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THE CONTRIBUTION OF SPAWNING PACIFIC-SALMON TO NITROGEN FERTILITY AND VEGETATION NUTRITION DURING RIPARIAN PRIMARY SUCCESSION ON AN EXPANSIVE FLOODPLAIN OF A LARGE RIVER

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ABSTRACT

Floodplain vegetation communities are mosaics of succession stages caused by erosion/redeposition as river channels migrate throughout their floodplains. Typically, plants colonizing alluvial deposits are severely N-limited, but N accumulates during succession, and this process determines long term fertility. The Kol River (Kamchatka, RU), received large annual N-subsidies from salmon and we sought to determine how salmon-N contributed to fertility during succession.

We constructed a vegetation chronosequence model and made N-fertility measurements within replicate succession stages before, during and after salmon runs. Natural abundance of ^{15}N was used as a tracer of salmon-N.

We found that new alluvial deposits were N-poor, containing < 200 kg-N ha^{-1} (to 10cm). However, soil-N increased more than 10X within 30 years and soils were N-rich henceforth. Net N-mineralization on young alluvial bars only provided a small fraction of the colonizing forest's N requirement, whereas soils in older forests provided abundant N. Negative correlation between foliar C:N and soil N during the first 20 years of succession indicated that the youngest succession stages were N-limited.

The salmon run commenced in midsummer and caused river water N to increase 3X. Subsequent late season flooding deposited an average of 25 kg-N ha^{-1} as salmon carcasses onto young alluvial bars during 2006, but deposition rates were 10 to 30X higher on other years. The N-pulse created by decomposing salmon on young alluvial bars was brief because subsequent flooding flushed these coarse soils, but colonizing willows assimilated N rapidly during this time and high foliar $\delta^{15}N$ (3 to 5‰) confirmed that salmon were a major N-source in early succession. Foliar $\delta^{15}N$ was abnormally high throughout the floodplain (1 to 5‰) indicating that older forests recycled salmon-N that accumulated during early succession.

All plant species that occurred during the first several centuries of succession had N-rich foliage (mean C:N 12 to 22). We conclude that salmon fertilized otherwise N-poor early succession annually, and built ecosystem N-pools during early succession, thereby allowing nitrophillic plant species to proliferate.

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TABLE OF CONTENTS

CHAPTER 2: THE CONTRIBUTION OF SPAWNING PACIFIC-SALMON TO SOIL NITROGEN FERTILITY DURING PRIMARY SUCCESSION IN A LARGE-RIVER FLOODPLAIN……...…………………………………………………………..53

LIST OF FIGURES

CHAPTER 1: PRIMARY VEGETATIVE SUCCESSION AND PEDOGENESIS ON AN EXPANSIVE FLOODPLAIN OF A LARGE SALMON RIVER

CHAPTER 2: THE CONTRIBUTION OF SPAWNING PACIFIC-SALMON TO SOIL NITROGEN FERTILITY DURING PRIMARY SUCCESSION IN A LARGE-RIVER FLOODPLAIN

CHAPTER 3: THE CONTRIBUTION OF SPAWNING SALMON TO FOLIAR NITROGEN NUTRITION DURING FLOODPLAIN PRIMARY SUCCESSION

CHAPTER 4: ANALYSIS OF FOLIAR $\delta^{15}N$ ACROSS A WIDE RANGE OF SALMON FERTILIZATION RATES IN RIPARIAN FORESTS THROUGHOUT THE PACIFIC-RIM

CHAPTER 5: SEASONAL INFLUENCE OF DECOMPOSING SALMON ON NITROGEN ASSIMILATION DYNAMICS OF GRAVEL-BAR WILLOWS

LIST OF TABLES

CHAPTER 1: PRIMARY VEGETATIVE SUCCESSION AND PEDOGENESIS ON AN EXPANSIVE FLOODPLAIN OF A LARGE SALMON RIVER

CHAPTER 2: THE CONTRIBUTION OF SPAWNING PACIFIC-SALMON TO SOIL NITROGEN FERTILITY DURING PRIMARY SUCCESSION IN A LARGE-RIVER FLOODPLAIN

CHAPTER 3: THE CONTRIBUTION OF SPAWNING SALMON TO FOLIAR NITROGEN NUTRITION DURING FLOODPLAIN PRIMARY SUCCESSION

CHAPTER 4: ANALYSIS OF FOLIAR δ^{15}N ACROSS A WIDE RANGE OF SALMON FERTILIZATION RATES IN RIPARIAN FORESTS THROUGHOUT THE PACIFIC-RIM

CHAPTER 5: SEASONAL INFLUENCE OF DECOMPOSING SALMON ON NITROGEN ASSIMILATION DYNAMICS OF GRAVEL-BAR WILLOWS

INTRODUCTION

Background

Pacific-salmon provide production and nutrient subsidies to freshwater ecosystems

Rivers of the northern Pacific-rim typically have low productivity, attributable to long cold winters, prolonged snowmelt-driven flooding, and low ion content. Consequently, Pacific-salmon *(Oncorhynchus spp.)* spawn and undergo early development in freshwaters, which serve as a refuge from predators, but then migrate to the ocean where they can attain much higher growth rates (Gross et al. 1988). Once in the ocean, juvenile salmon that initially weigh from less than one but up to tens of grams, grow to several kilograms, and then migrate back to their natal rivers to spawn and subsequently die. As spawning populations are often enormous relative to the size of these rivers, with up to several spawners per square meter of streambed, they can provide enormous production and nutrient subsidies to these otherwise oligotrophic freshwater ecosystems (Naiman et al. 2002).

It is well documented that spawning salmon are important food sources for the predators and scavengers living in and around salmon streams such as bears, eagles, foxes, otters, minks, invertebrates and resident fishes (eg- Cederholm, et al. 1989, Jauquet et al. 2003, and others). In addition to being consumed directly, nutrients imported by these salmon may also stimulate aquatic primary production (e.g. Wipfli et al. 1998, Wold and Hershey 1999, Chaloner and Wipfli 2002, Minakawa et al. 2002 and others). It has been shown that the growth of juvenile salmon, which often rear for several years in these freshwaters, may benefit from the presence of spawning adults (Bilby et al. 1998, Wipfli et al. 2003), and therefore, it is widely hypothesized that these nutrient and production subsidies act as a positive feedback mechanism that is essential in sustaining future salmon runs (eg. Michael 1995, Schmidt et al. 1998, Griswold et al. 2003, Schindler et al. 2003, Wilson et al. 2003, Wipfli et al. 2003). In light of the numerous recent studies demonstrating that so many organisms are directly dependent on these salmon runs, and that the nutrients imported by these salmon permeate entire ecosystems, Pacific-salmon are now recognized as “keystone species” (Naiman et al. 2002, Helfield and Naiman 2006), and there is increasing recognition that managers should also take into account the salmon’s ecological role when setting harvest rates, which have historically been as high as 60-90% of the adult population (Chen and Holtby 2002, Groot and Margolis 2003).

Pacific-salmon fertilize riparian vegetation

Numerous recent studies have found that salmon not only fertilize the freshwaters in which they spawn, but that they also fertilize riparian vegetation, with plants growing along spawning streams acquiring between up to 63% of their total foliar nitrogen from salmon (Bilby et al. 1996, Hildebrand et al. 1999, Helfield and Naiman 2001, Helfield and Naiman 2002, Bilby et al. 2003, and Mathewson et al. 2003). The finding that riparian vegetation assimilates salmon imported nitrogen has important implications because forests and soils have a much greater capacity to retain and recycle nutrients than in-stream processes. In fact, some research suggests that spawning salmon may not stimulate aquatic primary production in rivers with the densest runs, because the spawners dig up the streambed while building their nests, thereby preventing algal growth (Moore et al. 2004). Furthermore, aquatic primary production may be limited by factors other than nutrient availability, such as cold temperatures and flooding in these spawning streams (Chaloner et al. 2007). Given that stream nutrient concentrations decline to pre-salmon levels soon after carcass decomposition (Johnston et al. 2004, Chaloner et al. 2007), it is likely that much of these salmon nutrients would be rapidly discharged back to the ocean if not assimilated by the riparian zone. And, as terrestrial litter is often a much greater production source to streams than in-stream primary production (Cummins 1974), uptake by riparian vegetation may be a crucial pathway whereby salmon nutrients are assimilated and reallocated back to juvenile salmon. Salmon fertilization may have important implications for the ecology of the forests themselves, as forest growth is usually nitrogen limited, and several recent studies have found evidence that spawning salmon may increase plant growth and favor the abundance of nitrophillic species (Helfield and Naiman 2001-but see Kirchoff 2003, Bilby et al. 2003, Mathewson et al. 2003, Bartz and Naiman 2005).

Most research on the riparian assimilation of salmon nutrients has been conducted along small, relatively constrained stream reaches that do not expansive floodplains. In these small stream systems, nutrient transfer is primarily unidirectional, from the riparia to the mainchannel and then downstream (Cummins 1974, Hynes 1975, Vannote et al. 1980). Thus in order for salmon nutrients to fertilize riparian vegetation they must first be transported in the opposite direction, from the river channels to the riparian vegetation. Most studies have attributed this reverse flow of salmon nutrients to the activity of terrestrial vertebrate scavengers and predators which feed on the salmon and redeposit their nutrients in the forest (Ben-David et al. 1998, Hildebrand et al. 1999, Helfield and Naiman 2006). Several other studies have suggested that flooding (Cederholm et al. 1989, Ben David et al. 1998), hyporheic flow (O'Keefe and Edwards 2003), and aquatic insect emergence (Francis et al. 2006) may also deliver salmon nutrients to riparian vegetation. However, because these up-gradient pathways are relatively minor compared with down gradient nutrient flow in these small stream systems, this fertilization effect has been shown to occur over small scales, primarily within 25m, but up to 100m from streambanks (Ben-David et al. 1998, Hildebrand et al. 1999, Helfield and Naiman 2002, Bilby et al. 2003).

Retention of salmon imported nitrogen in floodplains

Whereas the recycling of salmon nutrients is well studied in small stream systems, this phenomenon is almost unstudied in expansive floodplains of large rivers. We surmise that the fertilization effect of spawning salmon is much greater in expansive floodplains not only because they have historically contained the largest aggregations of spawning salmon, but they should also have much greater capacity to assimilate salmon nutrients. Whereas constrained streams function like pipes that drain catchments and export matter downstream, the processes of flooding and hyporheic flow transfer nutrients reciprocally between aquatic and terrestrial habitats over large spatial scaes in large river floodplains (Junk et al. 1989, Stanford et al. 2005). Furthermore because river channels migrate throughout their floodplains over time, and salmon imported nutrients may be stored in riparian soils and biomass, we hypothesize that entire floodplains- which may be many kilometers wide- may be influenced by a legacy of salmon fertilization.

Our study site, a floodplain on the lower Kol River

Therefore we conducted the first detailed study of salmon fertilization of riparian vegetation in an expansive floodplain of a large (7th order) river. Our study site was a lower floodplain of the Kol River in southwestern Kamchatka (Russian Federation) (N53°49.506' E156°3.716'). We chose to work in southwestern Kamchatka because this region was extremely remote and consequently the entire Kol catchment was largely pristine with no roads or year-round inhabitants. Furthermore, most rivers in southwestern Kamchatka still receive very large salmon runs, whereas many runs have declined dramatically as a result of a variety of anthropogenic stressors on the North American side of the Pacific-rim (Nehlsen et al. 1991, www.stateofthesalmon.org). Up to five million pink salmon may return to spawn and die in the Kol per year, contributing up to 270,000 kg-N yr^{-1} to the river.

Our study floodplain was expansive (3.5km wide) and complex, exhibiting a "shifting habitat mosaic" succession pattern that is typical of alluvial floodplains in the northern Pacific-rim (Stanford et al. 2005). Rather than having a single mainchannel as is typical in constrained river reaches, the river formed a complex network of anastomosing channels in our study floodplain. This network of channels migrates throughout the floodplain over time, eroding existing terrestrial sites and redepositing them as bare alluvial deposits. New forests colonize these alluvial deposits, and as a result, the floodplain's vegetation community is a mosaic of different succession stages. Therefore, in order to determine how spawning salmon fertilize this floodplain it must be understood how salmon act as a nutrient source during primary succession.

Purpose and hypothesis formation

The overarching goal of this dissertation was to determine how spawning salmon contributed nitrogen to riparian forests and soils during primary succession on the Kol River floodplain. Floodplain primary succession is well studied in other temperate rivers, allowing us to (1) formulate hypotheses based on prior theoretical advances, (2) design our study based on proven methodologies and (3) compare our results from the Kol River floodplain to sites that did not recieve significant nutrient subsidies from spawning salmon. In particular, our research would not have been possible without the outstanding research published on primary succession and soil development in the Tanana River floodplain in Alaska (http://www.lter.uaf.edu/). The Tanana floodplain served as an excellent comparison site for our study because it is a similarly complex floodplain located in the Northern Pacific-rim that harbors many of the same early succession plant taxa (*Salix* and *Alnus sp.*) as occur on the Kol floodplain, but the Tanana receives minor nutrient subsidies from spawning salmon relative to the Kol River (very roughly 50 to hundreds of times fewer fish per stream kilometer or per unit flow during the growing season, respectively). In addition to the Tanana, floodplain succession studies conducted within the following river systems served as valuable comparison sites: The Hoh River, WA (Fonda 1974, Luken and Fonda 1983); The Porcupine River, AK (Farjon and Bogaers 1985); Tahish and Artlish Rivers, BC (Clement 1985); the Susitna River, AK (Helm and Collins 1997); The Tokachi River, JN (Nakamura et al. 1997); Agashashok River, AK (Rhoades et al. 2001); The Green and Yampa Rivers, CO (Adair et al. 2004); the Rekifune River, JN (Shin and Nakamura 2005); the Queets River, WA (Van Pelt et al. 2006); and the Middle Fork of the Flathead River, MT (Stanford unpublished).

By definition, primary succession begins with the vegetation's colonization of bare mineral substrates that have very low nitrogen concentrations (Walker and del Moral 2003) and therefore growth in early succession is usually severely nitrogen limited. Nitrogen fertility then improves over time as soils develop. As a result of this limitation, symbiotic nitrogen fixers are often important colonizers in early succession (Walker 1993), but nitrogen availability still limits their growth, as nitrogen-fixation is energetically expensive, requiring 8 to 12 grams of glucose per gram of nitrogen fixed (Gutschick 1981). By building ecosystem nitrogen pools, nitrogen fixers, and potentially salmon in the case of the Kol floodplain, may facilitate the growth of later succession species and have long term influence on a variety of functions in these ecosystems (eg. Fastie 1995, Vitousek and Walker 1989).

Our initial observations in the Kol River floodplain indicated that spawning Pink-salmon *(Oncorhynchus gorbuscha)* entered the river in mid-summer and spawned and died in late summer/early fall. Late season flooding, which occurs on most years in early to mid September, then washed their decomposing carcasses onto young gravel bars because these sites were adjacent to the main channel and flooded regularly. In contrast, older forest sites received few salmon carcasses because they were distant from the main channel and higher in elevation.

Therefore, we generated the working hypothesis that spawning salmon functioned to fertilize early succession in the Kol floodplain, thus promoting the colonization of young forests on these otherwise infertile gravel bars. Although we hypothesized that the intra-annual pulse in nutrient availability on gravel bars caused by salmon carcasses would likely be brief because carcasses decomposed rapidly and subsequent flooding flushes these coarse soils, we expected that salmon nutrients would be retained over time by accumulating fine sediments and plant biomass. Therefore while older forest sites may not receive annual salmon nutrient subsidies, it is likely that they recycle salmon nitrogen that accumulated in early succession. As a result of these salmon subsidies we expected that the Kol floodplain would be dominated by nitrophillic, fast growing plant species.

Chapter overview

This dissertation consists of five chapters which address the ideas set forth in the working hypothesis. The first three chapters document how the vegetation community, soil fertility and vegetation nutrition changed during succession. Chapter 1 sets the stage for the subsequent chapters by using mathematical models of vegetation growth, community development and soil nitrogen accumulation during the first several hundred years of primary succession to develop a chronosequence model for the Kol floodplain. We also quantified the flood deposition of salmon carcasses and compared primary succession in the Kol floodplain to other chronosequences that did not receive significant nutrient subsidies from spawning salmon. In Chapter 2 we used soil fertility measurements (total nitrogen, potentially mineralizeable nitrogen, dissolved inorganic nitrogen, and growing season net mineralization rate) to determine how mineral soil nitrogen fertility changed during the first century of succession. We also determined how these fertility measures changed seasonally and in relation to salmon carcass availability. Finally, we used ion exchange resin capsules to test whether spawning salmon created a seasonal pulse in nitrogen availability. In Chapter 3 we used foliar C:N ratios to indicate how the vegetation responded to changing nitrogen fertility during succession and we used the natural abundance of the ^{15}N isotope as a tracer of salmon-imported nitrogen during succession. We also compared foliar nitrogen concentrations in the floodplain to the uplands, as well as to typical values for deciduous forests. We concluded this chapter with a conceptual model of how vegetation nutrition and soil fertility interacted and changed together during succession. Chapter 4 presents a synthesis of studies of that have used natural abundance of the ^{15}N isotope as a tracer of salmon-nitrogen in foliage in order to determine whether foliar $\delta^{15}N$ is positively related to salmon run size at a diversity of rivers throughout the Pacific-rim. Furthermore, we used this synthesis to compare the relative size of the salmon fertilization effect in the Kol River to other salmon rivers. In Chapter 5 we used mainchannel nitrogen concentrations to determine the seasonality of salmon fertilization and we also used sequential whole willow harvests to determine whether colonizing willows assimilated nitrogen from decomposing salmon carcasses on a gravel bar, given that carcasses were not available until very late in the growing season.

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CHAPTER 1:

PRIMARY VEGETATIVE SUCCESSION AND SOIL NITROGEN ACCUMULATION ON AN EXPANSIVE FLOODPLAIN OF A LARGE SALMON RIVER

Abstract

Nitrogen limitation is usually severe in early primary succession, and the vegetation community both responds and contributes to changing nitrogen fertility as succession proceeds. Herein we document vegetation succession and soil development on a river floodplain (Kol River, Kamchatka, Russian Federation) that receives large nitrogen subsidies from spawning Pacific-salmon. We found that mathematical succession models were able to explain approximately half the variance in more than half of the soil and vegetation variables that we measured, indicating that the primary succession chronosequence concept was a good organizing principle for many of these variables. Similarly to floodplains in the Pacific-northwest, British Columbia, Alaska and Hokkaido we found newly formed gravel bars were colonized by willows (2 species of *Salix* and *Chosenia arbutifolia*) and alders (*Alnus hirsuta*), although alders were a relatively minor component of the forest community. Dense stands of colonizing trees trapped sediments forming raised floodplain benches that developed into gallery forests. Whereas floodplain forest communities in other regions of the northern Pacific-rim transitioned to more nitrogen-efficient tree species after approximately the first 100 years of succession, the Kol floodplain's forests transitioned into meadows of nitrophillic tall forbs, dominated by *Filipendula camtschatica,* after about the first century of succession. As in all types of primary succession, we found that new alluvial deposits were very nitrogen-poor on the Kol floodplain, containing less than 200 kg-N ha^{1} of total nitrogen (to 10cm). However, soil nitrogen increased rapidly during succession, and within 30 years the soil contained approximately 2,300 kg-N ha^{-1} (to 10cm + the litter layer). Unlike other Pacific-rim chronosequences, the period of most rapid nitrogen accumulation occurred while nitrogen fixing alder was a minor component of the forest community. Rather than alder, salmon-imported nitrogen and flood-deposited fine sediments could account for this nitrogen accumulation. Foliage of all the major vegetation species occurring during the first several hundred years of succession was nitrogen rich (foliar C:N 12 to 22) relative to both typical values for temperate forests, as well as other floodplains that did not have salmon-nitrogen subsidies. We therefore concluded that salmon likely promote the proliferation of nitrophillic vegetation in the Kol floodplain.

Introduction

Alluvial floodplains are dynamic interfaces between aquatic and terrestrial environments notable for their high biological diversity, productivity and ecosystem function rates (Gregory et al. 1991, Tockner and Stanford 2002, Stanford et al. 2005). The high biological diversity of floodplains is attributable to both the co-existence of aquatic and terrestrial species, and because the river continually reworks the floodplain by eroding existing sites and depositing new landforms, thereby creating a mosaic of diverse successional habitats. High productivity and ecosystem function rates in floodplains are attributable to both enhanced water and nutrient availability. Whereas rivers that flow in predominately constrained channels function like pipes, exporting nutrients from the riparia downstream (eg. Minshall et al. 1992, Cushing et al. 1993), the processes of flooding, channel migration, and groundwater exchange transfer nutrients reciprocally between aquatic and terrestrial habitats in large river floodplains (Junk et al. 1989, Stanford et al. 2005). And, because soils and forests have much greater nutrient retention capacity than streams, floodplains function to retain nutrients. Nutrient retention capacity is particularly high in the floodplain's young successional forests, as they rapidly accumulate biomass and soil nutrient pools (Walker and del Moral 2003).

Many rivers of the northern-Pacific rim receive large nutrient subsidies from Pacific-salmon which return from the ocean to their natal rivers to spawn and subsequently die. Given that floodplains retain nutrients whereas constrained reaches primarily export nutrients, we expected that floodplains are among the most important locations within catchment for the retention and recycling of salmon-imported nutrients. And, as vegetation growth is usually nitrogen limited in these floodplains, we also expected that salmon influenced the biological diversity, successional patterns and overall ecosystem functioning in floodplain forests.

Floodplain succession begins with pioneer vegetation species colonizing new alluvial substrate deposited by flooding. In gravel-bed floodplains these new alluvial deposits are composed of primarily of gravel and sand, and consequently these soils are very nitrogen poor. Nitrogen accumulates during primary succession as a result of biological nitrogen fixation and organic matter deposition. Thus, as in all types of primary succession chronosequences, including mines, glacial moraines, sand dunes, and volcanoes (Walker and del Moral 2003) vegetation growth is typically strongly nitrogen limited in early floodplain succession (Walker and Chapin III 1986, Sasaki et al. 2001, Adair and Binkley 2002).

In addition to plant growth, nitrogen limitation also controls community composition and development during primary succession. Some plants are adapted to nitrogen-poor conditions, and others nitrogen-rich conditions, and soil nitrogen availability is often a good predictor of species distribution (Chapin III et al. 1986). Not only do plants respond to nitrogen limitation, they also change site fertility both positively and negatively as succession proceeds, and these patterns are predictable during succession.

We reviewed published floodplain chronosequences around the northern Pacific-rim (which we define as north of 40°N latitude but south of the Arctic Circle), including sites in Washington State, British Columbia, Alaska, and Hokkaido in order to make some broad taxonomic and functional generalizations about overstory succession on floodplains in this region. The North American chronosequences had similar patterns of community development. Primary succession generally began with the colonization of alluvial bars by one or more of the following pioneer tree taxa: willows *(Salix sp.)*, alders *(Alnus sp.)* and/or cottonwoods *(Populus sp.)*, although a variety of herbaceous species may be briefly present at the onset of succession prior to full colonization by trees. Where willows were the initial colonizers they typically only persisted for the first decade or so, and then were usually replaced by alders, which dominated the community for several decades. Alders were often replaced by longer-lived *Populus* and sometimes maples *(Acer)* between fifty and one-hundred years. Deciduous trees were then replaced by, or coexisted with, conifers (either spruce *(Picea)* or hemlock *(Tsuga)*) which dominated after about the first century or more (Fonda 1974, Nanson and Beach 1977, Luken and Fonda 1983, Farjon and Bogaers 1985, Clement 1985, Viereck et al. 1993, Helm and Collins 1997, Van Pelt et al. 2006).

Relatively few studies have described floodplain vegetation dynamics on the Asian side of the northern Pacific-rim, and most of this research has been on Hokkaido. Similar to North American chronosequences, Nakamura et al. (1997) described that pioneer trees of the genus *Salix* and the closely related *Chosenia* and *Toisusu* genii, as well as *Alnus* and *Populus* colonized alluvial gravel bars at the onset of succession. These pioneers were replaced by two conifers, *Picea* and *Abies,* as well as occasional broadleaf deciduous trees of the genii *Ulmus, Fraximus* and *Acer* between 80 and 100 years after initial colonization. Shin and Nakamura (2005) found that the same genera also colonized alluvial bars in another small Hokkaido floodplain, but older floodplain benches were dominated by *Ulmus* and *Fraximus* forests rather than conifers.

We identified three main functional strategies for nitrogen use in these floodplain chronosequences. Firstly, colonizing willows and cottonwoods tend to be fast growing, and thus relatively nitrophillic in order to survive the stresses of flooding, fluctuating water tables and rapid sedimentation (Karrenberg et al. 2002). But, because new alluvial deposits are typically nitrogen poor, willows and cottonwoods rarely reach their growth potential in early succession. As a consequence, willows and cottonwoods typically have very plastic foliar nitrogen concentrations that respond strongly to fertilization (Walker and Chapin III 1986, Sasaki et al. 2001, Adair and Binkley 2002). For example, Hobbie et al. (1998) showed that willow foliage was nitrogen-poor at the onset of succession but nitrogen-rich as soils developed.

The other main nitrogen strategy for colonizing species is symbiotic nitrogen fixation, and alders are the most common nitrogen fixer in northern Pacific-rim floodplains. Alders often become the dominant tree in early succession despite the high energetic costs of nitrogen fixation, because early succession soils are nitrogen poor, giving them a strong competitive advantage. Alders may fix enormous quantities of nitrogen, with estimates commonly exceeding 100 kg-N ha^{-1} yr^{-1} (Binkley et al. 1994). This nitrogen is subsequently deposited into soils as nitrogen-rich litter (Binkley et al. 1994), ameliorating the infertility of early succession. Other species coexisting with alders are usually nitrogen-rich relative to when they grow without alder, and in some cases alders increase nitrogen fertility so greatly that coexisting species may not be nitrogen limited at all (Walker and Chapin III 1986, Hobbie et al. 1998, Rhoades et al. 2001).

The third strategy, occurring in later succession (after approximately the first century) is for plants to use nitrogen efficiently. Nitrogen-efficient species have low foliar nitrogen concentrations even in relatively fertile environments and thus are slow-growing. Also, their leaves typically have high concentrations of recalcitrant organic compounds. By depositing poor-quality litter, these plants decrease soil fertility. And, as plants respond to declining fertility by producing more recalcitrant litter, a positive feedback may occur whereby nitrogen limitation becomes progressively more severe in late succession (Berg and McClaugherty 1987, Van Cleve et al. 1993, Klingensmith and Van Cleve 1993, Schimel et al. 1996, Hobbie et al. 1998, Aerts and Chapin III 2000, Fierer et al. 2001) In Pacific-rim chronosequences, *Populus* and other later succession broadleaf deciduous trees tend to have lower foliar nitrogen concentrations than alders and willows, and the conifer trees occurring in the latest succession stages have especially nitrogen-poor, recalcitrant foliage (Walker and Chapin III 1986, Hobbie et al. 1998).

However, not all Pacific-rim floodplains may follow these patterns of changing nitrogen fertility as recent research suggests that spawning Pacific-salmon may fertilize riparian vegetation (Ben-David et al. 1998, Hildebrand et al. 1999, Helfield and Naiman 2001, Helfield and Naiman 2002, Bilby et al. 2003, Mathewson et al. 2003). However, rather than in the large floodplains where succession has been studied, salmon-nutrient research to date has been conducted primarily along small upland spawning streams. While nutrient transfer is primarily unidirectional (from the riparia to the stream) in small upland streams, terrestrial vertebrates feeding on the salmon, as well as flooding and hyporheic flow transport their nutrients in the opposite direction, from the streams to the riparia. This fertilization effect has been shown to occur over small spatial scales, primarily within 25m, but up to 100 m from the banks of these small salmon streams (Ben-David et al. 1998, Hildebrand et al. 1999, Helfield and Naiman 2002, Bilby et al. 2003).

In contrast, we hypothesized that the spatial distribution of salmon fertilization would be greater on the expansive floodplains of large salmon rivers due to the high reciporical terrestrial-aquatic connectivity occurring throughout enitre floodplains, which may be several kilometers wide. If substantial salmon-derived nutrients are transported by flooding from the networks of base flow channels into the riparia, or by entrainment in the alluvial aquifer through hyporheic exchange pathways (*sensu* Stanford et al. 2005) then it follows logically that salmon could dramatically influence the vegetation dynamics of these otherwise nitrogen-limited floodplain ecosystems.

Thus, we quantified primary succession on an expansive and structurally complex floodplain of a river in the Russian Far-East that receives enormous salmon subsidies. Our study site was the Kol River, Kamchatka, RU, a large (7th order) river. Up to five million pink salmon may return to spawn and die in the Kol, contributing up to 270,000 kg-N yr^{-1} to the river ecosystem. We developed a general working hypotheses that (1) spawning salmon were a major nitrogen source to colonizing forests with the potential to alleviate nitrogen limitation in early succession and (2) older floodplain forests recycled salmon-derived nitrogen that was imported in early succession (see also Chapters 2 and 3).

