University of Alberta

Factors Contributing to Variation in Lodgepole Pine (*Pinus contorta*) Response to Fertilization

by

©

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Abstract

Growth response of lodgepole pine [*Pinus contorta* Dougl. var. *latifolia* Engelm.] was assessed 8 years following repeated fertilization at Kenneth and Sheridan Creeks in the interior of British Columbia, Canada to examine mechanisms of tree and stand response to fertilization. Fertilization treatments examined were: control; periodic (every ~6 years); and, annual. Fertilization increased stand basal area and diameter growth at Sheridan but not significant at Kenneth. Fertilization caused a reduction in height increment at Kenneth while Sheridan was not affected. Measurements of sapwood hydraulic conductivity showed that lower branches of trees that were repeatedly fertilized conducted more water than lower branches of control trees. Results suggest that the higher flow capacity of lower branches may reduce the availability of water to support annual growth of the leader and upper branches in the trees fertilized annually and may be responsible for observed reductions in height growth. To further understand the implications of fertilization on tree growth, foliar nutrient concentrations, leaf area index (LAI) and needle longevity were examined. Annual fertilization likely induced copper (Cu) deficiency in these stands and was associated with decreased needle longevity when compared with the controls. While LAI was increased by fertilization, the differences were significant only at Sheridan. It is not clear if increased fertility in general or the Cu or iron (Fe) deficiencies induced by repeated fertilization were responsible for the changes in branch hydraulic conductivity observed.

A growth chamber experiment was conducted to quantify nitrogen (^{15}N) uptake dynamics in lodgepole pine seedlings at three different phenological stages (early spring, summer and fall). Thirty days after ^{15}N application in early spring, summer and

fall, the amount of ^{15}N recovered in seedlings as a percentage of the total ^{15}N fertilizer applied was 4, 43 and 33 %, respectively. Results suggest that low uptake of ^{15}N in the spring was associated with limited development of new roots as a result of low spring soil temperatures. The lack of unsuberized roots in spring, accompanied by low soil temperatures could be the key factors decreasing the effectiveness of early spring fertilization in the boreal forest.

Dedication

To my wife Eunice, Ezeiel, Zephan, and my father and mother.

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Chapter 1. General Introduction

In Canada, lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) occupies about 20 million hectares mostly distributed in Alberta and British Columbia (B.C.). This constitutes 22% of the total forest land in Western Canada and carries about 1.3 billion m^3 of merchantable timber (Kock 1995). In 2001-2002, its harvested volume of 22.1 million m^3 accounted for 32% of the total provincial harvest of 69.8 million m^3, making it the leading commercial tree species in B.C. (B.C. Ministry of Forests 2002). Reported stem biomass production for this species ranged from 1.9-2.1 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ on xeric sites and up to 4.2 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ on mesic sites in south east B.C. (Comeau and Kimmins 1989).

Despite the large volumes of lodgepole pine harvested in Western Canada, its growth and productivity are commonly limited by low nitrogen (N) supply (Yang 1985*a*, *b*, Weetman et al. 1988, Prescott et al. 1989) even though large reservoirs of N are usually found in boreal forest soils (Tamm 1991, Nasholm et al. 1998). This observation may be attributed to slow mineralization of soil organic matter because of low temperature and high C/N ratios that consequently limits N availability for plant growth (Fyles and McGill 1987, Tamm 1991, Cote et al. 2000). Fertilizing stands with N based fertilizer formulations either in single or repeated applications may improve soil N supply thus enhancing plant growth and productivity. However, stand responses are highly variable. Synchronizing stand fertilization with crop demand may increase the potential for improved productivity.

Leaf area index (LAI; the ratio of leaf surface area of a stand to the ground area the canopy projects over) is considered to be an important structural attribute of forest because leaves are the site for energy exchange, uptake of carbon dioxide by photosynthesis, and loss of water through transpiration (Pierce and Running 1988). LAI tends to stabilize for any particular stand after canopy closure; but can vary considerably between stands growing under the influence of different environmental conditions. The expected response when stands are fertilized with N fertilizers may include increased needle production and needle size, which can increase LAI (Brix 1983, Vose and Allen 1988) provided that needle longevity is not substantially reduced. The amount of leaf area on a tree depends upon both the rate of new needle production and the rate of loss of old needles, both of which are influenced by edaphic or climatic factors (Reich et al. 1995) as well as by crown closure. For instance, variation in needle longevity may be influenced by the amount of light within a canopy (Whitney 1982, Schoettle and Smith 1991, Schoettle and Fahey 1994, Ackerly 1999) or nutrient availability (Jonasson 1989, Son and Gower 1991, Gower et al. 1992, Raison et al. 1992). It has been shown that improved site fertility either through natural nutrient pulses or fertilization can decrease leaf longevity (Reich et al. 1995, Balster and Marshall 2000, Pensa and Sellin 2002, Niiemets and Lukjanova 2003). Over the long-term N fertilization increased branch wood biomass on low fertility sites (Mälkönen and Kukkola 1991) and enhanced shoot growth (Murthy and Dougherty 1997, Roberntz 1999). It is possible that by improving tree vigour, repeated (annual or periodic) fertilization may alter annual shoot growth patterns which may, in turn, influence needle retention and leaf area and therefore, overall patterns of tree growth. It is anticipated that repeated fertilization would increase foliar nutrient concentration leading to enhanced photosynthetic capacity of foliage and increased stand productivity, provided that uptake and utilization of the various nutrients by the plants are in balanced proportion (Ingestad 1979). However, the effects of repeated fertilization on needle longevity, and nutrient concentrations of various age-classes of needles have not been well documented.

Accelerated stand development and increased growth have been demonstrated for lodgepole pine following a single application of fertilizer, but responses have been variable (e.g., Cochran 1979, Yang 1998, Weetman et al. 1988, Brockley 2003). Since growth response of lodgepole pine to a single fertilizer application is usually short-lived (about 3-6 yr; McIntosh 1982, Brockley 1996), repeated fertilization may increase and sustain soil nutrient availability, alleviate nutrient limitations over an extended period (Weetman et al. 1995, Tamm et al. 1999, Kishchuk et al. 2002), and enhance tree growth provided that fertilization does not lead to an imbalance in the supply of other essential elements (Ingestad 1979).

Repeated fertilizer addition is also expected to provide larger and longer lasting growth responses than single applications. Increased stand basal area (BA) and volume increments have been demonstrated in pines (e.g., Mälkönen and Kukkola 1991, Weetman et al. 1995, Kishchuk et al. 2002) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Weetman et al. 1997) following repeated fertilization. However, gains from repeated fertilization may be offset by increased branch wood biomass (Mälkönen and Kukkola 1991), reduced height growth (Weetman et al. 1988, Brockley 1991, Tamm et al. 1999, Kishchuk et al. 2002,) and a decline in wood density (Yang 1988).

The pipe model theory proposed by Shinozaki et al. (1964 *a, b*) is based on the concept that a given unit of transpiring foliage is supplied with water by a corresponding unit of conducting sapwood area. However, differences in leaf area/sapwood area ratio between trees of the same species growing on different sites or in different positions in the canopy have led to attempts to create more general models of leaf area development in trees. Whitehead et al. (1984) proposed the hydraulic model based on Darcy's law and in contrast to the pipe model it explicitly takes into account many of the physical characteristics of the hydraulic pathway between stem and foliage. This model provides a theoretical basis for explaining variations in the relationship between leaf area and sapwood area. The model suggests that leaf area/sapwood area ratio is directly proportional to specific hydraulic conductivity and the water potential gradient in the stem and other xylem leading to the foliage and inversely proportional to the driving variable for transpiration represented by vapor pressure deficit and stomatal conductance.

Recent research suggests that the ability of sapwood to supply water to the crowns varies in response to edaphic and climatic factors (Sperry and Tyree 1990, Sellin 1993, Mencuccini and Grace 1996, Ryan and Yoder 1997). Moreover, water flow through sapwood is a function of tracheid anatomy and it changes with lumen diameter and length, both of which increases with site quality (Pothier et al. 1989*b*, Coyea and Margolis 1992). Studies indicate that specific hydraulic conductivity increases with improved site quality due to greater tracheid length and diameter in jack pine (*Pinus banksiana* Lamb.) on the better sites (Pothier et al. 1989*a*, 1989*b*). Protz et al. (2000) suggested that lower branches of unfertilized juvenile lodgepole self-pruned because they had lower specific hydraulic conductivity than upper branches. Dominant and co-dominant trees on medium sites have been shown to have higher hydraulic conductivity than suppressed trees (Reid et al. 2003). Silvicultural practices such as thinning can reduce specific hydraulic conductivity of trees immediately after treatment (Liu et al. 2003). By improving tree vigour, repeated fertilizer addition may cause changes to sapwood hydraulic characteristics which may, in turn, influence the pattern of tree growth response. Therefore, there is an obvious need to explore how repeated fertilization will affect the hydraulic architecture of lodgepole pine and it effect on tree growth. A number of plant parameters such as leaf area index (LAI), needle longevity, sapwood hydraulic conductivity and nutrient uptake can be measured to predict plant response to N fertilization. Knowledge of how these are coupled with soil nutrient availability to stimulate plant growth may provide a better understanding on how to manipulate stands to optimize plant growth.

In boreal and montane forests growth and development of conifers during the active growing period are strongly influenced by environmental factors. Soil temperature, soil moisture and nutrient availability may be the most important factors that limit growth. Nutrients are supplied to plant root surfaces through three mechanisms: (a) the growth of roots and mycorrhizae into the soil; (b) the mass flow of ions with the movement of soil water as a result of transpiration; and (c) the diffusion of ions toward the root surface when uptake rates exceed supply (Eissenstat and Van Rees 1994). Any factor that limits these processes will likely affect nutrient uptake and utilization. For example, low root zone temperature (RZT) limits root growth and elongation of conifer seedlings (e.g., Vapaavuori et al. 1992, Lyr and Garbe 1995) and may be linked to the reductions in metabolic activity and sink strength of roots, which results in a reduction of retranslocation of carbohydrates to roots (Hurewitz and Janes 1983). In conifers, new unsuberized fine roots have been shown to be more effective in water and nutrient uptake than older roots (Chung and Kramer 1975; Häussling et al. 1988), consequently, nutrient uptake may be enhanced by recent growth of new roots, particularly during the spring. Root zone temperature is reported to affect both water and ion transport (Markhart et al. 1979; Kennedy and Gonsalves 1988; Wan et al. 1999). Some nutrients may enter the plant passively following the flow of water; however, many are actively transported with enzyme-mediated reactions across root membranes (Ingestad 1982, Ryyppö et al. 1994) and may be reduced at low RZT (Bowen 1991, Wan et al. 1999).

Stand level fertilization is usually carried out at different times of the year (spring summer, fall) with different uptake response (e,g., Nason et al. 1988, Hulm and Killham 1990, Preston et al. 1990, Brockley 1995, Chang et al. 1996). The presumed causes of low uptake at various times of year were leaching, denitrificantion, rapid fixation and microbial immobilization (Preston et al. 1990, Fyles et al. 1994, Chang et al. 1996). Preston et al. (1990) applied labeled ammonium nitrate on snow at two forest sites in British Columbia. They attributed low recovery of the labeled isotope in plant tissues to leaching and denitrification but did not consider soil temperature as a factor that might limit uptake into the roots. During early spring, cold soils may inhibit nutrient movement to plant roots, and may limit uptake capabilities. Under these circumstances, it is apparent that simulating seasonal growing conditions (soil and air temperatures and photoperiod) in a growth chamber to study the uptake capability of lodgepole pine may provide insight into how fertilizer application can be synchronized with plant demand in order to optimize growth. This approach may provide useful information regarding how to fertilize in order to minimize losses *via* leaching and volatilization that can have attendant detrimental environmental consequences.

Thesis Overview

My objectives were to: (1) examine how tree growth and specific hydraulic properties of boles and branches vary with repeated fertilization of juvenile lodgepole pine stands, (2) examine the effect of repeated fertilization on leaf area index, branch characteristics (needle longevity, annual shoot growth and foliated shoot length) and stem growth of juvenile lodgepole pine stands, (3) quantify treatment effects on absolute nutrient concentrations and their ratios in foliage and (4) evaluate the effects of season of fertilizer application on ^{15}N uptake and allocation in lodgepole pine seedlings.

This thesis has been divided into five chapters. The current chapter introduces the study. Chapter 2 describes growth responses and sapwood hydraulic properties of young lodgepole pine stands following repeated fertilization. Chapter 3 describes the variation in leaf area index, branch characteristics (needle longevity, foliated shoot length and annual shoot length increment) and growth efficiency of young lodgepole pine stands following repeated fertilization. Chapter 4 deals with the use of labeled isotopes to assess seasonal plant N uptake and allocation in lodgepole pine seedlings under simulated climatic conditions within a growth chamber. The final chapter (Chapter 5) is a general discussion of research findings and recommendations for future research.

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Chapter 2. Growth Response and Sapwood Hydraulic Properties of Young Lodgepole Pine following Repeated Fertilization

Introduction

Accelerated stand development and increased growth have been demonstrated for lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm) following fertilization using nitrogen (N) alone or in combination with other elements, but responses have been variable (Cochran 1979, Yang 1985*a*, 1985*b*, 1998, Weetman et al. 1988, Brockley 1991, 1996, 2000, 2001, 2003*a*, 2003*b*). A recent assessment of 14-year growth response of young lodgepole pine to repeated fertilization showed a 46% increase in basal area over control trees (Kishchuk et al. 2002). Fertilization may increase photosynthetic capacity (by increasing leaf area index or increasing photosynthetic efficiency of the foliage) or reduce carbon allocation to fine root growth (Brix 1983, Gower et al. 1992, Haynes and Gower 1995), thus releasing carbon for stem growth. The effect of long-term N fertilization on Scots pine (*Pinus sylvestris* L.) however, resulted in a 25% increase in branch biomass on a low fertility site but not on a fertile site (Mälkönen and Kukkola 1991). Unless it is associated with an increase in photosynthetic output, increased allocation to branches may reduce stemwood response and negatively affect wood quality and lumber recovery.

Sapwood permeability to water flow has been shown to have a strong influence on photosynthesis and productivity because it affects stomatal conductance in response to dynamic water stress (Whitehead 1998) and will influence the leaf area that can be supported by a given area of sapwood. However, the ability of sapwood to supply water to the crowns varies in response to edaphic and climatic factors (Sperry and Tyree 1990, Sellin 1993, Mencuccini and Grace 1996, Ryan and Yoder 1997). Water flow through sapwood is a function of tracheid anatomy and it changes with lumen diameter and length, both of which increases with site quality (Pothier et al. 1989*b*, Coyea and Margolis 1992). Protz et al. (2000) suggested that crown recession (death of lower branches) is driven by reduction in branch sapwood hydraulic permeability, in addition to insufficient light to drive photosynthesis (Mäkelä 1997). More recently it has been shown that thinning stands resulted in reduced specific conductivity within trees immediately after treatment (Liu et al. 2003). Dominant and co-dominant trees on medium sites have been shown to have higher hydraulic conductivity than suppressed trees (Reid et al. 2003). By improving tree vigour, annual fertilization may cause changes to sapwood hydraulic characteristics and stomatal conductance which may, in turn, influence the magnitude and pattern of tree growth response. However, there have been no published studies on the effects of repeated fertilization on branch and bole sapwood hydraulic characteristics.

The objective of this study was to examine how tree growth and specific hydraulic properties of boles and branches vary with periodic and annual fertilization of juvenile lodgepole pine stands. The hypothesis tested was that trees from fertilized stands would have greater specific hydraulic conductivity of branch and bole sapwood because of a greater proportion of earlywood production than those in unfertilized stands. In addition, the hypothesis tested was that sapwood water-conducting properties of branches from different crown positions (top, middle and bottom) between and within treatments were similar.

Methods

Location and Site Description

The study was carried out on two sites (Kenneth Creek and Sheridan Creek) in the central interior of British Columbia. Both sites are part of a larger "maximum productivity" study established by the B.C. Ministry of Forests to document the long-term effects of various rates and frequencies of repeated fertilizer applications on the nutrition, growth and development of managed interior forests (Brockley 1999).

The Kenneth Creek site is located 74 km east of Prince George, B.C. (53° 49′ N 121° 47′ W) within the Willow variant of the wet cool subzone of the Sub-Boreal Spruce Biogeoclimatic Zone ($SBSwk_1$; DeLong 2003). Soil and vegetation descriptions indicate the site belongs to the Sxw-Huckleberry-Highbush Cranberry (05) site series. The soil moisture regime is mesic to sub-mesic and the soil nutrient regime is medium to poor. Derived from thick, well-sorted glaciofluvial outwash parent material, the soil is well drained, and stone free, with a fine to medium loamy sand texture. Although distinct Ae and Bf horizons are evident, the latter is too thin to meet the requirements of the

Podzolic order (Arocena and Sanborn 1999). The soil is therefore classified as an Eluviated Dystric Brunisol (Soil Classification Working Group 1998). After clearcutting and broadcast burning, the site was planted to lodgepole pine in the spring of 1983. At the time of installation establishment in 1993, the stand was 12 years old and had an average density of 1360 stems $\cdot ha^{-1}$. All treatment plots were thinned to a uniform density of 1100 stems $\cdot ha^{-1}$ during plot establishment. Stand growth characteristics at establishment are summarized in Appendix 1.

The Sheridan Creek site is located 7.5 km east of McLeese Lake, B.C. (52° 25′ N 122° 11′ W) within the Blackwater variant of the dry warm subzone of the Sub-Boreal Spruce Biogeoclimatic Zone ($SBSdw_2$; Steen and Coupe 1997). Soil and vegetation descriptions indicate the site belongs to the zonal SxwFd – Pinegrass (01) site series. The soil moisture regime is mesic and the soil nutrient regime is medium. It occurs on a moderately well drained, gently undulating morainal blanket. The rooting zone has a loamy texture with about 25% volume of gravel and cobbles of acidic, igneous intrusive lithology. There is a root restricting layer at a soil depth of about 35 cm, below which the texture is more clay rich with coarse fragments. The soil is classified as a Brunisolic Grey Luvisol (Soil Classification Working Group 1998). The site is occupied by naturally regenerated lodgepole pine that originated from a 1978 clear-cut and subsequent drag scarification. At the time of installation establishment in 1992, the 13-year-old stand had an average stand density of 20,000 stems $\cdot ha^{-1}$. All treatment plots were thinned to a uniform density of 1100 stems $\cdot ha^{-1}$ during plot establishment. Stand growth characteristics at establishment are summarized in Appendix 3.

Fertilization and Plot Establishment

A subset of three of the six fertilizer treatments applied in the larger "maximum productivity" project were used in this study. The three treatments were: 1) control (i.e., not fertilized); 2) periodic – fertilized every 6 years with a multi-nutrient blend containing 200 kg $\cdot ha^{-1}$ N, 100 kg $\cdot ha^{-1}$ phosphorus (P), 100 kg $\cdot ha^{-1}$ potassium (K), 50 kg $\cdot ha^{-1}$ sulphur (S), 25 kg $\cdot ha^{-1}$ magnesium (Mg), and 1.5 kg $\cdot ha^{-1}$ boron (B); 3) annual – fertilized yearly with nutrient blends customized to maintain foliar N concentration at approximately 16 g $\cdot kg^{-1}$ and other nutrients and nutrient ratios in balance with foliar N.

The 'annual' treatment was patterned after 'optimum nutrition' experiments performed in eastern Canada and Sweden, in which N was added annually in order to approximate steady-state N nutrition (Weetman et al. 1995; Tamm et al. 1999). Other macro- and micronutrients were added at rates and frequencies required to maintain an appropriate nutrient balance and to minimize growth limitations resulting from secondary deficiencies (see Ingestad 1979, Linder 1995). Treatment plots typically receive 100 to 200 kg ·N ·ha^{-1} each year. Other nutrients are usually added every 2 to 3 years. The frequency and rates of nutrient additions in the 'periodic' and 'annual' fertilizer treatments are summarized in Table 2-1. Urea (46-0-0, N-P-K) was the primary N source in both treatments. Additional sources of N were mono-ammonium phosphate (11-52-0, N-P-K) and ammonium nitrate (34-0-0, N-P-K). Phosphorus was added as monoammonium phosphate (11-52-0). Sulphate potash magnesia (0-0-22-22-11, N-P-K-S-Mg) was used as a primary source of K, S, and Mg. Potassium chloride (0-0-60, N-P-K), ammonium sulphate (21-0-0-24, N-P-K-S), and ProMag 36 (36% Mg and 6% S) were used to supply additional K, S, and Mg, respectively. Boron was supplied as granular borate (15% B). In all cases, fertilizer was applied shortly after snowmelt in the spring.

In the fall of 2000, foliar analysis of nutrient levels of current years foliage indicated probably copper (Cu) and iron (Fe) deficiencies or imbalanced in the annual treatment at Kenneth Creek (Table 3-1). In the spring of 2001 3 kg ·ha^{-1} of Cu and 10 kg ·ha^{-1} of Fe were added to the annual treatments at Kenneth to correct the deficiencies. This brought the N/Cu ratio in line with control and periodic fertilizations by the fall 2002 (Table 2-3). There was, however, little change in the N/Fe ratio after the application of Fe. It is worth mentioning that some of the added nutrients may have been lost from the Sheridan Creek site due to cattle grazing.

