Succession on Subalpine Placer Mine Spoil: Effects of Revegetation with Alnus viridis, Alaska, U.S.A

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Abstract

Alnus viridis seedlings were planted on placer mine spoil in an Alaskan subalpine watershed to bypass a seedling establishment bottleneck for *A. viridis*, and to evaluate the interaction between *A. viridis* and the dominant riparian woody plants, *Salix alaxensis* and *Populus balsamifera*. The study area was divided into 11 replicate blocks, each on a homogeneous recontoured spoil pile. Blocks were divided into two 0.01 ha plots, and treatments without (control) and with 84 planted *A. viridis* seedlings were randomly assigned to plots. After 10 years, the *Alnus* treatment had a dense stand of *A. viridis* 1–2 m tall, while the control had fewer, smaller seedlings. Compared to the control, planted *A. viridis* had a neutral effect on *S. alaxensis* and inhibited *P. balsamifera* at the seedling establishment stage, but facilitated the growth of established plants of both species, with many plants overtopping the *A. viridis* canopy. Compared to the control, *S. alaxensis* plants in the *Alnus* treatment had higher levels of foliar N and δ^{15}N values closer to those of *A. viridis*, indicating the importance of N fixation by *A. viridis*. Planting *A. viridis* accelerated the rate of succession by stimulating growth of woody dominants.

Introduction

Species of *Alnus* (alder) form nitrogen-fixing root nodules with the soil actinomycete *Frankia*, and often contribute large amounts of nitrogen to the soil profile (Crocker and Major, 1955; Van Cleve et al., 1971). The interaction between nitrogen-fixing plants and non-fixers is often complex, varying among sites, species, and life stages of species (Callaway, 1995; Callaway and Walker 1997). In primary succession following glacial retreat at Glacier Bay, *Alnus viridis* inhibited the establishment of *Picea sitchensis* but had a net facilitative effect on growth of established plants (Chapin et al., 1994; Fastie, 1995). In primary succession on river bars in interior Alaska, dense stands of *Alnus incana* had an overall negative effect on the establishment and growth of *Salix alaxensis* and *Populus balsamifera* (Walker and Chapin, 1986; Walker et al., 1986).

Alnus has been planted on many types of sites with the objective of adding nitrogen to the soil to facilitate the growth of other species. However, the interaction between planted *Alnus* and other woody plants varied among sites and species. On low-nitrogen soils, *Alnus* increased growth of non-fixers on some sites but out-competed and overtopped interplanted non-fixers on other sites; on fertile soils, interplanted non-fixers were either unaffected by *Alnus* or out-competed and overgrew *Alnus* (DeBell and Radwan, 1979; Hanson and Dawson, 1982; Binkley and Greene, 1983; Heilman and Stettler, 1985; Heilman, 1990).

Alnus has been planted to revegetate mine spoil (Plass, 1977; Heilman and Ekuan, 1982; Schlesinger and Williams, 1984). Mining for placer gold has severely disturbed many subarctic riparian ecosystems. Placer mining involved removing riparian vegetation and topsoil, excavating gravel (usually down to bedrock) from the stream channel, active floodplain, and/or old terraces and channels, and processing the gravel to remove the gold. Placer mining methods often buried or washed away topsoil, removed soil and organic material from alluvial gravels during processing, and left a deranged stream bordered by rock and gravel spoil piles. Recent regulations have reduced topsoil loss on new mines, but the topsoil has already been lost on the extensive areas of older placer mines that have been abandoned or are being remined.

Plant succession has been studied on subarctic placer spoil piles that have not been recontoured (Singleton et al., 1978; Rutherford and Meyer, 1981; Holmes, 1982; Durst, 1984, Deans, 1992) and recontoured placer spoil (Densmore, 1994). The dominant colonizers included *S. alaxensis*, *P. balsamifera*, and *A. incana* and/or *A. viridis*. However, on processed spoil with low levels of organic material and soil, plant cover was sparse even on sites as old as 60 years, and most trees and shrubs were not vigorous and were growing very slowly. On these sites, there were few or no *Alnus* plants, but those present grew vigorously even on the harshest sites. This suggested that establishment barriers limited *Alnus* density.

The objectives of this study were to determine if planting *A. viridis* seedlings would overcome the establishment bottleneck on subarctic placer mine spoil, and if the planted *A. viridis* would facilitate the establishment and growth of the dominant riparian woody plants, *S. alaxensis* and *P. balsamifera*. The research reported in this paper was part of long-term, multidisciplinary research on the restoration of a placer-mined watershed in Denali National Park and Preserve, Alaska.

Study Area

The Glen Creek watershed study area was located in the Kantishna mining area, a group of rugged hills within Denali National Park and Preserve (Fig. 1). The Glen Creek watershed is in the continental climatic zone of interior Alaska, but the continental pattern is modified by cooler summers and higher precipitation because of greater maritime influence and higher elevation. July averages 12°C, while January averages −18°C. Precipitation averages 48 cm annually with 72% occurring from June through September.