Herein we demonstrate that many attributes of forest community and soil development were predictable during primary succession in the Kol floodplain and we present models for these processes. Briefly, we found that newly exposed nitrogen-deficient gravel bars were colonized by young willows, and these willow stands then transitioned into mixed willow-alder gallery forests with a tall forb understory. At around 100 years the gallery forest senesced leaving a meadow of tall forbs, which eventually transitioned into grass-meadows and then possibly into heath over hundreds to thousands of years. Soil nitrogen accumulated most rapidly during the first 30 years of succession while nitrogen fixing alder trees were a minor component of the forest. Rather, this period of nitrogen accumulation corresponded to high nitrogen inputs from spawning salmon and sediment deposition. We conclude with a discussion of how the salmon subsidy may shape the vegetation community during succession.

Study System: the Kol River

The Kol River's headwaters originate in the central Kamchatka mountain range at an elevation of nearly 2000m and the river flows westward. The main channel has a minimum summer base flow of approximately 20 to 30 $m^3 s^{-1}$ in our study region, and the Kol is a seventh order river at its mouth. Approximately seventy percent of the catchment is tundra-dominated coastal plain below 150m.

Unlike the brown-water rivers originating in the coastal plane, the Kol and other large-rivers of the region have clear-water (except during extreme flooding) attributable to summer long snow and glacial melt in their mountain headwaters. Sediment laden floods originate with spring snowmelt and any time heavy rains occur, and the legacy of flooding has cut expansive braiding or anastomosing floodplain corridors (2.5 to 4 km wide in our study reach) through the tundra landscape.

Our study site was a large floodplain (N53°49.506' E156°3.716') of the lower Kol River approximately 6 to 10 km east of the river's confluence with the Sea of Okhotsk (Figure 1). The entire Kol catchment is largely pristine and was recently designated as a salmon conservation area by the Russian Government. Research was based out of a biostation run by the Wild Fishes and Biodiversity Foundation.

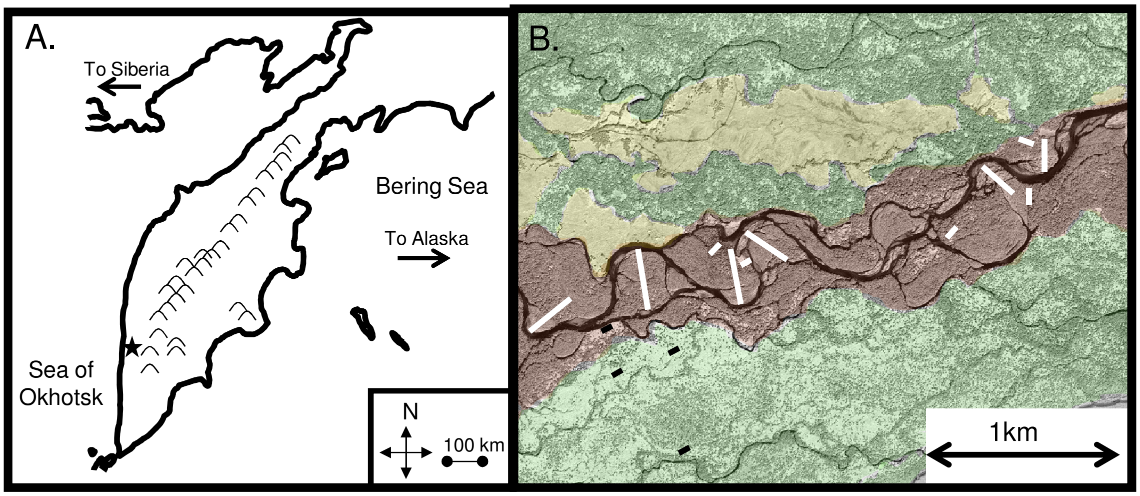

Figure 1. Map A: the Kamchatka Peninsula in the Russian far-east. The star shows the location of the Kol River. Map B: Satellite imagery from of the lower Kol floodplain in the region of our camp. The red shaded region shows the active floodplain which contains succession stages 0-IV. The green shading shows succession stage V in the passive floodplain. The yellow shading shows the grass meadows in the passive floodplain. The white lines show the study transects in the active floodplain. The black bars show the study transects in the passive floodplain. The original imagery before modification (lines and shading) was from the QuickBird satellitte and was provided by DigitalGlobe Inc. in 2004. We consider the active floodplain to be the area bounded by the main and secondary channels. The passive floodplain is the area outside of these channels and extends beyond the boundaries of this image to the floodplain margin. The ancient floodplain terrace is not shown in this image.

The Kol has runs of all six species of Pacific salmon as well as steelhead (*Oncorhynchus mykiss*), dolly-varden (*Salvelinus malma*), white spotted char (*Salvelinus kisutch*), spined sticklebacks (*Gasterosteus aculeatus*) and Pacific lamprey *(Lethenteron japonicum)*. In terms of biomass, Pink-salmon (*Oncorhynchus gorbuscha)* are by far the dominant fish species in this river with up to five-million adults return to spawn on even years. Odd year runs are approximately 10% of even years due to density dependent population processes occurring in the ocean (Quinn 2005). Given that the average mass of pink salmon is approximately 1.77 kg (SaRON unpublished data) and these fish are approximately 3.04% nitrogen and 0.36% phosphorus by body weight (Larkin and Slaney 1997) up to 270,000 kg of nitrogen and 31,500 kg of phosphorus are imported by spawning salmon on even years.

The coastal plain of south-western Kamchatka has a cold, wet, sub-oceanic (Krestov 2003) climate. The mean annual temperature of the coastal plain in this region is -0.9 °C and the mean temperatures of the coldest and warmest months are -14.9 and 12.2 °C respectively. The total frost-free period is 92 days (Sokolov 1974), and annual precipitation is approximately 789 mm. (Krestov 2003).

Soils outside the floodplain are Andisols and Histosols whereas floodplain soils are alluvial Entisols. Floodplain soils consisted of layers of sand and silt, and occaisionally layers of buried organic matter overlying gravel/cobble deposits.

Boreal and arctic vegetation communities of Kamchatka are generally species poor, particularly for trees (Grishin 1995). The majority of land-area outside the Kol floodplain is tundra, dominated by sedges (*Carex sp.*), ericaceous shrubs (*Vaccinium sp.* and *Empetrum sp.*), cloudberry (*Rubus chamaemorus*) and other species. Birch *(Betula ermanii)* forests with understories of tall-forbs (*Filipendula camtschatica, Senecio cannibifolius, Angelica ursina*), grasses and *Vaccinium sp.* occur on hills within the tundra landscape with better drainage. Floodplains are dominated by Salicaceaes trees including willows (*Salix sp. and Chosenia arbutifolia*) and cottonwoods (*Populus suaveolens*), as well as alder trees (*Alnus hirsuta*). In addition, floodplains contain meadows of grasses and tall (>3m) forbs (*Filipendula camtschatica*, *Senecio cannibifolius*, and *Urtica diocia*) (Krestov 2003). Known locally as “shellamanik,” these tall forb meadows are unique to the northeast Asia, and when growing in floodplains have some of the highest phytomass accumulation rates in the world (Walter 1981).

We used the term “active floodplain” to define the region of the floodplain bounded by the primary and secondary channels (see Figure 1). Active floodplain sites commonly received overland flows during annual flooding and erosion rates were sufficiently high such that the forests were usually less than 100 years old. This contrasts with the “passive floodplain” which we considered to be the region between the active channels and the modern floodplain margin. Passive floodplain forests were typically between 100 and hundreds of years old, and generally did not have annual overland flooding, but did flood during the higher flows. The passive floodplain contained numerous springbrooks and tertiary channels. We used the term “modern floodplain” to include both the active and passive floodplain regions. There was also an “ancient floodplain terrace” adjacent to the northern boundary of the modern floodplain. Considering that the ancient floodplain has converted into a tundra-heath community and there were no remnants of early succession species, this region was likely on the order of thousands of years old. There were no flowing channels, springbrooks or evidence of flooding in recent times in the ancient floodplain, but the abundance of swales and a tundra wall at its margin indicated that this region was once a floodplain of the Kol River.

Methods

Study site selection

Alluvial bars form as floodwaters deposit sediments along the inside margins of river-bends within the active zone of the floodplain. Thus an observer travelling perpendicularly away from river’s edge starts at the beginning of succession and walks into a series of progressively older forest patches, unless the chronosequence has been altered by channel avulsion. We selected six transects (shown in Figure 1), each beginning on an alluvial deposit occurring at the inside of a river bend. Preference was given to sites that were proximate to our camp and were actively growing (i.e., young forest stands adjacent to the river channel). Transects continued until they left the active floodplain, or passed into a distinctly younger succession stage. Each transect was approximately 300m long. Even-aged forest stands were then chosen as localized sites for detailed sampling along each study transect. Because trees colonized on bare alluvium at the beginning of succession, age of the oldest trees defined succession age. In total twenty-nine even-aged sampling sites were established within the six transects.

Our initial measurements revealed that trees eventually senesced, leaving fields of tall forbs in later succession. However, only one site within the active floodplain was sufficiently old enough to reach this succession stage in the vicinity of our transects. Therefore four additional 50 m transects within the passive floodplain were chosen as representatives of this stage, which we will refer to herein as stage V. These sites could not be aged because only rotting, senescent trees were present in these fields of tall forbs. Additionally, we observed that regions of the passive floodplain contained grass meadow communities that were nearly devoid of tree species or decomposing wood, indicating that this tall forb meadow succession stage is not a terminal climax; however we only modeled succession through stage V.

Vegetation and landscape measurements

Elevation (relative to the channel at base flow) and soil depth were measured every five meters along each of the six main study transects with a surveyor's sighting level/rod and a soil probe that measured soil depth up to 80 cm. These variables were also measured at points of significant topographic change.

Tree diameter and density by species was measured every 5 to 15 m (to avoid sampling the same trees repeatedly) on the six main study transects. Tree data was collected in 5x2 m belt transects in early succession pole-stands or using the point-centered quarter method (Cottam and Curtis 1956) in canopy tree stands. Density was determined as trees ha^{-1}.Absolute coverage was calculated as m^2 of wood ha^{-1} at breast-height using the tree density and diameter measurements. Frequency of occurrence by species was calculated as the percentage of sampling points where each species occurred. For each species relative density, relative cover and relative frequency were calculated as the percent contribution that each tree taxa made to the total value for these variables. Finally, importance value for each species was calculated by summing relative density, relative coverage and relative frequency. Only one species of willow tree was recognized and quantified in the initial three of the six study area transects, but we later realized two species were actually present. Therefore only half of the sites were used for data analysis that distinguished between these species, whereas data from all transects were used when modeling total *Salix* variables.

Canopy height was also determined every 10 m along the six main transects using a surveyors pole in young tree stands and by triangulation with a clinometer in older forest stands. Percent understorey cover was estimated visually in 5x2 m belt transects every 10 m along the main sampling transects.

The approximate age of each distinct forest stand was determined by counting tree rings from three or more of the largest trees (although only 2 trees were used at one site). Trees were cut down near the base in young pole-stands, whereas older trees were cored at waist height. Four years were added to the age of cored trees to account for the approximate time time that it takes trees to reach waist height. Stand age estimates were rough and become progressively less accurate the older sites became because there is a window in time (about a decade) during which trees colonize at the onset of succession and older sites were amalgamations of similarly aged forest stands.

Soil measurements

Soil samples were collected during August 2005 at each of the twenty-three even aged forest sites that were greather than nine years old. Five points were randomly chosen along 50 m transects within these sites and the litter layer (which we define as visually identifiable plant detritus on the soil surface) was then excavated within 100 cm^2 frame at each point. A mineral soil sample (which we define as beneath the litter layer and is a mixture of mineral sediments, humus and other organic matter) was then extracted using a bulk density corer (10 cm long by 5 cm diameter). In cases where the soil core sampler was obstructed by large plant roots the soil sample was taken at an adjacent spot without large roots. All five litter layer and mineral soil samples were then amalgamated to make one litter layer and one mineral soil sample per even-aged forest stand.

During August 2006 mineral soil was collected by excavating all soil within a 26 cm diameter circular frame to 10 cm depth on the six youngest gravel bars, because soils were too coarse to use the corer. Litter samples were not collected on new gravel bars because they were largely absent from these sites. The soil from three randomly chosen holes was amalgamated to make one sample for each of the six gravel bar sites. The volume of each hole was then determined by lining the holes with plastic and filling them with measured volumes of water.

Excavated soils were stored in a refrigerator for up to two days and then dried at 70°C for litter layer samples and at 46°C for mineral soils. The coarse and fine fractions of mineral soils were then separated using a 2 mm sieve. A subsample (with root hairs extracted) was then taken from the fine fraction and then pulverized to a fine powder with a mortar and pestle. Approximately 50 mg of this fine fraction was analyzed for total persulfate nitrogen according to Raveh and Avnimelech (1979). The total quantity of nitrogen (kg-N ha^{-1} to 10 cm depth) in the soil was then calculated by multiplying the nitrogen concentration of the soil by the mass of fine fraction per hectare.

Litter samples were ground to a powder using a hand mill and then subsampled. This subsampled powder was re-dried and then ground further in a spex mill. The resultant powder was analyzed for total nitrogen using a Fisons NA1500 elemental analyzer. Total litter-N ha^{-1} was determined by multiplying the mass of the litter layer per hectare by the concentration of nitrogen in the litter.

Salmon carcass measurements

We quantified terrestrially deposited carcasses approximately two weeks after fall flooding washed carcasses into the riparia. All carcasses were counted within 5 m of either side of each of the six main transects. Because the water level fluctuates on the earliest succession stages, a carcass was counted as terrestrial if it was amongst any vegetation. Total carcass mass per site was determined by multiplying the number of distinct carcasses or carcass remnants by the average adult wet mass in the Kol River, 1.77 kg for pink salmon and 3.43 kg for chum salmon (unpublished data). Total nitrogen deposited was estimated by multiplying total carcass biomass by 3.03%, the average % nitrogen content for salmon (Larkin and Slaney 1997). Thirty-percent of this nitrogen was then subtracted to account for losses in the river prior to salmon death (Mathisen et al. 1988). Mean carcass nitrogen deposition rates were calculated for each succession stage as defined in the succession model (presented in the results succession). Succession stage for each site was based on the age of each site as defined in the model, with the exception that one site that was 9 years old was considered stage I because more than half of the site was covered with a dense willow stand.

Foliar nitrogen concentrations

Foliage was collected during August 2006 at all study sites and along large transect that spanned the entire floodplain and was oriented perpendicularly to the river. Where present, foliage of two willows (*Salix*) species, alder (*Alnus*), and the forbs *Filipendula camtschatica*, and nettle (*Urtica diocia*) were collected from fully-developed leaves from the tops of the plants at our regular study transect as well as approximately every 200 m and 0, 10 and 50 m from every flowing channel along the large transect. Samples of *Carex*, grass and *Vaccinium* were also taken along the large transect. Leaves from three to five distinct plants were amalgamated to make one sample per site. The samples were dried at 60 to 80°C until brittle and then ground in a coffee grinder. This homogenate was then ground further in a spex-mill and re-dried. C:N ratios were determined on subsamples using a micro-Dumas combustion elemental analyzer at The University of Georgia Stable Isotope/Soil Biology Laboratory.

Statistical analysis

Vegetation and soil variables were regressed against succession age using the ordinary least squares algotithm. Tree density data was tested for conformance to mechanistic stand thinning models (Karev 2003, Karev 2006) (see Table 1). Absolute tree coverage, canopy height, understory coverage, soil depth, litter layer mass, and soil total nitrogen are all attributes of successional growth, therefore they were tested for conformance to the growth models reviewed by Fekeldulegn et al. (1999). All variables were also tested for conformance to the simpler empirical models available in SPSS. All statistical analyses were conducted using “SPSS 15.0” and “Graphpad Prism 5” computer programs.

Succession models were selected in favor of the highest R^2 values, however models were rejected if 0 was within the 95% confidence intervals of non-intercept parameters. Models were

Empirical models		Mechanistic models		Mechanistic models	
Model	**Equation**	**Tree density**[1]	**Equation**	**Growth**[2]	
Linear	$Y=b_0+b_1*t$	Voropanov	$N_t=B/(t^2)$	Chapmann Richards	$Y=B_0*(1-B_1*exp(-B_2*t)^{(1/(1-B3))}$
Logarithmic	$Y=b_0+b_1*ln(t)$	Khilmi	$N_t=N_0*exp(-A*(1-exp(-C*t))$	Richards	$Y=B0/(1+B_1*exp(-B2*X))^{(1/B3)}$
Inverse	$Y=b_0+b_1/t$	Power	$N_t=C*t^{(-K)}$	Von Bertalanffy	$Y=(B_0^{(1-B3)}-B_1*exp(-B_2*t))^{(1/1-B3)}$
Quadratic	$Y=b_0+b_1*t+b_2*t^2$	Kayanus	$N_t=(A+B*t)/(t^2)$	Weibull	$Y=B_0-B_1*exp(-B_2*t^{B3})$
Cubic	$Y=b_0+b_1*t+b_2*t^2+b_3*t^3$			Negative exponential	$Y=B_0*(1-exp^{(-B2*t)})$
Power	$Y=b_0*t^{b1}$			Monomolecular	$Y=B_0*(1-B_1*exp^{(-B2*t)})$
Compound	$Y=b_0*b_1^t$			Mitcherlich	$Y=(B_0-B_1*B_2^t)$
S-curve	$Y=exp(b0+b/t)$			Gompertz	$Y=B_0*exp(-B_1*exp(-B_2*t))$
logistic	$Y=1/(1/u+(b_0*(b_1^t))$			Logistic model	$Y=B_0/(1+B_1*exp(-B_2*t))$
growth	$Y=exp(b_0+b_1*t)$				
exponential	$Y=b_0*exp(b_1*t)$				

[1] after Karev 2003 and Karev 2006

[2] after Fekeldulegn et al. 1999

Table 1. Empirical and mechanistic models used to fit succession data

also rejected if visual inspection revealed unrealistic or exceptionally poor fits. In cases where two or more models produced similar fits, the better model was chosen using Akaike Information Criteria in the Graphpad Prism 5 program.

Significant differences in mean foliar C:N ratios among plant species were determined using the non-parametric Kruskal-Wallis test and Dunn post-hoc in the Graphpad Prism 5 program.

Results

Fits of the vegetation and soil variables to succession models

The succession models explained more than half of the variation in 22 of the 43 vegetation and soil variables tested (Table 2). In general, variation in mineral soil variables was explained very well by the succession models, whereas the litter layer variables were poorly explained. Variables associated with the most abundant trees, *Salix A* and *Salix B* tended to be better explained by the models than the less abundant *Chosenia arbutifolia.* Also, the coverage of the dominant understory species, *Filipendula camtschatica* was better explained by the models than the coverage of less abundant species.

Soil pedogenesis

Fine sediment (sand and smaller) accumulations averaged only 3 cm deep during initial tree colonization (sites less than five years), however soil depth increased rapidly (approximately 20 to 40 cm) during the first thirty years of succession (Figure 2) and by eighty years fine sediment depth typically ranged from 60 to >80 cm deep. Bulk density was highly related to succession age ($R^2 = 0.92$). Soils at the onset of succession had very high bulk density ranging from 1.9-2.2 g cm^{-3} and this declined precipitously to approximately 0.6 g cm^{-3} by thirty years. From thirty to eighty years bulk density declined more slowly and leveled off at approximately 0.5 g cm^{-3}.

Recently deposited alluvial bars were largely devoid of organic matter and therefore litter layer samples were not collected at sites less than five years old. Litter layer mass increased from approximately 20 t ha^{-1} at ten years to more than 40 t ha^{-1} at approximately thirty years (Figure 2). By eighty years litter accumulations typically exceeded 60 t ha^{-1}. However, there was very large variance from our model ($R^2 = 0.11$) and sites ranged from less than 10 t ha^{-1} to more than 80 t ha^{-1}. The tall forb meadows (i.e, the oldest sites, shown as stage V below) in the passive floodplain had more massive litter layers, with three of the four sites containing approximately 100 t ha^{-1} with the fourth site ca. 180 t ha^{-1}.

Table 2. Summary of mathematical succession model fits to soil and vegetation variables. Parameter standard errors (SE) listed in order of their sequence in the models.

Succession Parameter	**Model type**	**Equation**	**Applicable Age Range (years)**	**1st Param. SE**	**2nd Param. SE**	**3rd Param. SE**	**R^2**
Tree Density(trees ha^{-1})							
All trees	exponential	density=2.25*10^5*(exp(-0.102*age))	8 to 80	5.60*10^4	2.00*10^{-2}		0.81
Salix A.	exponential	density=1.23*10^5*(exp(-0.105*age))	8 to 80	1.28*10^4	8.67*10^{-3}		0.98
Salix B.	exponential	density=3.49*10^4*(exp(-0.0687*age))	8 to 80	1.02*10^4	1.99*10^{-2}		0.76
Alnus	no significant fit						---
Chosenia	s-curve	density=exp(2.64+57.6/age)	8 to 80	2.33	18.9		0.62
Tree Relative Density(%)							
Salix A	linear	rel density=-0.803*age+60.4	8 to 80	0.193	7.93		0.63
Salix B	linear	rel density=-0.422*age+24.0	8 to 80	0.134	5.5		0.50
Alnus	s-curve	rel density=exp(4.31+-52.9/age)	8 to 80	0.358	18.4		0.55
Chosenia	no significant fit						---
Tree Absolute Cover(m^2 ha^{-1})							
All trees	growth	abs. cov.=exp(2.80+0.0128*age)	8 to 80	0.18	3.42*10^{-3}		0.40
Salix A	linear	abs. cov.=-0.123*age+9.98	8 to 80	0.0545	2.24		0.34
Salix B	growth	abs. cov.=exp(1.42+0.0279*age)	8 to 80	0.471	7.28*10^{-3}		0.61
Alnus	s-curve	abs. cov=exp(3.26+-66.6/age)	8 to 80	0.404	22.5		0.60
Chosenia	no significant fit						---
Trees Relative Cover(%)							
Salix A	exponential	rel. cov.=91.3*(exp(-0.0385*age))	8 to 80	22.5	0.0126		0.68
Salix B	exponential	rel. cov.=21.0*(exp(0.0152*age))	8 to 80	4.65	4.03*10^{-3}		0.57
Alnus	s-curve	rel. cov.=exp(4.10+-49.5/age)	8 to 80	0.391	19.6		0.49
Chosenia	no significant fit						---
Trees Absolute Frequency(%)							
Salix A	linear	abs. freq.=-1.25*age+101	8 to 80	0.379	15.5		0.52
Salix B	exponential	abs. freq.=54.5*(exp(6.19*10^{-3}*age))	8 to 80	5.3	2.08*10^{-3}		0.44
Alnus	linear	abs. freq.=0.990*age+7.20	8 to 80	0.275	11.2		0.39
Chosenia	s-curve	abs. freq.=exp(2.14+17.7/age)	8 to 80	0.563	5.87		0.28

Table 2. Continued

Succession Parameter	**Model type**	**Equation**	**Applicable Age Range (years)**	**1st Param. SE**	**2nd Param. SE**	**3rd Param. SE**	**R^2**
Trees Relative Frequency(%)							
Salix A	linear	rel. freq.=-0.643*age+51.8	8 to 80	0.209	8.59		0.49
Salix B	compound	rel. freq.=30.8*(1.00^{age})	8 to 80	4.82	3.61*10^{-3}		0.05
Alnus	linear	rel. freq.=0.585*age+3.23	8 to 80	0.124	5.04		0.53
Chosenia	s-curve	rel. freq.=exp(1.69+15.3/age)	8 to 80	0.507	5.59		0.23
Tree Importance Value							
Salix A	exponential	imp. val.=262*(exp(-0.0341*age))	8 to 80	69.3	0.0115		0.66
Salix B	exponential	imp. val.=76.4*(exp(9.65*10^{-3}*age)	8 to 80	13.3	3.49*10^{-3}		0.40
Alnus	s-curve	imp. val. =exp(5.33+-45.3/age)	8 to 80	0.271	13		0.59
Chosenia	compound	imp. val. =57.1*(0.984^{age})	8 to 80	26.3	0.0157		0.09
Canopy Height(m)	gompertz	can. Height=11.8*exp(-3.77*exp(-0.109*age))	8 to 80	0.676	1.62	0.0306	0.80
%Understory Coverage							
Total	logarithmic	und. cov.=13.9+(41.7*ln(age))	8 to 80	21.7	14.8		0.28
Filipendula camtschatica	s-curve	und. cov.=exp(5.14+-90.6/age)	8 to 80	0.283	17.1		0.85
Urtica diocia	logarithmic	und.cov.=-22.3+(27.3*ln(age))	8 to 80	13.6	9.24		0.3
Grass	linear	und. cov.=-0.265*age+22.3	8 to 80	0.0961	3.91		0.28
Soil Variables							
Mineral soil bulk density (g cm^{-3})	inverse	und. cov.=0.373+6.68/age	3 to 80	0.0428	0.355		0.93
Mineral soil depth (cm)	linear	depth=0.693*age+10.4	4 to 80	0.133	5.09		0.54
Mineral soil total N (kg ha^{-1} to 10cm)	gompertz	min. N=1918*exp(-3.29*exp(-0.0994*age))	3 to 80	81.7	0.6	0.0148	0.92
Mineral Soil total N (mg g^{-1} to 10cm)	gompertz	min. N=4.08*exp(-3.58*exp(-0.0882*age))	3 to 80	0.311	1.11	0.0214	0.81
Mass litter layer (Tonnes ha^{-1})	compound	min. N=33.6*(1.01^{age})	3 to 80	7.45	4.70*10^{-3}		0.11
Litter layer total N (kg-N ha^{-1})	inverse	LL N=824-5460/age	8 to 80	10.3	2000		0.27
Total mineral soil + litter layer N (kg-N ha^{-1})	gompertz	TN=2517*exp(-4.37*exp(-0.14*age))	3 to 80	113	1.18	0.0234	0.9
Elevation	compound	elevation=0.216*1.02^{age}	4 to 80	0.0971	9.60*10^{-3}		0.12
Min. soil total N (mg g^{-1}) vs. Bulk density (g cm^{-3})	S-curve	TN=exp(-1.46+(1.30/age))	n/a	0.119	0.073		0.92

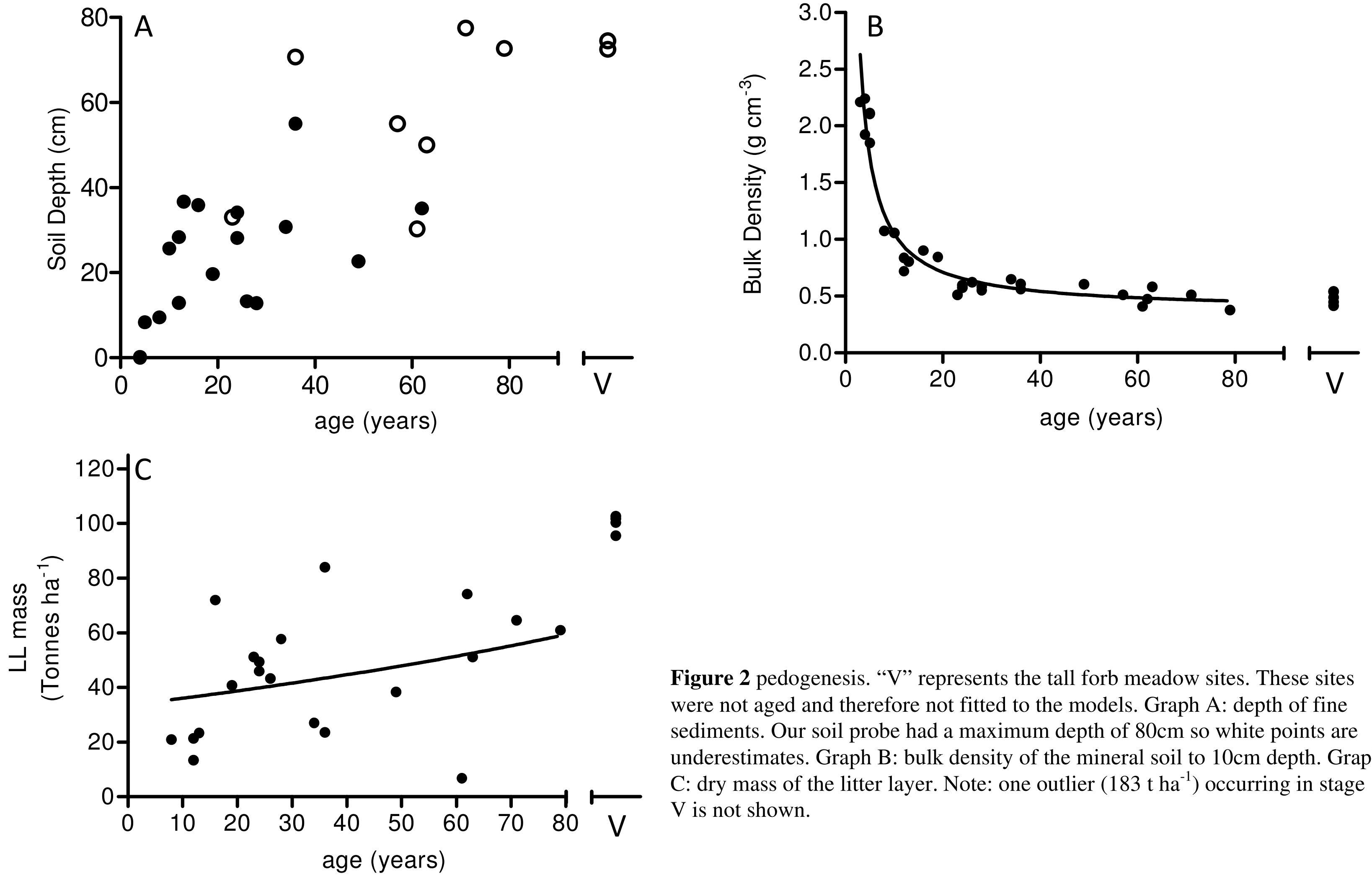

Figure 2 pedogenesis. "V" represents the tall forb meadow sites. These sites were not aged and therefore not fitted to the models. Graph A: depth of fine sediments. Our soil probe had a maximum depth of 80cm so white points are underestimates. Graph B: bulk density of the mineral soil to 10cm depth. Graph C: dry mass of the litter layer. Note: one outlier (183 t ha^{-1}) occurring in stage V is not shown.

