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N_2-fixation by Sitka alder in a young lodgepole pine stand in central interior British Columbia, Canada

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Abstract

Annual N_2-fixation by Sitka alder (*Alnus viridis* (Chaix) DC. ssp. *sinuata* (Regel) A.&D. Love) was estimated at 10–15 kg N ha^{-1} over three growing seasons in a young lodgepole pine (*Pinus contorta* Dougl. ex Loud.) stand in the Sub-Boreal Spruce biogeoclimatic zone of British Columbia (BC), Canada. Unlike the ambiguous evidence provided by ^{15}N natural abundance, the isotope dilution method indicated that >90% of the N in new alder tissues was derived from the atmosphere. Despite low light levels (18.1% of open sky values), alders growing under a mature lodgepole pine canopy (>150-year-old) obtained a similarly high proportion of their N requirements by N_2-fixation.

Keywords: Alder; Litterfall; Lodgepole pine; N_2-fixation

1. Introduction

The actinorhizal shrub Sitka alder (*Alnus viridis* (Chaix) DC. ssp. *sinuata* (Regel) A.&D. Love) is an important component of lodgepole pine (*Pinus contorta* Dougl. ex Loud.) stands in the Sub-Boreal Spruce biogeoclimatic zone (DeLong et al., 1993), as well as similar forest types in central and southern interior British Columbia (BC) (Haeussler and Coates, 1986). In young stands, Sitka alder can provide 50% or more cover, leading to competitive effects on the crop conifers. Offsetting this concern, this species has been shown to benefit site fertility through its symbiotic N_2-fixation, with estimates from the Pacific Northwest ranging from 20 to 150 kg N ha^{-1} per year (Binkley, 1986). Therefore, management of conifer stands with a significant Sitka alder component has to consider this tradeoff. Haeussler and Coates (1986) recognized a need for studies to determine if N_2-fixation by Sitka alder was beneficial to crop trees on interior BC sites.

Fertilization research has demonstrated widespread N deficiencies in lodgepole pine stands in central interior BC (Brockley, 1996), and significant N losses can occur from both biomass and forest floors during prescribed fires in this region (Kranabetter and Macadam, 1998). Symbiotic N_2-fixation may play an important role in restoring and maintaining soil N capital after natural and anthropogenic disturbances in these forests, so it is important to have a better understanding of its quantitative significance during early stand development.

To date, most of the relevant BC studies have involved southern interior sites. Simard (1990) observed that in 6–10-year-old naturally regenerated

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lodgepole pine stands in the Montane Spruce biogeoclimatic zone, Sitka alder cover up to 35% did not generally reduce pine growth. Later, Simard and Heineman (1996) refined this estimate, observing positive pine growth responses when alder cover was reduced from 22 to 15–18%. For similar stands, Sachs (personal communication) estimated annual N_2-fixation rates to be 1.5–8 kg ha^{-1} per year. Elsewhere in the BC southern interior, Mead and Preston (1992) used ^{15}N isotope dilution to demonstrate N_2-fixation by Sitka alder in a fertilized lodgepole pine stand, with approximately 50 kg N ha^{-1} accumulated by aboveground alder biomass in 8 years. In the only published study involving Sitka alder in the BC central interior, Ballard and Hawkes (1989) observed that proximity of this species enhanced the foliar N concentrations of white spruce (*Picea glauca* (Moech) Voss) planted on windrowed sites north of Prince George.

Sitka alder and other shrubby *Alnus* species can be very persistent in understories of conifer forest (Wurtz, 1995), surviving stand-destroying disturbances by regenerating from rootstocks. Our observation in central interior BC is that most Sitka alders in young conifer stands have regenerated in this manner, with recruitment of new seedlings restricted to areas of exposed mineral soil.

Previous studies have used three principal methods for detecting and quantifying N_2-fixation by *Alnus* spp. and other woody perennials, and each approach has following distinctive advantages and disadvantages.

