Nitrogen uptake by plants subsidized by Pacific salmon carcasses: a hierarchical experiment

Morgan D. Hocking and John D. Reynolds

Abstract: Bears (Ursus spp.) and other predators can capture and transport large numbers of Pacific salmon (Oncorhynchus spp.) to riparian areas beside small coastal streams, a process that may affect site productivity and local plant communities. We used a novel experimental manipulation of salmon carcasses to analyze understory plant uptake of salmon-derived N. A hierarchical before–after, control–impact design was used with the addition of chum salmon (Oncorhynchus keta (Walbaum in Artedi, 1792)) carcasses to forest sites along 11 streams on the central coast of British Columbia, Canada. Eight months after carcass placement, the foliar %N and δ15N in three herbaceous and one moss species had increased by an average of 14%–60% (%N) and 0.5–3.3‰ (δ15N) at treatment carcass sites versus control sites. Treatment effects for %N were typically greater than for δ15N. Nitrogen isotope signatures at carcass sites were highly variable (δ15N range = 30.1‰) and were mediated by plant species, stream salmon density, carcass mass, and individual plant foliar %N. These results show that understory plants use N from salmon during an important period of plant growth many months after carcasses were deposited in riparian areas. However, they also indicate that habitat variation across spatial scales from individual plants to streams needs to be considered when estimating the contribution of salmon to plant nutrition.

Résumé : Les ours (Ursus spp.) et autres prédateurs peuvent capturer et transporter un grand nombre de saumons du Pacifique (Oncorhynchus spp.) dans les zones riveraines le long de cours d’eau côtiers, un processus qui pourrait influencer la productivité du site et les communautés végétales locales. Nous avons utilisé une nouvelle manipulation expérimentale des carcasses de saumon pour analyser le prélèvement de N provenant du saumon par les plantes du sous-bois. Un plan expérimental hiérarchique avant–après avec témoin a été utilisé avec l’ajout de carcasses de saumon kétas (Oncorhynchus keta (Walbaum in Artedi, 1792)) dans des stations forestières le long de 11 cours d’eau sur la côte centrale de la Colombie-Britannique, au Canada. Huit mois après avoir placé les carcasses, %N et δ15N dans les feuilles de trois espèces d’herbacées et une espèce de mousses avaient augmenté en moyenne de 14 %–60 % (%N) et de 0,5 ‰–3,3 ‰ (δ15N) dans les stations traitées avec des carcasses versus les stations témoins. Les effets du traitement étaient typiquement plus importants sur le %N que sur δ15N. La signature isotopique de N dans les stations avec des carcasses était très variable (écart de δ15N = 30,1 ‰) et était influencée par les espèces végétales, la densité de saumon dans le cours d’eau, le poids des carcasses et le %N dans le feuillage de chaque plante. Ces résultats montrent que les plantes de sous-bois utilisent le N des saumons pendant une importante période de leur croissance plusieurs mois après que les carcasses aient été déposées dans les zones riveraines. Cependant, ils indiquent également qu’on doit tenir compte de la variation de l’habitat aux échelles spatiales allant des plantes individuelles au cours d’eau pour estimer la contribution du saumon à la nutrition des plantes.

[Traduit par la Rédaction]

Introduction

Anadromous Pacific salmon (Oncorhynchus spp.) affect biodiversity and ecosystem processes in streams throughout the Pacific Rim. Salmon are born in freshwater, with most populations migrating as juveniles to the ocean where they obtain >95% of their full body mass. As adults, salmon return to their natal streams to spawn and die, delivering marine-derived nutrients to aquatic and terrestrial habitats that are often resource limited (Willson and Halupka 1995; Gende et al. 2002; Naiman et al. 2002). Stream nutrient concentrations, such as NH4+, NO3−, and soluble reactive P, can be elevated during the spawning season, which subsequently affects the productivity of freshwater food webs (Johnston et al. 2004; Verspoor et al. 2010).

