

Effects of Sitka alder on the growth and foliar nutrition of young lodgepole pine in the central interior of British Columbia

R.P. Brockley and P. Sanborn

Abstract: The 6-year effects of differing levels of Sitka alder (*Alnus viridus* spp. *sinuata* (Regel) Á. Löve & D. Löve) retention (0, 500, 1000, and 2000 clumps/ha) on the development of retained alder and on the growth and foliar nutrition of 7-year-old naturally regenerated lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) were evaluated in a sub-boreal ecosystem in the central interior of British Columbia. Alder development was inversely related to alder retention density, with the largest height and crown width increments occurring at the lowest alder densities. Low to moderate levels of alder cover did not significantly inhibit the diameter or height growth of lodgepole pine. Even under high alder cover, growth was not reduced until alder cover exceeded 45%. Over the 6-year response period, lodgepole pine diameter and height increments under high alder cover were reduced by 10% and 12%, respectively, relative to the no-alder treatment. The effect of alder density on lodgepole pine foliar N was strongly linear, with the highest N levels measured in the high alder retention treatment. However, the positive impact of alder retention on foliar N resulted in probable imbalance of N relative to S and possibly P and K. Unless alleviated, nutritional imbalances may preclude reliable assessment of the competitive effects (i.e., light and soil resources) of alder density, if any, on lodgepole pine growth.

Résumé : Six ans après avoir conservé différentes densités d'aune vert (*Alnus viridus* spp. *sinuata* (Regel) Á. Löve & D. Löve) (0, 500, 1000 ou 2000 bouquets/ha), les effets sur le développement des aulnes résiduels et sur la croissance et la nutrition foliaire de la régénération naturelle de pin lodgepole (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) âgée de 7 ans ont été évalués dans un écosystème sub-boréal situé dans le centre intérieur de la Colombie-Britannique. Le développement de l'aune était inversement proportionnel à la densité de cette espèce; les plus forts accroissements en hauteur et en largeur de cime sont survenus aux plus faibles densités. Une couverture faible à modérée d'aune n'a pas significativement inhibé la croissance en hauteur ou en diamètre du pin lodgepole. Même sous un fort couvert d'aune, la croissance n'a pas été affectée tant que la couverture d'aune ne dépassait pas 45 %. Sur la période de six ans, l'accroissement en diamètre et en hauteur du pin lodgepole sous couvert dense d'aune a été réduit respectivement de 10 % et 12 % comparativement au traitement sans aune. L'effet de la densité de l'aune sur l'azote (N) foliaire du pin lodgepole était fortement linéaire et les concentrations les plus élevées de N ont été mesurées dans le traitement avec la plus grande quantité d'aulnes. Cependant, l'impact positif sur l'azote foliaire associé au maintien de l'aune a probablement entraîné un déséquilibre de N relativement au soufre et possiblement au phosphore et au potassium. À moins d'y remédier, les déséquilibres nutritionnels peuvent empêcher d'évaluer adéquatement les effets potentiels dus à la compétition (p. ex. lumière et ressources du sol) de l'aune sur la croissance du pin lodgepole.

[Traduit par la Rédaction]

Introduction

Sitka alder (*Alnus viridus* spp. *sinuata* (Regel) Á. Löve & D. Löve) is a common shrub species in lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) forests in the interior of British Columbia (Haeussler et al. 1990). Because it is moderately shade tolerant, a well-developed Sitka alder understory often persists under mature

forest canopies (Wurtz 1995). This shrub community usually remains relatively intact following clear-cut harvesting, and the increased light level promotes vigorous growth of the residual alder clumps. In regenerating stands, Sitka alder may increase in height and cover to a level where competition for light and soil resources and physical damage caused by whipping and snow press may negatively affect growth of the planted or naturally regenerated conifer crop species (Haeussler et al. 1990). In such situations, silviculturists recognize Sitka alder as a distinctive vegetation management challenge on dry to fresh sites in several biogeoclimatic zones in the central and southern interior of British Columbia (B.C. Ministry of Forests 1997a).

Twenty years of foliar data collected from immature lodgepole pine forests throughout the British Columbia interior indicate widespread N deficiencies (Ballard 1982; Weetman and Fournier 1982; Brockley 2001a; Krzic et al. 2002). Brockley (2001a) reported that three quarters of the

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52 lodgepole pine stands assessed had foliar N levels lower than 1.15%, indicating moderate to severe N deficiency (Ballard and Carter 1986). These inferred N deficiencies in lodgepole pine forests have been confirmed by favourable responses to N fertilization (Brockley 2000, 2001a). As an N-fixing species, Sitka alder can benefit site fertility through N additions, with accretion estimates from coastal British Columbia ranging from 20 to 35 kg N/ha annually (Binkley 1981, 1982; Binkley et al. 1984). In less productive interior forests, N fixation rates are apparently considerably lower: the only published study estimated a rate of approximately 6 kg/ha annually (Mead and Preston 1992). Nevertheless, a vigorous component of Sitka alder could potentially improve the nutritional status of young, N-deficient lodgepole pine forests. No studies have specifically studied the nutritional effects of Sitka alder on lodgepole pine. Ballard and Hawkes (1989) observed that proximity of Sitka alder enhanced the foliar N concentrations and leader growth of planted white spruce (*Picea glauca* (Moench) Voss) in the central interior of British Columbia. However, a previous study with Sitka alder indicated that increased N availability might disrupt the balance between foliar N and other essential nutrients (Binkley et al. 1984). Many studies have shown that proportions of nutrients relative to N are likely as important for tree growth as are the concentrations of individual nutrients (Ingestad 1979; Linder 1995).

Previous studies undertaken in British Columbia to document the effects of different amounts of Sitka alder cover on the growth of lodgepole pine have been conducted on southern interior sites (Simard 1990; Simard and Heineman 1996). Similar studies have not been conducted in the north-central interior, where the Sitka alder plant communities are similar but where environmental limitations to conifer growth may be quite different than in the southern interior. Also, previous studies have not documented the effects of differing levels of alder cover on lodgepole pine foliar nutrition. For the extensive Sub-Boreal Spruce (SBS) biogeoclimatic zone (DeLong et al. 1993), clear guidance is lacking on where the balance of advantage lies, that is, at what alder density are the likely benefits of N addition offset by competition with crop trees for light and soil resources and by the possible detrimental effects on foliar nutrient balance?