1. Although fast and inexpensive, acetylene reduction assays of root nodules are problematic for stony sites where root excavations are difficult. Results from this method are difficult to extrapolate to estimates of seasonal rates (Weaver and Danso, 1994).
2. The ^{15}N natural abundance method has been promoted as being well suited to field experiments with woody perennials (Virginia et al., 1989). In practice, the utility of this method is severely limited in many ecosystems by the diversity of soil N pools, the absence of appropriate reference plants, and other inherent complexities (Handley and Scrimgeour, 1997). For this method to be able to quantify N_2-fixation, Högberg (1997) recommended that the difference in $\delta^{15}N$ values between the reference and N_2-fixing species be at least 5‰. The best results from this approach are obtained from simple field settings such as can be found in primary successions (e.g. Hobbie et al., 1998).
3. ^{15}N isotope dilution is the most expensive method, and the choice of non-N_2-fixing reference species is of critical importance. Once established, labeled plots allow N_2-fixation processes during long-term stand development to be studied by sequential resampling (Mead and Preston, 1992).

The purpose of this study is to estimate N_2-fixation by Sitka alder at a representative BC central interior site where pre-existing clumps have regenerated in a young lodgepole pine stand. Although the extent of N_2-fixation by alder will be estimated by the ^{15}N isotope dilution method, a subsidiary objective is to examine complementary natural abundance data to compare the utility of both isotopic methods. Finally, N_2-fixation activity by Sitka alder will be examined in relation to the understory light environment of adjacent mature lodgepole pine forests.

2. Materials and methods

2.1. Study site

The principal study site (123°3′W, 53°41′N) is located in a 40 ha opening in the Vanderhoof Forest District, approximately 55 km southwest of Prince George, BC, at an elevation of 1030 m in the Stuart Dry Warm variant of the Sub-Boreal Spruce biogeoclimatic zone (DeLong et al., 1993). The site has a west aspect, with slopes ranging from 5 to 20%. Soils are medium-textured to coarse-textured (loam to sandy loam) with 30–40% gravels and cobbles and are classified as Brunisolic Gray Luvisols (Arocena and Sanborn, 1999; Soil Classification Working Group, 1998). The previous lodgepole pine forest was logged in 1987 and natural regeneration of pine occurred without prescribed burning or any subsequent thinning treatment. Stumps in this opening were too decayed to allow ring counting, but maximum ages of lodgepole pine trees in mature stands at four sites within 4 km of this opening ranged from 149 to 167 years. Virtually all of the alders at this site had regenerated from clumps inherited from the previous

stand, as evidenced by their large (up to 30 cm diameter) woody rootstocks. By 1995, pine density had reached 10,430 stems ha^{-1}, while alder density averaged 4100 clumps ha^{-1}, representing a mean alder cover of 51% (Sanborn et al., 2001). Similar or greater alder densities are common in young pine stands elsewhere in the Sub-Boreal Spruce zone in the Vanderhoof Forest District (DeLong, personal communication).

2.2. ^{15}N methods

The treatments for the isotope dilution experiment were installed in June 1996. Fourteen 2 m radius circular mini-plots were randomly scattered throughout the opening, each at least 20 m distant from the nearest main treatment plot for a related pine–alder competition study (Sanborn et al., 2001). Each mini-plot was centered on an alder clump of approximately average size (i.e. within 1 standard deviation (S.D.) of mean height and crown width) and pine seedlings within a 2 m radius were thinned so that no more than three average-sized seedlings remained. Additional thinning of pines to a density of approximately 1000 stems ha^{-1} was performed out to a radius of 5 m.