The retention of salmon nutrients in watersheds varies with the extent of stream disturbance by salmon themselves (Moore et al. 2007) and through shifts in stream substrate, forest harvesting and site slope (Tiegs et al. 2008; Holtgrieve et al. 2010) but also with the rate of salmon predation and terrestrial nutrient transfer by bears (Ursus spp.), wolves (Canis lupus Linnaeus, 1758), and other vertebrates (Reimchen 2000; Gende et al. 2001; Quinn et al. 2009). In small coastal streams, or in tributaries of larger rivers and lakes, vertebrate predators can transfer more than 50% of the spawning salmon to streamside areas (Helfield and Naiman 2006; Hocking and Reimchen 2006; Quinn et al. 2009). This creates hotspots of nutrient release that may be accessed by riparian plants (Gende et al. 2007; Holtgrieve et al. 2009).
Along with other pathways of salmon nutrient entry into terrestrial food webs, such as flooding and hyporheic water flow, salmon subsidies may ultimately affect riparian plant diversity (Wilkinson et al. 2005; Hocking and Reynolds 2011).

Correlational studies of the role of salmon nutrients in riparian plant nutrition have typically found increasing stable isotope ratios of heavy to light N (δ15N) in plant leaves across natural gradients in salmon spawning density (Bilby et al. 2003; Bartz and Naiman 2005; Nagasaka et al. 2006; Hocking and Reimchen 2009). This suggests that salmon provide an important source of N to streamside plants and is attributed to the fact that salmon carcasses have higher δ15N (~12‰) than terrestrial sources of N (~0‰). However, confounded with this δ15N-source-based approach is the fact that plant δ15N can also reflect site productivity, which itself may be influenced by salmon abundance (Pinay et al. 2003; Hocking and Reynolds 2011). For example, plant leaf δ15N broadly reflects the available N sources, rates of N cycling, and plant–mycorrhizal associations, which all influence N isotopic fractionation (Hogberg 1997; Evans 2001; Morris et al. 2005). Thus, simple correlations among locations between leaf N and numbers of salmon may be confounded by correlated differences in site productivity, which may amplify or obscure the true impacts of salmon on plant nutrient uptake.

Here, we use the first experimental approach with understory plants and salmon carcasses, based on a before–after, control–impact design, to analyze plant uptake of salmon-derived N. Chum salmon (Oncorhynchus keta (Walbaum in Arteri, 1792)) carcasses were placed along forest transects parallel to the stream channel in 11 watersheds on the central coast of British Columbia, Canada, intended to mimic natural salmon carcass transfer by wildlife that is widespread in this region (Hocking and Reimchen 2006; Darimont et al. 2008). Previous experiments in soils have shown that decaying salmon carcasses create biogeochemical hotspots including localized increases in soil NO3− and NH4+ concentrations, higher soil δ15N, and greater fluxes of N2O gas (Drake et al. 2005; Gende et al. 2007; Holtgrieve et al. 2009).

We hypothesized that salmon-derived N would be detectable in understory plants during the period of spring plant growth, over 8 months after the deposition of salmon carcasses. First, we predicted that nutrients derived from salmon would increase the mean and the variance of foliar δ15N and total N (%N) and that larger salmon carcasses would lead to increased N subsidies. Second, we predicted that plants in streams that had the lowest numbers of naturally spawning salmon would show the greatest increase in N uptake. Finally, we predicted that uptake by individual plants would depend on site productivity based on measures at the stream scale (salmon density, watershed size, and red alder density) and individual plant scale (foliar %N as a predictor of δ15N). For example, foliar %N is often positively correlated with foliar δ15N because they both index soil N availability and turnover, site productivity and differences in N uptake through mycorrhizae (Tilman 1988; Hobbie et al. 2000; Wardle et al. 2004; Craine et al. 2009; Kranabetter and MacKenzie 2010). Thus, building plant %N into models of plant δ15N may account for individual and microsite-level differences in these processes that are often difficult to determine and measure.

Materials and methods

Carcass experiment

We studied 11 small- to medium-sized streams (5–25 m bankfull width) on the central coast of British Columbia, Canada, near the Heiltsuk Nation village of Bella Bella (Table 1). Streams ranged from supporting no anadromous fish to high densities of spawning chum and pink salmon (Oncorhynchus gorbuscha (Walbaum, 1792)) and smaller numbers of coho salmon (Oncorhynchus kisutch (Walbaum, 1792)). This region receives some of the highest precipitation in North America (3000–4000 mm-year−1) and is classified within the Coastal Western Hemlock (CWH) biogeoclimatic zone (Pojar et al. 1987). Watersheds are accessible by boat only, and although some high-grade logging occurred in the 1930s and 1940s, human disturbances from road construction and forest harvesting remain minimal. Riparian plant communities are dominated by the shrubs salmonberry (Rubus spectabilis Pursh), false azalea (Menziesia ferruginea Sm.), salal (Gaultheria shallon Pursh), and blueberry (Vaccinium spp.), with a coniferous overstory of western hemlock (Tsuga heterophylla (Raf.) Sarg.). Sitka spruce (Picea sitchensis (Bong.) Carrière), western redcedar (Thuja plicata Donn ex D. Don), and amabilis fir (Abies amabilis Douglas ex J. Forbes). Densities of the deciduous red alder (Alnus rubra Bong.) are generally fairly low (an exception is the Clatspe River: Table 1). Canopy community structure (stems per hectare) was assessed along six 10 m wide belt transects extending 40 m perpendicular to the stream (Hocking and Reynolds 2011). Stream catchment areas were calculated using iM-apBC (Field and Reynolds 2011).