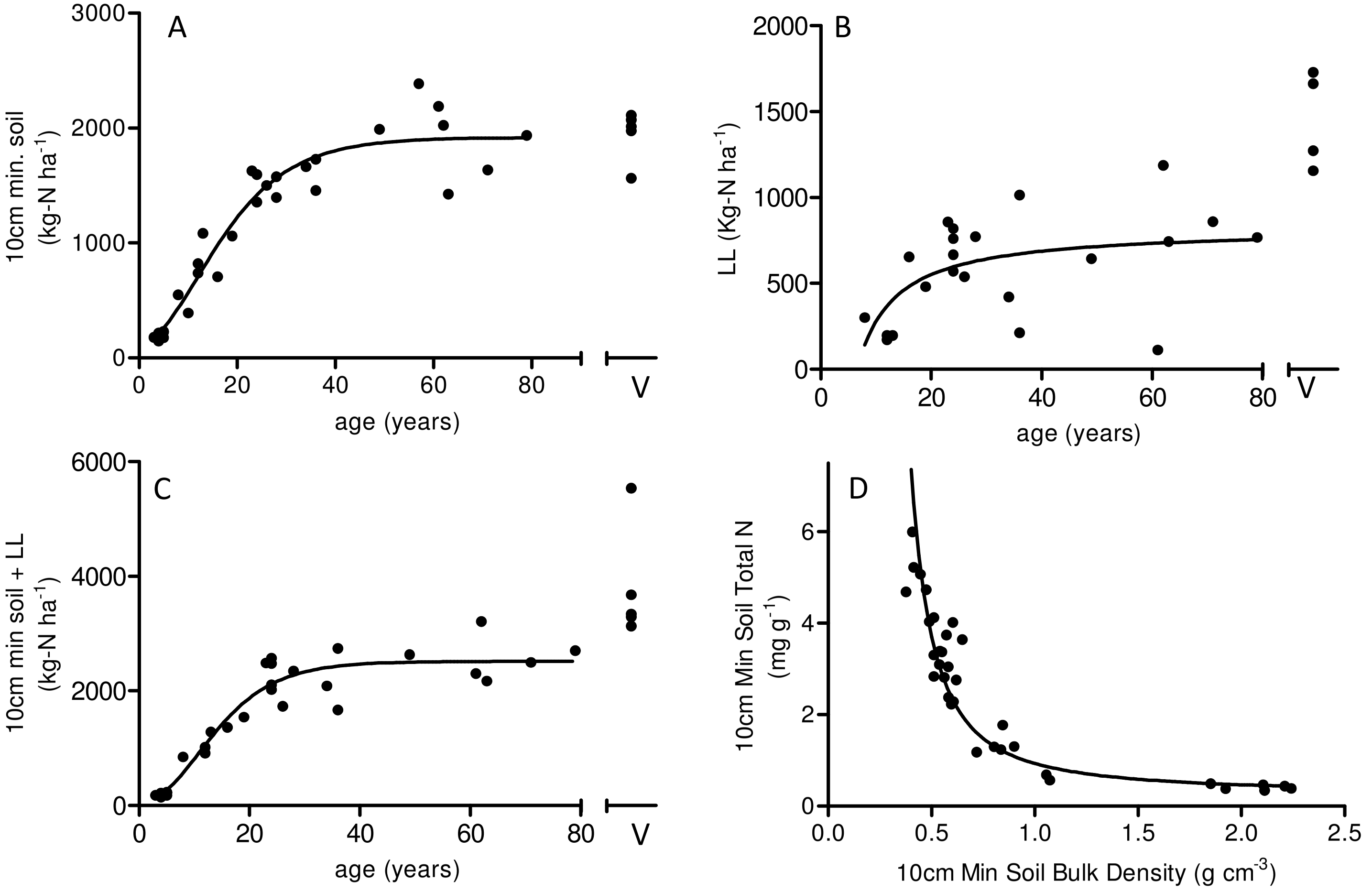

Figure 3. Soil nitrogen accumulation during succession. “V” represents the tall forb meadow community after most trees senescence. These sites were not aged and therefore not fitted to the models. Graph A: the accumulation of mineral soil nitrogen. Graph B: the accumulation of litter layer nitrogen Note: one outlier in stage V (3,423 kg-N ha^{-1}) is not shown. Graph C: the accumulation of total (10cm mineral soil+ litter layer) nitrogen, and graph D: the relationship between mineral soil nitrogen concentration and soil bulk density

Soils on the youngest alluvial bars had very low total nitrogen content. Mean nitrogen content of the top 10 cm of mineral soil was only 195 kg-N ha^{-1} from three to five years (Figure 3) and sites deviated very little from this mean (range: 145-232 kg-N ha^{-1}). Total soil nitrogen (top ten centimeters of mineral soil plus the litter layer) accumulated rapidly for the first thirty years of succession reaching 2,300 kg-N ha^{-1}. After this point, total nitrogen increased only slightly over the next fifty years, gaining an additional 200 kg-N ha^{-1}. The mineral soil accounted for approximately 70% to 80% of the total soil nitrogen between thirty and eighty years.

Whereas site age models accounted for most of the variation in the mineral soil total nitrogen (R^2=0.92) and total soil nitrogen variables (R^2=0.9), litter layer total nitrogen was not as well explained by our succession age model (R^2=0.27). While mineral soil total nitrogen content in the stage V passive floodplain sites was about equal to the oldest sites in the active floodplain, litter layer total nitrogen was elevated in the passive floodplain with respect to any of the younger sites. Figure 3 demonstrates that the total nitrogen concentration of the <2 mm fraction of the top 10 cm of mineral soil (expressed in mg g^{-1}) was well predicted by the bulk density of the soil (R^2 = 0.92). Sites with high bulk density contained very little nitrogen.

Vegetation chronosequence

Four tree species commonly occurred on the floodplain transects: two unknown species of willows (*Salix A* and *Salix B*) as well as a willow-like species (*Chosenia arbutifolia*) and alder (*Alnus hirsuta).* Between nine and twenty years after colonization, willows formed thick pole-stands, and average density was 6.9 trees m^{-2} at these sites. All species (Figure 4) were most dense during the first twenty years of succession indicating that there was no substantial recruitment during later succession. *Salix A* was the most abundant species at the beginning of succession but it was the first species to senesce, and by sixty years it rarely occurred. *Salix B* and then alders were the second and third most abundant species at the onset of succession, and *Salix B* became the dominant species after *Salix A* senesced. *Chosenia* density was highly variable and was only abundant at rocky sites on the elevated, drier portions of gravel bars.

We used absolute coverage (m^2 ha^{-1}of wood at breast height) (Figure 5) as an easily-measured surrogate for tree biomass. Mean total coverage was approximately 18 m^2 ha^{-1} on young alluvial bars (9 to 20 years) and coverage increased to 36 m^2 ha^{-1} at the mature forest sites (approximately 50 to 80 years). Coverage did not approach an asymptote in Figure 5, indicating that tree biomass continued to increase beyond our oldest active-floodplain sites. Relative coverage by species followed a similar pattern as tree density. *Salix A* had the highest coverage at the onset of succession, and comprised 60% of the total coverage, but its coverage was near 0 after about 50 years. Both *Salix B* and alder coverage increased across succession, while *Chosenia* showed no significant relationship with stand age. With respect to both density and coverage, *Salix B* and then alder were the dominant tree species in later succession (40 to 80 years).

Total understory coverage (Figure 6) was highly variable (8-77%) once tree colonization was nearly complete (ages 9 to 20 years). Three different vegetation types dominated the understory. Grasses were the most abundant single taxanomic group in the understory for the first thirty years of succession, although when added together, a diversity of forbs contributed as much as the grasses to total coverage. After thirty years, the understory community was dominated by stinging nettles *(Urtica diocia)* and after fifty years it was dominated by *Filipendula camtschatica. Filipendula* is a unique, broad-leaved, hollow-stemmed forb of the region that is notable for its extremely large size, high density, and prolific growth rates (see the last photograph in Figure 5). Occasional *Filipendula* plants were observed colonizing the initial succession stages, but this plant was sparsely distributed amongst dense young-tree stands. We observed that *Filipendula* spread by seeding and sending up new shoots from large rhizomes. *Filipendula* proliferated as succession proceeded, and between fifty and eighty years *Filipendula* covered on average about 45% of the land area in the understory. Once most of the trees had senesced in the passive floodplain, *Filipendula* coverage ranged from 63 to 88% of the land area, and the remaining area was largely covered by nettles (5 to 11%). *Filipendula* stands were often contiguous for several square kilometers in the passive floodplain (Figure 1).

All vegetation species occurring in the modern floodplain had high foliar nitrogen concentrations, with molar C:N ratios ranging from 12 to 27 (Table 3). The tree willows (*Salix A, Salix B,* and *Chosenia*) as well as the tall forb *Fillipendula camtschatica* all had very similar mean foliar C:N ratios ranging from 21to 22, whereas *Alnus* foliage was more nitrogen-rich (C:N 17) than the other trees. Foliage from *Urtica diocia* (C:N 12) was more nitrogen rich than all other species.

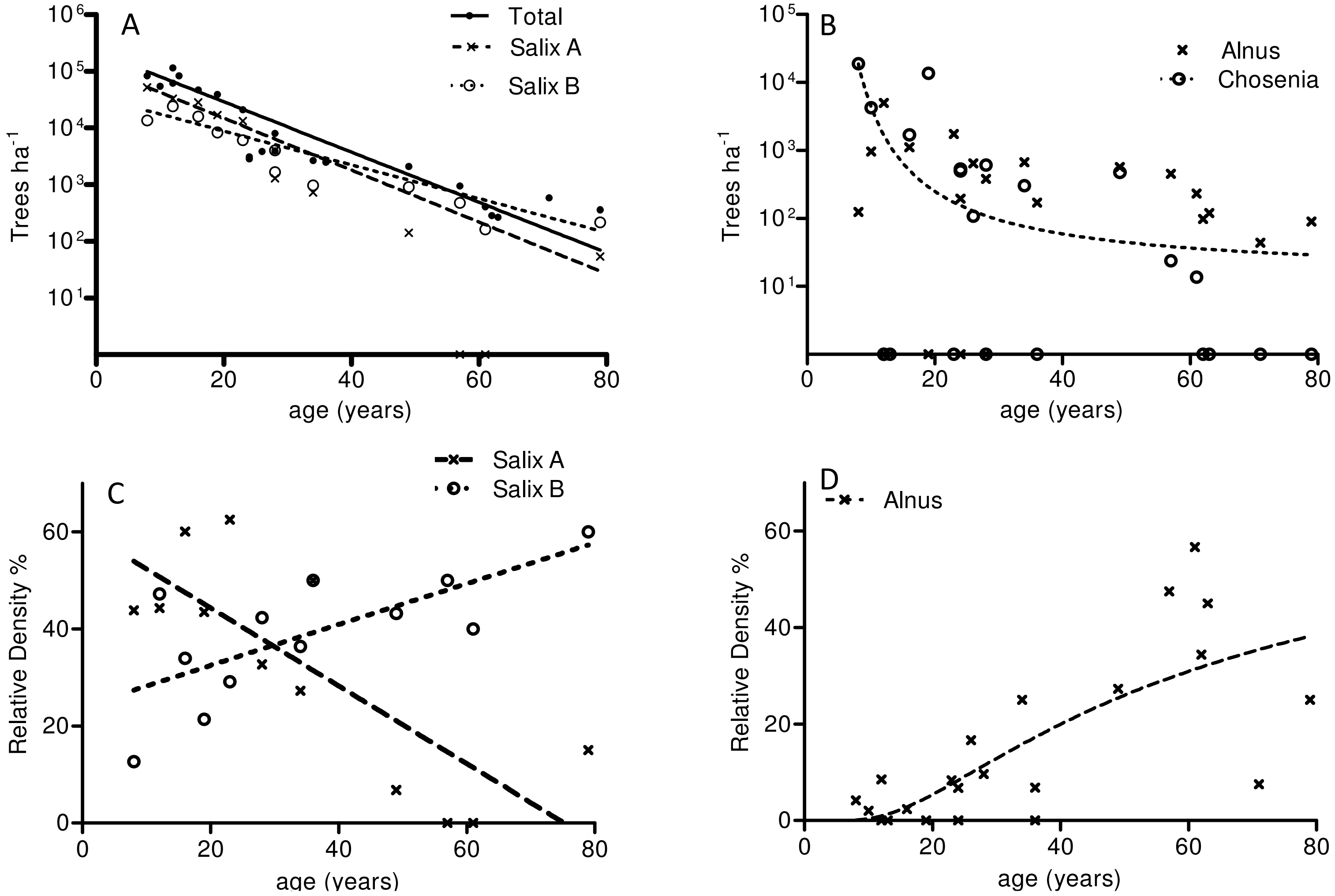

Figure 4. Changes in tree density during succession. Graphs A and B: absolute tree density. Graphs C an D: relative tree density.

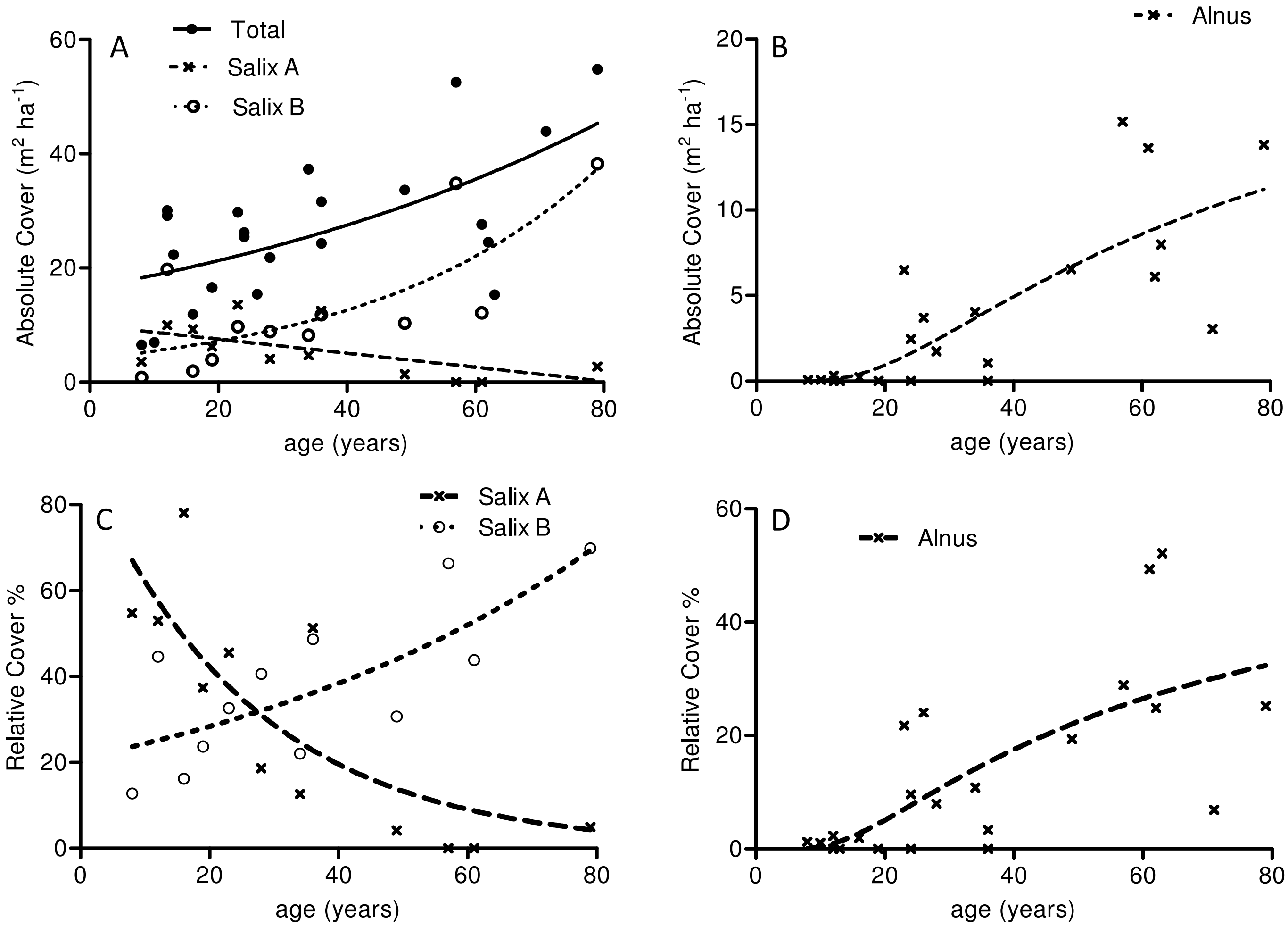

Figure 5. Changes in tree coverage during succession. Graphs A and B: absolute coverage at breast height. Graphs C and D: relative coverage

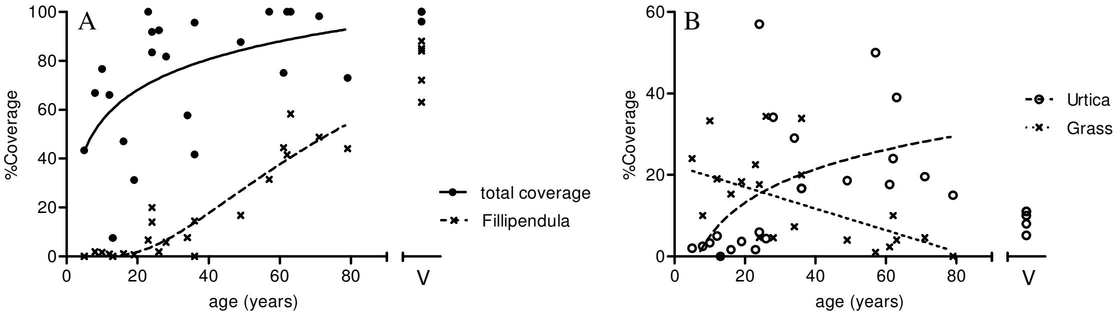

Figure 6. Changes in % coverage of understory species during succession

	mean	95%CI	N	significantly different than:
Alnus	16.9	16.1-17.7	30	*Salix B, Filc, grass*
Chosenia	19.9	17.9-21.8	20	*Urtica*
Salix A	20.8	18.9-22.7	23	*Urtica*
Salix B	22.1	20.7-23.4	48	*Alnus, Urtica*
Filipendula	21.2	19.7-22.8	48	*Alnus, Urtica*
Urtica	12.4	10.4-14.5	32	*Chos, SalixA, Salix B, Vacc, Care, grass*
Vaccinium	25.7	22.8-28.5	3	*Urtica*
Carex	25.0	11.9-38.1	3	*Urtica*
Grass	27.4	22.2-32.6	5	*Alnus, Urtica*

Significant differences detected using Kruskal Wallis test and Dunn post-hoc.

Table 3: Mean foliar C:N of dominant taxa in the modern floodplain. Filc-*Filipendula camtshatica.*

Conceptual model of floodplain succession

Based on the mathematical models of vegetation and soil variables we constructed a conceptual model of floodplain succession, as presented in Figure 7. Although succession is a continuous process, we similified the conceptualization of succession by defining six stages named for the dominant vegetation types.

Stage 0, "the bare alluvial-bar stage**"** (0 to 10 years): Newly deposited alluvial bars were composed primarily of cobble and gravel with sand filling the interstitial spaces of this matrix. In terms of cross-sectional elevation, alluvial bars are wedge-shaped, with a sloping shoreline along the mainchannel and a higher-elevation apex towards the far end of the alluvial bar. Because these alluvial bars were adjacent to the river they flooded extensively during the spring and fall.

Willow and *Chosenia* trees colonized during this stage. *Salix A* was the dominant tree species, followed by *Salix B*. *Chosenia* occurred sporadically, and primarily on the apex of these bars where willows do not grow as well. The time required for trees to fully colonize a site was highly variable, from less than five to more than ten years, and we observed that this is largely dependent on substrate size and flood extent. Fine sediments and total soil nitrogen content accumulated rapidly during this stage.

Stage I, "the alluvial-bar willow/*Chosenia* stage" (10 to 20 years): We considered young alluvial bars to have reached stage I when the majority of young gravel bars was covered in dense willow stands, and this typically took about ten years after initial colonization. Stage I sites typically flooded during highest spring and fall flows and dense tree stands promoted the deposition of fine sediments which accumulated rapidly during this stage. Sediments accumulated most rapidly in lower elevation regions of the bar and the apex was often preserved as a barren patch of xeric, coarse sediments. These coarse sediment patches often had sparse vegetation, but were considered part of the stage I site. Tree density was highest during this stage and the entire alluvial bars were often completely colonized with trees. *Salix A* was the most abundant tree species followed by *Salix B*. Alder trees established as fine sediments accumulated but they grew very slowly among the dense willow stands. Grasses were the dominant understory taxa. The soil litter layer began to accumulate during this stage, and total soil nitrogen accumulated rapidly.

Stage II, "the willow/*Chosenia* canopy stage" (20 to 30 years): *Salix A* and *B* formed a canopy, with *Salix A* being the dominant species. Tree stands thinned rapidly and the understory proliferated during this stage. Grasses were most abundant at the beginning of this stage but were then replaced by forbs, particularly *Urtica diocia*. Some of these stands flooded annually, but flooding became progressively less extensive as site age increased because younger alluvial bars adjacent to this stage buffered these sites from the main-channel, and elevation increased due to accumulating fine sediments. The litter layer continued to deepen and total soil nitrogen continued to accumulate, but then approached an asymptote by the end of this stage.

Stage III, "the willow/alder/*Chosenia* canopy stage" (30 to 50 years): *Salix A*, the dominant tree species until now, began to senesce and *Salix B* became the dominant canopy tree. Also, *Alnus* reached the canopy and grew rapidly. *Filipendula* proliferated and became the dominant understory species by the end of this stage. There was no significant accumulation of total soil nitrogen (to 10cm +litter layer) during this stage.

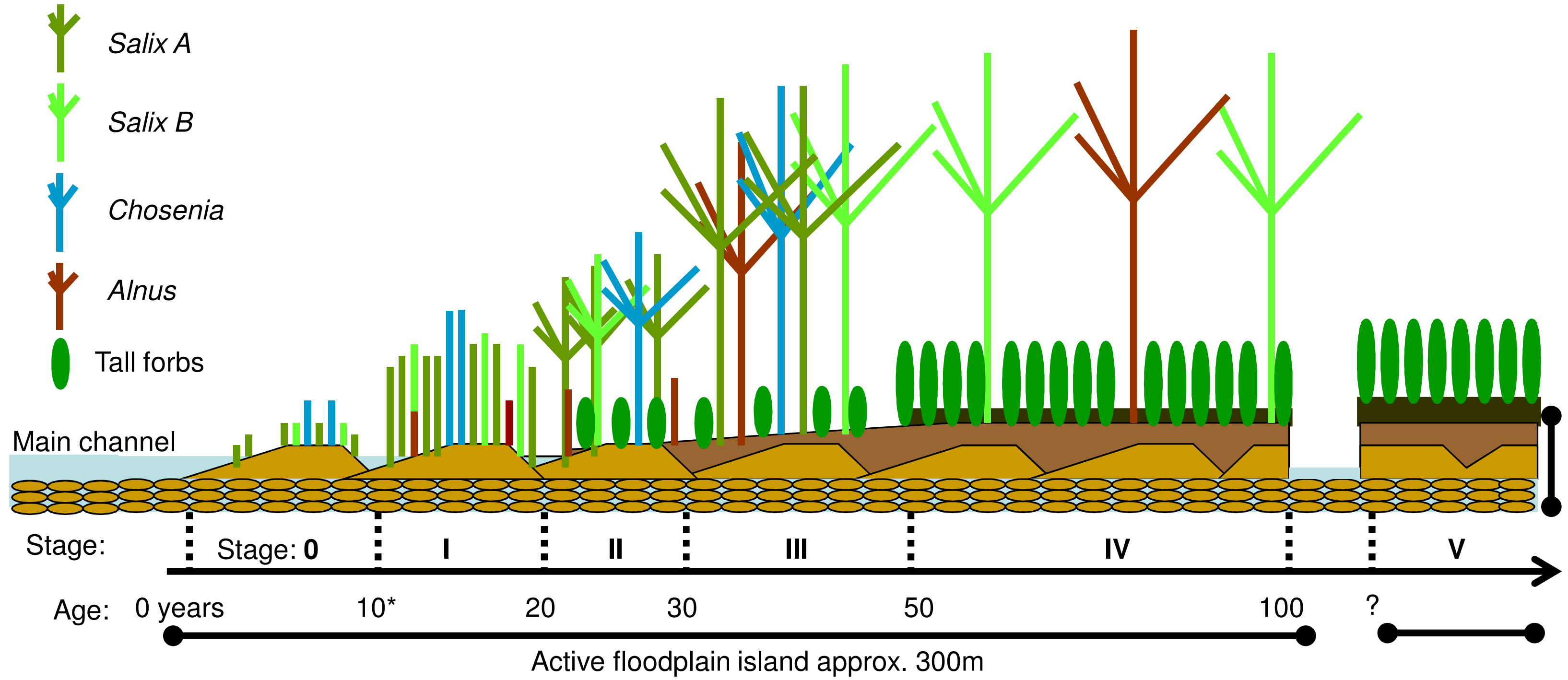

Figure 7. Conceptual model of primary succession in the Kol River floodplain. This model depicts six succession stages, five within the active floodplain and one within the passive floodplain. Stage 0 is “bare alluvial-bar;” Stage I is “alluvial bar willow/*Chosenia*;” Stage II is the “willow/*Chosenia* canopy;” Stage III is “willow/*Chosenia*/alder canopy;” and Stage IV is “declining willow, mature alder canopy;” and Stage V is “tall-forb meadow.” The age ranges for the succession stages are shown on the x-axis. *Note age ranges are approximate and rounded to the nearest decade. For example, colonization time can be highly variable depending on substrate conditions and it may take as little as 5 or nearly 10 years for a stage I willow stand to develop. “?” indicates that only relative age, rather than exact age was determined for stage V.

Stage	Total tree density (trees ha^{-1})	%willow	%alder	%chos.	Total tree cov. (m^{2}ha^{-1})	%willow	%alder	%chos.	Importance value: willow	alder I.V.	chos. I.V.
I	69000	86	2	12	18	86	1	13	241	13	45
	(39000-115000)	(65-100)	(0-9)	(0-35)	(7-29)	(61-100)	(0-2)	(0-39)	(173-300)	(0-36)	(0-120)
II	6900	81	8	11	24	61	13	26	211	38	51
	(2881-21106)	(75-90)	(0-16.7)	(0-17)	(15-30)	(36-78)	(0-24)	(0-33)	(176-245)	(0-64)	(0-92)
III	3840	77	15	9	32	67	8	16	207	49	35
	(2090-8104)	(50-100)	(0-27)	(0-23)	(24-37)	(35-100)	(0-19)	(0-46)	(124-300)	(0-81)	(0-95)
IV	480	63	36	1	36	67	31	2	185	110	5
	(267-952)	(40-93)	(7.5-57)	(0-3.3)	(15.-55)	(44-93)	(7-49)	(0-7)	(126-263)	(37-156)	(0-19)
V	n/a				n/a				n/a		

Stage	Total understory cover %	%grass	%nettle	% filk	Litter layer (kg ha^{-1})	Litter layer (kg-N ha^{-1})	Min. soil bulk density (g cm^{-3})	soil depth (cm)	Min. soil total N (mg g^{-1})	Min. soil total N (kg ha^{-1})	total soil N (min+LL) (kg-N ha^{-1})
0							2.1	3	0.4	195	195
							(1.9-2.2)	(0-8)	(0.3-0.5)	(145-232)	(145-232)
I	49	16	3	1	28700	333	0.9	24	1.1	765	1160
	(8-77)	(0-19)	(0-5)	(0-2)	(12800-52200)	(173-654)	(0.7-1.1)	(10-37)	(0.6-1.8)	(391-1084)	(848-1542)
II	90	17	21	10	47500	569	0.6	24	3.1	1509	2077
	(82-100)	(5-34)	(2-57)	(2-20)	(34600-66400)	(211-857)	(0.5-0.6)	(13-34)	(3.7-2.2)	(1357-1628)	(1668-2485)
III	71	16	20	10	59100	739	0.6	45	3.2	1709	2415
	(42-96)	(4-34)	(17-29)	(0-17)	(20600-67600)	(421-1015)	(0.5-0.6)	(23-71)	(2.3-4.0)	(1456-1988)	(2085-2744)
IV	91	4	28	45	57700	734	0.5	53	4.1	1933	2645
	(73-100)	(0-10)	(15-50)	(32-58)	(44400-84800)	(745-1187)	(0.4-0.6)	(30-78)	(2.4-6.0)	(1427-2386)	(2172-3210)
V	99	0	9	78	84400	1848	0.5	74	4.2	1948	3795
	(96-100)	0	(5-11)	(63-88)	(62200-131400)	(1155-3423)	(0.4-0.5)	(73-75)	(3.1-5.2)	(1563-2112)	(3132-5535)

Table 4. Means and ranges (in parenthesis) of vegetation and soil variables by succession stage. Mineral soil variables apply to ten centimeters depth.

