

Alder (*Alnus crispa*) effects on soils in ecosystems of the Agashashok River valley, northwest Alaska¹

Chuck RHOADES², Department of Forest Sciences, Colorado State University, Fort Collins, Colorado, U.S.A.

Hlynur OSKARSSON, RALA - Agricultural Research Institute, Reykjavik, ICELAND.

Dan BINKLEY, Department of Forest Sciences, Colorado State University, Fort Collins, Colorado, U.S.A.

Bob STOTTLEMYER, USGS Biologic Resources Division, Fort Collins, Colorado, U.S.A.

Abstract: At the northern limit of the boreal forest biome, alder (*Alnus crispa* [Ait.] Pursh) shrubs occur in a variety of ecosystems. We assessed the effects of individual alder shrubs on soil properties and understory plant tissue nitrogen in floodplain terraces, valley slopes and tussock tundra ridges. The three ecosystems differed with respect to soil properties and abiotic conditions and supported distinct plant communities. Alder increased resin-exchangeable soil N and NO₃ production significantly in each ecosystem. The greatest difference between alder canopy and surrounding soil NO₃ measured both under field and laboratory conditions occurred in floodplain sites. The shrub effect on soil pH and soil organic matter was greatest on tundra ridges. Alder shrubs also influenced the nitrogen nutrition of plants growing beneath their canopies. Plants growing below alder canopies had higher foliar nitrogen concentration and natural abundance ¹⁵N composition and lower carbon to nitrogen ratio than open-grown plants. Similar to soil N availability, understory plant leaf chemistry responded more to alder on floodplains than on slope or tundra ecosystems. This pattern suggests that understory plants rely more heavily on alder-fixed-N in this resource-poor ecosystem.

Keywords: arctic ecosystems, soil nitrogen isotopes, tundra, floodplain.

Résumé : À la limite nord de la forêt boréale, l'Aulne crispé (*Alnus crispa* [Ait.] Pursh) occupe différents milieux. Nous avons évalué l'effet d'aulnes individuels sur les propriétés du sol et la teneur en azote des tissus des plantes sous-jacentes, dans des plaines d'inondation, des versants de vallées et des crêtes de toundra herbacée. Les trois écosystèmes différaient au niveau des propriétés du sol et des conditions abiotiques et supportaient des communautés végétales distinctes. L'Aulne crispé a significativement augmenté la production de N résine-échangeable et de NO₃ du sol dans chaque écosystème. La plus grande différence entre le NO₃ sous un couvert d'aulnes et dans le sol adjacent, mesurée à la fois en conditions naturelles et contrôlées, s'est manifestée dans les plaines d'inondation. L'effet des arbustes sur le pH du sol et sa teneur en matière organique était maximal sur les crêtes toundriques. Les aulnes ont également influencé la nutrition en azote des plantes croissant sous leur couvert. Le feuillage des plantes croissant sous un couvert d'aulnes avait une concentration en azote et une composition en ¹⁵N d'abondance naturelle plus élevées et un rapport carbone:azote plus faible que les plantes de milieu ouvert. Tout comme pour la disponibilité du sol en N, la chimie foliaire des plantes sous-jacentes a mieux répondu à la présence de l'Aulne crispé dans les plaines d'inondation que dans les écosystèmes de versants ou de toundra. Ce patron suggère que les plantes sous-jacentes dépendent plus fortement de l'azote fixé par l'aulne dans cet écosystème pauvre en ressources.

Mots-clés : écosystèmes arctiques, isotopes de l'azote du sol, toundra, plaine d'inondation.

Introduction

The influence of *Alnus* trees and shrubs on ecosystem development and soil nutrient pools is well studied. Red alder (*Alnus rubra* Bong.) trees symbiotically fix in excess of 7 g N m⁻² annually in the Pacific Northwest (Binkley, Cromack & Baker, 1994), contribute to soil total N accumulation (Bormann, Cromack & Russell, 1994), and increase availability of soil N (Hart, Binkley & Perry, 1997) and P (Giardina *et al.*, 1995). When grown in mixed-species stands on N-poor soils, alder can increase the growth and nutrient content of associated conifers (Tarrant & Miller, 1963; Binkley *et al.*, 1992).

