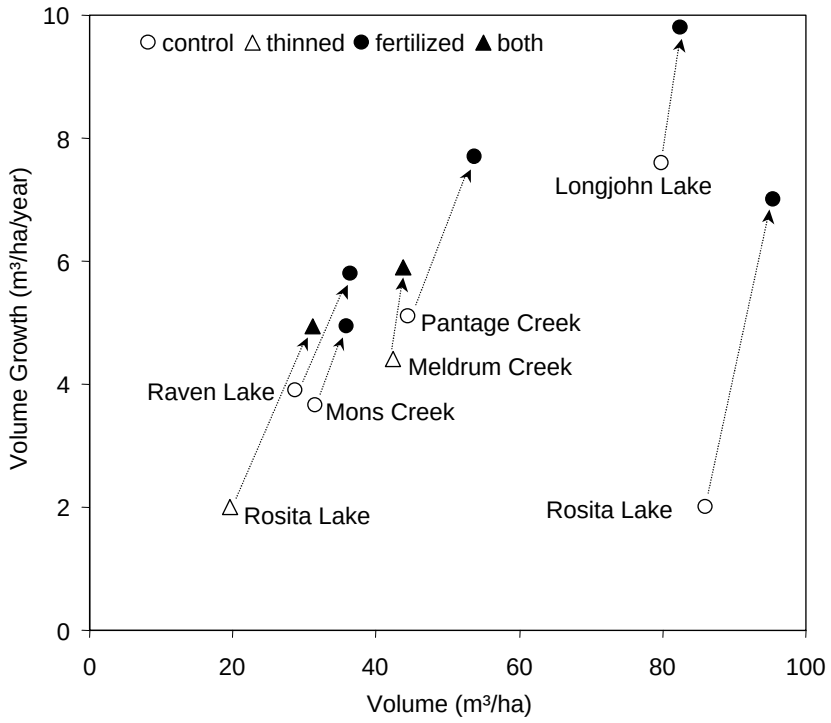

Figure 5. Productivity comparison between five lodgepole pine fertilizer trials within 150km of the repressed lodgepole pine stand in this study (Rosita Lake). Fertilizer response (indicated by arrows) is three years after fertilization and the other studies are in plantations or a thinned natural stand (Meldrum Creek). The fertilizer treatment on the other studies was 200 kg/ha nitrogen plus 50 kg/ha sulfur.

Most of the stands were planted on harvest-origin sites except for Meldrum Creek which is a thinned fire-origin non-repressed stand. Most of the stands are in the Sub-boreal Pine Spruce biogeoclimatic zone except for Meldrum Creek (one of the closer trials), which is in the Interior Douglas-fir zone. The details of the experimental design and treatments have been published (Brockley 2000). The control plots show a positive relationship between volume growth and standing volume except the repressed stand (Rosita Lake) is an outlier with the lowest volume growth and the highest standing volume. This relationship is to be expected when viewing stands of similar age and density because higher volume is the result of higher volume growth over time. The repressed stand does not fit within this relationship because it is older and has had more time to accumulate volume. Also, current annual volume growth is less than mean annual volume growth for the repressed stand while it is greater for the managed stands. High density in the repressed stand may also contribute to its higher volume because the stand would have been able to more fully capture the productive potential of the site at a younger age.

All of the fertilizer trials in non-repressed stands had similar responses (arrows in Figure 5) regardless of their position in the volume growth vs. standing volume relationship. In all cases the addition of 200 kg/ha nitrogen plus 50 kg/ha of sulfur increased the growth rate by around 2 m^3/ha/year. On fertilized only plots in this study, the average growth rate was increased by 5 m^3/ha/year. Whether this larger response is attributable to the more complete fertilizer mix or a greater nutrient deficiency cannot be determined from these data, but clearly the repressed stand treated with fertilizer is approaching the realm defined by the non-repressed stands. When thinning was combined with fertilization in the repressed stand the growth rate was increased by 3 m^3/ha/year, moving the stand within the range defined by the managed stands. The thinning treatment without fertilization in the repressed stand had no effect on volume growth rate (compared to control). Although the thinned only treatment has fallen in line with the managed stand control plots, it still has by far the lowest volume growth.

Continuing stand-level growth response to fertilizer is expected beyond the four-year measurement period due to the large increase in stand-level foliage biomass and the continuing elevated levels of sulfur and boron. Even with the decline of foliar nitrogen concentration to that of the control, the large increase in foliage biomass equates to an equally large increase in canopy foliar N content. How long this response will continue is unknown. A few studies have reported long-term responses to nutrient amendments (NCSFNC 1998, Turner et al. 2002, Albaugh *et al.* 2004). Foliar nitrogen remained below the critical value on fertilized plots suggesting that either higher rates or repeated application of nitrogen would produce additional response.

2.5.3 Growth Efficiency

Both increases in foliage biomass and growth efficiency contributed to the growth response. Strong growth efficiency responses have been observed on very nutrient poor sites elsewhere (Linder 1987, Albaugh et al. 2004).

The strong foliage biomass and growth efficiency gains associated with fertilization or thinning and fertilization suggest that the potential productivity of this site is quite high. Recent analyses

in other northern systems (Bergh *et al.* 1998) suggest greater levels of production are possible in northern forests than previously thought. The potential for increasing growth in these systems with nutrient management may not be as limited by temperature and moisture as previously thought.

Thinning alone reduced the amount of foliage per hectare for all trees but did not affect stand volume growth in year four because of increased growth efficiency. The thinning treatment has not altered the supply of resources; it has only reduced the number of trees competing for that limited supply. Fertilization alone increased foliage biomass per hectare and volume growth per hectare and had a large effect on growth efficiency of all-trees. Fertilization and thinning combined reduced foliage biomass and increased production through improved growth efficiency.

The growth efficiency increases due to fertilization could be due to both increased photosynthetic efficiency associated with higher foliar nutrient concentrations (Table 7, Linder 1987, Murthy *et al.* 1996) and increased above-ground carbon allocation due to improved soil fertility (Beets and Whitehead 1996, Haynes and Gower 1995, Albaugh et al. 2004). Fertilization increased growth efficiency for all trees and for thinned crop trees similarly (responses of 0.42 and 0.46 m^3/kg respectively) but had no effect on non-thinned crop trees (Table 6). The effect of light penetration on photosynthetic efficiency may also explain why growth efficiency was not increased by fertilization on non-thinned crop trees. The large fertilizer induced increase in foliage biomass on the non-thinned plots resulted in the highest foliage biomass and therefore shading, which may have counteracted any increases in crop tree growth efficiency due to improved foliar nutrition.

It is possible that the majority of increases in growth efficiency due to thinning for both all trees and crop trees are the result of increased photosynthetic efficiency due to light penetration deeper into the crown (Long and Smith 1990, Gillespie 1994). These effects were stronger for all trees than for crop trees (74% and 34% response respectively) because crop trees represent the best trees in the stand and had higher growth efficiency on control plots (0.99 m^3/kg) than all trees on control plots (0.46 m^3/kg). This is another indication that stand differentiation is occurring on this site not only with respect to trees size but also at a physiological level.

2.6 Conclusions

The condition of repression has clearly been overcome by a combination of thinning and fertilization. The additive effects of thinning and fertilization indicate that both treatments are needed to achieve the maximum response. The growth response was immediate and greater than found on nearby fertilizer trials. Stand volume growth was increased in year four after treatment from 2 to 7 m^3/ha/year with nutrient additions on non-thinned plots and to 5 m^3/ha/year when fertilizer was applied to thinned plots. Continuing stand-level growth response to fertilizer is expected due to the large increase in stand-level foliage biomass and the continuing elevated levels of sulfur and boron. The fertilizer treatment increased tree and stand growth through increases in both foliage biomass and growth efficiency. Thinning increased tree level growth by concentrating limited resources onto fewer trees. Boron appears to be the most limiting element followed by sulfur and nitrogen. Each of these elements has been identified as being limiting in non-repressed lodgepole pine in the region. The portability of these results to other repressed lodgepole pine stands or to repressed stands of other species depends on the understanding of the causal mechanisms of the growth response.

CHAPTER 3

REPRESSED LODGEPOLE PINE CROWN RESPONSE TO THINNING AND FERTILIZATION

3.1 Introduction

The large and immediate stand growth responses to thinning and fertilization described in Chapter 2 are associated with increases in foliage biomass and growth efficiency. Understanding how individual crowns and foliage within those crowns respond to increased nutrition and growing space will help to better understand the stand growth responses.

Pine foliage biomass can be increased a number of ways (Stenberg *et al.* 1994). Pine foliage biomass can be increased by making more and larger needles per fascicle, more fascicles per shoot, more shoots per branch, more branches per tree, or by increasing retention of older foliage. A fascicle is a bundle of needles attached at the base to the branch as a unit; lodgepole pine usually has two needles per fascicle. The number of fascicles in a shoot is determined in the fall of the previous year when the bud is set. It is therefore not possible to increase foliage biomass by increasing the number of fascicles during the first year after treatment unless additional shoots or branches are produced. The number of fascicles on a shoot can contribute to increased foliage biomass in subsequent years. At the level of the branch foliage biomass can be increased by either making more shoots or by increasing the amount of foliage on a shoot. Increased foliage on a shoot cannot be achieved the first year after fertilization by increasing the number of fascicles on a shoot but it can be achieved by increasing the weight of fascicles. Subsequent years can have both higher numbers and larger fascicles. Foliage biomass can also be increased through increased retention of old foliage cohorts or retention of old branches near the bottom of the live crown.

The factors that contribute to foliage response can vary vertically within the crown (whorl position), by year of production (cohort year), and by the rank within the branch structure (branch order) (Ford 1985, Whitehead *et al.* 1990, Raison *et al.* 1992a). A whorl is defined as all branches originating from the main stem within one annual stem growth section. The number of

whorls with live branches on a tree depends on its age and live crown length. A cohort is defined as all the foliage (or branches) produced during a single growing season. A lodgepole pine cohort of foliage usually remains on the tree for three to six years. Branch order is defined based on where the branch is attached to the rest of the tree. First order branches originate from the main stem, second order branches originate from first order branches, and so on. More higher order branches allow for higher crown density. All these factors can vary depending on genetics and site conditions (Lotan and Critchfield 1990).