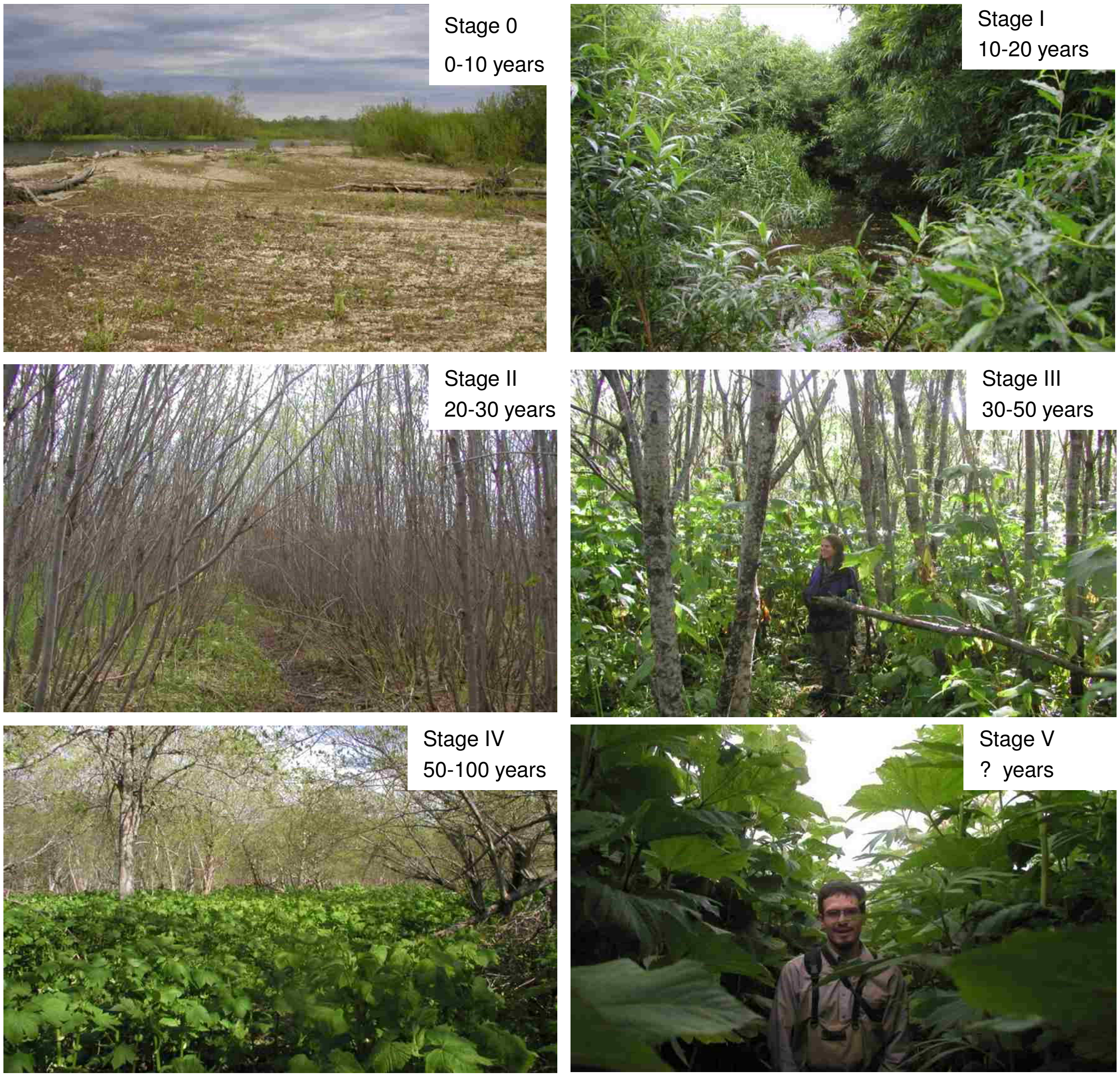

Figure 8. Photographs depicting the six succession stages corresponding to the model presented in Figure 7. *Note age ranges are approximate and rounded to the nearest decade. “?” indicates that only relative age, rather than exact age was determined for stage V.

Stage IV, “the declining willow, mature alder canopy stage” (50 to at least 100 years): this was the oldest stage that commonly occurred in the active floodplain. By this stage *Salix A* and *Chosenia* had senesced and rarely occurred. Large *Salix B* comprised a slightly greater proportion of the total coverage than mature alder and both these species filled the canopy at the beginning of this stage. However, these trees also began to rot and fall over, creating large canopy gaps. Very dense, tall stands of *Filipendula* and nettle proliferated in the gaps. There was no significant accumulation of total soil nitrogen (to 10 cm +litter layer) during this stage.

Stage V, "the tall-forb meadow stage"

Dense stands of *Filipendula* with lesser interspersed nettle dominated the tall-forb stage, and these stands were often continuous for several square kilometers. Mature *Filipendula* stems grew in densities exceeding 12 shoots m^{-2} and grew more than 3 m in height. Tall-forb meadow landscapes appeared as vast fields rather than distinct alluvial bar complexes because they formed from many historical bars and filled river channels, all coalesced by a thick blanket of sand and silts. These tall forbs produced large quantities of litter and a thick humus layer accumulated. Total litter layer nitrogen accumulated between stage IV and V, however total mineral soil nitrogen was roughly the same between these two stages. We are uncertain of the age of these sites because few, rotting *Salix B* and Alders remained. These sites occurred primarily in the passive region of the floodplain because site turnover time was short enough in the active floodplain to prevent this stage from developing.

We have observed that these tall forb meadows eventually transitioned into grass/short forb/woody shrub meadows which occur in the oldest region of the passive floodplain. A heath community, dominated by *Empetrum nigrum* and *Vaccinium sp*. may then replace this grass, but this heath only occurred in an ancient abandoned floodplain region that was adjacent to the modern floodplain. We estimated that the grass meadow community was on the order of hundreds of years old whereas the heath community was likely thousands of years old.

Table 4 summarizes the means and ranges of succession variables for our study sites when grouped by succession stage, and photographs illustrating typical examples of the succession stages 0 through V are shown in Figure 8.

Salmon carcasses

Nitrogen deposition from salmon carcasses was greatest at the "bare alluvial bar" succession stage (Figures 7 and 10). During September of 2006 an average of 25 kg-N ha^{-1} was deposited at these sites, but deposition rates were highly variable, ranging from more than 100 kg-N ha^{-1} to less than 3 kg-N ha^{-1}. Nitrogen inputs to all older succession stages were consistently low either because flood waters did not reach them or because dense vegetation of the earlier succession stages filtered out the carcasses. Although 2006 was predicted to be a high pink salmon year, runs were unusually low for all of western Kamchatka. We have data from several of the same sites collected during the previous high salmon year, 2004. Deposition rates in 2004 were roughly ten to thirty times higher for the youngest two succession stages (stage 0 and I), and similarly low for the older succession stages.

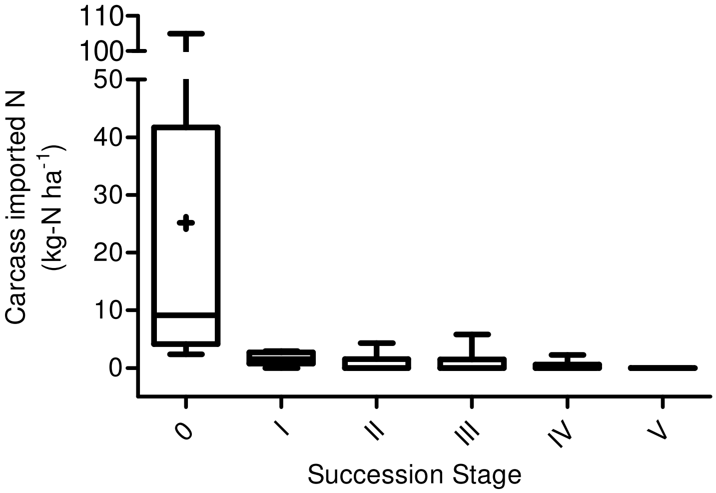

Figure 9. Boxplot depicting nitrogen imported from salmon carcasses by succession stage. Whiskers represent minimum and maximum values. The edges of the box are quartiles and the center bar is the mean. The "+" in stage 0 denotes the actual mean with one outlier included.

Figure 10. Photograph showing salmon carcasses washed up onto a stage 0 alluvial bar. This particular site received very high salmon carcass deposition rates.

Discussion

Succession modeling

We concluded that succession chronosequence concept was a good organizing principle for modeling many of the vegetation community and soil characteristics of the Kol floodplain. At least 50% of the variation in over half of the vegetation and soil variables could be explained by stand age alone (Table 2). In particular, soil variables such as total soil nitrogen and bulk density conformed extremely well to the succession models (R^2>0.90). Relative to the other soil variables, litter layer variables did not conform well to the models and this was likely due to the confounding effects of flooding, as the litter layer was washed away from heavily flooded sites, while sites with lesser flooding had large litter accumulations. With regards to the vegetation, the dominant, ubiquitous floodplain species (*Salix A* and *Salix B* and *Filipendula camtschatica*) tended to conform better to our models than rarer species, probably because rarer species had specific habitat microsite requirements. In particular, variables describing the Asian tree species *Chosenia arbutifolia* consistently showed poor relationship to succession models because they were not ubiquitous and we observed that only colonized the highest points of gravel bars among coarse substratum. *Chosenia's* microsite habitat requirement of coarse alluvia has also been documented Ishikawa (1987) and Ishikawa (1994).

While succession may be relatively predictable in floodplains with anastomosing to meandering channel systems like the Kol, succession was more chaotic in floodplains with braided channels (Nakamura et al. 1997, Gurnell et al. 2001, Shin and Nakamura 2005). Rather than segregating chronologically, pioneer trees (willows, alders and *Populus*) in floodplains with braided channels segregated into discrete spatial patches based on substrate quality and elevation.

Soil-nitrogen accumulation during succession

As in all types of primary succession (Walker and Moral del 2003) soil nitrogen was low at the onset of succession and accumulated over time in the Kol floodplain. We found that new alluvial bars were nitrogen poor, and only contained about 200 kg-N ha^{-1} (to 10 cm) (Figure 3). However, by thirty years soil nitrogen increased more than an order of magnitude to about 2,300 kg-N ha^{-1} (litter layer+10cm mineral soil). During the next fifty years soil nitrogen accumulated much more slowly, eventually leveling off at about 2,500 kg-N ha^{-1}.

In terms of quantity, the Kol's floodplain soils accumulated more nitrogen, more quickly than has been demonstrated in other Pacific-rim floodplain chronosequences. For example, in a floodplain of the Tanana River, Alaska, Walker (1989) found that young alluvial deposits initially contained similar quantities of nitrogen (400 kg-N ha^{-1} to 20 cm) as occurred on the Kol, but between twenty to fifty years mineral soils (to 20 cm) + forest floors on the Tanana contained roughly one-half to two-thirds (between 900 and 1,700 kg-N ha^{-1}) the nitrogen that the Kol's soils contained between twenty and fifty years (about 1,900 to 2,500 kg-N ha^{-1}). Soils in the Tanana floodplain then reached an asymptote at approximately 2,000 kg-N ha^{-1} by 100 years. Luken and Fonda (1983) also reported less nitrogen accumulation in the mineral soils of red-alder stands on a floodplain of the Hoh-River than we found at the Kol. By 65 years the Hoh's soils contained approximately 1,670 kg-N ha^{-1} to 15cm depth, whereas the Kol's mineral soils (to 10cm) contained about 1,900 kg-N ha^{-1} at the same age. Initially, total soil nitrogen accumulated much more rapidly in the Kol floodplain than in the Glacier Bay moraine chronosequence, but both chronosequences accumulated roughly the same level of nitrogen by 100 years. In Glacier Bay, the forest floor + 18cm of mineral soil had less than 500 kg-N ha^{-1} by 20 years, but the soil contained more than 2,500 kg-N ha^{-1} by approximately 100 years (Crocker and Major 1955.)

While even minute nitrogen inputs such as atmospheric deposition (Vitousek et al. 1989) and wind-blown arthropods (Edwards 1993) may be important nitrogen sources in otherwise nitrogen-poor early succession, the bulk of the nitrogen that accumulates over time usually originates from terrestrial nitrogen fixation (Walker 1993). This is particularly true in Pacific-rim chronosequences, because they are often dominated by alders, and alder stands typically fix enormous quantities of nitrogen, with annual fixation rates often exceeding 100 kg-N ha^{-1} yr^{-1} (Binkley et al. 1994). However, we found that alder was largely not responsible for the rapid nitrogen accumulation that we measured in early succession. Whereas more than 90% of total soil nitrogen accumulated during the first 30 years of succession, alder was a minor component of the forest community during this period, on average accounting for less than 6% of the total tree coverage (Figure 5). Alders did become a significant member of the forest community by succession stage IV (50 to 80 years), comprising more than 30% of the total coverage, however soil nitrogen (to 10 cm + the litter layer) only increased by approximately 100 to 200 kg-N ha^{-1} during this time.

Salmon-nitrogen import during succession

Rather than alder, our data suggests that the rapid accumulation of nitrogen that we observed in early succession was associated with the flood deposition of fine sediments and the import of salmon-nitrogen. That fine sediments play a crucial in nitrogen accumulation is evidenced by the very strong relationship between bulk density and mineral soil nitrogen concentration (R^2=0.92) that we found (Figure 3). Floodplains are a unique form of primary succession in that the sediment that forms new floodplain surfaces originates from pre-existing sites that have been eroded and redeposited. This being the case, early succession in floodplains may be considerably more fertile than the bare rock occurring at the onset of succession in volcanic, glacial moraines or abandoned mine chronosequences (Binkley et al. 1995 and Adair et al. 2004). However, early primary succession in floodplains is still typically nitrogen poor and nitrogen limited because deposited sediments are primarily mineral, and fertility improves dramatically as nitrogen, organic matter and topsoil accumulate during succession.

We found that spawned-out salmon carcasses were delivered to gravel bars with early successional vegetation because these sites were adjacent to the main channel and were regularly inundated with floodwaters (Figure 9). Approximately 25 kg-N ha^{-1} was deposited onto stage 0 alluvial bars during 2006. However this was an unusually low salmon year and there was little flooding. Inputs were between ten and thirty times higher on years with abundant salmon runs and typical flooding. Very few salmon carcasses flooded into stages III through V regardless of run size or flood extent because these sites were higher in elevation, farther from the main channel, and vegetation filtered out many of the salmon carcasses before floodwaters reached these sites. Whereas alders occurred later in succession, both maximal salmon carcass deposition and maximum nitrogen accumulation rates occured in early succession.

The carcass deposition rates that we quantified indicated that salmon were an important nitrogen source to the otherwise nitrogen deficient stages of early succession. Considering that forests typically assimilate between 25 to 100 kg-N ha^{-1} yr^{-1} (Chapin III et al. 2002) we concluded that salmon have the potential to provide a very large proportion, if not all of the nitrogen required annually by the vegetation colonizing alluvial bars, particularly during high run years (see Chapter 3). Furthermore, our estimates of salmon carcass deposition were comparable to atmospheric deposition rates that have caused nitrogen saturation (Aber et al. 1989). Also, our estimates of salmon-imported nitrogen were based solely on the flood-deposited salmon carcasses and other translocation processes, notably hyporheic flow (eg. O’Keefe and Edwards 2003, Helfield and Naiman 2006), overland flow, animals feeding on carcasses (Ben-David et al. 1998, Hildebrand et al. 1999, Helfield and Naiman 2006) and especially the flood deposition of fine sediments may be important in transporting salmon-nitrogen to these sites as well.

The fate of nitrogen imported from salmon carcasses is very different than alder-fixed nitrogen. Whereas alder-fixed nitrogen occurs in comparatively recalcitrant plant compounds, salmon flesh is extremely labile and did not persist in the environment. The major pink salmon die-off occurred in early-September, and most carcasses were consumed or decomposed within about a month. In particular, carcasses deposited on alluvial bars were voraciously consumed by gulls. Gulls occupied these alluvial bars for about twelve hours a day during the main salmon die-off, and then flew back to the coast during the night. Given that seabirds feeding on fish typically have a mean digestia retention time of six to eight hours (Hilton et al. 2000) and these adult birds excrete a similar quantity of nitrogen to what they consume, much of this salmon-derived nitrogen was excreted back onto the gravel bars as uric acid. We have observed that so much uric acid accumulated at some sites that the alluvial bars appeared speckled white.

Given that carcasses do not persist in the environment and alluvial bars at the onset of succession are composed primarily of coarse gravel and sand, the accumulation of fine sediments and biomass is crucial in retaining salmon-imported nitrogen in early succession. It has been shown experimentally that sediments do assimilate salmon imported nitrogen through both biotic and abiotic processes (Bilby et al. 1996). Also, willow stands commonly take up greater than 50 kg-N ha^{-1} yr^{-1}, and often more than 100 kg-N ha^{-1} year (Perttu and Kowalik 1997, Adegbidi et al. 2001, Sasaki and Nakatsubo 2007). Given these rates it would only take the developing forest stands 25 to 50 years to assimilate as much nitrogen as accumulated in early succession, and these plants function to retain this salmon-imported nitrogen by re-depositing it into the soil as more recalcitrant plant litter compounds.

As fine sediment deposition, salmon nitrogen import, and alders all occurred during the first 100 years of succession, we expected that there would be no increase in soil nitrogen between the oldest active floodplain sites (stage IV) and the passive floodplain sites (stage V). However, this was not the case. Figure 3 demonstrates that stage V sites had an additional 500-1000 kg-N ha^{-1} in the litter layer at most sites, although total nitrogen at one site was vastly elevated relative to the others. In contrast, the mineral soil contained roughly the same quantity of nitrogen in stages IV and V. There are several potential explanations for this unexpected nitrogen increase in the litter layer. Firstly, trees senesced between stages IV and V. Thus, the additional nitrogen may have come from the deposition of this woody biomass. Based on other studies quantifying woody biomass, this could account for about <500 kg-N ha^{-1} to 1,000 kg-N ha^{-1} (Bormann and Sidle 1990, Luken and Fonda 1983). Also, alder coverage probably continued to increase between our oldest active stage IV sites (Figure 5) before senescing by stage V and we suspect that alder continued to fix nitrogen during this time. This increase in litter layer nitrogen may have also resulted from the vegetation's long-term "mining" of deeper soil nitrogen and re-deposition of it on the soil's surface, and we did not measure soil nitrogen content below 10 cm depth.

Vegetation changes during succession

Similarly to other Pacific-rim chronosequences, succession on the Kol floodplain began with willows, alders and the willow-like *Chosenia* colonizing alluvial bars. However trees then senesced altogether, leaving a meadow of tall-forbs composed primarily of *Filipendula camtschatica* and *Urtica diocia*. We are unaware of any other study describing a successional transition from a forest community to a similar tall-forb community.

While the transition to this tall-forb community in late succession is the most glaring difference between the Kol's chronosequence and these other floodplains, the Kol's earliest succession stages also possessed some unique attributes. Firstly, while willows are typically short-lived and quickly replaced by alders in the North American chronosequences, we found that *Salix B*, persisted as the dominant tree species for more than 50 years (Figure 5). Secondly, whereas alders become the dominant tree or shrub species for several decades in most of these other floodplains, alder was of comparatively minor significance at the Kol, never achieving dominance. For example, we found that alder basal area reached its maximum during succession stage IV, at approximately $10m^2$ ha^{-1} and its mean relative cover was only 31% during this stage (Table 4). In comparison, alder basal area coverage was approximately two times that of the Kol at the Tanana floodplain in Alaska, three times that of the Kol at the Queets floodplain in Washington State, and four times that of the Kol in the Hoh River, Washington State during alder-dominated stages (Luken and Fonda 1983, Viereck et al. 1993, Balian and Naiman 2005).

Another unique feature of the Kol floodplain was that all the major vegetation species occurring during the first several hundred years of succession had very high foliar nitrogen concentrations, with molar foliar C:N ratios of nine different plant species ranging between 12.4 and 27.4 (Table 3, see also Chapter 3). In contrast, the global average for foliage in temperate forests is approximately 35.1 with a standard deviation of 19.9 (McGroddy et al. 2004). The high foliar nitrogen concentrations that we observed on the Kol floodplain likely reflected the high fertility resulting from salmon-imported nitrogen and to a lesser extent alder fixed nitrogen.

Implications: how could salmon subsidies influence vegetation dynamics?

Other salmon-derived nutrient studies conducted in small river systems have explored the ecological implications of these subsidies by comparing stream reaches with and without salmon. However, no natural migration barriers exist in the Kol and salmon spawn so densely throughout the system that no suitable control sites existed. Thus we used inference from the data discussed above to predict how salmon subsidies influence vegetation dynamics in the Kol floodplain.

Most obviously, salmon probably increase growth rates of the Kol floodplain's vegetation. It is well documented that photosynthesis rate is strongly positively correlated with foliar nitrogen concentrations (Field and Mooney 1986) and we found that vegetation occurring during the first several hundred years of succession had very high foliar nitrogen concentrations. We have also observed that the vegetation grows extremely densely and rapidly on the Kol floodplain. For instance, we measured that five-year old gravel-bar willows may grew more than a meter in height during the growing season, and the tall forb, *Filipendula camtschatica* grows more than three meters from May until the end of June. Furthermore, Walter (1980) reviewed Russian and Japanese studies of these tall-forb communities and found that when growing in floodplains, they had amongst the highest biomass accumulation rates of natural vegetation in the world. That the Kol floodplain's foliage is so nitrogen rich is remarkable considering that prior to the salmon run the Kol river is considered oligotrophic based on its very low conductivity (50 to 60 µS cm^{-1}) and baseflow nutrient concentrations (100-200 µg-N L^{-1} and 20-25 µg-P L^{-1} of total persulfate N and P respectively (Chapter 5 this volume)).

Nitrogen availability usually strongly limits vegetation growth on young alluvial bars (Walker and Chapin III 1986, Sasaki et al. 2001, Adair and Binkley 2002) but we found that salmon fertilize these early succession stages on the Kol, and this fertilization effect persists through the chornosequence (see also Chapter 3). Therefore loss of salmon runs in the Kol, perhaps due overfishing or climate change, may be expected to greatly increase nitrogen limitation in early succession. Future mature forest sites would also be expected to be less fertile if they did not receive salmon nitrogen subsidies in early succession.

In addition to growth rate, nitrogen fertility also influences community composition. Theoretically, increased nitrogen richness should favor the dominance of nitrophillic species (Tillman 1985, Aerts and Chapin III 2000) and several empirical studies have shown that salmon-nitrogen subsidies may have this effect in riparian communities (Bilby et al. 2003, Mathewson et al. 2003, Bartz and Naiman 2005).

One expected change in the vegetation community on the Kol floodplain with the loss of salmon would be increased alder abundance, as nitrogen fixation, which is energetically costly, would become progressively more profitable as fertility declined. While alders were the dominant early succession species in Pacific-rim chronosequences that did not have significant salmon subsidies, they were a comparatively minor component of the overall forest community in the Kol floodplain. We have observed that both alders and willows colonized early succession, but alders were quickly overtopped and grew extremely slowly amongst dense willow stands, and all other species were excluded in the most prolific willow stands, indicating that willow growth may have limited alder abundance.

Finally, without salmon we predict that the vegetation community would shift to a nitrogen efficient community at approximately 100 years, rather than the nitrophillic tall-forb community that currently dominates the passive floodplain. Because these tall-forb communities have some of the highest phytomass production rates in the world, (Walter 1981) the must require very high nitrogen fertility. Based on other written accounts describing floodplain forests in southwestern Kamchatka and Sakhalin, it appears that this tall-forb community is not limited to the Kol, but rather, is ubiquitous in large-river floodplains of this region (Walter 1981, Krestov 2003). The large rivers forming these floodplains have historically been major salmon-producers (Augerot 2005). Furthermore, we observed, and it has been documented that the growth of these species is greatly reduced in the uplands where there are no salmon nutrient subsidies relative to growth within the floodplains (Walter 1981).

In North American floodplains of the Pacific-rim, the vegetation shifts from pioneer willow, alder and poplar trees to nitrogen efficient conifer species at approximately 100 years of succession. However, even without salmon this would not occur on the Kol as conifers do not occur at low-elevations in this region of Kamchatka. Rather, without salmon, the community might transition to more nitrogen efficient birch forests or grasslands instead of the tall forb community, because birch trees are abundant outside of the floodplain and occasionally occur in the oldest regions of the floodplain. Birch trees also dominate Kamchatkan volcano seres (Grishin et al. 1996). We observed that the vegetation community in the Kol floodplain does eventually shift towards more nitrogen efficient species (grasses, *Vaccinium* and eventually *Empetrum*) during the oldest succession stages, but this transition to more nitrogen efficient species occurs much later in the Kol floodplain than has been documented in other floodplain chronosequences.

Conclusions

We concluded that the succession-chronosequence concept was a good organizing principle for understanding the range of variation in many soil and vegetation variables in the Kol floodplain. Our succession models were able to explain approximately half the variance in more than half of the vegetation and soil variables that we measured. Succession models were particularly good at explaining soil nitrogen accumulation during succession. As in all types of primary succession the Kol's floodplain soils were nitrogen poor (200 kg-N ha^{-1} to 10 cm) at the onset of succession. However these soils accumulated more nitrogen, more rapidly during succession than has been shown in other chronosequences, and by 20 years these soils contained approximately 2,300 kg-N ha^{-1} (to 10cm + litter layer). Unlike other Pacific-rim chronosequences, nitrogen-fixing alder was not the primary source of this accumulated nitrogen.

Rather, the rapid accumulation of nitrogen in early succession could be explained by the import of salmon-nitrogen, and the incorporation of this salmon nitrogen in rapidly accumulating fine sediments and forest biomass. We found that during early succession the vegetation community was similar to what has been described in other Pacific-rim chronosequences in that willows and alders colonized young alluvial bars. However early succession was different from these other chronosequences in that tree willows persisted for more than 100 years and alders were a relatively minor component of the forest community. Late succession was very unique relative to other chronosequences described to date in that the community transitioned from a willow/alder forest to a nitrophillic-tall forb community at approximately 100 years. Approximately 80% of total coverage was dominated by one species, *Filipendula camtschatica*. Finally, this chronosequence was also unique in that all the dominant species occurring during the first several hundred years of succession had very high foliar nitrogen concentrations, with molar C:N ratios ranging from 12 to 22. Thus, while not proven conclusively through experimentation, our results suggest that large annual nutrient subsidies from spawning Pacific-salmon create fertile soils and promote the proliferation of nitrophillic, fast-growing vegetation plant species in the Kol floodplain.

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CHAPTER 2:
THE CONTRIBUTION OF SPAWNING PACIFIC-SALMON TO SOIL NITROGEN FERTILITY DURING PRIMARY SUCCESSION IN A LARGE-RIVER FLOODPLAIN

Abstract

Nitrogen limitation is potentially severe in early primary succession because plants colonize nitrogen poor rock substrate, and fertility improves as soils develop. We sought to determine how soil nitrogen fertility changed during primary succession in the Kol floodplain chronosequence (Kamchatka, Russian Federation), and how soil fertility was influenced by the large annual subsidy of salmon-imported nutrients that this ecosystem received. We found that mineral soils at the onset of succession were nitrogen poor (200 kg-N ha^{-1}, to 10 cm), but soil nitrogen accumulated rapidly in early succession and total soil nitrogen was an order of magnitude higher in the floodplain's mature willow/alder canopy forests (ages 50 to 100 years). Potentially mineralizeable nitrogen and dissolved inorganic nitrogen pools also increased during succession and were consistently 3% and 0.3-0.4% (respectively) of total soil nitrogen. We concluded that net mineralization within the mineral soils of mature willow/alder canopy forests (50 kg-N ha^{-1} to 10cm per growing season) could probably satisfy the vegetation's annual nitrogen requirement, whereas net mineralization in early succession soils (6 kg-N ha^{-1}) could only provide a small fraction of required nitrogen. Thus, as in most other primary succession chronosequences, nitrogen limitation should have been severe in early succession. However, salmon spawned and died in late August and subsequent late season flooding washed their carcasses onto recently-formed alluvial bars, contributing between 0-100 kg-N ha^{-1} yr^{-1} (average 25 kg-N ha^{-1} yr^{-1}) as a pulse of labile nitrogen to these sites. Deposition rates were ten to thirty times higher on high salmon years. On average, annual nitrogen subsidies from spawning salmon vastly exceeded growing season soil net N-mineralization in the youngest succession stage, but this subsidy was short-term because subsequent flooding flushed this labile nitrogen from these coarse soils, and returned them to their infertile state. We concluded that salmon increased nitrogen availability in early succession for a brief period during the growing season, but salmon may also contribute to long-term fertility by building ecosystem nitrogen pools as biomass and fine sediments accumulate causing nitrogen retention capacity to increase during succession.