In southern and interior Alaska, the development of dense alder thickets form an important successional stage following deglaciation (Crocker & Major, 1955; Chapin *et al.*, 1994)

and silt-cap deposition in river floodplains (Van Cleve, Viereck & Schlenter, 1971; Van Cleve *et al.*, 1993). Along the Tanana River near Fairbanks, Alaska, Van Cleve, Viereck and Schlenter (1971) estimated average soil N accretion of 12 g m⁻²yr⁻¹ during the formation of 20 year-old *A. incana* [(L.) Moench spp. *tenuifolia* (Nutt.) Brietung] thickets. In fact, alder increases N cycling more than it affects total N capital (Clein & Schimel, 1995). Compared to earlier and later successional stages, soil N turnover was several-fold higher on alder-dominated river terraces due to inputs of N-rich litter (Van Cleve *et al.*, 1993; Clein & Schimel, 1995).

In spite of ample evidence of increased soil N availability under alder, few attempts have been made to trace alder-derived N into associated non-N-fixing plants. Binkley, Sollins and McGill (1985) attempted to use natural abundance isotope ratios to trace alder-fixed-N in various soil N pools and plant tissue. They found no pattern between Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] foliage

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²Author for correspondence. Present address: Department of Forestry, University of Kentucky, Lexington, KY 40546-0073, crchoa2@pop.uky.edu

grown in monospecific stands or in stands mixed with red alder. Natural abundance N isotope techniques have been used to identify the sources and forms of soil N taken up by plants in a variety of arctic ecosystems (Shulze, Chapin & Gebauer, 1994; Nadelhoffer *et al.*, 1996; Michelsen *et al.*, 1996). Differentiation based on N isotopes is possible because the $\delta^{15}\text{N}$ value of N-fixing plants approaches that of atmospheric N_2 gas (0‰) while plants relying on inorganic soil N forms are more depleted in ^{15}N (Shearer & Kohl, 1989). The isotope signature of foliage from alder (*Alnus crispa* [Ait.] Pursh) growing in tussock tundra on Alaska's North Slope was -1.5‰ , where graminoid *Carex* sp. and *Eriophorum vaginatum* L. foliage averaged $+2\text{‰}$ and ericaceous and *Salix* sp. shrubs averaged -4‰ (Nadelhoffer *et al.*, 1996). Further isotopic variation between species derives from differences in rooting depth, soil mycorrhizal associations, and form of N taken up by plants (Högberg, 1997). Paired comparisons of foliar $\delta^{15}\text{N}$ of plants growing beneath alder canopies and > 2 m beyond the canopy dripline may demonstrate uptake of alder-fixed-N by associated plants.

At the northern limit of the boreal forest in northwestern Alaska, *A. crispa* grows individually and in small patches across a variety of landscapes. While there has been abundant research on the influence of alder on soil properties within discrete ecosystems, few studies have considered the influence of alder over entire watersheds (Stottlemyer, 1992) or have evaluated alder effects among ecosystem types. The objective of this study was to measure the effect of *A. crispa* shrubs on soil and understory plant conditions in three distinct ecosystems where alder is common. We hypothesized that alder effects vary among arctic ecosystems and are most evident around isolated shrubs on resource-poor sites.

Material and methods

SITE DESCRIPTION

Research was carried out in the Agashashok River valley ($67^{\circ}28' \text{N}$ $162^{\circ}14' \text{W}$, elevation 120 m) approximately 35 km from its confluence with the Noatak River. The site is located within the Noatak National Preserve, at the western extent of the Brooks Range in the Baird Mountains. Summer (June to August) and winter (November to February) mean air temperature in Kotzebue, Alaska (80 km south of site) were 9.9 and -17.5°C , respectively from 1955

to 1990 (NOAA, 1998). Air temperature at the Agashashok site (shaded box at 1.5 m height) averaged 2°C higher than the Kotzebue averages during June through August of 1997 and 1998. Precipitation in Kotzebue averages 220 mm per year and is concentrated between July and September.