Interplanting of alder and pine at varying densities and proportions is one possible approach to the study of these interactions. However, several investigators have reported poor success in establishing planted Sitka alder in the interior of British Columbia.² An alternative method is to selectively remove or retain established alder in young plantations or naturally regenerated stands of lodgepole pine. Because most Sitka alder cover in young lodgepole pine stands in the SBS biogeoclimatic zone appears to originate from resprouted clumps established in the previous mature stands, this approach should produce stand conditions that are similar to those in managed forests throughout the region.

A long-term field experiment was established in 1995 to study the effects of differing levels of Sitka alder retention (0, 500, 1000, and 2000 clumps/ha) on the growth of young (~7 years old), naturally regenerated lodgepole pine thinned

to a uniform density of 1000 stems/ha. Ancillary studies were established to measure the (i) N fixation rate of Sitka alder, (ii) long-term changes in soil N availability associated with differing levels of alder retention, and (iii) decomposition rates and nutrient concentration changes in Sitka alder and lodgepole pine litter (Sanborn et al. 2001).

The N fixation rate of Sitka alder in this cutblock over three growing seasons has recently been reported by Sanborn et al. (2002). In this paper, we discuss the effects of differing densities of Sitka alder on the growth and development of lodgepole pine and Sitka alder during the 6 years following treatment. The effects of alder retention on lodgepole pine foliar nutrient levels and nutrient balance are also discussed.

Methods

Location and site description

The study site is located approximately 55 km southwest of Prince George (53°40'N, 123°39'W) in the Vanderhoof Forest District within the Stuart Dry Warm variant of the SBS biogeoclimatic zone (SBSdw3) (DeLong et al. 1993). Based on slope position, soil characteristics, and the dominant shrub and herb species, the site most clearly matches the submesic (04) site series for this variant. The site has a west aspect, with slopes ranging from 5% to 20% and a mean elevation of approximately 1030 m. The landform consists of a morainal blanket or veneer over igneous bedrock, with surface soil textures ranging from loam to sandy loam (30%–40% gravels and cobbles). Coarse-textured glacio-fluvial deposits occur in discontinuous eskers that extend across the western portion of the opening. This assemblage of landforms and materials is typical of the glaciated plateau in this subzone. The soil is classified as a Brunisolic Gray Luvisol (Soil Classification Working Group 1998). Additional details about the physical and chemical properties of the soil are provided in Arocena and Sanborn (1999).

The previous mature forest was clear-cut harvested in 1987 and subsequently naturally regenerated to a mixture of lodgepole pine and Sitka alder. Virtually all of the alder at this site had regenerated from clumps held over from the previous mature stand, as evidenced by their large woody rootstocks. At the time of trial establishment in 1995, the density of lodgepole pine was approximately 10 500 stems/ha, while the alder density averaged 4100 clumps/ha, representing a mean alder cover of 51% (Sanborn et al. 2001). Similar or greater alder densities are common on mesic and submesic sites in the SBSdw3 biogeoclimatic subzone and adjacent subzones (SBSdk and SBSmc3) (C. DeLong, B.C. Ministry of Forests, Prince George, B.C., personal communication). Measurements taken immediately following installation establishment indicated that initial heights of lodgepole pine trees and Sitka alder clumps averaged 1.5 m (range ~0.3–2.7 m) and 1.8 m (range ~0.6–2.9 m), respectively. The numbers of individual stems per alder clump were not systematically tallied. However, measurements taken for a companion study showed that average-sized clumps (within 1 SD of mean height and crown width) contained between 21 and 55 stems (Sanborn et al. 2001).

²D. Burgess. 1995. Interplanting Sitka alder with lodgepole pine. Canadian Forest Service, Chalk River, Ont. Unpublished report.

Experimental design

The experiment was laid out as a completely randomized design, with four treatments replicated three times for a total of 12 plots. The four treatments were (i) pine and no alder (i.e., complete eradication of alder clumps), (ii) pine and low alder (500 clumps/ha retained), (iii) pine and moderate alder (1000 clumps/ha retained), and (iv) pine and high alder (2000 clumps/ha retained). The alder distribution was too patchy to enable the establishment of a planned additional alder retention density (i.e., 4000 clumps/ha).

During May 1995, areas of uniform site conditions with high-density alder cover (~50% alder cover and 4000 alder clumps/ha) within the cutblock were identified for plot location. A total of twelve 0.08-ha rectangular treatment plots (25.28 m × 31.60 m) were established. Each of the four treatments was randomly assigned to three of the treatment plots.

The lodgepole pine in each treatment plot was manually thinned to a density of 1000 stems/ha (i.e., 80 trees per treatment plot) in May 1995. When selecting "leave" trees, an effort was made to maintain fairly even intertree spacing. This postthinning density is considerably lower than most operational prescriptions for young lodgepole pine. However, the objective in this study was to delay crown closure so that a vigorous Sitka alder understory would be maintained for a prolonged period.

The 500, 1000, and 2000 clumps/ha alder retention regimes were created by selecting alder "leave" clumps as per a grid pattern dictated by the alder retention density. All other clumps within each treatment plot were cut near ground level followed immediately with an application of glyphosate (trade name Vision™) to the cut stumps at a rate of 2.136 kg active ingredient/ha. Concentrated glyphosate was diluted at a rate of one part herbicide to two parts water. An inspection in the summer of 1996 indicated that the herbicide treatment had achieved at least 80% mortality in the alder, with no observed damage to the retained lodgepole pine. A followup glyphosate treatment was carried out in August 1996 to control resprouting of alder stumps. The followup treatment achieved at least 95% mortality of the treated alder clumps. In subsequent years, manual clipping was undertaken as needed to ensure complete control of the target alder clumps.

In October 1995, an additional 10-m buffer was created around each treatment plot within which lodgepole pine and alder clumps were thinned by brush saws to estimated densities of 1000 stems or clumps/ha. No herbicide was applied to the cut alder stumps within these buffers.

