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Salmon and alder as nitrogen sources to riparian forests in a boreal Alaskan watershed

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Abstract Anadromous Pacific salmon (*Oncorhynchus* spp.) transport marine-derived nitrogen (MDN) to the rivers in which they spawn. Isotopic analyses of riparian vegetation in a boreal Alaskan watershed indicate that trees and shrubs near spawning streams derive ~24–26% of their foliar nitrogen (N) from salmon. Basal area growth of white spruce (*Picea glauca*) is enhanced at sites receiving MDN inputs. This marine N subsidy appears to be less important to riparian ecosystems where symbiotic N fixation by alder (*Alnus crispa*) is prevalent, although salmon carcasses may nonetheless be an important source of other marine-derived nutrients affecting productivity in these forests. These findings illustrate the complexity of interactions surrounding riparian forests and the interconnectedness of river and riparian ecosystems.

Keywords *Alnus crispa* · Marine-derived nutrients · *Oncorhynchus* · *Picea glauca* · Riparian · Stable isotopes

Introduction

Anadromous Pacific salmon (*Oncorhynchus* spp.) are a source of allochthonous nutrients to the watersheds in which they spawn. Having spent most of their lives feeding and growing at sea, salmon returning to spawn and die in their natal streams carry marine-derived nutrients in their body tissues. Returning salmon are a seasonal food source for numerous mammal and bird species (Cederholm et al. 1989; Willson et al. 1998), and nutrients from decaying salmon carcasses are used by periphyton, aquatic macroinvertebrates, resident freshwater

fishes and juvenile salmon in spawning streams (Mathisen et al. 1988; Kline et al. 1990, 1993; Bilby et al. 1996; Wipfli et al. 1998). Consequently, annual spawning runs provide a mechanism for transporting nutrients from the northern Pacific Ocean to coastal freshwater and terrestrial ecosystems.

Recent studies have shown that terrestrial plants adjacent to spawning streams may derive as much as 18–24% of their foliar nitrogen (N) from salmon (Bilby et al. 1996; Ben-David et al. 1998; Hilderbrand et al. 1999; Helfield and Naiman 2001). Marine-derived nitrogen (MDN) may be transferred from spawning streams to riparian forests by flooding which deposits salmon carcasses on stream banks, through the downwelling of dissolved nutrients from spawning streams into shallow subsurface (i.e., hyporheic) flowpaths, or through dissemination of feces, urine and partially-eaten carcasses by terrestrial piscivores (Ben-David et al. 1998; Hilderbrand et al. 1999; Quinn and Buck 2000; Reimchen 2000). As a result of this nutrient subsidy, growth rates of riparian trees are significantly enhanced near spawning streams in coastal temperate forests of southeastern Alaska (Helfield and Naiman 2001). Because N is a limiting factor for plant growth in most northern and temperate forests (Epstein 1972; Chapin 1980; Chabot and Mooney 1985; Chapin et al. 1986), MDN may exert an important influence on nutrient cycling and productivity in watersheds supporting anadromous salmon.

However, the ecological significance of MDN inputs is not universal to all salmon-producing watersheds. Symbiotic N fixation by alder (*Alnus* spp.) is an important source of N in many forest ecosystems. Alder-fixed nitrogen (AFN), transferred to surrounding soils through root and nodule secretions and production of N-rich leaf litter, results in accelerated N cycling and increased N availability in forest soils, as well as in increased growth and foliar N content in sympatric conifers and understory plants (Binkley 1983; Binkley et al. 1985, 1992; Wurtz 1995; Vogel and Gower 1998; Rhoades et al. 2001). For example, N fixation by alder contributes approximately 156–164 kg N per ha annually to interior Alaska flood-

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plain ecosystems (Van Cleve et al. 1971; Klingensmith and Van Cleve 1993). In coastal temperate ecosystems of the Pacific Northwest, the dominant alder are typically early-successional species (e.g., *A. rubra*), which are abundant primarily on recently disturbed sites. In contrast, shrub alders of boreal ecosystems (e.g., *A. crispa*, *A. tenuifolia*) inhabit early-successional forests (Van Cleve et al. 1971; Van Cleve and Viereck 1981; Wurtz 1995), but also form long-term, stable communities (Wilson et al. 1985; Wurtz 2000), which may control soil N dynamics throughout the later stages of succession. In such areas, MDN inputs might not be as important to forest N budgets.

Here we examine the effects of MDN on riparian white spruce (*Picea glauca*) in a boreal forest ecosystem of southwestern Alaskan. The specific objectives of this study are to (1) quantify MDN uptake by riparian trees, (2) assess the effects of MDN inputs on the basal area growth of riparian trees, and (3) determine how these effects are influenced by the presence of alder.

Materials and methods

Study sites

The study area is in the Wood River Lakes system, southwestern Alaska, USA. The Wood River system comprises Lakes Aleknagik, Nerka, Beverly, Kulik and their tributaries, as well as the village of Aleknagik (59°17'N, 158°36'W; Fig. 1). The area is in a transitional climatic zone, with maritime as well as continental influences affecting weather patterns. Average summer temperatures range from 6 to 20° C, and average winter temperatures range from -15 to -6°C. Annual precipitation ranges from 250 to 340 cm, of which 200–250 cm falls as snow (Hartman and Johnson 1984). The river and lakes are generally ice-free from June through mid-November.