Introduction

Nitrogen is the nutrient that most commonly limits plant growth in temperate and boreal forests (Chapin III et al. 1986), and nitrogen-limitation is especially severe at the onset of primary succession because soils are composed of bare rock and nitrogen is nearly absent (Walker and del Moral 2003). Research documenting pedogenesis in other northern Pacific-rim chronosequences has demonstrated that nitrogen pools and mineralization rates are lowest at the onset of succession, but increase rapidly as succession proceeds due to nitrogen fixation and soil organic matter accumulation (Crocker and Major 1955, Klingensmith and Van Cleve 1993a, Van Cleve et al. 1993a, Van Cleve et al. 1993b, Kaye et al. 2003, Kielland et al. 2006).

The Kol River, Kamchatka, RU is a large (7th order) alluvial river with expansive floodplains, and vegetation communities within these floodplains are mosaics of successional patches (*sensu* Stanford et al. 2005, see also Chapter 1). In our study floodplain on the lower Kol River, succession began with the flood-deposition of gravel bars on the inside of river bends (stage 0). Dense willow *(Salix sp.)* stands colonized these gravel bars and facilitated the accumulation of fine sediments during flooding (stage 0-I). Within 50 years these sites developed into mature willow and alder *(Alnus sp.)* canopy forests (stage IV). After about the first century of succession willow and alder trees began to senesce and were replaced by meadows of nitrophillic tall forbs (stage V). Consistent with other chronosequences, Morris et al. (Chapter 1) found that total soil nitrogen (to 10 cm + litter layer) was extremely low at the onset of succession (<200 kg-N ha^{-1}) but increased more than an order of magnitude within thirty years.

However, in contrast to other chronosequences studied to date, the Kol floodplain receives enormous nitrogen subsidies from Pacific-salmon. These salmon return from the ocean to spawn and die in the Kol, importing up to 270,000 kg-N yr^{-1} into this otherwise oligotrophic river. We documented that these salmon died in late summer and late season flooding washed their decomposing carcasses onto young alluvial bars, as these sites were adjacent to the main channel and flooded regularly (Chapter 1). Therefore we hypothesized that salmon created a late-season pulse of plant-available nitrogen on these gravel bars, potentially alleviating nitrogen limitation at these otherwise infertile sites. We also hypothesized that salmon contributed to long term fertility by building forest nitrogen pools during succession.

The purpose of this study was to determine how soil nitrogen fertility changed during succession in the Kol floodplain, and how fertility was influenced by spawning salmon. Although many studies have demonstrated that salmon nitrogen is taken up by vegetation growing along spawning streams (Ben-David et al. 1998, Hildebrand et al. 1999, Helfield and Naiman 2001, Helfield and Naiman 2002, Bilby et al. 2003, Mathewson et al. 2003), very little research has explored how this nitrogen is stored and made available to vegetation. Terrestrial fertilization studies in other systems suggest that most of this nitrogen would be rapidly assimilated by the soil prior to being taken up by vegetation (Kaye et al. 2003, Brenner et al. 2005). Understanding how salmon nutrients are stored and recycled in pristine ecosystems such as the Kol is crucial in determining the consequences of salmon decline on ecosystem fertility.

Although the total quantity of nitrogen in the soil typically vastly exceeds the vegetation's requirement, nitrogen limitation occurs because plant-available dissolved inorganic nitrogen typically comprises a minute fraction of total soil nitrogen. Thus mineralization rate and the resultant pool of dissolved inorganic nitrogen are the variables that proximately determine fertility (Binkley and Hart1989), and these variables are controlled by many factors in addition to total soil nitrogen including: the size of the labile nitrogen pool and the quality of soil organic matter (Flanagan and Van Cleve 1983, Van Cleve et al. 1993b, Stump and Binkley 1993, Scott and Binkley 1997, Kaye et al. 2003), as well as environmental conditions such as temperature, soil moisture, sediment characteristics and geomorphology (Pastor et al. 1984, Nadelhoffer et al. 1991, Pinay et al. 1995, Hefting et al. 2004).

Therefore to assess how overall soil fertility changed during succession we measured potentially mineralizeable nitrogen under ideal conditions as well as in-field net N-mineralization rate and KCl extractable dissolved inorganic nitrogen pools. We also used ion-exchange resin capsules as an index of plant-available nitrogen. Since ion exchange resin is sensitive to both nitrogen originating from within the soil as well as external inputs, they were used to test whether decomposing salmon carcasses created a late-season pulse of plant available nitrogen in the earliest succession stages.

Specifically, we hypothesized that:

1) Prior to salmon carcass deposition all indices of soil fertility would increase during the first century of succession corresponding to the large accumulation of total soil nitrogen documented by Morris et al. (Chapter 1).

2) Prior to salmon carcass deposition nitrogen absorbed by ion exchange resin capsules would correlate well with the other soil nitrogen fertility indices, indicating that that the internal soil cycle was the primary source of plant-available nitrogen in the absence of salmon.

3) Ion exchange resin capsules would absorb the greatest amount of nitrogen at the youngest succession stages in late summer and early fall because late season flooding washes decomposing salmon carcasses onto these alluvial bars.

4) This late season-pulse in nitrogen availability on the young alluvial bars would be short term and these soils would be infertile again by the following spring because salmon carcasses decompose rapidly and subsequent fall and spring flooding flushes labile nitrogen from these coarse, rocky soils.

Study area

The Kol is a seventh-order river at its mouth and the main channel in our study region had a minimum summer base flow of approximately 20 to 30 $m^3 s^{-1}$. The Kol's headwaters originate in the central Kamchatka mountain range at an elevation of nearly 2000 m and the river flows westward. Roughly seventy percent of the catchment is tundra-dominated coastal plain below 150 m, although birch *(Betula sp.)* forests are present on hills within the tundra landscape. Permafrost generally does not occur in this watershed.

This study was conducted on a large, anastomosing floodplain (N53°49.506' E156°3.716') of the lower Kol River, Kamchatka, Russian Federation. Research was based out of a biostation operated by the Wild Fishes and Biodiversity Foundation. Our study reach, shown in Figure 1 was approximately 12 km upstream of the river's confluence with the Sea of Okhotsk. The floodplain was largely pristine with no roads or year-round inhabitants and the entire Kol catchment was recently designated as a salmon conservation area by the Russian government.

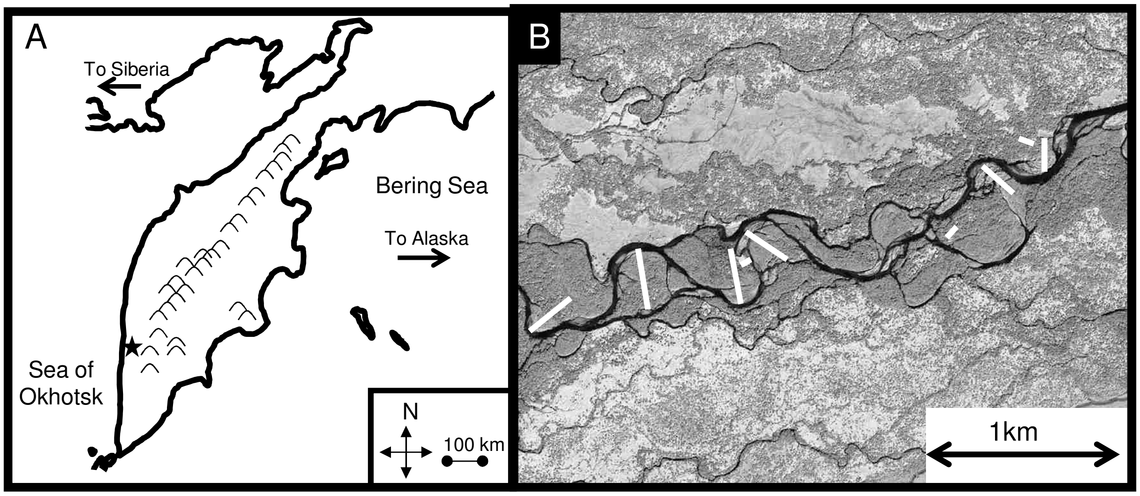

Figure 1. Map A: the Kamchatka Peninsula in the Russian far-east. The star indicates the location of the Kol River. Map B: Satellite imagery of the Kol Floodplain in the region of our camp. The white lines show the study transects. Original sattelite imagery before modification was from the QuickBird Satellite and was provided by DigitalGlobe Inc. in 2004.

The climate of the south-western Kamchatka is cold, wet, sub-oceanic (Krestov 2003). According to weather data collected in the town of Sobolevo, approximately 50 km north of the

Kol River, the mean annual temperature of the region is -0.9 °C. The mean temperatures of the coldest and warmest months are -14.9 and 12.2 °C respectively. The total frost-free period is 92 days (Sokolov 1974), and annual precipitation is approximately 789 mm. (Krestov 2003).

Morris et al. (Chapter 1) modeled the dominant vegetation succession pathway in the lower Kol floodplain and described six stages that occurred during the first several hundred years of succession. Briefly, succession began at stage 0 ("the bare alluvial bar stage" ages 0-10 years) with willows *Salix sp.* and the willow-like *Chosenia arbutifolia* colonizing bare alluvial deposits. Stage I, or the "alluvial-bar willow/*Chosenia* stage" occurred from 10-20 years when greater than half of these alluvial deposits were colonized by dense stands of two species of willow and the willow-like *Chosenia* tree. Stage II, or the "willow/*Chosenia* canopy stage" occurred from 20 to 30 years and was characterized by a canopy formed by the two willow species and *Chosenia,* with young alder trees (*Alnus hirsuta*) in the understory. Stage III, or the "willow/alder/*Chosenia* canopy stage" ranged in age from 30 to 50 years and was characterized by the senescence of one of the two willow species as well as *Chosenia.* A nitrophillic tall-forb understory composed of stinging nettle *(Urtica diocia)* and *Fillipendula kamtschatica* proliferated during this stage. Stage IV, or the "declining willow, mature alder canopy stage" ranged in age from 50 to at least 100 years and was the oldest stage that commonly occurred on the active region of the floodplain. During this stage the canopy was composed of mature willow and alder trees, and the understory was dominated by dense stands of *Filipendula kamtshcatica.* Stage V, or the "tall-forb meadow stage" occurred in the passive region of the floodplain. By this time most trees had senesced leaving vast meadows of >3 m tall forbs composed primarily of *Fillipendula kamschatica* with lesser nettles *(Urtica diocia).*

Concurrent with changes in the vegetation community, soils also developed during succession. Soils at the onset of succession were composed primarily of cobble and gravel with sand in the interstitial spaces. Through time flooding deposited layers of fine sediments and organic horizons formed. After the first 20 years of succession floodplain soils consisted of layers of sand and silt, and occaisionally, layers of buried organic matter overlying gravel and cobble. Surface organic matter accumulations ranged from being entirely absent at the most extensively flooded sites, to having a dense litter layer with A-horizons commonly up to 10 cm deep. Soils from three forest stands, aged approximately 30, 60 and hundreds of years old were were chosen for description during August of 2004. Midsummer Munsell colors for A horizons were typically either 2.5y3/2, 10yr 3/1-2 or 10yr 2/1-2 (Munsell 1994). Soil beneath the A horizon were most commonly 2.5y3/2-3 10yr3/3, or 10yr4/3. Redox motteling was occasionaly observed, particularly in deeper sediment layers. Soil pH (to approximately 5 cm) was measured at at least six points within each stand using a Kelway® Soil Acidity Tester and an Oakton® pH CON10 pH probe (approximately 50:50 soil water mix). Mean pH values were approximately 6 at all three forest sites and ranged from approximately 5.5 to 6.6 indicating that floodplain soils were consistently moderately acidic.

Methods

Selection of sampling sites

In order to contrast soil fertility between early and later succession all soil measurements were conducted at three succession stages: stage 0- alluvial deposits that were just beginning to be colonized by vegetation (generally 0 to 10 years old), stage I- alluvial deposits that were nearly fully colonized by willows (ages 10 to 20 years), and stage IV mature willow and alder forests (ages 50 to 100 years). Vegetation and soil attributes of these sites are summarized in Tables 1 and 2, and are described in detail in Chapter 1. Six replicates of stages 0 and IV and seven replicates of stage I were chosen in the vicinity of our camp along transects described in Chapter 1 (see Figure 1). One site aged 9 years old was included as a stage I site because more than half the site was covered in a dense willow stand. Soil sampling was conducted at random points chosen within 3 m on either side of 50 m transects running perpendicularly away from the river through the center of each succession stand. Multiple parallel transects were run through sites that were less than 50 m wide such that these shorter transects summed to approximately 50 m.

Soil bulk density

During the summers of 2005 and 2006 five replicate cores from the top 10 cm of mineral soil were taken using a 5 cm diameter bulk density soil corer at random points within each succession site. We considered the mineral soil to begin beneath the layer of visually identifiable plant detritus and consisted of both mineral sediments and where present soil humus. All five cores from each site were combined and dried at 46°C to determine water content and bulk density. The dried soils were then sieved to determine the mass of <3.3 mm and <2 mm soil fractions. Stage 0 soils contained cobbles and gravel and thus the soil corer could not be used at these sites. Therefore during the summer of 2006 all soil to 10 cm depth was collected within a 26 cm diameter circular frame at three random points within each stage 0 site. The total volume of these holes was determined by lining the hole with a plastic sheet and filling them with water.

Total persulfate-N

The total nitrogen content of the top 10 cm of mineral soils collected during bulk density sampling was quantified according to the persulfate digestion method described by Raveh and Avnimelech (1979). Briefly, an aliquot of the <2 mm fraction of dried soils was pulverized to a fine powder with a mortar and pestle. Approximately 50 mg of this fine fraction was then digested in an autoclave with persulfate. Devarda's alloy was then used to convert all inorganic nitrogen to ammonium. The ammonium content of the resulting extract was then determined colorometrically on a Perkin-elmer Lambda-1 spectrophotometer using the indophenol-blue-salicylate method described by Mulvaney (1996). The total quantity of nitrogen (kg-N ha^{-1} to 10 cm depth) in the soil was then calculated by multiplying the nitrogen concentration of the soil by the mass of the <2mm fraction per hectare.

Soil potentially mineralizeable-N (anaerobic incubation)

Potentially mineralizeable nitrogen (PMN) is a biological index that is useful for comparing the relative nitrogen mineralization potentials of soils incubated under identical conditions. In this study we used the waterlogged incubation method described by Bundy and Meisinger (1994). Briefly, two 5 g aliquots of the dried <3.3 mm fraction of the top 10 cm of soil (with the litter layer removed) collected from each site were placed into two screw-capped vials. One vial from each site was immediately extracted with 25 ml of 2 M KCl solution and the second vial was saturated with 12.5 ml of deionized water and capped. The vials receiving the DI water were then incubated at 40°C for 7 days. After the incubation an additional 12.5 ml of 4 M KCl was added to each vial to create a 2 M KCl extract. KCl extracts from the time-0 and time-7 soils were then shaken several times over 24 hours and then clarified by filtering through Whatman GF/A filters. The ammonium content of the KCl extracts was then determined using the indophenol-blue-salicylate method described by Mulvaney (1996). Potentially mineralizeable nitrogen was then determined by subtracting the ammonium content per gram of dry soil in time-0 soils from the time-7 soils. Potentially mineralizeable nitrogen was expressed as kg-N ha^{-1} by multiplying the mass of PMN per gram of soil by the total mass of <3.3 mm fraction per hectare at each site.

KCl extractable-DIN

Extractable NO_x-N and NH_4^+-N (in 2 M KCl) were determined on the time-0, 10c m soils (with the litter layer removed) collected as part of the buried bag net mineralization study according to the methods of Hart et al. (1994). During June and August 2006 five soil cores were

Stage	Total tree density (trees ha^{-1})	%willow	%alder	%chos.	Total tree cov. (m^{2} ha^{-1})	%willow	%alder	%chos.	Total understory cover %	%grass	%nettle	% filk
I	69000	86	2	12	18	86	1	13	49	16	3	1
	(39000-115000)	(65-100)	(0-9)	(0-35)	(7-29)	(61-100)	(0-2)	(0-39)	(8-77)	(0-19)	(0-5)	(0-2)
IV	480	63	36	1	36	67	31	2	91	4	28	45
	(267-952)	(40-93)	(8-57)	(0-3.3)	(15-55)	(44-93)	(7-49)	(0-7)	(73-100)	(0-10)	(15-50)	(32-58)

Table 1: Means and ranges (in parenthesis) for vegetation variables by succession stage, data from Chapter 1.

Succession Stage		Mass (tonne ha^{-1}) by fraction			Bulk density (g cm^{-3})			Water % mass		fine sed. depth (cm)	Forest floor			Carcass-N kg-N ha^{-1}	
		Total	<3.3mm	<2mm	Total	<3.3mm	<2mm	June '06	Aug. '06		(tonne ha^{-1})	Kg-N ha^{-1}	mol C:N	2005	2006
0	n=6	**1858**	**567**	**479**	**2.07**	**1.51**	**1.36**	**16.2**	**4.1**	**3**	**n/a**	**n/a**	**n/a**	**n/a**	**25**
	SE	*91*	*55*	*46*	*0.06*	*0.14*	*0.10*	*3.7*	*2.3*	*(0-8)*					*16*
I	n=7	**905**	**663**	**685**	**0.89**	**0.71**	**0.75**	**32.2**	**27.6**	**24**	**29**	**334**	**29.7**	**4**	**2**
	SE	*50*	*44*	*42*	*0.05*	*0.05*	*0.04*	*3.8*	*5.2*	*(10-37)*	*(13-52)*	*194*	*2.5*	*2*	*0*
IV	n=6	**485**	**446**	**479**	**0.48**	**0.44**	**0.48**	**48.4**	**43.2**	**53**	**58**	**734**	**28.7**	**3**	**0.4**
	SE	*31*	*37*	*40*	*0.03*	*0.04*	*0.04*	*3.5*	*2.0*	*(30-78)*	*(44-85)*	*159*	*1.6*	*1*	*0.4*

Table 2. Properties of the top 10cm of mineral soil and litter layer by succession stage, data from Chapter 1

Sample Period	Total N	PMN	KCL-extract	Net min	IER	River flow	Salmon Status
						spring flooding through June	prior to main run
Su '05	8/15-8/20/05				8/7-8/30/05	baseflow	spawning and major dieoff 3rd week of Aug.
						fall flooding 1st week of Sept.	
F '05					9/17-10/6/05	moderate flows after flooding	carcassses to complete decomp.
Sp '06			6/11/06	6/11-7/13/06	6/22-7/12/06	flood stage declining to baseflow	before run
Su '06		8/10-8/11/06	8/10-8/11/06	8/10-9/11/06	8/9-8/29/06	baseflow	in river prior to spawn
						minor fall flooding early Sept.	
F '06					9/10-9/30/06	moderate flows after flooding	few carcassses to complete decomp.

Table 3: Summary of sampling dates in relation to the pink salmon life history and river flow

taken at random points along each site transect and were amalgamated to make one sample per site. Samples were then refrigerated for up to 48 hours until they could be processed. In the laboratory, amalgamated soil samples were thoroughly mixed and three 10 g soil samples were then taken excluding particles >3.3 mm as well as root hairs. One of the subsamples was extracted 100 ml of 2 M KCl and the other two were dried at 48°C to determine the percent water content of the <3.3 mm fraction. The KCl extraction samples were shaken several times over the next 24 hours. The extracts were then clarified by passing them through Whatman GF/A filters. The NH_4^+-N content of the extracts was determined using the indophenol-blue-salicylate method and NOx-N was determined using the cadmium-reduction method (Mulvaney 1996). Mineral nitrogen content per hectare was determined by multiplying the mass of mineral nitrogen per gram of dry soil by the mass of <3.3 mm fraction per hectare at each site.

Net mineralization (buried bag method)

At each site five additional random soil cores sealed intact into 1mil polyethylene bags at the same time that the KCl extractable DIN samples were taken. The cores were placed upright back into their original holes and covered with a small quantity of soil. The cores were incubated in the ground for 30 days and then retrieved. Bags with obvious tears were discarded. Samples were extracted with 2 M KCl and analyzed for mineral nitrogen as described for the time-0 soils in the previous paragraph. Net mineralization rate was determined by subtracting the dissolved inorganic nitrogen content of the time 0 soils from the time 30 soils and dividing by the number of days of the incubation. Mineralization rate per gram of soil was converted to kg-N ha^{-1} day^{-1} by multiplying by the mass of <3.3 mm soil fraction per hectare.

Ion-exchange resin field incubation

Unibest PST-1 anion-cation exchange resin capsules were incubated during five sampling periods (see Table 3): August 2005, September-October 2005, June-July 2006, August 2006, and September-October 2006. Sampling was conducted at the same sites as the other soil nitrogen fertility measurements except that during spring flooding in 2006 additional sites were selected to determine how nitrogen availability compared between flooded and unflooded sites. Three resin capsules were placed at randomly chosen points within each site. A hole was made in the mineral soil with a 2 cm soil probe at approximately a 45 degree angle into the ground such that the final depth perpendicular to the soil surface was 10 cm. The resin capsules were placed in these holes and the core removed from the soil probe was placed in-tact back into the ground to cover the resin capsules. The soil probe could not be used on the youngest gravel bars, therefore the capsules were installed with a small hand shovel at these sites. The resin capsules were removed after 20 day incubation periods and frozen until they could be analyzed. The frozen capsules were then thawed, rinsed with ultra-pure deionized water and extracted three times sequentially with 25 ml of 2 M KCl per capsule. All three capsules from each site were extracted together to make one extract per site per season. The extracts were then clarified with Whatman GF/A filters and analyzed colorimetrically for NO_x-N and NH_4^+-N as described previously.

Statistical analysis

Statistical analyses were conducted using the Graphpad Prism 5 and SPSS for windows 15.0 computer programs. Means within each succession stage were compared using one-way ANOVA/Tukey post-hoc for the potentially mineralizeable and total soil nitrogen variables, and two-way repeated measures ANOVA/Tukey post-hoc were used for variables measured during different seasons. Prior to running the ANOVA's, variables were tested for conformance to the normal distribution with the Kolmogorov-Smirov test, and equality of variances with Bartlett's test. Variables were log transformed to improve conformance to these assumptions, but in several cases these assumptions were still violated (see Table 4). Because the repeated measures test required the deletion of data with missing pairs, we re-conducted these analyses using one-way ANOVA within each season prior running the Tukey test. ANOVA results presented in Table 4 are for the repeated measures test, but the post-hocs presented with these results are from the one-way analysis. Non-parametric Spearman's rho correlation coefficients were used to explore correlations between the nitrogen fertility indices and potential predictor variables.

Results

Both total nitrogen and potentially mineralizeable nitrogen (Figure 2 and Table 5) were lowest at the onset of succession (200 and 5.9 kg-N ha^{-1} respectively), increased in succession stage I and were highest in succession stage IV (1,933 kg-N ha^{-1} and 53.9 kg-N ha^{-1}.) Differences among succession stages were highly significant, $p<0.0001$ (Table 4). The fraction of total nitrogen that was potentially mineralizeable was consistently around 3% regardless of succession stage (Table 5).

Total dissolved inorganic nitrogen (ie. KCl extractable DIN) also increased significantly ($p<0.0001$) with succession and there were no significant differences between the spring and late summer sampling periods (Figure 3 and Table 5). Stage 0 soils contained approximately 0.8 kg-DIN ha^{-1} and this increased to 5.7 kg-DIN ha^{-1} in succession stage IV. Dissolved inorganic nitrogen was consistently 0.3-0.4% of total soil nitrogen (Table 5). In stages 0 and I the vast majority of dissolved inorganic nitrogen was NH_4^+-N, whereas roughly half was NO_x-N in succession stage IV.

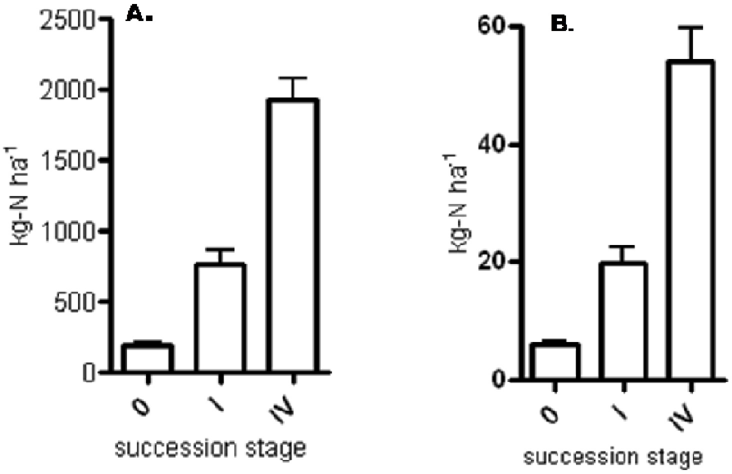

Figure 2. Total persulfate-N (A) and Potentially mineralizeable-N (B) +/- SE for the top 10cm of mineral soil by succession stage.

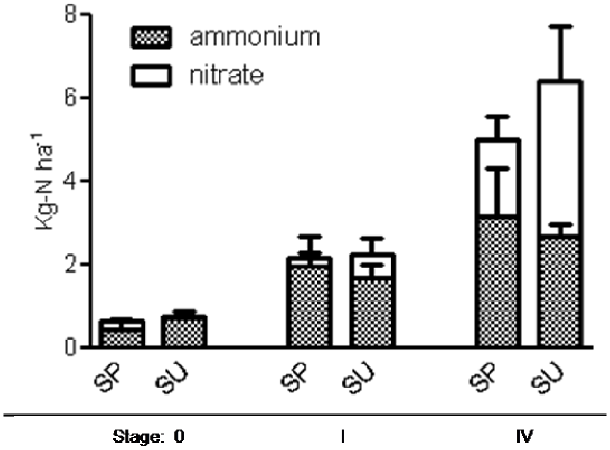

Figure 3. KCl-extractable dissolved inorganic-N +/- SE in the top 10cm of mineral soil by succession stage and season (spring and summer 2006).

Net N-mineralization rate also increased significantly ($p<0.0001$) with succession (Figure 4 and Table 5). Net mineralization in stage 0 was approximately 0.06 kg-N ha^{-1} day^{-1} and this increased to 0.53 kg-N ha^{-1} day^{-1} in stage IV. We also found that there were barely significant differences between seasons ($p=0.049$), and these differences occurred within succession stage I, while there was no difference between seasons in succession stages 0 or IV. In contrast to the dissolved inorganic nitrogen pools, which were dominated by ammonium, most of the net mineralized nitrogen was nitrified in every succession stage and season, with the exception of succession stage I during spring 2006. The total standing stock of KCl extractable dissolved inorganic nitrogen was roughly equivalent to net mineralization in 10-13 days.

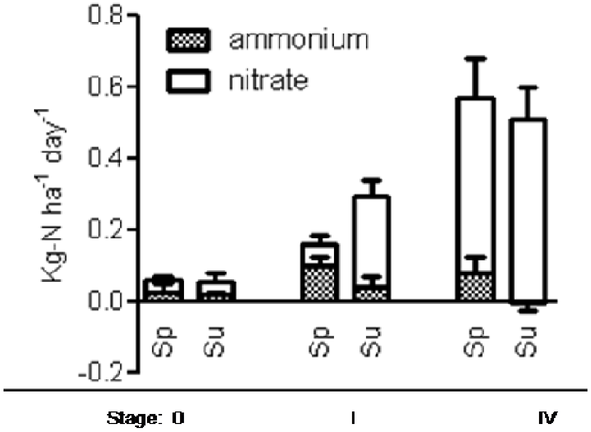

Figure 4. Net N-mineralization in the top 10cm of mineral soil by succession stage and season (spring and summer 2006).

When all seasons were averaged, the total quantity of nitrogen absorbed to ion exchange resin capsules also increased significantly ($p<0.0001$) with succession stage (Figure 5). However, unlike the other metrics of nitrogen fertility, there were highly significant differences among seasons ($p<0.0001$). When all sites were summed, summer of 2006 resin capsules absorbed significantly less nitrogen than in other seasons. Resin absorbed nitrogen among seasons was invariably low within stage 0 and invariably high within stage IV relative to stage I which fluctuated greatly between seasons. Resin absorbed nitrogen was about 50% lower in the summer than in the spring and fall within stage IV.

Succession stage I flooded extensively during the fall of 2005 and again in the spring of 2006. Resin absorbed nitrogen was higher during flooding than during the dry periods of summer and fall of 2006 (Figure 5). Figure 6 demonstrates that resin capsules at sites that were extensively flooded during the spring of 2006 typically absorbed more nitrogen than capsules at sites that did not flood. However, this was only true for stage I sites (greater than five years old) as younger (stage 0) sites that were flooded absorbed similar quantities of nitrogen as unflooded sites.