Measurement

An 18.96 m × 18.96 m (0.036 ha) assessment plot was established within each treatment plot to monitor the growth and development of retained lodgepole pine and alder clumps. The assessment plot was offset at one end of the treatment plot to reserve an area for future destructive sampling. Three sides of the assessment plot were surrounded by a 3.16-m buffer; the buffer on the fourth side was 9.48 m wide. Each assessment plot had 36 lodgepole pine trees and a number of alder clumps proportional to the specified alder retention density (i.e., 18, 36, and 78 clumps for the 500, 1000, and 2000 alders/ha densities, respectively). All re-

tained lodgepole pine and alder clumps within each assessment plot were permanently tagged.

Pretreatment alder percent cover was assessed using the line-intercept method, for which transects were located along the four sides and two diagonals of each assessment plot. Alder percent cover was based on the tally of points, at 1-m intervals along each transect, which fell beneath alder canopies. Post-treatment estimates of alder cover were obtained by reassessing the same transects during the summers of 1996 (first year), 1998 (third year), and 2001 (sixth year).

In October 1995, after installation of the treatments, the following measurements were obtained for each tagged pine tree and alder clump: total height, diameter at breast height (DBH) (pine only), and crown width (two dimensions at right angles, alder only). These measurements were repeated in the fall of 1998 (third year) and 2001 (sixth year). The straightened length of the tallest stem within each clump was used as the height measurement for Sitka alder. The initial 3- and 6-year DBH and height measurements were used to calculate 1- to 3-year and 4- to 6-year DBH and height increments. Approximately 30% of the lodgepole pine tagged trees were less than 1.3 m tall in 1995, so initial DBH measurements were not obtained from them. These short trees were evenly distributed among treatments. Only trees with initial DBH measurements were used for calculating 1- to 3-year and 4- to 6-year DBH increments.

Foliar analysis

Samples of the current year's foliage were collected from two lateral branches within the upper one third of the live crown on 10 lodgepole pine trees in each assessment plot in October 1995. One composite sample per plot, each sample consisting of equal amounts of foliage from each of the 10 trees, was prepared for the analysis of foliar nutrient concentrations. Using the same methodology, foliar sampling and analyses were repeated in 1998 (third year) and 2001 (sixth year). Foliage samples were frozen prior to oven-drying at 70 °C for 16–24 h. Dried composite samples were ground in an electric coffee grinder prior to shipment to a commercial laboratory for chemical analysis. The same commercial laboratory was used for all three sampling dates.

Dried foliage samples were digested using a variation of the sulphuric acid – hydrogen peroxide procedure described by Parkinson and Allen (1975). The digests were analyzed colorimetrically for N using the Berthelot (phenol-hypochlorite) reaction (Weatherburn 1967) in a Technicon autoanalyzer II. Total S was determined with a Leco SC-132 S analyzer. Inorganic sulphate S (SO₄) was extracted with 0.1 mol/L HCl (1 g foliage/20 mL HCl boiled for 20 min) followed by hydriodic acid reduction of the extract and bismuth colorimetry using the procedure of Johnson and Nishita (1952). A spectrophotometer was used for the determination of P using a procedure based on the reduction of the ammonium molybdiphosphate complex by ascorbic acid (Watanabe and Olsen 1965). Total Ca, Mg, and K were measured by atomic absorption spectrophotometry. After dry ashing, B was determined by the azomethine H colorimetric method described by Gaines and Mitchell (1979).

Data analysis

The effects of Sitka alder retention density on the height

and crown width development of alder and on the DBH increment, height increment, and foliar nutrient concentration of lodgepole pine were subjected to analysis of variance (ANOVA) using the general linear model procedure (SAS Institute Inc. 1989). One- to 3-year and 4- to 6-year DBH and height increments were calculated for all trees alive after 6 years and were adjusted by covariance analysis using initial DBH and height, respectively, as the covariates.

Orthogonal polynomial contrasts were used to test the linear and quadratic trends among the quantitative treatment means (Steel and Torrie 1980). Because the alder retention treatments were not equally spaced, the contrast coefficients were derived from first principles (Bergerud 1988).

Results

Sitka alder

The pretreatment percent cover of Sitka alder was similar in all alder retention treatments (49%–53%). One year after treatment, alder percent cover was reduced to 10%, 20%, and 38% for the low (500 clumps/ha), moderate (1000 clumps/ha), and high (2000 clumps/ha) alder retention treatments, respectively. Thereafter, the percent cover increased steadily and consistently in all treatments (Fig. 1a). By year 3, the alder percent cover in the high alder retention treatment had nearly recovered to the pretreatment level and by year 6 had exceeded this value. The crown width measurements of the retained alder clumps reflected recovery in percent crown cover, with the largest crown widths, and crown width increments, measured at the lowest alder densities (Fig. 1b).

Alder retention density had a significant effect on alder height increment during the 1- to 3-year and 4- to 6-year measurement periods (Table 1). The significant linear effect is clearly illustrated in Fig. 1c. For both measurement intervals, alder height increment was inversely related to alder retention density.