Each of the three treatments (control, periodic, annual) was replicated three times on both sites. Each treatment plot consists of an inner, 0.058-ha 'assessment' plot surrounded by a treated buffer. The assessment plot is offset at one end of the treatment plot to reserve an enlarged buffer area for destructive sampling. A 6.04 m buffer surrounds the three sides of the assessment plot; the buffer on the fourth side is 15.1 m wide. In 'periodic' and 'annual' treatment plots, fertilizer was uniformly broadcast by hand to the assessment plot and surrounding buffer. In keeping with intensive management goals, all stands were pruned to a lift height of 3 m in late September, 1999 at Sheridan, and in mid-October 2000 at Kenneth. Trees < 6 m in height were pruned to 50% of total height at both sites.

Tree Growth Assessment

At each study site, total height and diameter at breast height (DBH) were measured for all 64 trees within the inner assessment area of each treatment plot at the time of installation establishment and again in the fall of 2001 and 2002 (Appendix 1-4). DBH was measured using a diameter tape and heights were taken with a Forestor Vertex® hypsometer. This corresponded to growth response periods of 8 years at both study sites. Mean height, diameter and basal area increments were calculated as the arithmetic mean of individual tree measurement within a plot. Slenderness coefficient (tree total height/DBH) was calculated from these measurements. Treatment means were obtained by averaging the three replicate plots per treatment.

Stomatal Conductance

In August 2002, five average trees (trees with DBH near mean DBH) were selected from the assessment areas within each of the control and the annual treatment plots for stomatal conductance measurements. One lateral branch was clipped from the 3rd upper whorl on the east side of each tree with an aluminum pole pruner. Stomatal conductance was measured on the 3-cm terminal portion of the main leader of each branch (Protz et al. 2000) using a steady state porometer (LI-COR Li-1600. Inc., Lincoln, Neb.). Measurements were completed within 2 minutes of clipping, between 2 and 5 PM local time under full sunlight. Needles were then clipped from the branches, stored in ice and transported to the laboratory. Projected leaf area was determined using a flat-bed scanner and image analysis software (Sigma Scan Pro, SPSS Inc., Chicago, III). Stomatal conductance values were corrected for actual leaf areas and porometer boundary layer resistance.

Bole and Crown Assessment

In July 2001, two average trees were destructively sampled from the enlarged buffer area adjacent of the inner assessment area within treatment plots at both sites. A 100 cm bole section was cut from each selected tree at 1.3 to 2.3 m and stored in double wrapped polyethylene bags (0.15 mm thick) and kept cool during transport to the laboratory where they were frozen at -18 °C while awaiting tree ring analysis and bole conductivity measurements. The live crown of each felled tree was divided in three equal sections (top, middle and bottom). One average branch from each section was selected for laboratory hydraulic measurements and transported and stored in a similar fashion as the bole sections above. Two additional branches were sampled from each crown section and bagged separately in plastic bags, transported and stored in the laboratory as above, for later processing in the laboratory. Diameters (2 cm from the bole) of all remaining branches in each crown section were measured and their fresh (green) mass weighed with a calibrated spring balance.

Ring Analysis and Wood Density

In the laboratory, discs (2 cm thick) were cut from the bottom of the two bole sections per treatment plot and thawed. The surfaces of the discs were planed on the longest and shortest axis for ring width measurements. Earlywood, latewood, and total ring width were measured using a microscope and a stage micrometer for the most recent 7 or 8 annual rings. The two measurements were averaged and earlywood increment, latewood increment and percent earlywood were calculated for each sample. Percent earlywood for each sample was calculated by dividing the width of earlywood increment by the total ring width. Basic wood density was determined from oven dry weights of 10 cm discs cut above 1.3 m height, and green volume determined by water displacement.

Branch and Bole Specific Hydraulic Characteristics

The techniques used to measure bole and branch conductivity were similar to those described by Edwards and Jarvis (1982), Sperry et al. (1988), and Mencuccini et al. (1997). Bole specific hydraulic conductivity (${}_{BL}K_s$) measurements were made on a 20 cm long sub-section of the bole sample collected. Boles were re-cut 15 cm above 1.3 m height and 20 cm samples were collected; exact positions were adjusted so that no branch nodes were near the cut ends. This facilitated good sealing to the hydraulic conductivity apparatus. For branches specific hydraulic conductivity (${}_{BR}K_s$) was measured on a 10-15 cm long section taken from the second internode from the bole.

All bole and branch samples were cut while frozen to minimize the introduction of embolism to the cut ends. Freezing of lodgepole pine samples does not appear to have an impact on hydraulic conductivity measurements (Reid et al. 2003). Samples were then thawed overnight while submerged in filtered (0.2 μm) distilled water; 10 mM oxalic acid was added to the water to suppress growth of bacteria and fungi. After thawing, the remainder of the bark was peeled off, and the ends were planed with a sharp low angle block plane.

Each sample was installed into a constant head hydraulic conductivity apparatus using hanging water columns to generate 16.75 kPa of pressure head ($\Delta\Psi$) across bole and branch sections (after Protz et al. 2000). Plastic plumbing caps of approximately the same size as the bole or branch sections were modified to connect to the permeability tubing. Tire inner tubing of similar size was clamped to the cap and eventually to the bole or branch sample. Caps, tubing and wood samples were clamped tightly together (with additional rubber seals if needed) and the apparatus was carefully filled with (0.2 μm) degassed distilled water containing 10 mM oxalic acid. Samples were perfused in their natural direction of flow and outflow was constantly recorded using an electronic balance. Steady flow was usually observed after 5 minutes. Outflow perfusate temperature was recorded to correct for variations in water viscosity. After 30 minutes of steady flow, the perfusate was switched to a filtered (0.2 μm) solution of degassed acid fuchsin dye until a consistent standard color of outflow was observed. The dye stained the inflow end of the conducting sapwood to allow calculation of sapwood area (Protz et al. 2000). During the process of measurement of flow rate, the reservoir on the scale was covered to prevent evaporation from the pan. The dyed surface was re-cut 2 cm and then planed to obtain a clean surface. The dyed surface of the sample was scanned and the area of the dye surface, unstained sapwood, and heartwood was determined using image analysis software (Sigma Scan Pro, SPSS Inc., Chicago, Ill)

Specific hydraulic conductivity (K_s, m s^{-1}) describes the ability of sapwood to transmit water according to Darcy's law and was calculated as:

$$K_s = \frac{Q\,l}{A_s\,\Delta P} \qquad [1]$$

where Q is the volume flow rate ($m^3\,s^{-1}$) through the sample, l is the sample length (m), A_s is the conductive sapwood area (m^2), and ΔP is the pressure difference across the sample (m hydraulic head). All specific hydraulic conductivity measurements were corrected to 20 °C to account for changes in fluid viscosity with temperature.
The capacity of the bole or branch to supply water to foliage (Q^*, $m^3\,s^{-1}$) under a unit hydraulic gradient was determined according to Eq. [2] (Liu et al. 2003, Reid et al. 2003)

$$Q^* = K_s \, x \, A_s \qquad [2]$$

Equation [2] is identical to the hydraulic parameter described as hydraulic conductivity (k_h) by Tyree and Ewers (1991). A total of 36 bole and 108 branch samples were measured for both the Kenneth and Sheridan sites.

Leaf Area and Branch and Foliage Mass

The procedure used to determine tree leaf area, branch leaf area and branch wood mass was similar to that described by Monserud and Marshall (1999). Sub samples of foliage from each of the three sampled branches from each crown section were scanned to determine projected leaf area. Foliage specific leaf areas were determined as a ratio of leaf area and the dry mass of the scanned sub-samples. To estimate leaf area of each tree, ratios of dry foliage mass to total mass of the green branch were developed for each crown section for each tree using the three sub sampled branches from each crown section. Foliage mass per branch in each crown section was estimated as a product of total mass of the green branch of every individual branch in each crown section and the ratio of dry foliage mass to total mass of the green branch developed for each section. Branch leaf area (${}_{BR}A_L$) was estimated by multiplying foliate specific leaf area and dry foliage mass for the given branch in each section. Leaf area for each crown section was estimated by summing ${}_{BR}A_L$ of all branches in each crown section. Projected leaf area of each tree was calculated by summing the leaf area of all three crown sections. Branch mass was also estimated by developing ratios of dry branch mass to total mass of green branch for each crown section. Estimates of branch wood dry mass in each crown section were obtained by multiplying the total mass of the green branch of every individual branch in each crown section by the ratio of branch dry mass to total mass of the green branch develop for each section. In these stands, where pruning removed very large lower branches, it is possible that total branch wood mass/tree may have been underestimated thus mean branch estimates are reported.

Foliar Sampling and Analysis

Using an aluminum pole pruner, samples of current year's foliage were collected from two lateral branches within the upper one-third of the live crown of 10 trees per plot in the fall of 2002 (early October). Samples were frozen prior to oven-drying at 70° C for 16-24 h. One composite foliage sample per plot was prepared for total chemical analysis, each composite consisting of equal amounts of foliage from each of the 10 trees. Composite samples were ground prior to shipment to the B.C. Ministry of Forests analytical laboratory for chemical analysis.

Total N and total S were analyzed by combustion using the Fisons NA1500 NCS analyzer, followed by determination with an inductively coupled plasma spectrophotometer (ICP) with ARL 3560 ICP optical emission spectrometer. All other macro- and micronutrients were wet ashed with concentrated nitric acid (vanadium added as internal standard) and hydrogen peroxide, using a Questron QLab 6000 closed vessel microwave digestion system. The digest solutions were diluted with hydrochloric acid and individual nutrients determined by ICP as above.

Statistical Analysis

Data for Kenneth and Sheridan were analyzed separately. Differences in basal area (BA), DBH and height increments were first subjected to analysis of covariance using initial BA, DBH and heights, respectively as covariates. These covariates were not statistically significant ($P > 0.05$) at either location (Kenneth and Sheridan) except height at Sheridan was significant ($P = 0.03$); thus unadjusted treatment means are presented as well as adjusted treatment means for height increment at Sheridan. Analysis of variance (ANOVA) was used to test for treatment effects on tree growth characteristics, foliar chemistry and sapwood hydraulic variables. Where treatment effects were significant, the Student-Newman-Keuls test was used to compare treatment means.

Results

Changes in Tree Growth Characteristics and Foliar Analysis

Prior to fertilization, means of DBH, total height and basal area (BA) of trees were similar among treatments at both sites (Table 2-2). Repeated (periodic and annual) fertilization significantly lowered mean height increment of trees and ranked annual<periodic<control at Kenneth (Table 2-2). A significant decrease in height growth resulted in a decline in slenderness coefficient of fertilized trees at Kenneth (Table 2-2). At Sheridan, mean DBH and BA increments significantly increased with fertilization and ranked annual>periodic>control while height increments did not change (Table 2-2). A significant DBH increment of fertilized trees coupled with similar height growth resulted in a decline in slenderness coefficient of fertilized trees (Table 2-2).

At Kenneth, fertilization significantly increased N concentration in the current year's foliage (Table 2-3). Generally, repeated fertilization significantly increased most of the nutrient ratios except N/Ca, N/Cu and N/B (Table 2-3) while absolute levels of other macronutrients were not significantly affected by treatment. Note that there are no differences in ratios between annual and periodic treatment except N/P and N/Fe (Table 2-3). At Sheridan, annual fertilization significantly increased N concentration in the current year's foliage compared with the control and periodic (Table 2-3). Fertilization significantly increased absolute level of P and B while a significant decrease occurred for Ca levels (Table 2-3). Repeated fertilization significantly elevated the ratios of most of the nutrient elements except the ratio of N/Fe which slightly decreased at Sheridan (Table 2-3).

Diameter of Branch, Leaf Area and Mass of Branch Wood

At Kenneth, mean branch diameter and mean branch wood mass at the top, mid and bottom crown positions did not differ between treatments (Figure 2-1 a, c). Annual fertilization significantly decreased mean branch foliage mass at the mid and bottom crown position while the top sections did not show treatment effects (Figure 2-1 b). Bottom branches of the control trees carried 135% more foliage/branch compared with the annually fertilized trees. Mean branch foliage mass was greater at the mid crown position compared with bottom or top, within each fertilization treatment (Figure 2-1 b).

At Sheridan, annual fertilization significantly increased mean branch diameter and mean branch wood mass at the bottom of the crown compared with the periodic and control (Figure 2-1d, f) while mean foliage mass was similar (Figure 2-1 e). Mean branch wood mass of trees fertilized annually was significantly larger compared with that of periodic and control treatments at mid and bottom crown position. A similar trend existed at the top crown position, but differences were marginal ($P = 0.07$; Figure 2-1 f). Branch wood mass of bottom branches of annually fertilized trees was 67 and 94% greater than the control and periodic, respectively. Similarly, mid branch wood mass of annually fertilized trees was 109 and 120% larger than the periodic and control, respectively. Within each treatment, mean branch diameter, foliage mass and branch wood mass were significantly greater at mid crown and bottom compared with the top (Figure 2-1 d-e).

Hydraulic Parameters of Branch

At Kenneth, fertilization appeared to increase specific hydraulic conductivity (${}_{BR}K_s$) of bottom branches between treatments ($P = 0.09$; Figure 2-2 a) and slightly reduced branch leaf area/hydraulic capacity ratio (${}_{BR}A_L/{}_{BR}Q^*$) of bottom branches ($P = 0.06$; Figure 2-2 b). Leaf area of middle branches slightly increased with fertilization ($P = 0.07$), while bottom and top branches were similar (Figure 2-3 a). Within the control treatment ${}_{BR}K_s$, ${}_{BR}A_L/{}_{BR}Q^*$, ${}_{BR}A_L$ and ${}_{BR}Q^*$ were not significantly different among crown positions (Figure 2-2 a, b; 2-3 a, c), except sapwood area (${}_{BR}A_s$) which was significantly higher in the middle and bottom crown positions (Figure 2-3 b). Within the periodic treatment, the

${}_{BR}K_s$, and ${}_{BR}A_L/{}_{BR}Q^*$ were not significantly different at different crown positions. The mid crown branches had significantly larger ${}_{BR}A_L$ compared with top and bottom branches. There was a significant increase in ${}_{BR}A_s$ and ${}_{BR}Q^*$ of middle and bottom branches compared with top branches (Figure 2-3 b, c). Within the annual treatment, ${}_{BR}K_s$ significantly increased from top to bottom (Figure 2-2 a) while branch ${}_{BR}A_L/{}_{BR}Q^*$ ratio significantly increased from bottom to top (Figure 2-2 b). Middle branches had significantly larger ${}_{BR}A_L$ compared with the top and bottom while ${}_{BR}A_s$ and ${}_{BR}Q^*$ were significantly larger at mid and bottom crown positions compared with the top crown position (Figure 2-3 a-c).

At Sheridan, bottom branches of trees fertilized annually had significantly larger ${}_{BR}A_s$ than control or periodic fertilization, while those at the middle and top branches were similar between treatments (Figure 2-3e). Both fertilization treatments slightly increased ${}_{BR}Q^*$($P = 0.09$) of bottom branches while those at the top and middle branches were similar between treatments (Figure 2-3f). Within the control treatment, the bottom and middle branches had significantly larger ${}_{BR}A_s$ compared with the top while marginal increases occurred in ${}_{BR}A_L$ ($P = 0.08$) and ${}_{BR}Q^*$ ($P = 0.06$) at different crown positions (Figure 2-3d-f). Within the periodic treatment, there was a slight increase in ${}_{BR}K_s$ from top to bottom ($P = 0.08$; Figure 2-2 c). Branch leaf area slightly increased from top to bottom ($P = 0.07$) while ${}_{BR}A_s$ and ${}_{BR}Q^*$ significantly increased from top to bottom (Figure 2-3 d-f). Within the annual treatment, ${}_{BR}A_L/{}_{BR}Q^*$ ratio significantly declined from top to bottom (Figure 2-2 d) while ${}_{BR}A_s$ and ${}_{BR}Q^*$significantly increased from top to bottom (Figure 2-3 e, f).

Hydraulic Properties of Bole, Density of Wood and Stomatal Conductance (g_s)

At Kenneth, bole specific conductivity (${}_{BL}K_s$) was slightly higher in the annual treatment compared with the control and periodic treatments (Table 2-4, NS). Percent earlywood in the xylem produced from 1994 to 2000, bole sapwood area (${}_{BL}A_s$), ${}_{BL}A_L$, ${}_{BL}Q^*$ and leaf area/sapwood area ratio (S) were not significantly different (Table 2-4). There was a 1-4% decline in wood density with repeated fertilization compared with the control (Table 2-4, NS). At Sheridan, ${}_{BL}K_s$, percent earlywood in the xylem produced from 1993 to 2000,

$_{BL}A_s$, S and $_{BR}A_L/_{BR}Q^*$ were not significantly different while repeated fertilization significantly reduced wood density (13-20%) compared with the control (Table 2-4).

Stomatal conductances of foliage from upper branches were higher in the control than the annually fertilized plots at Sheridan (63.78 ± 5.25 and 49.27 ± 5.69, mmol m^{-2} s^{-1}). Similar trends were observed at Kenneth Creek (146.31 ± 10.40 and 120.41 ± 9.62, mmol m^{-2} s^{-1}).

Discussion

Results of this study suggest that fertilization increased specific hydraulic conductivity ($_{BR}K_s$) of lower branches thus changing the hydraulic architecture of trees following 7 or 8 years of fertilization. First, the lower branches of repeatedly (annual and periodic) fertilized trees had relatively higher $_{BR}K_s$ compared with the lower branches of the controls (Figure 2-2 a, c). The larger $_{BR}K_s$ of lower branches observed in this study is in contrast to the results of Protz et al. (2000) who suggested that lower branches of unfertilized juvenile lodgepole self-pruned because they had lower sapwood permeability than upper branches; in this study, fertilization appears to increase specific hydraulic conductivity of lower branches and will likely prolong branch life.

The higher $_{BR}K_s$ of bottom branches for the fertilized trees observed in this study may be related to a general increase in site quality. A similar trend was found for the boles ($_{BL}K_s$; Table 2-4). Other studies indicate that K_s increases with improved site quality due to greater tracheid length and diameter in jack pine (*Pinus banksiana* Lamb.) on better sites (Pothier et al. 1989*a*, 1989*b*). Even small differences in lumen diameters between treatments would have a significant effect since water transport through capillaries is proportional to the fourth power of lumen diameter (Sellin 1993, Tyree and Ewers 1991). The extent to which pruning may have affected K_s (boles and branches) was not clear from this study. However, there is evidence to suggest that pruning of balsam fir at different intensities did not have significant effect on K_s (Margolis et al. 1988).

At the branch level, trees from the fertilized treatments appear to have greater capacity to deliver water to foliage ($_{BR}Q^*$), but lower branches had relatively little leaf area relative to this capacity ($_{BR}A_L/_{BR}Q^*$; Figure 2-2b, d). This is in contrast to the suggestions of Sperry et al. (1988) that trees maintain a close balance between leaf area and bole hydraulic capacity to both maximize leaf area and minimize respiration cost. It would be expected that fertilized trees with greater $_{BR}A_s$ and higher $_{BR}Q^*$ would support greater leaf area but this was not the case in this study. Perhaps the decline in $_{BR}A_L/_{BR}Q^*$ from upper to lower branches is related to nutrient imbalances (see below). The combined increase in $_{BR}A_s$ and a decline in $_{BR}A_L$ of bottom branches of fertilized trees suggest that fertilized trees expended more photosynthates to develop structural mass but less leaf area than the control. The stomatal conductance (g_s) of upper branches of the control trees was also greater than that of annually fertilized trees. This may be related to the amount of water that is channeled to the lower branches. In fact, because the lower branches of the fertilized trees had higher $_{BR}K_s$ than upper branches and lower branches had large $_{BR}A_s$, water would flow to lower branches more easily than upper branches. In times of water stress (i.e., when root uptake is insufficient to supply total demand) the upper branch foliage of fertilized trees could experience water deficits compared with the control trees, which would explain the lower g_s I observed in upper branches of the fertilized trees. This suggests that on these sites, fertilization may result in increased water stress at the top of the tree. Thus, the higher flow capacity of lower branches may reduce the availability of water to support the annual growth of the leader and upper branches. It is also possible that the hydraulic limitations to the top of the tree reduced height growth of the fertilized trees (compare with Ryan and Yoder 1997).

At the tree level, DBH increment and BA increment were significantly higher in the annual treatments at Sheridan while the increases at Kenneth were not statistically significant (Table 2-2). The general increase in BA increment observed in this study is consistent with the 46% increase in BA in young lodgepole pine following repeated fertilization (Kishchuk et al. 2002). However, annual fertilization resulted in either a lack of or negative effect on height growth, consistent with observations of pine in other studies (Weetman et al. 1988, Brockley 1991, Tamm et al. 1999, Kishchuk et al. 2002). The increase in diameter coupled with reduced height growth resulted in a decline in slenderness coefficient (Table 2-2). Repeated fertilization also resulted in a significant decline in wood density at Sheridan (13-20%) while Kenneth was associated with a 1-4% decline (Table 2-4). The decline in wood density observed in this study suggests that any gains in BA and wood volume maybe offset by the decline in wood quality. A similar trend has been observed in lodgepole pine in the first 5-years after fertilization (Yang et al. 1988). Annually fertilized trees also allocated more growth to branch wood mass of bottom branches compared with the control (Figure 2-1c, f). Given that pruning removed some of the large branches from the bottom section, it is possible that branch wood biomass would have been greater had pruning not been done. These trends suggest that branch growth was more affected by annual fertilization than height growth. It is possible that the stand density of 1100 stems $\cdot ha^{-1}$ of the stands in this study, which is lower than what would normally be used for operational fertilization of pre-commercially thinned stands of lodgepole pine in British Columbia may have contributed to this shift in allocation of growth resources to lower branches. The observed allocation of growth to lower branches in this study is consistent with observed trends for Scots pine (*Pinus sylvestris* L.) following long-term N fertilization (Mälkönen and Kukkola 1991). Kishchuk et al. (2002) found that trees fertilized with higher rates of N developed large and distorted branches, and Hopmans and Flinn (1984) also observed heavy branching with increased supply of N and lack of apical dominance in boron deficient trees. The increased allocation to lower branches at the expense of top growth and the general decline in specific gravity of the bole at Sheridan, suggests a general decline in wood quality with fertilization.