Although many papers have described various needle or crown responses to treatments in several species including lodgepole pine (Gillespie *et al.* 1994, Sampson and Smith 1993, Binkley et al. 1995, Long and Smith 1984, Ford 1985, Vose *et al.* 1994, Kinerson et al. 1974), these responses have not been explored in combination or for repressed lodgepole pine.

3.2 Objectives

The extent to which needle, fascicle, and branch factors contributed to the increased foliage biomass of repressed lodgepole pine were addressed through the following questions:

1) What were the contributions of fascicle weight versus number, branch foliage weight versus number, retention, and extra needles per fascicle to the whole crown foliage biomass response to increased nutrition and growing space?

2) How did treatments affect the distribution of these variables vertically within the crown, across cohorts and across branch orders?

3.3 Methods

The data for this analysis come from the same destructively sampled trees that were used to estimate total foliage biomass per hectare in Chapter 2. This chapter will utilize the same data but will consider in more detail results at the level of the tree, whorl position, cohort, and branch order and for all the possible mechanisms of increased foliage biomass. See Chapter 2, section 3, for a more detailed description of the site, experimental design, and treatments.

3.3.1 Sampling and Measurements

Trees were selected to be both representative of their plots and to cover most of the range of variability in tree size. Data from these trees was used in both the regression analysis to produce the volume and foliage biomass equations presented in Chapter 2 as well as comparisons of treatment effects. Sampling across the range of tree sizes was critical to develop regressions applicable to the range of tree sizes present. Because of these requirements, a representative small, medium, and large tree was selected from each plot. Analysis of variance did not reveal any treatment effects on average pre-treatment sample tree height or DBH so these trees can be considered to represent the same population.

Three trees were harvested in August, 2001 from the treated buffer of each plot in the experiment described in Chapter 2. In addition to the volume (Equation 1) and foliage biomass equations (Equations 2 and 3) described in Chapter 2, these trees were also used for a more detailed analysis of the crown. Total height, DBH, and whorl lengths within the live crown were measured. Each whorl was identified by a number starting at 1 for the top most whorl and proceeding sequentially to the bottom of the live crown. If a whorl had no live branches it was included in the numbering of whorls even though no sample was collected. This means a given whorl number on one tree represents the same origination year as the equivalent numbered whorl on another tree. The live crown of each tree was divided into whorls and stored in a 4 degree C walk-in cooler until processed in the lab.

In the lab, each whorl was further divided into branch orders and cohorts and oven dried at 70 degrees C for at least 48 hours. Branches originating on the main stem were labeled 1^{st} order branches. Branches originating on 1^{st} order branches were called 2^{nd} order branches and so on. Most trees had up to 3^{rd} order branches but there were a few cases of 4^{th} and 5^{th} order branches. Foliage produced during the current growing season (2001) was called cohort 1. Foliage produced the year before sampling (2000) was called cohort 2. Trees held at most 6 cohorts (the oldest was produced in 1996).

Measurements were taken once all foliated branches were processed and dried. Each group of foliated shoots were uniquely identified based on their tree, whorl position, branch order, and

cohort. For each group of shoots, the foliage was separated from the shoots and the number of shoots were counted. Foliage was weighed and a randomly selected sub-sample of intact fascicles was used to determine fascicle weight and the number of fascicles with more than two needles. The number of fascicles in a sample was estimated by dividing the foliage biomass of that sample by the average fascicle weight. The number of fascicles with more than two needles was estimated by calculating the percentage of the sub-sample they represent and then multiplying that percentage by the total number of fascicles.

Summarization of this data, whether at the tree, whorl, cohort, or branch level, was accomplished using the following methods. Total foliage biomass and number of fascicles were calculated by summing all the samples. Average fascicle weight was calculated as a weighted average weighted by the number of fascicles in each sample. Average amount of foliage on a branch was calculated as a weighted average weighted by the number of branches in the sample. The number of foliated branches was calculated as the maximum number of branches for any whorl and branch order combination. This is because branches were divided into cohorts when they were counted so simply summing the number of branches across all samples would count each branch as many times as it had cohorts. It is also because not all branches had all cohorts. Foliage retention was estimated by calculating the average number of cohorts for each tree and for each whorl on each tree.

The relative contribution to the foliage biomass response of fascicle weight versus number and branch foliage weight versus number was calculated using a multiplicative method. Foliage biomass for a tree is equal to the number of fascicles for that tree times the average fascicle weight; therefore, equations 4 and 5 were used to calculate the percent contribution of each of these effects to the foliage biomass response (Equations 4 and 5).

Equation 4 Fascicle Weight Contribution = (((tfw – cfw) * cfn)/(tfb - cfb)) * 100

Equation 5 Fascicle Number Contribution = (((tfn – cfn) * tfw)/(tfb - cfb)) * 100

Where: tfw = treated fascicle weight
cfw = control fascicle weight
cfn = control fascicle number
tfb = treated foliage biomass
cfb = control foliage biomass
tfn = treated fascicle number

Total foliage biomass for a tree can also be calculated as the number of foliated branches times the average weight of foliage on a branch, therefore a similar set of equations was used to calculate the percent contributions of these variables (Equations 6 and 7).

Equation 6 Branch Foliage Weight Contribution = (((tbfw – cbfw) * cbn)/(tfb - cfb)) * 100

Equation 7 Branch Number Contribution = (((tbn – cbn) * tbfw)/(tfb - cfb)) * 100

Where: tbfw = treated branch foliage weight
cbfw = control branch foliage weight
cbn = control branch number
tfb = treated foliage biomass
cfb = control foliage biomass
tbn = treated branch number

3.3.2 Statistical Analysis

A randomized complete block analysis of variance (2 x 2 factorial with three replications) was used to examine the effects of thinning and fertilization on foliage biomass per tree, fascicle weight, fascicle number, branch foliage weight, branch number, the number of 3-needle fascicles, and retention.

Table 9. Design of the analysis of variance for all analyses.

Source of variation	Degrees of freedom
block	2
thinning (t)	1
fertilization (f)	1
interaction (t x f)	1
error	6
total	11

An alpha of 0.05 was used for the purpose of discussing significant main effects and interactions. These analyses were performed on whole tree means and for means for each whorl position for all variables. These analyses were also performed on foliage biomass, fascicle weight, and fascicle number for each cohort and on foliage biomass, branch foliage weight, and branch number for each branch order.

3.4 Results

3.4.1 Whole-tree Responses

Thinning and fertilization both had strong additive effects on tree-level foliage biomass (120% and 102% response respectively). The interaction of thinning and fertilization was weakly significant even though there was a large difference between the foliage biomass per tree on fertilized plots depending on whether or not they were thinned (Table 10).

Table 10. Treatment means and analysis of variance for whole-tree means.

	Foliage Biomass *g/tree*	Fascicle Weight *g/fascicle*	Fascicle Number per Tree	g Foliage per Branch	Number of Branches per Tree	3-needle Fascicles per Tree	Foliage Retention *cohorts/tree*
				Treatment Means			
Control	229	0.017	13,360	1.41	163	2	5.9
Thinned	511	0.022	22,273	2.10	244	8	5.6
Fertilized	472	0.021	22,159	1.34	354	13	5.8
Both	1,028	0.029	35,342	1.90	540	56	5.0
				Pr. > F			
Block	0.221	0.867	0.214	0.702	0.347	0.246	0.481
Thinned	**0.008**	**< 0.001**	**0.012**	**0.032**	0.127	**0.002**	**0.045**
Fertilized	**0.001**	**< 0.001**	**0.019**	0.931	**0.018**	**0.001**	0.180
Interaction	0.086	0.163	0.635	0.429	0.510	**0.006**	0.351

Both thinning and fertilization increased fascicle weight and the number of fascicles. The number of fascicles was 30% more responsive than fascicle weight at the whole-tree level for both thinning and fertilization effects. Thinning increased fascicle weight more than fertilization (34% vs. 28% response respectively) but fascicle number was increased equally by thinning and fertilization (62% vs. 61% response respectively).

Although both thinning and fertilization affected fascicle variables, branch variables were affected by one treatment or the other. The amount of foliage on a branch (branch foliage weight) was only increased by thinning and not by fertilization. The number of branches was only increased by fertilization and not by thinning. The amount of foliage biomass on a branch was greater on thinned plots while the number of branches was greater on fertilized plots. The branch number response was stronger due to fertilization (120% response) than the foliage weight response was to thinning (45% response).

The effects of both thinning, fertilization, and their interaction were statistically significant for the number of 3-needle fascicles but these numbers are so low they are not biologically significant. Even when thinning and fertilizer were both applied the total number of 3-needles fascicles only amounted to 0.16% of the total number of fascicles. This is not enough to have contributed to the foliage biomass response and so is not included in the remaining analyses.

Foliage retention was slightly reduced by thinning (less than a full cohort) but was not affected by fertilization. The reduction in foliage retention on thinned plots was small compared to the overall increase in foliage biomass due to thinning.

3.4.2 Relative Contributions to the Foliage Biomass Response

Of the possible mechanisms of increased foliage biomass, only increases in fascicle weight, fascicle number, branch foliage weight, and branch number could have contributed to increased foliage production on thinned and fertilized plots. Which of these mechanisms contributed more to the foliage biomass response and was the contribution affected by treatment?

About 80% of the increase in foliage biomass can be attributed to increases in number of fascicles regardless of treatment, with the remaining 20% being attributed to increases in fascicle weight (Table 11). Despite large treatment effects on growth and foliage biomass the relative contribution of these two variables remained unchanged.

Table 11. The effect of thinning and fertilization on the relative contribution of fascicle weight and number and branch foliage weight and number to the foliage biomass response.

	--- % Contribution to the Foliage Biomass Response ---			
	------ Fascicles -------		---------- Branches ----------	
	Weight[1]	Number[2]	Foliage Weight[3]	Number[4]
Thinned	23	77	40	60
Fertilized	23	77	-5	105
Both	20	80	10	90

[1] Calculated using Equation 4.
[2] Calculated using Equation 5.
[3] Calculated using Equation 6.
[4] Calculated using Equation 7.