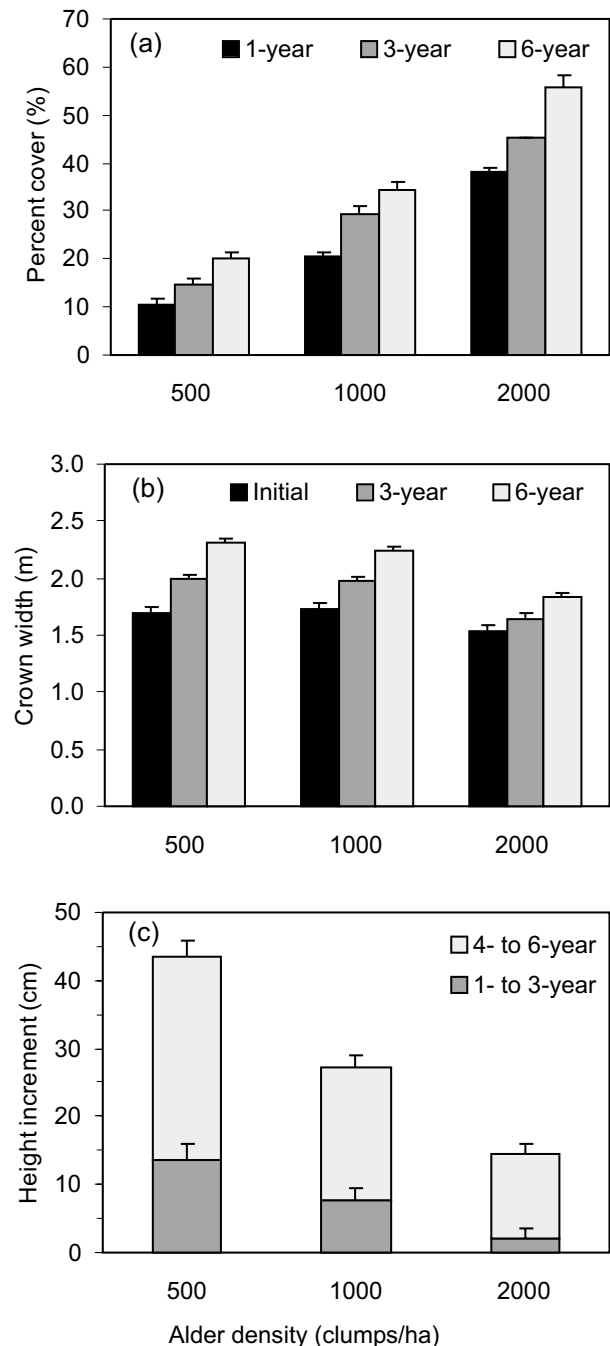
Lodgepole pine growth

Survival of lodgepole pine was apparently unaffected by varying densities of retained alder. After 6 years, survival ranged from 97% to 100% in the different treatments.

When the treatments were applied in 1995, the lodgepole pine trees were shorter than the retained alder clumps in all alder density treatments (Fig. 2). Three years later, however, pine had overtopped the retained alder in all treatments. By year 6, the height differential between pine and alder ranged from 151% to 184%.

Lodgepole pine DBH increment was significantly affected by Sitka alder during both the 1- to 3-year and 4- to 6-year measurement periods (Table 1). In the 1- to 3-year period, the effect was significantly quadratic, with 500 alder clumps/ha having a slight positive effect on DBH growth and 2000 alder clumps/ha having a slight negative effect (Fig. 3a). During the 4- to 6-year period, the effect of alder on DBH increment was linear, with less radial growth measured in the moderate and high alder retention densities than in the low-alder and no-alder treatments. Over 6 years, the effect was significantly linear (data not shown), with DBH increment in the high alder retention density 10% less than in the no-alder treatment.

Fig. 1. (a) Percent cover, (b) crown width, and (c) height increment of Sitka alder by year and alder retention treatment. Error bars represent standard error.



After 3 years, the various alder retention treatments had no effect on lodgepole pine height increment (Table 1; Fig. 3b). However, the effect of alder density on the height increment of pine was significant and linear during the 4- to 6-year period, with progressively less height growth with increasing alder density (Fig. 3b). Over 6 years, the effect was significantly linear (data not shown), with height increment in the high alder retention density 12% less than in the no-alder treatment.

Table 1. ANOVA summary table for 1- to 3-year and 4- to 6-year height increment of Sitka alder and 1- to 3-year and 4- to 6-year DBH and height increment of lodgepole pine showing variance ratios (*F*), *p* values, and mean square errors.

Source of variation	df	1- to 3-year		4- to 6-year	
		<i>F</i>	<i>p</i> > <i>F</i>	<i>F</i>	<i>p</i> > <i>F</i>
Sitka alder height increment					
Treatment	2	6.64	0.030	7.81	0.021
Linear	1	12.50	0.012	15.39	0.008
Quadratic	1	0.24	0.641	1.00	0.356
Mean square error	374	0.032		0.033	
Lodgepole pine DBH increment					
Treatment	3	4.60	0.037	5.99	0.019
Linear	1	3.96	0.082	17.49	0.003
Quadratic	1	7.61	0.025	0.29	0.605
Mean square error	279	0.208		0.249	
Lodgepole pine height increment					
Treatment	3	1.35	0.325	5.06	0.030
Linear	1	0.74	0.415	15.03	0.005
Quadratic	1	2.02	0.193	0.16	0.703
Mean square error	420	0.047		0.066	

Lodgepole pine foliar nutrition

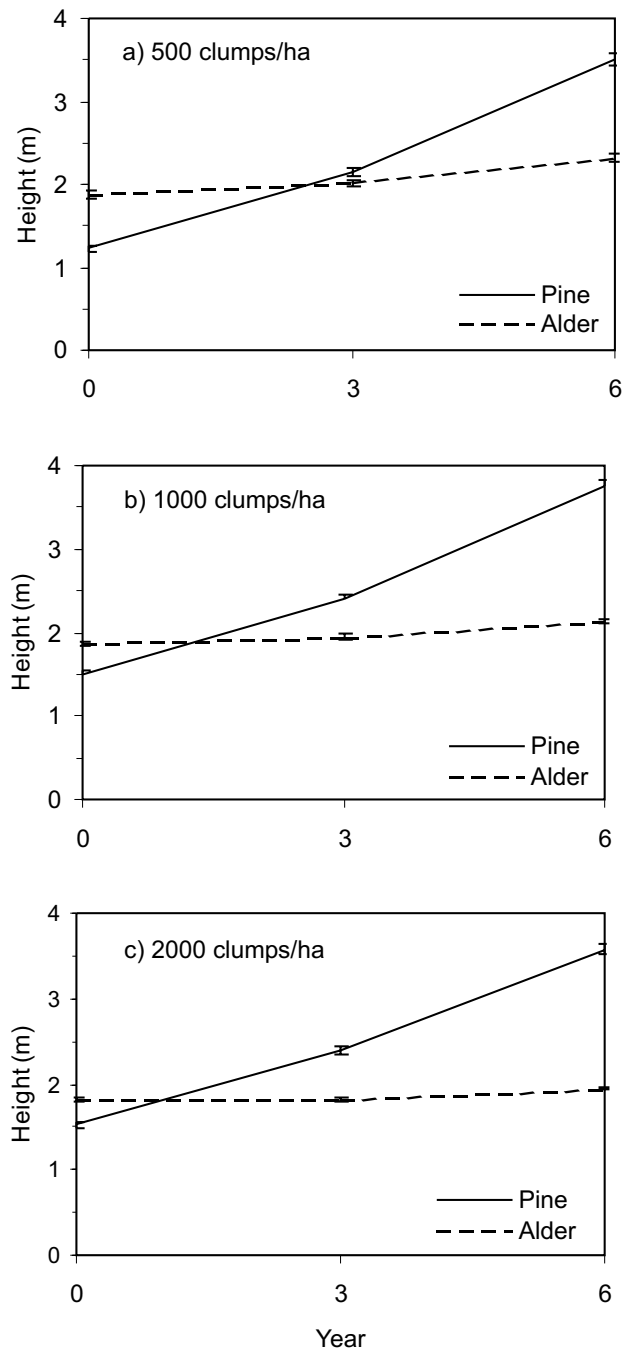
Initial lodgepole pine foliar N levels were high in all treatments, averaging 16.5 g/kg for the fall 1995 sampling (Fig. 4a). There was a significant treatment effect evident by year 3 (Table 2), with lodgepole pine in the no-alder treatment having lower foliar N levels than trees in the alder retention treatments (Fig. 4a). By year 6, the positive influence of retained alder on foliar N in lodgepole pine was clearly evident (Fig. 4a). The effect of alder density on foliar N was strongly linear (Table 2), with the lowest N levels occurring in the no-alder treatment and the highest N levels in the high-alder treatment.

