

Effects of repeated fertilization on needle longevity, foliar nutrition, effective leaf area index, and growth characteristics of lodgepole pine in interior British Columbia, Canada

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Abstract: We investigated the effects of repeated fertilization (either periodically every 6 years or annual fertilization) on needle longevity and growth response in two juvenile lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) stands in the interior of British Columbia, Canada. Annual fertilization decreased needle longevity by 23% at the Kenneth Creek site and by 30% at Sheridan Creek, compared with the control treatments at each site. At Sheridan, repeated fertilization significantly increased effective leaf area index, foliated shoot length, and annual shoot growth. However, none of these variables was significantly altered by repeated fertilization at Kenneth. At both locations, fertilization elevated nutrient concentrations in the current year's foliage. Annual fertilization increased nitrogen concentration in mid-crown branches of retained cohorts (1998–2002) at both study sites. Furthermore, annual nitrogen addition apparently induced or exacerbated copper and iron deficiency in these stands, especially at Kenneth Creek, which may be related to the premature loss of foliage. Nutrient imbalance may also be related to poor effective leaf area index and growth response at Kenneth Creek. Stem growth efficiency declined with annual fertilization at Kenneth Creek because of accelerated turnover of needles, increased allocation of growth to branches, and probably reduced photosynthetic capacity.

Résumé : Les auteurs ont étudié les effets d'une fertilisation répétée (soit périodiquement à tous les six ans ou annuellement) sur la longévité des aiguilles et la croissance de deux jeunes peuplements de pin lodgepole (*Pinus contorta* Dougl. var. *latifolia* Engelm.) situés à l'intérieur des terres en Colombie-Britannique, au Canada. La fertilisation annuelle a réduit la longévité des aiguilles de 23 % à la station de Kenneth Creek et de 30 % à celle de Sheridan Creek comparativement au traitement témoin dans chacune des stations. À Sheridan Creek, la fertilisation répétée a significativement augmenté l'indice de surface foliaire effective (LAI_e), la longueur des pousses avec du feuillage et la croissance annuelle des pousses. Cependant, aucune de ces variables n'a été significativement affectée par une fertilisation répétée à Kenneth Creek. Aux deux endroits, la fertilisation a augmenté la concentration des nutriments dans le feuillage de l'année. La fertilisation annuelle a augmenté la concentration d'azote dans les branches des cohortes qui avaient été retenues (1998–2002) au centre de la cime dans les deux stations. De plus, l'ajout annuel d'azote a apparemment provoqué ou aggravé des déficiences en cuivre et fer dans ces peuplements, particulièrement à Kenneth Creek, possiblement en lien avec la perte prématurée de feuillage. Le déséquilibre nutritif pourrait aussi être relié à un faible indice de surface foliaire et une croissance réduite à Kenneth Creek. L'efficacité de croissance de la tige a diminué avec la fertilisation annuelle à Kenneth Creek à cause du remplacement accéléré des aiguilles, de l'allocation accrue de croissance aux branches et de la réduction probable de la capacité photosynthétique.

[Traduit par la Rédaction]

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). LAI can vary considerably among stands growing in different environments. The amount of leaf area on a tree depends upon needle production and needle retention, both of which can be influenced by edaphic or climatic factors (Reich et al. 1995) as well as by crown closure.

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Several fertilization studies have attributed the increases in tree growth following nitrogen (N) additions to the combined positive effects of added N on leaf area and foliar photosynthetic rate. Evidence from these studies indicates that increased leaf area is the more important of these two mechanisms (Fagerstrom and Lohm 1977; Brix 1983; Vose and Allen 1988; Zhang 1993).

There have been conflicting reports on the effects of fertilization on growth efficiency (GE), defined as the amount of stem biomass growth per unit of foliage area (Waring 1983) or per unit intercepted radiation (Balster and Marshall 2000a). Several studies have reported an increase in GE following fertilization (Binkley and Reid 1984; Albaugh et al. 1998; Balster and Marshall 2000a). Other studies have found that GE is largely unaffected by nutrient additions (Vose and Allen 1988; Beets and Whitehead 1996; Samuelson et al. 2001). Furthermore, Will et al. (2002) reported higher GE in younger loblolly pine (*Pinus taeda* L.) stands than in older stands, following annual fertilization. Fertilization-induced increases in GE may be associated with increased efficiency of carbon assimilation or shifts in biomass allocation to above-ground (including stems) versus belowground components (Brix 1981; Waring 1983; Gower et al. 1992; Haynes and Gower 1995). Repeated (periodic or annual) fertilization and the stable nutrition that it provides are therefore expected to increase and sustain higher concentrations of foliar nutrients, which should lead to greater GE, provided that acquisition and utilization of other nutrients by the plant are in balanced proportions (Ingestad 1979). We suspect that when N fertilization induces nutrient imbalances, growth efficiency may not be improved and may even decline.

The effect of fertilization on longevity of needles has not been well addressed. Species with very long-lived foliage are most common on infertile soils in many ecosystems and biomes (Monk 1966; Chapin 1980; Reich et al. 1992). Such species generally have lower leaf N concentrations and lower photosynthetic capacities (Williams et al. 1989; Reich et al. 1991). However, trees with greater needle longevity often have higher 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).