In contrast to the consistent contribution of fascicle variables, branch variables contributed to the foliage biomass response in different proportions depending on treatment. Increases in the amount of foliage on a branch were more important to the response when thinning was applied alone. On thinned plots, increases in branch number accounted for 60% of the foliage biomass response versus 40% for the amount of foliage on a branch. The amount of foliage on a branch contributed either nothing (-5%) when fertilizer was applied alone, or very little (10%) when fertilizer was applied in combination with thinning.

Increased foliage retention did not contribute to the foliage response for any of the treatments. Thinning was the only treatment with a statistically significant effect on retention at the whole-tree level but this effect was negative (less retention) so could not have contributed to the response.

3.4.3 Vertical Distributions

The effects of thinning and fertilization on foliage biomass were statistically significant only for the top half of the crown (Table 12). Thinning effects extended three whorls lower in the crown than fertilizer effects. There was a significant interaction of thinning and fertilization only in the top three whorls, those initiated after fertilization.

The vertical distribution of foliage biomass within the crown had a consistent pattern for all treatments (Figure 6). The maximum amount of foliage occurred about one third of the way from the top of the tree with a roughly linear reduction toward the top and the bottom of the live crown. On control plots, the peak foliage biomass occurred on average at the 7^{th} and 8^{th} whorl positions from the top of the tree. Thinning and fertilization increased the magnitude of this pattern but did not affect where the peak whorls were located. A bulge in foliage biomass in the top three whorls can be seen for plots receiving the fertilizer treatment (Figure 6). The bottom of the live crown was the same (essentially the 22^{nd} whorl) for all treatments.

Table 12. Analysis of variance (probability of a greater F) for foliage biomass for each whorl position for the effects of blocks (Block), thinning (Thin), fertilization (Fert), and the interaction of thinning and fertilization (Int).

Whorl Position	Foliage Biomass			
	Block	Thin	Fert	Int
Top 1	0.353	**0.007**	**< 0.001**	**0.019**
2	**0.014**	**0.003**	**< 0.001**	**0.013**
3	0.900	**0.004**	**< 0.001**	**0.012**
4	0.825	**0.007**	**0.013**	0.349
5	0.205	**0.006**	**0.005**	0.098
6	0.126	**0.001**	**0.004**	0.190
7	0.736	**0.011**	**0.011**	0.159
8	0.466	**0.008**	**0.020**	0.196
9	0.667	**0.008**	**0.012**	0.178
10	0.227	**< 0.001**	**< 0.001**	0.065
11	0.445	**0.018**	**0.008**	0.668
12	0.477	**0.030**	0.186	0.850
13	0.455	**0.006**	0.059	0.480
14	0.153	**0.019**	0.127	0.737
15	0.366	0.135	0.921	0.868
16	0.862	0.103	0.346	0.859
17	0.525	0.054	0.636	0.271
18	0.463	0.136	0.161	0.348
19	0.847	0.114	0.158	0.238
20	0.355	0.762	0.116	0.564
21	0.479	0.327	0.311	0.252
22	0.726	0.196	0.146	0.185
23	0.636	0.521	0.446	0.497
24	0.811	0.185	0.314	0.499
25	.	.	.	.
Bottom 26	0.420	0.493	0.573	0.706

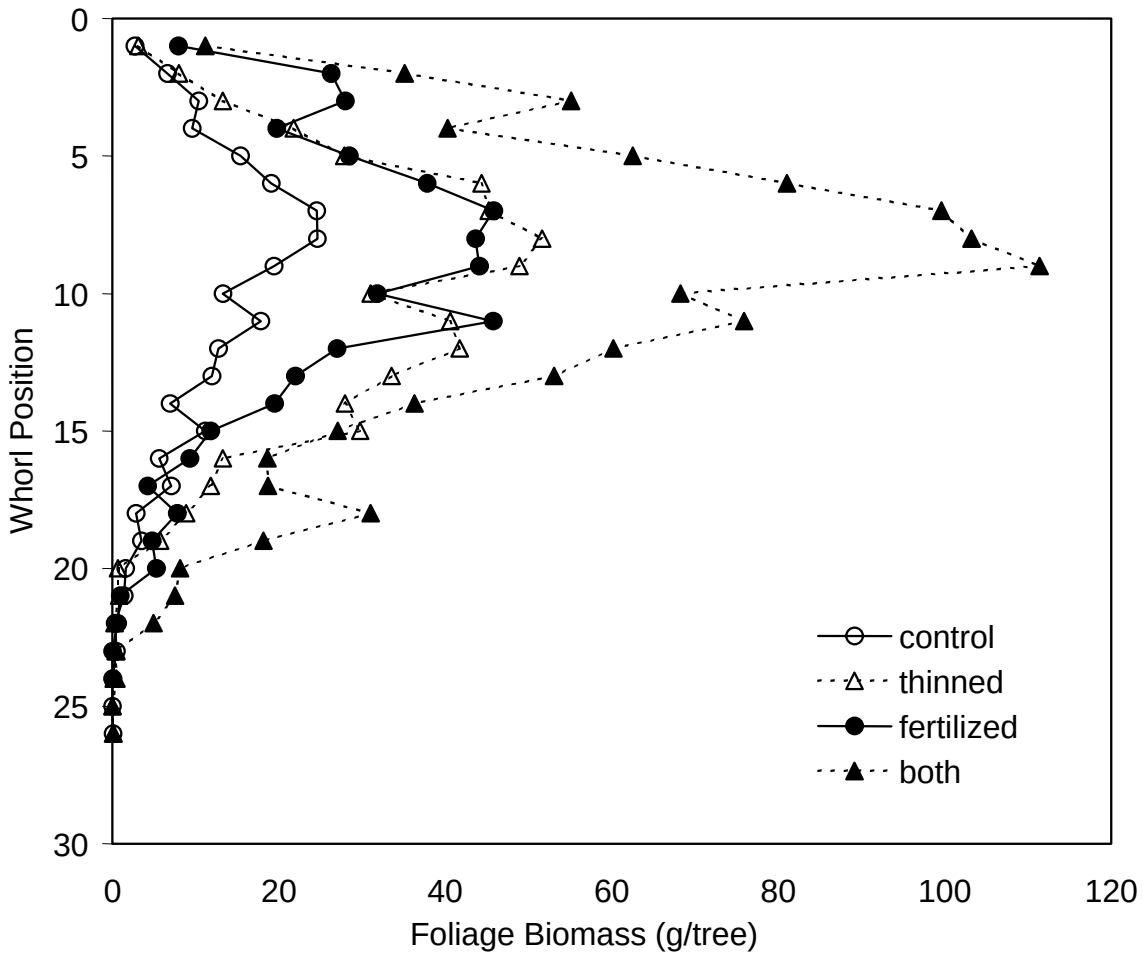

Figure 6. The effect of thinning and fertilization on the vertical distribution of foliage biomass from the top of the tree (whorl position 1) to the bottom of the live crown (whorl position 26).

Although thinning or fertilization alone produced similar responses in fascicle weight and number at the whole tree level (Table 10), their effects were vertically distributed differently (Table 13). Thinning and fertilization significantly increased fascicle weight throughout the crown, except thinning had no effect on the top-most whorls and fertilizer had no effect on the bottom-most whorls. Number of fascicles was significantly increased by thinning and fertilization only in the upper crown, although thinning had no effect on the top two whorls. The combined treatment resulted in a larger increase in fascicle weight and number throughout the crown than thinning or fertilizer alone (Figure 7A).

Table 13. Analysis of variance (probability of a greater F) for fascicle weight and number of fascicles for each whorl position for the effects of blocks (Block), thinning (Thin), fertilization (Fert), and the interaction of thinning and fertilization (Int).

	Fascicle Weight				Fascicle Number			
Whorl	Block	Thin.	Fert.	Int.	Block	Thin.	Fert.	Int.
Top 1	0.974	0.272	**0.030**	0.762	0.748	0.354	**0.002**	0.465
2	0.723	0.225	**0.005**	0.735	0.127	0.153	< **0.001**	0.223
3	0.719	**0.036**	**0.002**	0.871	0.786	**0.053**	**0.002**	0.083
4	0.483	0.176	**0.013**	0.585	0.781	**0.018**	0.081	0.737
5	0.306	**0.016**	**0.004**	0.389	0.365	**0.024**	**0.027**	0.288
6	0.963	**0.054**	**0.022**	0.841	0.233	**0.008**	**0.044**	0.524
7	0.488	**0.001**	**0.001**	**0.052**	0.893	**0.048**	**0.049**	0.504
8	0.653	**0.005**	**0.008**	0.092	0.489	**0.024**	0.074	0.610
9	0.510	**0.001**	**0.001**	0.171	0.811	**0.020**	**0.034**	0.561
10	0.968	< **0.001**	**0.001**	0.479	0.273	**0.023**	**0.012**	0.596
11	0.972	**0.001**	**0.001**	0.291	0.586	0.236	0.096	0.769
12	0.509	< **0.001**	**0.001**	0.138	0.454	0.148	0.525	0.753
13	0.894	**0.001**	**0.005**	0.502	0.355	0.058	0.282	0.968
14	0.293	< **0.001**	**0.001**	0.112	0.147	0.104	0.367	0.293
15	0.911	**0.008**	0.219	0.588	0.163	0.279	0.784	0.620
16	0.754	< **0.001**	**0.031**	0.120	0.788	0.430	0.567	0.867
17	0.614	< **0.001**	0.097	**0.014**	0.260	0.194	0.933	0.452
18	0.483	**0.005**	**0.036**	0.148	0.476	0.284	0.194	0.740
19	0.632	< **0.001**	**0.008**	**0.040**	0.622	0.447	0.351	0.486
20	0.742	**0.048**	0.964	0.676	0.322	0.633	0.218	0.988
21	0.441	**0.012**	0.241	0.082	0.518	0.546	0.383	0.286
22	.	.	.	.	0.943	0.402	0.183	0.294
23	.	.	.	.	0.579	0.598	0.366	0.541
24	.	.	.	.	0.897	0.204	0.450	0.561
25	.	.	.	.	.	.	.	.
Bottom 26	.	.	.	.	0.398	0.511	0.534	0.719

The vertical distribution of fascicle weight and number of fascicles followed consistent patterns that were altered by treatment only in magnitude (Figure 7A). Fascicles were heavier in the upper crown (Figure 7A), but were more abundant in the middle crown (Figure 7B). Fascicle weight increased moving down through the top three to four whorls and then decreased linearly toward the bottom of the live crown. The vertical distribution of the number of fascicles followed a pattern similar to the vertical distribution of foliage biomass.