Highly-enriched (98 atom% ^{15}N) $(NH_4)_2SO_4$ was applied in solution at the rate of 0.2 g ^{15}N m^{-2} on 13 June 1996, immediately after sampling of foliage from alder, pine and other major woody and herbaceous species growing on the mini-plots (birch-leaved spirea (*Spiraea betulifolia* Pall. ssp. *lucida* (Dougl. ex Greene) Taylor and MacBryde), black huckleberry (*Vaccinium membranaceum* Dougl. ex Hook.), bluejoint (*Calamogrostis canadensis* (Michx.) Beauv.), fireweed (*Epilobium angustifolium* L.), red raspberry (*Rubus idaeus* L. var. *strigosus* (Michx.) Maxim) for determination of ^{15}N natural abundance. Foliar sampling was repeated on 20 August 1996 and 12 August 1997.

To determine if N_2-fixation was occurring in alders under the mature pine forest canopy, we created four more mini-plots in a similar manner on 23 June 1997. These were located 200 m–4 km from the main study site and were chosen so as to contain alder clumps of average size under an overstory canopy density typical of the mature pine stands in the vicinity. Foliar sampling of alder and associated shrubs and herbs (birch-leaved spirea, black huckleberry, prickly rose (*Rosa acicularis* Lindl. ssp. *sayi* (Schwein.) W.H. Lewis)) was carried out immediately before labeling, and repeated on 12 August 1997.

In early August 1998, foliar sampling was repeated, and four mini-plots in the main opening were randomly selected for more complete destructive sampling of other biomass components of alder and associated plants (fine branches, main stems, fine roots, reproductive structures). Composites of forest floor, and 0–20 and 20–35 cm depth mineral soil were prepared from 10 random locations in each of these four mini-plots. Each composite was split in the laboratory, with half air-dried and the remainder kept refrigerated in a field-moist condition.

Plant, forest floor and mineral soil samples were ground to pass a no. 40 sieve (0.425 mm) and analyzed for total N by the semimicro-Kjeldahl method, with mercuric oxide used as the catalyst. The distillates, collected in boric acid–ethanol, were dried at 70 °C. The ammonium N was converted to dinitrogen gas using the Rittenberg reaction with alkaline lithium hypobromite, and analyzed for ^{15}N enrichment using a Vacuum Generators Sira nine mass spectrometer. NH_4^+–N and NO_3^-–N were extracted with 2 M KCl from field-moist forest floor and mineral soils, with analysis by distillation with MgO and Devarda's alloy and titration with HCl. NO_3^-–N was barely detectable, so isotope analysis was performed on composited samples of the distillates of the NH_4^+ and NO_3^- species.

The pre-labeling foliar ^{15}N natural abundance data from 1996 were used to calculate the proportion of alder N derived from atmosphere (FN_{dfa}):

$$FN_{dfa} = \frac{\delta^{15}N_0 - \delta^{15}N_t}{\delta^{15}N_0 - \delta^{15}N_a}$$

where $\delta^{15}N_a$ is the ^{15}N natural abundance of fixed N for the N_2-fixing plant grown in an N-free medium, $\delta^{15}N_t$ is the $\delta^{15}N$ value for the N_2-fixing species growing in the field, and $\delta^{15}N_0$ is the $\delta^{15}N$ value for the non-fixing reference species (Shearer and Kohl, 1986). We did not measure $\delta^{15}N_a$ directly, but used published values for other *Alnus* species: −0.3‰ (Binkley et al., 1985) and −1.9‰ (Domenach et al., 1989).

For the isotope dilution experiment involving the labeled mini-plots, the percentage of N in the alder

tissues that was derived from the atmosphere ($\%N_{dfa}$) was calculated as (Warembourg, 1993)

$$\%N_{dfa} = \left\{1 - \frac{^{15}\text{N atom}\% \text{ excess (fixing plant)}}{^{15}\text{N atom}\% \text{ excess (non-fixing plant)}}\right\} \times 100$$

2.3. Above-ground biomass production

Litterfall was monitored from May 1996 through May 1999 in three (25.28 m × 31.60 m) associated plots in which alder cover had been slightly reduced to approximately 40% (2000 clumps ha^{-1}) in 1995 (Sanborn et al., 2001). Twenty littertraps (33 cm diameter), based on a design by Högberg et al. (1987), were deployed in each plot. Most of the litterfall occurred during September and October, so traps were emptied twice yearly (late October, early May). Litter materials were dried to constant weight at 70 °C before sorting and weighing, and determination of N content with a LECO CHN-600 Elemental Analyzer.

