Holocene soil-geomorphic surfaces influence the role of salmon-derived nutrients in the coastal temperate rainforest of Southeast Alaska

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ABSTRACT

The influence of salmon-derived nutrients (SDN) is widely accepted as a potential factor in the maintenance of aquatic and terrestrial productivity in North American Coastal rainforests. Holocene alluvial landforms are intimately connected with the return of anadromous salmon, but the influence of the soils that occupy these landforms and support this important terrestrial–aquatic ecological coupling have not been examined in SDN studies. We used paleo-ecologic information, soil resource inventories and measurements of soil morphology to construct a soil-geomorphic model for alluvial landforms along salmon spawning channels on Prince of Wales Island, Southeast Alaska, USA. Post-glacial sea-level rise, crustal uplift and subsidence combined with Holocene sediment deposition have formed alluvial terraces and floodplains along rivers on Prince of Wales Island. These alluvial landforms have soils that are mapped as Entisols (Tonowek soil series) and Spodosols (Tuxekan soil series). We propose a soil-geomorphic model where the Spodosols located on terraces are estimated to derive from sediments deposited after the stabilization of landscape approximately 8 kybp to 6 kybp. The stability of these soils is reflected through mature soil development with organic matter accumulation and podzolization. Our model identifies Entisols on floodplains developed from alluvial deposition in the latter Holocene that have soil morphologic features consistent with recent deposition and limited soil development. We used this soil-geomorphic model to test the hypothesis that the terrestrial end-member value commonly used to quantify nitrogen (N) loading on soils through stable isotope analysis differs by soil type and found that the two soil types had significantly different N isotopic (δ^{15}N) values more consistent with soil development than SDN loading. The use of a soil-geomorphic model provides a means to stratify alluvial landforms and constrain the natural variability encountered in studies of riparian nutrient cycles associated with the feedbacks between SDN and terrestrial ecosystems to improve estimates of the fate of SDN in soils and vegetation.

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1. Introduction

The influence of salmon-derived nutrients (SDN) is widely accepted as a potential factor in the maintenance of aquatic and terrestrial productivity in nutrient-limited forests of the North American Pacific Coastal rainforests (Ben-David et al., 1998; Bilby et al., 1998; Willson et al., 1998; Wipfli et al., 1998; Naiman et al., 2002). The biogeomorphological interaction among alluvial land-forms, riparian vegetation and stream channels provides spawning habitat for salmon, and the nutrients from salmon promote the growth and maintenance of trees that perpetuate stream channel attributes conducive to the successful rearing of young salmon (Naiman et al., 2002). Understanding the specific mechanisms related to the biogeomorphic feedback associated with SDN is complicated by soil heterogeneity and the potential for vastly different cycling and storage of nutrients in the terrestrial system. Post-glacial chronose-quences of soils and ecosystems have provided a model for soil-geomorphic development in glacially derived soils in post-glacial valleys of the North Pacific Coastal rainforests (Crocker and Major, 1955; Ugolini, 1968; Chapin et al., 1994), but we have not found any studies that provide a model for Holocene soil geomorphology and alluvial landforms connected with the return of anadromous salmon.

The mass spawning of chum (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*) occurs in low-gradient river systems that can be

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identified by geomorphic, soil, and vegetation attributes (Naiman et al., 2005). The SDN from these mass spawning salmon is transferred from the aquatic to the terrestrial ecosystem via multiple pathways including bears (Quinn et al., 2009) and other piscivores (Merz and Moyle, 2006), as well as floods (Ben-David et al., 1998; Fellman et al., 2008). The SDN can be directly applied to the soil through the deposition of carcasses, or indirectly through feces and urine of piscivorous animals. The consumption of carcasses by insects and subsequent re-distribution through multiple trophic pathways can also spread SDN in the terrestrial ecosystem (Reimchen et al., 2003). Therefore, SDN are distributed on soils in irregular patterns with varying amounts of material and nutrient concentration. The most consistent patterns associated with SDN are concentration plumes that are greatest at the stream edge near the spawning salmon and decrease in a perpendicular direction away from the stream (Ben-David et al., 1998).

Quantifying the impact of the SDN nutrient subsidy on plant growth uses several approaches that either directly or indirectly measure some aspect of soils. The 'Riparian zone' is often invoked as a homogeneous soil-geomorphic surface associated with alluvial landforms. However, homogeneity in terrestrial plant communities often masks soil variability on alluvial landforms (Merrill and Benning, 2006). Reference reaches above barriers to salmon migration (e.g., waterfalls) are also used as 'control' reaches, thus allowing a comparison of stream reaches with and without the influence of SDN. However, natural barriers to salmon migration, such as waterfalls, reflect distinct geomorphic changes that influence soil and vegetation communities that can confound SDN studies. In zones above barriers, the classic floodplain is often limited by the physiography of steep valley sides and constrained channels (Montgomery, 1997). Greater growth rates of trees have been noted in salmon reaches compared to non-salmon-bearing reaches above a barrier (Helfield and Naiman, 2001). However, these growth rates may have been related to differences in vegetation communities rather than the presence of SDN (Kirchhoff, 2003) and subsequent speculation noted that vegetation differences and growth rates above and below the salmon barrier may have been due to geomorphologic and soil factors, not necessarily the presence of salmon (Naiman et al., 2002). Higher N concentrations were found in a non-salmon-bearing reach compared to a salmon-bearing reach, contrary to the hypothesized influence of SDN (Bartz and Naiman, 2005). However, the potential influence of specific soil types was not investigated that may have impacted the N variability in the riparian zone.