The area's topography consists of rolling hills and low mountains with summits of approximately 500–1,000 m, as well as an extensive network of valley troughs excavated by repeated glaciations during the Pleistocene. The underlying bedrock consists of weakly metamorphosed Mesozoic sedimentary and volcanic rocks (Manley et al. 2001). Soils are primarily well-drained Typic Haplocryods, formed in silty volcanic ash over gravelly glacial drift or loam till (Rieger et al. 1979; Soil Survey Staff 1998). At lower elevations (i.e., <150 m), the vegetation is a boreal forest association of white spruce and paper birch (*Betula papyrifera*) with cottongrass (*Eriophorum* spp.). These forests are interspersed with areas of moist tundra featuring poorly drained organic soils, shallow permafrost tables and a vegetative cover of mosses and low shrubs. Hill slopes and some alluvial floodplains are dominated by dense stands of green alder (*A. crispa*). Available N is typically the limiting nutrient for growth in Alaskan white spruce forests (Van Cleve and Zasada 1976; Chapin et al. 1986; Schulze et al. 1994).

Apart from recreational and subsistence hunting and fishing associated with the village and nearby fishing lodges, the watershed has been almost entirely unaffected by land use disturbances. The Wood River system is a major producer of sockeye salmon (*O. nerka*) to the Bristol Bay fishery. Since 1950, annual escapement has ranged from 230,000 to 2,970,000 (Alaska Department of Fish and Game 1950–1992, D.E. Rogers, unpublished data 1993–97, Rogers and Rogers 1998). Bristol Bay streams and lakes have been characterized extensively regarding patterns of sockeye escapement, spawning behavior and predation by bears (Jensen and Mathisen 1983; Eggers and Rogers 1987; Blair and Quinn 1991; Blair et al. 1993; Quinn and Buck 2000; Ruggerone et al.

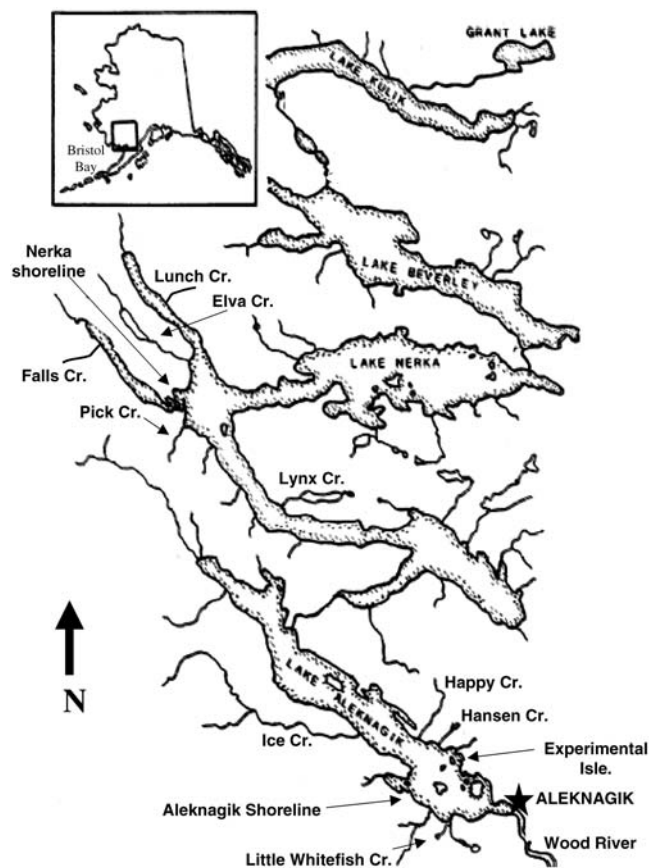


Fig. 1 The Wood River Lakes System (adapted from Rogers and Rogers 1998)

2000; Gende et al. 2001), and are known to be significantly enriched by biogenic inputs of salmon-borne, marine-derived nutrients (Donaldson 1967; Mathisen 1972; Mathisen et al. 1988; Kline et al. 1993; Eastman 1996).

Sample collection and analyses

Data were collected at ten riparian sites in the Wood River system (Fig. 1). Of these, seven were adjacent to tributaries of Lakes Aleknagik and Nerka (Elva Creek, Hansen Creek, Happy Creek, Ice Creek, Little Whitefish Creek, Lynx Creek, Pick Creek), and 3 were adjacent to the lakes themselves (Experimental Island, Aleknagik shoreline, Nerka shoreline). To evaluate the effects of MDN on riparian vegetation, we divided these sites into spawning sites (i.e., sites adjacent to streams with spawning salmon) and reference sites (i.e., sites adjacent to streams or shorelines without salmon). Sites with mean spawning densities of ≥ 0.5 fish per meter stream length, based on 1957–1997 escapement data, were considered spawning sites (Table 1). Apart from the absence of spawning salmon, reference sites were comparable to spawning sites in terms of physical and ecological characteristics (Table 2). To evaluate the effects of N-fixation by alder on sympatric white spruce, a further distinction was made between alder sites (i.e., $\geq 2\%$ green alder, by stem, in the riparian zone) and non-alder sites (i.e., no alder present in the riparian zone).