In October of 2006, we placed 9–10 chum salmon carcasses in the forest riparian zone of each watershed along a ~100 m transect parallel to each stream and within 10 m of the stream channel. Most of these carcasses had some carcass scavenging by vertebrates, although we chose fish that were largely intact rather than smaller remnants. Chum carcasses were weighed (grand mean = 3.5 ± 0.1 kg) and placed beside selected indicator plant species including lanky moss (Rhytidiadelphus loreus (Hedw.) Warnst.), bunchberry (Cornus canadensis L.), foamyflower (Tiarella trifoliata L.), and false lily-of-the-valley (Maianthemum dilatatum (Alph. Wood) A. Nelson & J.F. Macbr.). Bunchberry, foamyflower, and false lily-of-the-valley are all common understory perennial herbs with arbuscular mycorrhizal associations that facilitate plant access to N, P, and other nutrients (Kranabetter and MacKenzie 2010). Lanky moss forms the dominant ground cover across our sites and is hypothesized to be able to access nutrients through the soil substrate (Wilkinson et al. 2005) and via atmospheric deposition directly through the foliar tissues (Solga and Frahm 2006; Liu et al. 2008).

At the time of carcass placement, we took foliar samples from one plant individual for each indicator species present at the carcass site and also from a paired control site 2 m away. Each site had a lanky moss sample and had one or two of the three herbaceous indicator species. Carcass sites were marked and then monitored for a 2–3 week period to determine rates of disturbance of the carcasses. The majority of carcasses in our 11 watersheds were not disturbed (105/117), although we had originally used one additional watershed that we removed from the experiment because of re-
Salmon population data

Fisheries and Oceans Canada monitors salmon spawning populations in two of our 11 study watersheds, with data extending 60 years to 1950. From fall 2006 to 2009, we partnered with the Heiltsuk Integrated Resource Management Department based in Bella Bella, British Columbia, to inventory salmon populations in small streams not consistently surveyed by Fisheries and Oceans Canada. This included the remaining eight streams supporting salmon populations from this study. Fish in all streams were counted during at least three separate years (seven of 10 streams had all four years). The area-under-the-curve estimation method was used for cases when three or more counts occurred for a stream in a given year (English et al. 1992). When we had one or two counts, or if salmon abundance was very low, the peak live plus dead estimate method was used (30 of 74 estimates). The method used did not affect population estimates. In cases when both methods were used, strong correlations were observed between area-under-the-curve and peak live plus dead estimates for both chum ($R^2 = 0.932, n = 37$) and pink salmon ($R^2 = 0.964, n = 23$), with no difference in means by method (paired $t$ tests: $p > 0.18$). Stream residency times of 10 days (live chum salmon) and 20 days (live pink salmon) were assumed.

Based on counts from 2006 to 2009, we derived an index of salmon spawning density (SD) (kilograms of salmon biomass per metre of spawning length) for each stream:

$$[1] \quad SD = \sum \frac{(N_i \times W_i)}{SL}$$

where $N$ is the number of adult salmon, $i$ is the salmon species (chum or pink salmon), $W$ is salmon mass (chum salmon: 3.5 kg, pink salmon: 1.2 kg), and $SL$ is the length of the stream in which salmon spawned (metres). The lengths of the spawning sections of streams were obtained from individual stream walks. Salmon spawning density was log ($x + 1$) transformed for the analysis.

