Fertilization of Riparian Vegetation by Spawning Salmon: Effects on Tree Growth and Implications for Long-Term Productivity

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Abstract.   Anadromous Pacific salmon (*Oncorhynchus* spp.) transport marine-derived nitrogen (MDN) to the rivers in which they reproduce. Isotopic analyses indicate that trees and shrubs near spawning streams derive approximately 22 - 24% of their foliar nitrogen (N) from spawning salmon. As a consequence of this nutrient subsidy, growth rates are significantly increased in Sitka spruce (*Picea sitchensis*) near spawning streams. As riparian forests affect the quality of instream habitat through shading, sediment and nutrient filtration and production of large woody debris (LWD), this fertilization process serves not only to enhance riparian production, but may also act as a positive feedback mechanism by which salmon-borne nutrients improve spawning and rearing habitat for subsequent salmon generations and maintain the long-term productivity of river corridors along the Pacific coast of North America.

*Key words: Alaska; feedback; fertilization; forest growth;   marine-derived nutrients; nitrogen; nutrient cycling; river; riparian forest; salmon; Sitka spruce (*Picea sitchensis*); stable isotopes.*

INTRODUCTION

As the interface between terrestrial and aquatic ecosystems, the riparian zone is inherently characterized by linkages across ecosystem boundaries. In forested landscapes, these linkages are normally thought of in terms of how the riparian zone mediates the transfer of materials and energy from upland ecosystems and influences the physical and ecological characteristics of rivers and streams. For example, the riparian canopy regulates stream temperatures through shading and provides allochthonous organic matter via litterfall, while root systems stabilize banks and filter lateral sediment and nutrient inputs, thereby controlling instream sediment and nutrient dynamics (Peterjohn and Correll 1984, Gregory et al. 1991, Naiman and D camps 1997, Naiman et al. 1998, 2000). Riparian trees are also a source of large woody debris (LWD), which, among other functions, retains sediments and alters channel morphology and flow regimes (Harmon et al. 1986, Fetherston et al. 1995, Bilby and Bisson 1998). These effects are often essential to the maintenance of spawning and rearing habitat for salmonid fishes, to the extent that the preservation of riparian buffer zones (i.e., zones of relatively intact riparian vegetation in otherwise altered watersheds) is required by many North American jurisdictions for mitigating the detrimental effects of anthropogenic disturbance (Murphy 1995).

Nonetheless, the linkages between river and riparian ecosystems are not unidirectional. Fluvial disturbances such as flooding, erosion and sediment deposition affect successional patterns as well as soil composition and nutrient dynamics in riparian zones, which in turn affect patterns of vegetation growth and species composition (Richards 1982, Naiman and D camps 1997, Naiman et al. 1998). In coastal watersheds of the Pacific Northwest, spawning migrations of anadromous Pacific salmon (*Oncorhynchus* spp.) represent another potentially important vector for transfer of nutrients and organic matter from streams to riparian forests.

Pacific salmon spend most of their lives and do the majority of their life's growth at sea before returning to freshwater to spawn and die in their natal streams. Returning salmon provide 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 incorporated into freshwater biota at various trophic levels (Mathisen et al. 1988, Kline et al. 1990, 1993, Bilby et al. 1996, Wipfli et al. 1998). Consequently, annual spawning migrations provide a mechanism for transporting nutrients from the fertile northern Pacific Ocean to relatively nutrient-poor freshwater and terrestrial ecosystems.

Recent studies using stable isotope tracers have shown that salmon-borne, marine-derived nitrogen (MDN) is incorporated into the foliage of terrestrial vegetation adjacent to spawning streams (Bilby et al. 1996, Ben-David et al. 1998, Hilderbrand et al. 1998). Despite awareness of MDN inputs to riparian zones, there has been no quantification of the ecological implications of this nutrient subsidy for riparian ecosystems. Given that nitrogen (N) availability is the limiting factor for terrestrial plant growth in most northern and temperate forests (Chabot and Mooney 1985, Kimmins 1997), MDN inputs may have an important effect on riparian forest growth. To the

extent that riparian vegetation enhances instream habitat for salmonid fishes, this process may serve as a positive feedback mechanism maintaining long-term salmon production as well as riparian habitat in coastal watersheds. Here we examine the effects of salmon-borne nutrients on the riparian forests of two Alaskan watersheds. The specific objectives of this study were (1) to determine the extent to which riparian plants acquire MDN from salmon carcasses, and (2) to assess the effects of MDN on the basal area growth of riparian trees.