Field sampling occurred between June and August in 1997, 1998 and 1999. At each site, we established 4–6 transects extending perpendicularly from the stream or lakeshore. Transects were spaced randomly at intervals of at least 100 m. Sampling points were designated at 5 m, 25 m, 50 m and 100 m from the edge of

Table 1 Spawning and alder designations of study sites

Site	Stream length (km)	Mean escapement 1957–97	Mean spawning density (fish/m) 1957–97	Spawning designation	Alder in riparian zone (%)	Alder designation
Hansen Cr.	2.10	3,986	1.90	Spawning	0	Non-alder
Happy Cr.	6.45	5,165	0.80	Spawning	4	Alder
Ice Cr.	16.13	8,622	0.53	Spawning	2	Alder
Lynx Cr.	2.26	2,921	1.29	Spawning	0	Non-alder
Pick Cr.	4.03	10,776	2.67	Spawning	0	Non-alder
Elva Cr.	4.84	319	0.07	Reference	15	Alder
Experimental Is.	NA	0	0	Reference	0	Non-alder
L. Aleknagik shoreline	NA	0	0	Reference	15	Alder
L. Nerka shoreline	NA	0	0	Reference	19	Alder
Little Whitefish Cr.	1.29	190	0.15	Reference	0	Non-alder

Table 2 Comparison of physical and ecological characteristics (mean \pm 1 SE) of spawning and reference sites with and without alder. Single-factor ANOVA indicate no significant differences among site categories ($\alpha=0.05$)

Site characteristic	Spawning sites		Reference sites		$P (F_{3, 6} > F_{obs})$
	Alder	No alder	Alder	No alder	
Slope ($^{\circ}$)	2.7 \pm 0.6	2.8 \pm 1.9	5.0 \pm 1.1	4.4 \pm 0.2	0.43
Canopy cover (%)	63 \pm 2.4	53 \pm 11.1	50 \pm 8.8	51 \pm 10.5	0.82
Stem density (trees/ha)	1,630 \pm 257	1,006 \pm 232	1,159 \pm 75	1,001 \pm 155	0.20
Basal area density (m ² /ha)	31 \pm 6.0	36 \pm 14.3	35 \pm 6.2	33 \pm 7.0	0.98
Percent white spruce (by stem)	33 \pm 16.5	57 \pm 18.1	46 \pm 5.5	55 \pm 5.0	0.65
Percent green alder (by stem)	3 \pm 0.9	0 \pm 0.0	16 \pm 1.3	0 \pm 0.0	<0.0001

the active channel or high water mark along each transect ($n=223$). At each sampling point, we used a spherical densiometer to measure canopy cover and a hand-held clinometer to measure transect slope. Stem density, basal area density and overstory species composition were measured using the point-centered quarter method (Mueller-Dombois 1974). Foliage and increment core samples were collected from the nearest canopy white spruce (i.e., having its crown at canopy level with unobstructed access to direct sunlight) at each sampling point. Foliage samples were taken from the canopy at a height of approximately 3 m, and increment cores were taken from the bole as close as possible to the base of the tree, using a 5-mm-diameter manual borer. Where available, we also collected foliage samples of feltleaf willow (*Salix alaxensis*), balsam poplar (*Populus balsamifera*) and green alder. Additional poplar, willow and alder samples were collected at two supplementary reference sites (Falls Creek, Lunch Creek) where no spruce trees were present.

Foliage samples were dried at 50 $^{\circ}$ –60 $^{\circ}$ C for 48 h and ground to a fine (i.e., <212 μ m) powder for chemical analyses. Foliar carbon (C) and N contents were measured with a Lehman 440 CHN analyzer for determination of foliar C:N ratios. Stable isotope ratios (¹⁵N:¹⁴N) were measured with a Micromass Sira II mass spectrometer and MMS Dumas combustion system at Mountain Mass Spectrometry in Evergreen, Colorado.

Increment cores were dried, mounted on wooden blocks and sanded for analyses of annual growth rings. Ring widths were measured to the nearest 0.01 mm using a Henson incremental measuring stage and dissecting microscope with video display. Ring widths were converted to annual basal area increments by the equation

$$BAI = w \times 2\pi r \quad (1)$$

where BAI is annual basal area increment (mm²), w is annual ring width (mm) and r is the radius of the tree (mm), calculated as the cumulative total of all previous years' ring widths. Basal area growth (mm²/year) was then calculated as the mean BAI per year for each sample tree.

Physical and ecological characteristics of spawning and reference sites were compared with analyses of variance (ANOVA). Stable isotope data were analyzed with two-sample t -tests, ANOVA and Fisher's protected least significant difference (PLSD) to determine the effects of spawning versus reference sites and alder versus non-alder sites. Although C:N and basal area growth data were not normally distributed, these were also analyzed with ANOVA because of the robustness of the test with respect to deviations from normality (Srivastava 1959; Tiku 1971; Zar 1999). Correlations among physical and ecological factors affecting growth rates of sample trees were analyzed using Spearman's rho correlation coefficients.