Nutrient retranslocation, defined as the process of an element being depleted from older plant components and made available for new growth, can provide substantial amounts of nutrients for new growth (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). In several studies, percentage of nutrient retranslocated was 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). Actual studies of improved site fertility either through natural nutrient pulses or fertilization have shown decreased leaf longevity with increased nutrient supply (Reich et al. 1995; Balster and Marshall 2000b; Harrington et al. 2001; Pensa and Sellin 2002; Niimets and Lukjanova 2003; Bauer et al. 2004). Reasons for the decrease in needle longevity were related to resource-use efficiency, shading

in the crown interior, or retranslocation from old to new foliage. Previous studies suggest that nutrient imbalance (mainly N/magnesium ratio) result in reduced foliage retention (Oren et al. 1988; Liu and Huettl 1991). Stone (1968) also reported that iron (Fe) deficiency could lead to premature needle drop.

Foliar N concentration has been used to estimate net photosynthesis because of the strong coupling between the two (e.g., Field and Mooney 1986) and also to predict stand basal area response (Brockley 2000). Most lodgepole pine fertilization experiments that examined growth responses usually focused on current year's foliar N (Brockley 2000; Kishchuk et al. 2002). Given the strong relationship between foliar N and stand productivity, we anticipate that repeated fertilization would increase foliar N across all age-classes, thereby increasing growth and GE.

This paper presents results from a study designed to examine the effects of repeated fertilization on needle longevity, branch growth characteristics, effective LAI (LAI_e), periodic annual increment of stem (basal area, volume and biomass), and GE of juvenile lodgepole pine stands. In addition we examine the effects of repeated fertilization on foliar nutrient concentrations for the range of needle cohorts in these stands.

Materials and methods

Location and site description

The study was carried out on two sites, Sheridan Creek and Kenneth Creek, which are part of a larger "maximum productivity" study established by the British Columbia 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; Brockley and Simpson 2004).

The Kenneth Creek site is 74 km east of Prince George, British Columbia (53°49'N, 121°47'W; 820 m elevation) within the willow variant of the wet, cool subzone of the Sub-Boreal Spruce biogeoclimatic zone (SBSwk₁; DeLong 2003). Vegetation and soil descriptions indicate the site belongs to the Sxw-Huckleberry – Highbush Cranberry (05) site series. The soil nutrient regime is medium to poor, and the soil moisture regime is mesic to submesic. Soil is derived from thick, well-sorted glacial-fluvial outwash. The soil is well drained and stone free with a fine to medium loamy sand texture and is classified as an Eluviated Dystric Brunisol (Soil Classification Working Group 1998). The site was clear-cut in 1981, and lodgepole pine was planted in spring of 1983. In 1993 the plots had an average density of 1360 stems·ha⁻¹ and were thinned to a uniform density of 1100 stems·ha⁻¹.

The Sheridan Creek site is located 7.5 km east of McLeese Lake, British Columbia (52°25'N, 122°11'W; 975 m elevation) within the southern Fraser Basin variant of the dry, warm southern subzone of the Sub-Boreal Spruce biogeoclimatic zone (SBSdw₂; Steen and Coupe 1997). Vegetation and soil descriptions indicate the site belongs to the zonal SxwFd – Pinegrass (01) site series. The soil nutrient regime is medium, and the soil moisture regime is mesic. Soils within this area occur 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, igne-

Table 1. Nutrient application rates by treatment and year at Kenneth Creek and Sheridan Creek.

Treatment	Nutrient element (kg·ha ⁻¹)	Year										Total
		1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	
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
Annual	N	—	200	200	200	—	100	100	150	100	100	1150
	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	—	—	—	1.5	4.5
	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
Annual	N	200	200	200	200	—	100	100	150	100	100	1350
	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	—	—	—	1.5	4.5

ous, 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 more coarse fragments. The soil is classified as a Brunisolic Grey Luvisol (Soil Classification Working Group 1998). At the time of trial establishment, the site was occupied by a naturally regenerated lodgepole pine stand that originated following a 1978 clear-cut. In 1992 the plots had an average density of 20 000 stems·ha⁻¹ and were thinned to a uniform density of 1100 stems·ha⁻¹.

Fertilizer treatment and plot establishment

Subsets of three of the six fertilizer treatments applied in the larger “maximum productivity” project were examined in this study. The three treatments were (1) control (i.e., no fertilization); (2) periodic: fertilized every 6 years; and (3) annual: fertilized yearly with nutrient blends customized to maintain foliar N concentration at about 16 g·kg⁻¹ and other nutrients and nutrient ratios in balance with foliar N in the current year’s foliage. In addition to N, the intent of the experiment was to add other macro- and micro-nutrients at rates and frequencies required to maintain an appropriate nutrient balance and to minimize growth limitations resulting from secondary deficiencies (Ingestad 1979; Linder 1995) (Table 1).

Each of the three treatments 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 three sides of the assessment plot; the buffer on the fourth side is 15.1 m wide. In the “periodic” and “annual” treatment plots, fertilizer was uniformly broadcast by hand to the assessment plot and surrounding buffer shortly after snowmelt in the spring. The stands were pruned to a lift height of 3 m in late September 1999 at Sheridan and in mid-October 2000 at Kenneth. Trees less than 6 m in height were pruned to 50% of total height at both sites. Initial stand conditions and conditions at the time of this study are presented in Table 2 and are presented in greater detail in Amponsah et al. (2004).