Alder shrubs are found on floodplain terraces, valley slopes and tussock tundra interfluvies within the Agashashok river valley. Within the floodplain, individual alder shrubs are widely spaced along the edges of abandoned river channels on 10-20 cm thick silt caps overlaying river cobbles. Soil texture is loamy (10% clay, 42% silt and 48% sand). Floodplain vegetation is dominated by *Dryas integrifolia* subsp. *integrifolia* (M. Vahl), a woody-stemmed prostrate plant intermingled with sparse shrubs and forbs (Table I). Alder regenerates in dense clumps (about 800 to 1000 shrubs ha^{-1}) on steep valley slopes (60-70%). Soils beneath valley slope alder stands are shallow, rocky and appear to have formed on mudslides. Soil texture is clay loam (29% clay, 32% silt and 39% sand). The well-drained, sloping soils have relatively high shrub and flowering plant species diversity. Within wet tussock tundra, alder occur both in evenly-spaced stands (Chapin, McGraw & Shaver, 1989) and concentrated along surface drainage features. Thaw depth of the tundra soils extends from the soil surface to 30-40 cm by mid-summer. Tundra mineral soils contain 26% clay, 34% silt and 40% sand. Tussock tundra is dominated by *Eriophorum vaginatum* (cotton grass) with a mixture of erect and prostrate ericaceous plants.

SAMPLING AND ANALYSIS

To assess the effect of alder clumps on soil properties, a variety of field and laboratory soil tests were performed on soils sampled beneath alder canopies and in adjacent open areas. *In situ* soil N and P availability and movement were measured using ion exchange resin bags located at 5 cm depth, beneath the forest floor or moss layer (Binkely, 1984). In floodplain and slope ecosystems this depth was located within mineral soil, while in the tundra it fell within the compacted organic layer found above the permafrost. Resin bags were prepared by sealing 14 mL of cation resins (Sybron Chemi-cals, Inc., ID# C-251) and 14 mL of anion resins (Sybron Chemicals, Inc., ID# ASB-1P) into separate nylon stockings. Resin bags were installed in mid-June, cutting a small slit in soils with a serrated knife, inserting the paired cation and anion resin bags, and gently replacing the moss or litter layer. Exchange resins were removed after 40

TABLE I. Dominant plants of three ecosystem types of the Agashashok River valley. Nomenclature follows Hultén (1968).

Ecosystem type	Shrub strata	Herbaceous strata	Ground cover
Floodplain terrace	<i>Salix alaxensis</i> (Anderss.) Cov. <i>S. brachycarpa</i> ssp. <i>niphochlada</i> Nutt. <i>Shepherdia canadensis</i> (L.) Nutt. <i>Potentilla fruticosa</i> L.	<i>Epilobium latifolium</i> L. <i>Oxytropis campestris</i> (L.) DC. <i>Hedysarum alpinum</i> L. <i>Senecio lugens</i> Richards.	<i>Dryas integrifolia</i> M. Vahl <i>Arctostaphylos rubra</i> (Rehd. & Wilson) Fern. <i>Salix reticulata</i> L.
Valley slope	<i>Salix planifolia-pulchra</i> Cham. <i>S. glauca</i> L. <i>S. lanata</i> L. <i>Vaccinium uliginosum</i> L.	<i>Equisetum arvense</i> <i>Boykinia richardsonii</i> (Hook.) Gray <i>Dodecatheon frigidum</i> Cham. & Schlecht. <i>Papavar macounii</i> Greene	<i>Dryas octopetala</i> L. <i>Salix reticulata</i> L. <i>Andromeda polifolia</i> L. <i>Cassiope tetragona</i> (L.) D. Don
Tussock tundra ridge	<i>Vaccinium uliginosum</i> L. <i>Betula nana</i> L. <i>Salix planifolia-pulchra</i> Cham.	<i>Eriophorum vaginatum</i> L. <i>Carex</i> spp. <i>Rubus chamaemorus</i> L. <i>Petasites hyperboreus</i> Rydb.	<i>Ledum palustre</i> L. spp. <i>decumbens</i> (Ait.) Hult. <i>Vaccinium vitis-idaea</i> L. <i>Empetrum nigrum</i> L.

days, refrigerated, and extracted with 2 M KCl. Soil NO_3 , NH_4 , and PO_4 were analyzed with a Lachat continuous-flow spectrophotometer (Lachat Instruments, Milwaukee, Wisconsin). Resin bags were located beneath alder (< 1 m from center of shrub clump) and in open sites (> 2 m from edge of alder canopy). On sloping sites, sample pairs were oriented along the contour to minimize contamination from adjacent shrubs. In dense stands it may not have been possible to avoid downhill soil N creep from uphill shrubs. Six alder canopy / canopy inter-space pairs were studied in two replicate floodplain, slope and tundra ecosystems located within 3 km of one another.