Stable isotope analysis

Plant indicator samples were dried and then ground into a fine powder with a heavy duty Wig-L-Bug grinder (Pike Technologies, Madison, Wisconsin). Ground plant samples (0.9–2.5 mg dry mass) collected in the fall were assayed for N and C isotope natural abundance using a Finnigan Delta Plus mass spectrometer interfaced via Conflo II to a NC2500 elemental analyzer at the Stable Isotope in Nature Laboratory (SINLAB) at the University of New Brunswick, Fredericton, New Brunswick. Ground plant samples (2.4–3.2 mg dry mass) collected in the spring were assayed for N and C isotopes using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at the University of California Davis Stable Isotope Facility. Isotopic signatures are expressed in delta notation ($\delta$) as ratios in parts per mil ($\permil$) deviations from known isotopic standards according to

$$[2] \quad \delta^{15}N \text{ or } \delta^{13}C \text{ (per mil)} = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000$$

where $R$ is the ratio of the heavy isotope ($^{15}N$ or $^{13}C$)/light isotope ($^{14}N$ or $^{12}C$). Ten plant samples from each of lanky moss, bunchberry, and foamflower (total $n = 30$ samples) processed at SINLAB were rerun at the University of California Davis and compared using repeated-measures ANOVA. Small but significant effects of lab were observed for $\delta^{15}N$, $\%N$, $\delta^{13}C$, and $\%C$. Significant lab × species effects were observed for $\%N$ and $\delta^{13}C$. We therefore standardized SINLAB stable isotope data to University of California Davis data (Supplementary data Table S1).¹

Model selection

We use a model selection approach using the Akaike information criterion (AIC) to evaluate the relative importance of the candidate set of hypotheses for each dependent variable.

Table 1. Habitat and chum (Oncorhynchus keta) and pink salmon (Oncorhynchus gorbuscha) population data (2006–2009) for the watersheds in this study.

<table>
<thead>
<tr>
<th>Watershed</th>
<th>Spawning length (m)</th>
<th>Bankfull width (m)</th>
<th>Chum salmon mean</th>
<th>Pink salmon mean</th>
<th>Salmon index (kg·m⁻¹)</th>
<th>Catchment area (km²)</th>
<th>Red alder density (stems·ha⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ada</td>
<td>435</td>
<td>11.1</td>
<td>1033</td>
<td>317</td>
<td>7.4</td>
<td>9.8</td>
<td>43</td>
</tr>
<tr>
<td>Bullock Square</td>
<td>296</td>
<td>8.4</td>
<td>233</td>
<td>140</td>
<td>2.5</td>
<td>2.8</td>
<td>38</td>
</tr>
<tr>
<td>Clatshe</td>
<td>900</td>
<td>22.8</td>
<td>1688</td>
<td>8388</td>
<td>16.8</td>
<td>24.3</td>
<td>291</td>
</tr>
<tr>
<td>Fannie Left</td>
<td>1500</td>
<td>12.8</td>
<td>1094</td>
<td>4049</td>
<td>5.1</td>
<td>16.4</td>
<td>19</td>
</tr>
<tr>
<td>Kill</td>
<td>453</td>
<td>3.5</td>
<td>394</td>
<td>275</td>
<td>2.9</td>
<td>0.5</td>
<td>62</td>
</tr>
<tr>
<td>Mosquito Left</td>
<td>250</td>
<td>5.7</td>
<td>115</td>
<td>252</td>
<td>2.7</td>
<td>2.1</td>
<td>91</td>
</tr>
<tr>
<td>Neckas</td>
<td>2100</td>
<td>17.7</td>
<td>11489</td>
<td>29214</td>
<td>34.6</td>
<td>16.0</td>
<td>24</td>
</tr>
<tr>
<td>Ripley Bay</td>
<td>0</td>
<td>14.7</td>
<td>0</td>
<td>0</td>
<td>0.0</td>
<td>15.7</td>
<td>0</td>
</tr>
<tr>
<td>Roscoe Trib 1</td>
<td>250</td>
<td>14.1</td>
<td>361</td>
<td>844</td>
<td>8.8</td>
<td>8.5</td>
<td>62</td>
</tr>
<tr>
<td>Spiller Trib 1</td>
<td>80</td>
<td>7.7</td>
<td>9</td>
<td>73</td>
<td>1.5</td>
<td>2.3</td>
<td>24</td>
</tr>
<tr>
<td>Webster</td>
<td>800</td>
<td>16.5</td>
<td>1307</td>
<td>837</td>
<td>5.2</td>
<td>23.9</td>
<td>No data</td>
</tr>
</tbody>
</table>