The bedrock geology of the Glen Creek watershed is faulted and folded quartzite and hornblende schist of the Birch Creek Formation. The study area on lower Glen Creek was covered in the middle Wisconsin with glacial ice from the Alaska Range, and gravel and rocks deposited by the glacier were mixed with bedrock material in the alluvial gravels.
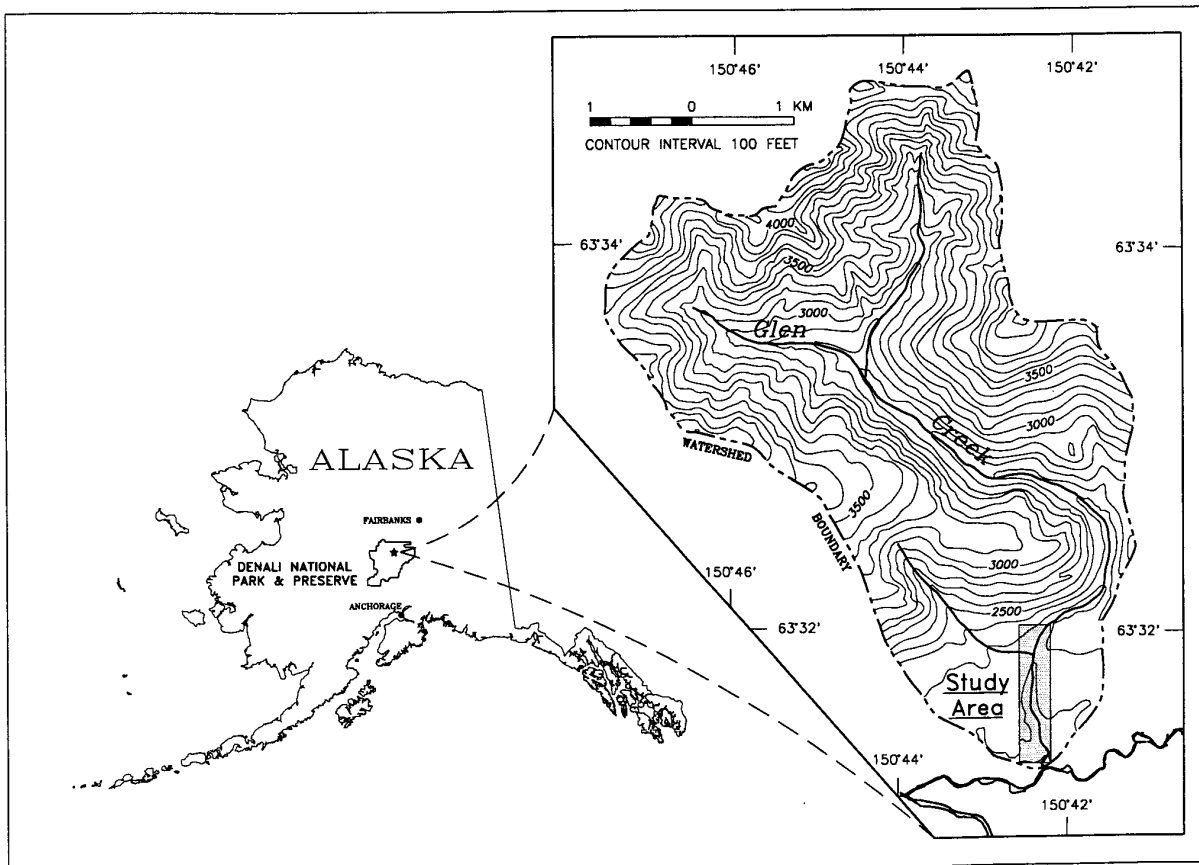
FIGURE 1.   Map showing location of study area.

The Glen Creek watershed was hand-mined from 1906 to 1941. The stream was diverted and dammed, and topsoil and fines were washed away, but the disturbed area was limited relative to later mining. In the 1970s, the study area on lower Glen Creek was extensively mined with the bulldozer/washplant method. The mining severely disturbed the vegetation in the study area, but the predisturbance vegetation was inferred from remnants and adjacent less-disturbed watersheds at the same elevation. In these watersheds the floodplain above the annual flood level was dominated by *S. alaxensis* 1.5–3.0 m tall, mixed with varying amounts of *A. viridis* 1.0–3.0 m tall and *P. balsamifera* saplings. The understory usually included the low shrub *Dasiphora floribunda* and the grass *Calamagrostis canadensis*. Higher areas had mature *P. balsamifera* and young *Picea glauca*, and old terraces were dominated by the shrubs *Betula nana*, *S. pulchra*, and scattered mature *P. glauca*.

In 1988, 9–15 years after mining had ceased, the study area was dominated by unstable gravel and rock spoil piles 3–8 m tall. Some of these piles were still unvegetated; others had scattered *S. alaxensis* and *P. balsamifera* seedlings which were 8–9 years old but only 5–20 cm tall, and little or no *A. viridis*; and some piles had scattered to complete cover of *A. viridis* 0.5–1 m tall interspersed with small *S. alaxensis*. Most of the topsoil in the mined area was gone.

Reclamation of the study area began in August 1988, when the location and composition (topsoil, gravel, boulders, etc.) of spoil piles were mapped and the area above the active floodplain was recontoured. The recontouring redistributed spoil to reduce and stabilize slopes, covered washed boulders and cobbles with finer spoil, and respread the available topsoil and fines. The stream channel and active floodplain were recontoured and stabilized in 1992, and the design and results of this part of the reclamation project are reported elsewhere (Karle and Densmore, 1994, 2001).

Undisturbed vegetation and naturally revegetated areas from the 1906–1941 mining surrounded the recontoured area and provided a fairly uniform seed source for *S. alaxensis* and *A. viridis*, but *P. balsamifera* trees were more scattered.

Methods

EXPERIMENTAL DESIGN

A randomized complete block design was used for the study. The reclamation grading produced 11 distinct areas of recontoured spoil above the active floodplain, each of which had been a spoil pile. A replicate block (10 × 22 m) was established on each of the 11 recontoured spoil piles in June 1989. Each block was as homogeneous as possible for factors such as aspect, slope, substrate characteristics, depth to the water table, and seed rain. Furthermore, the composition of each spoil pile was determined during the recontouring process, ensuring that the study addressed primary succession on known substrates without the legacy effect of buried vegetation and/or topsoil.