Soil samples, composited from 3 soil cores, were taken within 1 m of resin bag locations beneath alder canopies and in open areas. Six alder canopy and open site pairs were sampled at one site per ecosystem type. In floodplain and slope ecosystems, soil was collected from the upper 10 cm of mineral soil. Tundra soil was sampled from the active rooting zone. At the time of sampling this consisted of compacted, well-decomposed organic horizon (Oa) found in the 10 cm immediately above frozen mineral soil.

Soil N availability was estimated by a 90-day laboratory incubation of field-moist soils maintained at constant temperature (5°C) and moisture conditions. Following incubation, soil NO_3 and NH_4 were extracted with 2 M KCl and analyzed as above by Lachat continuous-flow spectrophotometry. Total C and N were analyzed by dry combustion using a LECO CHN-1000 element analyzer. Soil was dried, sieved to pass a 2 mm mesh, and ground prior to total element analysis. Soil pH was measured in 1:1 fresh soil to deionized water and 0.01 M CaCl_2 solutions. Extractable cations (Ca^{2+} , Mg^{2+} , K^+) were quantified in 1 M NH_4NO_3 extracts by inductively coupled plasma spectroscopy.

To assess the amount and source of nitrogen available to plants growing beneath alder canopies, foliage N and C content and natural abundance isotope composition were compared between canopy and open-grown plants. Tissue was sampled from the dominant ground cover species in each ecosystem type (Table I). Green leaves of *Dryas integrifolia*, *Dryas octopetala* L., and *Ledum palustre* L. ssp. *decumbens* (Ait.) Hult. were clipped on floodplain, valley slope, and tundra sites, respectively. Both *Dryas integrifolia* and *D. octopetala* are non-nodulated, unlike *D. drummondii* Richards that grows in southern Alaska (Kohls *et al.*, 1994). Plant tissue was dried and ground prior to total element and isotope analysis. Foliage total C and N were analyzed by dry combustion as described above. Stable N isotopes were analyzed in N_2 gas samples following sample combustion. Ratios of $^{15}\text{N}/^{14}\text{N}$ were measured using a Finnegan MAT Delta-S dual inlet ratio mass spectrometer. Measurement of stable N isotope ratios is expressed in per thousand (‰) units using delta notation (δ) to characterize change relative to an atmospheric N_2 standard (Shearer & Kohl, 1989), where $\delta^{15}\text{N} = \{[(^{15}\text{N}/^{14}\text{N})_{\text{sample}}] / (^{15}\text{N}/^{14}\text{N})_{\text{reference}}\} - 1\} \times 1000$. Standard deviation for repeated measurements of a homogenized standard sample was 0.2‰ $\delta^{15}\text{N}$.

Height and diameter of individual alder canopies were measured for all sample shrubs ($n = 6$ per ecosystem). Basal diameter of four dominant stems of each shrub were measured near ground level using calipers. Shrub age was estimated on a limited number of stem cross-sections ($n = 1$

to 5 per ecosystem). Alder litter inputs were sampled from 25 cm × 50 cm plastic trays secured beneath alder crowns in August 1997 and emptied in June 1998. Leaf litter N content and natural abundance N isotope composition were analyzed by dry combustion and mass spectrometry as described earlier.

The effect of alder shrubs on soil N availability, soil nutrients, and ground cover tissue properties were compared within the three ecosystems. Within each ecosystem independent sample *t*-tests evaluated differences between shrub and open site means (SPSS Inc., 1997). In addition to alder canopy effects, it was possible to test the statistical significance of ecosystem differences on resin N and P, as *in situ* resin incubations were carried out in replicate sites per ecosystem. The interaction term between alder shrub and the ecosystem type tests the consistency of alder effects on resin-exchangeable nutrients across ecosystems. Analysis of variance main effects were alder, ecosystem, and site (SPSS Inc., 1997). The alder canopy effect (canopy *versus* open soil difference) was compared between the three distinct ecosystems by one-way analysis of variance.