¹Supplementary data are available with this article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/x2012-045.
(%N and \(\delta^{15}N\)). AIC evaluates the predictive power of models with different combinations of variables based on the principal of parsimony, balancing optimal model fit with the number of parameters used (Burnham and Anderson 1998). We performed four analyses separated by indicator species groups and dependent variables: (1) lanky moss %N, (2) lanky moss \(\delta^{15}N\), (3) herbaceous species %N, and (4) herbaceous species \(\delta^{15}N\). Species separation was done because lanky moss and herbaceous arbuscular mycorrhizae plants are predicted to vary in their pathways of N uptake (Solga and Frahm 2006; Kranabetter and MacKenzie 2010) and because lanky moss has substantially lower foliar %N. Further, because false lily-of-the-valley was only sampled in the spring, herbaceous species models were simplified to include only spring data.

**Mixed-effects models**

Due to the hierarchical structure of the data set, we used mixed-effects modeling to account for the lack of independence and correlation structure among samples across different scales (McMahon and Diez 2007; Zuur et al. 2009). First, we chose the most parsimonious random structure using minimum AIC\textsubscript{c} scores with a model that included the full set of fixed explanatory variables based on a priori hypotheses (Supplementary material Table S2). We excluded all three-way or greater interaction terms because none were predicted to be important. We set stream as a random effect and also applied a compound symmetry correlation structure among samples from carcass treatment – control pairs, nested within carcass sites, nested within streams. Because of observed heterogeneity in the residuals that violated assumptions of equal variances, we tested for the inclusion of variance identity parameters for carcass treatment and stream effects. Generally, we found higher variance in \(\delta^{15}N\) and %N at treatment carcass sites versus control sites. The only exception was with lanky moss where higher leaf %N and mass at carcass sites varied from 0% to 4% versus 0% to 3% at control sites that lacked carcasses than at control sites that lacked carcasses (all \(F < 1.5, all p < 0.015\); exception is lanky moss %N: \(F_{[97,293]} = 0.82, p = 0.25\) (Fig. 1). In all species and across all watersheds, \(\delta^{15}N\) signatures from spring carcass sites varied from \(-15.6\%e\) to \(14.5\%e\) (range = 30.1%), while control sites varied from \(-1.3\%e\) to 9.3% (range = 20.6%\%e). Leaf %N values varied from 1.1% to 60% (range = 4.9%) at experimental carcass sites and from 0.5% to 3.8% (range = 3.3%) at control sites. Increased %N and \(\delta^{15}N\) variation at carcass sites compared with control sites means that these models perform better when a parameter that accounts for unequal variances is included (see Materials and methods).

**Results**

**Effects of carcass addition**

After 8 months, the addition of salmon carcasses led to increases in leaf %N by an average of 14%–60%, depending on plant species, compared with control sites (Fig. 1). We also observed elevated \(\delta^{15}N\) signatures in the herbaceous species by 1.3%–3.3%\%e. For lanky moss, we found only a marginal mean \(\delta^{15}N\) increase of 0.5%\%e. Overall, the top models in each analysis explained 49%–69% of the variation in leaf %N or \(\delta^{15}N\) (pseudo-\(R^2\) values in Table 2).

Carcass treatment effects were observed in all top models (Table 2). Significant coefficients for treatment were observed in the top model in both lanky moss analyses. In the herbaceous \(\delta^{15}N\) model, treatment effects were greater in individuals with higher leaf %N (treatment \(\times\) foliar %N interaction). In the herbaceous %N models, a significant main effect of treatment was observed as well as treatment effects that varied by plant species (treatment \(\times\) plant species interaction).

Leaf %N and \(\delta^{15}N\) values were more variable at sites where we added carcasses than at control sites that lacked carcasses (all \(F > 1.5, all p < 0.015\); exception is lanky moss %N: \(F_{[97,293]} = 0.82, p = 0.25\) (Fig. 1). In all species and across all watersheds, \(\delta^{15}N\) signatures from spring carcass sites varied from \(-15.6\%e\) to 14.5% (range = 30.1%), while control sites varied from \(-1.3\%e\) to 9.3% (range = 20.6%\%e). Leaf %N values varied from 1.1% to 60% (range = 4.9%) at experimental carcass sites and from 0.5% to 3.8% (range = 3.3%) at control sites. Increased %N and \(\delta^{15}N\) variation at carcass sites compared with control sites means that these models perform better when a parameter that accounts for unequal variances is included (see Materials and methods).