Branch sampling

In August 2002, three trees were selected within each treatment plot at each site. The protocol used to sample branches was similar to the procedure described by Balster and Marshall (2000b). One branch (an axis that originates from the bole of the tree) was cut from east, west, and south sides of the selected trees from mid-crown height. These branches were actively growing and had clearly defined segments where older needle cohorts had been shed. This enabled ageing the last living cohort and ensured that the

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

	Treatment		
	Control	Periodic	Annual
Pretreatment (Kenneth Creek; 1993)			
DBH (cm)	8.71 (0.26)	8.74 (0.20)	9.29 (0.38)
Total height (m)	5.50 (0.17)	5.58 (0.06)	5.72 (0.13)
Posttreatment (Kenneth Creek; 2001)			
DBH (cm)	15.2 (0.39)	15.9 (0.03)	16.0 (0.27)
Total height (m)	10.9 (0.12)	10.7 (0.11)	9.9 (0.12)
Pretreatment (Sheridan Creek; 1992)			
DBH (cm)	4.67 (0.06)	4.45 (0.25)	4.85 (0.05)
Total height (m)	4.23 (0.15)	4.09 (0.17)	4.23 (0.08)
Posttreatment (Sheridan Creek; 2001)			
DBH (cm)	9.9 (0.17)	11.2 (0.29)	11.9 (0.07)
Total height (m)	8.2 (0.13)	8.2 (0.32)	8.0 (0.15)

Note: Numbers in parentheses represent 1 SE ($n = 3$). DBH, diameter at breast height.

treatment effect on needle longevity could be assessed accurately. Branches were transported on ice to the laboratory and stored at $-18\text{ }^{\circ}\text{C}$ until processed.

Branch characteristics and N–P–K analysis of different age-classes of needles

Needle age-class (longevity of needles) and shoot characteristics were assessed and quantified along the first-order axis of each branch. Longevity of needles was quantified by counting annual needle cohorts, distinguished by the presence of second-order branches along the axis of each main branch and (or) by bud scars. Any cohort with greater than 40% of the fascicles still green was counted as a retained cohort. 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 when foliage was attached. Unit fascicle mass was calculated from a subsample of 50 fascicles selected at random from each shoot and averaged over each treatment. The survivorship of fascicles in each needle age-class was determined by dividing the number of retained fascicles by the sum of the number of fascicle scars and retained fascicles.

Foliage from each needle age-class was oven-dried at $70\text{ }^{\circ}\text{C}$ for 16–24 h and weighed. Subsamples 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 phosphorus (P) in the digests were determined with a Technicon autoanalyzer II, and potassium (K) was analyzed with a SpectrAA 880 Varian atomic absorption spectrometer at the University of Alberta Natural Resources analytical laboratory. Results were expressed as concentrations (grams per kilogram of dry mass) and contents (micrograms per fascicle) of N, P, and K.

Sampling and chemical 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 early

October of 2000. Samples were frozen prior to oven-drying at $70\text{ }^{\circ}\text{C}$ for 24 h. One composite foliage sample per plot was prepared for analysis, with each composite consisting of equal amounts of foliage from each of the 10 trees. Composite samples were ground prior to analysis at the British Columbia Ministry of Forests analytical laboratory.

Total N and total sulfur (S) were analyzed by combustion using the Fisons NA1500 NCS analyzer, followed by determination with an inductively coupled plasma spectrophotometer (ICP) with an ARL 3560 ICP optical emission spectrometer. All other macro- and micro-nutrients 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 described previously.

Estimates of LAI_e and intercepted radiation

Hemispherical photographs were taken using a Nikon Coolpix 990 digital camera and a 7-mm fisheye lens converter mounted level on a tripod. Fifteen photographs of the canopy, excluding the understory vegetation, were taken within each plot in July 2001. Photographs were taken at the centre of mapped grid squares (approx. $5\text{ m} \times 5\text{ m}$) established in each plot at about 1.0 m 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), which calculates LAI by inversion of gap fraction data (Welles 1990). The Poisson model was used, so needle and crown clumping were ignored, and estimates were LAI_e (Chen and Black 1992) rather than true LAI and also included woody plant area. We used a manual threshold, 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, thus separating branches from open sky. The photos were then analyzed by SLIM to calculate LAI_e with respect to the location of the camera (Comeau et al. 2002). The fraction of radiation intercepted by the canopy was calculated from the hemispherical photographs based on calculations of both diffuse and direct sunlight below and above the canopy. SLIM calculates the amount of direct (beam) and diffuse radiation penetrating gaps in the canopy over the growing season. Beam radiation is calculated by tracking the location of the sun in relation to canopy gaps, while diffuse radiation is calculated using gap fraction data for each of 480 overhead sky segments on the photograph. Transmittance was calculated as the ratio of understory photosynthetic photon flux density (PPFD) to overstory PPFD, and absorbance was calculated by subtracting transmittance from 1.0.

Stand growth characteristics

At each study location, total height and diameter at breast height (DBH) were measured for all 64 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. DBH was measured using a steel diameter tape, and heights were taken with a

Forester Vertex[®] hypsometer. Periodic annual increment (PAI) of height and basal area (BA) were calculated for each tree within a plot. Treatment means were obtained by averaging the three replicate plots per treatment.

In July 2001, two trees 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 a 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 the bark in cubic centimetres, D is DBH outside the bark in centimetres, and H is total height in metres (R.P. 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 ($P < 0.05$; $r^2 = 0.94$). Wood density was determined from oven-dry masses of 10-cm-thick discs cut above 1.3 m height, and green volume was determined by water displacement. Individual tree PAI of stem volume in each of the treatment plots at Kenneth (1999–2002) and Sheridan (1998–2001) were determined using these equations. PAI of stem volume was converted to biomass based on the average wood density of each treatment. 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. Growth efficiency (GE; stem biomass growth per unit intercepted radiation or foliage area) was calculated by dividing stand-level PAI of stem biomass by the proportion of intercepted radiation (IR) or LAI_e.