Results

ALDER EFFECTS

Alder increased soil N availability *in situ* and in the laboratory incubation for all three ecosystems (Figures 1 and 2). Overall, resin- NO_3 was 7-fold higher beneath alder shrubs compared to a 3-fold increase in NH_4 . Beneath alder, resin- NO_3 averaged about 30% of total resin-N, compared to only about 15% in open soils. The effect of alder on resin- NO_3 and NH_4 was greatest in floodplain and tundra, respectively. Following the 90-day incubation, alder soil contained 3 to 30 times more NO_3 than open soils (Figure 2). Alder had positive, negative and no effect on NH_4 concentrations following incubation of floodplain, slope, and tundra sites, respectively. Resin-P was also significantly higher ($P < 0.06$) beneath alder shrubs (Table II). Relative to open sites, resin-P was 1.2, 13.5 and 10-fold greater beneath alder in floodplain, slope, and tundra ecosystems. Total soil N and C increased by 50% under tundra alder ($P < 0.1$), but had little effect on total C and N pools in the other ecosystems (Table III).

Soil pH decreased by 0.1 to 0.5 units beneath alder shrubs (Table III). Shrubs changed soil acidity to the greatest extent in tundra where total soil N also increased substantially. There was no discernible zone of influence on soil pH beneath individual valley slope alder. Extractable cations differed little between alder and open soils on floodplain or valley slopes. In tundra soils, the sum of NH_4NO_3 extractable cations was 1.6 times higher under alder canopies than in open sites. Interestingly, both extractable cations and soil acidity increased beneath alder crowns (Table III). This apparent disparity probably results from increased soil organic pools beneath shrub canopies that both augment the number of cation exchange sites and the total quantity of organic acid in the soil (Binkley & Sollins, 1990).

The natural abundance N isotope composition of alder litter inputs was close to atmospheric N_2 levels (‰), ranging from -1.8‰ in leaf litter, -1.5‰ in roots and -2.0‰ in woody debris. Relative to open-grown ground cover plants, those growing below alder canopies had higher

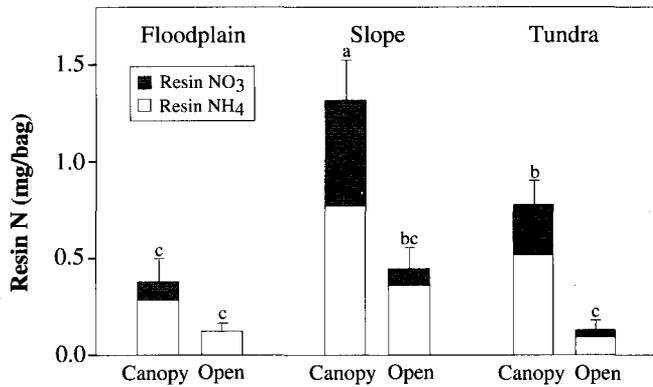


FIGURE 1. Ion exchange resin NH₄ and NO₃ for alder canopy and open soils on three arctic ecosystem types. Bars report mean of six trees in two replicate sites per ecosystem type with standard error of the mean. Similar letters indicate that means do not differ at a 0.05 significance level.

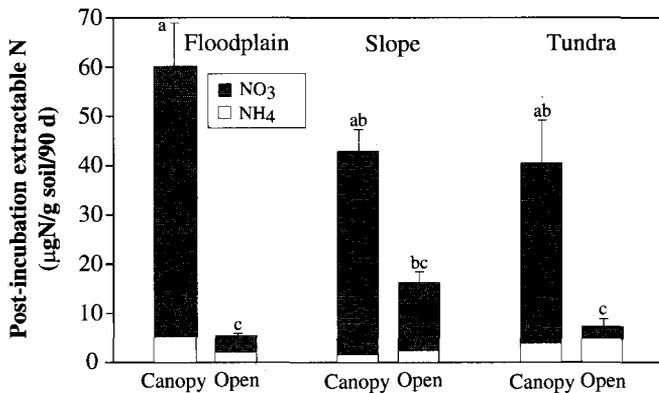


FIGURE 2. Extractable soil N following 5°C incubation. Bars report mean of six trees per ecosystem type with standard error of the mean. Similar letters indicate that means do not differ at a 0.05 significance level.

TABLE II. *F*-ratio and significance levels of analysis of variance testing alder shrub, ecosystem, and replicate site effects on resin N and P.