Each block was divided into two 0.01 ha (10 × 10 m) plots with a 2-m-wide walkway between the plots. Plots in each pair were randomly assigned to the control or to the planted *A. viridis* treatment (hereafter referred to as the *Alnus* treatment). A 14.1-m transect was laid out diagonally across each plot immediately after planting, and foot traffic was confined to one side of the transect to avoid disturbance to small seedlings and developing biological soil crusts.

PROPAGATION AND PLANTING OF A. VIRIDIS

Alnus viridis seeds were collected on 1–4 September 1988 from riparian stands approximately 10 km downstream of the study site.

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Alnus viridis nodules and soil from around *A. viridis* roots were collected at the study site on 14 September 1988. The seeds and soil were stored frozen, and the nodules were stored at 3°C. Seedlings were propagated in greenhouses at the Alaska State Forest Nursery with methods based on those of DeBell et al. (1988). Seedling containers were Leach cells 2.5 cm in diameter and 10 cm long (capacity 45 cm^3). The propagation medium was 1 part peat moss to 1 part vermiculite, with calcium sulfate added and pH 5.5–6.0. The propagation medium was inoculated with the nitrogen-fixing symbiont *Frankia* by mixing 5 L of soil from around *A. viridis* roots and 0.3 L of ground *A. viridis* nodules into each 1.0 m^3 of propagation medium. Each container was seeded with 10–20 *A. viridis* on 9–10 March 1989. Seedlings were fertilized throughout greenhouse propagation with a liquid solution (formulation 7% N, 40% P, 17% K). A low nitrogen/high phosphorous fertilizer was selected to promote root growth without inhibiting nodule formation (Burgess and Peterson, 1987). Six weeks after seeding, seedlings were thinned to one per container. At this time 30 seedlings were randomly selected, washed, measured, and examined for nodules. Seedlings were 2–3 cm tall and all were nodulated. Seedlings were moved outside the greenhouse to harden off on 16 May. On 1 June, 30 randomly selected seedlings were measured and examined for nodules before the seedlings were planted in the field sites. Total seedling branch length was 23 ± 1 (mean ± SE) cm, and all seedlings were well nodulated, with 34 ± 4 nodules per seedling.

On each *Alnus* treatment plot, 84 *A. viridis* seedlings were planted on 8–13 June 1989. Seedlings were planted in clusters of seven 0.75 m apart on twelve 2.5-m centers. Each seedling was watered once at time of planting with approximately 1 L of a liquid fertilizer solution (formulation 9% N, 45% P, 15% K), and was also fertilized with slow-release MagAmp (formula 7% N, 52% P, and 6% K) sprinkled around its base. Each *A. viridis* seedling received a total of 0.56 g N, 3.80 g P, and 0.58 g K. These fertilizers were selected to stimulate root growth while minimizing any negative effects of added nitrogen on nodule formation and function (Burgess and Peterson, 1987).

VEGETATION MEASUREMENTS

Vegetation was measured in August 1998, after 10 growing seasons. Cover was estimated along a 10-m transect in each plot. The transect was centered along the side of the diagonal transect that had not been walked on. Vascular plant cover was estimated by species, and ground cover was estimated as rock, soil, biological soil crust, or litter. Biological soil crust was defined as a surface layer of soil cyanobacteria, lichens, and mosses (Belnap, 2003). To measure species composition, vascular plant taxa present in a 0.5 × 10 m plot adjacent to the transect were recorded.

The density and height of *S. alaxensis*, *P. balsamifera*, and *A. viridis* and the density of other woody plants were measured in a 50 m^2 subplot, the half of the 10 × 10 m plot that had not been walked on. Only plants >10 cm tall and in a free-to-grow status were counted and measured. Plants that were <10 cm tall 10 years after disturbance were more likely to remain stunted and/or be out-competed. Free-to-grow seedlings were defined as those whose terminal leaves had the typical sun morphology, while suppressed seedlings were those where all leaves had the typical shade morphology. Leaves with sun morphology were thicker and greener (and in *S. alaxensis* more tomentose) than their shaded counterparts. *Alnus viridis* branches from the base, and the planted *A. viridis* were intertwined so that individual plants could not be reliably distinguished; therefore, the number of plants was estimated at 40 plants/50 m^2 based on counts made in 1994. The height of planted *A. viridis* was measured at 12 random sites in each plot.

FOLIAR TOTAL N AND ^{15}N ABUNDANCE

Foliar nitrogen content and natural abundance of ^{15}N were measured in *S. alaxensis* and planted *A. viridis* growing in three replicate blocks. Three *S. alaxensis* plants were sampled in each treatment plot on 31 July 1998. Three *A. viridis* plants were sampled in each *Alnus* treatment plot on 21 August 1998. For each plant, a sample of 3–5 fully expanded leaves was collected from the current year's growth twigs. Samples were dried for 48 h at 55°C. Total foliar N and stable nitrogen ratios were measured to determine if *S. alaxensis* was utilizing fixed N$_2$ from the planted *A. viridis*. The stable isotope ratio is expressed in thousandths following classical delta notation ($\delta^{15}N = [(R_{sample} - R_{reference})/R_{reference}] \times 1000$), where $R = {}^{15}N/{}^{14}N$. Atmospheric N$_2$ is the ultimate reference value, with a value of zero. N$_2$ fixing plants have $\delta^{15}N$ values closer to that of atmospheric N$_2$ than non-N$_2$ fixing plants. Non-N$_2$ fixing plants such as *S. alaxensis* will have $\delta^{15}N$ values closer to N$_2$ fixing plants such as *A. viridis* if the non-fixing plants utilize biologically fixed N before soil processes modify $\delta^{15}N$. Total N content and isotope ratios were measured on a Carlo Erba 1500 CN analyzer linked to a VG Victor Isotech Cira Series II mass spectrometer in the Duke University Phytotron.