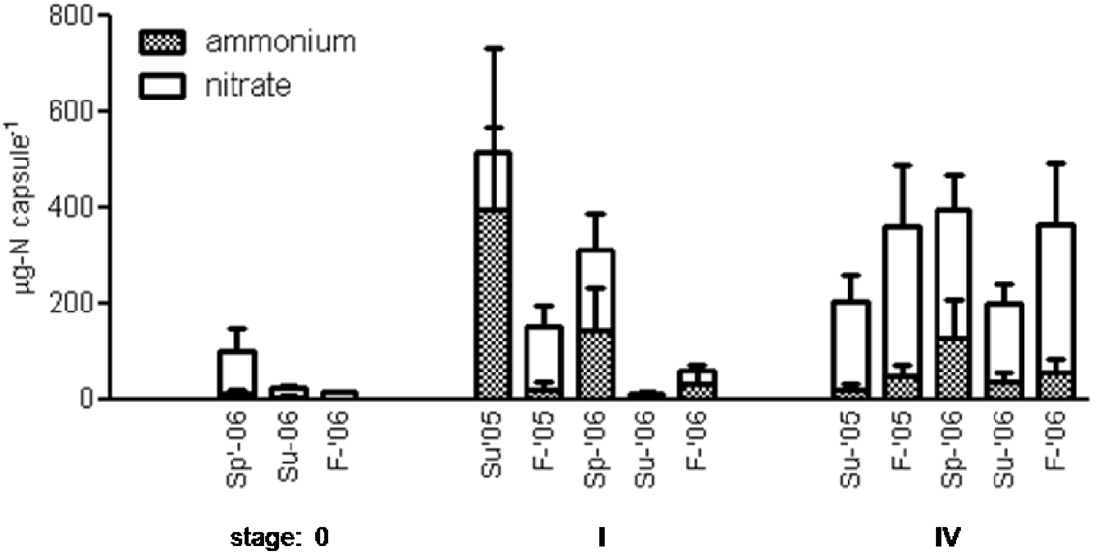

Figure 5. Dissolved inorganic nitrogen absorbed by ion exchange resin capsules (at 10cm soil depth) by succession stage and season. Summer 2005-baseflow and during salmon dieoff; Fall 2005-after carcass decomposition and after late season flooding; Spring 2006-during flooding and before salmon run; Summer 2006-baseflow and before salmon dieoff, Fall 2006- after salmon dieoff and after fall flooding, very few decomposing salmon carcasses.

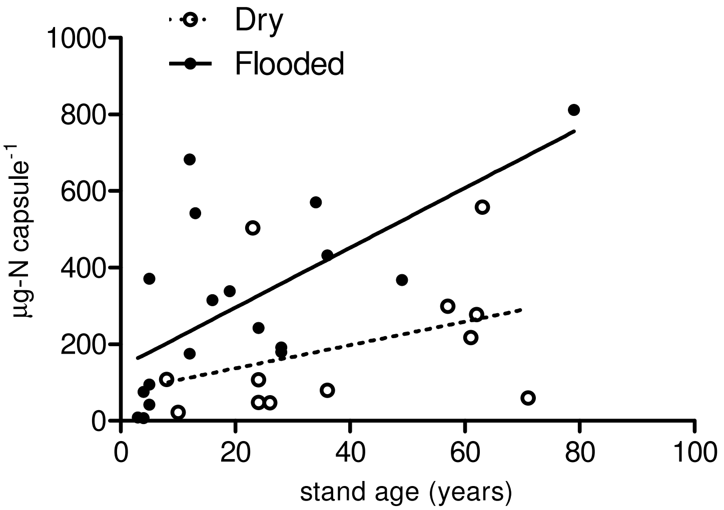

Figure 6. Dissolved inorganic nitrogen absorbed by ion exchange resin capsules at 10cm soil depth in flooded and unflooded forest stands by succession stage. These samples were taken during spring of 2006.

Within stage I, resin absorbed nitrogen was highest during the summer of 2005 and this period corresponded to the maximum time of pink salmon spawning and death. There was no significant relationship between the quantity of carcass imported nitrogen and resin absorbed nitrogen within stage I during the summer of 2005 (Figure 7), however sites receiving salmon carcasses in general had higher resin absorbed nitrogen than sites that did not. In contrast, the salmon spawn and death occurred after the resin incubation period during the summer of 2006 and resin absorbed nitrogen was much lower at this time than in the previous year. Unfortunately, resin capsules were not used in succession stage 0 when salmon carcasses were available during the summer of 2005 and therefore we cannot determine whether salmon increased nitrogen availability at these sites during this time. Fall resin capsule incubations in 2005 and 2006 occurred after the main period of salmon spawning and death and resin absorbed nitrogen was low in stages 0 and I during these times.

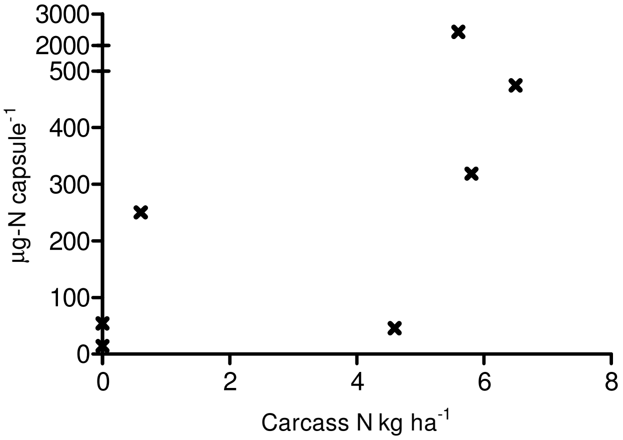

Figure 7. Dissolved inorganic nitrogen absorbed by ion exchange resin capsules verses salmon carcass N deposition in succession stage I sites during summer of 2005.

Mineral soil total nitrogen was highly correlated with stand age (ρ=0.91) and highly negatively correlated with bulk density (ρ=-0.92) (Table 6). Potentially mineralizeable nitrogen was also highly correlated with these variables, but had the greatest correlation with mineral total nitrogen (ρ=0.96).

For both spring and summer samplings, total net mineralization and the total quantity of KCl extractable dissolved inorganic nitrogen were also highly correlated with stand age, bulk density, soil total nitrogen and potentially mineralizeable nitrogen (Table 6). Net nitrification was strongly correlated with age in the spring; and age, bulk density, total nitrogen and potentially mineralizeable nitrogen in the summer. In both spring and summer total KCl extractable nitrogen was better correlated with total soil nitrogen and potentially mineralizeble nitrogen than net mineralization rates.

In the fall of 2005 and summer and fall of 2006 total nitrogen absorbed to ion exchange resin were correlated with most of the other soil nitrogen fertility indices. Resin absorbed nitrogen during the summer of 2006 was more strongly correlated with KCl extractable nitrogen than mineralization rate. During spring 2006 (during flooding, but without salmon) total nitrogen absorbed per resin capsule was weakly correlated with total and potentially mineralizeable nitrogen and more strongly correlated with % soil water and KCl extractable ammonium. In contrast, total nitrogen and nitrate absorbed per resin capsules during the summer of 2005 (in the presence of salmon) was not correlated with any other soil variable that we measured.

Discussion

Plants colonize nitrogen-poor mineral substrate at the onset of primary succession, and consequently nitrogen limitation is usually severe (Walker and del Moral 2003.) However, the Kol River floodplain chronosequence is unique relative to other chronosequences studied to date in that it receives enormous annual nutrient subsidies from spawning Pacific-salmon which have the potential to ameliorate severe nitrogen limitation in early succession. We hypothesized that: 1) prior to seasonl salmon carcass availability all indices of soil fertility would increase during the first 100 years of succession; 2) prior to salmon carcass availability nitrogen absorbed by ion exchange resin capsules would correlate well with the other soil nitrogen fertility indices; 3) ion exchange resin capsules would absorb the most nitrogen at the youngest succession stages when decomposing salmon carcasses were available; and 4) the late season pulse in nitrogen availability from salmon carcasses on the young alluvial bars would be brief, with sites being infertile again by the following spring.

Hypothesis 1

Our results strongly supported our first hypothesis that soil nitrogen fertility would increase with succession stage. Mineral soils at the onset of succession (stage 0) had extremely low total nitrogen (<200kg-N ha^{-1} to 10cm), but nitrogen content was an order of magnitude higher in succession stage IV (Figure 2, Table 5). Potentially mineralizeable nitrogen and dissolved inorganic nitrogen also increased with succession, and were consistently 3% and 0.3-0.4% respectively of the total soil nitrogen (Table 5). Many other studies have found that total soil nitrogen is a poor indicator of plant-available nitrogen (eg. Nadelhoffer et al. 1983, Flanagan and Van Cleve 1983) and nitrogen availability is be better correlated with other factors, such as soil organic matter quality (Flanagan and Van Cleve 1983, Van Cleve et al. 1993b, Stump and Binkley 1993, Scott and Binkley 1997, Kaye et al. 2003) or environmental conditions including

log Total N by stage	**Bartlett's P**	**ANOVA p**		
one-way ANOVA	0.20	<0.0001		
	SS	df	MS	F
Treatment	2.994	2	1.497	112.800
Residual	0.212	16	0.013	
Total	3.207	18	0.013	
Tukey post-hoc	All comparisons significant			

log PMN by stage	Bartlett's P	ANOVA p		
one-way ANOVA	0.71	<0.0001		
	SS	df	MS	F
Treatment	2.758	2	1.379	74.170
Residual	0.298	16	0.019	
Total	3.056	18		
Tukey post-hoc	All comparisons significant			

log total KCl-N by stage and season
repeated measures ANOVA

	p-value	SS	Df	MS	F
Interaction	0.778	0.031	2	0.157	0.256
season	0.378	0.051	1	0.051	0.832
stage	<0.0001	3.815	2	1.908	20.760
subjects	0.238	1.194	13	0.092	1.498
residual		0.797	13	0.061	

Tukey post-hoc[1] SP significant: 0-IV, I-IV SU significant: All
-one-group summer group failed normaility even with log transform

log net minerlization by stage and season
repeated measures ANOVA

	p-value	SS	Df	MS	F
Interaction	0.046	0.200	2	0.100	3.947
season	0.049	0.120	1	0.120	4.721
stage	<0.001	5.265	2	2.633	19.800
subjects	0.003	1.729	13	0.133	5.252
residual		0.329	13	0.025	

Tukey post-hoc[1] SP: all significant SU significant: 0-I, 0-IV
-one spring group failed normaility even with log transform

log total resin absorbed N by stage and season
2-way ANOVA

	p-value	SS	Df	MS	F
Interaction	<0.001	4.896	6	3.089	3.089
season	<0.001	6.492	4	1.623	6.145
stage	<0.001	9.965	2	4.983	18.865
residual		17.960	68	0.264	

Tukey post-hoc Across all dates: all significant Seasons: Su'05-Su'06, Fa'05-Su'06, Sp'06-Su'06
-repeated measures could not be used due to missing values

log total KCl-NH_4-N by stage
repeated measures ANOVA

	p-value	SS	Df	MS	F
Interaction	0.145	1.081	2	0.540	2.243
season	0.153	0.545	1	0.545	2.264
stage	0.002	6.095	2	3.048	10.210
subjects	0.342	4.476	15	0.298	1.239
residual		3.613	15	0.241	

Tukey post-hoc[1] SP significant: 0-I, 0-IV SU: All significant

- summer not log transformed for post hoc
-spring transform failed Bartlets

log net nitrification by stage
repeated measures ANOVA

	p-value	SS	Df	MS	F
Interaction	0.034	0.008	2	0.004	4.460
season	0.014	0.007	1	0.007	7.989
stage	0.001	0.133	2	0.066	13.350
subjects	0.002	0.065	13	0.005	5.806
residual		0.011	13	0.001	

Tukey post-hoc[1] SP significant: 0-IV, I-IV SU: All significant

spring failed bartlets even if log trans

log total KCl-NOx-N by stage
repeated measures ANOVA

	p-value	SS	Df	MS	F
Interaction	0.143	5.693	2	2.847	2.269
season	0.117	3.537	1	3.537	2.819
stage	0.013	47.690	2	23.840	6.130
subjects	0.026	50.560	13	3.889	3.100
residual		16.310	13	1.255	

Tukey post-hoc[1] SP significant: 0-IV, I-IV SU significant: 0-IV, I-IV
-spring transform failed Bartlets

[1] -post hoc conducted using one-way anova with each season separate to include deleted values without replicates excluded in the repeated measures ANOVA

Table 4. ANOVA results testing for significant differences between stage and season for N-fertility indices.

Stage	Total N	PMN	% of total	DIN Pool	% of total	Min. per season	% of total
0	195	5.9	3.04	0.8	0.4	5.5	2.6
	(145-231)	(3.8-8.4)	(2.1-3.7)	(0.46-1.1)	(0.2-0.6)	(1.7-11.5)	(1.0-4.9)
I	**765**	19.8	2.7	2.31	0.3	20.7	3.1
	(391-1084)	(12.1-31.7)	(1.7-4.9)	(0.78-3.6)	(0.1-0.4)	(8.6-26.5)	(0.8-6.6)
IV	**1933**	53.9	2.8	5.69	0.3	49.1	2.7
	(1427-2386)	(36.9-67.2)	(1.9-4)	3.4-8.7	(0.2-0.4)	(19.3-68.7)	(1-4.5)
DIN pool is mean KCl extractable NO_x-N+NH_4-N							
Min per season calculated by multiplying the mean daily mineralization rate by 92 frost free days in the growing season.							

Table 5. Summary of nitrogen pools and total growing season net mineralization for the top 10 cm of mineral soil. Values expressed as kg-N ha^{-1}.

temperature, soil moisture, sediment size and geomorphology (Pastor et al. 1984, Nadelhoffer et al. 1991, Pinay et al. 1995, Hefting et al. 2004). The strong correlation between total soil nitrogen and the other nitrogen fertility indices that we observed in this study reflected the extreme differences in total nitrogen between early and later succession. Factors other than total nitrogen have greater influence on nitrogen availability when sites with narrower ranges of total soil nitrogen are compared.

Net N-mineralization rate adequately quantifies plant-available soil nitrogen in all but the least fertile ecosystems (Schimel 2004). Because we found no significant differences between seasons for stage 0 or IV, we multiplied average daily net mineralization rates by the annual average of 92 frost free days in southwestern Kamchatka (Sokolov 1974) to calculate total net mineralization for the entire growing season. We calculated that net mineralization (mineral soil to 10cm) in stages 0 and IV were approximately 5.5 and 48.8 kg-N ha^{-1} growing season^{-1} respectively. While our estimate of net mineralization was reasonable for succession stage 0, it was underestimated for succession stage IV because we did not measure net mineralization in the litter layer. In a review of 11 forest mineralization studies, Stump and Binkley (1993) found that the litter layer contributed about equally to total net mineralization as the mineral soil. Therefore, net mineralization in stage IV at the Kol was likely closer to 100 kg-N ha^{-1} growing season^{-1}. Given that temperate and boreal forests typically assimilate 25 to 100 kg-N ha^{-1} yr^{-1} (Chapin III et al. 2002) we conclude that the soils of succession stage 0 could only provide a small fraction of the annual nitrogen requirement of colonizing willow stands, whereas net mineralization within succession stage IV probably adequately supplied or exceeded the forest's requirement.

Considering that other studies have found a great deal of variation in estimates of net mineralization rate between incubation periods (eg. klingensmith and Van Cleve 1993, Kielland et al. 2006) our whole growing season estimates of net mineralization were admitadely rough, as they were only based on two month-long incubations. Other seasonal factors that were missed during our incubations, such as freeze-thaw cycles and periodic flood disturbances may cause

							Net N-mineralization rate (spring or summer)			KCl extractable N (spring or summer)		
	Age	**Bulk density**	**Bulk density <2mm**	**10 cm min. soil total N**	**Potentially mineralize. N**	**Soil %H20**	**total**	**NH_4**	**NO_x**	**total**	**NH_4**	**NO_x**
Mineral Soil N-pools (kg-N ha^{-1})												
Total N	0.91**	**-0.92****	-0.86**									
PMN	0.93**	-0.94**	-0.95**	**0.96****								
Litter Layer												
C:N ratio	N	N	N	N	N							
kg-N ha^{-1}	0.50*	**-0.65****	-0.47*	0.54**	N							
Spring net N-mineralization rate (kg-N ha^{-1} day^{-1})												
total	0.85**	-0.85**	**-0.91****	0.88**	0.89**	0.80**						
NH_4-N	N	N	N	N	N	N						
NO_X-N	0.48**	N	**-0.55***	0.48*	0.54*	N						
Spring KCl extractable N (kg-N ha^{-1})												
Total	0.78**	-0.89**	-0.79**	0.84**	0.83**	**0.91****	0.62**	N	N			
NH_4-N	0.71*	-0.82**	-0.70**	0.71**	0.72**	**0.84****	0.49*	0.60**	N			
NO_X-N	N	N	N	N	N	N	N	-0.53*	**0.77****			
Summer net N-mineralization rate (kg-N ha^{-1} day^{-1})												
total	0.72**	-0.73**	-0.79**	0.76**	**0.82****	0.64**						
NH_4-N	N	N	N	N	-0.52*	**-0.55***						
NO_X-N	0.74**	-0.77**	-0.82**	0.81**	**0.85****	0.70**						
Summer KCl extractable N (kg-N ha^{-1})												
Total	0.82**	-0.82**	-0.87**	0.87**	**0.94****	0.79**	0.72**	-0.57*	0.77**			
NH_4-N	0.79**	-0.80**	-0.81**	0.80**	**0.90****	0.82**	0.75**	-0.57*	0.79**			
NO_X-N	0.81**	-0.76**	**-0.85****	0.84**	0.85**	0.76**	0.63**	-0.58*	0.71**			
RC Summer 2005 (µg-N capsule^{-1})												
total	N	N	N	N	N	N	N	N	N	N	N	N
NH_4-N	N	N	N	N	N	N	-0.71*	N	**-0.85****	-0.67*	-0.68*	-0.65*
NO_X-N	N	N	N	N	N	N	N	N	N	N	N	N
RC Fall 2005 (µg-N capsule^{-1})												
total	N	-0.63*	-0.64*	**0.76****	0.63*							
NH_4-N	N	N	N	N	N							
NO_X-N	N	N	-0.55*	**0.70***	0.57*							
RC Spring 2006 (µg-N capsule^{-1})												
total	0.43*	-0.35*	-0.37*	0.37*	0.46*	**0.66****	N	0.65**	N	0.55*	0.65**	N
NH_4-N	N	N	-0.38*	N	N	N	N	**0.68****	N	N	N	-0.52*
NO_X-N	0.43*	N	N	N	0.49*	0.51*	N	N	N	**0.52***	0.46*	N
RC Summer 2006 (µg-N capsule^{-1})												
total	**0.76****	-0.69**	-0.66**	0.74**	0.65**	N	N	-0.59*	0.55*	0.71**	0.65**	0.66**
NH_4-N	N	-0.55**	-0.45**	0.39*	0.54*	0.51*	N	**-0.62****	N	0.57*	0.58*	N
NO_X-N	0.70**	-0.62**	-0.63**	0.71**	0.63**	N	N	-0.6*	0.54*	**0.71****	0.64**	0.66**
RC Fall 2006 (µg-N capsule^{-1})												
total	0.62**	-0.66**	**-0.67****	0.65**	0.66**							
NH_4-N	0.52*	-0.52*	**-0.55***	0.54*	0.52*							
NO_X-N	0.62**	-0.66**	-0.67**	0.67**	**0.68****							

Note: soil percent water, mineralization rate, and KCl extractable N only measured once during spring and summer. Spring or summer resin capsules tested for correlatation with either spring or summer variables even if they were not from the same year.
**:significant correlation at the 0.01 level; and *: significant at the 0.05 level (2-tailed). N=not significant (p>0.05)
-Bolded values signify highest correlation coefficients, shaded values indicate that a correlation was not tested.

Table 6. Spearman rho correlations between N availability indices and environmental variables.

actual net mineralization to be greater than our estimates. Nevertheless, our results were sufficient to demonstrate the low fertlility of early succession and the high-fertility later succession.

Net N-mineralization rates have been studied extensively in many other forest ecosystems and reviews conducted by Binkley and Hart (1989) and Scott and Binkley (1997) conclude that soils in temperate forests typically mineralize between 15 and 115 kg-N ha^{-1} yr^{-1}. Thus growing season net mineralzation within the Kol's early succession (stage 0 and I) soils was low relative to this average, whereas the Kol's mature forest soil (stageIV) would likely be near the high end of this range if the litter layer were included.

The pattern of increasing net mineralization with succession that we documented on the Kol is consistent with what has been shown in other chronosequences, although there were considerable differences between the magnitudes of these rates among different floodplains. In the Tanana River floodplain, Alaska, Van Cleve et al. (1993b) found that total annual net mineralization in the forest floor and top 5cm of mineral soil was 2.6 kg-N ha^{-1} in four year old willow *(Salix sp.)* stands, and maximized at 16 kg-N ha^{-1} yr^{-1} in 107 year old poplar *(Populus balsamifera)* stands. This maximal rate is considerably lower than the net mineralization rate that we measured in stage IV (49 kg-N ha^{-1} season^{-1}) on the Kol floodplain. Walker and Chapin III (1986) found that the Tanana's vegetation responded to this increasing nitrogen availability during succession with increased foliar nitrogen concentrations.

Adair et al. (2004) also measured net mineralization across succession in cottonwood stands *(Populus sp.)* on the Green and Yampa river floodplains in Northwestern Colorado. As on the Kol and Tanana floodplains, net mineralization in the Yampa floodplain was lowest in the youngest succession stages (0-20 year old cottonwood stands), approximately 15 kg-N ha^{-1} yr^{-1} (to 20cm) and increased to 29 kg-N ha^{-1} yr^{-1} in stands greater than 100 years old. However, in contrast to all of these other chronosequences. Adair et al. (2004) found that mineralization rate was highest in the youngest succession stages on the Green River, at nearly 79 kg-N ha^{-1} yr^{-1}. Adair et al. (2004) recognized that this was a unique pattern relative to other chronosequences, and suggested that it was likely due to geomorphic changes associated with flow regulation by an upstream dam. As was the case in the Tanana floodplain, foliar nitrogen concentrations were significantly correlated with net-N mineralization in the Green and Yampa Rivers.

Whereas most of the mineralized nitrogen was usually nitrified in the soils of the Kol floodplain, the vast majority of dissolved inorganic nitrogen in succession stages 0 and I and roughly half of that in stage IV was ammonium. High nitrification rates yet a low standing nitrate pool is commonly observed (eg. Nadelhoffer et al. 1983) and is attributable to nitrate's greater mobility in the soil and its tendency to be lost through leaching and denitrification. The high nitrification rates that we observed in late succession further indicated that the Kol's mature forest soils were particularly nitrogen rich, as Pacific-rim forest soils are typically dominated by ammonium (Van Cleve et al. 1993b, Kielland et al. 2006) except when nitrogen availability greatly excceds the microbial communitie's nitrogen demand, as often occurs when alders fix enormous quantities of nitrogen (Van Cleve et al. 1993b, Hobbie et al. 1998, Rhoades et al. 2001, Brenner et al. 2005).

Hypotheses 2 and 3

We found support for our second hypothesis; that in the absence of salmon, resin absorbed nitrogen originated primarily from the soil (Figure 5, Table 6). When all seasons within each succession stage were averaged, resin absorbed nitrogen was lowest in stage 0 and highest in stage IV; the same increasing pattern with succession that occurred with all other indices of soil nitrogen fertility. A similar increase in resin absorbed nitrogen with succession was also documented on the Yampa and Green River floodplains by Adair et al. (2004). However, unlike the other soil fertility indices, resin absorbed nitrogen also varied greatly with season, and during summer 2005 we found no correlation between resin absorbed nitrogen and the other soil fertility indices. In addition resin absorbed nitrogen during spring 2006 correlated much less strongly with the other soil fertility indices than did resin absorbed nitrogen during the fall 2005 and summer and fall of 2006 sampling periods. Our results indicated that the altered fertility patterns we observed during the summer 2005 and spring 2006 were likely driven by two factors: flooding and fertilization with salmon carcasses.

Extensive flooding (without salmon carcasses) occurred during the spring 2006 resin capsule incubation period. Overland flow periodically inundated many of our young (stages 0 and I) succession sites because they were adjacent to the main channel and were lower in elevation than older forest stands. In contrast, only one mature forest (stage IV) site received overland flow. We found that resin absorbed nitrogen in stage I was greatly increased during spring flooding relative to non-flood/non-salmon sampling periods, and nearly to the levels of resin capsules in stage IV. Figure 6 provides evidence that the spring increase in resin absorbed nitrogen was in fact due to flooding. Resin capsules at sites with overland flow absorbed nearly twice the nitrogen as at sites that did not flood, however, this was only true for sites greater than five years old.

Flooding could increase resin absorbed nitrogen in several ways. For one, flowing floodwaters may import nitrogen to these sites. Also, the physical disturbance associated with flooding, waterlogging and drying may enhance mineralization (Baldwin and Mitchell 2000). Our data suggests that disturbance is the stronger effect. Stage I sites likely showed greater response to flooding than stage 0 sites because they contained vastly more organic matter, fine sediments and nitrogen, and flooding probably increased nitrogen availability and mobility from within the soils. Flooding may have also enhanced ion diffusion and mass flow of the soil solution, and like plant roots, resin capsules are sensitive to both of these factors (Binkley and Hart 1989).

The timing of the salmon dieoff corresponded to the summer resin incubation period in late August in 2005. During this time, we found evidence in support of our third hypothesis, that salmon introduce a pulse of labile nitrogen into otherwise infertile early succession. Salmon spawned in the main channel and their decaying carcasses accumulated along stage 0 and I alluvial bars that were adjacent to the main channel. We observed that fluctuating water levels and several species of gulls, which fed on the carcasses, delivered salmon nutrients to these early succession stages. Mean resin absorbed nitrogen was actually highest in succession stage I during 2005, and in contrast to the other seasons, ammonium, rather than nitrate, comprised the majority of the resin absorbed nitrogen during this time. Ammonium is the direct product of carcass decomposition and Drake et al. (2005) found that carcass derived ammonium was not nitrified until approximately a one-month after the onset of decomposition. Furthermore, Figure 7 shows that in general, stage I sites that received salmon carcasses had elevated resin absorbed nitrogen relative to those that did not. We expect that resin capsules at stage 0 sites would have absorbed even more nitrogen during the late summer of 2005, as they received even more carcasses, however resin capsules were not used in stage 0 sites during this period.

Rather than uniformly fertilizing the soil of early succession, salmon carcasses create “hot-spots” of nitrogen availability. Drake et al. (2005) found that each decomposing carcass influenced nutrient availability on about 2.5 m^2 of soil. While not measured in this study, we suspect that the area that each carcass influenced in the Kol was larger than what Drake et al. (2005) found because they protected their carcasses from terrestrial vertebrates, whereas we observed that gulls dispersed these nutrients in the Kol floodplain. Even so, we observed that some regions of alluvial bars received many carcasses and other regions received little or none. Since we installed resin capsules randomly at a rate of approximately 1 capsule per 100 m^2, whereas carcasses were deposited at a rate of 1 per 30 m^2 in stage I during 2005, it is very likely that these capsules missed carcass hot-spots at many of these sites. In retrospect, the use of three resin capsules per site was sufficient to discriminate fertility among succession stages, but a greater number should have been used to detect the “hotspots” on years of low salmon abundance. While comprising a small area, these localized nitrogen flushes may still be very important to the plant community because we observed that even young (<5 yr old) willows often had roots that were more than a meter long, and these roots formed extensive networks.

Western Kamchatka's pink salmon runs are usually about ten times higher on even years than it is on odd years, and we originally designed this study to compare the fertilization effect on a low and high year, 2005 and 2006. Unfortunately, pink salmon runs were extremely depressed throughout western Kamchatka in 2006 and of a similar magnitude as low salmon years. Furthermore, 2006 was also a very dry year and the water level was low during the main spawning period. What carcasses did occur were distant from our study sites and were not deposited into the riparia until early September, after the summer resin incubation period. Therefore, in contrast to 2005, we did not see any elevated nitrogen concentrations at stage I or stage 0 sites during the summer of 2006. Rather, resin absorbed nitrogen was lowest during this period, and we were unable to test for the much more extreme fertilization effect of a high salmon year.

Although we were unable to prove with resin capsules that salmon carcasses created a late season pulse of nitrogen at stage 0 sites the fact that these sites received 25 kg-N ha^{-1} on a low salmon year and deposition rates were estimated to be about 10 to 30X higher on high salmon years with typical flooding (Chapter 1) indicates that salmon imported nitrogen is almost assuredly the largest source of plant available nitrogen to these early succession sites. Even on a low salmon year, 2006, the quantity of nitrogen imported by the salmon probably exceeded net mineralization during the entire growing season.