Stable isotope analyses

Isotopic ratios of ¹⁵N:¹⁴N are generally higher in marine systems than in terrestrial or freshwater environments, and elevated ¹⁵N:¹⁴N ratios in terrestrial biota are often indicative of marine enrichment (Schoeninger et al. 1983; Owens 1987). These ratios are expressed as $\delta^{15}\text{N}$ values, which represent the per mil deviation in ¹⁵N abundance from atmospheric N₂, the recognized isotopic standard. $\delta^{15}\text{N}$ values are calculated as

$$\delta^{15}\text{N} = (R_{\text{sample}} - R_{\text{standard}}) / (R_{\text{standard}}) \times 1,000 \quad (2)$$

where R is the ratio of ¹⁵N to ¹⁴N. Observed $\delta^{15}\text{N}$ values may be converted to MDN percentages using a two-source mixing model (e.g., Kline et al. 1990; Bilby et al. 1996). The mixing model calculates MDN percentages as

$$\%MDN = [(SAM - TEM) / (MEM - TEM)] \times 100 \quad (3)$$

where %MDN is the percent MDN in a given sample, SAM is the observed $\delta^{15}\text{N}$ of the sample, TEM is the terrestrial end member (i.e., $\delta^{15}\text{N}$ value representing 0% MDN) and MEM is the marine end member (i.e., $\delta^{15}\text{N}$ value representing 100% MDN). In this study, SAM was calculated as the mean foliar $\delta^{15}\text{N}$ of each species

at spawning sites, TEM was the mean $\delta^{15}\text{N}$ of conspecific foliage at reference sites without alder, and MEM was the mean $\delta^{15}\text{N}$ of sockeye salmon carcass tissue. The model assumes that isotopic fractionation associated with N uptake is negligible, as is likely the case where N is limiting (Nadelhoffer and Fry 1994).

Results and discussion

MDN enrichment of riparian vegetation

Foliar $\delta^{15}\text{N}$ of spruce, willow and poplar was significantly higher at spawning sites relative to reference sites (Fig. 2). The only species for which there was no significant difference between spawning and reference sites was green alder. That alder $\delta^{15}\text{N}$ was relatively constant among study sites and similar to values reported for alder grown experimentally in N-free soils (Binkley et al. 1995; Vogel and Gower 1998) suggests that alder were obtaining N primarily through fixation of atmospheric N_2 rather than from soil N pools. Mixing model calculations indicate an average of approximately 24% MDN in spruce, 24% MDN in poplar, 26% MDN in willow and <1% MDN in alder at spawning sites (Table 3). In terms of spatial distribution, spruce $\delta^{15}\text{N}$ values were highest in individuals within 25 m of spawning streams (Fig. 3). This was expected, as the majority of salmon carcasses were typically found within spawning streams or their immediate vicinity. Among sample points closest to spawning streams, certain areas were used consistently by brown bear (*Ursus arctos*) for feeding on salmon. These areas were characterized by matted-down grasses and recurrent deposition of bear feces and partially eaten salmon carcasses throughout the spawning season. Foliar $\delta^{15}\text{N}$ was significantly higher in spruce growing at these bear middens relative to other sample points at comparable distances from spawning streams or at reference sites (Fig. 4). These patterns are consistent with the results of previous studies demonstrating spatial correlations between foliar $\delta^{15}\text{N}$ values and piscivore activity (Ben David et al. 1998; Hilderbrand et al. 1999).

It should be recognized that foliar $\delta^{15}\text{N}$ values might be influenced by factors other than MDN inputs. Differences in foliar $\delta^{15}\text{N}$ may reflect differences in rooting depths and soil N pools (Schulze et al. 1994; Handley and Scrimgeour 1997), as well as isotopic fractionation associated with microbial N processing in soils (Nadelhoffer and Fry 1994), all of which vary spatially within any given watershed according to differences in slope, elevation and soil texture. For example, studies of non-salmon bearing watersheds have reported increased foliar $\delta^{15}\text{N}$ in plants growing in valley bottoms relative to more upland sites, due to greater soil N availability and net nitrification potential (Garten 1993). In our study, foliar $\delta^{15}\text{N}$ decreased with increasing upland distance at reference sites as well as spawning sites (Fig. 3), suggesting differences in soil N processing associated with changes in elevation and proximity to the water table, yet the difference between near (i.e., within 25 m) and far (i.e., beyond 25 m) samples was significant only

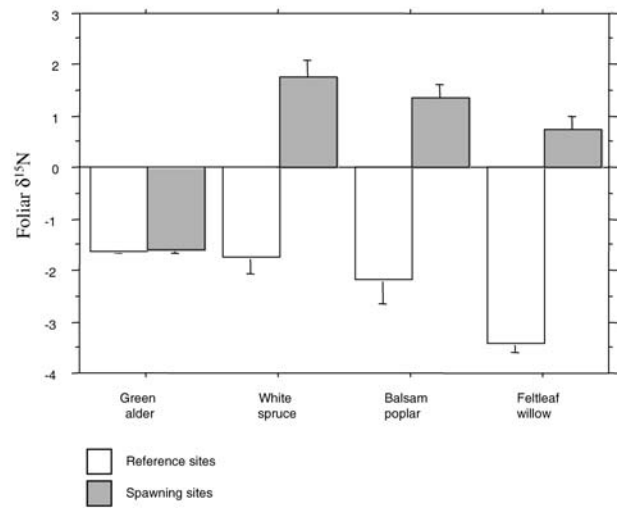


Fig. 2 Foliar $\delta^{15}\text{N}$ of riparian vegetation at spawning and reference sites. Two-sample *t*-tests indicate significant differences for white spruce [$t_{221(2)}=7.34$, $P<0.0001$], balsam poplar [$t_{34(2)}=6.92$, $P<0.0001$] and feltleaf willow [$t_{17(2)}=10.36$, $P<0.0001$], but not for green alder [$t_{60(2)}=0.29$, $P=0.77$]. Data are mean values +1 SE