Estimating above-ground alder biomass and production presented significant difficulties. Although the clumps seldom exceeded 2.5 m in either height or diameter, each could contain 50 or more stems, making it impractical to use biomass estimation equations based on individual stems, as was done by Wurtz (1995) and Binkley (1982). Instead, we developed calibration equations based on the above-ground biomass of entire clumps ($n = 50$) which were measured (maximum height, maximum horizontal crown width, second width measurement at 90° to first) and weighed after destructive sampling in late May, 1998. These equations were to be applied to the measurements made in 1995 and 1998 on the alders ($n = 234$) retained in the three assessment plots of the 2000 clump ha^{-1} retention treatment in the main thinning study.

2.4. Light environment in the mature stands

The light environment of the alders in the four labeled mini-plots under the mature lodgepole pine canopy was estimated from paired open sky and understory measurements taken using LAI-2000 plant canopy analyzers (LI-COR Inc., Lincoln, NB). Other studies have shown that diffuse non-interceptance (DIFN) values provided by this sensor provide unbiased estimates of average growing season fractional transmittance (% of open-sky light) (Gendron et al., 1998; Comeau et al., 1998; Machado and Reich, 1999). Measurements were taken using two sensors under overcast sky conditions on 21 June 1999. One sensor recorded open sky readings at 30 s intervals, while the second was used to take measurements just above the alder at each of the four mini-plots under the pine canopy. After merging open sky and below-canopy data, DIFN was calculated using measurements from the upper four sensor rings (0–58° from vertical).

3. Results and discussion

Approximately 80% of the mean annual above-ground litterfall of 583.9 kg ha^{-1} consisted of alder components, with only a minor contribution from the young pine trees (Table 1) (almost all of the ''other'' litter category consisted of alder seeds released during fall and early winter). Litterfall from the young pine trees contributed only 14% of the total. Alder components comprised 86% of the annual litterfall N return of 10 kg ha^{-1}. Alder leaf samples (August 1996–1998) from the ^{15}N-labeled mini-plots had total N concentrations ranging from 20.6 to 22.6 g kg^{-1}, as compared with a mean N concentration of 19.7 g kg^{-1} in alder leaf litter, indicating that little retranslocation occurred before abscission.

We tested several simple and multiple regressions of the alder clump measurement variables and their

Table 1
Annual litterfall and nitrogen return (May 1996–May 1999) for plots with retention of 2000 alder clumps and 1000 lodgepole pines ha^{-1}

Component	Litterfall biomass (kg ha^{-1})		Total nitrogen (kg ha^{-1})	
	Mean	S.D.	Mean	S.D.
Alder leaves	379.0	158.5	6.9	3.1
Alder seed cones	42.6	19.7	0.6	0.3
Pine needles	79.7	65.1	0.9	0.8
Twigs	18.2	15.1	0.2	0.2
Deciduous leaves	8.2	11.2	0.2	0.3
Herbaceous	12.4	7.0	0.1	0.1
Other	43.9	27.6	1.1	0.8
Total	583.9	264.6	10.0	4.7

Table 2
Alder biomass and annual growth (kg ha^{-1}) increment for plots with retention of 2000 clumps ha^{-1} (1995–1998)

Plot number	Biomass		Annual growth
	1995	1998	
2	4570	5819	416
4	5210	5938	242
5	5099	5774	225
Mean	4960	5843	295

transformations, and the best fit ($r^2 = 0.916$) was obtained for a regression with the *Y*-intercept forced through zero:

$$\text{biomass} = 0.09311 \times \text{DIAMS}$$

where DIAMS is the simple product of the two perpendicular diameter measurements for each clump. Including the numbers of stems per clump as a predictive variable in multiple regressions did not improve the strength of this relationship.