Statistical analysis

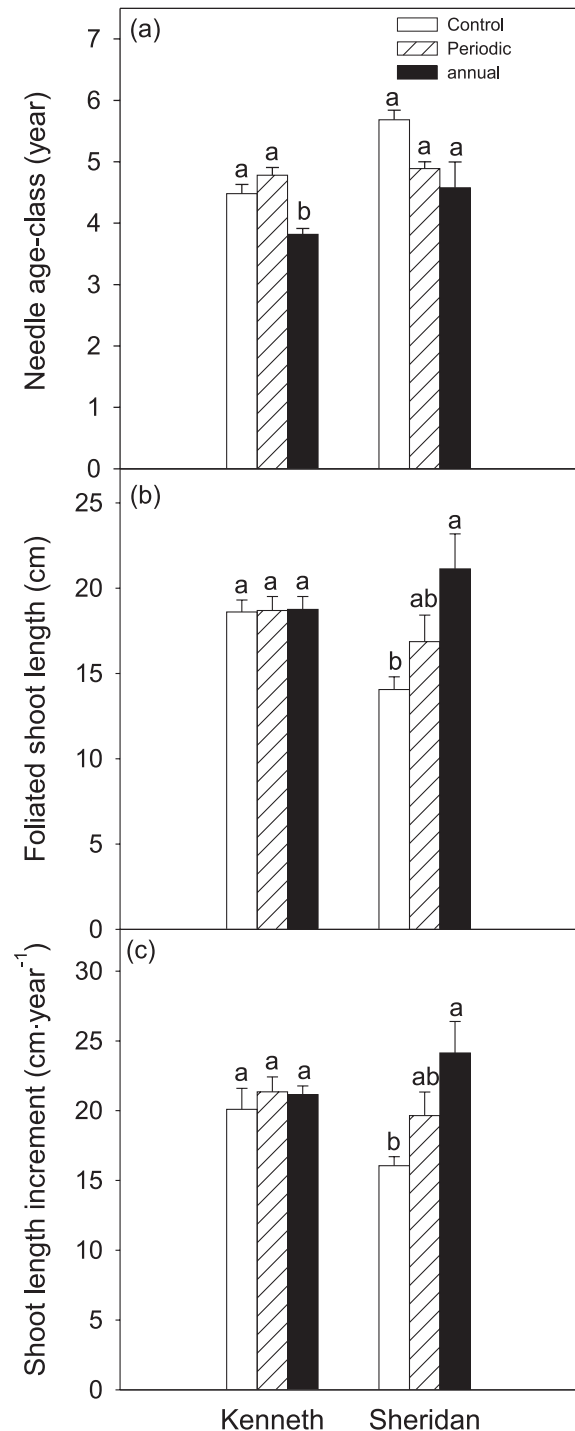
Data for Kenneth and Sheridan were analyzed separately. One-way analysis of variance (ANOVA) was used to test for treatment effects on needle longevity, 2000 foliar nutrient levels, and growth response variables. Given that plot is an experimental unit, the three sample trees were averaged per plot and used for analysis of needle longevity and growth response. Repeated measures (Proc Mixed) with compound symmetry covariance structure was used to test for a treatment effect (with Tukey adjustments at $p = 0.05$) and trends on survivorship, fascicle mass, and foliar nutrient data (N–P–K).

Results

Branch characteristics

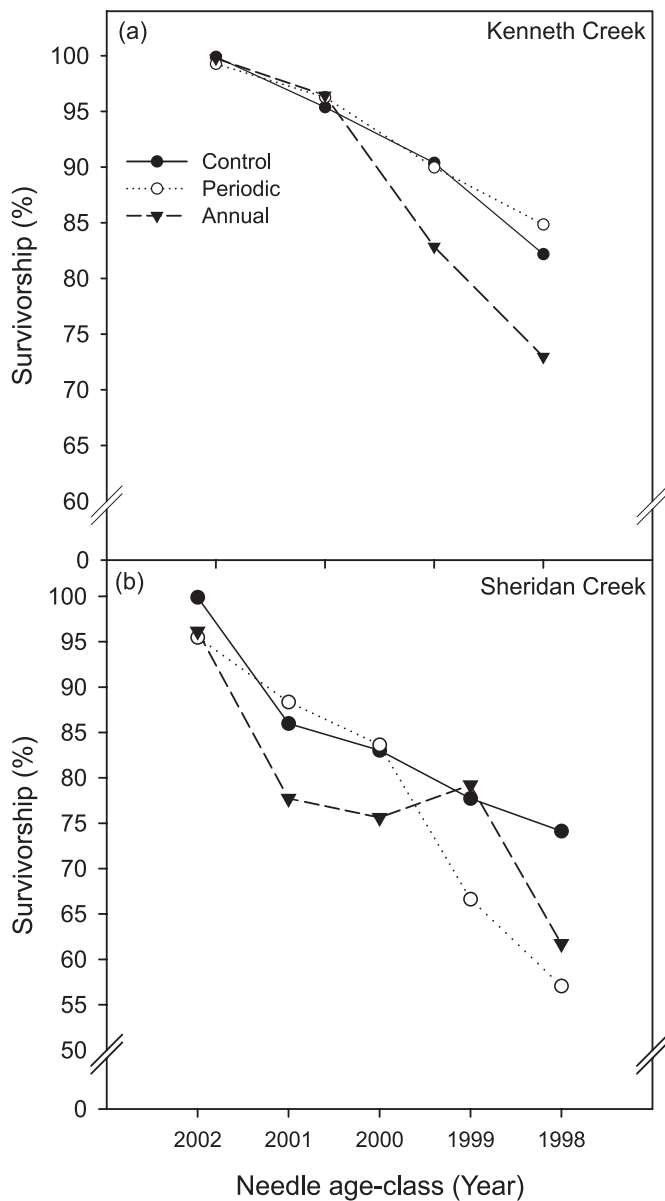
At Kenneth Creek, annual fertilization significantly decreased the mean number of needle age-classes compared with periodic and control treatments (Fig. 1a; $p = 0.005$). On average, annual fertilization decreased needle longevity by 23%. However, mean foliated length and annual shoot-length increment of mid-crown branches were unaffected by fertilization (Fig. 1b, $p = 0.980$; Fig. 1c, $p = 0.714$). There was a significant decline in fascicle survivorship with age for all three treatments (Fig. 2a), but the annual treatment showed a steeper decline (significant interaction between annual fascicle survivorship and treatment). However, the overall treatment effect on fascicle survivorship was not significant.