With the possible exception of S, foliar levels of other nutrients were relatively unaffected by treatment (Table 3). However, treatment effects were evident in the balance of foliar N relative to several other nutrients. In years 3 and 6, there were significant treatment effects for foliar N/S, N/P, and N/K (Table 2), with lodgepole pine in the no-alder treatment having lower ratios than trees in the various alder retention treatments (Figs. 4b, 4c, and 4d). A strong linear relationship between alder density and foliar N/S was present in years 3 and 6 (Table 2). This is clearly illustrated in Fig. 4b, with progressively higher ratios with increasing alder density. Significant linear relationships were also detected for foliar N/P and N/K (Table 2; Figs. 4c and 4d). For N/P, there was also a significant quadratic effect in year 6 (Table 2; Fig. 4c).

Discussion

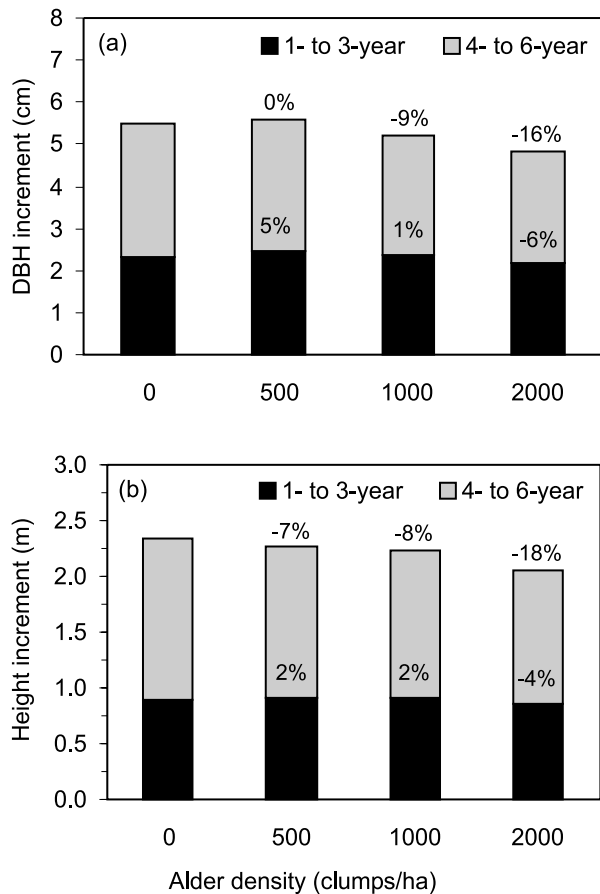
In central British Columbia, Sitka alder typically reaches a mature height of only 3 m (Haeussler et al. 1990). These growth characteristics undoubtedly make it a less serious competitor than the taller-growing red alder (*Alnus rubra* Bong.) in coastal ecosystems (Harrington and Deal 1982; Binkley et al. 1984). Nevertheless, the Sitka alder at this site

Fig. 2. Height development of lodgepole pine and Sitka alder at different alder retention densities: (a) 500, (b) 1000, and (c) 2000 clumps/ha. For each year, plotted values are means of all measurements combined. Error bars represent standard error.



is exhibiting vigorous growth. After 6 years, mean alder height across all alder retention densities is 2.05 m, with the tallest clumps and largest height increments being associated with the lowest alder density. Fourteen years after harvest, the retained clumps in all of the alder retention treatments continue to produce significant height and crown width increment. At the high alder retention density, the mean crown cover of 56% surpasses the 30%–50% cover estimate for fully mature alder cover in the Montane Spruce biogeo-

Fig. 3. (a) Diameter and (b) height increment of lodgepole pine by measurement period and alder retention treatment. Numbers above bars indicate change relative to the no-alder treatment for each measurement period.



climatic zone in the southern interior (B.C. Ministry of Forests 1997a).

Simard (1990) observed that Sitka alder cover up to 35% did not generally reduce the growth of 6- to 10-year-old naturally regenerated lodgepole pine stands in the Montane Spruce biogeoclimatic zone in south-central British Columbia. Simard and Heineman (1996) refined this estimate, observing that pine growth in the more productive Interior Cedar–Hemlock biogeoclimatic zone was better when alder cover was reduced from 22% to 15%–18%. To date, the results from the present study indicate that low to moderate levels of alder cover do not significantly inhibit the DBH or height growth of young lodgepole pine in north-central British Columbia. Even at the highest alder retention density (2000 clumps/ha), DBH and height growth of lodgepole pine were not reduced until alder cover exceeded 45%. Over the entire 6-year response period, DBH and height increments under high alder cover were reduced by 10% and 12%, respectively, relative to the no-alder treatment. In absolute terms, mean DBH and height reductions were 6 mm and 28 cm, respectively. Growth reductions of a similar magnitude were reported by Simard and Heineman (1996). Conversely, significant increases in the growth of black spruce (*Picea mariana* (Mill.) BSP) and Sitka spruce (*Picea sitchensis* (Bong.) Carrière) were associated with high densi-