MATERIALS AND METHODS
Study sites
        Our study area comprises two watersheds on Chichagof Island in southeast Alaska, USA. The Kadashan and Indian rivers flow into Tenakee Inlet near the village of Tenakee Springs (57° 52' N, 135° 18' W). The area's climate is maritime, with moderate temperatures throughout the year. Annual precipitation is approximately 236 cm, most of which falls as rain during the snow-free period between April and December (Ben-David et al. 1998, Pollock et al. 1998). At lower elevations (< 150 m), the vegetation is a coastal, old-growth forest association of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*), with a well-developed understory dominated by devil's club (*Oplopanax horridus*), huckleberry (*Vaccinium* spp.) and raspberry (*Rubus* spp.). Floodplain soils are Entisols, most likely resulting from flooding and silt deposition, with thin (< 5 cm) organic horizons. Upland soils are typically mature Spodosols developed on glacial deposits, upraised beach terraces and unconsolidated colluvium, with organic horizons of variable depth, but generally greater than 5 cm (Hanley and Hoel 1996). Available N is typically the limiting nutrient in area soils (Harris and Farr 1974).
        The Kadashan River drains an area of approximately 140 km^2, with a mean summer discharge of 4.9 m^3/s. The Indian River drains an area of approximately 57 km^2, with a mean summer discharge of 1.8 m^3/s. Both rivers support dense spawning populations of pink salmon (*O. gorbuscha*), as well as lesser spawning runs of chum (*O. keta*) and coho salmon (*O. kisutch*). Pink spawning occurs in summer (July - September), with annual escapement ranging from 30,000 to 125,000 spawners in the Kadashan and 200 to 45,000 spawners in the Indian River (USDA Forest Service, Alaska Dept. of Fish and Game, unpublished data). Each returning pink salmon carries approximately 65 g of N in its body tissues (Larkin and Slaney 1997), almost all of which is of marine origin. Therefore, annual spawning migrations bring as much as 8,000 and 3,000 kg of MDN to the Kadashan and Indian rivers, respectively.

Sample collection and analyses
        To evaluate the effects of MDN on riparian vegetation, we divided the two watersheds into spawning sites (i.e., sites adjacent to reaches with spawning salmon) and reference sites (i.e., sites adjacent to reaches without salmon). Each watershed contained one spawning site and one reference site. The Indian River reference site was located above a series of waterfalls blocking anadromous fish, while the Kadashan reference site was adjacent to a series of smaller tributaries above the upstream extent of spawning in the watershed. Reference sites were chosen so as to be, apart from the absence of salmon, as similar as possible to spawning sites in terms of physical and ecological characteristics (see Table 1).
        Field sampling occurred in August of 1998 and 1999. At each site, we established four transects, extending laterally from the stream and spaced at 100 m intervals. Sampling points were designated at 5 m, 25 m, 50 m and 100 m from the active channel along each transect, and at random points between transects (n = 76). 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 and overstory species composition were measured using the point-centered quarter method (Mueller-Dombois 1974). Foliage and increment core samples were taken from the nearest canopy Sitka spruce (i.e., having its crown at canopy level with access to direct sunlight) at each sampling point. Increment cores were collected with a 5 mm-diameter manual borer. Where available, we also collected foliage samples of devil's club, fern (*Dryopteris dilatata* and *Athyrium filix-femina*) and red alder (*Alnus rubra*).