Applying this equation to the individual alder clump measurements in the three main treatment plots with retention of 2000 clumps ha^{-1}, we obtained a mean annual above-ground biomass increment of 295 kg ha^{-1} (1995–1998; Table 2). During the same interval, alder cover increased from 38 to 45% in this treatment. For estimation of N accretion, we attributed all of this increment to woody tissues, since our annual litterfall data showed no trend in leaf biomass over the same 3-year-period. Destructive sampling of alder biomass components from four labeled mini-plots in 1998 yielded mean (±S.D.) total N concentrations of 5.8 ± 0.5 g kg^{-1} for main woody stems, 9.5 ± 0.4 g kg^{-1} for twigs (<5 mm diameter) and 11.0 ± 1.6 g kg^{-1} for fine (<2 mm diameter) roots.

Pre-labeling ^{15}N natural abundance data indicated that, on average, alder had higher δ^{15}N values than almost all associated species growing on the mini-plots (Table 3). Grab samples of foliage collected in August 1995 from this site had displayed a similar pattern, with all species except birch-leaved spirea having slightly higher δ^{15}N values than alder (data not shown).

Unfortunately, these ^{15}N natural abundance data provided little useful insight into N_2-fixation by Sitka alder at this site. Not only were the differences in δ^{15}N values between alder and the reference species much smaller than Högberg (1997) recommended, but this method usually yielded negative estimates of FN_{dfa} since δ^{15}N values for alder did not lie between those for the non-fixing reference species and for alders grown in an N-free medium (Table 3).

In contrast, isotope dilution provided unambiguous evidence for N_2-fixation by Sitka alder. For the 14 mini-plots located in the young opening, $\%N_{dfa}$ ranged from approximately 90–95%, depending on the reference species (Table 4). Comparison of excess ^{15}N abundance data for various biomass components revealed that the labeling of young tissues in the non-fixing reference species was sufficiently uniform that analysis of current-year foliage would provide reasonable estimates of $\%N_{dfa}$.

By the 1998 sampling date, almost three full growing seasons had elapsed since the application of the ^{15}N tracer to the mini-plots in the young opening.

Table 3
^{15}N natural abundance, and calculated proportion of alder N derived from atmosphere (FN_{dfa}), for foliage collected 13 June 1996, prior to labeling of mini-plots in young opening

Species (number of samples)	δ^{15}N (‰)		FN_{dfa} (%)[a] ($\delta^{15}N_a = -0.3$ ml)	FN_{dfa} (%)[a] ($\delta^{15}N_a = -1.9$ ml)
	Mean	S.D.		
Sitka alder (14)	2.88	0.86		
Birch-leaved spirea (5)	3.08	1.03	6	4
Black huckleberry (9)	2.17	1.39	−29	−17
Bluejoint (6)	1.85	0.82	−48	−27
Fireweed (13)	2.44	1.33	−16	−10
Lodgepole pine (14)	2.23	1.73	−26	−16
Red raspberry (7)	1.66	0.90	−62	−34

[a] Proportion of alder foliar N derived from atmosphere, assuming $\delta^{15}N_a = -0.3$ ml (*A. rubra*; Binkley et al., 1985) or −1.9 ml (*A. glutinosa*; Domenach et al., 1989).

Table 4
Isotope dilution results: proportion of Sitka alder N derived from atmosphere ($\%N_{dfa}$), based on excess ^{15}N abundance in foliage of selected reference species (August 1998)

Species	Young opening ($\%N_{dfa}$)		Mature stands ($\%N_{dfa}$)	
	Mean	S.D. (*n*)	Mean	S.D. (*n*)
Birch-leaved spirea			89.83	8.12 (2)
Black huckleberry	93.45	3.51 (11)	95.77	3.79 (4)
Fireweed	91.66	6.47 (12)		
Lodgepole pine	94.64	2.63 (14)		
Prickly rose			78.62	1.62 (2)
Red raspberry	93.54	3.40 (8)		