Fig. 1. Mean number of needle age-classes, annual shoot-length increment, and foliated shoot length of mid-crown branches of lodgepole pine at Kenneth Creek and Sheridan Creek. Means with the same letters are not significantly different at $p = 0.05$ according to a Student–Newman–Keuls test ($n = 3$). Error bars indicate ± 1 SE. Note multiple comparisons between treatments were restricted to each site.



At Sheridan Creek, fertilization resulted in a slight but nonsignificant decrease in the number of needle age-classes (Fig. 1a, $p = 0.061$); treatments were ranked control > periodic >

Fig. 2. Mean fascicle survivorship of retained cohorts from mid-crown branches of lodgepole pine at Kenneth and Sheridan Creek.



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 (Fig. 1b, $p = 0.042$; Fig. 1c, $p = 0.047$). In general, there was a significant decline in fascicle survivorship with age for all three treatments (Fig. 2b). However, the overall treatment effect on fascicle survivorship was not significant (Fig. 2b).

N-P-K concentration and content of different needle age-classes

At Kenneth, annual fertilization significantly increased mean foliar N concentration and content compared with the periodic and control treatments (Fig. 3a, $p = 0.007$; Fig. 3b, $p = 0.045$). While N concentration tended to decline with needle age, N content often increased, especially in the control treatment,

but was variable in the periodic and annual treatments (Fig. 3b). In general, P and K concentrations were similar between treatments (results not shown; $p = 0.395$ and $p = 0.270$, respectively).

At Sheridan, annual fertilization significantly increased mean N concentrations and content of foliage of the retained cohorts compared with the periodic and control treatments (Fig. 3d, $p = 0.009$; Fig. 3e, $p = 0.011$). There was a general decline in N concentration with age. In contrast, N content tended to have its highest levels in the 2-year-old fascicles (Fig. 3e), which also had the largest fascicle mass (Fig. 3f). Mean P concentration averaged over all "retained cohorts" was not significantly different between treatments ($p = 0.709$). Annual fertilization significantly increased mean K concentration compared with control and periodic treatments (results not shown; $p = 0.025$).

Mass of fascicles

At Kenneth Creek, there was a general increase in mean fascicle mass with age, and while there was a trend for increased mass of fascicles in the annual fertilization, there was no significant difference across treatments (Fig. 3c, $p = 0.127$). In contrast, the 2-year-old cohort tended to have the largest fascicle mass for the three treatments at Sheridan Creek (Fig. 3f). For mean mass of all fascicles at Sheridan Creek, there was no significant difference among treatments ($p = 0.384$).

Nutrient concentration of the current year's foliage collected in 2000

At Kenneth, both periodic and annual fertilization significantly elevated foliar concentrations of N and boron (B) in the current year's foliage collected in 2000 (Table 3). Annual fertilization increased S concentration and decreased foliar levels of copper (Cu), calcium (Ca), and zinc (Zn) compared with control and periodic treatments (Table 3). Annual fertilizer addition increased foliar N/Cu and N/Fe ratios compared with the control or periodic treatment at Kenneth Creek. The ratio of N/Cu of the annual treatment was about 2.5 greater than that of the periodic treatment and 3.4 times greater than that of the control (Table 3).