Main Effect	NO ₃	Resin NH ₄	P
Alder	31.77	15.63	3.57
	0.00	0.00	0.06
Ecosystem	11.09	6.85	1.50
	0.00	0.00	0.23
Site	0.74	1.00	0.26
	0.39	0.32	0.61
Alder × ecosystem	5.45	1.01	1.76
	0.01	0.37	0.18

TABLE III. Alder effects on soil properties on three arctic ecosystem types. Mean and significance value (*p*-value) of paired *t*-test (*n* = 6).

Ecosystem	Type	Total % Carbon	Nitrogen	C:N	Soil pH		Extractable Cations mmol _c kg ⁻¹		
					Water	CaCl ₂	Ca	Mg	K
Floodplain	Canopy	7.098	0.4	19.9	7.8	7.3	307.4	24.3	0.8
	Open	6.619	0.3	19.7	8.0	7.4	299.0	23.9	0.5
	<i>p</i>	0.59	0.41	0.92	0.03	0.00	0.76	0.89	0.15
Slope	Canopy	12.224	0.8	15.9	6.6	6.0	348.7	51.7	0.7
	Open	12.033	0.7	16.3	6.7	5.9	316.2	49.5	1.4
	<i>p</i>	0.88	0.97	0.46	0.92	0.47	0.29	0.53	0.07
Tundra	Canopy	22.452	1.2	18.1	5.3	4.5	375.5	57.6	2.1
	Open	14.829	0.8	19.0	5.8	4.8	243.2	33.5	1.6
	<i>p</i>	0.10	0.09	0.31	0.01	0.06	0.14	0.08	0.29

foliar nitrogen concentration and δ¹⁵N (Table IV). Leaf δ¹⁵N of alder understory plants was 2.4, 1.8 and 0.6‰ greater (*i.e.* closer to the isotopic signature of atmospheric N) than open-grown floodplain, slope and tundra plants. The difference between canopy- and open-grown plant tissue N (*F*-test: 8.6; *P* < 0.008), C:N ratio (*F*-test: 9.0; *P* < 0.007), and δ¹⁵N (*F*-test: 3.2; *P* < 0.09) differed significantly among the three ecosystems. Alder shrub effects on plant tissue chemistry were greatest on floodplains, followed by slope and tundra ecosystems.

ECOSYSTEM AND LANDSCAPE DIFFERENCES

The three ecosystems differed significantly with regard to most soil properties (Table III). The coarse-texture floodplain soils were warmer and drier (11°C and 72% gravimetric soil moisture at 5 cm) than the fine-texture tundra soils (5°C and 140% moisture). Conditions on valley slopes were intermediate (8°C and 86% moisture). Valley slope sites support the largest shrubs that in turn generate twice the leaf litter of floodplain or tundra alder (Table V). The 3 landscapes differed significantly with regard to most soil properties (Table III). The coarse-texture floodplain soils were much warmer and drier (11°C and 72% gravimetric soil moisture at 5 cm) than the fine-texture tundra soils (5°C and 140% moisture). Conditions on valley slopes were intermediate (8°C and 86% moisture). Valley slope sites support the largest shrubs that generate twice the litterfall of floodplain or tundra alder (Table V). The age of alder shrubs appears to increase from floodplain to slope and tundra.

Resin and post-incubation N were comparable between alder-free floodplain and tundra soils (Figures 1 and 2). The less-densely-stocked slope #2 had similar resin-N as open site soil in tundra and floodplain ecosystems. The denser stand (slope site #1), however, contained 2.4 times the resin-N of slope site #2. Resin-P was more than 4-fold higher in open floodplain than tundra soils (data not shown); open valley slope soil had intermediate resin-P.

Total soil N and C mirrored the trend in abiotic conditions; soil organic matter pools were highest in the cold, wet tundra soils and lowest on the warm, dry floodplain (Table III). Soil acidity was greatest in the tundra as was the change in pH measured in 0.01 M CaCl₂ (1.0 pH unit). Periodic deposition of silt by floodwater contributes soluble cation salts and weatherable minerals that maintain the slightly alkaline pH of the floodplain soils.

TABLE IV. Leaf N and C content and natural abundance isotope ratio for dominant ground cover species in each ecosystem type (Mean and SE of mean; n = 3). Alder effect was analyzed using an independent sample t-test within each ecosystem.