SOIL CHARACTERISTICS

Soil texture samples were taken from each replicate block during the first growing season following recontouring. Each textural sample was taken from a pit approximately 20 cm in depth and diameter. Three textural samples were taken from each block and combined for particle size analysis. The proportions of cobble, gravel, and soil (<2.0-mm fraction) were measured. The proportions of sand, silt, and clay in the soil were determined by the Bouyoucos hygrometer method (Gee and Bauder, 1986). Soil samples for other parameters were taken from each replicate block in August 1989, and again from each plot within each block in August 1998. All samples were taken from a pit 15 cm in depth and diameter. In 1989, nine samples from each block were combined into one for analysis. In 1998, six samples were combined into one for nutrient analysis. Samples were divided into litter, biological soil crust, and mineral soil subsamples.

The soil fraction (particle size <2.0 mm) was analyzed for pH, organic matter, total nitrogen, and extractable phosphorous. Soil pH was measured with a pH meter in 1:1 soil/water paste. Organic matter content was estimated by loss of weight on ignition (for 7 h at 400°C) (Nelson and Sommers, 1982). Nitrogen content was determined by Kjeldahl analysis (Bremner and Mulvaney, 1982). Extractable phosphorous was measured with the Olsen (Olsen and Sommers, 1982) or Mehlich III method (Tran and Simard, 1993), depending on pH. The University of Alaska Agricultural and Forestry Experiment Station did all soil analyses.

DATA ANALYSIS

The Statistical Analysis System (SAS Institute Inc., 2000) was used for data analysis. Mean ± SE was calculated for all variables. Proportions were arcsine transformed before analysis. The analysis of variance for a randomized complete block design (ANOVA) procedure or the multivariate analysis of variance for a randomized complete block design (MANOVA) procedure were used to determine if variables differed significantly ($P < 0.05$) between treatments. An ANOVA that takes blocking into account is an efficient way of correcting for the effects of spatial autocorrelation (Legendre et al., 2004). Wilks' lambda was used as the test criterion for MANOVA (Morrison, 1976). The Ryan-Einot-Gabriel-Welsch multiple range test was used to compare treatment means for individual variables.

The ANOVA procedure was used to determine if total density of *S. alaxensis* and *P. balsamifera* differed significantly between treatments. Total density of *A. viridis* was not statistically analyzed because total density for the *Alnus* treatment was based on an estimated value with unknown error. *Salix alaxensis* and *P. balsamifera* plants on each

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TABLE 1

Density of *Alnus viridis*, *Salix alaxensis*, and *Populus balsamifera* by height category on control and *Alnus* treatments.

	Control[a]	*Alnus*	F	P[b]
Alnus viridis				
11–50 cm	5.5 ± 3.8	1.0 ± 0.5	1.35	0.2727
51–150 cm	5.1 ± 1.5	13.0 ± 2.6	4.66	0.0563
>150 cm	0.0 ± 0.0	26.0 ± 2.8	89.81	0.0001
Wilks' Lambda for MANOVA			199.95	0.0001
Salix alaxensis				
11–50 cm	37.5 ± 11.0	8.7 ± 2.2	6.13	0.0328
51–150 cm	2.0 ± 1.1	19.5 ± 4.9	18.91	0.0014
>150 cm	0.0 ± 0.0	8.9 ± 2.0	19.11	0.0014
Wilks' Lambda for MANOVA			7.88	0.0090
Populus balsamifera				
11–50 cm	97.4 ± 32.6	15.2 ± 4.2	7.28	0.0224
51–150 cm	2.5 ± 1.7	10.1 ± 3.0	6.66	0.0274
>150 cm	0.0 ± 0.0	2.8 ± 1.0	7.97	0.0181
Wilks' Lambda for MANOVA			3.94	0.0536

[a] Values are mean ± SE plants per 50 m^2; $n = 11$ replicate blocks.
[b] Probability values for cover variables from MANOVA for complete randomized replicate block design.

TABLE 2

Biotic cover in control and *Alnus* treatments.

	Control[a]	*Alnus*	F	P[b]
Cover (%)				
Alnus viridis	4.9 ± 2.6	79.2 ± 2.8	188.98	<.0001
Other woody taxa	3.4 ± 1.0	3.2 ± 1.0	0.04	0.8421
Graminoid	2.7 ± 1.7	9.5 ± 4.3	5.21	0.0456
Forb	1.9 ± 0.9	0.2 ± 0.1	3.63	0.0859
Biological soil crust	8.2 ± 1.7	7.0 ± 1.6	0.20	0.6656
Litter	7.3 ± 3.5	69.6 ± 4.2	336.59	<.0001
Wilks' Lambda for MANOVA			42.49	0.0004

[a] Values are mean ± SE; $n = 11$.
[b] Probability values for cover variables from MANOVA for complete randomized replicate block design.

plot and *A. viridis* plants on each control treatment plot were divided into three height categories: 11–50 cm, 51–150 cm, and >150 cm. Height data for individual *A. viridis* plants was not available for the intertwined stands on the *Alnus* treatment plots. For these plots, the proportion of the random *A. viridis* height measurements within each height category was multiplied by the estimated density of 40 *A. viridis* plants per plot to generate an estimate of plants per height category. MANOVA was used to determine if the number of *A. viridis*, *S. alaxensis*, and *P. balsamifera* plants in each height category differed significantly between treatments. Values for percentage cover of *A. viridis*, other woody taxa, graminoids, forbs, biological soil crust, and litter were analyzed using MANOVA to determine if individual cover variables differed significantly between treatments. The number of vascular plant taxa was analyzed with ANOVA. MANOVA was used to determine if foliar N content and relative abundance of foliar ^{15}N differed significantly between treatments. Mineral soil pH, organic matter, total N, and extractable P were analyzed using MANOVA to determine if baseline and treatment values differed significantly.