In contrast to the large fluctuations evident in stage I, resin capsules at the stage IV sites absorbed invariably high quantities of nitrogen regardless of season, because they typically neither flooded extensively nor received significant salmon carcasses relative to the high nitrogen content of their soils. For example stage IV sites received approximately 2kg-N ha^{-1} from salmon carcasses in 2005 and 0.4 kg-N ha^{-1} in 2006. In contrast, the top 10cm of mineral soil at these sites contained nearly 2,000 kg-N ha^{-1} of total nitrogen, 54 kg-N ha^{-1} of potentially mineralizeable nitrogen, and mineralized net mineralization was nearly 50 kg-N ha^{-1} per growing season. Thus the vast majority of nitrogen absorbed by resin capsules at stage IV sites originated from within the soil rather than from decomposing salmon carcasses.

Our final hypothesis, that the pulse in nitrogen availability from salmon carcasses would be short term, was supported in this study. We observed that the carcasses delivered to early succession were largely decomposed within weeks because gulls, and in some cases maggots and bears voraciously consumed the salmon. While much of this nitrogen was potentially returned to these sites as bird guano, nearly all visual remains of salmon and guano were washed away with subsequent fall flooding. Following fall flooding, resin absorbed nitrogen was again very low in the early succession stages. In addition to resin capsules, all the other of soil nitrogen fertility indices also indicated that early succession stages were infertile in the spring and summer of 2006 as well, despite having received large quantities of salmon carcasses in the previous years (late summer of 2005).

Our conclusion that on an annual scale, the fertilization effect of salmon is brief, contrasts with Drake et al. (2005) who found that decomposing salmon carcasses increased soil nitrogen availability all winter long and into the following spring. This probably occurred because Drake et al. (2005) placed carcasses on organic-rich soils, whereas we found that most carcasses were deposited onto gravel bars in the Kol floodplain, and these gravel bars' coarse soils were flushed during subsequent fall and spring flooding. Significant salmon-imported nitrogen is likely only retained in early succession as retention capacity improves during succession from the accumulation of fine sediments and the re-deposition of plant assimilated salmon nitrogen as litter (Chapter 1).

Conclusions

We found that in the absence of salmon, early succession soils had very low total nitrogen, potentially mineralizeable nitrogen, and KCl extractable dissolved inorganic nitrogen. Furthermore we found that net-mineralization in early succession soils could only provide a small fraction of the forest's annual nitrogen requirement. In contrast, soils in mature forests were nitrogen rich and net-mineralization could likely provide the majority of the vegetation's nitrogen requirement.

However, the extreme nitrogen infertility of early succession may be temporarily alleviated by a late season pulse of labile nitrogen entering the soils from spawned-out salmon, which during one season we detected using ion exchange resin capsules. In Chapter 1 we found that the quantity of labile nitrogen imported to stage 0 alluvial bars from decomposing salmon carcasses averaged 25 kg-N ha^{-1} growing season^{-1} on a low salmon year, but was approximately 10 to 30 times higher on high salmon years. Even on this low salmon year the quantity of nitrogen imported by the salmon exceeded net-mineralization within the top 10cm of soil (approximately 5.5 kg-N ha^{-1}), indicating that salmon were the largest nitrogen source to colonizing vegetation. However, we found that the salmon fertilization effect in early succession lasted several weeks at most, as carcasses were rapidly decomposed and subsequent fall flooding flushed young gravel bars, reverting them back to their infertile states. Spring flooding, even without salmon also appears to increase nitrogen availability in early succession.

This study suggests that the primary short-term function of salmon carcasses in the Kol floodplain is to alleviate strong nitrogen limitation on early succession alluvial bars in late summer. Thus, if the pink salmon run were lost or drastically overharvested, as has occurred in many other large rivers in the Pacific-rim, there may be an immediate effect of increased nitrogen limitation in early succession. While the annual pulse of nitrogen availability caused by decomposing carcasses appears to be brief, spawning salmon likely also have a long-term fertilization effect by building vegetation and soil nitrogen pools in early succession, in concert with the growth of soil nitrogen retention capacity due to accumulating fine sediments and plant litter in early succession. Thus although the annual salmon input to the mature forest succession stage (stage IV) is minor, the high nitrogen fertility that we observed at these sites is likely attributable in part to the legacy of salmon nutrient inputs these sites received in early succession.

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CHAPTER 3:
THE CONTRIBUTION OF SPAWNING SALMON TO FOLIAR NITROGEN NUTRITION DURING FLOODPLAIN PRIMARY SUCCESSION

Abstract

As is typical in floodplain primary succession, vegetation in the Kol River floodplain colonizes nitrogen-poor alluvial bars, and fertility improves as soils develop during succession. However, unlike other chronosequences studied to date, the Kol floodplain receives large annual nitrogen subsidies from spawning Pacific-salmon. The purposes of this study were to 1) determine how foliar nitrogen concentrations change during succession and 2) use the natural abundance of the ^{15}N isotope in foliage to trace nitrogen sources during succession. We found that foliage in both the active and passive floodplain regions was nitrogen-rich (mean molar C:N 21 and 26 respectively) relative to the uplands (C:N 32), other Pacific-rim floodplains, as well as the global average for temperate broadleaf forests (C:N 35 McGroddy et al. 2004). Furthermore, foliage of non nitrogen-fixers in both the active and passive floodplains was enriched with ^{15}N isotope (mean $\delta^{15}N$ 2‰ to 3‰ respectively), confirming that salmon were a major nitrogen source to the vegetation. Foliar C:N ratios suggested that vegetation may have been nitrogen-limited for a brief period at the onset of succession (approximately 20 years) but this limitation was rapidly satiated as soil fertility increased during succession. Elevated foliar $\delta^{15}N$ values of non-nitrogen fixing species (averaging 4‰) indicated that salmon were a major nitrogen source for colonizing vegetation during early succession. After the first 20 years, nitrogen was probably not limiting for at least the next 60 years of succession, and declines in foliar ^{15}N by 2‰ indicated that *Alnus*-fixed nitrogen and nitrogen mineralized from fine sediments were the major sources of plant-available nitrogen during this time. Older sites in the passive floodplain did not receive major annual nitrogen inputs. Rather, negative correlation between foliar C:N and $\delta^{15}N$ indicated that these sites recycled nitrogen imported in early succession. Despite being distant from river channels and not receiving salmon carcass deposits for hundreds of years, elevated foliar $\delta^{15}N$ (3 to 4‰) at sites within the passive floodplain indicated these sites were still enriched with salmon-imported nitrogen. While other studies conducted in the riparian zones of static upland streams have found that salmon-nitrogen fertilization is limited to small scales, primarily within 25 m, but up to 100 m from the streambank, we conclude that salmon fertilized the entire 2.5 km wide modern floodplain of the Kol River. This occurs because the river moves across the floodplain in both space and time and salmon-nitrogen imported in early succession is stored in soils and forest biomass.

Introduction

At the onset of primary succession vegetation colonizes bare rock environments with very low plant-available nitrogen. Consequently, vegetation growth may be severely nitrogen limited during this time (Vitousek and Walker 1989, Vitousek et al. 1989b, Walker and del Moral 2003). As a result of this limitation, symbiotic nitrogen fixers are often important colonizers in early succession (Walker 1993), but nitrogen availability still limits plant growth as the energetic cost of nitrogen fixation is high, approximately 8 to 12 g of glucose per gram of nitrogen fixed (Gutschick 1981). Over the long term, symbiotic nitrogen fixers function to build ecosystem nitrogen pools and may facilitate the growth of later successional species (Walker and del Moral 2003). Given that some plants are adapted to nitrogen poor conditions, while others nitrogen rich conditions, and changes in soil fertility can elicit changes in community composition (Aerts and Chapin III 2000), nitrogen inputs in early succession may have long-term influence on a wide range of ecosystem properties (eg. Fastie 1995, Vitousek and Walker 1989).

The floodplain of the lower Kol River (Kamchatka, Russian Federation) is a mosaic of successional habitats (*sensu* Stanford et al. 2005), caused by the constant erosion of existing sites and the deposition of new alluvial deposits as river channels migrate throughout the floodplain. Succession begins in the Kol flooodplain with the colonization of bare gravel bar deposits by young willow *(Salix and Chosenia)* trees, which gradually develop into canopy forests when sites persist rather than being eroded away. Nitrogen-fixing alder *(Alnus)* trees proliferate upon reaching the canopy within 20 to 30 years, and for the next 60 years forests have a mixed willow and alder canopy with a tall forb understory. Eventually, the willow and alder trees senesce, leaving vast meadows of tall forbs with scattered remnant trees. After hundreds of years, these tall-forb meadows eventually transition into grass-meadows. The oldest sites (likely thousands of years old) consist of a heath community that occurs on an ancient terrace (abandoned floodplain) adjacent to the modern floodplain. (see Chapter 1)

Based on the very low net N-mineralization rates that we quantified on gravel bars at the onset of succession (Chapter 2), we hypothesized that colonizing vegetation should be strongly nitrogen limited. However, the Kol floodplain receives enormous nutrient subsidies from pink salmon *(Oncorhynchus gorbuscha)*, that mature in the ocean and spawn and die in this river. We found that flooding in early September deposited decomposing salmon carcasses onto these young gravel bars, importing an average of 25 kg-N ha^{-1} to these sites on a year with low salmon abundance. Carcass deposition rates were approximately ten to thirty times higher on abundant salmon years (Chapter 1). In contrast, few carcasses were deposited in older forest stands.

Therefore we developed a general working hypothesis that spawning salmon were a major nitrogen source to colonizing forests with the potential to alleviate nitrogen limitation. And, as soil nitrogen accumulates most rapidly during early succession, we hypothesized that vegetation in older forests recycled salmon-imported nitrogen acquired in early succession. (Chapter 1)

Because salmon are enriched with the ^{15}N stable isotope ($\delta^{15}N$ = 9‰ for pink salmon in the Kol floodplain B. Ellis unpublished) relative to terrestrially-fixed nitrogen ($\delta^{15}N$ typically -2 to 0 ‰, reviewed by Nadelhoffer and Fry 1994), nitrogen stable isotopes have been used as natural tracers of salmon-imported nitrogen (Bilby et al. 1996, Ben-David et al. 1998, Hildebrand et al. 1999, Helfield and Naiman 2001, Helfield and Naiman 2002, Mathewson et al. 2003, Bilby et al. 2003, Bartz and Naiman 2005). Some studies have found that riparian vegetation growing along spawning streams may benefit from this fertilization through increased foliar nutrient concentrations (Helfield and Naiman 2001, Helfield and Naiman 2002, Bilby et al. 2003) and increased growth rates (Helfield and Naiman 2001-but see Kirchoff 2003); or this fertilization may cause changes in community composition (Bilby et al. 2003). While these studies unanimously showed that vegetation incorporated salmon-imported nitrogen, this fertilization occurred over very small scales, primarily within 25m, but up to 100m from the stream banks streambanks (Ben-David et al. 1998, Hildebrand et al. 1999, Helfield and Naiman 2002, Bilby et al. 2003). However, all of the aforementioned studies were conducted in relatively static riparian communities along upland streams where nutrient transfer is primarily unidirectional, from the uplands to the stream. In contrast, this study was conducted in a dynamic large-river floodplain. Because (1) river channels migrate throughout expansive alluvial floodplains over time, (2) nutrient transfer is reciprocal between the mainchannel and riparia in floodplains (*sensu* Junk et al. 1989), and (3) nutrients are stored in the rapidly accumulating soils and biomass of young successional communities (Walker and del Moral 2003), we expected that salmon nutrient fertilization would occur over much greater scales in the Kol River floodplain than has been shown previously.

The natural abundance of the ^{15}N isotope has also been used to track nitrogen inputs and internal cycling processes in primary succession (Vitousek et al. 1989a, Kohls et al. 1994, Hobbie et al. 1998, Kohls et al. 2003, Hobbie et al. 2005). For example all of aforementioned studies found that foliage of non N-fixers was highly depleted in ^{15}N (mean $\delta^{15}N$ for different species ranged from -8‰ to -4‰) at the onset of succession because colonizing vegetation relied on nitrogen imported with atmospheric deposition, which was also highly depleted in ^{15}N. After this initial period where atmospheric deposition was the main nitrogen source Hobbie et al. (1998) and Kohls et al. (2003) found that symbiotic nitrogen fixers rapidly built plant-available nitrogen pools during succession in the Glacier Bay moraine chronosequence, and foliar δ^{15}N of non-fixers approached the values of the fixers as they assimilated this biologically-fixed nitrogen. In contrast, foliar δ^{15}N remained very low for hundreds of years in chronosequences with low nitrogen fixation rates (Vitousek et al. 1989a, Kohls et al. 1994). Thus the overarching conclusion of these studies was that in early succession, when internal soil nitrogen cycling is low and nitrogen inputs are comparatively high, foliar δ^{15}N primarily reflected nitrogen inputs.

In cases where different sites have access to the same nitrogen sources, differences in foliar δ^{15}N is driven by overall site fertility, as evidenced by a negative correlation between foliar δ^{15}N and foliar C:N found in nearly all studies (eg. Vitousek et al. 1989a, Garten 1993, Garten and Van Miergot 1994, Koopmans et al. 1997, Emmett et al. 1998, Kitayama and Iwamoto 2001). This occurs because under relatively nitrogen rich conditions soil nitrogen cycling is "open," in which case nitrification and nitrogen losses enrich foliar δ^{15}N. On the other hand, nitrogen cycle is "tight" under low-fertility conditions causing high fractionation and a depletion foliar δ^{15}N (Högberg 1997). Therefore Vitousek et al. (1989a) concluded that foliar δ^{15}N increased in late succession because the vegetation community switched from nitrogen to phosphorus limitation whereas Hobbie et al. (1998) and other secondary succession studies (Wang et al. 2007) concluded that foliar δ^{15}N decreased in late succession because vegetation became progressively more nitrogen limited. Thus, these studies suggest that in the absence of major nitrogen inputs in late succession, foliar δ^{15}N should increase under increasingly fertile conditions or decrease if nitrogen limitation became progressively more severe.

In this chapter we sought to determine how spawning salmon contributed to vegetation nutrition during primary succession in the Kol floodplain. We used foliar C:N ratios to determine the nutritional status of the floodplain vegetation and how this changes during succession and we also used the ^{15}N isotope as a natural tracer of nitrogen inputs during succession.

We proposed the following hypothesis for the entire modern floodplain (active + passive regions):

- because of the very large fertilization effects of salmon and to a lesser extent *Alnus* we expected foliar C:N to be low relative to typical values for temperate broadleaf forests, other Pacific-rim floodplains, as well as relative to the uplands.
- because salmon are enriched in ^{15}N, we expected foliar δ^{15}N to be high relative to typical values for temperate broadleaf forests, other Pacific-Rim floodplains as well as relative to the uplands.

We proposed the following hypothesis for the young forests (<100 years old) that occur in the active region of the floodplain:

- foliar $\delta^{15}N$ would be elevated at the onset of succession because salmon were the major nitrogen source during this time
- foliar $\delta^{15}N$ would be lower during *Alnus* inhabited succession stages relative to the onset of succession
- there would not be a negative correlation between foliar C:N and foliar $\delta^{15}N$, indicating that foliar $\delta^{15}N$ in this region was driven by nitrogen inputs rather than by internal cycling processes

In contrast, we proposed the following hypothesis for the older forests (>100 years old) that occur in the passive floodplain:

- foliar $\delta^{15}N$ would be negatively correlated with foliar C:N, indicating that the passive floodplain recycled nitrogen imported in early succession; and
- there would be an increase in foliar $\delta^{15}N$ with succession if foliar C:N indicated that the vegetation was very nitrogen rich and a decrease in foliar $\delta^{15}N$ in late succession if foliar C:N indicated that nitrogen became progressively more limiting in late succession.

Study area

The headwaters of the Kol River (Kamchatka, Russian Federation) originate in the central Kamchatka mountain range at an elevation of nearly 2000 m and the river flows westward (see Figure 1). Roughly seventy percent of the catchment is tundra-dominated coastal plain below 150 m and the Kol is a seventh-order river at its mouth. The entire catchment is largely pristine. This study was conducted on a expansive floodplain (N53°49.506’ E156°3.716’) of the lower Kol River, approximately 6 to 10 km due east of the rivers mouth at the Sea of Okhotsk (Figure 1). Research was based out of a biostation operated by the Wild Fishes and Biodiversity Foundation (Petropavlovsk, Kamchatsky) and the Wild Salmon Center (Portland, Oregon). The main channel adjacent to our camp had a minimum summer base flow of approximately 20 to 30 $m^3 s^{-1}$.

We used the term “active floodplain” to define the region of the floodplain bounded by the primary and secondary channels (see Chapter 1). Active floodplain sites commonly received overland flows during annual flooding and erosion rates were sufficiently high such that the forests were usually less than100 years old. This contrasts with the “passive floodplain” which we considered to be the region between the active channels and the modern floodplain margin. Passive floodplain forests were between 100 and hundreds of years old, and generally did not have annual overland flooding, but did flood during the higher flows. The passive floodplain

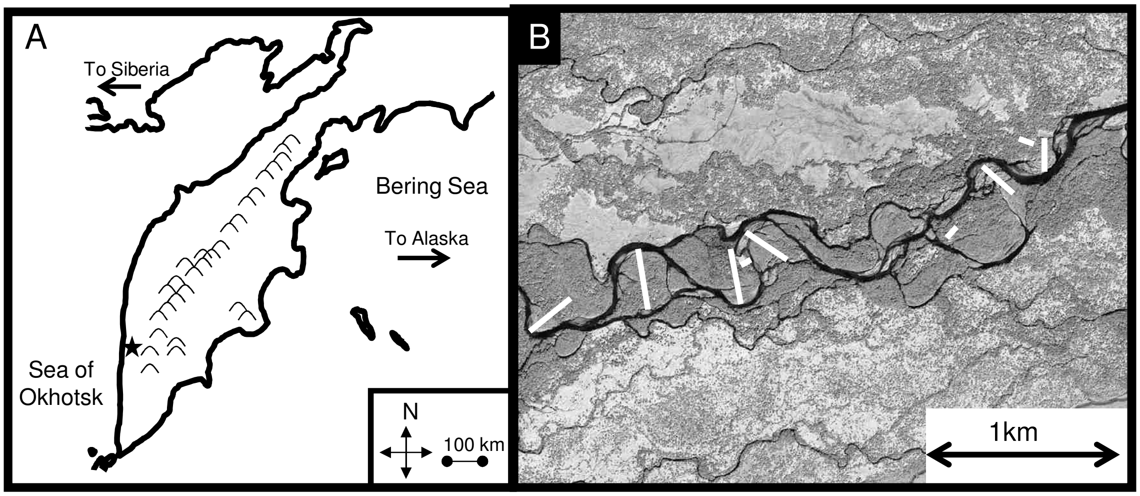

Figure 1. Map A: the Kamchatka Peninsula in the Russian far-east. The star indicates the location of the Kol River. Map B: Satellite imagery of the Kol Floodplain in the region of our camp. The white lines show the study transects. Original sattelite imagery before modification was from the QuickBird Satellite and was provided by DigitalGlobe Inc. in 2004.

contained numerous springbrooks and tertiary channels. We used the term “modern floodplain” to include both the active and passive floodplain regions. There was also an “ancient floodplain terrace” on the northern end of the modern floodplain. There were no flowing channels, springbrooks or evidence of flooding in recent times in the ancient floodplain, but the abundance of swales and a tundra wall at its margin indicated that this region was once a floodplain of the Kol River.

Morris et al. (Chapter 1) modeled the dominant vegetation succession pathway in the lower Kol floodplain and proposed six succession stages during the first several hundred years of succession. Briefly, succession began at stage 0 (“the bare alluvial bar stage” ages 0-10 years) with willows *Salix sp.* and the willow-like *Chosenia arbutifolia* colonizing bare alluvial deposits. Stage I, or the “alluvial-bar willow/*Chosenia* stage” occurred from approximately 10-20 years when more than half of the land area of these alluvial deposits was colonized by two species of willow and the willow-like *Chosenia* tree. Stage II, or the “willow/*Chosenia* canopy stage” occurred from 20 to 30 years and was characterized by a canopy formed by the two willow species and *Chosenia* with young alder trees (*Alnus hirsuta*) in the understory. Stage III, or the “willow/alder/*Chosenia* canopy stage” ranged in age from 30 to 50 and was characterized by the senescence of one of the two willow species as well as *Chosenia*. The canopy was closed and shared by willow and alder trees, and a nitrophillic tall-forb community composed of stinging nettle *(Urtica diocia)* and *Filipendula camtschatica* grew prolifically in the understory. Stage IV, or the “declining willow, mature alder canopy stage” ranged in age from 50 to at least 100 years and was the oldest stage that commonly occurred in the active region of the floodplain. The canopy was composed of mature willow and alder trees and began to open during this stage due to tree senescence. The understory was dominated by dense stands of *Filipendula camtschatica*. Stage V, or the "tall-forb meadow stage" occurs in the passive region of the floodplain. By this time most trees had senesced leaving vast meadows of >3m tall forbs composed primarily of *Filipendula camtschatica*, with lesser abundance of nettles *(Urtica diocia)*. We have not aged stage V sites using tree cores because remaining trees had rotted trunks.

The quantitative succession models presented in Chapter 1 only considered succession until stage V, however we have observed that the tall-forb meadows were eventually replaced by a grass/short forb/woody shrub meadow community (stage VI), which was then replaced by a heath community composed primarily of the evergreen shrub *Empetrum sp*. as well as *Vaccinium sp.* in the most ancient regions of the floodplain (stage VII). The grass meadow community is probably hundreds of years old and the heath community is likely thousands of years old. A summary of forest community variables across succession is presented in Table 1.

In the coastal plain, the majority of land-area outside the floodplain was arctic tundra, dominated by sedges (*Carex sp.*), ericaceous shrubs (*Vaccinium sp*. and *Empetrum sp.*) cloudberry (*Rubus chamaemorus*) and other species. Birch *(Betula ermanii)* forests with understories of tall-forbs (*Filipendula camtschatica, Senecio cannibifolius, Angelica ursina*), grasses and *Vaccinium sp*. occurred on hills within the tundra landscape.

The climate of the south-western Kamchatka is cold, wet, sub-oceanic (Krestov 2003). According to weather data collected in the town of Sobolevo, approximately 50 km north of the Kol River, the mean annual temperature of the region is -0.9 °C. The mean temperatures of the coldest and warmest months are -14.9 and 12.2 °C respectively. The total frost-free period is 92 days (Sokolov 1974), and annual precipitation is approximately 789 mm (Krestov 2003). Soils outside the floodplain are Andisols and Histosols whereas floodplain soils are alluvial Entisols. Floodplain soils consisted of layers of sand and silt, and occaisionally, layers of buried organic matter overlying gravel and cobble deposits. Surface organic matter accumulations ranged from being entirely absent at the most extensively flooded sites, to having a dense litter layer and A-horizons commonly up to 10cm deep. Redox motteling was occasionaly observed, particularly in deeper sediment layers. Mean soil pH values (to approximately 5 cm) average approximately 6 and range from approximately 5.5 to 6.6 indicating that floodplain soils are moderately acidic (see Chapter 2).

Stage	Typical Age Range	Tree density (trees ha^{-1})	%willow	%alder	%chos.	Tree cov. (m^{2} ha^{-1})	%willow	%alder	%chos.	Total understory cover %	%grass	%nettle	% filk	fine sed. depth (cm)	10 cm min soil-N (kg-N ha^{-1})	L. Layer (kg-N ha^{-1})	L. Layer mol C:N	Salmon carcasses 2006 (kg-N ha^{-1})
0	0-10	Vegetation beginning to colonize, mostly bare												3	200	n/a	n/a	25
														(0-8)	(150-230)			(2-105)
I	10-20	69000	86	2	12	18	86	1	13	49	16	3	1	24	770	330	30	2
		(39000-115000)	(65-100)	(0-9)	(0-35)	(7-29)	(61-100)	(0-2)	(0-39)	(8-77)	(0-19)	(0-5)	(0-2)	(10-37)	(390-1080)	(170-650)	(22-42)	(0-3)
II	20-30	35000	81	8	11	24	61	13	6	90	17	21	10	24	1510	570	32	1
		3000-21000	(75-91)	(0-17)	(0-17)	(15-30)	(36-78)	(0-24)	(0-14)	(82-100)	(5-34)	(2-57)	(2-20)	(13-34)	(1360-1630)	(210-860)	(28-38)	(0-5)
III	30-50	4000	77	15	9	32	67	8	16	71	16	20	10	45	1710	740	30	0
		(2000-8000)	(50-100)	(0-27)	(0-23)	(24-37)	(35-100)	(0-19)	(0-46)	(42-96)	(4-34)	(17-29)	(0-17)	(23-71)	(1460-1990)	(420-1020)	(24-40)	0
IV	50-100	500	63	36	1	36	67	31	2	91	4	28	45	>50	1930	730	29	0
		(300-1000)	(40-93)	(8-57)	(0-3)	(15-55)	(44-93)	(7-49)	(0-7)	(73-100)	(0-10)	(15-50)	(32-58)	(30-78)	(1430-2390)	(1103-1190)	2	(0-2)
V	hundreds?	Tall forbs with few remaining willow and alder trees								99	0	9	78	>70	1950	1850	30	0
										(96-100)	0	(5-11)	(63-88)		(1560-2110)	(1160-3420)	(23-39)	0
VI	hundreds?	Grassland/short forb/woody shrub community, not measured																0
																		0
VII	thousands?	Empetrum nigra and Vaccinium sp. Heath, not measured																0

Table 1: means and ranges (in parenthesis) for vegetation and landscape variables by succession stage (from Chapter 1). Chos .= *Chosenia arbutifolia.* L. Layer=litter layer

Methods

Trans-floodplain transect

On August fifth and sixth of 2006 foliage was sampled along a 7.5 km long transect that was perpendicular to the river from the uplands on the north, across the floodplain to the uplands on the south (Figure 2). This transect crossed the river immediately adjacent to our camp. Using a handheld Garmin eTrex GPS, sampling points were selected approximately every 200 m along the transect, except at flowing channels, in which cases sampling points were chosen, 0, 10 and 50 m from the channel banks. These additional points were meant to increase the sample size of younger successional communities which generally comprised a smaller area than the older forest stands. The vegetation community was described at each point and foliage was collected from the two most abundant of the following taxa: (*Vaccinium, Carex, Salix, Filipendula camtschatica*, *Betula, grass and Empetrum nigrum*). Where available, whole leaves were amalgamated from three individual plants, and only fully mature leaves from the top of the plants were collected.

Sample points were grouped according to the following habitats: "active floodplain" (AF) which included all young successional forests (stages0-IV) in the region of the mainchannels; passive floodplain (PF) which included all sites between the active floodplain and the modern floodplain boundaries and consisted primarily of succession stages V and VI; ancient heath (AH) which included an ancient abandoned floodplain region now dominated by heath (succession stage VII); and finally "tundra/birch forest" (TU) which included all points outside the floodplain in the uplands. These regions are shown in Figure 2.

Chronosequence transects

Six transects were established within the floodplain to sample an array of points within the vegetation chronosequence (detailed in Chapter 1). Briefly, thetransects began on the inside of river meanders in the region of our camp and extended perpendicularly away from the river channel into the riparian forest. Smaller, 50 m long sub transects were established in the middle of even aged forest stands along the six larger transects. Three additional fifty meter transects were established in the active floodplain region to gain additional replicates of succession stages 0 and IV. In addition, five 50 m transects were established in the passive floodplain in succession stage V along pre existing trails. Each even aged stand was aged using tree cores from the largest trees, and mineral soil total nitrogen content (to ten centimeters) and total *Alnus* basal area coverage was determined according to the methods described in Chapter 1. Stand age could not be determined for stands older than eighty years because older trees had rotted trunks. One site aged 9 years old was grouped into succession stage I because more than half the land area on that

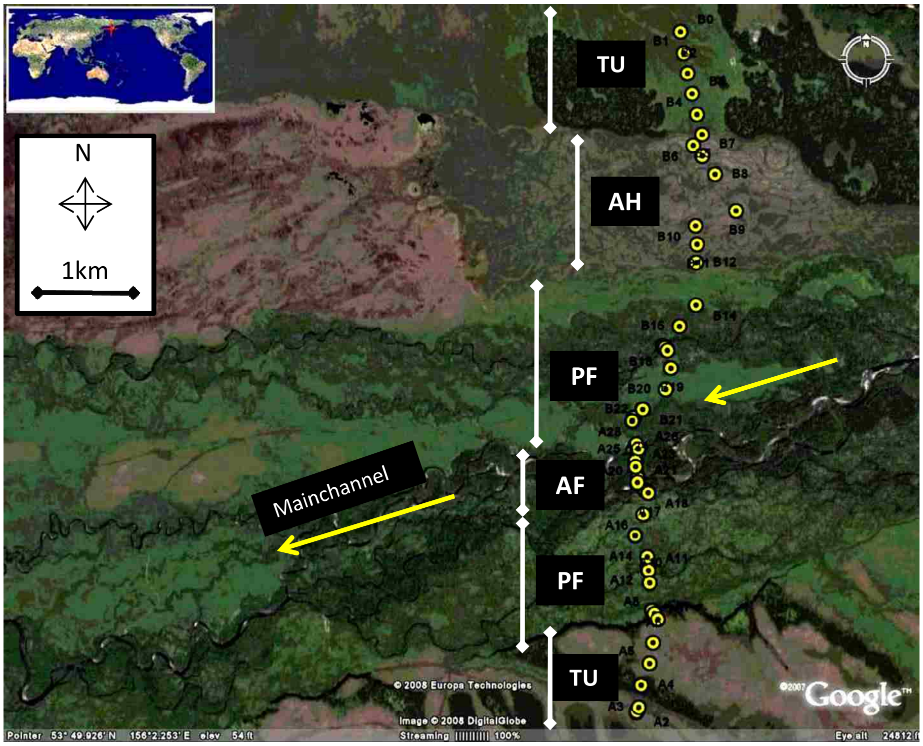

Figure 2. Map showing the trans-floodplain sampling transect. Region abbreviations are as follows: TU-tundra/birch forest uplannds; AH-ancient heath floodplain; PF-passive floodplain; and AF-active floodplain. Sampling points shown with yellow dots. Original map, without modifications (regions, lines, arrows, and other text) from "Google Earth 2007".

the gravel bar was colonized by a dense willow stand.