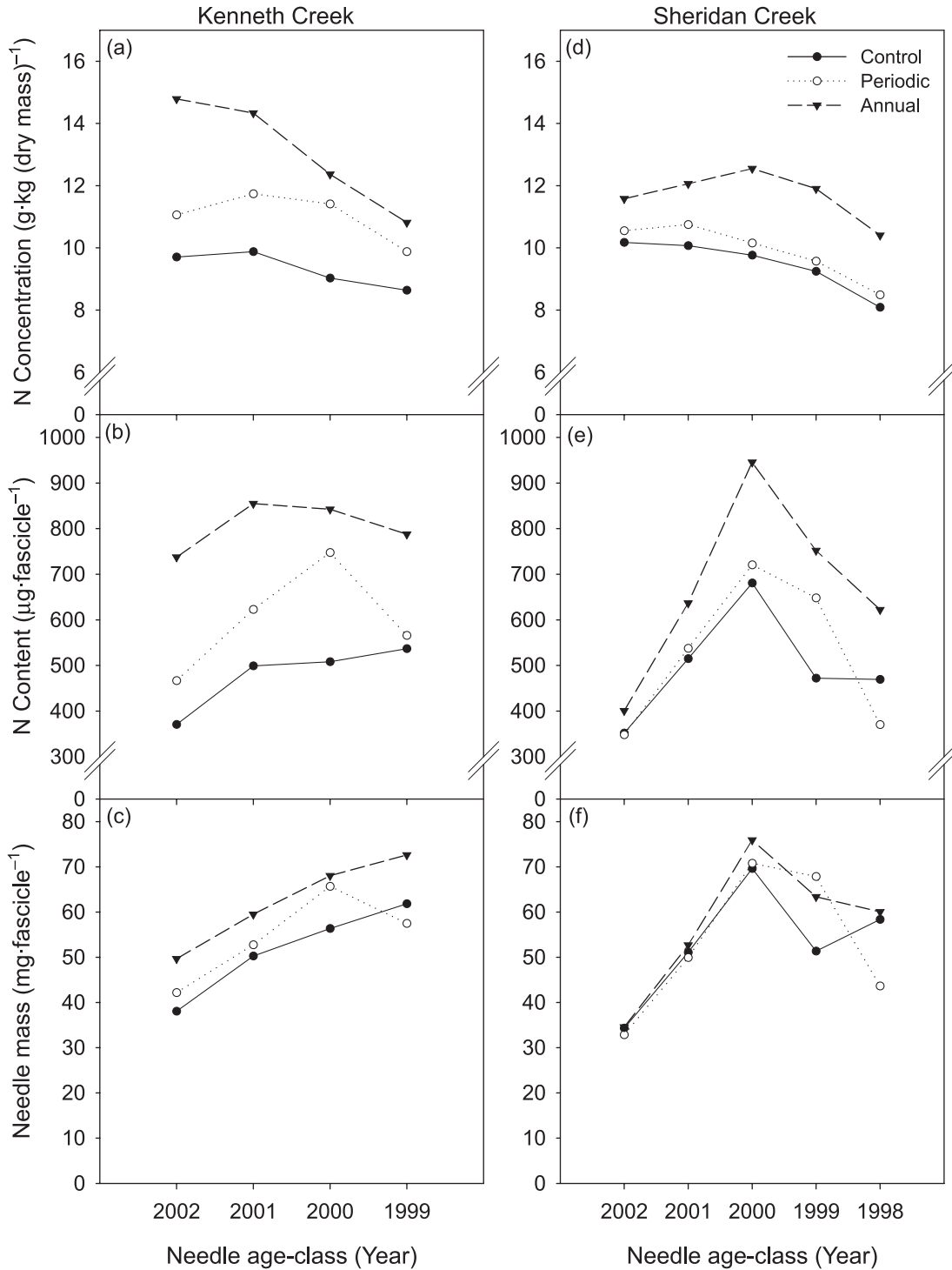
At Sheridan, treatment affected N, P, and S concentrations in the current year's foliage in 2000, and ranked annual > periodic > control, while B was ranked periodic > annual > control (Table 3). Repeated fertilization increased the ratios of N/Cu and N/Fe, but differences were not statistically significant at this site (Table 3).

Stand growth characteristics

Annual fertilization significantly reduced growth efficiency (GE; PAI stem biomass per unit intercepted radiation or LAI_e), PAI of height, stem biomass, and volume, and these were ranked periodic > control > annual at Kenneth (Table 4). PAI of basal area and stem volume per tree were greater in the periodic treatment compared with the annual and control treatments. There were no treatment effects on LAI_e and the proportion of intercepted radiation (IR) at Kenneth (Table 4).

At Sheridan Creek, PAI of stem volume, PAI of stem biomass, IR, and LAI_e were increased by fertilization at the stand level. In contrast, GE was not significantly affected by fertilization. At the tree level, fertilization significantly in-

Fig. 3. Mean foliar nitrogen concentration and content and mass of fascicle for different age-classes in retained cohorts from mid-crown branches of lodgepole pine at Kenneth Creek and Sheridan Creek.



creased PAI of basal area and stem volume. Treatment effect on PAI of height was significant and ranked periodic > annual, control (Table 4).

Growth rates during the 3-year period examined in this study (6–9 years after start of fertilization) provide only a short period of evaluation and may not entirely reflect preceding or subsequent rates of growth. A more complete summary of

growth response results in these stands are presented in Brockley and Simpson (2004).

Discussion

Our results show that annual fertilization decreased longevity of needles on mid-crown branches of lodgepole pine

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

Nutrient element	Treatment			<i>p</i> value
	Control	Periodic	Annual	
Kenneth Creek				
N (g·kg ⁻¹)	12.93 (0.38)b	15.30 (0.51)a	15.60 (0.10)a	0.004
P (g·kg ⁻¹)	1.21 (0.04)a	1.27 (0.01)a	1.29 (0.03)a	0.197
K (g·kg ⁻¹)	4.53 (0.25)a	4.49 (0.11)a	4.69 (0.14)a	0.702
Ca (g·kg ⁻¹)	1.59 (0.09)a	1.48 (0.08)a	1.20 (0.07)b	0.031
Mg (g·kg ⁻¹)	0.92 (0.02)a	0.88 (0.05)a	0.83 (0.01)a	0.154
S (g·kg ⁻¹)	0.78 (0.03)b	0.74 (0.03)b	1.01 (0.02)a	<0.001
Cu (mg·kg ⁻¹)	3.1 (0.3)a	2.6 (0.2)a	1.1 (0.1)b	0.002
B (mg·kg ⁻¹)	12.7 (1.8)b	25.3 (2.2)a	21.9 (1.2)a	0.006
Fe (mg·kg ⁻¹)	26.4 (0.9)a	29.4 (6.0)a	22.3 (0.4)a	0.405
Zn (mg·kg ⁻¹)	44.8 (1.6)a	45.3 (2.5)a	36.7 (1.7)b	0.040
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
Sheridan Creek				
N (g·kg ⁻¹)	12.43 (0.48)b	13.93 (0.58)b	16.40 (0.60)a	0.007
P (g·kg ⁻¹)	1.22 (0.02)b	1.43 (0.05)a	1.51 (0.02)a	0.002
K (g·kg ⁻¹)	4.32 (0.22)a	4.71 (0.19)a	4.59 (0.09)a	0.323
Ca (g·kg ⁻¹)	1.80 (0.12)a	1.73 (0.14)a	1.37 (0.03)a	0.068
Mg (g·kg ⁻¹)	1.02 (0.05)a	0.93 (0.03)a	0.94 (0.06)a	0.371
S (g·kg ⁻¹)	0.78 (0.04)c	1.00 (0.07)b	1.26 (0.05)a	0.002
Cu (mg·kg ⁻¹)	2.8 (0.1)a	3.1 (0.1)a	2.9 (0.1)a	0.177
B (mg·kg ⁻¹)	16.5 (0.9)b	25.0 (1.2)a	24.6 (0.3)a	<0.001
Fe (mg·kg ⁻¹)	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/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