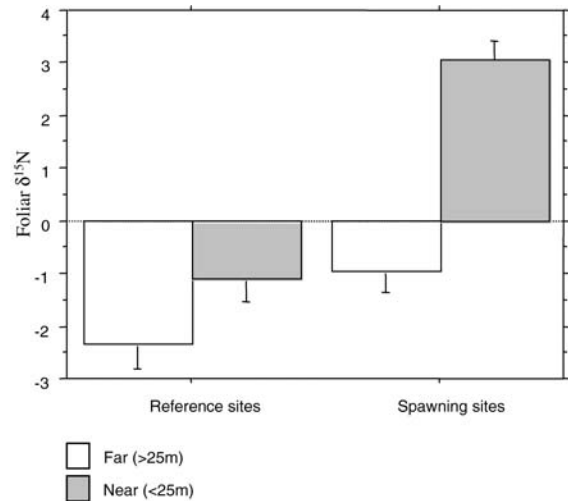


Fig. 3 Foliar $\delta^{15}\text{N}$ of riparian white spruce at spawning and reference sites. Two-factor ANOVA indicates a significant salmon effect (i.e., spawning vs. reference sites, $F_{1,219}=38.97$, $P<0.0001$), a significant effect of distance from the stream (i.e., within 25 m vs beyond 25 m, $F_{1,219}=34.90$, $P<0.0001$), and a significant interaction effect of salmon and distance ($F_{1,219}=9.61$, $P<0.005$). Fisher's PLSD indicates a significant difference between near and far spawning sites ($P<0.0001$), but not between near and far reference sites ($P=0.06$). Data are mean values +1 SE

at spawning sites. This, combined with overall increased $\delta^{15}\text{N}$ values at spawning sites and at bear middens in particular, suggests that observed patterns of foliar $\delta^{15}\text{N}$ were primarily due to MDN enrichment rather than edaphic factors.

Table 3 Mean percent marine-derived nitrogen (%MDN) in riparian foliage at spawning sites, as calculated by two-source mixing model. %MDN ranges were calculated as the range of values obtained using the range of potential Sample, Terrestrial end

Species	Marine end member ±95% CI (n)	Terrestrial end member ±95% CI (n)	Sample ±95% CI (n)	% MDN (range)
White spruce	12.62±0.31 (10)	-1.74±0.64 (89)	1.77±0.64 (134)	24 (16–33)
Balsam poplar	12.62±0.31 (10)	-2.17±0.92 (16)	1.36±0.51 (20)	24 (15–32)
Feltleaf willow	12.62±0.31 (10)	-3.42±0.32 (6)	0.72±0.50 (13)	26 (21–31)
Green alder	12.62±0.31 (10)	-1.63±0.07 (49)	-1.61±0.12 (13)	<1 (-1–2)

member and Marine end member values within 95% confidence intervals. Mixing model calculations and terms are described in Materials and methods

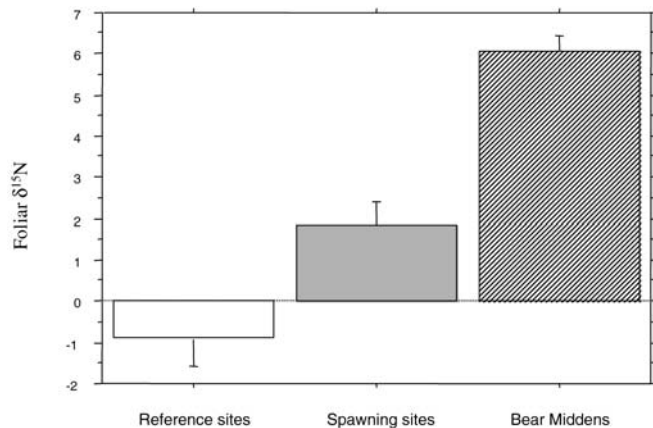


Fig. 4 Foliar $\delta^{15}\text{N}$ of riparian white spruce at bear middens and non-bear influenced sample points within 10 m of the stream at spawning and reference sites. Single-factor ANOVA indicates a significant difference between sample categories ($F_{2, 81}=48.79$, $P<0.0001$). Fisher's PLSD indicates significant differences between bear middens and non-bear spawning sites ($P<0.0001$), and between bear middens and reference sites ($P<0.0001$). Data are mean values +1 SE

Use of AFN by white spruce

MDN uptake by white spruce appears to be influenced by the presence of alder. Spruce $\delta^{15}\text{N}$ was significantly increased at spawning sites relative to reference sites only among non-alder sites (Fig. 5a). Mixing model calculations indicate an average of approximately 36% MDN in spruce at spawning sites without alder, as compared with 2% MDN at spawning sites with alder (Table 4). At alder-influenced reference sites, spruce $\delta^{15}\text{N}$ was similar to alder $\delta^{15}\text{N}$ (Fig. 2) and significantly increased relative to non-alder reference sites (Fig. 5a), suggesting that spruce use AFN where available. At alder-influenced spawning sites, spruce $\delta^{15}\text{N}$ was similar to alder $\delta^{15}\text{N}$ and significantly decreased relative to non-alder spawning sites. This could be due to preferential use of AFN over MDN, or to preferential uptake of ^{14}N from both MDN and AFN as a result of increased N availability in the presence of both N sources. Where forest growth is not N-limited, N uptake by trees may discriminate against the ^{15}N isotope (Nadelhoffer and Fry 1994). In the latter case, the mixing model's assumption of negligible frac-