Results

After 10 years, the density of *A. viridis* seedlings that naturally colonized from seed in the control treatment (10.6 ± 4.9) was lower than the estimated density of 40 live planted *A. viridis* per plot in the *Alnus* treatment. In the control treatment, 52% of the *A. viridis* plants were ≤50 cm tall, and the remainder were ≤150 cm tall; in comparison, 65% of the planted *A. viridis* were >150 cm tall (Table 1). The density of *S. alaxensis* that naturally colonized from seed was not significantly different between the control and *Alnus* treatments (40.4 ± 1.6 and 37.1 ± 6.8, respectively; $F = 0.06$, $P = 0.8075$). However, 93% of the *S. alaxensis* plants in the control were ≤50 cm tall, while 77% of *S. alaxensis* in the *Alnus* treatment were >50 cm

tall, with the most vigorous plants >200 cm tall. The density of *P. balsamifera* that colonized from seed was significantly higher in the control than in the *Alnus* treatment (99.9 ± 33.9 and 28.1 ± 6.6, respectively; $F = 5.71$, $P = 0.0379$). However, 97% of the plants in the control were ≤50 cm tall, compared to the *Alnus* treatment where 54% of the plants were ≤50 cm tall, but the most vigorous plants were >150 cm tall.

Alnus viridis cover was significantly higher in the *Alnus* treatment than in the control, and the planted *A. viridis* provided 85% of the vascular plant cover in these plots (Table 2). The cover of other woody plant taxa was not significantly different between treatments. The *Alnus* treatment had significantly more graminoid cover than the control plots. Forb cover was a minor component in both treatments. The cover of biological soil crust was not significantly different between treatments. The biological soil crust was dominated by two nitrogen fixers, the cyanobacteria *Microcoleus vaginatus* and the soil lichen *Collema tenax* (Belnap, personal commun., 1993) and by colonizing mosses. The cover of litter was significantly higher in the *Alnus* treatment, covering most of the ground surface. The number of vascular plant species present was not significantly different between the control and the *Alnus* treatment (12.8 ± 9.9 and 15.1 ± 9.9, respectively; $F = 4.10$, $P = 0.0735$).

Foliar N content was not significantly different between *A. viridis* plants and *S. alaxensis* plants in the *Alnus* treatment, but was significantly lower in *S. alaxensis* plants growing in the control treatment (Table 3). Foliar δ^{15}N values for *S. alaxensis* plants growing in the *Alnus* treatment were intermediate between values for *A. viridis* and values for *S. alaxensis* plants in the control treatment, but were not significantly different from either. However, values for *S. alaxensis* plants in the control treatment were significantly lower than values for *A. viridis* plants. All plants sampled had δ^{15}N values lower than that of atmospheric N_2.

The texture of the mine spoil was 14.2 ± 5.2% cobbles, 62.4 ± 5.2% gravel, 18.5 ± 0.4% sand, 3.8 ± 0.2% silt, and 1.1 ± 0.2% clay. The soil fraction (sand, silt, and clay) was classified as a loamy sand.

Mineral soil pH declined significantly between year 1 and year 10 for both control and *Alnus* treatments, but the decline was greater in the *Alnus* treatment (Table 4). Extractable P increased significantly in the *Alnus* treatment but not in the control. Organic matter and total N in mineral soil declined significantly in both treatments, but the control had significantly less organic matter than the *Alnus* treatment. Variables for the biological soil crust were similar in the two treatments, and the crust had a lower pH and higher levels of P, total N, and organic matter than the mineral soil. The nitrogen-rich litter layer was mostly *A. viridis* leaves.

TABLE 3

Total nitrogen content and relative abundance of ^{15}N in foliage of *Alnus viridis*, and of *Salix alaxensis* growing in control and *Alnus* treatments.

	Alnus viridis	*Salix alaxensis*[a] Control	*Alnus*	F	P[b]
Foliar [15]N	−1.27 ± 0.07*a*	−4.44 ± 0.90*b*	−2.30 ± 0.29*ab*	8.53	0.0360
Foliar total N (%)	3.32 ± 0.07*a*	1.60 ± 0.13*b*	3.22 ± 0.19*a*	37.95	0.0025
Wilks' lambda for MANOVA				7.13	0.0183

[a] Values are mean ± SE, *n* = 3: values within a row with the same letter are not significantly different at the 0.05 level.

[b] Probability values from MANOVA for complete randomized replicate block design.

Discussion

Our study showed that planting *Alnus viridis* seedlings at the beginning of primary succession on freshly recontoured placer mine spoil had complex effects on the succession of dominant woody plants. Planting *A. viridis* seedlings created a dense stand 1–2 m tall after 10 years. In contrast, the natural establishment of *A. viridis* from seed on the control treatment resulted in fewer, much smaller seedlings. Greenhouse inoculation with *Frankia* ssp. was not a factor in the establishment and growth of planted seedlings. In an auxiliary experiment, inoculated and uninoculated *A. viridis* seedlings were grown in the greenhouse and planted in the study area (Densmore, unpublished data). At the end of the first growing season, the nodule biomass per seedling did not differ between inoculated and un-inoculated seedlings. Furthermore, naturally established seedlings were well nodulated. Other studies have also shown effective levels of *Frankia* in Alaskan soils (Huss-Danell et al., 1997, 1999).