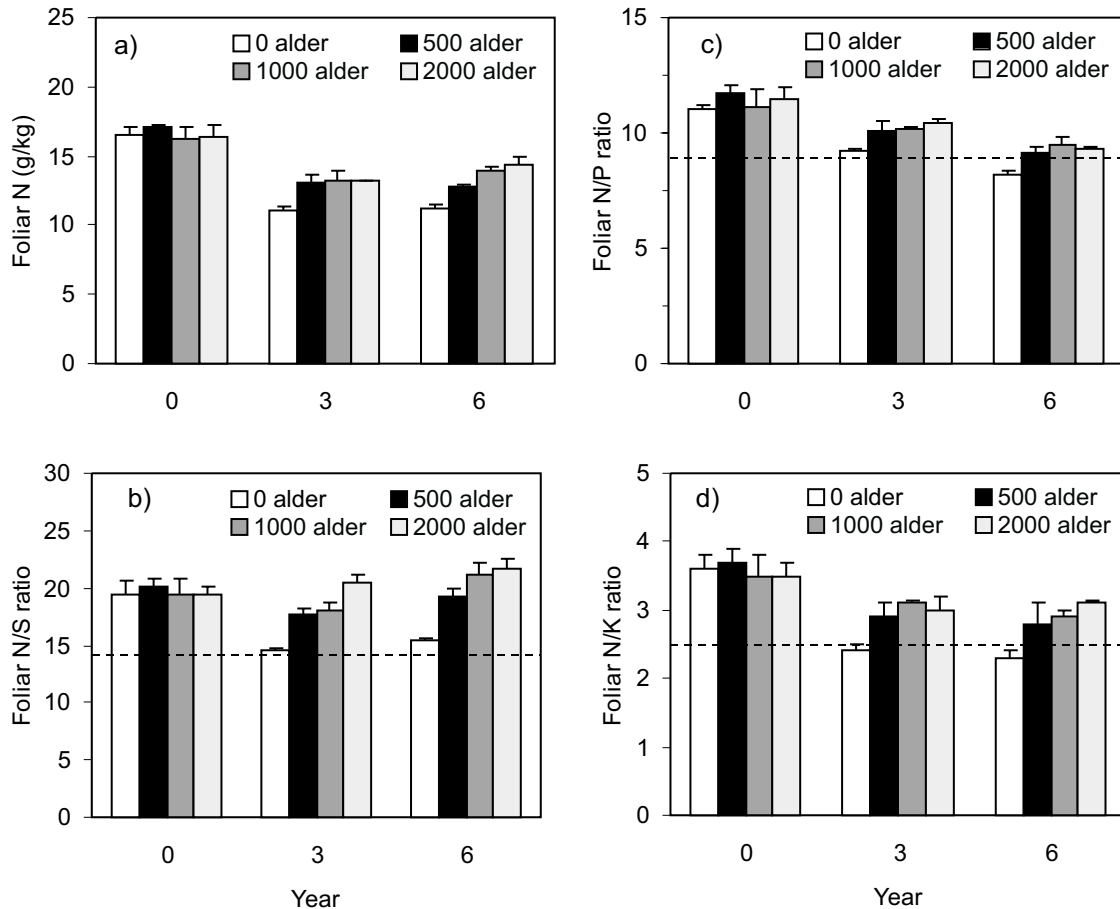
ties of green alder (*Alnus crispa* (Ait.) Pursh) in Newfoundland (Hudson 1993). Improved foliar N levels and protection from severe winter weather were suggested as possible explanations for the beneficial effects of alder on conifer plantation performance.

Simard (1990) and Simard and Heineman (1996) reported that stem diameter of lodgepole pine was more affected than height growth by alder competition. These observations are consistent with those reported from lodgepole pine thinning research, where stem radial increment is much more sensitive than height to changes in stand density (Johnstone 1985). In fact, there is evidence that some degree of crowding is required to maximize height growth of lodgepole pine (Johnstone 1981, 1982). In the present study, however, relative DBH and height increments were similarly affected by alder competition. Even at the lowest alder retention density, there was a small negative effect on lodgepole pine height increment in the 4- to 6-year measurement period.

Given the relatively large height differential between lodgepole pine and Sitka alder by year 6 (184%), it seems likely that soil resources (e.g., moisture and temperature) are more important than light availability in limiting pine growth in the high alder retention treatment at our study site. Results from alder competition studies in south-central British Columbia also indicate that competition for soil resources is more important than light availability in limiting the growth of lodgepole pine. Simard (1990) reported that DBH responses of lodgepole pine resulted not from removal of alder alone but rather from removal of alder, herbs, and low-growing shrubs. Maximum and minimum soil temperatures at 5 and 30 cm depth were considerably lower under an alder and herb canopy compared with a treatment where vegetation was completely removed (Simard 1990). Simard and Heineman (1996) reported that manual cutting of alder caused a significantly greater reduction in Sitka alder height and cover than glyphosate treatment, but lodgepole pine growth was not correspondingly better. Although soil moisture was less affected than soil temperature, soil water potential in the summer was significantly higher where all vegetation had been removed than where shrubs and herbs remained (Simard and Heineman 1996).