**Effects of foliar %N at the individual plant scale**

We observed positive relationships between %N and \(\delta^{15}N\) in all species, with \(\delta^{15}N\) model performance increasing when individual plant foliar %N was included as a predictor (Fig. 2; Table 2). In lanky moss, the relationship between %N and \(\delta^{15}N\) did not differ when carcasses were added. In the herbaceous models, %N and \(\delta^{15}N\) values varied by plant species, and there were strong plant species \(\times\) %N and treatment \(\times\) %N interactions. Foamflower and false lily-of-the-valley typically had higher mean %N and \(\delta^{15}N\), stronger treatment effects on %N and \(\delta^{15}N\), and shallower control slopes of \(\delta^{15}N\)–%N compared with bunchberry. For all herba-
Effects of experimental carcass mass at the site scale

In lanky moss, higher %N and δ¹⁵N values were observed from larger experimental carcasses (significant treatment × carcass mass interactions) (Fig. 3; Table 2). For example, some δ¹⁵N values at small experimental carcasses were highly depleted in δ¹⁵N (−5 to −15‰), while δ¹⁵N values from large carcasses were enriched (up to +10‰). In the herbaceous species, relationships between carcass mass and %N or δ¹⁵N were weak and were not present in the top models.

Effects of salmon density and catchment area at the stream scale

Leaf %N and δ¹⁵N values were higher at streams that had higher densities of spawning salmon (kilograms of salmon biomass per metre of spawning length) (Fig. 4; Table 2). Differences in stream salmon density also affected the impacts of carcass additions on total N uptake. Plants at streams with lower salmon densities showed greater increases in %N with carcass addition than streams with higher salmon density (treatment × salmon spawning density interactions). In contrast, important treatment × salmon spawning density interactions for δ¹⁵N were not observed.

Discussion

Our experiments provide evidence of salmon nutrient uptake in four common riparian plant species during a period of late spring plant growth 8 months after salmon carcass placement. Using a hierarchical design, significant variation in leaf %N and δ¹⁵N was accounted for by including differences among streams in background densities of spawning salmon, the mass of the carcasses that were added, the plant species, and, for δ¹⁵N, individual plant foliar %N. These experimental results complement previous correlational studies on the role of salmon in riparian plant nutrition and account for several compounding variables that are discussed below.

Our experiment shows that salmon nutrient addition can affect total N cycling to plants at multiple scales. At the
smallest scale near salmon carcasses, inorganic N inputs to soils can exceed 10 g N·m⁻²·year⁻¹ (Gende et al. 2007), which we show can increase plant leaf %N by 14%–60% depending on plant species. In the herbaceous species, the greatest responses were observed in false lily-of-the-valley, and to a lesser extent foamflower, compared with bunchberry. Both false lily-of-the-valley and foamflower are nitrophilic, commonly found in nutrient-rich areas, and can capitalize on available N more effectively than bunchberry, which is a nutrient-poor indicator (Klinka et al. 1989; Morris et al. 2005; Kranabetter and MacKenzie 2010).

At larger scales across streams, %N values in control plants sampled from riparian areas showed an increase with spawning salmon density (kilograms per metre). While this pattern has been observed previously in correlational studies (Kranabetter and MacKenzie 2010). With high rates of bear predation on salmon (e.g., 50% of the salmon run), N inputs from the salmon–bear association can average over 2 g N·m⁻²·year⁻¹ along each side of the stream and contribute roughly 25% of the riparian N budget (Helfield and Naiman 2006; Quinn et al. 2009). Thus, an across-stream gradient in productivity may be partly driven by salmon nutrient subsidies to riparian areas (Helfield and Naiman 2002; Drake and Naiman 2007; Hocking and Reynolds 2011). We recognize the limitations of our data set (n = 11 streams) when extrapolating to the stream scale, as there are likely to be many habitat factors that drive riparian productivity in addition to salmon density (e.g., large variation in Fig. 4). At a much larger scale, Hocking and Reynolds (2011) modeled the role of salmon and habitat across 50 streams in this same region and found that the physical features of watersheds such as stream size, slope, and canopy community mediate the effect of salmon subsidies on plant biodiversity. Our experimental approach supports these findings and provides evidence that N deficiencies can still remain in riparian areas that support high salmon abundance.

For example, treatment and control curves of %N by salmon density fail to fully converge (see Fig. 4). In sites that are nutrient-poor indicator (Klinka et al. 1989; Morris et al. 2005; Kranabetter and MacKenzie 2010).