Thinning significantly increased the amount of foliage on a branch and fertilization increased the number of branches at the whole tree level (Table 10). There was no statistically significant effect of thinning on branch number or fertilization on branch foliage weight at the whole tree level. However, thinning and fertilization affected both size and number of branches for certain whorls.

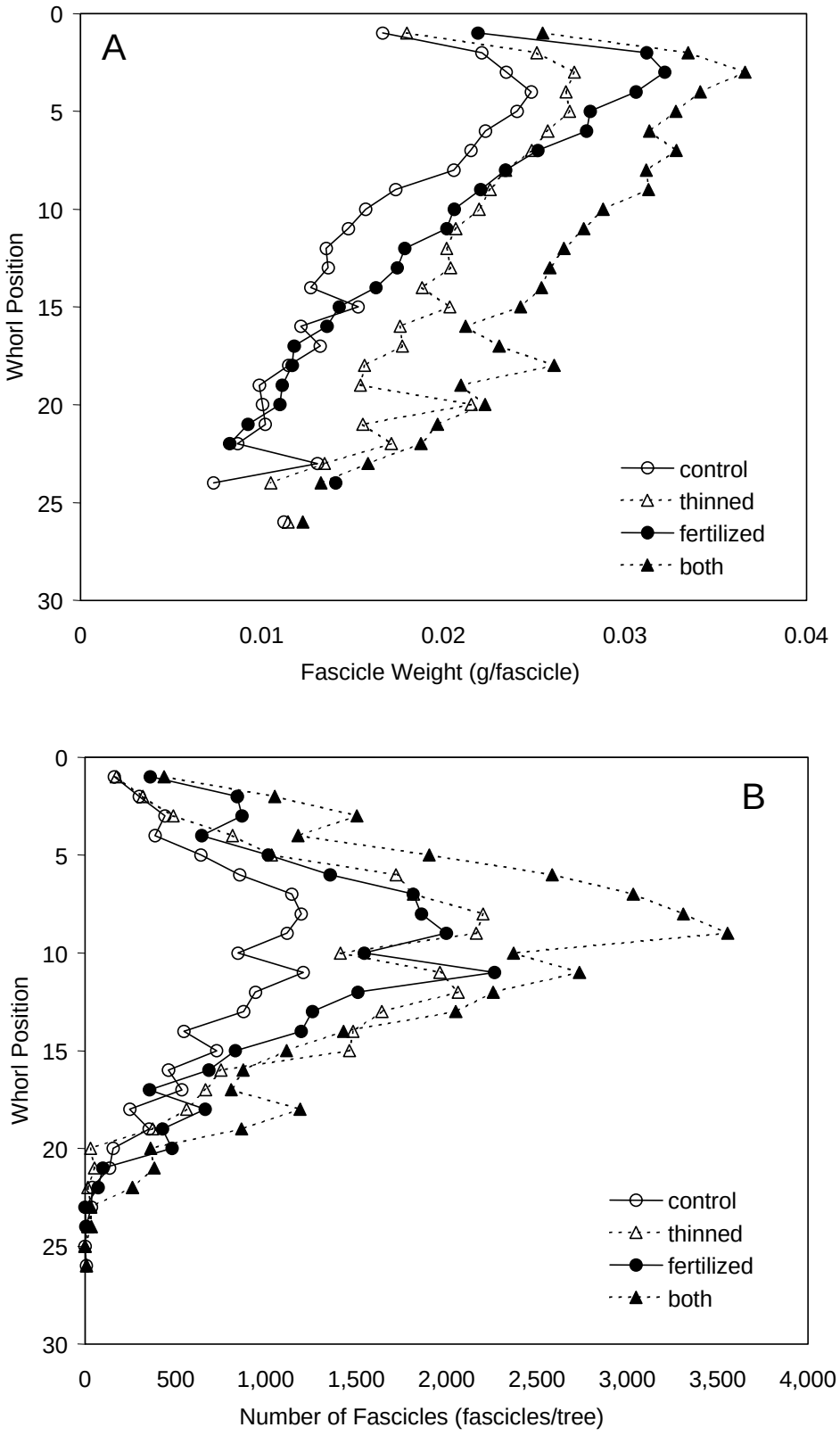

Figure 7. The effect of thinning and fertilization on the vertical distribution of (A) fascicle weight and (B) number of fascicles from the top of the tree (whorl position 1) to the bottom of the live crown (whorl position 26).

The amount of foliage on a branch was increased by thinning mostly in the lower crown and was only sporadically significant in top of the crown (Table 14). Fertilizer mostly increased the amount of foliage on a branch on the whorls that were initiated after fertilization (whorls 1 through 3). Thinning increased the number of foliated branches from the 4th whorl down to the 10th whorl. The number of foliated branches was increased by fertilization from the top of the crown down to the 14th whorl (Table 14).

Table 14. Analysis of variance (probability of a greater F) for the amount of foliage on a branch and the number of branches for each whorl position for the effects of blocks (Block), thinning (Thin), fertilization (Fert), and the interaction of thinning and fertilization (Int).

	Amount of Foliage on a Branch				Number of Foliated Branch			
Whorl	Block	Thin	Fert.	Int.	Block	Thin	Fert.	Int.
Top 1	0.383	0.083	**0.004**	0.147	0.568	0.912	**0.033**	0.587
2	0.501	0.231	**0.005**	0.915	0.760	0.497	**0.001**	0.436
3	0.230	**0.042**	**0.005**	0.629	0.507	0.191	**0.007**	0.121
4	0.930	0.624	0.174	0.924	0.880	**0.006**	**0.038**	0.377
5	0.595	0.542	0.653	0.569	0.355	**0.021**	**0.012**	0.204
6	0.264	0.282	0.884	0.922	0.400	**0.009**	**0.013**	0.300
7	0.600	0.181	0.792	0.977	0.688	**0.033**	**0.015**	0.251
8	0.678	0.830	0.243	0.514	0.367	**0.013**	**0.010**	0.265
9	0.595	0.091	0.641	0.457	0.893	**0.012**	**0.004**	0.150
10	0.784	**0.049**	0.263	0.104	0.430	0.065	**0.005**	0.172
11	0.816	0.072	0.549	0.181	0.698	0.318	**0.036**	0.696
12	0.677	**0.018**	0.625	0.242	0.596	0.276	0.152	0.812
13	0.873	**0.003**	0.529	0.360	0.441	0.165	0.075	0.642
14	0.832	**0.009**	0.149	0.137	0.270	0.290	0.084	0.870
15	0.829	**0.011**	0.180	0.585	0.225	0.558	0.346	0.745
16	0.597	**0.038**	**0.032**	0.696	0.896	0.598	0.162	0.882
17	0.641	**0.021**	0.139	0.581	0.425	0.419	0.203	0.419
18	0.563	**0.039**	0.799	0.960	0.312	0.590	0.077	0.867
19	0.060	**0.003**	0.660	**0.031**	0.678	0.840	0.284	0.840
20	0.488	**0.021**	**0.051**	0.095	0.229	0.474	0.208	0.752
21	0.397	0.104	0.876	0.556	0.563	0.952	0.370	0.500
22	.	.	.	.	0.893	0.802	0.187	0.562
23	.	.	.	.	0.629	0.666	0.399	0.521
24	.	.	.	.	0.850	0.203	0.347	0.347
25	.	.	.	.	.	.	.	.
Bottom 26	.	.	.	.	0.579	0.468	1.000	0.468

The amount of foliage on a branch and the number of foliated branches follow similar vertical distribution patterns to fascicle weight and the number of fascicles (Figure 8). Like fascicle weight, thinning and fertilization treatments had little effect on the shape of these patterns but had large effects on the magnitude. The maximum number of branches, however, peaked around five whorls lower in the crown than the maximum number of fascicles.