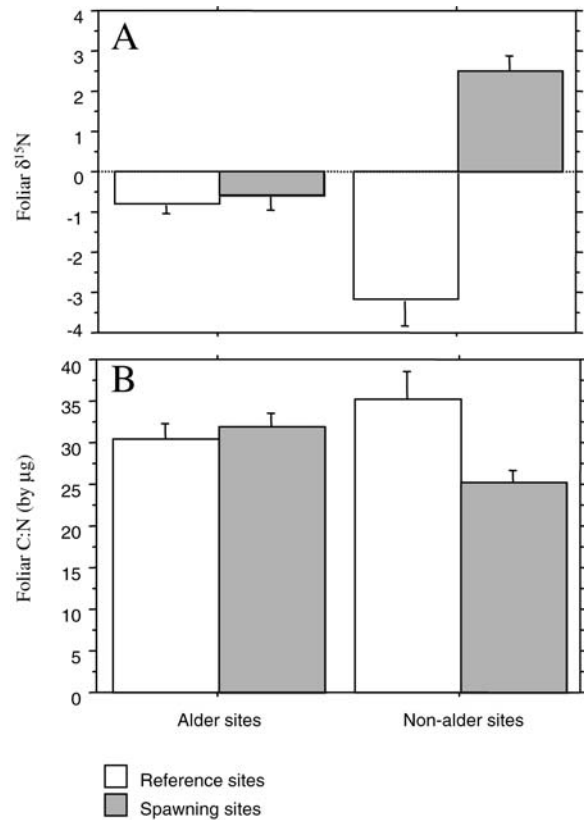


Fig. 5a, b Foliar $\delta^{15}\text{N}$ and C:N of riparian white spruce at spawning and reference sites with and without alder. **a** Two-factor ANOVA indicates no significant alder effect ($F_{1, 219}=0.53$, $P=0.47$), but a significant salmon effect ($F_{1, 219}=36.50$, $P<0.0001$) and a significant interaction effect of alder and salmon ($F_{1, 219}=31.67$, $P<0.0001$). Fisher's PLSD indicates a significant difference between spawning and reference sites without alder ($P<0.0001$), but not between spawning and reference sites with alder ($P=0.78$). **b** Two-factor ANOVA indicates no significant alder effect ($F_{1, 89}=0.19$, $P=0.66$), or salmon effect ($F_{1, 89}=3.73$, $P=0.06$), but a significant interaction effect of alder and salmon ($F_{1, 89}=7.28$, $P<0.01$). Fisher's PLSD indicates a significant difference between spawning and reference sites without alder ($P<0.005$), but not between spawning and reference sites with alder ($P=0.57$). Data are mean values +1 SE

tionation would be violated, and %MDN would be underestimated. In either case, the data suggest that MDN might not be as important to riparian spruce where AFN is available.

Table 4 Mean percent marine-derived nitrogen (%MDN) in foliage of white spruce at spawning sites with and without alder, as calculated by two-source mixing model. %MDN ranges were calculated as the range of values obtained using the range of potential

Sites	Marine end member ±95% CI (n)	Terrestrial end member ±95% CI (n)	Sample ±95% CI (n)	% MDN (range)
With alder	12.62±0.31 (10)	-0.78±0.49 (53)	0.58±0.77 (32)	2 (8–11)
Without alder	12.62±0.31 (10)	-3.16±1.29 (36)	2.51±0.75 (102)	36 (25–46)

Sample, Terrestrial End Member and Marine End Member values within 95% confidence intervals. Mixing model calculations and terms are described in Materials and methods

Foliar C:N was highest at non-alder reference sites (Fig. 5b), suggesting decreased N availability where neither MDN nor AFN are present. As with $\delta^{15}\text{N}$, differences in spruce C:N between spawning and reference sites were significant only among non-alder sites (Fig. 5b). Previous studies have demonstrated that the effects of alder on soil N availability are inversely related to background soil fertility (Binkley 1983; Wurtz 1995; Rhoades et al. 2001). Accordingly, we might expect to see a diminished effect of AFN at spawning sites, where salmon carcasses entail increased soil nutrient capital. Here, the relationship is reversed: The effects of MDN on N availability appear to be tempered by the presence of AFN.

In addition to localized inputs from riparian alder, study sites receive some AFN from adjacent hill slopes. Hill slope alder may fix significant amounts of atmospheric N, which, given the dominance of alder at higher elevations throughout the Wood River system, are leached down slope to non-alder as well as alder sites. The magnitude of these inputs will vary according to the proportion of alder coverage within the watershed, as well as geomorphic and climatic factors such as slope, soil texture and rainfall. Nonetheless, if leaching rates are comparable to those reported for other boreal Alaskan forests (e.g., Van Cleve et al. 1983), a relatively small proportion (i.e., <1%) of hill slope AFN is leached to the riparian zone, and confounding effects on observed patterns of foliar N and $\delta^{15}\text{N}$ are likely minimal.

Effects on forest growth and community composition

As with foliar N content, spruce basal area growth was lowest at non-alder reference sites (Fig. 6a). That growth rates were significantly increased at sites with either AFN or MDN inputs (i.e., alder-influenced reference and non-alder spawning sites) suggests that growth at non-alder reference sites was limited by N availability. Overall, spruce growth was most strongly correlated with foliar N and $\delta^{15}\text{N}$ (Table 5), suggesting that N availability was the most important variable affecting growth.