The interaction between the planted *A. viridis* and the dominant colonizers varied with species, and also with the life stage of each species. For *S. alaxensis*, the interaction appeared to be neutral for the seedling establishment stage. After 10 years, plants were abundant both with and without planted *A. viridis*. However, the planted *A. viridis* facilitated *S. alaxensis* growth. *Salix alaxensis* was much taller in the *Alnus* treatment than in the control treatment. The vigorous growth of *S. alaxensis* in the planted *A. viridis* stands created a stand structure with *S. alaxensis* overtopping *A. viridis*.

For *P. balsamifera*, the interaction was negative for the seedling establishment stage. After 10 years, *P. balsamifera* plants were much more abundant without planted *A. viridis*. The effect of the planted *A. viridis* on seedling establishment differed between *S. alaxensis* and *P. balsamifera* because *P. balsamifera* grew more slowly than *S. alaxensis*, and *P. balsamifera* seedlings were shaded or overwhelmed by litter. The density of vigorous *P. balsamifera* growing with planted *A. viridis* was still sufficient for development of a dense mature stand. The planted *A. viridis*, however, facilitated the growth of the *P. balsamifera* seedlings that survived the competitive effect of *A. viridis* on seedling establishment and early growth. Many of the *P. balsamifera* plants growing with planted *A. viridis* were >50 cm tall, with some plants overtopping the *A. viridis* canopy; in contrast, almost all the seedlings in the control treatment were <50 cm tall.

The planted *A. viridis* also facilitated the growth of graminoids; cover was much higher in the *Alnus* treatment than in the control. Graminoid cover was dominated by *Calamagrostis canadensis*, an important component of the herbaceous understory of naturally established mature *S. alaxensis* and *A. viridis* stands in this area.

Two lines of evidence supported the importance of N-fixation by the planted *A. viridis*. First, *S. alaxensis* plants growing with planted *A. viridis* had higher levels of foliar N than *S. alaxensis* in control plots. Second, measurements of the relative abundance of foliar ^{15}N showed that values for *S. alaxensis* plants growing with planted *A. viridis* were intermediate between values for *A. viridis* and values for *S. alaxensis* plants growing in the control plots. This indicated that *S. alaxensis* plants growing in the *Alnus* treatment were using biologically fixed N more directly, because the δ^{15}N values for nitrogen-fixing plants such as *A. viridis* are close to atmospheric N_2, and the values shift away as fixed N is cycled through plants and soil microorganisms (Binkley et al., 1985; Shearer and Kohl, 1986; Kielland, 2001). Similar results were obtained in a study comparing the abundance of ^{15}N in *P. nigra* grown with and without *A. glutinosa* (Kurdali et al., 1990)

TABLE 4

Soil characteristics at beginning of study (year 1) and after 10 years in control and *Alnus* treatments.

	n	Year 1[a]	*n*	Control	*n*	*Alnus*	F	P[b]
Mineral soil								
pH	11	7.56 + 0.10*a*	10	6.88 ± 0.12*b*	11	6.53 ± 0.13*c*	42.91	<.0001
Extractable P (ppm)	11	1.73 + 0.19*a*	10	2.10 ± 0.48*a*	11	3.84 ± 0.49*b*	11.05	0.0007
Organic matter (%)	11	1.59 ± 0.16*a*	10	0.42 ± 0.20*b*	11	0.80 ± 0.17*c*	17.72	<.0001
Total N (%)	11	0.027 ± 0.004*a*	10	0.008 ± 0.002*b*	11	0.006 ± 0.001*b*	50.60	<.0001
Wilks' Lambda for MANOVA							20.78	<.0001
Biological soil crust								
pH		—	6	6.01 ± 0.24	11	5.67 ± 0.14	2.20	0.1984
Extractable P (ppm)		—	6	7.00 ± 1.39	11	12.09 ± 2.38	1.58	0.2642
Organic matter (%)		—	6	2.63 ± 0.56	11	2.80 ± 0.51	0.55	0.4900
Total N (%)		—	6	0.050 ± 0.020	11	0.047 ± 0.015	0.32	0.5948
Wilks' Lambda for MANOVA							1.16	0.5121
Litter								
Total N (%)		—		—	11	3.138 ± 0.045		

[a] Values are mean ± SE; values within a row with the same letter are not significantly different at the 0.05 level. Dashes indicate that no biological soil crust or litter was present.

[b] Probability values from MANOVA for complete randomized replicate block design.

Changes in soil characteristics also contributed to vegetation differences between control and *Alnus* treatments. Soil changed from baseline conditions in both treatments, but the *Alnus* treatment differed from the control. Soil with planted *A. viridis* had a lower pH than soil on control plots, a change which often occurs under *Alnus* stands (Van Cleve et al., 1971; Walker, 1989). Extractable P increased between the first and tenth year in the *Alnus* treatment but not in the control treatment. Higher levels in the *Alnus* treatment were related to greater decrease in pH that made P more available. Organic matter and total N within the mineral soil declined both with and without planted *A. viridis*. The biological soil crust contributed some N to the soil profile, and the planted *A. viridis* deposited substantial amounts of nitrogen-rich leaf litter, but the added N was apparently rapidly incorporated in plant biomass or lost to leaching or denitrification. Other studies in interior Alaska have shown increased N levels under *Alnus* stands, but these stands were 15 years old or older (Van Cleve et al., 1971; Walker, 1989). The results of this study are consistent with Dawson et al. (1983), who found increased N levels in a 3-year-old *Alnus* stand only within 15 cm of the stems of some plants.