Accordingly, the degree of variability between mini-plots in the calculated $\%N_{dfa}$ was considerably smaller than that reported by Mead and Preston (1992) for estimates of Sitka alder N sources made only 1 year after tracer application. However, this earlier study involved much higher total N application rates (100 kg ha^{-1}), leading to considerable uptake of applied mineral N by alder during the year after application. In contrast, we used an N application rate of only 2 kg ha^{-1}, resulting in little apparent disturbance to N_2-fixation by Sitka alder in our labeled mini-plots. For this reason, it would not have been necessary to wait more than 2 years to estimate $\%N_{dfa}$ for alder at this site. Foliar sampling conducted during the year of tracer application yielded a mean N_{dfa} value (89%) which was very similar to our 1998 results, based on the same four reference species.

Combining the data for litterfall, biomass production, N concentration, and $\%N_{dfa}$ (mean of 93% for four reference species in 1998), we conservatively estimate stand-level N_2-fixation at 9.6 kg ha^{-1} per year in the young opening, based only on above-ground components. This estimate would be increased if we had determined the proportion of woody biomass production occurring as small-diameter (<5 mm) twigs, which had a higher N content than the main stems (9.5 versus 5.8 g kg^{-1}). However, the major omissions from this estimate are for the below-ground processes. Alder fine root production was not measured, but if this process is comparable in magnitude to leaf litterfall, an additional 4 kg N ha^{-1} per year could be involved. This assumption may be reasonable, based on the limited data for this species. In his study of a 5-year-old Sitka alder stand on Vancouver Island, BC, Binkley (1982) did not measure fine root production, although he reported that root biomass was almost 1.7× higher than leaf biomass. Thus, a realistic range of estimated N_2-fixation rates in our young stand would 10–15 kg N ha^{-1} per year.

N_2-fixation would also be underestimated if direct transfer of fixed N was occurring from alder to associated non-fixing species through mycorrhizal linkages. However, field evidence for this process is still lacking, and pot experiments have provided contradictory evidence (Arnebrant et al., 1993; Ekblad and Huss-Danell, 1995).

After 26 months, the bulk of the ^{15}N label was still present in the forest floor. If the current-year tissues of the non-fixing species obtained most of their N from the uptake of soil NH_4^+, the ^{15}N atom% excess data for soils and biomass suggest that N uptake occurred from both forest floor and mineral soil, consistent with our observations of fine root distributions (Tables 5 and 6). However, the full picture is undoubtedly more complex, given recent evidence that other species of pine and *Vaccinium* can also take up organic nitrogen directly (Näsholm et al., 1998).

For the ^{15}N-labeled mini-plots established under mature pine canopies, the sparse understory made it difficult to obtain samples of non-fixing species, and only black huckleberry occurred in all four mini-plots. Nevertheless, our 1998 foliage analyses suggested that

Table 5
Distribution of excess ^{15}N among biomass components of non-fixing reference species for destructively-sampled mini-plots in young opening (August 1998)

Species	Component	*n*	^{15}N atom% excess	
			Mean	S.D.
Black huckleberry	Leaves	3	0.1925	0.0503
	Young stems	3	0.1901	0.0464
	Old stems	3	0.2652	0.0212
	Fine roots	3	0.1724	0.0716
Fireweed	Leaves	3	0.1467	0.0407
	Stems	3	0.1619	0.0332
	Fine roots	3	0.1680	0.0571
Lodgepole pine	1998 foliage	4	0.2094	0.0193
	1998 branches	4	0.2070	0.0099
	1997 foliage	4	0.2281	0.0433
	1997 branches	4	0.2034	0.0290
	Main stem	4	0.1978	0.0244
	Fine roots	4	0.1997	0.0339

Table 6
Total N and ($NO_3^- + NH_4^+$)–N concentrations, and ^{15}N atom% excess in forest floors and mineral soil from labeled mini-plots in young opening (August 1998)[a]