That growth rates were similar at alder-influenced reference and non-alder spawning sites suggests that AFN and MDN are equally useful for spruce growth. However, it should be recognized that AFN and MDN inputs might differ significantly in their effects on soil

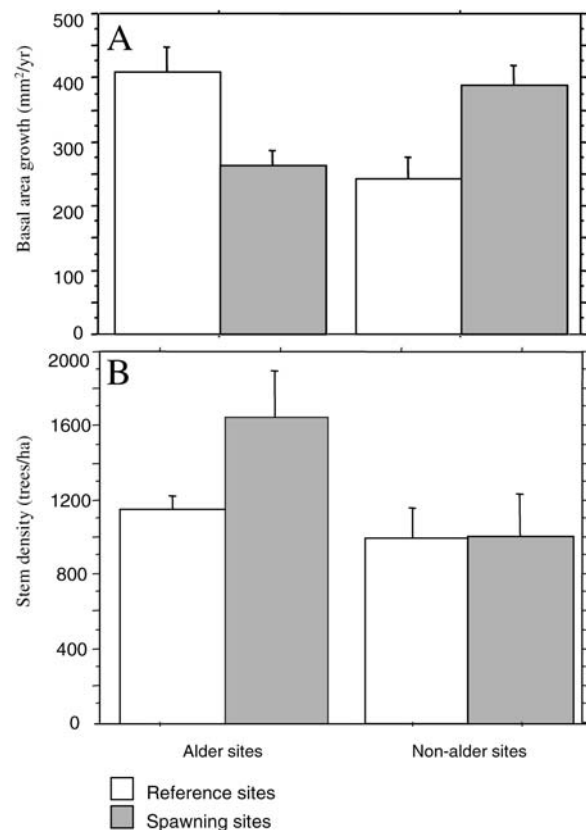


Fig. 6a, b Basal area growth of white spruce and stem density at spawning and reference sites with and without alder. **a** Two-factor ANOVA indicates no significant alder effect ($F_{1, 181}=0.23$, $P=0.63$), or salmon effect ($F_{1, 181}=0.001$, $P=0.98$), but a significant interaction effect of alder and salmon ($F_{1, 181}=12.19$, $P<0.001$). Fisher's PLSD indicates a significant difference between spawning and reference sites with ($P<0.05$) and without alder ($P<0.01$). Data are mean values +1 SE

microbial community dynamics. Salmon carcass tissues and piscivore wastes are expected to introduce comparatively large amounts of labile organic matter to riparian soils, which may result in rapid turnover of microbial communities and increased N availability to plants, as is typically reported for soils under AFN fertilization (Binkley 1983; Binkley et al. 1985, 1992; Vogel and Gower 1998; Rhoades et al. 2001). Alternatively, labile organic matter inputs associated with MDN may result in increased microbial production and intensified competi-

Table 5 Spearman's rho correlations for factors affecting basal area growth of white spruce

	Basal area growth (m ² /year)	Distance from stream (m)	Canopy cover (%)	Slope (°)	Stem density (trees/ha)	Foliar δ ¹⁵ N	Foliar C:N
Basal area growth (m²/year)							
Correlation coefficient		-0.205**	0.006	0.022	-0.025	0.438**	-0.364**
<i>P</i> (two-tailed)		0.005	0.950	0.833	0.735	<0.001	0.001
<i>n</i>		185	116	96	185	185	85
Distance from stream (m)							
Correlation coefficient	-0.205**		-0.338**	-0.117	-0.053	-0.537**	0.039
<i>P</i> (two-tailed)	0.005		<0.001	0.238	0.431	<0.001	0.707
<i>n</i>	185		128	104	223	223	93
Canopy cover (%)							
Correlation coefficient	0.006	-0.338**		0.286**	0.004	0.312**	0.188
<i>P</i> (two-tailed)	0.950	<0.001		0.003	0.967	<0.001	0.158
<i>n</i>	116	128		104	128	128	58
Slope (°)							
Correlation coefficient	0.022	-0.117	0.286**		-0.210*	-0.173	0.369**
<i>P</i> (two-tailed)	0.833	0.238	0.003		0.033	0.080	0.006
<i>n</i>	96	104	104		104	104	54
Stem density (trees/ha)							
Correlation coefficient	-0.025	-0.053	0.004	-0.210*		0.194**	-0.036
<i>P</i> (two-tailed)	0.735	0.431	0.967	0.033		0.004	0.730
<i>n</i>	185	223	128	104		223	93
Foliar δ¹⁵N							
Correlation coefficient	0.438**	-0.537**	0.312**	-0.173	0.194**		-0.488**
<i>P</i> (two-tailed)	<0.001	<0.001	<0.001	0.080	0.004		<0.001
<i>n</i>	185	223	128	104	223		93
Foliar C:N							
Correlation coefficient	-0.364**	0.039	0.188	0.369**	-0.036	-0.488**	
<i>P</i> (2-tailed)	0.001	0.707	0.158	0.006	0.730	<0.001	
<i>n</i>	85	93	58	54	93	93	

** Significant correlation at $\alpha=0.01$

* Significant correlation at $\alpha=0.05$

tion between plants and soil decomposers for imported N, potentially decreasing N availability to plants (e.g., Shaver and Chapin 1980; Jonasson et al. 1996; Schmidt et al. 1997). That foliar N content in spruce was increased at non-alder spawning sites relative to non-alder reference sites (Fig. 5b) suggests that competition with soil microbes does not affect white spruce under MDN fertilization.