Both with and without planted *A. viridis*, the composition of the dominant woody plant community was similar to the plant communities that established naturally in this area on floodplains along unmined streams and on placer mine spoil with favorable moisture and nutrient conditions. After 10 years, the net effect of planting *A. viridis* was to accelerate the rate of succession by stimulating growth of woody dominants. These results generally agreed with studies of primary succession in Glacier Bay, Alaska (Chapin et al., 1994; Fastie, 1995), but differed from the studies of primary riparian succession on the Tanana River in interior Alaska, where *A. incana* inhibited *S. alaxensis* to the point of eliminating it (Walker and Chapin, 1986; Walker et al., 1986). This difference between two riparian sites only 120 miles apart emphasizes how plant interactions in primary succession vary with species and site characteristics (Callaway, 1995; Callaway and Walker, 1997). The species of *Alnus* on the Tanana River, *A. incana*, grows to a height of 6–9 m, twice as tall as *A. viridis* (1–4 m) (Viereck and Little, 1972). *Salix alaxensis*, which grows to a height of 4.5–9 m, can overtop *A. viridis* but is likely to remain in the understory of a stand of *A. incana*. The substrate also differed between the sites. The placer mine spoil was course-textured and low in nutrients (similar to glacial till in Glacier Bay), while the riparian substrate was fine-textured with higher nutrient levels.

On the other hand, the *S. alaxensis* and *P. balsamifera* plants growing without planted *A. viridis* were still so small that their role in the developing plant community was not ensured. In the study area, plants of this size persisted but remained stunted on dry, low-nutrient sites, while succession proceeded in the direction of shrub tundra. Longer-term studies are needed to determine if successional pathways diverge between plots with planted *A. viridis* and control plots.

Planting *A. viridis* may be an effective restoration technique on severely disturbed subarctic sites throughout the range of the species. Planting seedlings can create a productive stand of *A. viridis* on sites that would otherwise remain largely unvegetated for many years, improving aesthetic and habitat values. Planting may also facilitate growth of dominant successional species such as *S. alaxensis* and *P. balsamifera* if growth is limited by low levels of soil nitrogen.

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References Cited

Belnap, J., 2003: The world at your feet: desert biological soil crusts. *Frontiers in Ecology and the Environment,* 1: 181–189.

Binkley, D., and Greene, S., 1983: Production in mixtures of conifers and red alder: the importance of site fertility and stand age. *In: I.U.F.R.O. symposium on forest site and continuous productivity.* U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, General Technical Report PNW-163, 112–117.

Binkley, D., Sollins, P., and McGill, W. B., 1985: Natural abundance of nitrogen-15 as a tool for tracing alder-fixed nitrogen. *Soil Science Society of America Journal,* 49: 444–447.

Bremner, J. M., and Mulvaney, C. S., 1982: Nitrogen-total. *In:* Page, A. L., Miller, R. H., and Keeney, D. R. (eds.), *Methods of Soil Analysis, Part 2, Chemical and Microbial Properties.* Madison, Wisconsin: Agronomy Society of America, Agronomy Monograph 9: 595–624.

Burgess, D., and Peterson, R. L., 1987: Effect of nutrient conditions on root nodule development in *Alnus japonica*. *Canadian Journal of Botany,* 65: 1658–1670.

Callaway, R. M., 1995: Positive interactions among plants. *The Botanical Review,* 61: 306–349.

Callaway, R. M., and Walker, L. R., 1997: Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology,* 78: 1958–1965.

Chapin, F. S., Walker, L. R., Fastie, C. L., and Sharman, L. C., 1994: Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs,* 64: 149–175.

Crocker, R. L., and Major, J, 1955: Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. *Journal of Ecology,* 43: 427–448.

Dawson, J. O., Dzialowy, P. J., Gertner, G. Z., and Hansen, E. A., 1983: Changes in soil nitrogen concentration around *Alnus glutinosa* in a mixed, short-rotation plantation with hybrid *Populus*. *Canadian Journal of Forest Research,* 13: 572–576.

Deans, A., 1992: *Environmental factors influencing the natural revegetation of placer mine tailings in interior Alaska.* M.S. thesis. Colorado School of Mines, Golden, Colorado, 119 p.

DeBell, D. S., and Radwan, M. A., 1979: Growth and nitrogen relations of coppiced black cottonwood and red alder in pure and mixed plantings. *Botanical Gazette,* 140: 97–101.

DeBell, D. S., Radwan, M. A., Ruekema, D. L., Zasada, J. C., Harms, W. R., and Cellarius, R. A., 1988: *Increasing the productivity of biomass plantations of alder and cottonwood in the Pacific Northwest.* U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Annual Technical Report, 135 pp.

Densmore, R. V., 1994: Succession on regraded placer mine spoil in Alaska in relation to initial site characteristics. *Arctic and Alpine Research,* 26: 60–69.

Durst, J. D., 1984: *Small mammals in relation to natural revegetation of gold dredge tailings at Nyac, Alaska.* M.S. thesis. University of Alaska, Fairbanks, 105 pp.

Fastie, C. L., 1995: Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology,* 76: 1899–1915.

Gee, G. W., and Bauder, J. W., 1986: Particle size analysis. *In:* Klute, A. (ed.), *Methods of Soil Analysis Part 1, Physical and Mineralogical Methods.* Madison, Wisconsin: Agronomy Society of America, Agronomy Monograph 9: 383–412.