Neither soil temperature nor soil moisture was measured in the present study. However, forest soils in subboreal ecosystems are generally too cold for maximum root growth of seedlings, and the removal of competing vegetation has been reported to significantly increase soil temperature (Dobbs and McMinn 1977; McMinn 1982). Also, Ballard and Hawkes (1989) inferred that the beneficial effects of broadcast burning on the growth of planted white spruce were attributable to soil warming caused by removing the insulating effects of vegetation and forest floor. Soil moisture deficits are likely less prevalent in moist sub-boreal ecosystems than in drier climates in the southern interior. However, a strong relationship between forest productivity (as measured by site index) of lodgepole pine and soil moisture regimes within the SBS biogeoclimatic zone was reported by Wang et al. (1994). Our study site has a slightly dry actual soil moisture regime and a predicted site index of 18 m at 50 years of age (B.C. Ministry of Forests 1997b), representing intermediate productivity for the SBSdw3 subzone. According to DeLong et al. (1993), submesic sites with high soil coarse fragment

Fig. 4. (a) Foliar N concentration, (b) N/S ratio, (c) N/P ratio, and (d) N/K ratio in current-year foliage of lodgepole pine by alder retention treatment and year. Error bars represent standard error. The dashed horizontal line represents a “critical” level above which a probable nutrient imbalance (i.e., deficiency) relative to N is indicated (Brockley 2001b).



content (>70%) within this subzone have significantly reduced soil moisture retention, resulting in a drought hazard for a significant portion of the growing season. The coarse fragment content at our submesic study site was only moderate (30%–40%). However, relatively low summer precipitation (225–300 mm), combined with significant evaporative demand and interception of precipitation by the alder canopy, likely makes this site susceptible to periodic growing season soil water deficits (D. Spittlehouse, B.C. Ministry of Forests, Victoria, B.C., personal communication).

As an N-fixing species, Sitka alder has a potentially important role in maintaining long-term productivity in N-deficient lodgepole pine stands in the interior of British Columbia. This role needs to be considered when evaluating the significance of short-term competitive interactions with pine early in stand development. On some sites, the competitive effects of Sitka alder on crop trees may be outweighed by the long-term benefits of N accretion. Measurements made over a 3-year period at this site indicate that symbiotic N fixation by alder in the 2000 clump/ha treatment is contributing 10–15 kg N/ha annually (Sanborn et al. 2002). Although such amounts may seem small, when projected over the entire period prior to canopy closure, the cumulative N accretion may largely offset typical N losses from wildfire and (or) harvesting in these ecosystems. Moreover, since Sitka alder can persist as an understory shrub throughout

stand development, this N accretion will continue, although likely at a reduced rate. Even under the canopies of 150-year-old pine stands near this site, Sitka alder was able to meet almost all of its N requirements from fixation (Sanborn et al. 2002).

Sitka alder clumps are long-lived and may survive more than one stand-destroying disturbance. Their long-term persistence leads to localized nutrient enrichment, particularly in the forest floor. Measurements at this site in 1995 found that forest floor total N and mineralizable N concentrations were significantly higher under alder clumps relative to locations between clumps (Sanborn et al. 2001). Total N in the 0–20 cm mineral soil was also enriched under alder clumps, although less dramatically than in the forest floor.

The relatively high foliar N levels (~16.5 g/kg) measured in lodgepole pine foliage prior to the application of the alder treatment regimes are not surprising given the young age of the trees and soil N enrichment resulting from N fixation and more rapid N cycling from the vigorous alder cover. What is surprising, however, is the rapidity of decline in foliar N within the no-alder treatment. After 3 years, lodgepole pine foliar N concentration in the no-alder treatment was only 11.0 g/kg, indicating moderate to severe N deficiency (Ballard and Carter 1986; Brockley 2001b). The elimination of alder litterfall (and thus reduced N additions to the soil N pool) may partially account for the rapid decline in lodge-

Table 2. ANOVA summary table for lodgepole pine foliar N concentration, N/S ratio, N/P ratio, and N/K ratio by year showing variance ratios (*F*), *p* values, and mean square errors.

Source of variation	df	Initial		3-year		6-year	
		<i>F</i>	<i>p</i> > <i>F</i>	<i>F</i>	<i>p</i> > <i>F</i>	<i>F</i>	<i>p</i> > <i>F</i>
Foliar N							
Treatment	3	0.28	0.839	5.50	0.024	10.38	0.004
Linear	1	0.16	0.702	7.73	0.024	26.07	0.001
Quadratic	1	0.00	0.947	7.46	0.026	5.03	0.055
Mean square error	8	1.202		0.655		0.554	
Foliar N/S							
Treatment	3	0.12	0.945	16.21	0.001	12.03	0.002
Linear	1	0.02	0.880	43.93	0.001	26.95	0.001
Quadratic	1	0.05	0.825	2.06	0.189	9.09	0.017
Mean square error	8	2.761		1.082		1.973	
Foliar N/P							
Treatment	3	0.30	0.825	5.04	0.030	5.52	0.024
Linear	1	0.12	0.742	10.53	0.012	9.25	0.016
Quadratic	1	0.02	0.878	3.63	0.093	7.19	0.028
Mean square error	8	0.847		0.176		0.178	
Foliar N/K							
Treatment	3	0.21	0.886	3.52	0.068	4.49	0.040
Linear	1	0.42	0.535	6.45	0.035	9.97	0.013
Quadratic	1	0.00	0.998	4.04	0.079	2.65	0.142
Mean square error	8	0.131		0.081		0.083	

Table 3. Mean foliar nutrient concentrations of lodgepole pine by alder retention regime 6 years after treatment.

Treatment	N (g/kg)	P (g/kg)	K (g/kg)	Ca (g/kg)	Mg (g/kg)	S (g/kg)	SO ₄ (mg/kg)	B (mg/kg)
No alder	11.2 (0.35)	1.37 (0.03)	4.93 (0.03)	1.90 (0.12)	0.74 (0.03)	0.73 (0.02)	11.3 (1.5)	8.3 (0.9)
500 clumps	12.7 (0.18)	1.40 (0.06)	4.60 (0.60)	1.70 (0.20)	0.78 (0.04)	0.67 (0.03)	10.0 (0.1)	8.7 (0.3)
1000 clumps	13.9 (0.38)	1.47 (0.03)	4.77 (0.15)	1.67 (0.15)	0.74 (0.07)	0.66 (0.02)	9.3 (0.7)	8.0 (0.6)
2000 clumps	14.3 (0.67)	1.53 (0.09)	4.63 (0.18)	1.83 (0.07)	0.84 (0.06)	0.66 (0.00)	10.0 (0.1)	7.0 (0.6)
LSD ^a	1.40	0.188	1.053	0.458	0.169	0.070	2.61	2.03

Note: For each treatment, values represent means of three composite samples. Numbers in parentheses indicate standard error.