The foliar nutrient concentrations of the current year's foliage show that fertilization, especially annual fertilization, elevated the level of N in trees at both locations. Fertilization effects on other nutrient elements were variable contrary to the expected elevated levels in the foliage. Although attempts to maintain current foliar N concentration at 16 $g \cdot kg^{-1}$ was almost successful, foliar nutrient imbalances may have been induced by repeated N additions (Ingestad 1979). Fall 2002 foliar nutrient data suggest that N/Cu and N/Fe ratios were higher and imbalanced at Kenneth and N/Fe at Sheridan (Table 2-3). According to Ingestad (1979), an optimum foliar N/Cu and N/Fe balance ratio is about 3000-3500 and 150, respectively. Although the ratio of N/Fe was above the suggested optimum N/Fe balance for all three treatments at both locations, the ratio for the annual treatment at Kenneth was about 40% higher than the control and the periodic fertilization and may be related to the poor growth performance of the annually fertilized trees at this location. It is likely that N/Cu and perhaps the N/Fe imbalance may be responsible for the large and distorted branches and the resulting unusual hydraulic architecture observed at Kenneth (Table 3-1 and 3-2). Other studies have also reported induced copper deficiency in other coniferous trees following N fertilizer application (Turvey and Grant 1990). The differences in growth response between the two locations may be related to climatic, site, and soil factors, and or to genetics (see site description). Further studies of fertilized stands will be needed to determine if the unusual hydraulic architecture observed was the result of generally high nutrient status or nutrient imbalances caused by repeated fertilization. Further studies might also be done to determine if there is a genetic basis for the relatively low growth response and disrupted hydraulic architecture at Kenneth under the annual fertilization.

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Table 2-1. Nutrient application rates (kg $\cdot ha^{-1}$) by treatment and year at Kenneth Creek and Sheridan Creek.

Treatment	Nutrient Element	Year									Total
		1993	1994	1995	1996	1997	1998	1999	2000	2001	
Kenneth Creek											
Control	-	-	-	-	-	-		-	-		-
Periodic	N		200						200		400
	P		100						100		200
	K		100						100		200
	S		50						50		100
	Mg		25						25		50
	B		1.5	-	-	-	1.5	-	1.5		3.0
Annual	N		200	200	200	-	100	100	150	100	1050
	P		100	100	-	-	50	-	50		300
	K		100	100	-	-	50	-	50		300
	S		50	50	17	-	49	-	63	11	240
	Mg		25	25	100	-	50	-	32	50	282
	B		1.5	-	-	-	1.5	-	-		3.0
	Cu		-	-	-	-	-	-	-	3	3
	Fe		-	-	-	-	-	-	-	10	10
Sheridan Creek											
Control	-	-	-	-	-	-	-	-	-		-
Periodic	N	200					-	200			400
	P	100					-	100			200
	K	100					-	100			200
	S	50					-	50			100
	Mg	25					-	25			50
	B	1.5	-	-	-	-	-	1.5			3.0
Annual	N	200	200	200	200	-	100	100	150	100	1250
	P	100	100	100	-	-	50	-	50		400
	K	100	100	100	-	-	50	-	50		400
	S	50	50	50	17	-	49	-	63		279
	Mg	25	25	25	100	-	50	-	32		257
	B	1.5	-	-	-	-	1.5	-	-		3.0

Table 2-2. Mean tree growth characteristics of lodgepole pine stands at Kenneth Creek and Sheridan Creek.

	Treatment			
Site/tree growth variables	Control	Periodic	Annual	*P*-values
Pretreatment (Kenneth Creek)				
DBH (cm)	8.71 (0.26)a	8.74 (0.20)a	9.29 (0.38)a	0.359
Total height (TH; m)	5.50 (0.17)a	5.58 (0.06)a	5.72 (0.13)a	0.523
Basal area (m^2) x 10^{-3}	6.08 (0.36)a	6.11 (0.30)a	6.90 (0.58)a	0.381
Slenderness coefficient (TH/DBH)	0.64 (0.02)a	0.64 (0.01)a	0.62 (0.01)a	0.620
Post-treatment (1993-2002)				
DBH increment (cm)	6.49 (0.24)a	7.15 (0.18)a	6.72 (0.09)a	0.104
Total height increment (m)	5.42 (0.08)a	5.11 (0.11)b	4.20 (0.03)c	<0.001
Basal area increment (m^2) x 10^{-3}	12.34 (0.74)a	14.00 (0.17)a	13.65 (0.19)a	0.075
Slenderness coefficient	0.73 (0.02)a	0.68 (0.01)ab	0.63 (0.01)b	0.010
Pretreatment (Sheridan Creek)				
DBH (cm)	4.67 (0.06)a	4.45 (0.25)a	4.85 (0.05)a	0.253
Total height (m)	4.23 (0.15)a	4.09 (0.17)a	4.23 (0.08)a	0.751
Basal area (m^2) x 10^{-3}	1.79 (0.04)a	1.62 (0.18)a	1.92 (0.04)a	0.242
Slenderness coefficient	0.92 (0.02)a	0.94 (0.01)a	0.87 (0.02)a	0.121
Post-treatment (1992-2001)				
DBH increment (cm)	5.23 (0.20)b	6.70 (0.20)a	7.05 (0.09)a	0.001
Total height increment (m)	3.93 (0.04)a	4.09 (0.16)a	3.78 (0.13)a	0.267
Basal area increment (m^2) x 10^{-3}	6.10 (0.29)c	8.37 (0.39)b	9.50 (0.15)a	0.001
Slenderness coefficient	0.84 (0.02)a	0.74 (0.02)b	0.68 (0.01)b	0.003

NOTE: For each installation variable, treatment means with different letters are significantly different at $\alpha = 0.05$. Numbers in parentheses represent standard error. (n=3).

Table 2-3. Fall 2002 foliar nutrient levels of current's year foliage (Upper crown).

Site/variables	Treatment: Control	Periodic	Annual	*P*-values
<u>Kenneth Creek</u>				
N (g kg^{-1})	11.37 (0.23)c	13.10 (0.26)b	15.13 (0.55)a	0.001
P (g kg^{-1})	1.30 (0.05)a	1.35 (0.03)a	1.37 (0.01)a	0.475
K (g kg^{-1})	4.38 (0.08)a	4.46 (0.07)a	4.60 (0.23)a	0.567
Ca (g kg^{-1})	1.28 (0.17)a	1.25 (0.19)a	1.24 (0.10)a	0.976
Mg (g kg^{-1})	0.79 (0.03)a	0.80 (0.01)a	0.88 (0.01)a	0.051
S (g kg^{-1})	0.85 (0.05)a	0.83 (0.00)a	0.91 (0.02)a	0.281
Cu (mg kg^{-1})	1.9 (0.5)a	2.1 (0.4)a	2.2 (0.3)a	0.872
B (mg kg^{-1})	18.7 (3.2)a	19.2 (3.2)a	20.4 (4.8)a	0.950
Fe (mg kg^{-1})	25 (3)a	28 (1)a	24 (3)a	0.447
Zn	41 (2)a	43 (1)a	44 (1)a	0.324
N/K	2.60 (0.09)b	2.94 (0.10)ab	3.30 (0.19)a	0.029
N/P	8.75 (0.36)b	9.71 (0.30)b	11.07 (0.38)a	0.009
N/Ca	9.11 (0.96)a	10.91 (1.44)a	12.38 (0.94)a	0.205
N/Mg	14.35 (0.35)b	16.31 (0.39)a	17.22 (0.81)a	0.028
N/S	13.49 (0.53)b	15.72 (0.31)a	16.70 (0.61)a	0.010
N/Cu	7329 (2392)a	6767 (1284)a	7285 (1006)a	0.966
N/Fe	460 (38)b	468 (19)b	646 (66)a	0.046
N/B	655 (137)a	724 (131)a	863 (255)a	0.730
<u>Sheridan Creek</u>				
N (g kg^{-1})	12.00 (0.20)b	11.63 (0.30)b	15.73 (0.20)a	<0.001
P (g kg^{-1})	1.35 (0.03)b	1.50 (0.02)a	1.49 (0.03)a	0.009
K (g kg^{-1})	4.77 (0.08)a	4.64 (0.19)a	4.54 (0.13)a	0.547
Ca (g kg^{-1})	1.45 (0.03)a	1.27 (0.07)b	1.00 (0.03)c	0.002
Mg (g kg^{-1})	0.99 (0.04)a	1.03 (0.01)a	0.92 (0.05)a	0.226
S (g kg^{-1})	0.93 (0.05)a	0.90 (0.04)a	1.02 (0.02)a	0.160
Cu (mg kg^{-1})	3.2 (0.1)a	3.5 (0.2)a	3.1 (0.2)a	0.294
B (mg kg^{-1})	13.9 (0.8)c	18.8 (1.0)b	25.5 (0.6)a	0.001
Fe (mg kg^{-1})	34 (1)a	34 (3)a	33 (3)a	0.960
Zn	49 (3)a	48 (2)a	44 (2)a	0.379
N/K	2.52 (0.08)b	2.51 (0.09)b	3.47 (0.11)a	<0.001
N/P	8.90 (0.32)b	7.77 (0.12)c	10.55 (0.28)a	0.001
N/Ca	8.26 (0.07)b	9.27 (0.75)b	15.76 (0.40)a	<0.001
N/Mg	12.11 (0.31)b	11.34 (0.43)b	17.31 (1.29)a	0.004
N/S	12.99 (0.85)b	12.91 (0.29)b	15.43 (0.15)a	0.024
N/Cu	3760 (145)b	3337 (110)b	5179 (371)a	0.004
N/Fe	357 (16)a	349 (33)a	488 (49)a	0.054
N/B	867 (49)a	620 (27)b	617 (22)b	0.003

For each installation and nutrient variable, treatment means with different letters are significantly different at $\alpha = 0.05$. Numbers in parentheses represent standard error. (n=3).

Table 2-4. Mean hydraulic characteristics and wood density for boles of sampled trees from lodgepole pine stands following initial fertilization.

Site/ variables	Control	Treatment Periodic	Annual	*P*-values
Kenneth Creek				
Percent earlywood (%; 1994-2000)	83.86 (1.20)a	82.64 (1.02)a	81.82 (1.03)a	0.393
Sapwood area ($_{BL}A_S$; cm^2)	89.89 (8.68)a	103.87 (8.36)a	100.99 (13.09)a	0.649
Leaf area ($_{BL}A_L$; m^2)	20.31 (1.89)a	24.56 (2.33)a	19.28 (2.19)a	0.160
S ($_{BL}A_L$ / $_{BL}A_S$; m^2 cm^{-2})	0.23 (0.01)a	0.24 (0.02)a	0.19 (0.01)a	0.145
Specific conductivity ($_{BL}K_s$; ms^{-1} x 10^{-5})	0.91 (0.19)a	0.95 (0.18)a	1.45 (0.19)a	0.063
Hydraulic capacity ($_{BL}Q^*$; m^{3}s^{-1} x 10^{-8})	8.53 (2.05)a	10.53 (2.50)a	14.17 (1.48)a	0.285
$_{BL}A_L$/ $_{BL}Q^*$ (m^2/ m^{3}s^{-1} x 10^8)	3.88 (1.51)a	3.35 (0.95)a	1.39 (0.15)a	0.321
Wood density (g cm^{-3})	0.35 (0.004)a	0.35 (0.004)a	0.34 (0.008)a	0.301
Sheridan Creek				
Percent earlywood (%; 1993-2000)	79.36 (2.76)a	82.85 (1.31)a	78.72 (1.96)a	0.132
Sapwood area ($_{BL}A_S$; cm^2)	62.44 (8.46)a	60.61 (7.20)a	72.90 (6.93)a	0.384
Leaf area ($_{BL}A_L$; m^2)	11.02 (1.55)a	12.10 (1.99)a	14.40 (2.29)a	0.383
S ($_{BL}A_L$/ $_{BL}A_S$; m^2 cm^{-2})	0.18 (0.01)a	0.20 (0.01)a	0.19 (0.02)a	0.414
Specific conductivity ($_{BL}K_s$; ms^{-1} x 10^{-5})	1.50 (0.18)a	1.80 (0.18)a	1.80 (0.19)a	0.365
Hydraulic capacity ($_{BL}Q^*$; m^{3}s^{-1} x 10^{-8})	8.80 (0.86)a	10.41 (1.01)a	12.81 (1.25)a	0.163
$_{BL}A_L$/ $_{BL}Q^*$ (m^2/ m^{3}s^{-1} x 10^8)	1.26 (0.16)a	1.21 (0.24)a	1.13 (0.13)a	0.848
Wood density (g cm^{-3})	0.39 (0.012)a	0.34 (0.006)b	0.32 (0.009)b	0.015

For each installation variable, treatment means with different letters are significantly different at α = 0.05. Numbers in parentheses represent standard error. (n=3).

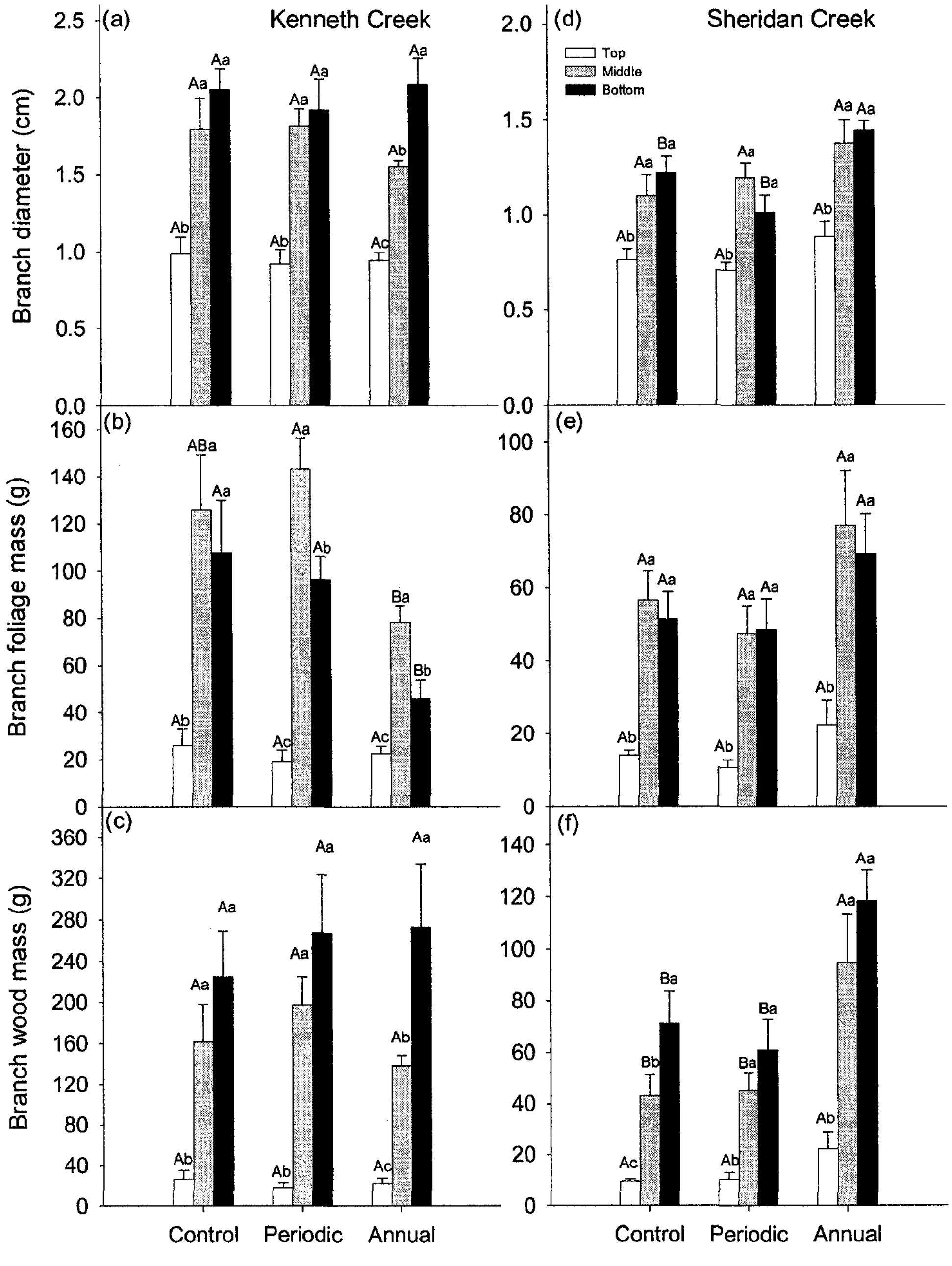

Figure 2-1. Mean branch diameter, foliage mass and branch wood mass of branches from different crowns positions of fertilized and unfertilized lodgepole pine trees at Kenneth and Sheridan. Bars with the same lowercase letter among crown positions within each fertilization treatment, and bars with the same uppercase letter among fertilization treatments within each crown position are not significantly different at α = 0.05 according Student-Newman-Keuls test. (n=3). Error bars indicate ± (SE).

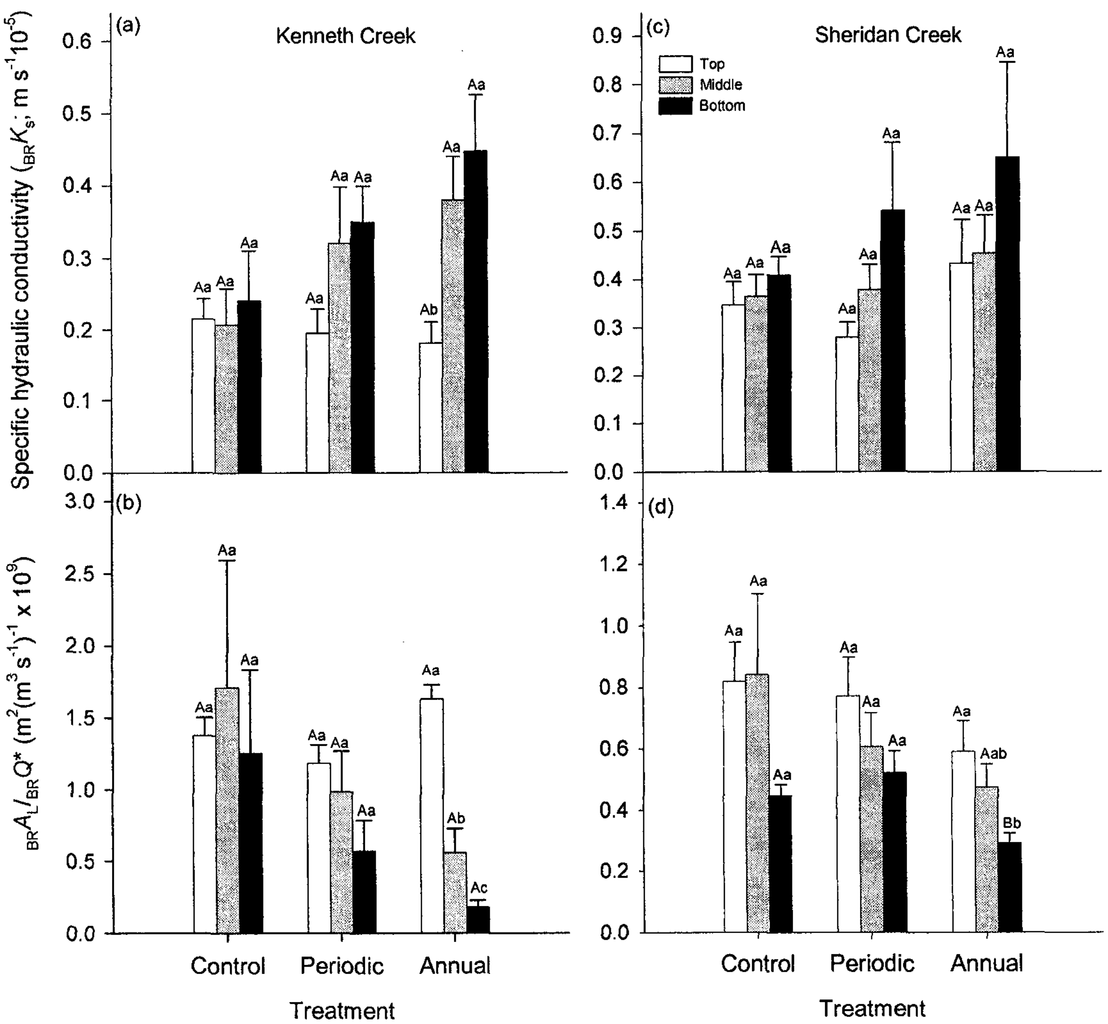

Figure 2-2. Mean branch specific hydraulic conductivity ($_{BR}K_s$) and leaf area/hydraulic capacity ratio ($_{BR}A_L/_{BR}Q^*$) of branches from different crowns positions of fertilized and unfertilized lodgepole pine trees at Kenneth and Sheridan. Bars with the same lowercase letter among crown positions within each fertilization treatment, and bars with the same uppercase letter among fertilization treatments within each crown position are not significantly different at $\alpha = 0.05$ according Student-Newman-Keuls test. (n=3). Error bars indicate ± (SE).