	Total N (g kg^{-1})	($NO_3^- + NH_4^+$)–N (mg kg^{-1})	^{15}N atom%	
			Total N	$NO_3^- + NH_4^+$
Forest floor	1.16 (0.10)	82.6 (6.7)	0.1869 (0.0399)	0.3545 (0.0672)
Mineral soil				
0–20 cm	0.08 (0.03)	1.8 (1.3)	0.0280 (0.0115)	0.0678 (0.0228)
20–35 cm	0.05 (0.01)	1.9 (1.0)	0.0345 (0.0076)	0.0677 (0.0267)

[a] Means (S.D.); $n = 4$.

approximately 80–95% of the N in the alder tissues originated from the atmosphere (Table 4). This proportion was comparable to that observed in the full-light conditions of the young opening, even though understory light levels averaged only 18.1% of open sky values (S.D. = 4.3). Although we did not obtain the biomass production data needed to estimate N_2-fixation rates, Sitka alder appears to obtain most of its N requirements through fixation in these mature lodgepole pine forests.

The N_2-fixation rates estimated for this site are below the range of values for Sitka alder cited by Binkley (1986), but slightly above those found in the southern interior of BC (Sachs, personal communication; Mead and Preston, 1992). Are amounts in the order of 10–15 kg N ha^{-1} per year significant in the context of long-term site productivity and soil fertility? If rates of this magnitude operate until crown closure is attained by the lodgepole pines, estimated to occur at age 18 years for the unthinned stand at this site, the estimated cumulative amounts of N fixed would approach 200–300 kg ha^{-1}. N increments of this magnitude are significant when compared with the existing N pool in the forest floor (769 kg ha^{-1} at this site in 1995; (Sanborn et al., 2001)) and the levels of N loss reported to occur from prescribed burning in the BC central interior (105 kg ha^{-1} from slash, 288 kg ha^{-1} from forest floor (Kranabetter and Macadam, 1998)).

Although prescribed fire was not employed at this site, and its use has generally declined in interior BC over the past decade, fire is historically part of forest ecosystems in the Sub-Boreal Spruce zone (DeLong and Tanner, 1996). The presence of a persistent symbiotic N_2-fixing shrub in these forests provides a natural mechanism for recovery of soil nutrient capital after stand-initiating disturbances. The importance of this role played by Sitka alder is reinforced by the apparent persistence of its N_2-fixation activity even in stands exceeding 150-year-old. During stand development in such lodgepole pine forests, N_2-fixation rates may reach their minimum levels during the period of densest shading in the years after full crown closure is attained. Future sampling of the remaining ^{15}N-labeled mini-plots at this site, in conjunction with the long-term biomass production data from the associated pine–alder competition study (Sanborn et al., 2001), will indicate whether such a trend occurs.

4. Conclusions

Eleven years after harvesting of a lodgepole pine stand in the Sub-Boreal Spruce zone of interior BC, the N_2-fixation rate by Sitka alder at a density of 2000 clumps ha^{-1} (45% cover) was estimated at approximately 10–15 kg ha^{-1} per year, depending on the magnitude of the unmeasured below-ground contribution. Almost all of the Sitka alder clumps at this site were inherited from the previous stand, and their vigorous regrowth from pre-existing root systems would allow N_2-fixation to reach maximum rates rapidly after harvesting or natural disturbance. The amounts of N potentially fixed prior to pine crown closure are of similar magnitude to N losses observed from operational prescribed burning in BC central interior forests.

Rates of N_2-fixation by Sitka alder are likely at a maximum during the open canopy conditions of early stand development, but ^{15}N isotope dilution and light transmittance data indicate that N_2-fixation activity continues under a mature lodgepole pine canopy (>150-year-old).

The ^{15}N isotope dilution technique provided unambiguous evidence for N_2-fixation by alder, in contrast to ^{15}N natural abundance data.

In conjunction with the continuing biomass production measurements at this site, the remaining ^{15}N-labeled mini-plots will permit N_2-fixation rates to be estimated during and after crown closure.

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