### Table 2. Parameter estimates (±SE) for the top models in each analysis.

<table>
<thead>
<tr>
<th>Analysis</th>
<th>Parameter</th>
<th>Value</th>
<th>SE</th>
<th>df</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lanky moss foliar %N</td>
<td>Intercept</td>
<td>0.80</td>
<td>0.15</td>
<td>290</td>
<td>5.34</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>(R² = 0.69)</td>
<td>Treatment</td>
<td>0.55</td>
<td>0.11</td>
<td>290</td>
<td>4.80</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Season</td>
<td>0.14</td>
<td>0.03</td>
<td>290</td>
<td>4.64</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Salmon density</td>
<td>0.21</td>
<td>0.07</td>
<td>9</td>
<td>3.03</td>
<td>0.014</td>
</tr>
<tr>
<td></td>
<td>Carcass mass</td>
<td>-0.0001</td>
<td>0.0002</td>
<td>86</td>
<td>-3.14</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Treatment × salmon density</td>
<td>-0.10</td>
<td>0.030</td>
<td>290</td>
<td>-3.41</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Treatment × carcass mass</td>
<td>0.0001</td>
<td>0.0003</td>
<td>290</td>
<td>3.18</td>
<td>0.002</td>
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<td>1.03</td>
<td>290</td>
<td>-4.87</td>
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<tr>
<td>(R² = 0.50)</td>
<td>Treatment</td>
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<td>1.43</td>
<td>290</td>
<td>-2.73</td>
<td>0.007</td>
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<td>Season</td>
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<td>0.33</td>
<td>290</td>
<td>-6.86</td>
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<td>Salmon density</td>
<td>1.16</td>
<td>0.39</td>
<td>9</td>
<td>3.01</td>
<td>0.015</td>
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<tr>
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<td>2.92</td>
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<td>Carcass mass</td>
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<td>0.0002</td>
<td>86</td>
<td>0.74</td>
<td>0.46</td>
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<td>Treatment × carcass mass</td>
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<td>0.0004</td>
<td>290</td>
<td>2.68</td>
<td>0.008</td>
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<td>198</td>
<td>10.22</td>
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<tr>
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<td>Treatment</td>
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<td>0.20</td>
<td>198</td>
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<td>0.008</td>
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<td>197</td>
<td>2.16</td>
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Note: R² values are derived from the linear relationship of observed versus model-fitted data for each analysis.
Fig. 2. Positive relationships between foliar $\delta^{15}N$ by %N vary by plant species, (A) lanky moss (*Rhytiadelphus loreus*), (B) bunchberry (*Cornus canadensis*), (C) foamflower (*Tiarella trifoliata*), and (D) false lily-of-the-valley (*Maianthemum dilatatum*), and are often steeper at experimental carcass sites (solid circles, solid line) compared with control sites (open circles, broken line). Predicted lines are derived from top model parameter estimates (Table 2).

Fig. 3. Foliar $\delta^{15}N$ values in lanky moss (*Rhytiadelphus loreus*) increase with experimental chum salmon (*Oncorhynchus keta*) carcass mass at (A) carcass treatment sites but not at (B) control sites. Multiple lines represent the predicted relationships for each watershed (random intercept by watershed).
trient limited, pulsed nutrient inputs can cause rapid microbial responses that transform existing soil organic materials into forms (e.g., NO$_3^-$ and NH$_4^+$) that are more readily available to plants (Wardle 2002; Kranabetter et al. 2005; Gende et al. 2007). This may partially explain our greater treatment effects on leaf %N than on $\delta^{15}$N. For example, Bump et al. (2009) observed rapid foliar %N responses to wolf-killed moose carcasses and lagged increases in foliar $\delta^{15}$N.