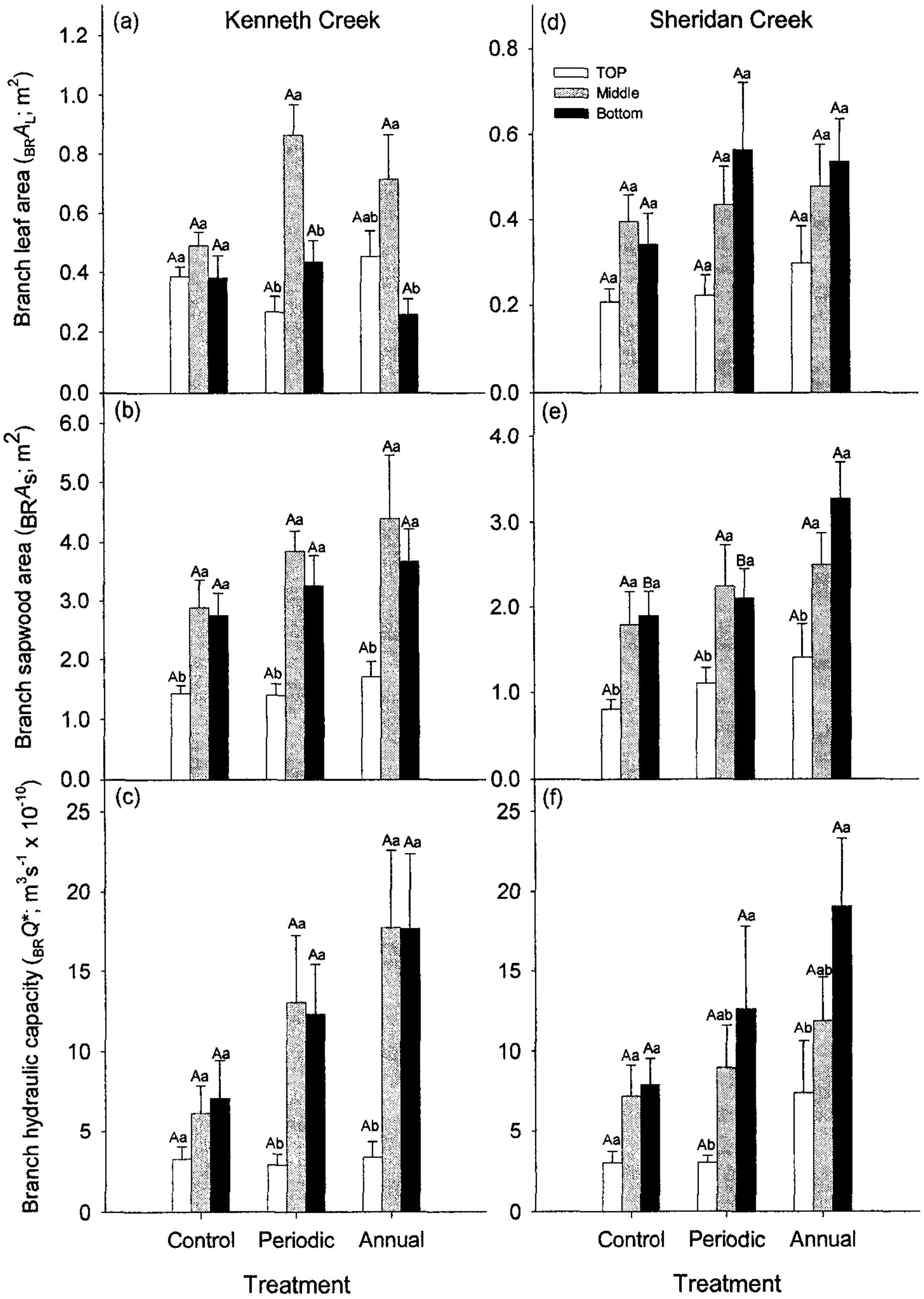

Figure 2-3. Mean branch leaf area ($_{BR}A_L$), sapwood area ($_{BR}A_s$) and hydraulic capacity ($_{BR}Q^*$) of branches from different crowns positions of fertilized and unfertilized lodgepole pine trees at Kenneth and Sheridan. Bars with the same lowercase letter among crown positions within each fertilization treatment, and bars with the same uppercase letter among fertilization treatments within each crown position are not significantly different at $\alpha = 0.05$ according Student-Newman-Keuls test. (n=3). Error bars indicate ± (SE).

Chapter 3. Effects of Repeated Fertilization on Needle Longevity, Growth Efficiency and Leaf Area Index of Lodgepole Pine Stands.

Introduction

Leaf area index (LAI; leaf area per unit ground area) is considered to be one of the major factors that influences forest productivity and stand dynamics (Waring and Schlesinger 1985, Oliver and Larson 1996). The amount of leaf area on a tree depends on needle production and retention, both of which vary with edaphic and climatic factors (Reich et al. 1995). Trees with greater needle longevity have higher productivity (Schoettle 1990, Reich et al. 1991, 1992, Gower et al. 1993) and nutrient use efficiency (NUE; as measured in photosynthate produced per unit nutrient uptake over the life of the foliage) (Chapin 1980, Son and Gower 1991). Repeated fertilization would be expected to increase foliar nutrient concentration. This should enhance photosynthetic capacity of foliage to increase stand productivity, provided that acquisition and utilization of the nutrient by the plant are in balanced proportion (Ingestad 1979). However, the effects of repeated fertilization on longevity of needles, or the nutrient concentration of various age classes of needles has not been well documented.

Three theories attempt to explain why needles on conifer branches are retained for different periods of time. First, the light limitation hypothesis suggests that as lateral branches form new needles and grow outwards each year, older needles are gradually buried deeper into the crown of the tree. Thus, on fast growing trees, older needles might become shaded below their light compensation point (Schoettle and Fahey 1994). Reduced light interception after shading contributes to a decline in carbon gain through at least two mechanisms: a) lower light levels directly reduce photosynthetic rates due to energy limitations; b) as older needles become shaded, nitrogen (N) allocation to younger needles are favored thus reducing N concentration and photosynthetic capacity of older needles (Field 1983). Under reduced light, the ability of older needles to maintain a positive carbon balance becomes a major factor contributing to their longevity (McMurtrie et al. 1986, Schoettle and Smith 1991, 1998, Ackerly 1999).

Secondly, the nutrition hypothesis suggests that species with long-lived foliage are most common on infertile soils in many ecosystems and biomes (Monk 1966, Chapin 1980, Reich et al. 1992). Such species have been shown to have generally lower leaf N concentrations and lower photosynthetic capacities (Williams et al. 1989, Reich et al. 1991). Thus, increased needle longevity has been suggested as an important mechanism to reduce annual nutrient and C demand to produce new foliage and to cope with low N availability (Chapin 1980, Chabot and Hicks 1982). Moreover, improved site fertility either through natural nutrient pulses or fertilization has been shown to decrease leaf longevity (Reich et al. 1995, Balster and Marshall 2000, Harrington et al. 2001, Pensa and Sellin 2002, Niiemets and Lukjanova 2003) in support of the above contention (Chapin 1980, Reich et al. 1992). The nutrition hypothesis may also be related to nutrient use theory, suggesting that long-lived foliage has higher NUE (Chapin 1980).

Thirdly, nutrient retranslocation, defined as the process of an element being depleted from older plant components and made available for new growth has been demonstrated to provide substantial amounts of nutrients for the construction of new needles each year (Lim and Cousens 1986, Helmisaari 1992). Nutrient withdrawal from older leaves has been suggested as a possible cause of leaf senescence and death (Maillette 1982, Lange et al. 1987, Schoettle and Fahey 1994) because of possible reduction in photosynthetic capacity. However, retranslocation may be regulated by N supply, growth sinks, nutrient uptake rates, size of plant nutrient reserves or age of trees (Nambiar and Fife 1987, Munson et al. 1995, Hawkins et al. 1998). In several studies, rates of retranslocation were either unaffected across nutrient gradients (Fife and Nambiar 1984, Birk and Vitousek 1986, Nelson et al. 1995) or increased in plants growing in fertile environments (Nambiar and Fife 1987, Proe and Millard 1994, Munson et al. 1995, Salifu and Timmer 2003). Furthermore, retranslocation is not necessarily related to leaf senescence but may occur in all needle age-classes during spring and early summer when growth is intensive (Fife and Nambiar 1982, Fife and Nambiar 1984). It is not clear which of the above theories explain the variation in needle longevity anticipated following repeated fertilization.

The objectives of this study were to: 1) examine the effect of repeated fertilization on needle longevity, annual shoot growth, foliated shoot length, LAI and stemwood growth efficiency in juvenile lodgepole pine stands; and 2) quantify the effects of repeated fertilization on foliar nutrient concentrations and nutrient ratios in these stands.

Methods

Location and Site Description

The study was carried out on two sites: 1) Sheridan Creek; and 2) Kenneth Creek which are part of a larger "maximum productivity" study established by the B.C. Ministry of Forests to document the long-term effects of various rates and frequencies of repeated fertilizer applications on the nutrition, growth and development of managed interior forests (Brockley 1999). A thorough description of the sites, fertilizer treatment and plot establishment are given in chapter 2.

Stand Growth Characteristics

At each study location, total height and diameter at breast height (DBH) were measured for all trees within the inner assessment area of each treatment plot in the fall of 1999 at Kenneth and 1998 at Sheridan and again in the fall of 2001 at Sheridan and 2002 at Kenneth (Appendix 2 and 4). DBH was measured using a steel diameter tape and heights were taken with a Forestor Vertex® hypsometer.

In July 2001, two trees (same trees as in Chapter 2) were destructively sampled from each plot and their stemwood volumes calculated based on the geometric forms assumed by portions of a tree stem (Husch et al. 1982). Volume of these sampled trees was estimated using standard volume equation developed for lodgepole pine of harvest origin for Sheridan Creek ($V = 4186 + 34.04D^2H$) and another of plantation origin for Kenneth Creek ($V = 5482 + 35.28D^2H$), where V is volume inside bark in cubic centimeters, D is DBH outside bark in centimeters, and H is total height in meters (Brockley unpublished data). To test for bias, estimated stemwood volumes were regressed on calculated stemwood volumes for each location. Estimated and calculated volumes were positively related for Sheridan ($P <0.05$; r^2 0.98) and Kenneth ($P <0.05$; r^2 0.94). Individual tree periodic annual increment (PAI) of stem volume in each of the treatment plots at Kenneth (1999-2002) and Sheridan (1998-2001) were determined using the equations above. PAI of stem volume was converted to biomass based on the average wood density of each treatment (Chapter 2; Table 2-4). Stand PAI of stem biomass per hectare was obtained by summing individual PAI of stem biomass in each plot and converting plot area to a per hectare basis. Stem growth efficiency was calculated by dividing stand level PAI of stem biomass by leaf area index (LAI).

Branch Sampling

In August 2002, one dominant, one co-dominant and one suppressed tree were selected from the assessment areas within each treatment plot per site. The protocol used to sample branches was similar to the procedure described by Balster and Marshall (2000). At both locations one branch (an axis that originates from the bole of the tree; i.e., first-order branch) was cut from east, west and south sides of the trees from mid crown height. These branches were actively growing and had shoots without needles, which were older than the oldest cohorts with needles on each branch. This enabled ageing the last living cohort and ensured that treatment effect on needle longevity could be assessed accurately. Branches were transported on ice to the laboratory and stored at -18 °C until processed.

Growth Characteristics of Branches and N P K Analysis of Different Age-Classes of Needles

Needle longevity and shoot characteristics were assessed and quantified on each 1^{st} order branch. Needle age-class was quantified by counting annual needle cohorts, distinguished by the presence of second order branches along the axis of each main branch and/or bud scars. Any cohort with greater than 40% of the fascicles still green was counted as alive. If multiple flushes on the same year was suspected, a cut was made below and above the internode to ensure each cohort belonged to the same year's growth. Annual shoot growth and foliated shoot length (length of the shoot with firmly attached fascicles) were also measured. The mean shoot growth increment was calculated from all the increments of shoot growth from those years of shoot growth that had foliage attached. Unit fascicle mass was calculated from a subsample of fifty fascicles selected at random from each shoot and averaged over each treatment for each cohort. The survivorship of fascicles in each needle age-class was determined by dividing the number of living fascicles by the sum of the number of fascicle scars and living needles.

Foliage from each needle age-class was oven dried at 70 ° C for 16-24 h, and weighed. Sub-samples of foliage were composited by plot per treatment for each needle age-class and ground prior to analysis. Samples were digested in concentrated sulphuric acid followed by oxidation with hydrogen peroxide. Total N and P in the digests were determined with a Technicon autoanalyzer II and K was analyzed with atomic absorption spectrometer spectraa 880 Varian. Results were expressed as concentrations (g $\cdot$kg^{-1} dry wt.) and contents (µg $\cdot$fascicle^{-1}) of N, P and K.

Sampling and Nutrient Analysis of Current Year's Foliage

Using an aluminum pole pruner, samples of current year's foliage were collected from two lateral branches within the upper one-third of the live crown of 10 trees per plot in the fall of 2000 and 2001 (early October). Samples were frozen prior to oven-drying at 70° C for 16-24 h. One composite foliage sample per plot was prepared for analysis, each composite consisting of equal amounts of foliage from each of the 10 trees. Composite samples were ground prior to analysis at the B.C Ministry of Forests analytical laboratory. Analytical procedure used for all macro- and micronutrients was similar.

Estimation of LAI with Hemispherical (fisheye) Photography

Hemispherical photographs were taken using a Nikon Cooplix 990 digital camera and a 7mm fisheye lens converter mounted level on a tripod. Fifteen photographs of the canopy, excluding the understory vegetation were taken within each plot. Photographs were taken at the centre of mapped grid squares (≈ 5 m x 5 m) established in each plot at about one meter above ground level with the top of the camera oriented northward. The camera was set to slightly overexpose the photographs to ensure good contrast between sky and foliage. To prevent glare from direct sunlight, photographs were taken early in the morning or late in the evening or under conditions of uniform cloud cover. Each photograph was analysed using the Spot Light Interception Model (SLIM) (Comeau et al. 2002). In SLIM leaf area index is calculated by inversion of gap fraction data (Welles 1990). The Poisson model was used, so needle and crown clumping were ignored, and estimates were effective LAI (Chen and Black 1992) rather than true LAI. A manual threshold was used, marking parts of the photographs as being sky or foliage to direct the program in its conversion of individual pixels to black and white (binary) information. The photos were then analyzed by SLIM to calculate LAI with respect to the location of the camera (Comeau et al. 2002).

Fine Root Sampling and Analysis

In August 2001, 15 soil cores were sampled from the center of the 15 grid squares within each treatment plot at Kenneth Creek. Soil cores were obtained by driving a sharp-edged steel tube, 7.0 cm inside diameter into the soil to a depth of 40 cm. Individual cores were placed in polyethylene bags and transported on ice to the laboratory and stored at -18 °C until processed. In the laboratory, roots were washed to separate them from soil and organic material. Live and dead pine roots were separated from other roots (grasses, shrubs etc.). Pine fine roots (<5 mm) were visually compared to sections of wire having diameters of 5 mm or were checked with calipers and separated from root > 5 mm. Live sorted pine root and non pine roots were dried at 70 °C for 72 hours and weighed.

Statistical Analysis

Data for Kenneth and Sheridan were analyzed separately. Analysis of variance (ANOVA) was used to test for treatment effects on longevity of needles, leaf area index, PAI of stem biomass, stem growth efficiency and fine root biomass and other variables. Data analyses on survivorship, N concentration and content were performed on age-classes 0-4 and 0-5 for Kenneth and Sheridan, respectively, because of limited data for age-classes 5 and 6. Where treatment effects were significant, the Student-Newman-Keuls test was used to compare treatments.

Results

Branch Characteristics

At Kenneth, six age-classes of needles (from current-year up to 5 years) were counted in the control and the periodic treatments while four age-classes (from current-year up to 3 years) were counted for mid crown branches of the annual treatment. Annual fertilization significantly decreased the mean number of needle age-classes compared with periodic and control treatments (Figure 3-1a). However, mean foliated length, and annual shoot length increment of mid crown branches were unaffected by fertilization (Figure 3-1b, c). The fascicle survivorship of age-classes 0 to 2 were similar between treatments while age-class 3 was significantly different and ranked as periodic>control>annual (Figure 3-2a). Generally, within each treatment, there was a significant decline in survivorship with needle age (Figure 3-2a).

At Sheridan, seven age-classes of needles (from current-year up to 6 years) were counted in the control while six age-classes (from current-year up to 5 years) were counted for the periodic and annual treatments. Fertilization tended to decreased the number of needle age-classes ($P = 0.06$) (Figure 3-1a); treatments were ranked control>periodic>annual. Mean annual shoot length increment and foliated shoot length were significantly larger in the annual treatment compared with periodic and control, and can be ranked annual>periodic>control (Figure 3-1b, c). The fascicle survivorship of age-classes 0 to 4 were similar between treatments (Figure 3-2b).. In general, the survivorship of the current-year needles within each treatment was significantly higher compared with all other age-classes.

N P K Concentration and Content of Different Needle Age-Classes

At Kenneth Creek, mean foliar N concentration was significantly greater in the annual treatment; treatments can be ranked as annual>periodic=control for age-classes 0-3 (Figure 3-3 a). Within the control treatment, N concentration in age-class 4 was significantly lower compared with needles in the age-classes 0-3 (Figure 3-3 a). Within the periodic treatment, N concentrations were similar among age-classes (Figure 3-3 a). Within the annual treatment, N concentrations in age-classes 0 and 1 needles were significantly greater compared with age-classes 2 and 3 (Figure 3-3 a). There was a general decline in P and K concentrations with age in all three treatments and P and K values were similar in all age-classes between treatments (Figure 3-4 a, 3-5 a). At Sheridan, N concentration of foliage in age-classes 1-4 was significantly higher in the annual treatment than the control or periodic (Figure 3-3 d). Within the each treatment, N concentration significantly declined in age-classes 4 and 5. Mean P and K concentrations were significantly lower in older foliage in all three treatments. Mean P and K concentrations were similar in all age-classes between treatments except K concentration of age-class 2 was significantly higher in the annual treatment compared with control and periodic (Figure 3-4 c, 3-5 c).

Mean foliar N content was significantly higher in the annually fertilized trees and can be ranked as annual>periodic>control for age-classes 0-4 at Kenneth (Figure 3-3 b). Within the control and the annual treatments, N content was not different between age-classes (Figure 3-3 b). N content was higher, however in the age-class 2 foliage compared with the other age-classes within the periodic treatment (Figure 3-3 b). Mean P and K contents were unaffected by treatment in all age-classes except current-year foliage, where contents were higher in the annual treatment compared to control and periodic treatments (Figure 3-4 b, 3-5 b). The N content increased with age and peaked in age-class 2 foliage and then significantly declined in age-class 3 to 4 needles, in all three treatments (Figure 3-3 e). Mean P and K contents were unaffected by treatment in all needle age-classes except current year foliage, where contents were higher in the annual treatment compared to control and periodic treatments (Figure 3-4 d, 3-5 d).

Mass of Fascicles

At Kenneth, mean mass of fascicles of age-class 0 was largest in the annual treatment compared to control and periodic (Figure 3-3 c). Within each treatment, mass of fascicle significantly increased with age (Figure 3-3 c). At Sheridan, mean mass of fascicle of age-class 4 was lowest in the periodic compared control and annual treatments (Figure 3-3 f).

Nutrient Concentration of the Current Year's Foliage From 2000 and 2001

At Kenneth, fertilization significantly elevated foliar concentrations of N and boron (B) in the current year's foliage of 2000 (Table 3-1). In addition, annual fertilization increased sulfur (S) concentration and decreased concentrations of copper (Cu), calcium (Ca) and Zinc (Zn) (Table 3-1). Generally, fertilization increased most of the nutrient ratios except N/K, N/P and N/Fe (Table 3-1) while absolute levels of other macronutrients were not affected by treatment. The ratio of N/Cu of the annual treatment was about 2.5 greater than the periodic treatment and 3.4 times greater than the control treatment (Table 3-1). The absolute levels of N and B were higher in the current year's foliage of 2001, in fertilized treatments particularly the annual (Table 3-2). Annual fertilization decreased absolute levels of Ca, magnesium (Mg), Cu and Zn relative to the control and periodic treatments. There was a significant treatment effect on all the ratios except N/S and N/B

(Table 3-2). The ratios of N/Cu and N/Fe were 1.6 and 5.6 times higher in the annual treatment compared with the control treatments.

At Sheridan, treatment affected N, P, and S concentrations in the current year's foliage of 2000; and ranked annual>periodic>control while B was ranked periodic>annual>control (Table 3-1). Repeated fertilization elevated the ratios of most elements except the ratio of N/S and N/B which decreased slightly (Table 3-1). In the 2001 foliage samples, N, P and S were higher in the fertilized treatments and ranked annual>periodic>control while Ca was lower in the annual treatment (Table 3-2). The annual treatment had higher N/K, N/Ca, N/Mg and N/Fe compared with the control and periodic (Table 3-2).

Stand Growth Characteristics

Annual fertilization reduced growth efficiency, PAI of stem biomass and volume while treatment effect on roots of other species was marginal ($P= 0.08$) and ranked periodic>control>annual at Kenneth (Table 3-3). There were no treatment effects on live pine fine root biomass, LAI and LAI/pine root biomass ratio at Kenneth (Table 3-3). At Sheridan, stem volume increment and LAI were greater on fertilized plots. Fertilization slightly increased PAI of stem biomass ($P=0.08$) while growth efficiency was marginally reduced by annual fertilization at Sheridan ($P = 0.09$) (Table 3-3).

