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Author: Roseann V. Densmore

Source: Arctic, Antarctic, and Alpine Research, 37(3) : 297-303

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: https://doi.org/10.1657/1523-0430(2005)037[0297:SOSPMS]2.0.CO;2
Succession on Subalpine Placer Mine Spoil: Effects of Revegetation with *Alnus viridis*, Alaska, U.S.A.

Roseann V. Densmore

U.S. Geological Survey, Alaska Science Center, 1011 East Tudor Road, Anchorage, Alaska 99503, U.S.A.
roseann_densmore@usgs.gov

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 δ¹⁵N 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 stichensis* 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-competited 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 Ekuian, 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.
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 *Salix alaxensis* 1.5–3.0 m tall, mixed with varying amounts of *Agrimonia viridis* 1.0–3.0 m tall and *Populus 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.
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 cm³). 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 treatment plot on 21 August 1998. For each plant, a sample fixing plants. Non-N SE) cm, A. viridis S. alaxensis was not statistically analyzed because plants on each 1 (mean of A. viridis and were intertwined so that individual plants could not Salix alaxensis growing in three treatment was based on an estimated value, ¼. The stable isotope of S. alaxensis was measured in a 50 m seedling received a total of 0.56 g N, 3.80 g P, by mixing 5 L of soil from around A. viridis 6 plant 84, S. alaxensis and 10 m plot adjacent to the transect were recorded. 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 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 m² 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 tormentose) 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 m² 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 15N ABUNDANCE

Foliar nitrogen content and natural abundance of 15N 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 N₂ from the plant A. viridis. The stable isotope ratio is expressed in thousandths following classical delta notation (δ²⁰¹⁵N = ([Rsample − Reference]/[Reference] × 1000), where R = N²/²⁰¹⁵N. Atmospheric N₂ is the ultimate reference value, with a value of zero. N₂ fixing plants have δ¹⁵N values closer to that of atmospheric N₂ than non-N₂ fixing plants. Non-N₂ fixing plants such as S. alaxensis will have δ¹⁵N values closer to N₂ fixing plants such as A. viridis if the non-fixing plants utilize biologically fixed N before soil processes modify δ¹⁵N. Total N content and isotope ratios were measured on a Carlo Erba 1500 CN analyzer linked to a VG Victor Isetech 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 (Bremmer 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. 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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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 15N 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. A. 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 δ15N 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 δ15N values lower than that of atmospheric N2.

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.

<table>
<thead>
<tr>
<th></th>
<th>Foil $^{15}$N</th>
<th>Foil total $N$ (%)</th>
<th>Wilks’ lambda</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Alnus viridis</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>$-1.27 \pm 0.07a$</td>
<td>$-4.44 \pm 0.90b$</td>
<td>$2.30 \pm 0.29ab$</td>
</tr>
<tr>
<td>Alnus</td>
<td>$3.32 \pm 0.07a$</td>
<td>$1.60 \pm 0.13b$</td>
<td>$3.22 \pm 0.19a$</td>
</tr>
</tbody>
</table>

$^a$ 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 uninoculated 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 *Alnus* treatment. This indicated that *S. alaxensis* plants growing in the *Alnus* treatment were using biologically fixed N more directly, because the $\delta^{15}$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; Kielstad, 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.

<table>
<thead>
<tr>
<th></th>
<th>n Year 1$^a$</th>
<th>n Control</th>
<th>n</th>
<th>Alnus</th>
<th>$F$</th>
<th>$P^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mineral soil</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pH</td>
<td>11 7.56 ± 0.10a</td>
<td>10 6.88 ± 0.12b</td>
<td>11 6.53 ± 0.13c</td>
<td>42.91 &lt;.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Extractable P (ppm)</td>
<td>11 1.73 ± 0.19a</td>
<td>10 2.10 ± 0.48a</td>
<td>11 3.84 ± 0.49b</td>
<td>11.05 0.0007</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Organic matter (%)</td>
<td>11 1.59 ± 0.16a</td>
<td>10 0.42 ± 0.20b</td>
<td>11 0.80 ± 0.17a</td>
<td>17.72 &lt;.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total N (%)</td>
<td>11 0.027 ± 0.004a</td>
<td>10 0.008 ± 0.002b</td>
<td>11 0.006 ± 0.001b</td>
<td>50.60 &lt;.0001</td>
<td></td>
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</tr>
</tbody>
</table>

Wilks’ Lambda

for MANOVA

20.78 <.0001

Biological soil crust

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>Alnus</th>
<th>$F$</th>
<th>$P^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH</td>
<td>6 6.01 ± 0.24</td>
<td>11 5.67 ± 0.14</td>
<td>2.20 0.1984</td>
<td></td>
</tr>
<tr>
<td>Extractable P (ppm)</td>
<td>6 7.00 ± 1.39</td>
<td>11 12.09 ± 2.38</td>
<td>1.58 0.2642</td>
<td></td>
</tr>
<tr>
<td>Organic matter (%)</td>
<td>6 2.63 ± 0.56</td>
<td>11 2.80 ± 0.51</td>
<td>0.55 0.4900</td>
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</tr>
<tr>
<td>Total N (%)</td>
<td>6 0.050 ± 0.020</td>
<td>11 0.047 ± 0.015</td>
<td>0.32 0.5948</td>
<td></td>
</tr>
</tbody>
</table>

Wilks’ Lambda

for MANOVA

1.16 0.5121

Litter

<table>
<thead>
<tr>
<th></th>
<th>Total N (%)</th>
<th>n</th>
<th>$F$</th>
<th>$P^b$</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>3.138 ± 0.045</td>
<td>11</td>
<td>1.16 0.5121</td>
<td></td>
</tr>
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</table>

$^a$ 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.

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 was 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.

Acknowledgments

This work was supported by funding and logistical support from the U.S. Geological Survey, National Park Service Alaska Regional Office Minerals Management Branch, and Denali National Park and Preserve, with special assistance from A. R. Carter and P. Spencer. D. Schramm designed and directed the spoil recontouring. J. Van Horn, M. Pope, M. Emerz, M. and A. Vander Meer, J. Forbes, T. Ledwith, D. Kogel, J. Knudsen, and J. Kuty provided field assistance.

The manuscript benefited from comments from D. Derksen, D. Helm, P. Spencer, and M. Udevitz.

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