Foliage samples were dried at 50 - 60ºC for 48 hours and ground to a fine powder for chemical analyses. Foliar N content was determined using a Lehman 440 CHN analyzer. Isotope ratios (^{15}N:^{14}N) were measured with a Finnigan MAT DELTA^{plus} isotope ratio mass spectrometer (IRMS) in the stable isotope laboratory at the University of Washington's School of Oceanography. 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

$$BAI = rw \times 2\pi r \tag{1}$$

where BAI is annual basal area increment, rw is annual ring width and r is the radius of the tree, calculated as the cumulative total of all previous years' ring widths.

Stable isotope analyses

Isotopic ratios of ^{15}N to ^{14}N are generally higher in marine systems than in terrestrial or freshwater environments, and elevated ^{15}N:^{14}N ratios in terrestrial biota are indicative of marine enrichment (Schoeninger et al. 1983, Owens 1987). These ratios are expressed as δ^{15}N values, which represent the per mil deviation in ^{15}N abundance from atmospheric N_2, the recognized isotopic standard, and are calculated as

$$\delta^{15}N = ((R_{sample} - R_{standard})/ R_{standard}) \times 1000 \tag{2}$$

where R is the ratio of ^{15}N to ^{14}N. Observed δ^{15}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

$$\%MDN = ((SAM - TEM)/(MEM-TEM)) \times 100 \tag{3}$$

where %MDN is the percent MDN in a given sample, SAM is the observed δ^{15}N of the sample, TEM is the terrestrial end member (i.e., δ^{15}N value representing 0% MDN) and MEM is the marine end member (i.e., δ^{15}N value representing 100% MDN). In this study, SAM was calculated as the mean foliar δ^{15}N of each species at spawning sites, TEM was the mean δ^{15}N of conspecific foliage at reference sites, and MEM was the mean δ^{15}N of salmon carcass tissue. The model assumes that isotopic fractionation associated with N uptake is negligible.

RESULTS AND DISCUSSION
MDN enrichment of riparian vegetation

Foliar N content and δ^{15}N of Sitka spruce, devil's club and fern were significantly higher at spawning sites relative to reference sites (Table 2). The only species for which there was no significant difference was red alder, which derives most of its N through fixation of atmospheric N_2, and would therefore be less likely to sequester MDN inputs. Mixing model calculations indicate an average of approximately 24% MDN in Sitka spruce, 22% MDN in devil's club, 22% MDN in fern and 1% MDN in red alder at spawning sites (Table 3). It should be recognized that the temporal scale over which MDN enrichment occurs is at this point unknown. Whereas observed MDN percentages in vegetation may reflect the proportions of total soil N pools derived from salmon annually, these values might also reflect a gradual accumulation of smaller MDN inputs over many years. In the latter case, annual MDN inputs would not be as important as suggested by mixing model calculations. Nonetheless, the fact that increased δ^{15}N values at spawning sites corresponded with decreased foliar C:N ratios (Table 2) suggests that MDN inputs do provide important nutrient subsidies to the riparian forest.

In terms of spatial distribution, foliar δ^{15}N of Sitka spruce was highest in individuals closest to the stream (i.e., within 25 m of the active channel), although the elevated δ^{15}N signal was evident in trees as far as 100 m from spawning streams (Fig. 1). In addition to MDN inputs, foliar δ^{15}N values may be influenced by isotopic fractionation associated with microbial N processing in soils (Nadelhoffer and Fry 1994). For example, studies of non-salmon bearing watersheds have found increased foliar δ^{15}N in plants growing in valley bottoms, due to greater soil N availability and net nitrification potential relative to more upland sites (Garten 1993). In our study, foliar δ^{15}N was significantly influenced by the presence of salmon, but not by upland distance from the stream (Fig. 1). This, combined with lower C:N ratios at spawning sites (Table 2), suggests that observed increases in foliar δ^{15}N were due to MDN enrichment rather than edaphic factors. Nitrogen fixation by red alder might also affect N isotope distribution in forest soils and non-N fixing plants, but since alder comprised a relatively small proportion of the riparian forest at both spawning and reference sites (Table 1), alder-fixed N was likely not an important factor affecting δ^{15}N patterns in our samples