Growth rates were not increased at sites with both MDN and AFN inputs (i.e., alder-influenced spawning sites, Fig. 6a), possibly as a result of density-dependent factors. Previous studies have demonstrated that intra- and interspecific competition can limit the basal area growth response of Alaskan white spruce to N fertilization (Van Cleve and Zasada 1976; Yarie et al. 1990), and the fact that stem densities were greatest at alder-influenced spawning sites (Fig. 6b) may account for decreased growth rates at these sites, despite the availability of MDN and AFN. It is also possible that the combination of MDN and AFN inputs may lead to N saturation at alder-influenced spawning sites. Due to the short growing

season and relatively short contact time between soil and drainage water in these northern boreal forest, area soils and vegetation have relatively low capacities for N retention and may be prone to N saturation (i.e., availability of N in excess of biological demand). Under N saturation, biomass production of white spruce would not be limited by N supply (Näsholm et al. 1997). Other effects of N saturation include increased net nitrification and increased nitrate losses via leaching, which would result in increased foliar δ¹⁵N (Aber et al. 1989, 1991; Näsholm et al. 1997), potentially confounding interpretations of isotope data with respect to MDN uptake. That δ¹⁵N was not increased at alder-influenced spawning sites suggests that these sites are not N saturated.

While N fixation by alder may reduce the importance of MDN inputs to riparian conifers, MDN inputs may in turn reduce the proportional abundance of alder in the riparian forest. Alder were generally more abundant at reference sites relative to spawning sites (Table 2), and comprised more than 10% of the riparian forest only at reference sites (Table 1). It is possible that consistent an-

nual MDN inputs from spawning salmon entail a decreased competitive advantage for N-fixing species such as alder, resulting in decreased alder abundance at MDN-influenced sites. However, the data do not necessarily suggest a causal relationship. Given the ability of alder to colonize newly disturbed habitats, sites with frequent fluvial disturbances are more likely to be dominated by alder. Such frequently disturbed streams are also unstable as nursery habitat for salmon, and may be less likely to support spawning populations. Accordingly, alder and salmon abundance may be inversely correlated, but both may be controlled by broader geomorphic factors (e.g., slope, valley shape) rather than by each other.

Implications for river and riparian ecosystems

There is an increasing body of evidence to suggest that anadromous salmon are an important source of allochthonous nutrients to the watersheds in which they spawn (Cederholm et al. 1999; Naiman et al. 2002). Here we have demonstrated that riparian trees may derive as much as 36% of their foliar N from MDN transported by salmon, and that foliar N content and growth rates are enhanced in riparian areas receiving MDN inputs. To the extent that riparian trees affect the quality of instream habitat through shading, sediment filtration and production of large woody debris (Meehan et al. 1977; Harmon et al. 1986; Gregory et al. 1991; Naiman and Décamps 1997; Bilby and Bisson 1998; Naiman et al. 1998), this marine fertilization process serves not only to enhance riparian production, but may also act as a positive feedback mechanism by which nutrients from salmon carcasses help to improve spawning and rearing habitat for subsequent salmon generations. Moreover, increased N in riparian foliage increases litterfall rates and enhances the nutritional quality of litter delivered to the stream (Binkley 1983; Vogel and Gower 1998), potentially enhancing aquatic productivity. MDN inputs to riparian plants might also affect terrestrial browsers such as moose (*Alces alces*) and snowshoe hare (*Lepus americanus*). Plants with higher foliar N contents are more nutritious and palatable (Bryant 1987; Pastor et al. 1988), and spatial distributions of MDN may therefore influence patterns of browsing, which in turn affects nutrient cycling, successional processes and plant species composition in riparian ecosystems (McInnes et al. 1992; Kielland and Bryant 1998; Suominen et al. 1999).

The influence of alder is somewhat confounding. Marine N subsidies appear to be less important to riparian ecosystems where alder are present, but further research is needed to fully characterize the effects of AFN and MDN on microbial dynamics, N availability and nutrient limitation in riparian soils. If forest growth is not N-limited at alder-influenced sites, salmon carcasses may nonetheless be an important source of other marine-derived nutrients. For example, each mature sockeye returning to freshwater contains approximately 10–13 g of phosphorus (P) in its body tissues, almost all of which is of

marine origin (Mathisen et al. 1988; Larkin and Slaney 1997). Spruce growth is P-limited in many northern forests (Brække 1996), and P availability may also limit alder growth and nitrogenase activity in boreal Alaskan floodplain forests (Uliassi et al. 2000). Accordingly, salmon-borne nutrients may have direct or indirect effects on riparian productivity even where AFN is the dominant source of N.

These findings illustrate the complexity of interactions surrounding northern riparian ecosystems. Marine nutrients carried upstream by spawning salmon affect patterns of riparian growth and productivity, which in turn affect the physical habitat and nutrition of terrestrial browsers as well as juvenile salmon. These interactions are mediated by piscivorous animals who rely on salmon populations for their own dietary needs, such that the long-term viability of salmon populations, riparian forests and terrestrial wildlife are all mutually dependent.

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