Ecosystem Sample Species		C %	Leaf Tissue		$\delta^{15}\text{N}$ ‰
			N %	C:N	
FLOODPLAIN					
<i>Dryas integrifolia</i>	Canopy	46.03	2.00	23.31	-5.81
		1.1	0.2	1.7	0.1
	Open	47.60	1.13	42.21	-8.20
		1.2	0.1	0.9	0.2
	t-test p-value	0.377	0.000	0.002	0.004
SLOPE					
<i>Dryas octopetala</i>	Canopy	49.52	2.31	21.82	-1.75
		0.5	0.2	2.1	0.4
	Open	46.70	1.47	31.92	-3.63
		2.6	0.1	1.7	0.7
	t-test p-value	0.393	0.042	0.023	0.107
TUNDRA					
<i>Ledum palustre</i>	Canopy	52.59	1.74	30.33	-4.58
		0.3	0.0	0.7	0.5
	Open	53.68	1.37	39.26	-5.18
		0.3	0.0	0.9	0.1
	t-test p-value	0.025	0.000	0.000	0.30

TABLE V. Alder shrub age, size, and leaf litter from replicate sites (n = 6 shrubs per site) in three ecosystems.

Ecosystem	Site	Age ¹ yr	(n)	Canopy		Stem ² Diameter cm	Leaf Litter g m ⁻² yr ⁻¹
				Height m	Diameter m		
Floodplain	1	23	(5)	1.1	3.3	5.5	85.9
	2	nd ³		0.9	2.3	3.9	119.9
Slope	1	49	(3)	2.5	3.8	4.7	247.9
	2	nd		3.3	4.4	6.1	273.0
Tundra	1	53	(1)	1.7	3.2	4.3	184.2
	2	nd		1.7	3.0	3.6	106.8

¹ Mean of basal cross-sections of 1-5 main stems

² Mean basal caliper of 4 main stems per clump

³ nd: Not determined

Discussion

Our study quantifies the dramatic effect of alder shrubs on soil N pools within three different arctic ecosystem types. In each ecosystem, understory plant N uptake is linked to alder-fixed soil N. The soil enrichment pattern and the relationship between alder-N and understory plant N uptake varies between floodplain terrace, valley slope and tundra ridge ecosystems. Community- and ecosystem-specific response to alder-fixed N will determine the degree to which alder may direct ecosystem development.

Varying soil properties, abiotic conditions, and disturbance regime combine to influence both alder growth and ecosystem-specific shrub effects. On floodplain silt-caps, for example, isolated shrubs are exposed to both strong winds and seasonal floodwaters that scour leaf litter from beneath shrub canopies and reduce N return to the soil. Not only does the floodplain environment limit N accumulation beneath alder canopies, soil conditions may also limit N retention within the soil profile. The coarse floodplain soil provides a well-oxidized environment that favors inorganic N production, as during our laboratory incubation (Figure 2). However, the low clay content of floodplain soils may limit their ability to retain soil N or sequester organic inputs.

Sloping areas generally have better drainage and deeper active (thawed) layers than level, tundra ecosystems. Establishment of dense, productive alder stands on slopes of the Agashashok River valley appears to have followed soil slumping and the exposure of a mineral soil seedbed. Valley-slope alder stands support the largest shrubs with the greatest litterfall (Table V). These stands return 5.2 g N m⁻²yr⁻¹ compared to 2.1 and 2.9 g N m⁻²yr⁻¹ annually on floodplain and tundra landscapes, respectively.

Greater shrub density and productivity combine with topography to dilute the soil resource-island beneath individual alder crowns on valley slopes. Larger soil N (resin, incubation, total) and soil acidity responses beneath floodplain and tundra alder as compared to slope ecosystems indicate that nutrient transport homogenizes hill-slope alder effects. In previous work, we measured increased soil N availability extending more than 10 m down-slope from the edge of a red alder stand into a pure Douglas-fir stand in western Washington (Rhoades & Binkley, 1992). On tundra slopes, Valentine (1990) found that zones of enriched available soil N extended 3 to 6 m down-slope of individual alder shrubs. As alder density increased, discrete "islands" of higher soil N around individual alders overlapped and disappeared.