Effects of MDN on riparian forests

As a consequence of MDN inputs, Sitka spruce growth is enhanced near spawning streams. Among trees within 25 m of the stream, where MDN inputs are greatest, mean annual basal area growth was more than tripled at spawning sites relative to reference sites (Fig. 2). This enhanced growth rate corresponds to a requirement of approximately 86 years to attain a diameter at breast height (dbh) of 50 cm at spawning sites, as compared with 307 years at reference sites. The data do not suggest a direct correlation between foliar δ^{15}N and tree growth (Fig. 3), as trees growing in areas with spawning salmon likely receive some threshold level of added nutrients above which growth is no longer nutrient-limited. Growth rates were more variable at spawning sites, likely due to microsite differences in light availability or other potentially growth-limiting factors, but total annual growth per unit forest area (m^2/ha/yr) was more than three times higher at spawning sites relative to reference sites (Fig. 4).

Given the dominance of western hemlock at reference sites (Table 1), spruce growth rates were likely affected to some extent by interspecific competition. However, since canopy cover was similar at spawning and reference sites (Table 1) and all cores were taken from canopy rather than sub-canopy or understory trees, the effects of canopy competition on growth patterns of individual samples were likely unimportant. Moreover, dendrochronological analyses of increment cores indicated no significant difference between spawning and reference sites in suppression or release events earlier in the lives of sample trees ($P[Z_{50(2)} > 0.65] > 0.50$). This suggests that overtopping by hemlock is not the primary factor responsible for decreased spruce growth at reference sites relative to spawning sites.

Implications for stream habitat

The influence of riparian vegetation on the quality of spawning and rearing habitat for salmonid fishes has been well documented. Shading by streamside trees moderates stream temperatures, controlling rates of embryo development and maintaining optimal timing of life history events (Beschta et al. 1987). Bank stabilization and sediment filtration by riparian roots minimize erosion and siltation, which threatens embryo survival by restricting intragravel flow and oxygenation of redds (Chapman 1988). Litter inputs provide allochthonous organic matter supporting production of aquatic insects, which are an essential food source for juvenile salmon (Meehan et al. 1977).

Riparian forests also enhance stream habitat through the production of LWD. Among other functions, LWD traps sediment and increases the structural complexity of stream channels (Keller and Swanson 1979, Harmon et al. 1986, Bilby and Ward 1991, Fetherston et al. 1995, Bilby and Bisson 1998), thereby creating preferred habitat for spawning and rearing (Bjornn and Reiser 1991). Instream LWD also creates areas of low flow velocity and shear stress, providing shelter from winter high flows and bed scour (Murphy et al. 1985, McMahon and Hartman 1989), which are important causes of mortality in overwintering fry and incubating embryos (McNeil 1964). Overall, the presence of LWD in spawning streams enhances production of salmonid fishes (Fausch and Northcote 1982, Murphy et al. 1985, Crispin et al. 1993).

The influence of LWD on stream habitat is controlled to a large extent by the size of LWD pieces. Larger pieces typically persist longer in streams, as they take longer to decompose and are more difficult to flush downstream (Anderson et al. 1978, Murphy and Koski 1989). Size of LWD is especially important in larger rivers (e.g., > 10 m wide) where only the largest pieces (i.e., > 50 cm in diameter) can withstand high flows and remain in the channel (Bilby and Ward 1989). In our study, trees near spawning streams reached this threshold diameter more than 200 years earlier than their counterparts at reference sites. The height of riparian trees also affects LWD recruitment. The majority of LWD inputs originate within a distance from the stream that is equivalent to the height of the tallest trees in the riparian forest. The probability of a tree entering the stream when it falls increases with the height of the tree relative to its distance from the channel's edge (Van Sickle and Gregory 1990). To the extent that taller, wider trees are more likely to enter and persist in streams, MDN subsidies to riparian growth enhance the beneficial effects of LWD on spawning habitat. By enhancing the growth of riparian trees and the production of LWD, MDN inputs to the riparian zone might therefore serve as a positive feedback mechanism by which spawning salmon help to enhance the survivorship of subsequent salmonid generations.