Discussion

Results from this study suggest that annual fertilization decreased longevity of needles on mid crown branches of lodgepole pine following 7 or 8 years of fertilization. First, mean longevity of needles declined by 23% in the annual treatment at Kenneth Creek and 30 % at Sheridan Creek compared with the control. This is consistent with reported decreases in needle longevity on fertile sites either through fertilization or natural nutrient pulses (Brix 1981, Shaver 1981, Balster and Marshall 2000, Niiemets and Lukjanova 2003). Secondly, periodic fertilization tended to increase the number of cohorts compared with the annual and control treatment at Kenneth but this was not the case at Sheridan where the controls had more needle age-classes (Figure 3-1a). Thirdly, there was a general decrease in survivorship with needle age in all three treatments; the annual treatment however, tended to have a steeper decline in survivorship in the 2 and 3-year-old needle classes compared with the current and 1-year-old needles at Kenneth. A similar trend in decreased survivorship with annual fertilization was observed at Sheridan (Figure 3-2b). Aerts (1989) observed a similar decline in leaf survivorship following fertilization of *Erica tetralix* L. Although the general decline in needle survivorship with age is a natural phenomenon, it appears to be accelerated by repeated fertilization.

Repeated fertilizer addition generally increased N concentrations in current year's foliage (2000 and 2001) of upper crown position and in foliage of mid crown branches at both locations (Tables 3-1 and 3-3, Figure 3-3 a, d). However, fertilization effects on other nutrient elements were variable, contrary to the expected elevated levels in the foliage. Although the goal of increasing and maintaining current foliar N concentration at 16 $g \cdot kg^{-1}$ was almost successful, foliar nutrient imbalances may have been induced by repeated N additions (Ingestad 1979). According to Ingestad (1979), an optimum foliar N/Cu and N/Fe balance ratio is about 3000-3500 and 150, respectively. The foliar data for fall 2000 and 2001 (Tables 3-1 and 3-2) show that the ratios of N/non added nutrients such as Cu and Fe (N/Cu and N/Fe) were well above those values, indicating that Cu and Fe deficiencies were likely induced at both locations by the repeated fertilization treatments. Similar results for the effects of repeated fertilization on added and non-added nutrients have been reported by Tamm et al. (1999) and Kishchuk et al. (2002). These ratios were very high in the annual treatment, suggesting that annual fertilizer addition may have exacerbated these imbalances. It is plausible that copper deficiency induced in the fertilized treatment was more pronounced in the older foliage of the mid crown because Cu was retranslocated to meet the demand of the younger needle age-class (Everett and Thran 1992, Nieminen and Helmisaari 1996); and may have resulted in the early loss of the older needles in the annual treatment (Kozlowski and Pallardy 1997).

Leaf senescence and death are thought to be related to nutrient withdrawal (Maillette 1982, Lange et al. 1987, Schoettle and Fahey 1994). Since the greatest N concentration and content in all needle age-classes of mid crown branches was in the annual treatment at both sites N withdrawal out of the older foliage does not appear to be the primary factor controlling early loss of older foliage in the fertilized treatments. While there was a decline in nutrient concentration with age, the concentrations in 4 year-old or older needles were still not exceptionally low in the fertilized stands and compare well with the current year foliar N of the control and the periodic (Figure 3-3a, d). At Sheridan, the N concentration and content in the foliage of the periodic and control were similar except there appeared to be a decline in concentration in the 3 and 4-year-old needles. It is worth mentioning that even N content in the 5-year old needles was relatively higher in the control than the periodic yet the control carried more needle age-classes. Despite the elevated N in the foliage of the annually fertilized trees, this treatment had the least foliage retention consistent with other observations indicating short-lived foliage on more productive site (Chabot and Hicks 1982) (Figure 3-1).

Results from this study also suggest that light limitation was not the most important factor limiting survival of the older foliage (Williams et al. 1989, Schoettle and Fahey 1994) for two reasons: a) the stands at both sites had space between the crowns , b) total light levels at one meter (estimated from fisheye photos of canopy) were 23%, 24% and 25% in the annual, periodic and control treatments respectively at Kenneth; and 29%, 35% and 43% in the annual, periodic and control treatments respectively at Sheridan. These light levels suggest that foliage on branches at mid crown positions were probably not shaded below reported light compensation points (28 to 87 $\mu mol \cdot m^{-2} \cdot s^{-1}$) for lodgepole pine (Dykstra 1974; Carter and Smith 1988; Landhäusser and Lieffers 2001). Although some amount of shading within the canopies cannot be totally discounted, differences in light conditions are unlikely to have a large negative effect on carbon balance in older foliage (McMurtrie et al. 1986, Schoettle and Smith 1991, 1998, Ackerly 1999). A potential limitation to use of light levels from the fisheye photos is that it does not give estimates of light levels within the crown of trees thus the extent of light limitation within the crowns (particularly mid crown branches) could not be determined and may affect the interpretation of results in relation to the light hypothesis.

The expected outcome of stand level fertilization is to increase stand leaf area and photosynthetic efficiency. Fertilization significantly increased leaf area index at

Sheridan but only a marginal increase was observed at Kenneth and may be related to the relative increase in foliage mass with treatment (Brix 1983). Also, fertilization significantly increased foliated shoot length and annual shoot growth increment at Sheridan but there was no treatment effect at Kenneth. This observation suggests that carbon (C) allocation to branch growth was uniform or consistent at Kenneth but not Sheridan.

Stem growth efficiency appeared to decline with fertilization at both locations (Table 3-3). This relative decline in growth efficiency may be attributed to the more rapid turn over of needles (Figure 3-2) and increased crown growth of fertilized trees (O'Hara 1988). Thus, the amount of C that could be allocated to stem or height growth may be channeled to produce new needles and to support branch growth. Estimates of fine roots in this study compare well with the values reported by Comeau and Kimmins (1988) for lodgepole pine growing on mesic sites in the Rocky Mountains of southeastern British Columbia.

In summary, repeated fertilization of lodgepole pine stands reduced needle longevity. Annual N addition may have induced or exacerbated Cu deficiency in these stands, which may be related to early foliage loss. The accelerated foliage loss could reduce nutrient storage in foliage before crown closure thus limiting the size of nutrient capital for internal cycling after crown closure (Miller 1981, 1995). The decline in growth efficiency with fertilization was likely due to accelerated turnover of needles, and increased allocation of growth to needles and branches, and self-shading due to increases in leaf-area index.

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Table 3-1. Fall 2000 foliar nutrient levels of current year's foliage (Upper crown).

	Treatment			
Site/variables	Control	Periodic	Annual	*P* value
Kenneth Creek				
N (g/kg)	12.93 (0.38)b	15.30 (0.51)a	15.60 (0.10)a	0.004
P (g/kg)	1.21 (0.04)a	1.27 (0.01)a	1.29 (0.03)a	0.197
K (g/kg)	4.53 (0.25)a	4.49 (0.11)a	4.69 (0.14)a	0.702
Ca (g/kg)	1.59 (0.09)a	1.48 (0.08)a	1.20 (0.07)b	0.031
Mg (g/kg)	0.92 (0.02)a	0.88 (0.05)a	0.83 (0.01)a	0.154
S (g/kg)	0.78 (0.03)b	0.74 (0.03)b	1.01 (0.02)a	< 0.001
Cu (mg/kg)	3.1 (0.3)a	2.6 (0.2)a	1.1 (0.1)b	0.002
B (mg/kg)	12.7 (1.8)b	25.3 (2.2)a	21.9 (1.2)a	0.006
Fe (mg/kg)	26.4 (0.9)a	29.4 (6.0)a	22.3 (0.4)a	0.405
Zn (mg/kg)	44.8 (1.6)a	45.3 (2.5)a	36.7 (1.7)b	0.040
N/K	2.88 (0.24)a	3.41 (0.18)a	3.33 (0.10)a	0.156
N/P	10.71 (0.48)a	12.01 (0.29)a	12.11 (0.32)a	0.065
N/Ca	8.15 (0.39)c	10.39 (0.78)b	13.11 (0.65)a	0.004
N/Mg	14.03 (0.63)b	17.52 (0.86)a	18.89 (0.45)a	0.005
N/S	16.59 (0.32)b	20.70 (0.49)a	15.46 (0.31)b	< 0.001
N/Cu	4318 (476)b	5913 (296)b	14489 (1477)a	< 0.001
N/Fe	492 (29)a	556 (91)a	701 (18)a	0.093
N/B	1062 (141)a	611 (40)b	717 (33)b	0.024
Sheridan Creek				
N (g/kg)	12.43 (0.48)b	13.93 (0.58)b	16.40 (0.60)a	0.007
P (g/kg)	1.22 (0.02)b	1.43 (0.05)a	1.51 (0.02)a	0.002
K (g/kg)	4.32 (0.22)a	4.71 (0.19)a	4.59 (0.09)a	0.323
Ca (g/kg)	1.80 (0.12)a	1.73 (0.14)a	1.37 (0.03)a	0.068
Mg (g/kg)	1.02 (0.05)a	0.93 (0.03)a	0.94 (0.06)a	0.371
S (g/kg)	0.78 (0.04)c	1.00 (0.07)b	1.26 (0.05)a	0.002
Cu (mg/kg)	2.8 (0.1)a	3.1 (0.1)a	2.9 (0.1)a	0.177
B (mg/kg)	16.5 (0.9)b	25.0 (1.2)a	24.6 (0.3)a	< 0.001
Fe (mg/kg)	38.0 (4.7)a	33.1 (1.5)a	34.8 (1.6)a	0.542
Zn	50.3 (1.1)a	52.8 (2.7)a	48.1 (1.7)a	0.296
N/K	2.90 (0.22)a	2.96 (0.01)a	3.58 (0.20)a	0.054
N/P	10.22 (0.33)a	9.75 (0.30)a	10.85 (0.53)a	0.226
N/Ca	6.94 (0.22)c	8.12 (0.43)b	11.97 (0.23)a	< 0.001
N/Mg	12.26 (0.87)b	15.03 (0.16)ab	17.59 (1.73)a	0.042
N/S	15.97 (0.50)a	13.99 (0.39)b	12.99 (0.34)b	0.006
N/Cu	4528 (375)a	4551 (232)a	5659 (232)a	0.052
N/Fe	334 (30)b	421 (18)ab	474 (39)a	0.045
N/B	762 (72)a	558 (19)b	667 (32)ab	0.058

NOTE: For each installation and nutrient variable, treatment values with different letters are statistically significant at $\alpha = 0.05$. Numbers in parentheses represent standard error. (n=3).

Table 3-2. Fall 2001 foliar nutrient levels of current year's foliage (Upper crown).

	Treatment			
Site/variables	Control	Periodic	Annual	*P* value
Kenneth Creek				
N (g/kg)	12.13 (0.44)b	14.17 (0.27)b	16.20 (0.35)a	< 0.001
P (g/kg)	1.38 (0.04)a	1.53 (0.01)a	1.39 (0.06)a	0.094
K (g/kg)	4.79 (0.15)a	4.92 (0.18)a	4.89 (0.34)a	0.923
Ca (g/kg)	1.65 (0.07)a	1.37 (0.10)a	0.85 (0.07)b	0.001
Mg (g/kg)	1.02 (0.03)a	0.92 (0.03)b	0.78 (0.00)c	< 0.001
S (g/kg)	0.70 (0.05)a	0.89 (0.02)a	0.86 (0.07)a	0.073
Cu (mg/kg)	2.8 (0.1)a	2.0 (0.2)b	0.7 (0.1)c	< 0.001
B (mg/kg)	15.9 (2.4)b	25.0 (1.4)a	22.3 (1.1)a	0.025
Fe (mg/kg)	27.1 (0.7)a	27.1 (0.9)a	22.5 (0.7)b	0.008
Zn	48.6 (1.2)a	50.2 (1.7)a	37.4 (1.9)b	0.003
N/K	2.54 (0.15)b	2.89 (0.16)ab	3.33 (0.16)a	0.033
N/P	8.78 (0.33)b	9.26 (0.21)b	11.66 (0.38)a	0.001
N/Ca	7.36 (0.23)b	10.45 (0.95)b	19.36 (1.80)a	< 0.001
N/Mg	11.95 (0.56)b	15.43 (0.56)b	20.86 (0.37)a	< 0.001
N/S	17.62 (1.58)a	15.94 (0.62)a	19.13 (1.35)a	0.274
N/Cu	4419 (342)b	7195 (1267)b	24578 (4359)a	0.003
N/Fe	449 (26)b	525 (26)b	721 (13)a	< 0.001
N/B	800 (114)a	571 (31)a	731 (36)a	0.147
Sheridan Creek				
N (g/kg)	11.73 (0.47)c	13.17 (0.37)b	14.73 (0.29)a	0.004
P (g/kg)	1.19 (0.04)b	1.36 (0.03)a	1.38 (0.01)a	0.005
K (g/kg)	4.40 (0.03)b	4.68 (0.05)a	4.26 (0.05)b	0.001
Ca (g/kg)	1.70 (0.05)b	1.84 (0.11)b	1.37 (0.05)a	0.012
Mg (g/kg)	0.98 (0.01)a	1.04 (0.01)a	0.96 (0.04)a	0.161
S (g/kg)	0.72 (0.05)b	0.87 (0.02)a	0.96 (0.03)a	0.007
Cu (mg/kg)	2.6 (0.0)a	3.1 (0.1)a	2.7 (0.2)a	0.065
B (mg/kg)	16.8 (2.8)a	22.1 (1.1)a	18.7 (0.6)a	0.191
Fe (mg/kg)	29.2 (0.3)a	30.5 (2.4)a	26.8 (1.0)a	0.279
Zn	49.5 (2.2)b	57.8 (1.7)a	47.7 (0.4)b	0.010
N/K	2.67 (0.10)b	2.82 (0.09)b	3.46 (0.04)a	< 0.001
N/P	9.86 (0.21)a	9.69 (0.36)a	10.67 (0.17)a	0.073
N/Ca	6.90 (0.33)b	7.21 (0.62)b	10.75 (0.44)a	0.002
N/Mg	11.95 (0.64)b	12.63 (0.52)b	15.36 (0.86)a	0.028
N/S	16.44 (0.51)a	15.08 (0.30)a	15.36 (0.28)a	0.092
N/Cu	4513 (181)a	4296 (104)a	5443 (414)a	0.049
N/Fe	402 (19)b	437 (35)b	551 (13)a	0.011
N/B	728 (95)a	599 (37)a	791 (25)a	0.157

NOTE: For each installation and nutrient variable, treatment values with different letters are statistically significant at $\alpha = 0.05$. Numbers in parentheses represent standard error. (n=3).

Table 3-3. Periodic annual increment of stem volume and biomass (PAI), leaf area index (LAI), fine root biomass, growth efficiency (PAI/LAI) and LAI/pine root ratios of lodgepole pine stands.

	Treatment			
Site/ variables	Control	Periodic	Annual	*P*-values
Kenneth Creek				
PAI stem volume (m^3 ha^{-1} y^{-1} ; 1999-2002)	10.95 (0.55)ab	11.86 (0.25)a	9.61 (0.47)b	0.031
PAI stem biomass (Mg ha^{-1} y^{-1}; from 1999-2002)	3.88 (0.15)a	4.16 (0.12)a	3.28 (0.15)b	0.010
Pine fine root biomass (< 5 mm; Mg ha^{-1})	5.5 (0.08)a	5.29 (0.74)a	4.10 (0.58)a	0.390
Non pine roots	4.11(0.37)a	5.64 (1.09)a	2.93 (0.27)a	0.081
LAI (m^2 m^{-2})	2.29 (0.13)a	2.44 (0.17)a	2.72 (0.05)a	0.122
LAI/pine fine root ratio	0.43(0.04)a	0.49 (0.12)a	0.69 (0.10)a	0.184
Growth efficiency (Mg ha^{-1} y^{-1}/m^2 m^{-2})	1.70 (0.03)a	1.71 (0.09)a	1.20 (0.04)b	0.002
Sheridan Creek				
PAI stem volume (m^3 ha^{-1} y^{-1}; 1998-2001)	3.84 (0.25)b	5.69 (0.45)a	5.97 (0.24)a	0.007
PAI stem biomass (Mg ha^{-1} y^{-1}; from 1998-2001)	1.44 (0.11)a	1.95 (0.19)a	1.93 (0.13)a	0.081
LAI (m^2 m^{-2})	1.29 (0.06)c	1.76 (0.05)b	2.26 (0.04)a	< 0.001
Growth efficiency (Mg ha^{-1} y^{-1}/m^2 m^{-2})	1.11 (0.04)a	1.13 (0.11)a	0.86 (0.01)a	0.091

NOTE: For each installation and variable, treatment values with different letters are statistically significant at $\alpha = 0.05$. Numbers in parentheses represent standard error. (n=3)

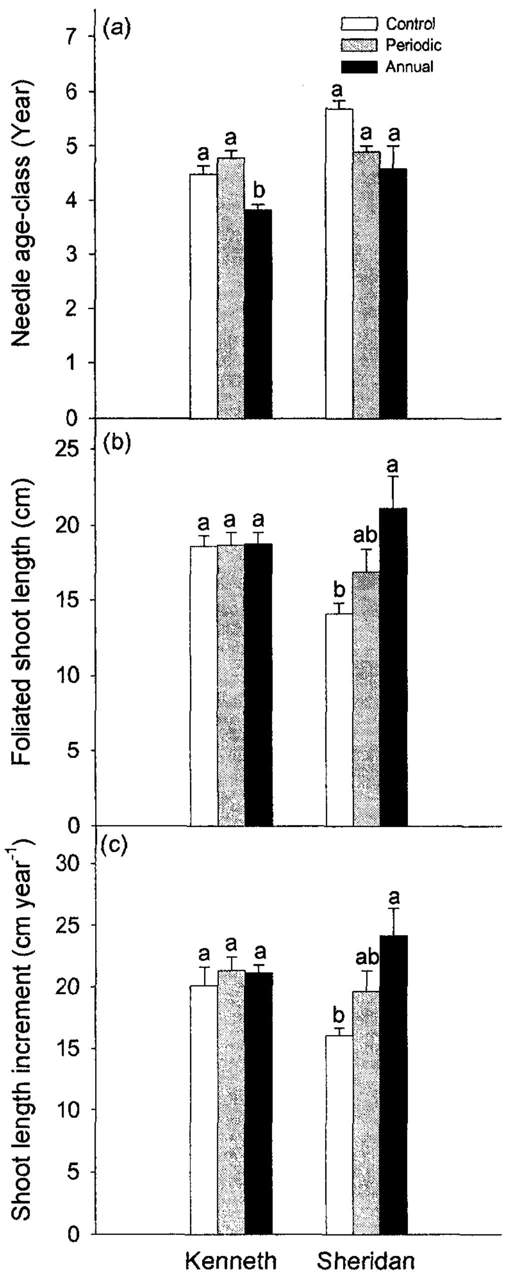

Figure 3-1. Mean needle age-classes, annual shoot length increment, foliated shoot length and needle mass shoot $^{-1}$ of mid crown branch of lodgepole pine at Kenneth and Sheridan Creek. Means with the same letters are not significantly different at $\alpha = 0.05$. Error bars indicate ± (SE). (n=3).