Transects that extend perpendicular to the stream channel capture the diffusion of SDN distribution, but can cross various soil types (Ben-David et al., 1998; Bilby et al., 2003; Bartz and Naiman, 2005). Nitrogen concentrations varied with distance from the stream across four landform categories in one SDN study, but there was no identification of soil type or evaluation of nutrient concentrations related to soil factors (Bilby et al., 2003). Soil map units identified in regional soil surveys have not provided the resolution for partitioning specific soil types for field studies (see Bartz and Naiman, 2005 use of Reiger et al., 1979). The only study we have encountered with a specific soil type identified and isolated as an experimental unit highlighted how soil heterogeneity in texture, pH, and cation exchange capacity may have influenced SDN cycling (Drake et al., 2005).

The δ^{15}N natural abundance method is commonly used in SDN research as a tracer to determine the source and sinks of N in riparian zones (Drake et al., 2006; Gende et al., 2007). However, variable soil-geomorphic features associated with the cycling of nitrogen can confound the use of tracers such as δ^{15}N. Nitrogen has two stable (i.e. non-radioactive) isotopes, ^{14}N and ^{15}N, with the vast majority being ^{14}N. Because of the relatively small difference in the proportion of ^{15}N/^{14}N relative to a standard, N isotopes can be effective tracers in ecological studies (Rundel et al., 1989; Lajtha and Michener, 1994). The δ^{15}N source is assumed to be provided by the salmon, while the

sinks for δ^{15}N are assumed to be vegetation, microbial communities, and soil surfaces. A mixing model can determine the amount of N provided by SDN through a mathematical expression with known values of the δ^{15}N for the marine and terrestrial end-members (adapted from Kline et al., 1990, 1993):

$$\%SDN = \frac{SAM-TEM}{MEM-TEM} \times 100\%$$

Where the %SDN is the percentage of salmon-derived N in the sample of vegetation or soil, SAM is the δ^{15}N of a representative sample of vegetation or soil, TEM is the δ^{15}N of the terrestrial end-member (assumed to be a sample that has obtained 100% of its N from terrestrial sources), and MEM is the δ^{15}N of the marine end-member (assumed to be a sample that has obtained 100% of its N from marine sources). The N loading rate provided by SDN is calculated from measured or estimated values for the end-members.

Natural fractionation through nitrification, denitrification and NH_4^+ volatilization influence the isotopic fractionation of δ^{15}N and cause problems in determining augmentation of N by salmon in soils and vegetation with the δ^{15}N method (Högberg, 1997). Högberg (1997) notes that δ^{15}N is not a "conservative, unchanging tracer" and the texture, moisture conditions and abundant carbon substrate in riparian soils lead to intense, sustained nitrogen cycling (Bedard-Haughn et al., 2003; Pinay et al., 2003; Luxhøi et al., 2004) that causes a pronounced fractionation of N (Naiman et al., 2005). Trees may discriminate against the heavier δ^{15}N isotope when forest growth is not N-limited, such as riparian zones (Nadelhofer and Fry, 1994) leaving an enriched δ^{15}N signature. Therefore, both vegetation and soil processes lead to fractionation and concentration of δ^{15}N, which diminishes the isotopic ratio and can render the δ^{15}N natural abundance method ineffective in determining N loading through SDN.

Recent attempts have been made to link the ecological aspects of ecosystems, such as stream systems, to geomorphology (Renschler et al., 2007). The study of eco-geomorphology describes the integration of physical, chemical, and biological components of ecosystems (Thoms and Parsons, 2002). The related field of soil geomorphology has emerged as an important study of the linkage between soils and landforms (Birkeland, 1999; Wysocki et al., 2000) and the soil-geomorphic approach provides a means to build models that can address the confounding influence of soil variability in studies of SDN. Soil geomorphology combines landform arrangement and differentiation with the process of soil formation and provides a means to constrain the variability in ecological function related to soils (Daniels and Hammer, 1992; Gerrard, 1992). While soil state-factor theory (Jenny, 1941; Amundson and Jenny, 1997) can be applied to alluvial soils in riparian zones in order to understand ecological function (Van Cleve et al., 1991), the soil geomorphological template can link the biological feedback mechanisms to the paleo-environmental template of Holocene landscape evolution. The eco-geomorphological feedback between SDN and terrestrial ecosystems can be improved through an understanding of alluvial soil geomorphology.

This study was designed to address the need for integrating alluvial soil geomorphology with the deposition of SDN on terrestrial ecosystems in North Pacific coastal rainforests. Our goal was to establish a model for soil geomorphology of Holocene alluvial landforms in salmon spawning streams of Southeast Alaska. We established relationships between soil attributes and landforms through replicated descriptions and characterization of several soils in Holocene alluvial deposits along salmon spawning streams on Prince of Wales, Island, Southeast Alaska, USA. We then used these alluvial soil types to test the hypothesis that the concentration of isotopic nitrogen (δ^{15}N), commonly used as a tracer of SDN, was related to alluvial soil type.