We observed substantial variability in N isotopes, especially at salmon carcass sites ($\delta^{15}$N range = 30.1‰) compared with control sites ($\delta^{15}$N range = 20.6‰) and approaching the $\delta^{15}$N range observed in a global data set of vascular plant species (Craine et al. 2009). Plant $\delta^{15}$N variation reflects the range of soil N sources, plant–mycorrhizal associations, and fractionation processes during N transformations in ecosystems (Hogberg 1997; Hobbie et al. 2000; Evans 2001). Beside salmon streams, the wide range in plant $\delta^{15}$N will partly reflect the mosaic and long-term legacy of the pinpoint nutrient deposits from salmon carcasses. However, interpreting plant $\delta^{15}$N in correlational studies of salmon ecosystems is challenging because higher rates of gaseous N losses at sites with higher productivity can also lead to soil $\delta^{15}$N enrichments (Hogberg 1997; Pinay et al. 2003). Furthermore, at sites that are N limited, there is increased dependence on mycorrhizal fungi, which transfer isotopically depleted N to their host plants (Hobbie et al. 2000; Kranabetter and MacKenzie 2010). Both processes result in variable soil to plant N isotopic fractionation that confounds estimates of salmon-derived N in plants (e.g., Morris et al. 2005). We suggest that one way to account for these processes is to include %N as a predictor of $\delta^{15}$N. Positive correlations between foliar %N and $\delta^{15}$N suggest that both %N and $\delta^{15}$N can be used as indicators of site primary productivity (Kahmen et al. 2008; Craine et al. 2009). We show a significant positive slope between %N and $\delta^{15}$N that varies by plant species and is steeper with the addition of salmon carcasses. The positive slope in bunchberry at control sites and the absence of this relationship in false lily-of-the-valley and foamflower at control sites suggest that mycorrhizal fungi may play a greater role in transferring N to bunchberry than to the other herb species. This result parallels observations by Morris et al. (2005) in a nearby salmon-bearing watershed who found that false lily-of-the-valley leaf $\delta^{15}$N was similar to soil $\delta^{15}$N, while bunchberry leaf $\delta^{15}$N was highly depleted relative to soil. Thus, while our experiments confirm that plants take up N derived from salmon carcasses, we caution against quantifying the amount of N contributed from salmon using $\delta^{15}$N measurements alone. This means that previous estimates of percent salmon-derived or marine-derived N in plants that use constant marine and terrestrial end-members may be incorrect. Here, observed increases in $\delta^{15}$N across the index of salmon density probably reflect a combination of increasing site productivity and long-term salmon subsidies with a $\delta^{15}$N-enriched salmon source of N.

Fig. 4. Mean (± SE) foliar (A and C) %N and (B and D) $\delta^{15}$N in (A and B) lanky moss (Rhytidiadelphus loreus) and (C and D) herbaceous understory plants from spring treatment chum salmon (Oncorhynchus keta) carcass sites (solid circles) and spring control sites (open circles) in watersheds that vary by salmon density (per metre of spawning length). Predicted lines are derived from the top model parameter estimates (Table 2) where solid lines represent treatment and broken lines represent control. Note the differences in the %N and $\delta^{15}$N scales.

A) Lanky moss

B) Lanky moss

C) Herbaceous species

D) Herbaceous species

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Hocking and Reynolds

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Another complexity to interpreting $\delta^{15}\text{N}$ involves the dual N uptake pathways of some nonvascular plants, shown here by the $\delta^{15}\text{N}$ variation in lanky moss. Many species of mosses can take up N not only from the substrate but also by absorption from the air directly through the leaf surface (Solga and Frahm 2006; Liu et al. 2008). We hypothesize that some lanky moss samples were highly enriched in $\delta^{15}\text{N}$ (e.g., $+10\%_\text{e}$) due to substrate N uptake, while others were highly depleted (e.g., $-15\%_\text{e}$) due to foliar uptake of volatilized NH$_3$, which is $\delta^{15}\text{N}$ depleted (Hogberg 1997). NH$_3$ volatilization is likely an important process during the decay of salmon carcasses (Gende et al. 2007; Holtgrieve et al. 2009).

In conclusion, we provide the first experimental evidence that salmon carcasses shift N use in plants during an important period of spring plant growth many months after carcasses were deposited in forest areas, including substantial increases in total N (%N) in leaf tissues. Increasing foliar % N (and declining C/N ratio) is associated with greater plant palatability and litter quality, faster N cycling, and a shift in plant resource allocation towards stem and leaf growth rather than root development and foliar defense (Tilman 1988; Wadle et al. 2004). These patterns are consistent with shifts towards higher total N, increased tree growth, and nutrient-rich plant communities across larger-scale gradients in salmon spawning density where salmon subsidies ultimately influence riparian productivity (Helfield and Naiman 2006; Drake and Naiman 2007; Hocking and Reynolds 2011). However, we also caution that these impacts can be spatially restricted.

References


Hobbie, E.A., Macko, S.A., and Williams, M. 2000. Correlations...