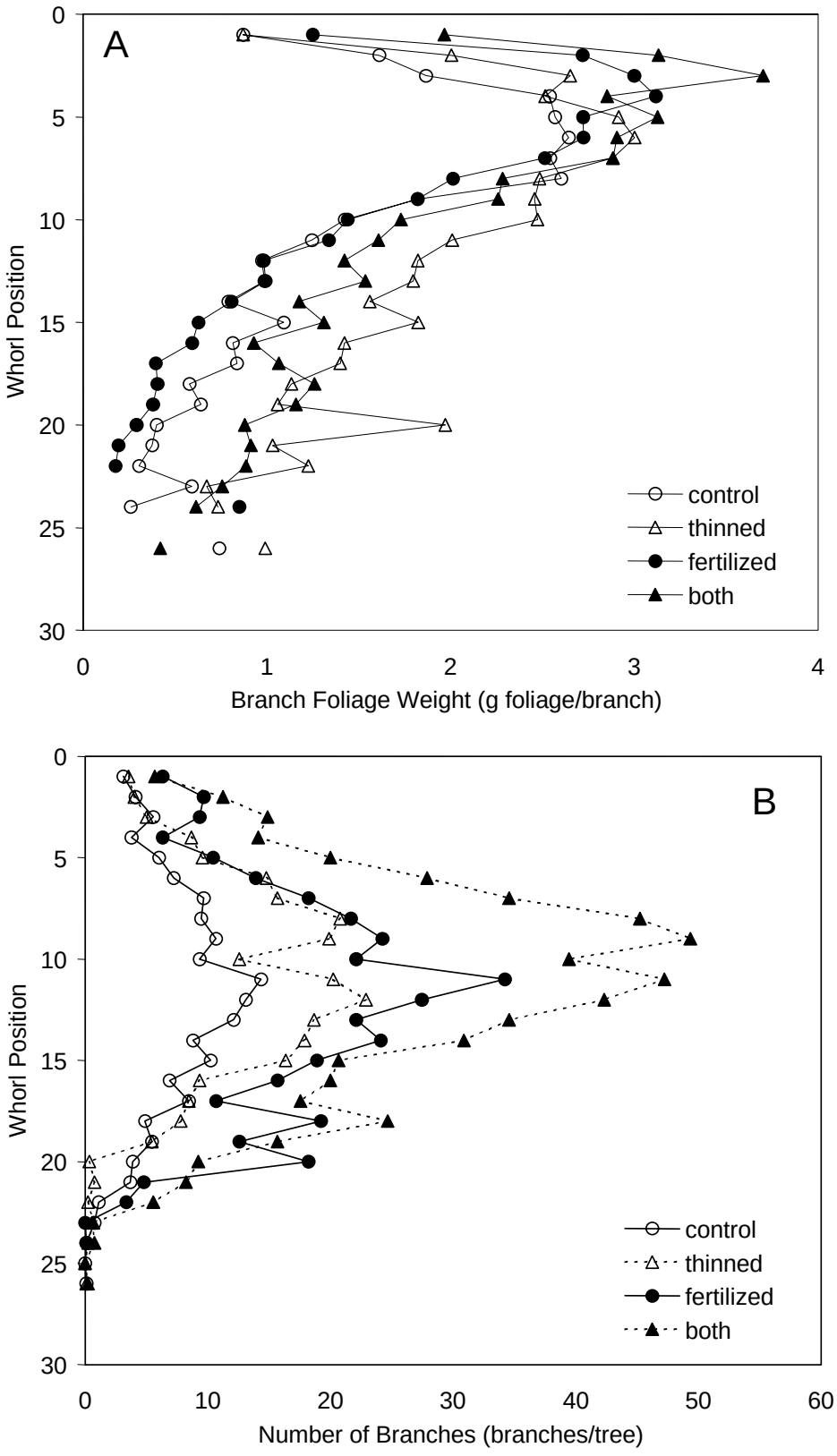

Figure 8. The effect of thinning and fertilization on the vertical distribution of (A) branch foliage weight and (B) branch number from the top of the tree (whorl position 1) to the bottom of the live crown (whorl position 26).

The general pattern was more foliated branches in whorls in the middle crown with branches in the upper crown holding more foliage. The average amount of foliage on a branch increased moving down through the top three to four whorls as branches grew longer and accumulated more cohorts. Below the highest seven whorls the average amount of foliage on a branch declined as branches produced less of each cohort in the lower whorls.

Although the shape of the patterns of branch foliage weight and number of branches were not affected by treatment, there was a shift toward the top of the tree in terms of the position of the maximums for these distributions. Branch foliage weight was greatest on control and thinned plots from the 3rd to the 8th whorls, fertilizer shifted this up to the 4th whorl, and applying both thinning and fertilizer together shifted it to the 3rd whorl. The 11th and 12th whorls had the most foliated branches on control, thinned and fertilized plots, while thinning and fertilization together shifted this up to the 9th whorl.

The retention of cohorts was not a contributing factor in the vertical foliage biomass response pattern. What trends were observed in the vertical distribution were small and only sporadically statistically significant. Differences in foliage retention were statistically significant at the whole-tree level only for the thinning effect. However, at the whorl-level the thinning effect on the average number of cohorts was only significant for the 9th whorl and fertilizer was significant for the 5th and 6th whorls.

The vertical patterns of cohort retention in the upper and lower crown were unaffected by treatment but the mid-crown area of stable cohort numbers had fewer cohorts on plots that were both thinned and fertilized (Figure 9). Although the effect of thinning on retention of cohorts is significant at the whole-tree level, there were no consistent trends to the statistical significance by whorl (Table 15).

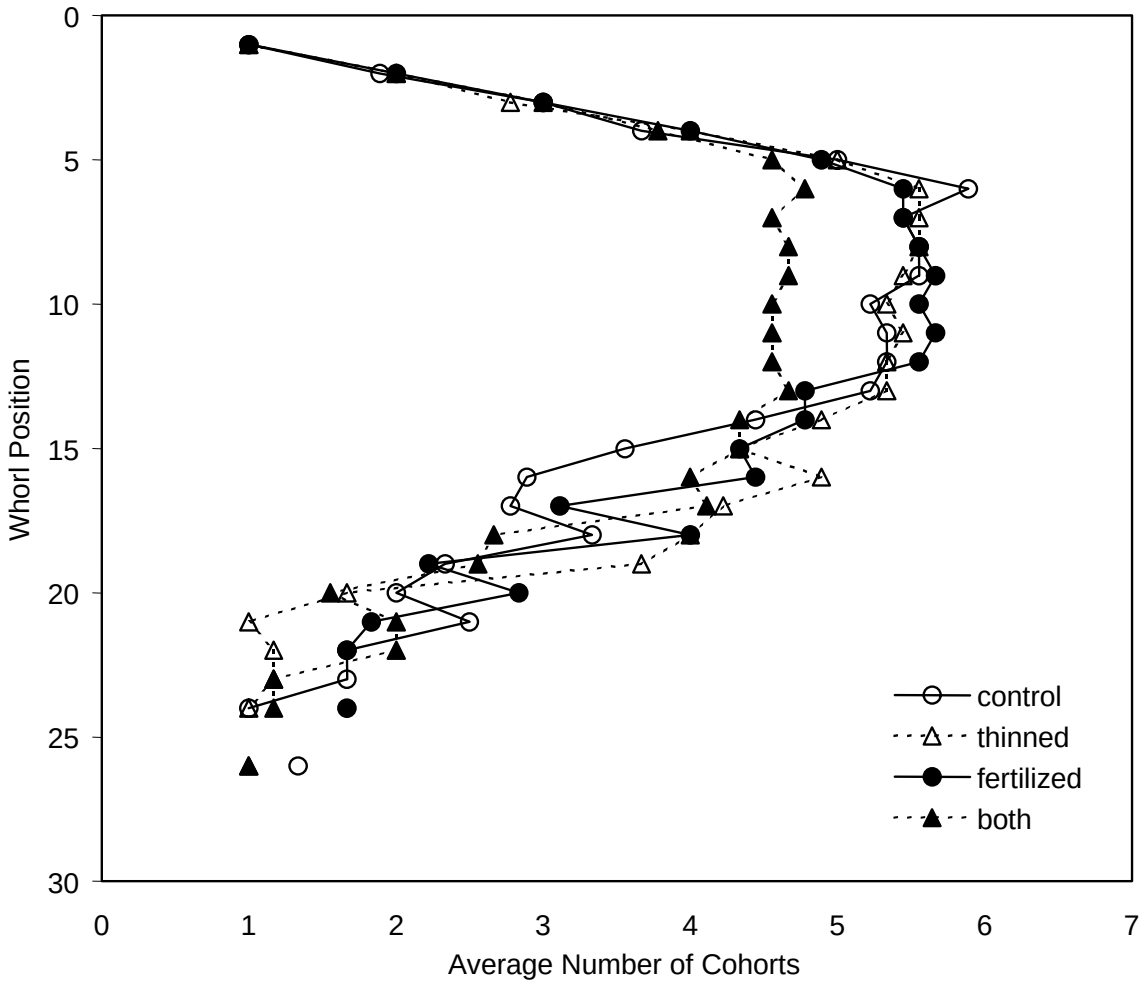

Figure 9. The effect of thinning and fertilization on the vertical distribution of the number of cohorts of foliage from the top of the tree (whorl position 1) to the bottom of the live crown (whorl position 26).

Table 15. Analysis of variance (probability of a greater F) for the number of foliage cohorts for each whorl position for the effects of blocks (Block), thinning (Thin), fertilization (Fert), and the interaction of thinning and fertilization (Int).

	Average Number of Cohorts			
Whorl	Block	Thin	Fert.	Int.
Top 1	.	.	.	.
2	0.422	0.356	0.356	0.356
3	0.422	0.356	0.356	0.356
4	0.140	0.750	0.750	0.147
5	0.670	0.097	**0.017**	0.097
6	0.866	0.093	**0.050**	0.531
7	0.479	0.264	0.165	0.165
8	0.579	0.124	0.124	0.124
9	0.330	**0.045**	0.180	0.090
10	0.422	0.175	0.471	0.103
11	0.226	0.082	0.291	**0.044**
12	0.477	0.170	0.420	0.170
13	0.256	1.000	0.253	0.810
14	0.094	1.000	0.796	0.321
15	0.083	0.495	0.495	0.495
16	0.271	0.163	0.521	**0.047**
17	0.501	0.116	0.873	0.750
18	0.318	0.619	0.619	0.167
19	0.133	0.270	0.407	0.493
20	0.349	0.464	0.903	0.432
Bottom 21	0.276	0.363	0.528	0.076

3.4.4 Foliage Cohort Distributions

Foliage cohort distributions were far more plastic in their response to treatment than the vertical distributions. Treatments affected both the magnitude and pattern of foliage cohort distributions.

Thinning, fertilization, and interaction effects were all statistically significant for foliage biomass in the youngest three cohorts (Table 16). Only the interaction term was statistically significant for foliage biomass on the 1998 and 1997 cohorts. There were large increases in the amount of foliage biomass on the youngest cohorts, especially with the combined treatment (Figure 10). The oldest cohort had less foliage biomass on thinned plots but this difference was very small and did not take much away from the overall foliage biomass increase due to thinning.

Table 16. Analysis of variance (probability of a greater F) for foliage biomass, fascicle weight, and number of fascicles for each cohort year for the effects of blocks (Block), thinning (Thin), fertilization (Fert), and the interaction of thinning and fertilization (Int).