Hanson, E. A., and Dawson, J. O., 1982: Effects of *Alnus glutinosa* on hybrid *Populus* height growth in a short-rotation intensively cultured plantation. *Forest Science,* 28: 49–59.

Heilman, P. E., 1990: Growth and status of *Populus* in mixture with red alder on recent volcanic mudflow from Mount Saint Helens. *Canadian Journal of Forest Research,* 20: 84–90.

Heilman, P., and Ekuan, G., 1982: Nodulation and nitrogen fixation by red alder and Sitka alder on coal mine spoils. *Canadian Journal of Forest Research,* 12: 992–997.

Heilman, P., and Stettler, R. F., 1985: Mixed, short-rotation culture of red alder and black cottonwood: growth, coppicing, nitrogen fixation, and allelopathy. *Forest Science,* 31: 606–613.

Holmes, K. W., 1982: *Natural revegetation of gold dredge tailings at Fox, Alaska.* M.S. thesis. University of Alaska, Fairbanks, 197 pp.

Huss-Danell, K., Uliassi, D., and Renberg, I., 1997: River and lake sediments as sources of infective *Frankia* (*Alnus*). *Plant and Soil,* 197: 35–39.

Huss-Danell, K., Sverrisson, H., Hahlin, A., and Danell, K., 1999: Occurrence of *Alnus*-infective *Frankia* and *Trifolium*-infective *Rhizobium* in circumpolar soils. *Arctic and Alpine Research,* 31: 400–406.

Karle, K. F., and Densmore, R. V., 1994: Stream and floodplain restoration in a riparian ecosystem disturbed by placer mining. *Ecological Engineering,* 3: 121–133.

Karle, K. F., and Densmore, R. V., 2001: Results from a channel restoration project: hydraulic design considerations. *In: Proceedings of the 2001 Wetlands Engineering and River Restoration Conference*, American Society of Civil Engineers, Reno, NV.

Kielland, K., 2001: Stable isotope signatures of moose in relation to seasonal forage composition: a hypothesis. *Alces,* 37: 329–337.

Kurdalli, F., Domenach, A. M., and Bardin, R., 1990: Alder-poplar associations: determination of plant nitrogen sources by isotope techniques. *Biology and Fertility of Soils,* 9: 321–329.

Legendre, P., Dale, M. R. T., Fortin, M., Casgrain, P., and Gurevitch, J., 2004: Effects of spatial structures on the results of field experiments. *Ecology,* 85: 3202–3214.

Morrison, D. F., 1976: *Multivariate Statistical Methods.* New York: McGraw-Hill Book Co.

Nelson, D. W., and Sommers, L. E., 1982: Total carbon, organic carbon, and organic matter. *In:* Page, A. L., Miller, R. H., and Keeney, D. R. (eds.), *Methods of Soil Analysis, Part 2, Chemical and Microbial Properties.* Madison, Wisconsin: Agronomy Society of America, Agronomy Monograph 9, 539–552.

Olsen, S. R., and Sommers, L. E., 1982: Phosphorous. *In:* Page, A. L., Miller, R. H., and Keeney, D. R. (eds.), *Methods of Soil Analysis Part 2, Chemical and Microbial Properties.* Madison, Wisconsin: Agronomy Society of America, Agronomy Monograph 9: 403–430.

Plass, W. T, 1977: *Growth and survival of hardwoods and pine interplanted with European alder.* U.S. Department of Agriculture, Forest Service. Research Paper NE-376.

Rutherford, C., and Meyer, K., 1981: *Revegetation on gold dredge tailings, Nyac, Alaska.* U.S. Department of Interior, Bureau of Land Management, Alaska State Office, Anchorage. Technical report, 51 pp.

SAS Institute Inc., 2000: *Statistical Analysis System.* Cary, North Carolina, U.S.A.

Schlesinger, R. C., and Williams, R. D., 1984: Growth response of black walnut to interplanted trees. *Forest Ecology and Management,* 9: 235–243.

Shearer, G., and Kohl, D. H., 1986: N_2-fixation in field settings: estimations based on natural ^{15}N abundance. *Australian Journal of Plant Physiology,* 13: 699–756.

Singleton, G. A., Steen, O. A., Weagle, K., and Weir, D., 1978: *Fish and wildlife habitat recovery in placer mined areas of the Yukon.* Canadian Department of Indian Affairs and Northern Development, Serial no. OSU80-00045, 131 pp.

Tran, T. S., and Simard, R. R., 1993: Mehlich III-extractable elements. *In:* Carter, M. R. (ed.), *Soil Sampling and Methods of Analysis.* Ann Arbor, Michigan: Lewis Publishers, 43–49.

Van Cleve, K., Viereck, L. A., and Schlentner, R. L., 1971: Accumulation of nitrogen in alder (*Alnus*) ecosystems near Fairbanks, Alaska. *Arctic and Alpine Research,* 3: 101–114.

Viereck, L. A., and Little, E. L., 1972: *Alaska trees and shrubs.* Fairbanks, Alaska: University of Alaska Press.

Walker, L. R., 1989: Soil nitrogen changes during primary succession on a floodplain in Alaska, U.S.A. *Arctic and Alpine Research,* 21: 341–349.

Walker, L. R., and Chapin, F. S., 1986: Physiological controls over seedling growth in primary succession on an Alaskan floodplain. *Ecology,* 67: 1508–1523.

Walker, L. R., Zasada, J. C., and Chapin, F. S., 1986: The role of life history processes in primary succession on an Alaskan floodplain. *Ecology,* 67: 1243–1253.