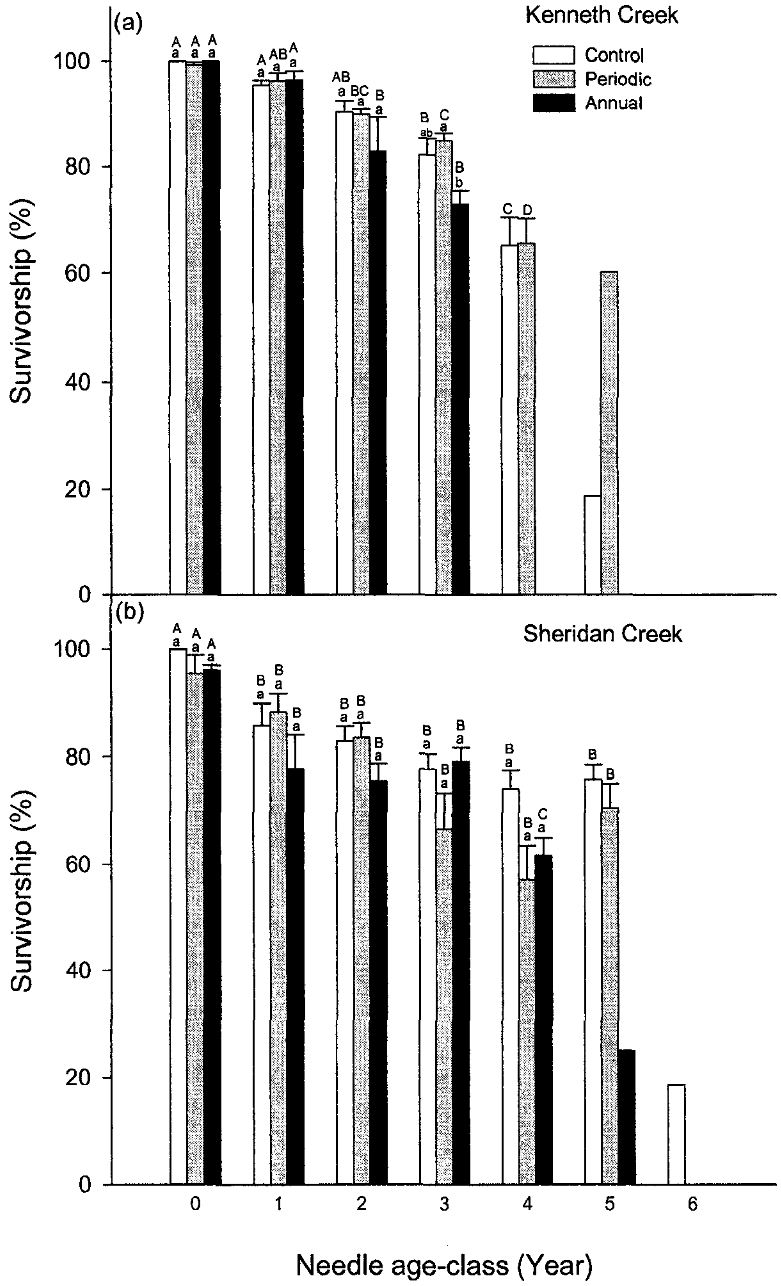

Figure 3-2. Means survivorship of needles of different age-classes from mid crown branches of lodgepole pine at Kenneth and Sheridan Creek during 2002. Age-class 0 represents current year. Bars with the same lowercase letter for different treatments within an age-class were not significant (α = 0.05 according Student-Newman-Keuls test). Similarly, the upper case letters tested if there were differences in response across the age classes within a treatment. Error bars indicate ± (SE). (n=3)

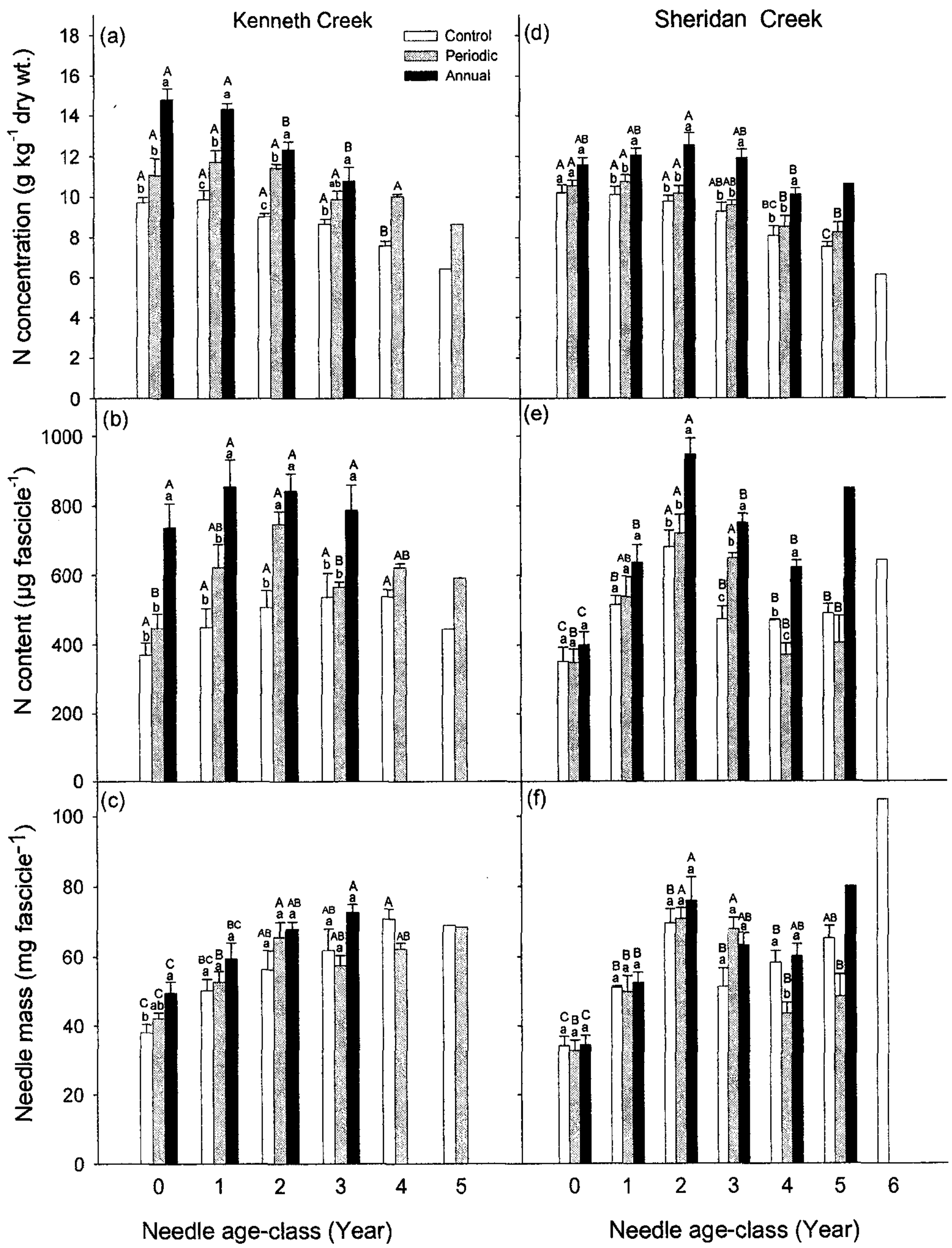

Figure 3-3. Mean nitrogen concentration (g ·kg^{-1}) and content (µg fascicle $^{-1}$) and mass of fascicle (mg fascicle $^{-1}$) for different age-classes of lodgepole pine at Kenneth and Sheridan Creek. Age-class 0 represents current year. Bars with the same lowercase letter for different treatments within an age-class were not significant (α = 0.05 according Student-Newman-Keuls test). Similarly, the upper case letters tested if there were differences in response across the age classes within a treatment. Error bars indicate ± (SE).

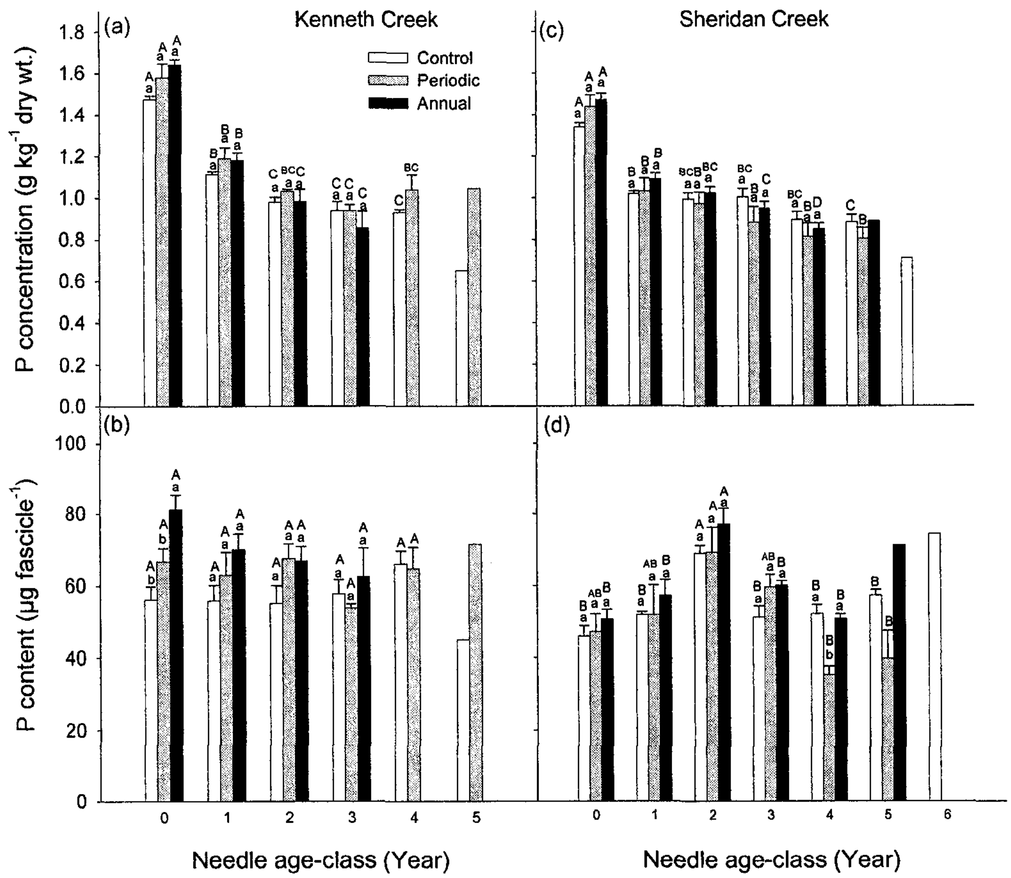

Figure 3-4. Mean Phosphorus concentration (g ·kg^{-1}) and content (µg fascicle $^{-1}$) and needle mass (mg fascicle $^{-1}$) for different age-classes of lodgepole pine at Kenneth and Sheridan Creek during 2002. Age-class 0 represents current year. Bars with the same lowercase letter for different treatments within an age-class were not significant (α = 0.05 according Student-Newman-Keuls test). Similarly, the upper case letters tested if there were differences in response across the age classes within a treatment. Error bars indicate ± (SE).

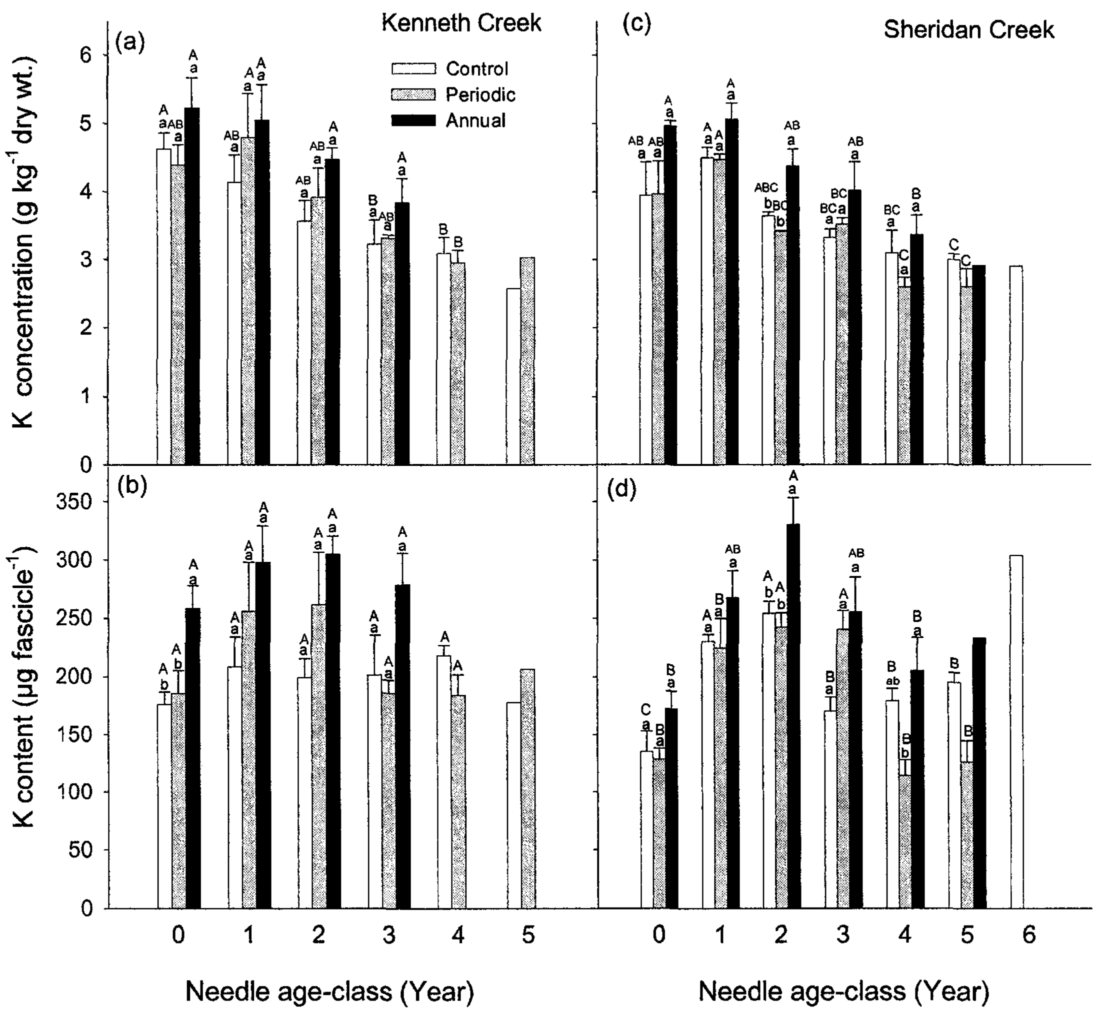

Figure 3-5. Mean Potassium concentration (g ·kg-1) and content (µg fascicle -1) and needle mass (mg fascicle -1) for different age-classes of lodgepole pine at Kenneth and Sheridan Creek during 2002. Age-class 0 represents current year. Bars with the same lowercase letter for different treatments within an age-class were not significant (α = 0.05 according Student-Newman-Keuls test). Similarly, the upper case letters tested if there were differences in response across the age classes within a treatment. Error bars indicate ± (SE).

Chapter 4. Seasonal nitrogen uptake and allocation in young *Pinus contorta* in response to ^{15}N fertilization

Introduction

Growth and productivity of lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) stands in the boreal forest are often hampered by low soil nitrogen (N) availability (Yang 1985, Weetman et al. 1988, Prescott et al. 1989) due to slow mineralization of soil organic matter (Fyles and McGill 1987, Tamm 1991, Cote et al. 2000). Hence, there is interest in fertilizing lodgepole pine stands with N fertilizers in an attempt to improve N supply, which may promote uptake and tree growth. In some cases, only a small portion of the applied N is taken up by tree roots and translocated to above ground plant tissues (Miller et al. 1976, Chang et al. 1996, Preston et al. 1990) which may contribute to substantial variation in growth response of crop trees to N fertilization (Cochran 1979, Yang 1998, Brockley 1996). One source of this variation may be the failure to synchronize the timing of fertilizer application with the time when plant demand for nutrients is high and roots are active allowing exploitation of applied fertilizer.

Fertilizing stands in early spring, as sometimes practiced in northern Alberta, may be out of synchrony with plant demand since uptake during this period may be limited by slow root growth associated with low spring soil temperature (Folk et al. 1995, Iivonen et al. 1999, Wan et al. 1999). Root zone temperature is reported to affect both water and ion transport (Markhart et al. 1979, Kennedy and Gonsalves 1988, Wan et al. 1999) and either of these changes could alter shoot growth (Landhäusser et al. 1996, Landhäusser and Lieffers 1998, Iivonen et al. 1999) by limiting the supply of water and nutrients to the expanding tissue. For example, N uptake via mass flow or diffusion (e.g. NH_4^+) may be limited due to low rates of water uptake at low soil temperature associated with increased root resistance and water viscosity (Lawrence and Oechel 1983, Lopushinsky and Kaufmann 1984, Goldstein et al. 1985). Similarly, low soil temperature may reduce the activity of enzymes on the membrane responsible for positive ion uptake, e.g. H^+-ATPase (Ryyppö et al. 1994) thereby reducing active transport of N.

Forest tree species readily absorb NH_4^+ ions into roots (Haynes 1986), however, its availability after fertilization is often affected by nitrification, immobilization or binding to exchange sites. There is evidence that NH_4^+ produced by hydrolysis from urea fertilizer may become fixed to organic matter (Foster et al. 1985), thus limiting its availability for uptake and use by plants. Hence, there is a need for a better understanding of fertilizer uptake and distribution dynamics within plant tissues. For instance, it is not known whether applied fertilizer uptake will be most effective within two weeks, or whether uptake will be higher thereafter. Understanding these uptake processes may provide insight into how fertilizer application can be synchronized with plant N demand and may be useful for minimizing losses *via* leaching and volatilization with detrimental environmental consequences. Understanding might also allow better returns from expenditures on fertilization.

In fertilization studies that involve the use of ^{15}N, it is critical to discriminate between the various N pools in the plant-soil system: native N, non labeled fertilizer N, and N derived from labeled fertilizer (NDFF). ^{15}N isotopes can be effectively used for such studies (Nômmik 1990). The method is precise, and allows tracing and quantification of fertilizer N as it enters, is transformed, or leaves the system under study (Nômmik 1990). Hence, the tracer approach has been widely used to discriminate between native N and fertilizer N. Thus, current uptake was labeled with ^{15}N to facilitate direct quantification of isotopic N that is derived from applied fertilizer, and its distribution in structural tissues of lodgepole pine seedlings.

The objectives of this study were to compare plant N uptake and partitioning in tissues of lodgepole pine after early spring, summer and fall applications of $(^{15}NH_4)_2SO_4$. The hypothesis tested was that ^{15}N uptake would be lower immediately following early spring fertilization than following summer or fall applications.

Materials and Methods

Soil and Plant Material

Soil (top 20 cm) used for this study was collected from 76-year-old lodgepole pine stands located near Edson, Alberta (53°25' N, 117°05' W, 900 m elevation). Soils in this area are dominantly Orthic Gray Luvisols (Alberta Soil survey Report 1972). At the start of our experiment, soil chemical characteristics were: total N 1.2 g $\cdot kg^{-1}$, total P 574 mg $\cdot kg^{-1}$,

$pH_{(H_2O)}$ 5.4, Ca 5.53 cmol(+)kg^{-1}, Mg 1.0 cmol(+)kg^{-1}, K 0.27 cmol(+)kg^{-1}, and Na 0.08 cmol(+)kg^{-1}. The textural class of the soil was a silt loam with 9% clay, 32% sand and 59% silt.

One-year-old dormant (container grown 225 plug stock seedlings, root plug size 4 cm diameter and 10 cm long) lodgepole pine seedlings were obtained from a commercial nursery. The stock was grown from a seedlot collected in the "upper foothills region" near Hinton, Alberta. On June 22, 2001, seedlings were planted in plastic pots (15 cm diameter self-watering with false bottom and no drainage hole) containing 1.5 kg of soil described above. Prior to planting, each pot was fitted with a plastic tube into the false bottom to enable suctioning of water should drainage water accumulate after watering. To determine the amount of water to add at watering, four pots were watered to saturation and allowed to drain for three days. The difference in weights of saturated pots and drained pots after three days was used as a guide for watering. Seedlings were grown in a greenhouse (day/night temperature of 21/18 °C and 18 hours photoperiod) for two weeks. Plants were fertilized with 1.0 g per liter of fertilizer on June 22, 2001 (NPK 10-52-10) to enhance root growth and on July 20 with (NPK 30-10-10). Plants were moved outdoors at the end of July and left to grow throughout the summer and fall. Seedlings were over wintered outside and covered with straw in mid-December to prevent frost damage.

Experimental Setup

In mid-January 2002, frozen seedlings in the water tight pots were placed into a water bath system which was assembled in a growth chamber. Seedlings were thawed for one week in darkness at a soil temperature of 2 °C and an air temperature of 10 °C. The water bath system consisted of nine watertight plastic boxes (90 x 90 x 20 cm) in which chilled water was circulated to achieve the required soil temperatures (Landhäusser and Lieffers 1994). The water temperatures in the baths were regulated by thermostats. The chilled water was evenly dispersed in the water baths through a network of perforated hoses in the bottom of the baths. An overflow pipe returned surface water back to the chilling unit. By submerging pots in the baths specific soil temperature were maintained. Seasonal soil and air temperatures and photoperiod conditions (early spring, summer and fall) typical for northern Alberta in the growth chamber were simulated (Table 4-1). During the growing period, the pots were moved to different positions in the baths to compensate for possible spatial variation in growth chamber conditions.

The experimental used a 3 by 3 factorial design, testing three different seasons of fertilizer application (early spring, summer and fall; Table 4-1) and three sample collection times (3, 7 and 30 days after fertilization) as fixed main effects. Each treatment combination was replicated six times. I selected 108 uniform seedlings and randomly assigned 36 to each of the three simulated seasons. Eighteen of the 36 seedlings were randomly assigned to the three sampling times after fertilization while the remaining 18 received no fertilizer. All of the seedlings used in the experiment were placed in the growth chamber and water bath at the same time. However, fertilizer was applied during the simulated early springtime, or delayed until the seedlings had entered the summer or fall periods of their annual growth (Table 4-1). Each simulated season lasted 30 days. An additional 3 days was allowed between seasons to enable seedlings to adjust to the next growing conditions by regulating growing conditions in the growth chamber. The entire experiment lasted 129 days (Table 4-1). Other than fertilizer applied in 2001, no additional fertilizer was applied prior to the ^{15}N application in 2002. Seedlings received 150 mg N per pot [simulating operational silvicultural prescription of 200 kg N ha^{-1} under field conditions] based on the area of the pot. The general fertilization rates employed in silvicultural practice vary from 100- 200 kg N ha^{-1} (Miller et al. 1976, Hulm and Killham 1990, Nômmik 1990; Chang et al. 1996, Staples et al. 1999, Chang and Preston 2000). Each pot was treated with $(^{15}NH_4)_2SO_4$ (21-0-0-24S, ISOTEC Inc. USA) enriched to 5.13 atom % ^{15}N. Chelated (EDTA 42% and DTPA 13%) micronutrients were applied at the rate of 0.03 g per liter and phosphorus (P) supplemented by KH_2 P_2O_5 (0-52-34) at the rate of 60 kg ha^{-1} to avert deficiency of other nutrients. All nutrients were applied in solution form. Seedlings were not over watered thus eliminating the problem of loss of water or ^{15}N fertilizer which might have resulted due to suctioning of excess water.