Cohort	Foliage Biomass				Fascicle Weight				Fascicle Number			
year	Block	Thin	Fert.	Int.	Block	Thin.	Fert.	Int.	Block	Thin.	Fert.	Int.
2001	0.535	**0.001**	**0.001**	**0.019**	0.800	0.106	0.439	0.764	0.290	**0.001**	**< 0.001**	**0.028**
2002	0.515	**< 0.001**	**< 0.001**	**0.011**	0.321	**< 0.001**	**< 0.001**	0.333	0.470	**0.003**	**0.004**	0.174
1999	0.199	**< 0.001**	**0.002**	**0.020**	0.157	**< 0.001**	**< 0.001**	**0.019**	0.164	**0.001**	0.610	0.822
1998	0.163	0.342	0.294	**0.038**	0.473	**0.027**	0.816	0.544	0.139	0.114	0.490	0.072
1997	0.200	0.753	0.300	**0.042**	0.654	0.857	0.463	0.136	0.182	0.538	0.423	0.083
1996	0.059	0.087	0.609	0.072	0.299	0.590	0.087	0.188	0.060	0.117	0.454	0.086

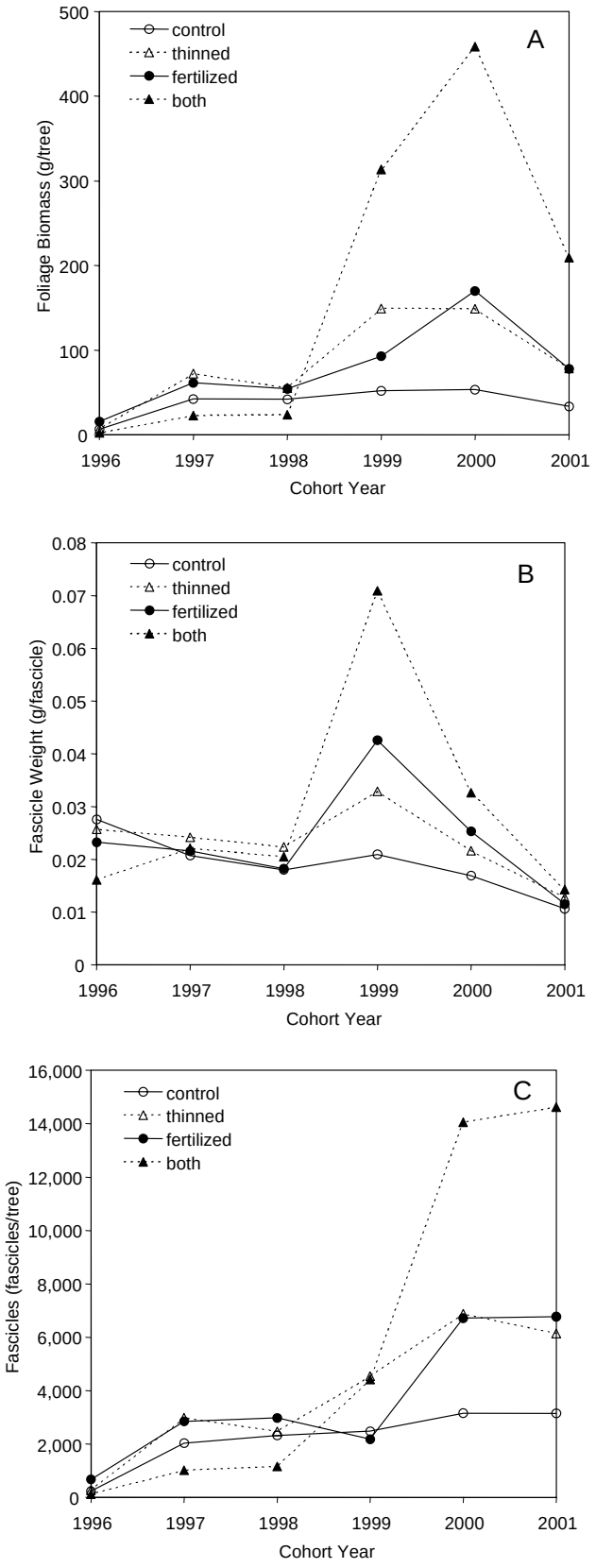

Figure 10. The effect of thinning and fertilization on the distribution of (A) foliage biomass, (B) fascicle weight, and (C) number of fascicles for each cohort.

3.4.5 Branch Order Distributions

There were not enough observations for analysis of variance on 4th or 5th order branches. Foliage biomass was significantly increased by thinning on 1st, 2nd, and 3rd order branches but not the main stem (Table 17). Fertilization, however, significantly increased foliage biomass on the main stem as well as 1st and 2nd order branches. Thinning significantly increased the amount of foliage per branch on 1st and 2nd order branches while fertilization increased foliage per branch on the main stem and 1st order branches. The number of foliated branches was significantly increased by fertilization on 1st through 3rd order branches but thinning had no effect on the number of branches.

Table 17. Analysis of variance (probability of a greater F) for foliage biomass, branch foliage weight, and number of foliated branches for each branch order for the effects of blocks (Block), thinning (Thin), fertilization (Fert), and the interaction of thinning and fertilization (Int).

Branch	Foliage Biomass				Branch Foliage Weight				Foliated Branch Number			
Order	Block	Thin	Fert.	Int.	Block	Thin	Fert.	Int.	Block	Thin	Fert.	Int.
Stem	**0.002**	0.203	**< 0.001**	**0.008**	0.186	0.130	**< 0.001**	0.666	.	.	.	.
1st	0.140	**< 0.001**	**< 0.001**	0.082	0.345	**0.002**	**0.006**	0.455	0.391	0.179	0.081	0.798
2nd	0.480	**0.005**	**0.011**	0.138	0.842	**0.007**	0.602	0.894	0.386	0.083	**0.012**	0.445
3rd	0.248	**0.049**	0.071	0.492	0.525	0.176	0.189	0.587	0.353	0.359	**0.045**	0.623

The shape of the pattern of foliage across branch orders was fixed and unaltered by treatment but the magnitude of the pattern was significantly altered by treatment (Figure 11). The majority of foliage biomass was found on 1st and 2nd order branches. On 1st order branches, both the amount of foliage on a branch and the number of branches contributed to increased foliage biomass, but on 2nd order branches the majority of the foliage biomass can be attributed to the number of branches.

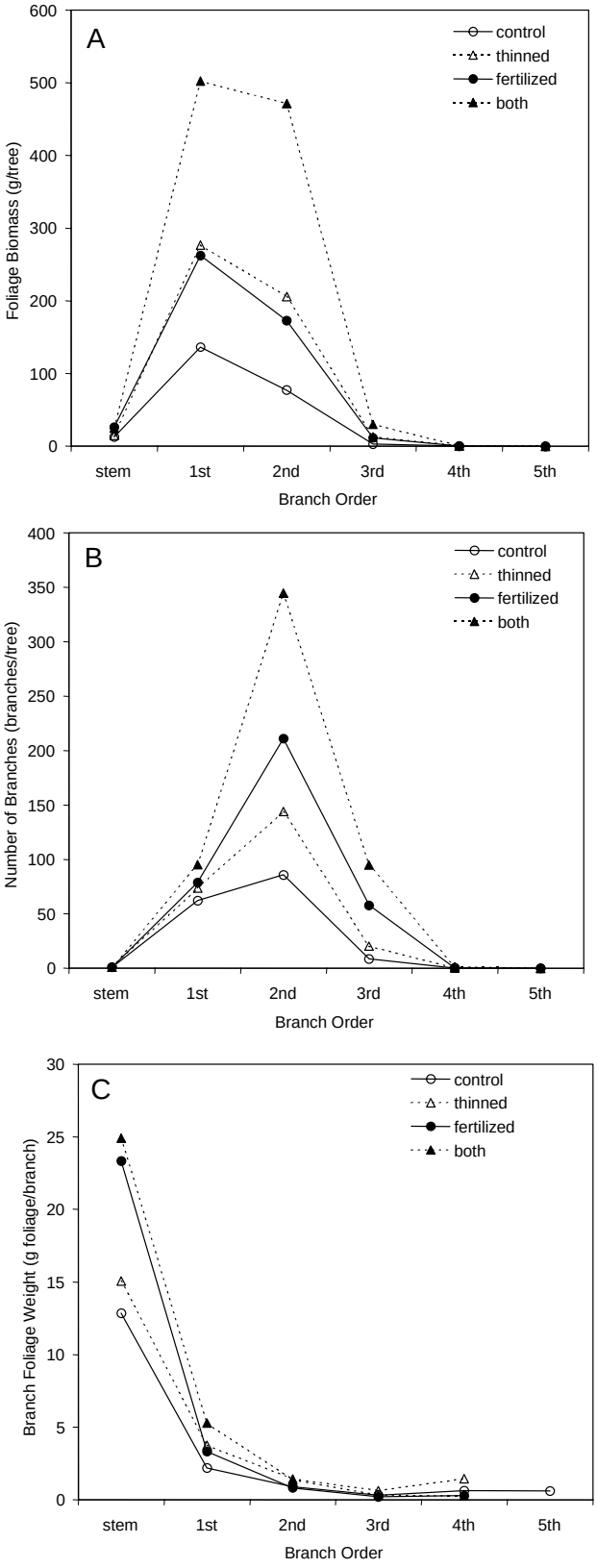

Figure 11. Distribution of (A) foliage biomass, (B) number of branches, and (C) amount of foliage per branch across branch order three years after fertilization and four years after thinning.

3.5 Discussion

3.5.1 Whole-tree Responses

As expected, thinning and fertilization had large positive effects on foliage biomass per tree (Raison *et al.* 1992b, Gillespie *et al.* 1994 , Vose *et al.* 1994). At the fascicle level, fascicle weight was increased by thinning and fertilization (Table 10) as has been found for several species (Brix 1981, Weetman and Fournier 1982, Valentine and Allen 1990, Raison *et al.* 1992a). However, the principal contribution (almost 80% regardless of treatment) to the whole tree foliage biomass response was due to increases in the number of fascicles (Table 11). The two factors that influenced this increase in fascicle number (branch number and number of fascicles per branch) varied by treatment. Fertilization had a stronger effect on increasing branch number than thinning while only thinning increased the number of fascicles on a branch. Others have shown increases in branch number to thinning and/or fertilization (Brix 1981, Gillespie *et al.* 1994). Thinning increased the average amount of foliage on a branch (Figure 8A) more than the combined treatment because the combined treatment had foliage distributed over many more branches (Figure 8B). Since the useful life of a branch is many years longer than that of a fascicle, an increase in the number of branches with fertilization could result in a longer lasting affect on the crown than increases in the number of fascicles with thinning.