Several pathways exist for the transfer of MDN from streams to riparian vegetation. Summer floods deposit salmon carcasses on streambanks, and dissolved nutrients from carcasses decomposing in the stream may downwell into shallow subsurface (i.e., hyporheic) flowpaths, where they can be transported to the rooting zones of some riparian plants. In addition, riparian zones may be enriched through dissemination of feces, urine and partially-eaten carcasses by brown bear (*Ursus arctos*) and other salmon-eating fauna. Salmon carcasses provide an important seasonal food source for a wide range of mammals and birds, and a significant proportion of total spawner biomass may be consumed by predators and scavengers (Cederholm et al. 1989, Willson et al. 1998, Ben-David et al. 1998). Recent studies have reported significant spatial correlations between piscivore activity and foliar $\delta^{15}N$ and in riparian zones adjacent to salmon-bearing waters (Ben-David et al. 1998, Hilderbrand et al. 1999). These findings suggest that piscivores act as significant vectors for MDN enrichment of riparian vegetation.

Although many Alaskan stocks remain healthy, Pacific salmon have disappeared from or are in serious decline throughout most of their historical spawning range in North America (Stouder et al. 1997, Gresh et al. 2000). In addition to the resultant cultural and economic consequences, these declines may have important long-term ecological implications for freshwater and terrestrial ecosystems of the Pacific coast. Here we have shown that riparian plants derive a significant proportion of their foliar N from spawning salmon, and that riparian growth rates are significantly enhanced by this nutrient subsidy. This fertilization process may in turn affect the quality of instream spawning and rearing habitat and reproductive success of salmon populations, so that declines in spawning density may result in degraded riverine habitat and further declines in salmon

production over the long term. To the extent that this depensatory cycle is mediated by piscivorous animals that depend on the availability of salmon and riparian habitat for their own survival, the viability of salmon populations, riparian forests and terrestrial piscivores are mutually dependent. These findings have potentially important implications for fisheries management, endangered species legislation and ecological restoration, as traditionally-focused, single-species management approaches will likely be inadequate to address the complexity of interactions between salmon stocks and the river and riparian ecosystems upon which they depend.

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TABLE AND FIGURE CAPTIONS

TABLE 1.   Physical and ecological characteristics of spawning and reference sites. Data are mean values ± 1 SD. Two-sample t-tests indicate no significant differences between spawning and reference sites ($\alpha = 0.05$).

TABLE 2.   Mean $\delta^{15}N$ values and carbon:nitrogen (C:N) ratios in the foliage of riparian vegetation at spawning and reference sites. * denotes significant difference between spawning and reference sites, as determined by two-sample t-tests ($\alpha = 0.05$).

TABLE 3.   %MDN in Sitka spruce foliage at spawning sites, as calculated by two-source mixing model.

FIG. 1.   Mean foliar $\delta^{15}N$ in riparian Sitka spruce at spawning and reference sites. Two-factor ANOVA indicates a significant salmon effect (i.e., spawning vs. reference sites $P[F_{1,72} > 67.38] < 0.0001$), no significant effect of distance from the stream (i.e., within 25 m vs.beyond 25 m $P[F_{1,72} > 0.11] > 0.50$), and no significant interaction effect of salmon and distance ($P[F_{1,72} > 2.72] = 0.10$). Mean ± 1 SE are plotted.

FIG. 2.   Annual basal are growth (mm^2/yr) of riparian Sitka spruce at at spawning and reference sites. Two-factor ANOVA indicates a significant salmon effect (i.e., spawning vs. reference sites $P[F_{1,48} > 6.60] = 0.01$), no significant effect of distance from the stream (i.e., within 25 m vs.beyond 25 m $P[F_{1,48} > 0.78] = 0.38$), and a significant interaction effect of salmon and distance ($P[F_{1,48} > 6.41] = 0.01$). Mean ± 1 SE are plotted.