^aLeast significant difference (*p* = 0.05).

pole pine foliar N following alder eradication at this study site. However, data from a companion study indicated that mean annual input of alder leaves in treatment plots with retention of 2000 alder clumps/ha averaged 379 kg/ha, representing a total annual N input of only 6.9 kg/ha (Sanborn et al. 2002). This is a very small amount of N relative to the 1850 kg total N/ha in the forest floor and upper mineral soil (0–20 cm) at the study site (Sanborn et al. 2001). It is also a small amount relative to typical annual N mineralization rates (20–40 kg/ha) for forest soils (Binkley and Hart 1989). Also, Berg and Cortina (1995) reported that net N release from several types of litter, including gray alder (*Alnus incana* (L.) Moench), does not typically occur until mass loss reaches about 40%–50%. For alder litter, it may take 1–2 years to reach this threshold (Berg and Ekbohm 1991).

The rapid decline in lodgepole pine foliar N following alder eradication, coupled with the strong positive linear trend between foliar N and retained alder density, may offer indirect field evidence for the occurrence of a direct N transfer mechanism between the roots of Sitka alder and lodgepole pine. In a laboratory study, Arnebrant et al. (1993) reported

that European black alder (*Alnus glutinosa* (L.) Gaertn.) and lodgepole pine were interconnected by mycelium of the ectomycorrhizal fungus *Paxillus involutus* (Fr.) Fr. They estimated that about 20% of the N in the lodgepole pine was derived from fixation, which strongly indicated a net transfer of N from the alder to the pine via this shared hyphal pathway. Although likely of low ecological significance, the net transfer of a small amount of fixed N from gray alder and Scots pine (*Pinus sylvestris* L.) was reported by Ekblad and Huss-Danell (1995). At our study site, Varga (1998) found that lodgepole pine and Sitka alder shared mycorrhizal fungi of two genera, although this did not prove that actual interspecies linkages existed below ground.

Based on published foliar diagnostic criteria, foliar nutrient ratio data indicated probable imbalances of N relative to S, P, and K in all treatments prior to alder manipulation in 1995 (Kelly and Lambert 1972; Ingestad 1979; Linder 1995). In years 3 and 6, lower foliar N levels resulted in more favourable N/S, N/P, and N/K in the no-alder treatment. In the 500, 1000, and 2000 alder clumps/ha retention treatments, however, these foliar nutrient ratios remained

above, or close to, probable "critical" levels throughout the study period. The effects of the differing alder retention treatments on the foliar N and S status of lodgepole pine are consistent with the results reported from fertilization research studies in the central interior of British Columbia (Brockley and Sheran 1994; Brockley 1996, 2000, 2001a). In studies with lodgepole pine, foliar N/S ratios often increase dramatically after N fertilization. Accumulated evidence indicates that S deficiencies, either aggravated or induced by N additions, are responsible for the unresponsiveness of some lodgepole pine stands to N additions. Favourable growth responses to combined applications of N and S have been documented in many of these stands (Brockley 2000). In the present study, the foliar SO_4 levels measured in pine foliage within the various alder retention treatments in years 3 and 6 also indicate probable S deficiency and suggest that foliar N may not be fully utilized in protein synthesis (Kelly and Lambert 1972). At these levels of N and SO_4 , a regression model developed for lodgepole pine would predict a small growth response to fertilization with N alone, even where foliar N levels are deficient (Brockley 2000). The imbalance of N relative to S in lodgepole pine growing in association with alder in this study is partly caused by elevated N levels and partly by lower S levels in foliage. Because aboveground estimates of lodgepole pine biomass were not obtained, it is not possible to state with certainty whether lower foliar S concentrations are attributable to dilution resulting from increased pine biomass or to reduced uptake of soil S. However, Brockley and Sheran (1994) reported reduced S uptake following N fertilization of lodgepole pine in the central British Columbia interior. Similarly, by combining the foliar biomass and foliar nutrient data reported by Binkley et al. (1984), the lower foliar S levels in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) grown in association with Sitka alder can be attributed to reduced S uptake.

The imbalance of N relative to P is consistent with the results reported for Douglas-fir growing in association with Sitka alder and red alder on Vancouver Island (Binkley et al. 1984). Impaired P nutrition may have limited the performance of both alder and Douglas-fir. Decreased P availability under red alder cover was also hypothesized by Van Miegroet et al. 1990.

The beneficial effect of retained Sitka alder on lodgepole pine foliar N and the apparent negative effect of alder on foliar nutrient balance pose some interesting problems when interpreting the pine and alder growth data. Although competition with Sitka alder for light and soil resources may be largely responsible for the smaller DBH and height growth of pine in the moderate- and high-alder treatments, it is possible that foliar nutrient imbalances resulting from higher N levels may also have contributed to these results. Also, the height growth potential of pine in all treatments at this site may have been partially suppressed by low soil B availability. Visible symptoms of B deficiency were not present in this study. However, foliar B levels within the range measured in this study (6–8 mg/kg) have been shown to inhibit the height growth of lodgepole pine in the absence of acute B deficiency symptoms (Brockley 1990, 2003). Unless alleviated, nutritional imbalances may preclude reliable assess-

ment of the competitive effects (i.e., light and soil resources) of alder density, if any, on lodgepole pine growth.

Low soil availability of S (possibly also P and K) may also be affecting the growth performance and N fixation activity of Sitka alder on this site. A bioassay of soil samples from a red alder – Douglas-fir stand showed that red alder seedlings produced double the biomass and four times the N fixation per plant when P and S were added (Binkley 1986). The indication that N accretion by Sitka alder may exacerbate nutritional problems (especially S and B) that are known to exist on interior sites may have implications regarding the future growth and management of lodgepole pine growing in association with alder. Further research is warranted to examine whether the growth of lodgepole pine growing under similar conditions, as well as the growth and N accretion potential of Sitka alder, can be improved by the application of S and B (possibly also P and K), with and without added N fertilizer.

Given the small absolute differences in DBH and height growth among the various alder retention treatments to date, forest practitioners should likely assign a low priority to the control of Sitka alder on submesic sites in the SBS biogeoclimatic zone. Brushing may only be needed in cases where alder density is uniformly high (i.e., >45%) or where the removal of localized patches is necessary to release individual pine trees. The monitoring of this experiment will continue so that the effects of Sitka alder density on the growth and nutrient status of lodgepole pine can be documented over the long term.

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