Retention of foliage cohorts (Table 16) and retention of live branches in the lower crown (Figure 8B) had very little impact on the foliage biomass response to thinning and fertilization. Others have found positive effects (Miller and Miller 1976, Linder and Rook 1984) and negative effects (Raison *et al.* 1992b) or little impacts (Brix 1981, Vose and Allen 1991) on needle retention. The positive effects were observed in open stands (Vose *et al.* 1994). Foliage retention did not significantly contribute to the foliage response and treatments had little effect on the vertical pattern of cohort retention (Figure 9).

3.5.2 Vertical Response Patterns

The average number of cohorts in a whorl increased by one for each whorl moving down from the top of the tree, as each whorl has an additional cohort one year older than the whorl above (Figure 9). This pattern is because the top-most whorl can only produce the most recent cohort

and the second whorl from the top can only produce the most recent two cohorts. The sixth whorl from the top of the tree is the highest whorl that can display the oldest cohort. Below the sixth whorl there was no change in the number of cohorts until the 13th whorl from the top of the tree. Below the 13th whorl the number of cohorts declined until there was only one cohort on average at the base of the live crown. This decline in the number of cohorts in the lower crown is because of both lower retention of the older cohorts and less production of younger cohorts. This suggests that even greater foliage biomass response may be possible since there appeared to be no effects of self-shading or increased production in the lower crown.

The pattern of increasing foliage biomass from the top of the tree down to the whorls where maximum foliage biomass occurs is due to the time required to build the structure of higher branch orders and foliage cohorts. Second order branches cannot be produced until a whorl begins its second growing season and third order branches cannot be produced until the third growing season. The eighth whorl from the top of the tree is the highest whorl that can have a six-year-old cohort on a third order branch and it was the whorl with the most foliage biomass (Figure 6). The decline in foliage biomass below the peak whorls toward the bottom of the live crown is interesting because these whorls have had time to accumulate all the branch orders and cohorts. This reduction in foliage biomass is due to the strong reduction in production of new cohorts as well as less retention of older cohorts in the lower crown positions (Figure 9). The lower production of new cohorts in the lower crown may be due to lower light (Vose *et al.* 1994) and/or lower nutrition (Gillespie *et al.* 1994, Zhang *et al.* 1997). Because of the low stand leaf area and the low nitrogen nutrition even after fertilization (Table 7), the lack of foliage production in the lower crown could be due to poor nutrition, especially on thinned plots where light levels are high in the lower crown. If this is true then additional foliage biomass response may be possible in the lower crown with either a higher fertilizer rate or a repeated application.

Although thinning and fertilization treatments did not alter the relative vertical (according to whorl position) foliage distribution pattern, they did have a large positive effect on the scale (Figure 6). Similar results were reported by Vose (1988) for loblolly pine, another shade intolerant pine. Thinning and fertilization have affected both relative and absolute foliage distributions in Douglas-fir (Brix 1981), possibly because of greater shade tolerance. Vose (1988) suggested that the vertical distribution of foliage can provide some insight into the

importance of light and the amount of foliage self-shading in intolerant species such as pines. Thinning and fertilization increased the amount of foliage in the peak whorls equally, but thinning had a greater effect in the lower crown as would be expected with higher light levels in the lower crown (Figure 6). Fertilization had a greater effect on the top three whorls, which were produced entirely after fertilization. Foliage biomass at the bottom of the live crown was not affected by treatments in this study despite large increases in foliage biomass (Figure 6). This suggests that light may still not be limiting even in the fertilized only plots, and the trees could possibly display more foliage before shading becomes a factor.

The increase in fascicle weight in the top-most whorls (Figure 7A) is because fascicles continue to increase in weight as they age (see control plots on Figure 10B). The top-most whorl may produce large fascicles but they will continue to increase in weight throughout their life, which may be as long as six years (although most of the weight increase occurs in the first three years). Below the 3rd or 4th whorl position from the top of the tree, fascicle weight declined as smaller fascicles were produced in the lower whorls. Fascicles at the bottom of the live crown are approximately half the weight on average of fascicles at the top of the crown (Figure 7A). Similar fascicle weight gains with time and similar crown position effects have been reported for loblolly pine (Zhang and Allen 1996). Fertilization without thinning produced the greatest amount of foliage biomass per hectare (Table 5) and therefore the most shading. This shading may have contributed to the lack of increase in fascicle weight or number below the 15th whorl from the top of the tree. However, the effect of this shading was not enough to affect the position of the bottom of the live crown (Figure 6). Fascicle weight in the lower crown was much higher on thinned plots, which would have little or no shading from the side although these trees also had greater access to soil resources due to increased growing space.

3.5.3 Cohort Response Patterns

The distribution of foliage across cohorts can provide some information concerning changes in the crown through time since a cohort is defined as the foliage produced during one growing season. However, care must be taken in these interpretations because these data were collected at one point in time. Different cohorts, therefore, represent foliage of varying age in addition to the changes caused by the treatments.

There was no significant loss of fascicles on the most recent three cohorts so foliage data from these cohorts can be considered to represent production. In contrast, any treatment effects observed on cohorts produced prior to treatment must be due to differences in retention but none of these effects were statistically significant (Table 16).

There were no differences in foliage biomass on control plots for the 1997-2000 cohorts indicating that the same amount of foliage was produced each year on control plots and the trees were producing foliage at a constant rate (Figure 10A). However, the oldest and youngest control cohorts both had less foliage biomass. In the oldest cohort this is due to senescence of fascicles (Figure 10C). The lower foliage biomass in the youngest cohort is because these fascicles have not finished elongation (Figure 10B) and does not mean the foliage production is diminishing in the third year after fertilization. Even though the fascicles on the youngest cohort were smaller than older cohorts (Figure 10B) the response of the number of fascicles has increased since treatment and the elevated level has been maintained even in the youngest cohort (Figure 10C). If the fascicle weight of the youngest cohort continues to increase at the same rate as the previous cohort, then the foliage biomass will be equal to the previous cohort (when compared at equal ages) since there was little difference in the number of fascicles produced over the last two years. It is not possible from these data to predict how long the elevated foliage biomass will remain but there is no evidence that the response is beginning to diminish. Since these trees hold needles for up to six years, the elevated foliage biomass will likely last at least that long. If foliar boron and sulfur concentrations continue to remain elevated on fertilized plots (Table 7), increased foliage biomass could last much longer.

The increase in foliage biomass on the cohort produced during the first growing season after fertilization (1999 cohort) was due entirely to increased fascicle weight (Figure 10B) with no difference due to the number of fascicles (Figure 10C). For pines, the number of fascicles on a shoot is determined when the bud is set in the fall. When there is a sudden increase in the resources available for growth (such as after a fertilization treatment) foliage biomass cannot be increased by making more fascicles during the first growing season. Foliage biomass response is limited to the plasticity of fascicle weight since the number of fascicles has already be set at the end of the previous growing season (Weetman and Fournier 1982, Valentine and Allen 1990).

The number of fascicles can be increased during the second and subsequent growing seasons provided resource availability remains elevated. The much larger foliage biomass response (Figure 10A) from the cohort produced two growing seasons after fertilization (2000 cohort) was due mostly to an increase in the number of fascicles (Figure 10C), while increased fascicle weight contributed a significant but smaller amount (Figure 10B).

Foliage biomass responded the first growing season following application of fertilizer but the response was delayed by one year after thinning which was applied a year before fertilization. As a result, the increased foliage biomass response to both the thinning and fertilization treatments can only be seen in the three most recent cohorts (Figure 10A and Table 16). By considering the way thinning alters the availability of resources it may be possible to develop some hypotheses about what happened. The effect of thinning on light availability (especially in the lower crown) is immediate, so the lack of immediate response would suggest that light was not the most limiting resource to foliage biomass production. Uptake of soil resources, such as nutrients and water, would not be immediately increased after thinning because the remaining trees would require time to expand their root systems and exploit the soil no longer occupied by their competitors. It may have taken some time for resources to be increased for the remaining trees. This could be another indication of the importance of nutrition on this site.

3.5.4 Branch Order Response Patterns

Control tree foliage was displayed mostly on 1st and 2nd order branches with much smaller amounts of foliage on the main stem and higher branch orders (Figure 11A). This pattern is a function of both the number of branches (Figure 11B) and the amount of foliage on a branch (Figure 11C). On control trees, the number of branches increased as the branch order increased up to 2nd order branches. This is a function of the way branch orders are organized. Each main stem can have a limited number of 1st order branches and each 1st order branch can have a limited number of 2nd order branches and so on. This trend does not continue because there is a limit to how many branches a tree can produce and maintain. The number of 3rd order branches on control trees drops off substantially and 4th and 5th order branches were present only sporadically. In addition to the number of branches being limited, the amount of foliage displayed on a branch diminishes as branch order increases. The main stem had more foliage

than a first order branch (Figure 11C). A first-order branch had more foliage than a 2nd order branch.

Ford (1985) suggested that trees on better sites would have more branches at higher orders than trees on poor sites. This is consistent with the increase in 2nd order branches as well as the smaller increase in 3rd order branches observed in this study with improved nutrition (Figure 11B). There were no significant treatment effects on 1st order branches. Thinning did not improve site quality and had no effect on the number of branches, which is also consistent with Ford (1985).

Species with the flexibility to produce higher branch orders may have a greater ability to increase foliage biomass when resource availability increases, because they have more shoot tips. By increasing the number of higher-order branches a tree will also increase the complexity of its crown architecture, which permits a higher density crown that can intercept more light (Stenberg *et al.* 1994). However, producing higher branch orders has diminishing returns on increased foliage biomass. The higher the branch order, the smaller the branch and the less foliage a branch will display (Figure 11C).