FIG. 3.   Annual Sitka spruce basal area growth (mm^2/yr), expressed as a function of foliar $\delta^{15}N$ at spawning and reference sites.

FIG. 4.   Annual basal area growth per unit area ($m^2/ha/yr$) of riparian Sitka spruce at spawning and reference sites. Mean ± 1 SE are plotted.

TABLE 1

Site Characteristic	Spawning Sites	Reference Sites	$P(t_{2(2)} > t_{obs})$
Average slope (deg)	**7.2** ± 6.7	**7.1** ± 1.2	0.60
% canopy cover	**87** ± 0.9	**85** ± 2.0	0.35
Stem density (trees/ha)	**361** ± 55	**478** ± 264	0.50
Basal area (m²/ha)	**108** ± 6.7	**122** ± 9.4	0.33
% Sitka spruce (by m²)	**68.2** ± 16.9	**26.1** ± 3.1	0.09
% western hemlock (by m²)	**28.3** ± 18.5	**71.0** ± 9.5	0.14
% red alder (by m²)	**3.4** ± 1.6	**1.3** ± 2.8	0.70
Median Sitka spruce age (yrs)	**137** ± 3.9	**139** ± 20.2	0.64

TABLE 2

Species	C:N		$\delta^{15}N$	
	$\pm$ 1 SE (n)		$\pm$ 1 SE (n)	
	REFERENCE	SPAWNING	REFERENCE	SPAWNING
Sitka spruce (*Picea sitchensis*)	**39.21** $\pm$ 2.01 (10)	**32.73*** $\pm$ 1.46 (10)	**-3.34** $\pm$ 0.33 (32)	**0.63*** $\pm$ 0.32 (44)
Devil's club (*Oplopanax horridus*)	**17.21** $\pm$ 0.46 (11)	**15.75*** $\pm$ 0.57 (11)	**-0.91** $\pm$ 0.38 (22)	**2.24*** $\pm$ 0.34 (28)
Fern (*Dryopteris dilatata, Athyrium filix-femina*)	**19.62** $\pm$ 1.01 (10)	**16.88*** $\pm$ 0.86 (10)	**-3.05** $\pm$ 0.42 (19)	**0.62*** $\pm$ 0.36 (27)
Red alder (*Alnus rubra*)	**16.51** $\pm$ 0.89 (10)	**16.56** $\pm$ 1.14 (10)	**-1.04** $\pm$ 0.09 (10)	**-0.91** $\pm$ 0.11 (21)

Note: Dryopteris dilatata and *Athyrium filix-femina* are grouped together because no significant differences in foliar C:N or $\delta^{15}N$ were detected between the two species [$P(t_{44(2)} > 1.85) > 0.05$].

TABLE 3

	Marine End Member ± 95% CI (n)	Terrestrial End Member ± 95% CI (n)	Sample ± 95% CI (n)	%MDN (range)
Sitka spruce (*Picea sitchensis*)	13.39 ± 0.89 (4)	-3.34 ± 0.63 (32)	0.63 ± 0.62 (44)	24 (16 - 32)
Devil's club (*Oplopanax horridus*)	13.39 ± 0.89 (4)	-0.91 ± 0.74 (22)	2.24 ± 0.66 (28)	22 (12 - 32)
Fern (*Dryopteris dilatata, Athyrium filix-femina*)	13.39 ± 0.89 (4)	-3.05 ± 0.82 (19)	0.62 ± 0.70 (27)	22 (13 - 32)
Red alder (*Alnus rubra*)	13.39 ± 0.89 (4)	-1.04 ± 0.17 (10)	-0.91 ± 0.22 (21)	1 (-2 - 4)

Note: %MDN ranges were calculated as the range of values obtained using the range of potential Sample, Terrestrial End Member and Marine End Member values within 95% confidence intervals. Mixing model calculations and terms are described in *Materials and methods*.

Figure 1

Figure 2

Figure 2

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Figure 3

Figure 4