Harvest and Measurements

Seedlings were destructively sampled 3, 7 or 30 days after applying the labeled fertilizer. Six seedlings were randomly sampled for analysis of ^{15}N and total N at each sampling time from both fertilized and unfertilized pots. After harvest, roots were separated from soil, and the seedlings were separated into roots, stems and needles. The soil was sieved and any remaining roots recovered and washed. Plant materials were oven dried for 48 hours at 68° C. Plant samples were ground with a Wiley Mill and ball-milled. Soil samples were air dried and fine ground in a Sieteknik mill. Total N and ^{15}N abundance was analyzed using Automatic Nitrogen Analyzer Model 1500 coupled to a stable isotope ratio analyzer (SIRA 10) mass spectrometer (VG Isogas, Middlewich, Cheshire, England). The mass spectrometer comprised of an automatic Dumas system (Carlo Erba) for total N and a flow-through system for the nitrogen gas generated for isotope ratio analysis using a triple collector system. The ^{15}N data are reported as the percent N derived from labeled fertilizer (%NDFF); and total ^{15}N content (mg) in plant tissues and soil components calculated from Eq. [1]:

$$\%NDFF = \left[\frac{(A - B)}{(C - B)}\right]100 \qquad [1]$$

Where A = atom % ^{15}N in fertilized plant tissues, B = atom% ^{15}N in unfertilized plant tissues, C = atom% ^{15}N in applied fertilizer. Total N content in plant tissues (TN; mg) was estimated as N concentration multiplied by plant tissue dry weight. Total ^{15}N recovered in the plant was calculated as a product of %NDFF and TN. Labeled N content per plant was calculated by summing the ^{15}N in different tissues. Total soil ^{15}N content was calculated using the same procedure based on soil weight.

Statistical Analysis

Analysis of variance (ANOVA) was performed on all experimental variables using general linear models (SAS Institute 2001). Response variables that did not conform to homogeneity of variance and normality requirements were weighted with the reciprocals of their variance (Steel et al. 1997). Means and standard errors were reported on unweighted variables. Tukey's multiple range test was used to evaluate differences between treatment means at $\alpha = 0.05$.

The linear model for the ANOVA is given as:

$$Y_{ijk} = \mu + S_i + T_j + ST_{ij} + \varepsilon_{(ij)k} \qquad [2]$$

where Y_{ijk} is seedling dry weight, %NDFF, ^{15}N content or N concentration of the kth replicate (k = 1…,6), estimated at jth time (j =1, 2, 3), from the ith simulated season (i =1, 2, 3); μ = overall mean; S_i = fixed effect of the ith simulated season; T_j = fixed effect of the jth sampling time; followed by the interaction effects ST_{ij} and ε is error associated with measured seedling, N content or concentration from replicates.

Results

^{15}N Uptake and Distribution in Plant Tissues

Uptake of ^{15}N was greatest following summer fertilizer application, intermediate in fall and lowest in spring ($P < 0.001$; Table 4-2). When compared to ^{15}N uptake in early spring seedlings 30 days after fertilizer application, ^{15}N uptake by the whole plant increased by 828% in fall and 1130% in summer (Table 4-2). Difference in ^{15}N uptake do not differ significantly between summer and fall 30 days after fertilization ($P = 0.276$). Similar to seasonal response, ^{15}N uptake in plant tissues was lowest at 3 days after fertilization but increased with sampling time up to day 30 ($P < 0.01$) (Table 4-2). There was a significant season × sampling time interaction ($P < 0.001$). This relates to the uniform increase in ^{15}N uptake in fall and summer fertilization over the three sampling times, compared to the early spring fertilization, where there was a sharp increase in ^{15}N uptake between days 7 and 30, in contrast to the small increase between days 3 and 7.

Following fertilization in early spring, about 4% of applied ^{15}N was detected in the seedlings at 30 days. This was partitioned in the order of 8%in needle, 20%in stem and 72% in root (Table 4-2). During summer, about 43% of applied ^{15}N was recovered in the plant 30 days after fertilization. Of this amount, 47% was found in the needle, 8% in stem and 47% in root, suggesting that needles and roots were major sinks for nutrients.

For the fall treatment, the amount of ^{15}N absorbed after 30 days was 33% of applied ^{15}N. The trend in ^{15}N partitioning in the fall was similar to summer with 36% in needles, 8% in stems and 56% in roots (Table 4-2), again demonstrating that roots and needles were major sinks for nutrients.

Percent N derived from tracer (%NDFF) in plant tissues was highest following summer fertilizer application, lower in fall and least in spring (P <0.001; Figure 4-1). Similar to seasonal response, %NDFF uptake in plant tissues was lowest at 3 days after fertilization but increased with sampling time up to day 30 ($P < 0.001$). Season × sampling time interaction was significant for needles, stem and roots %NDFF ($P < 0.001$; Figure 4-1). This relates to the more uniform increase in %NDFF uptake following fall and summer fertilization over the three sampling times, compared to the early spring fertilization, where there was a sharp increase in %NDFF uptake between days 7 and 30, compared to the observed trend between days 3 and 7.

Recovery of ^{15}N in Soil Component

The amount of applied fertilizer N that remained in the soil was greatest in early spring followed by fall and least in summer ($P < 0.001$) and decreased with time ($P < 0.01$). There was a significant season × sampling time interaction ($P < 0.001$). The interaction reflects the slow decline in labeled fertilizer between 3 and 7 days, followed by a steeper decline between 7 and 30 days in the spring fertilization, compared with the uniform decline with time for labeled N following fall and summer treatments. Total recovery of ^{15}N labeled fertilizer in the soil over the entire period of the study ranged from 48% in the fall treatment or 72 mg to 95% in the early spring treatment or 143 mg of the applied ^{15}N in the treated pots (Table 4-2).

Total N Concentration in Plant Tissues

The concentration of N in plant tissues selected for the fertilized and un-fertilized treatments were similar prior to treatment. There was a general decline in whole plant N, starting from spring and progressing to summer and fall. However, N concentrations in the fertilized seedlings did not decline as much as the unfertilized seedlings. Note that only in the springtime, was there actually a decline in the average N concentration of the whole plant after the time of fertilization.

Plant Growth Response

Needle, root and whole plant dry weights of the seedlings increased with season ($P < 0.001$) and with sampling time ($P < 0.001$– 0.02; Figure 4-2), while stem dry weight did not change with time ($P = 0.184$). When compared to initial seedling dry weight (7 g plant^{-1}) at the start of the experiment, total plant dry weight increased to mean values of 11 g in spring, 23 g in fall and 25 g in summer (Figure 4-2d) at the 30 day sampling time. Similarly, mean needle dry weight increased to 6 g in spring, 10 g in fall and 12 g in summer (Figure 4-2a) compared to initial needle dry weight (3 g plant^{-1}). There was a significant season x sampling time interaction for all plant components ($P = 0.009$ – 0.035). This relates to the more continuous increase in size of the spring seedlings over the 30 day period, compared to the more stable biomass for the summer and fall seedlings (Figure 4-2). Low soil temperatures resulted in restricted root growth throughout the 30 day experimental period in the early spring. However, compared with the initial status (3 g plant^{-1}), root dry weight increased to 9 g in summer and 10 g in fall, by the 30 day sampling period for each period of fertilization (Figure 4-2c).

Discussion

The results of this study show that the highest uptake of applied fertilizer in lodgepole pine seedlings occurred in summer, followed closely by fall fertilization, while the lowest uptake occurred in early spring. Higher root growth in summer probably increased the number of new fine roots thus root absorption surface, which probably accounted for the improved ^{15}N uptake. Another plausible explanation could be that higher root zone temperature in summer resulted in increased root water flow (Wan et al. 1999) thereby increasing active transport of N.

Despite having seedlings that were well established in pots and contained fine roots developed during the previous growing season, low soil temperatures in spring limited the capacity of these seedlings to take up the applied labeled isotope. It appears that uptake occurred only after new roots had developed (by day 30) in the spring seedlings.

Low soil temperatures may have reduced water absorption and therefore nutrient uptake by increasing the viscosity of water and lowering membrane permeability to water (Kaufmann 1975, 1977, Running and Reid 1980, Bowen 1991, Wan et al. 1999). In conifers, new unsuberized roots have been shown to be more effective in water and nutrient uptake than older roots (Chung and Kramer 1975, Häussling et al. 1988). Hence, slow root growth in early spring may have played a key role in reducing water and N uptake. Moreover, low rates of ^{15}N uptake during early spring may be related to changes in the structure of the membrane lipid bilayer in roots at low soil temperature (Simon 1974), and the reduction of activity of enzymes on the membrane responsible for positive ion uptake, e.g. H^+-ATPase (Ryyppö et al. 1994). Most of the ^{15}N absorbed in early spring was still in the roots 30 days after fertilization (Figure 4-1). This observation agrees with the results of Proe and Millard (1995) who observed increased partitioning of ^{15}N to roots 2 weeks following spring (May) fertilization of 3 year old Sitka spruce. It is likely that the slow transport of N may have limited the movement of ^{15}N into the aboveground plant parts, hence may also have contributed to the decline in N concentration in both fertilized and unfertilized plants with time during early spring (Table 4-3). The decline in N concentration with time indicates a dilution effect, signifying that growth rate was higher than N uptake rate (Imo and Timmer 1992, Salifu and Timmer 2003*b*). Although there was expansion of foliage in early spring (by 30 days) it apparently was not an effective N sink. Presumably, the N stored in the roots would have been transported to the expanding needles as the season progressed but would not have stimulated growth of current foliage.

During the fall, shoot elongation and needle expansion had ceased and seedlings were in the process of or had set buds. Increased N in plant tissues (needles and roots) following fertilization in fall may provide nutrient reserves for use when N uptake is often low during early spring (van den Driessche 1985*b*, Chapin et. al. 1986, Atkin 1996). The 43% recovery in seedlings of the total ^{15}N applied for the summer fertilization is higher than reports from other studies (Knowles and Lefebvre 1972, Salifu and Timmer 2003*a*). For example about 8-12% of applied urea ^{15}N was recovered in black spruce seedlings over one growing season (Knowles and Lefebvre 1972). Similarly, reported recoveries averaged 12-19% of applied $^{15}NH_4{}^{15}NO_3$ between 60 and 120 days after application to black spruce (Salifu and Timmer 2003*a*). The differences could be due to species, length of study and growing medium used. For example, Salifu and Timmer (2003*a*) used fine sand as a growing medium compared with the silt loam used in our study. Furthermore, recoveries based on ^{15}N studies in the field ranged from 5-25% in Sitka spruce (Hulm and Killham 1990, Chang et al. 1996), and lodgepole pine (Preston et al. 1990). It is possible that more ^{15}N would have been recovered in the plants with time, but the trajectories of uptake with time (Figure 4-1) suggest that the trend had not plateaued by the end of 30 days. Also, the tissue N concentration (Table 4-3) did not appear to have reached the suggested ranges of optimal foliar N concentrations of 1.38-2.66% for lodgepole pine seedlings (van den Driessche 1984*a*, 1984*b*).

The total ^{15}N recovery in the soil-plant system in this study ranged from 80-96% of the total amount applied. Recoveries in pots ranged from 88-95% in early spring, 48-83% in the fall and 57-87% in the summer (Table 4-2). The amount of ^{15}N not accounted for ranged between 4 and 20%. This ^{15}N was presumably lost from the system by our inability to separate all soil particles from the rooting system before washing.

In summary, the highest ^{15}N uptake by lodgepole pine seedlings occurred following application of N fertilizer during summer; uptake was lower in fall and was the least in spring. The uptake of fertilizer continued for at least 30 days following application. Early spring fertilization may be less effective in promoting N uptake since low soil temperatures limited the ability of roots to absorb and transport N. Thus, early spring fertilization may leave fertilizer in the soil and available for uptake by non-target understory species or soil microbes that might be able to function at lower temperatures. Nutrients in solution could also be leached into deep strata or off site if there is significant precipitation or snow melt (Preston et al. 1990). Fall fertilization resulted in increased N reserves in both roots and needles which could be retranslocated to meet sink demand for new spring growth to compensate for plants inability to take up soil N (Chapin et. al. 1986, Atkin 1996). Furthermore, the likelihood of reduced potential N losses through volatilization during the fall, as a result of cooler temperatures, suggests that fall could be a good time for fertilization. However, since there are fewer active sinks for growth at this time, N would need to be stored in tree tissues in order to be available for growth in the spring of the following year. While summer fertilization resulted in the highest rates of uptake, substantial losses of N may occur during warm and dry weather through volatilization under field conditions (Nason et al. 1988); consequently summer fertilization should be done with caution. In areas where summers are characterized by moist and humid conditions, N uptake may be optimized.

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Table 4-1. Growing conditions during three simulated seasons for lodgepole pine seedlings used in the ^{15}N uptake experiment in a growth chamber.

	Simulated Seasons			
	Early spring Day (0-30)	Late Spring Day (33-63)	Summer Day (66-96)	Fall Day (99-129)
Photoperiod (hours/day)	15	17	18	12
Relative humidity%	60	60	60	60
Air temperature(Day\night) °C	12\8	15/12	20\17	14\10
Soil temperature°C (Day\night)	4\3	8/6	19\15	11\10
Light ($\mu mol.m^{-2}.s^{-1}$)	350	350	350	350

Table 4-2 Amount of fertilizer ^{15}N recovery in lodgepole pine seedlings and soil compartment.

	Total ^{15}N content (mg)							
	Recovery in pot-plant system							
Sampling time (days)	Needle	stem	root	plant	soil	total	Unaccounted	Total % recovery of applied fertilizer
Early spring								
3	0.03a (0.01)	0.05a (0.01)	0.86a (0.01)	0.94a (0.10)	140.73fg (1.96)	141.67	8.33	94.45
7	0.10a (0.02)	0.12b (0.01)	1.23a (0.16)	1.45a (0.16)	143.06f (1.66)	144.51	5.5	96.33
30	0.43b (0.08)	1.03cd (0.23)	3.79b (0.42)	5.25b (0.63)	131.42eg (2.69)	136.67	13.35	91.10
summer								
3	3.32c (0.57)	1.33d (0.13)	9.79c (0.48)	14.44d (1.01)	124.04e (3.19)	138.48	11.53	92.31
7	13.93d (1.20)	3.02e (0.21)	15.81de (1.80)	32.76e (1.62)	103.74bd (3.60)	136.50	13.49	91.01
30	29.09e (2.91)	5.14f (0.29)	30.08f (1.64)	64.31f (4.54)	72.10a (6.35)	136.41	13.59	90.94
fall								
3	0.72ab (0.22)	0.47cd (0.04)	8.18c (0.87)	9.37c (0.68)	128.16cdef (7.51)	137.53	12.47	91.69
7	6.56c (1.17)	1.61d (0.16)	11.50cd (1.70)	19.67d (2.81)	100.18bcf (5.78)	119.85	30.15	79.90
30	17.45d (1.66)	3.80e (0.22)	27.27ef (3.14)	48.52f (4.50)	85.69ab (8.06)	134.21	15.78	89.48

NOTE: Within a column, treatment means with different letter are significantly different at $\alpha= 0.05$. Numbers in parentheses are standard error. (n=6).

Table 4-3. Total N concentrations in fertilized and unfertilized lodgepole pine seedlings after early spring, summer and fall growing seasons; and sampled 3, 7 and 30 days.

Sampling Time (days)	Treatment[1]	N concentration (mg g^{-1} dry weight) Whole plant	Needle	Stem	root
Early spring					
3	unfertilized	16.13 (0.62)	16.85 (0.76)	10.47 (0.57)	18.25 (0.46)
7		16.61 (0.39)	17.25 (0.42)	10.08 (0.34)	19.45 (0.54)
30		14.30 (0.44)	15.20 (0.79)	9.97 (0.22)	15.87 (0.65)
3	fertilized	16.50 (0.75)	17.28 (0.58)	10.73 (0.50)	18.35 (1.34)
7		15.11 (0.04)	16.82 (0.46)	9.32 (0.30)	16.38 (0.66)
30		14.18 (0.88)	14.02 (0.94)	9.27 (0.65)	17.48 (1.25)
Summer					
3	unfertilized	9.00 (0.32)	8.98 (0.37)	4.65 (0.21)	11.20 (0.45)
7		8.50 (0.43)	8.52 (0.60)	4.52 (0.24)	10.25 (0.22)
30		7.90 (0.20)	7.43 (0.28)	4.13 (0.14)	9.78 (0.27)
3	fertilized	8.30 (0.20)	8.58 (0.50)	4.24 (0.11)	10.10 (0.44)
7		9.80 (0.43)	10.65 (0.54)	5.43 (0.31)	10.65 (0.61)
30		10.50 (0.45)	11.33 (0.76)	5.68 (0.25)	11.20 (0.22)
Fall					
3	unfertilized	6.60 (0.11)	6.80 (0.21)	3.75 (0.12)	7.76 (0.28)
7		7.50 (0.46)	8.37 (0.38)	4.67 (0.16)	7.60 (0.22)
30		7.30 (0.45)	7.57 (0.26)	5.02 (0.12)	7.52 (0.35)
3	fertilized	7.60 (0.44)	7.63 (0.37)	4.38 (0.16)	8.78 (0.38)
7		7.80 (0.84)	8.57 (0.52)	4.63 (0.26)	8.03 (0.35)
30		9.90 (0.80)	11.02 (0.44)	5.57 (0.25)	10.32 (0.54)

NOTE: Numbers in parentheses are standard error. (Means =6 plants/sampling date). [1]Labeled N supplied at 0 and 150 mg $seedling^{-1}$

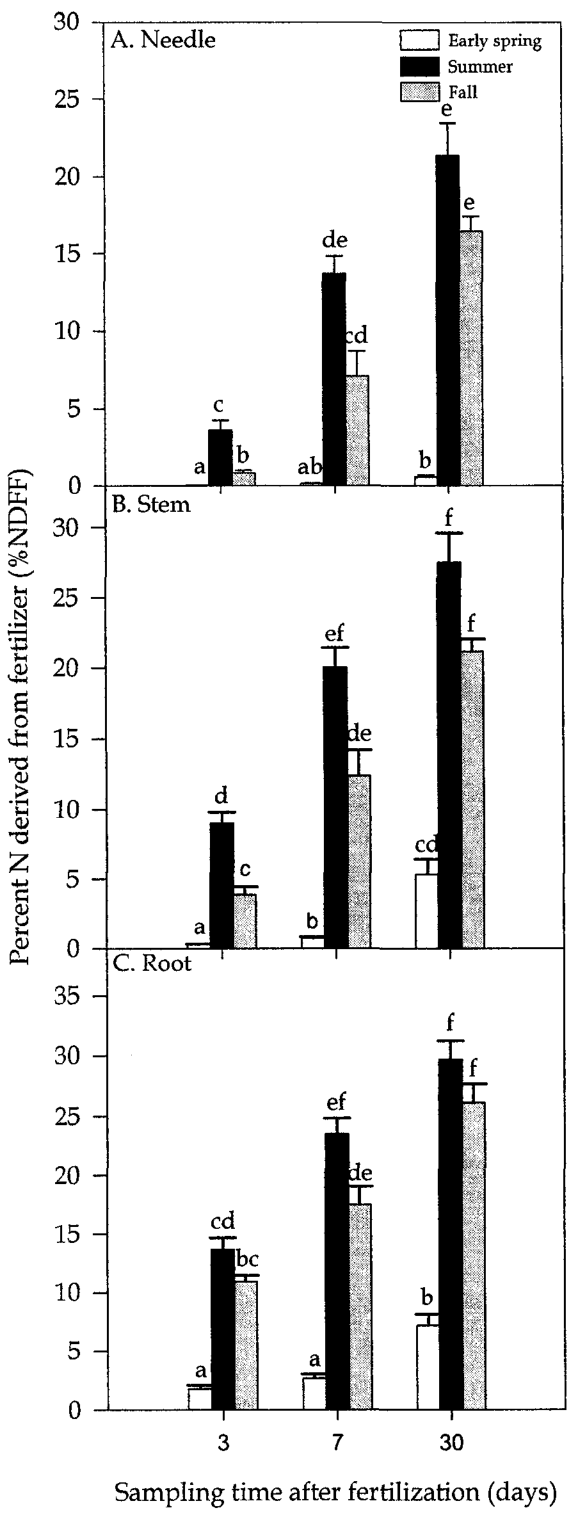

Figure 4-1. The %NDFF (percent N derived from labeled fertilizer) of tissue from needle (A) stem (B) and roots (C) of lodgepole pine seedling, and sampled at 3, 7 and 30 days after fertilizer application in early spring, summer or fall. Means with different letter are significant at $\alpha = 0.05$ (n=6).