Alder shrubs appear to be a stable, long-lived component of the tussock-tundra community. The oldest alder sampled (53 years) was growing within tundra (Table V). Alder shrubs are often nestled in small basins of tussock vegetation where they resprout repeatedly following tundra fires. The cold, wet tundra soil conditions favor the formation of organic matter beneath alder crowns.

Soil N availability beneath alder canopies is well correlated with shrub height (Figure 3). Although the relation between alder height and open-site resin-N may provide a site index of alder growth, differences in shrub age, stand density, and herbivory complicate comparisons. Within the Agashashok River valley, the activity of herbivores (moose and caribou) is heaviest along floodplain terraces and stream drainages (C. Rhoades, pers. observ.). The small stature of floodplain alder may therefore result from herbivory compounding the low nutrient status of the floodplain soils.

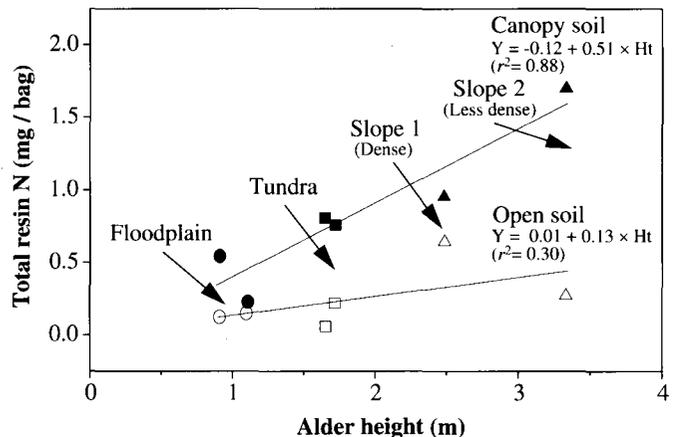


FIGURE 3. Relation between soil N availability and height of individual alder clumps. Symbols are means of six alder shrubs or open samples for each site replicate. Solid symbols denote canopy samples, open symbols denote open samples.

Conversely, the larger size of valley slope alder may result from lighter herbivory combined with more favorable soil and abiotic factors.

Soil N accumulated beneath tundra and floodplain alder at about $4.5 \text{ g m}^{-2}\text{yr}^{-1}$, based on 50 and 25 year-old average shrub ages in the two ecosystems. Mineral soil nitrogen accretion (0-10 cm) averaged $1.5 \text{ g m}^{-2}\text{yr}^{-1}$ in a 23-year-old mixed Sitka alder (*A. sinuata* [Regel] Rydb.) and Douglas-fir stand on a low-fertility site in southern British Columbia (Binkley, Cromack & Baker, 1984). Assuming that the Agashashok valley-slope alder regenerated 50 years ago on mineral substrate containing similar total N as open floodplain soils, soil N may have increased by around $7.5 \text{ g m}^{-2}\text{yr}^{-1}$ in the upper 10 cm of mineral soil. This rate is 60% of that of the *A. incana* thickets growing on Tanana river terraces (Van Cleve, Viereck & Scelenter, 1971). In Tanana alder stands, shrubs reach more than 4 m tall with average stem diameters of 7 cm and support more than 7000 alder stems ha^{-1} as compared to 1000 shrubs ha^{-1} on Agashashok valley slopes.

Soil N is the principal soil nutrient limiting plant production in many arctic (Shaver & Chapin, 1991) and alpine (Bowman *et al.*, 1993) ecosystems. The increase in foliar N of plants growing near alder indicates that the understory plants are exploiting the zone of increased soil N availability beneath the shrubs. The higher natural abundance N isotope signature of the below-canopy plants further demonstrates the linkage between alder-fixed N and understory plant N uptake. While the magnitude of the alder effect on plant tissue varied between ecosystems, we are unable to separate ecosystem differences from species-specific responses of the understory sample species. The largest alder effect on soil and understory leaf chemistry (*Dryas integrifolia*) occurred on the floodplain terrace, suggesting a closer link between plant N uptake and alder-fixed-nitrogen in this nutrient-poor ecosystem. A similar zone of soil enrichment occurred beneath tundra alder, yet *Ledum palustre* tissue did not respond as dramatically. While this study demonstrates a link between alder-originated soil N and understory plant N uptake, further work is required to resolve how this pattern varies between understory plant species and ecosystems.

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