3.6 Conclusions

Increased nutrition and growing space both resulted in increases in foliage biomass, but the mechanisms of these increases were different for the two treatments. Fascicles responded to both thinning and fertilization while branch variables were affected by one treatment or the other. Both thinning and fertilization increased total foliage biomass, fascicle weight, and number of fascicles. The average amount of foliage on a branch was only increased by thinning while the number of branches was only increased by fertilization. Number of fascicles was more important to the foliage biomass response than fascicle weight and the relative contribution to the response was similar for all treatments. The importance of branches to the foliage biomass response was, however, different depending on treatment. The increase in foliage biomass on fertilized plots was due entirely to an increase in the number of branches while on thinned plots number of branches accounted for only 60% of the increase in foliage biomass. When thinning and

fertilization were applied together number of branches accounted for 90% of the foliage biomass response. Increased retention of old foliage or branches was of little importance to the increase in foliage biomass when compared to the increase in the production of new foliage. Fertilization without thinning produced the greatest amount of foliage biomass per hectare and therefore the most shading. This shading may have contributed to the lack of increase in fascicle weight or number below the 15th whorl. However, the lack of treatment effects on foliage biomass at the bottom of the live crown, the position of the bottom of the live crown, and the steady reduction in the number of cohorts toward the base of the live crown, all suggest that even greater foliage biomass response is still possible since there appeared to be no evidence of self-shading or increased production in the lower crown. Because of the low stand leaf area and the low nitrogen nutrition even after fertilization, the lack of foliage production in the lower crown could be due to poor nutrition, especially on thinned plots where light levels are high in the lower crown. If this is true then additional foliage biomass response may be possible in the lower crown with either a higher fertilizer rate or a repeated application. Foliage responded immediately to the fertilization treatment but was delayed by one year for the thinning treatment. Treatments did not alter the whorl (vertical) distributions of foliage and branch variables but did increase the magnitude of these patterns. Treatments did affect both the pattern and magnitude of the distribution of foliage across cohorts. Cohorts were the most plastic distributions followed by branch orders and then whorls.

CHAPTER 4

REPRESSED LODGEPOLE PINE RESEARCH AND MANAGEMENT

4.1 Causes and Symptoms of Repression

The term repression (or stagnation) defines a stand condition of slow growth and very high density associated with dense natural regeneration after wildfire (Lotan 1975, Bassman 1985, Lotan and Critchfield 1990, Tinker and Romme 1994). Although considered to be an irreversible physiological dysfunction by some authors (Mitchell and Goudie 1980, Goudie 1980, Keane 1985, Worrall *et al.* 1985, Keane and Weetman 1987, Worrall 1995), the large increases in stand growth reported in this trial (Table 6) and Farnden and Herring (2002) indicate that the growth per area of these repressed stands was limited primarily by nutrient deficiencies similar to those found in non-repressed lodgepole pine (Weetman *et al.* 1988, Cochran 1989, Brockley 1990 and 2001b, Marshall *et al.* 1991, Kishchuk and Brockley 2002, Kishchuk *et al.* 2002). These nutrient deficiencies may be due in part to the inherent low fertility of the region and also to the loss of nutrients during the stand-establishing fire (Stone 1990).

Results of this study suggest that repression is not caused by an irreversible physiological dysfunction because both thinning and fertilization produced immediate responses that would not be possible if something were wrong with the trees. This study has demonstrated the greater confidence in inferring a cause and effect relationship that can be obtained through a manipulative trial (Romesburg 1981, Hurlbert 1984). For example, although low hydraulic conductivity has been observed in repressed trees (Reid *et al.* 2003), results from this trial would indicate that this is a symptom rather than a cause. The rapid tree-level response in volume growth, foliage biomass, and growth efficiency observed in this study both when density was reduced and when nutrition was improved, indicates that any observed physiological dysfunction is reversible and can be attributed to poor nutrition and a lack of growing space.

Results from this trial indicate that poor nutrition is responsible for the low productivity per hectare while high density results in the division of limited resources amongst many individuals

resulting in a reduction in individual tree growth. Growth efficiency is also reduced by poor nutrition and limited growing space. Very low growth efficiency in repressed stands can explain why growth is so poor relative to the amount of foliage biomass but this low growth efficiency can be manipulated with fertilization and thinning and so must also be a symptom rather than a cause of repression.

4.2 Implications For Management

The additive effects of fertilization and thinning indicate that both treatments are needed to achieve the maximum effect on tree-level growth (Table 5). Stand-level growth was increased only by fertilization indicating the importance of nutrition on stand level productivity. Repressed stands need both reduced stocking and nutrient additions to reach the site's growth potential. Fertilization alone may only result in a slow process of accelerated stand development and thinning alone does not ameliorate the fundamental nutrient limitation. A complete fertilizer mixture (Table 3) may result in long-term improvement in site quality, which could make fertilization and thinning a financially attractive method for improving the productivity and value of repressed stands. Stand growth rates on fertilized plots compare well with non-repressed lodgepole pine in the area and are much higher than would be expected for a repressed stand (Figure 5). Bergh *et al.* (1998) suggested that the growth potential of boreal species is much higher than currently realized with appropriate nutrient management.

It is possible that the post-treatment growth rates observed in this study are still far below the site potential and that the limits set by temperature and moisture may be not be as constraining as previously thought. There may be other nutrient and density management strategies that could produce even greater growth by producing higher stand-level foliage biomass and further increases in growth efficiency.

However, forest managers must consider not only the potential for large increases in timber yield with large-scale intensive nutrient management, but also the tremendous power for change on other parts of the ecosystem. Repressed stands have been a part of the natural ecosystem for a long time. Low productivity forests have low leaf area that permits light to reach the forest floor

where other plants and lichens important to wildlife habitat can be found. Managing these forests to reach their potential productivity would greatly increase the amount of foliage, which would block almost all direct sunlight from reaching the forest floor. The resulting annual needle fall would cover the ground in a thick layer of decomposing organic matter that could, over time, enrich soil fertility and improve soil moisture. The impact of these changes in the ecosystem should be weighed against the economic benefits associated with increased productivity. Perhaps applying these ideas to a limited number of carefully selected intensively managed stands has the potential to increase wood production sufficiently to reduce the need for extensive stand management and harvesting.

The management strategies of rehabilitation and spacing currently used in repressed stands need to be reconsidered in light of these new results. Given the results of this study, it seems unlikely that replanting repressed sites is a financially viable alternative since it wastes what little growth has accumulated and does not address the fundamental nutrient limitation of the site.

4.3 Implications for Future Research

Although a low supply of soil boron, sulfur, and nitrogen appears to have most limited growth in this repressed lodgepole pine stand, a more general conclusion might apply to repressed stands in other areas and for other species. Amelioration of resource limitations and density reduction to concentrate resources onto fewer crop trees may provide the best opportunities for improving productivity of repressed stands, but additional research is needed.

While the results of this study suggest there is no longer a justification to search for a physiological cause of repression, the results of this study do suggest some possible directions for future research into the physiological symptoms of repression. Why did increased growth efficiency contribute so much to the response and what was the relative importance of the possible mechanisms of increased growth efficiency (photosynthetic efficiency, respiration, and biomass partitioning)? Why is the relationship between diameter and foliar biomass (Appendix B) so weak on control trees yet so strong on treated trees? The relationship between conducting tissue and foliage seems to be different on control plots, which supports recent findings by Reid

et al. (2003) that show reduced hydraulic conductivity in repressed trees. How does this vary by crown class?

How repeatable are the results from this study for other areas or for other species in a repressed condition? Was the severe nutrient limitation of this stand typical of repressed lodgepole pine stands or might other resource limitations be involved on other sites? What is the potential productivity of a repressed stand? Would a different fertilizer mixture or rate or repeated application produce even greater growth, foliage biomass, and/or growth efficiency response? What will be the longevity of the thinning and fertilizer responses?

The question of portability of these results to other repressed lodgepole pine stands or to repressed stands of other species can be resolved with additional trials to replicate this experiment in other locations and with better characterization of the mechanisms responsible for the observed low growth efficiency.

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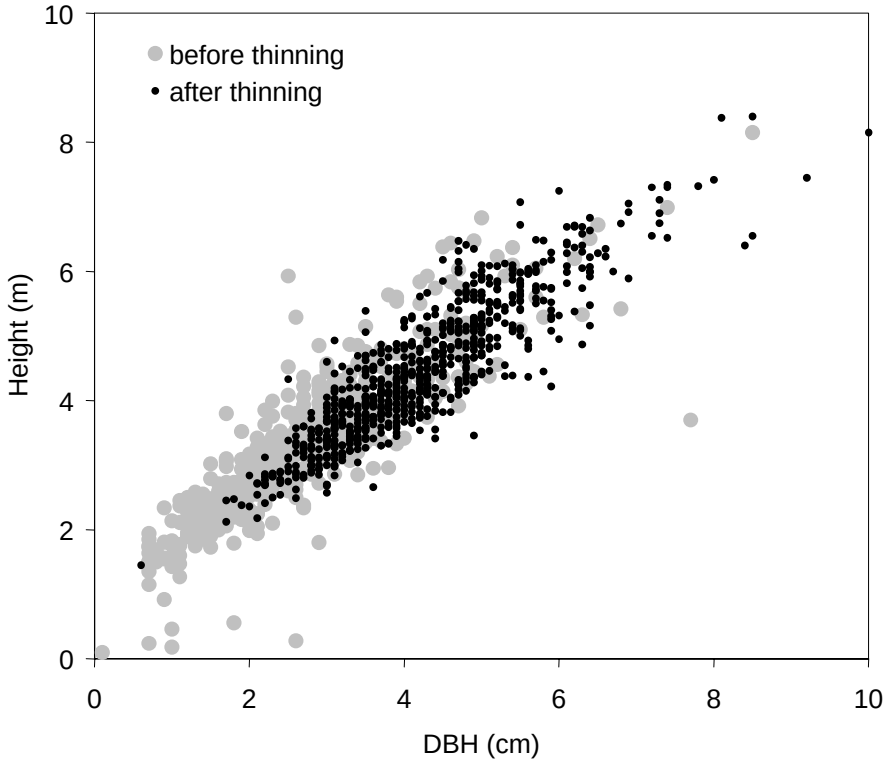
APPENDIX

A. EFFECT OF THINNING ON HEIGHT AND DIAMETER DISTRIBUTIONS FOR ALL TREES ON THINNED PLOTS.



B. RELATIONSHIP BETWEEN FOLIAGE BIOMASS AND DIAMETER FOR THE 36 DESTRUCTIVELY SAMPLED TREES AND THE REGRESSION EQUATIONS USED TO ESTIMATE FOLIAGE BIOMASS.