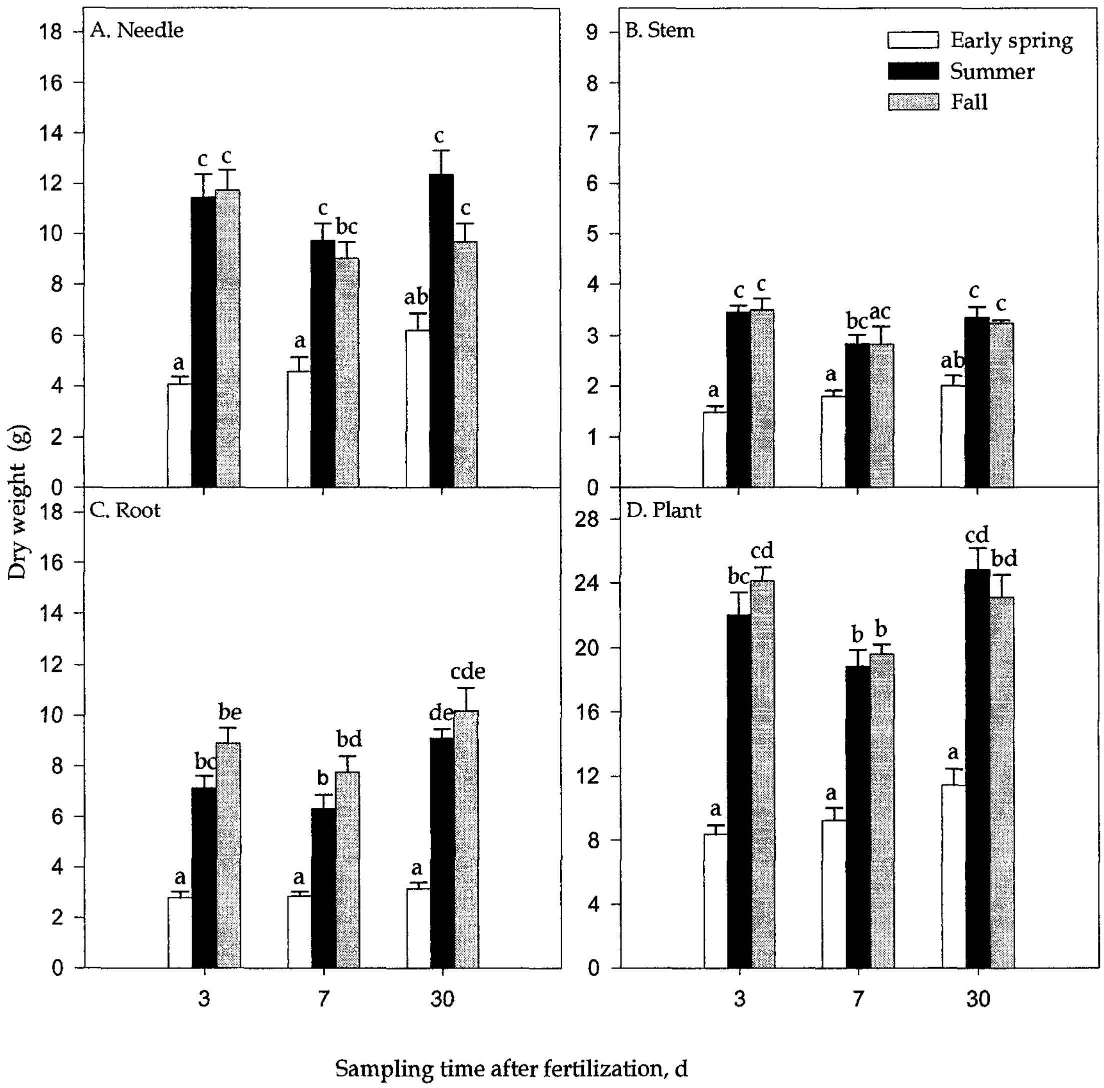

Figure 4-2. Mean dry weights of needle (A), stem (B), root (C) and whole plant (D) of lodgepole pine seedling at 3, 7 and 30 days after fertilizer application in early spring, summer or fall. Means with different letter are significant at $\alpha = 0.05$ (n=6).

Chapter 5. General Discussion

The focus of this dissertation was three-fold: 1) to assess the effects of repeated fertilization on growth response and sapwood hydraulic characteristics of lodgepole pine stands (Chapter 2); 2) to examine the effects of repeated fertilization on needle longevity, leaf area index, stem growth efficiency and periodic annual increment of stem wood (Chapter 3); and 3) to evaluate the effect of season of fertilizer application on plant nitrogen (N) uptake and partitioning in tissues of pine seedlings under controlled conditions (Chapter 4).

The annual fertilization treatment was patterned after 'optimum nutrition' experiments conducted in Eastern Canada and Sweden (Weetman et al. 1995, Tamm et al. 1999) where edaphic and climatic conditions are different from that of central interior British Columbia (B.C). The fertilization experiment was established by the B.C. Ministry of Forests, under the direction of Mr. Robert Brockley. The poor growth response observed in this study (especially at the Kenneth Creek site) suggests that fertilization rates and frequencies, and micronutrient supplements should be calibrated for the central interior B.C. based on soil and climatic conditions in that Biogeoclimatic Zone.

In chapter 2, stand level DBH, BA and height increments at two locations (Kenneth Creek and Sheridan Creek) 8 years following repeated fertilization were assessed. Treatments had no significant effect on DBH and BA increments at Kenneth but were significant at Sheridan. Fertilization had a negative effect on height growth at Kenneth while height was similar among treatments at Sheridan. At both study locations, there was a consistent trend of greater allocation of growth to lower branches in the fertilized treatments while leaf area on those branches was lower. The mechanisms that might explain the observed poor growth performance and reduced height at Kenneth Creek were not clear. Consequently, I measured sapwood hydraulic conductivities of boles and branches of trees in all three treatments to examine if these could explain some of the variations in growth and nutritional responses. This study revealed that lower branches of fertilized trees had higher sapwood hydraulic conductivity than the controls. However, despite the larger capacity of lower branches of fertilized trees to supply water there was actually less foliage on these branches.

To further examine the implications of the larger water supply capacity of lower branches of fertilized trees relative to the controls, stomatal conductance (g_s) of upper branches of trees in the controls and the annual treatments was measured. Results indicate that the control trees had greater g_s than the annually fertilized trees. The greater water supply capacity of lower branches compared with the upper branches of fertilized trees suggests that more water will be delivered to lower branches than upper branches. In times of soil moisture deficit the upper branch foliage of fertilized trees could experience larger water deficits compared with the control trees as indicated by the low g_s of upper branches in the annual treatment. Under such circumstances fertilization may result in increased water stress at the top of the tree and may reduce the availability of water to support the annual growth of the leader and upper branches (Ryan and Yoder 1997). I propose that the changes in hydraulic architecture of fertilized trees observed in this study may be linked to the reduction in height growth; and may account for negative effect of fertilization on height growth in other pine studies (e.g., Weetman et al. 1988, Brockley 1991, Tamm et al. 1999, Kishchuk et al. 2002). Protz et al. (2000) suggested that lower branches of unfertilized juvenile lodgepole self-pruned because they had lower specific hydraulic conductivity than upper branches. In this study, fertilization appeared to increase sapwood hydraulic conductivity of lower branches and will likely prolong branch life because of greater water supply capacity and may delay crown recession until full crown closure. This will likely encourage carbon allocation to branch wood growth at the expense of height growth or stem growth. Clearly, this is exactly the opposite response to that desired by forest managers.

Although the intended target for optimum foliar N concentration of 16 g/kg was almost successfully achieved, copper (Cu) and iron (Fe) deficiencies were either induced or exacerbated in these stands. The variable effect of repeated fertilization on tree growth suggest that: (a) fertilization responses may be site specific and response may be related to stand, soil and climatic factors, and, (b) nutrient imbalance induced or exacerbated by repeated fertilization may result in poor growth responses (Ingestad 1979). The overall implication of annual fertilization is that it will prolong life of lower branches and may increase knots and knots sizes which may reduce wood quality. To avoid serious reductions in wood quality, stand density management that would minimize lateral branch growth before crown closure and fertilization practice (e.g. balanced periodic additions of required elements) that could improve soil nutrient availability to enhance growth and productivity is of utmost interest.

Contributions

- Sapwood hydraulic problems developed in the fertilized stands thus changing the hydraulic architecture of trees. As a result lower branches of fertilized trees conducted more water than the upper branches of the control trees. The hydraulic problems affected the ability of fertilized trees to supply water to support annual leader growth.
- Increases in longevity and size of lower branches will delay vertical crown recession thus necessitating early pruning in order to encourage C allocation to height or diameter growth.
- Large and distorted branches developed when trees were annually fertilized and was related to nutrient imbalance.

Directions for future studies

- Is it possible that hydraulic architecture of trees will change in all cases when stands are repeatedly fertilized at varying stand densities?
- This study assumed that the whole sapwood area of both bole and branches conducted water but this may not necessarily be the case (Reid et al. 2003). Measurements are needed for these stands to quantify the proportion of the sapwood that actually conducts water.
- There is evidence that tracheid anatomy (lumen diameter and length) changes with site quality (Pothier et al. 1989*b*, Coyea and Margolis 1992). The extent to which repeated fertilization would affect tracheid anatomy is not known. Future studies should examine tracheid anatomy to document treatment effects.
- Absolute foliar N levels were elevated with repeated fertilization but did not necessarily translate to expected growth response. This suggests that using absolute levels of nutrients in the foliage to predict fertilization response may not always provide reliable. Thus further biochemical studies are needed to

characterize and quantify N pools in fertilized plant tissues. For instance, there is evidence that arginine is the most readily available form of N stored in plants; and assumed the most responsive to N fertilization (Kim et al. 1997). Such studies could be useful in improving our ability to predict plant response to fertilization.

- Further studies might also be done to determine if there is a genetic basis for the relatively low growth response and disrupted hydraulic architecture at Kenneth under t annual fertilization.

Chapter 3 presents a study that examined the effects of repeated fertilization on needle longevity, leaf area index (LAI), periodic annual increment (PAI) of stem biomass, annual shoot growth and growth efficiency. In addition, foliage nitrogen (N), phosphorus (P) and potassium (K) concentrations were quantified for all different age-classes in each treatment. The expected increase in LAI with repeated fertilization was achieved at Sheridan, while there was a marginal increase in LAI at Kenneth. I also found that annual fertilization generally reduced needle life span. The higher foliar N concentration in the annual treatment relative to the control suggests that higher photosynthetic efficiency was achieved in these stands. However, the higher needle production and more rapid turnover in the annual fertilization treatment in general may have reduced the potential LAI that would have been achieved in these treatments. In fact, the PAI of stemwood biomass of trees at both locations did not vary with treatment. In contrast, stem growth efficiency tended to be lower in the fertilized treatments. The lack of growth response to annual fertilization, particularly at Kenneth may be attributed to allocation of carbon to needle and branch production and the decreased longevity of needles on the branches.

Although previous studies suggest that short-lived needles are characteristic of high productivity sites (e.g., Reich et al. 1995, Balster and Marshall 2000, Pensa and Sellin 2002, Niiemets and Lukjanova 2003), annual fertilization of the stands examined in this study led to reduced needle longevity with foliar analysis suggesting that this may be due to Cu deficiencies. Previous studies on needle longevity have used the light hypothesis, nutrient limitation hypothesis, nutrient withdrawal (retranslocation), and cost-benefit analysis to explain variation in needle longevity. Generally, high nitrogen status of the fertilized treatments suggest that the nutrient limitation theories can not be invoked to explain the decreased needle longevity and needle survivorship observed in this study. Hence, nutrient imbalance or deficiency (Cu) identified in this study may have contributed to the accelerated foliage loss observed following fertilization.

Contributions

- Annual fertilization likely resulted in early foliage loss and may be related to nutrient imbalance or deficiencies (e.g., Cu). This phenomenon could reduce nutrient storage in foliage before crown closure thus limiting the size of nutrient capital for internal cycling after crown closure (Miller 1981, 1995).
- Lack of growth response of the annual treatment (especially at Kenneth) was related to the higher needle turn over (decreased needle longevity) and increased allocation of C to branch growth at the expense of height or stem growth.

Directions for future studies

- Further study to examine copper availability, distribution and internal cycling, as well as its interaction with nitrogen fertilization is required.
- Future studies should examine foliage retention at different heights. This would provide useful information about the portion of the canopy that contributes to leaf area development when trees are fertilized.
- Further study to examine light levels and photosynthesis of needle age-classes at different heights is required.

A study of seasonal N uptake by lodgepole pine seedlings was conducted in a growth chamber (Chapter 4) to investigate if the variable growth response of lodgepole pine to fertilization noted by others (e.g., Cochran 1979, Yang 1998, Weetman et al. 1988, Brockley 2000, 2001, 2003*a*, 2003*b*) could be explained by the timing of application. For this study, seasonal growing conditions (soil and air temperatures and photoperiod) representing early spring, summer and fall were simulated and seedlings fertilized with $(^{15}NH4)_2SO_4$ to quantify effects of season of application on uptake and distribution in plant tissues. The highest ^{15}N uptake occurred in summer followed by fall and the least was in the early spring period. The greater part of the ^{15}N that was taken up in early spring was in the roots while summer and fall uptake were partitioned into roots, stem and needles. Preston et al. (1990) attributed low recovery of labeled ammonium nitrate applied on snow at two forest sites in British Columbia to leaching, denitrification, and undetermined factors including rapid fixation and microbial immobilization of ammonium N and other growth limiting nutrients (e.g., boron and sulfur. Summer fertilization can result in substantial loss of N under warm conditions when urea is used as the source of N (Nason et al. 1988). Since most forest fertilization uses urea, summer application may not produce desired growth responses even though my results show that uptake was best during summer. Fall fertilization built up nutrient reserves in the foliage and could be retranslocated to meet sink demand in early spring when low soil temperature limits new root growth and nutrient uptake (Chapin et al. 1986, Häussling et al. 1988, Atkin 1996, Wan et al. 1999).

Contributions

- I have shown that early spring conditions and spring phenology of pine roots limits N uptake, therefore fertilizing stands during early spring is not recommended. Although this was conducted in a growth chamber, results from other studies indicate similar responses under field conditions (Munson and Timmer 1989; Malik and Timmer 1996).
- Also, higher ^{15}N uptake during summer and fall growing conditions shows that N supply and demand was synchronized thus N uptake can be optimized when stands are fertilized during this period. This knowledge is valuable to support decisions on how to match fertilizer addition with plant demand for optimum nutrient acquisition and utilization that will lead to enhanced growth.

Directions for future studies

- Further field studies should be established to quantify ^{15}N uptake and to determine whether uptake of N following early spring fertilization in the field is different from what was observed in the growth chamber. In addition, field studies should examine longer-term responses of trees to fertilizer application in different seasons. Such studies will help match fertilization with plant demand to improve nutrient uptake and utilization that stimulates growth.

- Future studies should also endeavor to quantify late spring uptake responses.
- Further studies are required to document the fate of labeled isotopes in natural pine ecosystems. For instance, if applied on snow during early spring, will the fertilizer run off when snow melts?

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APPENDICES

Appendix 1. Growth characteristics of lodgepole pine stands at establishment (Kenneth Creek, 1993).

Treatment	Plot	Variable	Mean	Standard deviation	Minimum	Maximum	N
	6	DBH	9.78	1.52	5.10	12.80	64
Annual	14		9.25	1.16	6.20	12.00	64
	17		8.63	0.88	6.40	10.70	64
	3		9.23	1.17	6.90	12.10	64
Control	8		8.39	1.03	6.70	10.80	64
	18		8.51	1.43	5.20	11.60	64
	4		9.13	1.32	6.00	12.80	64
Periodic	10		8.42	0.99	6.10	10.90	64
	12		8.67	1.07	7.00	11.10	64
	6	Height	5.91	0.71	4.05	7.22	64
Annual	14		5.64	0.58	3.72	6.95	64
	17		5.55	0.48	4.53	6.47	64
	3		5.69	0.55	4.62	6.89	64
Control	8		5.67	0.58	4.32	7.07	64
	18		5.16	0.70	3.87	6.36	64
	4		5.67	0.57	4.55	7.28	64
Periodic	10		5.58	0.47	4.77	6.50	64
	12		5.48	0.58	4.19	7.31	64
	6	HLC	0.15	0.16	0	1.00	64
Annual	14		0.28	0.16	0	0.90	64
	17		0.41	0.18	0.10	0.85	64
	3		0.37	0.13	0.15	0.80	64
Control	8		0.29	0.16	0	0.80	64
	18		0.34	0.12	0.10	0.70	64
	4		0.25	0.15	0	0.65	64
Periodic	10		0.29	0.13	0	0.85	64
	12		0.26	0.08	0	0.50	64

Note: HLC= Height to live crown

Appendix 2. Growth characteristics of lodgepole pine stands following initial fertilization in 1994 (Kenneth Creek).

Treatment	Plot	Variable	Mean	Standard deviation	Minimum	Maximum	N
			1999				
	6	DBH (cm)	14.97	2.19	10.30	20.00	61
Annual	14		14.69	2.01	10.50	18.50	64
	17		14.17	1.55	10.30	18.20	63
	3		14.28	1.55	10.70	17.90	64
Control	8		13.05	1.27	9.50	16.10	62
	18		13.94	1.98	9.90	18.40	64
	4		14.30	1.91	9.80	20.40	64
Periodic	10		14.16	1.32	10.70	17.20	64
	12		14.21	1.49	11.30	17.90	63
	6	Height (m)	8.70	0.96	6.20	10.40	61
Annual	14		8.49	0.80	6.10	10.40	64
	17		8.45	0.72	6.80	9.80	63
	3		9.11	0.78	7.10	10.70	64
Control	8		9.17	0.67	7.50	10.90	62
	18		8.65	0.83	6.50	10.50	64
	4		8.85	0.77	7.40	10.50	64
Periodic	10		9.05	0.68	7.30	10.70	64
	12		8.80	0.85	6.80	11.10	63
			2002				
	6	DBH (cm)	16.45	2.67	10.40	22.20	61
Annual	14		15.93	2.45	10.50	21.70	64
	17		15.60	2.07	10.80	20.90	63
	3		15.72	1.75	12.10	20.20	64
Control	8		14.48	1.45	9.90	17.80	62
	18		15.41	2.28	10.50	20.90	64
	4		15.95	2.29	10.10	23.10	64
Periodic	10		15.87	1.44	12.60	19.50	64
	12		15.87	1.76	12.40	20.40	63
	6	Height (m)	10.14	1.23	6.80	12.60	61
Annual	14		9.78	0.92	7.30	11.70	64
	17		9.83	0.99	6.50	11.60	63
	3		10.96	0.85	8.70	12.80	64
Control	8		11.14	0.77	9.40	13.30	62
	18		10.70	0.91	8.20	12.70	64
Periodic	4		10.61	0.82	8.80	12.30	64
	10		10.91	0.78	8.90	12.90	64
	12		10.55	0.90	8.10	13.20	63

Appendix 3. Growth characteristics of lodgepole pine stands at establishment (Sheridan Creek, 1992).

Treatment	Plot	Variable	Mean	Standard deviation	Minimum	Maximum	N
	5	DBH	4.85	0.94	2.90	7.80	64
Annual	10		4.84	0.96	3.30	7.30	64
	13		4.66	0.96	2.50	6.80	64
	2		4.79	0.87	3.50	7.00	64
Control	12		4.62	0.77	3.30	6.30	64
	15		4.62	1.11	2.40	8.20	64
	4		4.50	0.79	3.00	6.50	64
Periodic	8		4.82	0.97	3.20	7.20	64
	18		3.94	0.85	2.60	5.90	64
	5	Height	4.33	0.56	2.92	5.61	64
Annual	10		4.23	0.57	3.17	5.64	64
	13		4.03	0.51	2.58	5.11	64
	2		4.53	0.56	3.36	6.39	64
Control	12		4.10	0.49	3.02	5.15	64
	15		4.06	0.70	2.46	6.27	64
	4		4.09	0.49	3.17	5.35	64
Periodic	8		4.38	0.55	3.14	5.54	64
	18		3.75	0.48	2.81	4.85	64
	5	HLC	0.67	0.24	0.20	1.30	64
Annual	10		0.53	0.14	0.30	0.95	64
	13		0.47	0.14	0.30	0.95	64
	2		0.69	0.27	0.15	1.50	64
Control	12		0.56	0.21	0.20	1.30	64
	15		0.63	0.20	0.30	1.30	64
	4		0.53	0.18	0.20	1.10	64
Periodic	8		0.71	0.24	0.35	1.30	64
	18		0.62	0.17	0.35	1.20	64

Note: HLC= Height to live crown

Appendix 4. Growth characteristics of lodgepole pine stands following initial fertilization in 1993 (Sheridan Creek).

Treatment	Plot	Variable	Mean	Standard deviation	Minimum	Maximum	N
			1998				
	5	DBH (cm)	9.68	1.54	5.40	14.00	60
Annual	10		9.93	1.72	6.40	14.20	60
	13		9.74	1.35	6.90	13.00	57
	2		8.40	1.24	5.60	11.20	62
Control	12		8.39	1.17	6.00	11.40	62
	15		8.60	1.48	4.30	13.20	63
	4		9.32	1.26	6.80	12.40	62
Periodic	8		9.36	1.55	5.90	12.70	60
	18		8.45	1.37	6.10	12.20	59
	5	Height (m)	6.59	0.82	4.30	8.20	60
Annual	10		6.93	0.87	5.30	9.15	60
	13		6.62	0.73	5.10	8.25	57
	2		7.25	0.80	5.60	10.00	62
Control	12		6.88	0.75	5.30	8.40	62
	15		6.77	0.88	4.60	9.30	63
	4		6.90	0.65	5.20	8.75	62
Periodic	8		7.24	0.85	5.60	9.00	60
	18		6.21	0.81	4.50	7.70	59
			2001				
	5	DBH (cm)	11.79	1.92	6.00	16.50	60
Annual	10		12.03	2.12	7.10	16.30	60
	13		11.91	1.66	8.10	15.20	57
	2		9.75	1.49	6.40	12.90	62
Control	12		9.73	1.36	6.80	13.00	62
	15		10.24	1.67	5.20	14.90	63
	4		11.57	1.49	8.80	15.20	62
Periodic	8		11.29	1.84	6.70	15.90	60
	18		10.60	1.62	7.30	15.10	59
	5	Height (m)	7.92	0.94	4.80	9.70	60
Annual	10		8.30	0.87	6.40	10.35	60
	13		7.80	0.81	5.90	9.30	57
	2		8.40	0.93	6.20	11.15	62
Control	12		8.09	0.81	6.00	9.60	62
	15		7.99	0.94	5.10	10.50	63
Periodic	4		8.37	0.71	6.70	10.20	62
	8		8.62	0.91	6.60	10.50	60
	18		7.57	0.95	5.50	9.30	59