Note: For each installation and nutrient variable, treatment values with different letters are statistically significant at $p = 0.05$ according to Student–Newman–Keuls test. Numbers in parentheses represent 1 SE ($n = 3$).

following 7 or 8 years of fertilization. First, mean longevity of needles declined by 23% in the annual treatment at Kenneth Creek and by 30% at Sheridan Creek, compared with the control. This is consistent with reported decreases in needle longevity observed in long-term N fertilization experiments of other conifers (Balster and Marshall 2000b; Bauer et al. 2004) and fertile sites (Pensa and Sellin 2002; Niimets and Lukjanova 2003). The average needle longevity of unfertilized lodgepole pine in this study was 5 years at Kenneth Creek and 6 years at Sheridan Creek and is within the range of needle longevity (4–13 years) reported by Critchfield (1957) and the average range of (5–18 years) reported by Schoettle (1990) for lodgepole pine in the Rocky Mountains. Secondly, periodic fertilization tended to increase the number of retained 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. Thirdly, the annual treatment tended to have a steeper decline in survivorship in the 2- and 3-year-old needles compared with the current and 1-year-old needles at Kenneth. A similar trend in decreased survivorship with annual fertilization was observed at Sheridan (Fig. 2b). Aerts (1989) also observed a decline in leaf survivorship following fertilization of *Erica tetralix* L.

Other studies of needle longevity contradict our finding of decreased needle longevity in response to fertilization (Miller

and Miller 1976; Turner and Olson 1976; Reader 1978; Brix 1981; Lajtha and Whitford 1989; Gholz et al. 1991). These studies are based on short-term measurements (1 or 2 years), which may not fully elucidate the effect of fertilization on needle life. Another theory to explain the discrepancy between our study and previous literature is that reduced redistribution of N from older foliage to new foliage (Monk 1966; Turner and Olson 1976; Shaver 1983) may have allowed greater survival of older foliage in previous studies. Since the highest N concentration and content in all needle age-classes (including 4-year-old needles) was in the annual treatment at both sites, N withdrawal out of the older foliage is unlikely to be responsible for premature loss of older foliage in the fertilized treatments. While there was a decline in nutrient concentration with needle age, the concentrations in 4-year-old or older needles in the annually fertilized stands compare well with the current-year foliar N of the control and the periodic fertilization treatments. For these reasons, we feel that N withdrawal was likely not responsible for premature loss of older foliage in the fertilized treatments in our study.

Light limitation does not seem to be the main cause of reduced survival of older foliage in fertilized trees in this study for two reasons: (1) the canopies of the stands at both sites were not closed, suggesting that foliage on branches at mid-crown positions were probably not shaded below light-

Table 4. Stand- and tree-level growth characteristics and effective leaf area index (LAI_e) of lodgepole pine stands in response to fertilization treatments.

Variable	Treatment			
	Control	Periodic	Annual	<i>p</i> value
Kenneth Creek				
PAI height (m·year ⁻¹ ·tree ⁻¹ ; 1999–2002)	0.65 (0.02)a	0.60 (0.01)a	0.45 (0.02)b	<0.001
PAI basal area × 10 ⁻³ (m ² ·year ⁻¹ ·tree ⁻¹ ; 1999–2002)	1.12 (0.04)	1.32 (0.03)	1.16 (0.07)	0.054
PAI stem volume × 10 ⁻² (m ³ ·year ⁻¹ ·tree ⁻¹ ; 1999–2002)	1.00 (0.04)ab	1.08 (0.02)a	0.89 (0.06)b	0.050
PAI stem volume (m ³ ·ha ⁻¹ ·year ⁻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 ·year ⁻¹ ; 1999–2002)	3.88 (0.15)a	4.16 (0.12)a	3.28 (0.15)b	0.010
Effective LAI _e (m ² ·m ⁻²)	2.29 (0.13)	2.44 (0.17)	2.72 (0.05)	0.122
Intercepted radiation (IR)	0.74 (0.02)	0.76 (0.01)	0.77 (0.02)	0.593
Growth efficiency (GE _{AL} ; Mg·ha ⁻¹ ·year ⁻¹) [†]	1.70 (0.03)a	1.71 (0.09)a	1.20 (0.04)b	0.002
Growth efficiency (GE _{IR} ; Mg·ha ⁻¹ ·year ⁻¹) [†]	5.17 (0.08)a	5.46 (0.08)a	4.24 (0.25)b	0.004
Sheridan Creek				
PAI height (m·year ⁻¹ ·tree ⁻¹ ; 1998–2001)	0.40 (0.01)b	0.47 (0.01)a	0.43 (0.02)ab	0.027
PAI basal area × 10 ⁻³ (m ² ·year ⁻¹ ·tree ⁻¹ ; 1998–2001)	0.71 (0.02)b	1.14 (0.06)a	1.24 (0.01)a	<0.001
PAI stem volume × 10 ⁻² (m ³ ·year ⁻¹ ·tree ⁻¹ ; 1998–2001)	0.36 (0.02)b	0.54 (0.04)a	0.59 (0.02)a	0.002
PAI stem volume (m ³ ·ha ⁻¹ ·year ⁻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 ·year ⁻¹ ; from 1998–2001)	1.44 (0.11)	1.95 (0.19)	1.93 (0.13)	0.081
Effective leaf area index (m ² ·m ⁻²)	1.29 (0.06)c	1.76 (0.05)b	2.26 (0.04)a	<0.001
Intercepted radiation (IR)	0.53 (0.002)c	0.60 (0.002)b	0.66 (0.004)a	<0.001
Growth efficiency (GE _{AL} ; Mg·ha ⁻¹ ·year ⁻¹)	1.11 (0.04)	1.13 (0.11)	0.86 (0.01)	0.091
Growth efficiency (GE _{IR} ; Mg·ha ⁻¹ ·year ⁻¹)	2.71 (0.21)	3.25 (0.31)	2.90 (0.18)	0.332

Note: For each installation and variable, treatment values with different letters are statistically significant at $p = 0.05$ according to Student–Newman–Keuls test ($n = 3$). Numbers in parentheses represent 1 SE. PAI, periodic annual increment.

[†]GE_{AL} was calculated as PAI stem biomass per unit LAI_e, and GE_{IR} was calculated as PAI stem biomass per unit intercepted radiation.

compensation points (Dykstra 1974; Carter and Smith 1988; Landhäusser and Lieffers 2001); and (2) at Kenneth, where LAI_e was highest and relatively uniform across treatments, the annual treatment had the largest drop in fascicle survivorship. Thus, although we cannot totally eliminate the possibility that shading within the canopies had an impact on survivorship of foliage, it is likely other factors were the cause for the difference in survivorship.

Despite improved foliar N, neither tree growth nor LAI_e was stimulated by repeated fertilization at Kenneth Creek. We speculate that induced nutrient deficiencies caused by foliar imbalance of N relative to nonadded micronutrients (i.e., Cu and Fe) may explain these results at Kenneth and may also have contributed to the needle loss and significant decline in GE in the annual treatment. Twisting of stems and branches and rosetting of terminal shoots are clearly evident in annual treatment plots at Kenneth, where foliar Cu levels (1–2 mg·kg⁻¹) are within the range associated with visual symptoms of Cu deficiency in *Pinus radiata* D. Don (Will 1985; Turvey and Grant 1990). These symptoms were not observed at Sheridan, where foliar Cu and Fe levels were higher in the annual treatment compared with the control and periodic treatments. Induced micronutrient deficiencies (B and (or) Cu) were suggested as possible reasons for stem deformities and height disruptions in repeatedly fertilized Scots pine (*Pinus sylvestris* L.) trials in Sweden (Tamm et al. 1999). Similar symptoms were also observed in an intensively fertilized lodgepole pine stand in southern British Columbia (Kishchuk et al. 2002).

Low foliar Cu and Fe levels, and high N/Cu and N/Fe ratios, may be related to the coarse-textured soils derived from

glaciofluvial outwash at Kenneth Creek. Other studies indicate that Cu deficiency may occur on acidic, sandy soils (Stone 1968; Will 1985; Turvey and Grant 1990). Furthermore, Stone (1968) suggested that Fe deficiency can be found in stands growing on “leached acid sandy soils from siliceous materials low in Fe bearing minerals”. In other studies, foliar nutrient imbalances caused by high N inputs have been linked to poor tree growth, higher leaf turnover rates, and reduced leaf area (Oren and Zimmerman 1989; Bauer et al. 2004). Micronutrient levels were not measured in older foliage at Kenneth Creek. However, we speculate that retranslocation of nutrients from older to younger foliage (Everett and Thran 1992; Nieminen and Helmisaari 1996) may have exacerbated N/Cu and (or) N/Fe foliar imbalances, thereby accelerating the loss of older needles (Kozłowski and Pallardy 1997).

At the individual tree and stand level, fertilization increased periodic annual increment (PAI) of basal area and volume at Sheridan Creek, consistent with growth responses observed in a similar experiment with lodgepole pine (Kishchuk et al. 2002). This increase in PAI at Sheridan appears to be positively related to the increases in LAI_e (Brix 1983) and light interception. At Kenneth Creek, there was a trend for a decline in PAI and growth efficiency with annual fertilization, relative to the control. First, there was poor needle retention at this site, which was reflected in only a small (nonsignificant) increase in LAI_e. Secondly, as the decline in PAI with annual fertilization was opposite to the small gain in LAI_e, there was probably a decline in photosynthetic efficiency or in the proportion of growth allocated to stemwood. Bauer et al. (2004) reported a similar decline in photosynthetic efficiency following fertilization of red pine (*Pinus resinosa* Ait.), where most of the

foliar N was accumulated as amino acids, possibly caused by foliar nutrient imbalances, reduced needle retention, and decoupling of the photosynthesis–N relationship.

In summary, annual fertilization resulted in reduced needle longevity, but overall there was little impact on stand leaf area at Kenneth Creek. At the same time there was a negative effect on height increment and stem volume increment. In contrast, at Sheridan there was greater branch growth and stand leaf area, and some of the productivity indicators suggested greater growth with annual fertilization. While results from the Sheridan site are consistent with other studies that suggest that increases in stem volume growth following fertilization are largely related to increases in LAI (Albrektson et al. 1977; Brix 1981, 1983; Colbert et al. 1990; Linder et al. 1987; Vose and Allen 1988), results from the Kenneth Creek site underscore the need to provide a balanced supply of required nutrients, since induction of deficiencies of other elements through excessive application of one element (N in this study), may result in reduced needle retention, reduced growth efficiency, and negative growth responses.

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