Foliage from all of these study transects was collected during the third week of July in 2006. Where available, the following dominant taxa were collected in stages 0 through V: *Alnus hirsuta, Chosenia arbutifolia, Salix sp. A,Salix sp. B, Filipendula camtschatica* and *Urtica diocia*. Leaves from five replicate plants collected along the entire transect were amalgamated to make one sample per species per site. Foliage was collected from mature leaves near the tops of the plants only. In addition, results from the large floodplain transect analysis (described previously) were grouped according to succession stages V, VI and VII and added to the succession analysis. Each point along the trans-floodplain transect within stages V through VII was considered a separate replicate site.

Foliage processing and analysis

Whole leaves (including the petiole) were refrigerated in zip-loc bags until they could be dried, usually within 24 hours after collection. Leaves were dried until brittle at approximately 70°C in an oven and then re-sealed in zip-loc bags at the field camp. Samples were exported from Russia to the USA following detailed government protocols. In the laboratory at the Flathead

Lake Biological Station (The University of Montana), samples were re-dried at 60 to 80°C and then ground in a coffee grinder. This homogenate was then subsampled and ground further in a SPEX ball mill. This powder was then subsampled and sent to the University of Georgia Stable Isotope Laboratory where it was analyzed for total carbon and nitrogen as well as the ratio of ^{15}N to ^{14}N isotopes using a combustion GC/MS system. Nitrogen concentration was reported as molar carbon to nitrogen ratios. ^{15}N concentration was reported in $\delta^{15}N$ units which is the parts per thousand deviation of the sample's ^{15}N:^{14}N from atmospheric N_2's ^{15}N:^{14}N which is 0.003675. Therefore $\delta^{15}N = ((R_{sample}R_{N2})/(R_{N2}))*1000$.

Statistical analysis

For the successional analysis, stages V through VII could not be aged because any remaining trees had rotted trunks and could not be cored. Therefore sites 0 through IV were also divided into categorical variables by succession stage. Differences in mean foliar C:N and $\delta^{15}N$ for the region or succession stage was determined using ANOVA followed by the Tukey post-hoc. In cases where the hypothesis that the data conformed to a normal Gaussian distribution was rejected using the Komogorov-Smirnov test, the data were log transformed prior to running the ANOVA. If the data still did not conform to a normal distribution following log transformation the data were analyzed using the non-parametric Kruskal-Wallis test followed by the Dunn post-hoc. In cases where only two groups were compared a T-tests were used. All correlation analyses utilized the non-parametric Spearman-rho test because the correlations were typically non-linear. All statistical analyses were conducted using the "Graphpad Prism version 5.00" and "SPSS for Windows 15.0" computer programs.

Results

Foliar C:N

We found significant differences in foliar C:N ratios among all regions in our large study transect (Figure 3 and Table 2), with the exception that the tundra/birch forest was not significantly different from the passive floodplain when the nonparametric test was used rather than the ANOVA test. When all species were combined, molar foliar C:N ratios were lowest (21) in the active floodplain, followed by the passive floodplain (26), tundra/birch forest uplands (32) and then then ancient heath region (46). The differences among these regions were driven both by differences in the same taxa among regions, as well as the occurrence of different growth

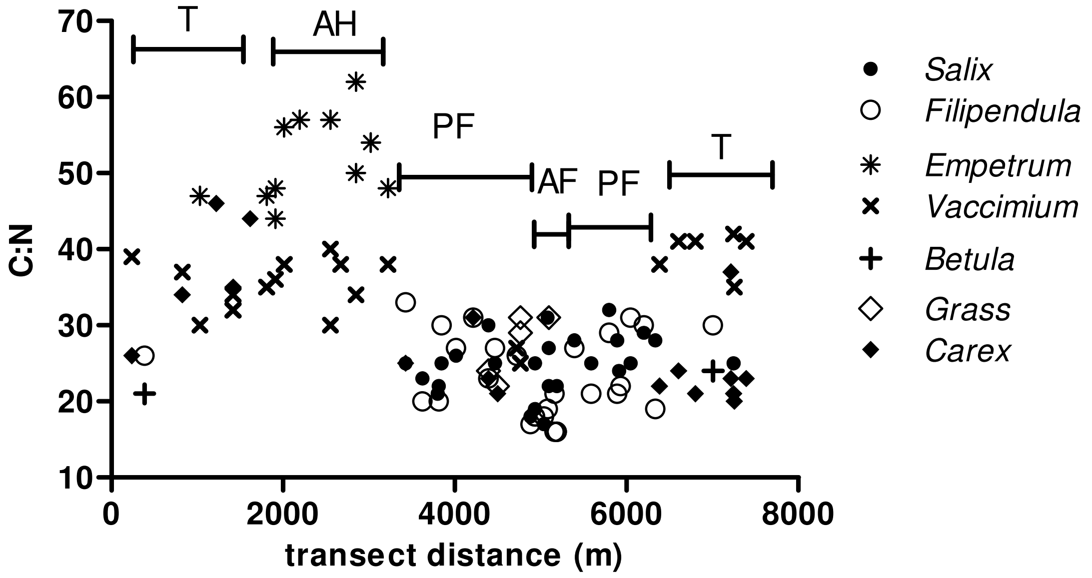

Figure 3. Foliar C:N along the trans-floodplain sampling transect. Region abbreviations are as follows. TU-tundra/birch forest uplands; AH-ancient heath floodplain; PF-passive floodplain; and AF-active floodplain.

	Tundra/Birch forest	Ancient Heath	Passive Floodplain	Active Floodplain	Statistics
Salix	**25**		**26^{AF}**	**22.6^{PF}**	T-test; p=0.0444
95% CI, N	n/a; 1		24.4 to 27.6; 16	18.6 to 26.7; 8	
Filipendula	**28**		**25.7^{AF}**	**17.7^{PF}**	kruskal Wallis/Dunn p=0.0003
	n/a; 2		23.3 to 28.1; 17	16.4 to 18.9; 9	
Vaccinium	**36.9^{PF}**	**36.3^{PF}**	**$25.7^{AH,TU}$**		ANOVA/Tukey; p=0.0003
	34.5 to 39.3; 13	33.2 to 39.4; 7	22.8 to 28.5; 3		
Empetrum	**47**	**52.9**			
	na; 1	48.5 to 57.3; 9			
Grass			**26.5**	**31**	
			19.8 to 33.2; 4	na; 1	
Carex	**28.9**		**25**		log trans. T-test n/s
	23.4 to 34.5; 13		18.1 to 31.9; 4		
Betula	**22.5**				
	na; 2				
total mean	**$32^{AH,AF}$**	**45.6^{all}**	**$26.1^{AH,PF}$**	**20.6^{all}**	Kruskal Wallis/Dunn p<0.0001
95% CI; N	**29.2 to 35.1; 32**	**40.5 to 50.8; 16**	**24.9to27.2; 44**	**18.2 to 23.0; 20.6**	

Table 2. Foliar C:N of samples collected along the large floodplain transect grouped by species and habitat. Superscripts show that a species mean within one habitat is significantly different from another habitat's mean.

forms among regions. For example, *Salix* and *Filipendula camtschatica* were both more nitrogen-rich in the active floodplain (C:N 23 and 18 respectively) than they were in the passive floodplain (26 for both species); likewise, *Vaccinium* was more nitrogen rich in the passive floodplain (26) than in the tundra/birch forest (36) or the ancient floodplain heath (37) communities. The ancient heath community was dominated primarily by the nitrogen poor (mean C:N 53) ericaceous shrub *Empetrum nigrum*, which did not commonly occur in the modern floodplain. The tundra/birch forest uplands exhibited a wide range of C:N ratios, containing both relatively nitrogen rich taxa (*Betula* C:N 22.5 and *Salix* C:N 25) as well as nitrogen poor species (*Empetrum nigrum* C:N 47 and *Vaccinium* C:N 37). In contrast, the passive floodplain had a very narrow range in C:N ratios with mean values per taxa only ranging from 25 to 27.

We also found highly significant differences in foliar C:N ratios when the data were grouped by succession stage (Figure 4 and Table 3). When all taxa were grouped together we found that foliar C:N ratios were relatively high at the onset of succession (stage 0 C:N 24), decreased in succession stage I (C:N 18) and leveled off between 16 and 17 in succession stages II through IV. Foliar C:N in succession stage 0 was significantly higher than stages I through IV, and there were no statistically significant differences between stages I through IV. After stage IV, foliar C:N ratios increased significantly stepwise in stage V (C:N 21), stage VI (C:N 27) and VII (C:N 46).

Salix B and *Filipendula camtschatica* were abundant in succession stages 0 through VI and exhibited the same U-shaped pattern as the overall mean foliar C:N ratio. While these changes tended to be significant for *Salix B*, in many post-hoc comparisons the differences were not significant for *Filipendula camtschatica*. Foliar C:N of the tree species *Chosenia arbutifolia* and *Salix A* followed the same pattern as the other species in stages 0 through III, but these tree species were mostly senesced by succession stage IV and therefore could not be assessed for an increase in C:N in later succession. *Alnus* foliar C:N was slightly higher in stage 0, was lowest in succession stages I through III and increased again in stages IV through V, but these changes were very slight relative to the other species and were not significant. In contrast, *Urtica diocia* exhibited the same pattern of elevated C:N ratios in early succession as the other species, but it's C:N ratios did not increase in late succession. Instead, C:N ratios remained low in stages II through V. Whereas the same group of species were found in succession stages 0 through V,

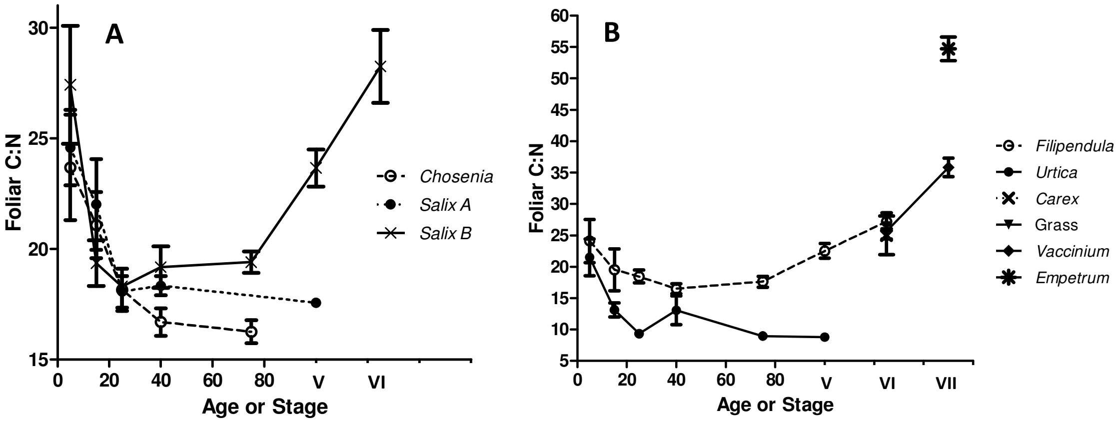

Figure 4. Foliar molar C:N grouped by succession stage. Graph A shows all the tree species (except *Alnus*) and B shows non-tree species. Typical succession stage 0 sites range in age from 0 to 10 years old; stage I - 10 to 20 years; stage II - 20 to 30 years; stage III – 30 to 50 years and stage IV – 50 to 100 years. Note-one site aged 9 years old considered stage I because more than half the site was covered in a dense tree stand. Foliar means for stages 0 through IV were plotted according to the X-axis point at the center of the age range for a particular stage. Stages V, VI and VII were not aged. Error bars show standard error.

	Succession Stage								
	0	I	II	III	IV	V	VI	VII	
Alnus	18.2	15.5	16	16.8	18.3	19.3			ANOVA/Tukey
se; N	3.3; 2	0.8; 7	0.6; 8	0.4; 4	0.5; 6	0.3; 3			p=0.0245
Chosenia	23.7	21.1	18.2	16.7	16.3				ANOVA/Tukey
se; N	2.4; 5	1.5; 5	1.0; 5	0.6; 3	0.5; 2				p=0.0456
Salix A	24.6^{II}	22	18.1^{0}	18.3		17.6			ANOVA/Tukey
se; N	1.7; 6	2.1; 6	0.7; 8	0.4; 2		n/a; 1			p=0.0221
Salix B	$27.4^{,I,II,III,IV}$	$19.4^{0,V,VI}$	$18.3^{0,V,VI}$	$19.2^{0,VI}$	$19.4^{0,VI}$	$23.7^{I,II}$	$28.3^{I,II,III,IV}$		ANOVA/Tukey
se; N	2.7; 5	1.0; 8	0.3; 6	0.9; 5	0.5; 6	0.8; 14	1.7; 4		p<0.0001
Filipendula	24.1	19.5	18.4	16.5^{VI}	17.6	22.5	27.2^{III}		Kruskal-wallis/Dunn
se; N	3.4; 5	3.3; 5	1.0; 8	0.8; 5	0.9	1.2; 15	1.1; 6		p<0.0043
Urtica	$21.5^{I,II,III,IV,V}$	13.1^{0}	9.3^{0}	13.1^{0}	9^{0}	8.8^{0}			ANOVA/Tukey
se; N	2.9; 6	1.1; 5	0.4; 8	2.3;3	0.2; 6	0.2; 4			p<0.0001
Vaccinium							25.7^{VI}	35.8^{VII}	T-test p
se; N							0.7; 3	1.5; 6	p=0.0013
Empetrum								54.7	
se; N								1.9; 7	
Carex							25		
se; N							3.1; 3		
Grass							26.5		
se; N							2.1; 4		
mean	$23.8^{I,II,III, IV}$	$18.4^{0,VI,VII}$	$16.2^{0,V,VI,VII}$	$16.9^{0,V, VI,VII}$	$16^{0,V,VI,VII}$	$21.1^{II,III,IV, VII}$	$26.7^{I,II,III,IV,VII}$	$46^{II,III,IV,V,VI}$	Kruskal Wallis/Dunn
	1.1; 29	0.8; 36	0.6; 43	0.6; 22	0.9; 24	0.9;37	0.7; 20	3.0; 13	p<0.0001

-Superscripts denote that a succession stage is significantly different from another succession. significance level =0.05.
-Column and row means calculated from each datapoint.

Table 3. Mean foliar C:N grouped by species and succession stage. This table corresponds to Figure 4.

stages VI and VII were dominated by other late succession species. Thus the higher foliar C:N ratios exhibited in these stages were primarily due to changes in growth form.

The rapid decline in foliar C:N ratios from stage 0 through I and leveling off in stages II through IV is mirrored the rapid increase in soil fertility during early succession. Foliar C:N ratios for most species in the active floodplain , as well as the mean for all plants in the active floodplain, were highly negatively correlated with both age and total soil nitrogen content (Table 4). In turn, site age and total mineral soil nitrogen content are highly correlated with each other (Chapter 2). Age and soil nitrogen variables were not collected for succession stages V through VII and therefore correlations between foliar C:N ratios and potential predictor variables were not evaluated for these sites.

	Age (years)	Soil N (min+LL) (kg-N ha^{-1})	Min. Soil N (Kg-N ha^{-1})	Alder Cover (m^2 ha^{-1})
Alnus	0.369 (0.058)	0.191 (0.370)	0.278 (0.161)	0.309(0.125)
Chosenia	-0.704 (0.001)	-0.707 (0.002)	-0.690 (0.001)	-0.539 (0.017)
SalixA	-0.697 (<0.001)	-0.606 (0.005)	-0.629 (0.002)	-0.679 (0.001)
SalixB	-0.491 (0.006)	-0.369 (0.058)	-0.444 (0.014)	-0.366(0.051)
Filipendula	-0.355 (0.069)	-0.195 (0.360)	-0.298 (0.131)	-0.111 (0.589)
Urtica	-0.581 (0.001)	-0.502 (0.009)	-0.553 (0.002)	-0.509 (0.006)
Total*	-0.531 (<0.001)	-0.469 (<0.001)	-0.485 (<0.001)	-0.394 (<0.001)

Table 4. Spearman rho correlation coefficients of foliar C:N verses age, total soil N (litter layer + 10 cm mineral soil), total 10 cm mineral soil N, and alder cover for active floodplain plants only. p-values are in parenthesis.

Foliar δ^{15}N

We found that the trans-floodplain transect could be divided into two statistically distinct regions as regards foliar δ^{15}N: the tundra/birch forest/ the ancient heath floodplain and the passive/active floodplain (Figure 5 and Table 5). Mean foliar δ^{15}N was higher in the passive floodplain (3.3‰) than the active floodplain (2.2‰), but the difference was not statistically significant. In contrast with the modern floodplain, foliar δ^{15}N in the tundra/birch forest and the ancient heath floodplain were both negative, with the tundra/birch forest (-2‰) slightly depleted from atmospheric N_2 (0‰) whereas the ancient heath floodplain was more highly depleted (-4.9‰). The differences among these regions were driven both by differences in the same species among regions, as well as the occurrence of different growth forms among regions. For example, *Salix* and *Filipendula camtschatica* were both more enriched with ^{15}N in the passive floodplain (δ^{15}N 3.8‰ and 3.1‰) than in the active floodplain (δ^{15}N 2.9‰ and 1.5‰). In contrast, *Filipendula camtschatica* was slightly depleted from atmospheric N_2 in the tundra/birch forest (δ^{15}N -0.7‰). *Vaccinium* was enriched with ^{15}N relative to atmospheric N_2 in the passive

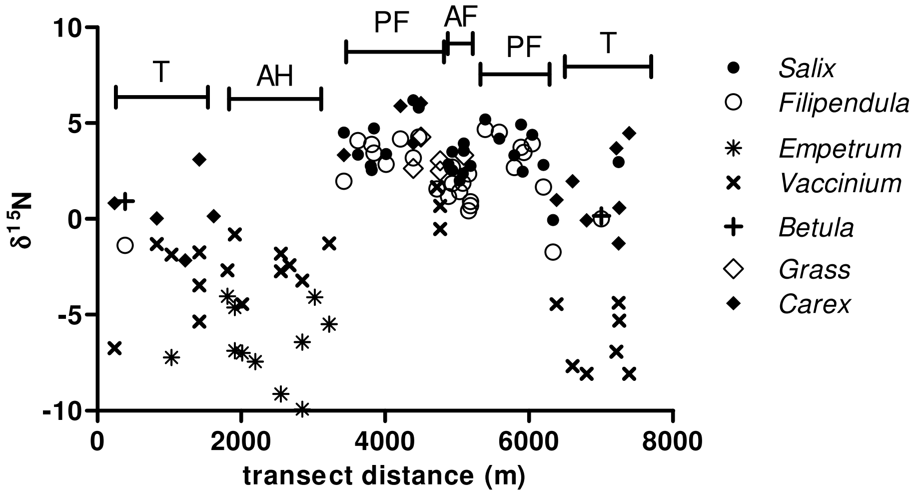

Figure 5. Foliar $\delta^{15}N$ (‰) along the trans-floodplain sampling transect. Region abbreviations are as follows. TU-tundra/birch forest uplands; AH-ancient heath floodplain; PF-passive floodplain; and AF-active floodplain

	Tundra/Birch forest	Ancient Heath	Passive Floodplain	Active Floodplain	
Salix	**3** na; 1		**3.8** 3.0 to 4.6; 16	**2.9** 2.4 to 3.5; 8	T-test p=0.1552
Filipendula	**-0.7^{PF}** na; 2		**$3.1^{TU,AF}$** 2.3 to 3.9; 17	**1.5^{PF}** 0.9 to 2.1; 9	ANOVA/Tukey p=0.0008
Vaccinium	**$-5^{PF,AH}$** -6.5 to -3.6; 13	**-2.4^{TU}** -3.5 to -1.2; 7	**0.6^{TU}** -2.1 to 3.3; 3		ANOVA/Tukey p=0.0006
Empetrum	**-7.2** n/a; 1	**-6.8** -8.3 to -5.3; 9			
Grass			**3.1** 1.8 to 4.4; 4	**3.3** n/a; 1	
Carex	**1.0^{PF}** -0.2 to 2.3; 12		**4.8^{TU}** 2.6 to 7.0; 4		T-test p=0.0034
Betula	**0.5** n/a; 2				
total mean **95% CI; N**	**$-1.9^{AF,PF}$** **-3.2 to -0.6; 32**	**$-4.9^{AF,PF}$** **-6.3 to -3.4; 16**	**$3.3^{TU,AH}$** **2.8 to 3.8; 44**	**$2.2^{TU,AH}$** **1.7 to 2.7; 18**	Kruskall Walllis/ Dunn p<0.0001

Table 5. $\delta^{15}N$ (‰) of foliage samples collected along the large floodplain transect grouped by species and habitat. Superscripts show that a species mean within one habitat is significantly different from another habitat's mean.

floodplain (δ^{15}N 0.6‰), but depleted in the ancient heath (δ^{15}N -2.4‰) and depleted to an even greater extent in the tundra (δ^{15}N -5.0‰). The ericaceous shrub *Empetrum nigrum,* was the most depleted species (δ^{15}N -6.8‰), and occurred almost exclusively in the ancient heath region.

We also found that the dominant species in the tundra/ birch forest stage exhibited a wide range in mean foliar δ^{15}N, from an average of -5‰ for *Vaccinium*, all the way to +1‰ for *Carex*. *Empetrum nigrum* and *Salix* were even lower and higher respectively, but were only sampled once each. In contrast, the two most abundant taxa in the active floodplain, *Salix* and *Filipendula camtschatica* were very similar in their δ^{15}N values, 1.5‰ and 2.9‰.

With the exception of the N_2 fixing *Alnus* trees, there were also strong patterns to the change in foliar δ^{15}N across succession (Figure 6 and Table 6). *Alnus* foliage exhibited no statistically significant differences among any succession stages and had a very narrow range of mean δ^{15}N values among stages (-0.9‰ to -0.5‰). When *Alnus* foliage was excluded, foliar δ^{15}N was highest and roughly the same for succession stages 0 and I (4.2‰ and 4.4‰ respectively), was lowest in succession stages II through IV (range 2.1‰ through 2.4‰) and then increased again to 4‰ and 3.4‰ in succession stages V and VI, and finally declined to -5‰ in succession stage VII.

Salix B, *Filipendula camtschatica* and *Urtica diocia* all were abundant in succession stages 0 through V and exhibited the same general U-shaped pattern as the mean. *Salix A*, was abundant in stages 0 through III and like the mean was enriched in ^{15}N during succession stages 0 and I relative to stages II and III. Aside from *Alnus*, the only other species that did not exhibit the same general pattern as the total mean was *Chosenia arbutifolia* which was generally high throughout succession stages 0 through IV.

The two tree *Salix* tree species were typically about 1‰ enriched in ^{15}N relative to the two forbs, *Filipendula kamtschatica* and *Urtica diocia*. The late succession ericaceous shrubs (*Vacccinium and Empetrum nigrum*) that replaced the early succession species were depleted in ^{15}N relative to the early succession species and co-occurring non-ericaceous species. *Vaccinium* δ^{15}N declined dramatically from 0.6‰ in succession stage VI to -2.9‰ in succession stage VII.

We found that within the active floodplain foliar δ^{15}N and C:N were significantly and positively correlated (Figure 7 and Table 7) when all species were considered, as well as for four out of the six individual species studied. In contrast, foliar δ^{15}N and C:N were strongly and negatively correlated in both the ancient heath floodplain and the birch forest/tundra uplands. When all species were considered, there was no significant correlation in the passive floodplain, but there was a negative correlation for *Filipendula camtschatica* in this region. With the exception of the passive floodplain, correlations were generally stronger and more highly

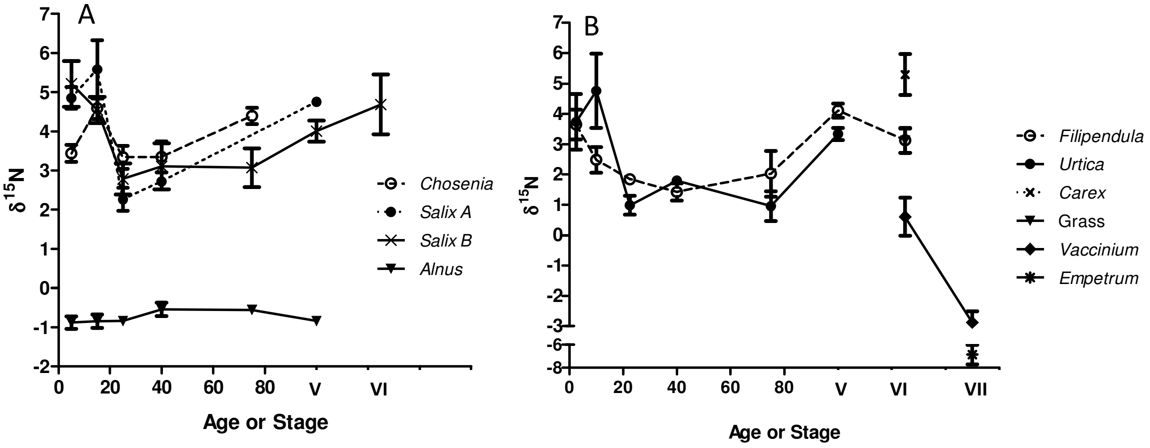

Figure 6. Foliar $\delta^{15}N$ (‰) grouped by succession stage and species. Graph A shows all the tree species and B shows non-tree species. Typical succession stage 0 ranges in age from 0 to 10 years old; stage I - 10 to 20 years; stage II - 20 to 30 years; stage III – 30 to 50 years and stage IV – 50 to 100 years. Note-one site aged 9 years old considered stage I because more than half the site was covered in a dense tree stand. Foliar means for stages 0 through IV were plotted according to the X-axis point at the center of the age range for a particular stage. Stages V, VI and VII were not aged.

	Succession Stage								
	0	I	II	III	IV	V	VI	VII	
Alnus	-0.9	-0.8	-0.8	-0.5	-0.6	-0.8			ANOVA/Tukey p=0.3151
se; N	0.2;2	0.2;7	0.2; 8	0.2; 4	0.1; 6	0.1; 0.1			
Chosenia	3.4^{I}	$4.6^{0,II}$	3.3^{I}	3.3	4.4				
se; N	0.2; 5	0.3; 5	0.3; 5	0.4; 3	0.2; 2				ANOVA/Tukey p=0.0139
Salix A	4.9^{II}	$5.6^{II,III}$	$2.3^{0,I}$	2.7^{III}		4.8			ANOVA/Tukey p=0.0002
se; N	0.3; 6	0.7; 6	0.3; 8	0; 2		na;1			
Salix B	5.2^{II}	4.5	2.8^{0}	3.1	3.1	4	4.7		Kruskal Walllis/Dunn p=0.0083
se; N	0.6; 5	0.3; 8	0.4; 6	0.6; 5	0.5; 6	0.3; 14	0.8; 4		
Filipendula	$3.7^{II,III}$	2.5^{V}	$1.8^{0,V}$	$1.4^{0,V}$	2^{V}	$4.1^{I,II,III,IV}$	3.1		ANOVA/Tukey p<0.0001
se; N	0.5; 5	0.4; 5	0.1; 8	0.3; 5	0.8; 4	0.2; 15	0.4; 6		
Urtica	3.7^{II}	$4.8^{II,IV}$	$1^{0,I}$	1.8	1^{I}	3.3			ANOVA/Tukey p=0.0015
se; N	0.9; 6	1.2; 5	0.3; 8	0.1; 3	0.5; 6	0.2; 4			
Vaccinium							0.6^{VII}	-2.9^{VI}	T-test p=0.0013
se; N							0.6; 3	0.4; 6	
Empetrum								-6.9	
se; N								0.9; 7	
Carex							4.8		
se; N							0.7; 4		
Grass							3.1		
se; N							0.4; 4		
total mean[1]	$4.2^{II,III,IV,VII}$	$4.4^{II,III,IV,VII}$	$2.1^{0,I,V}$	$2.4^{0,I,V,VII}$	$2.3^{0,I,V,VII}$	$4^{II,III,IV,VII}$	3.4^{VII}	$-5^{0,I,III,IV,V,VI,VII}$	Kruskal Wallis/Dunn p<0.0001
	0.3;27	0.3; 29	0.2; 35	0.3; 18	0.4; 18	0.2; 34	0.4; 20	0.7; 13	

[1]-excludes alder

-Superscripts denote that a succession stage is significantly different from another. significance level =0.05.

-Column and row means calculated from each datapoint

Table 6. Foliar $\delta^{15}N$ (‰) grouped by succession stage and species. This table corresponds to Figure 6.

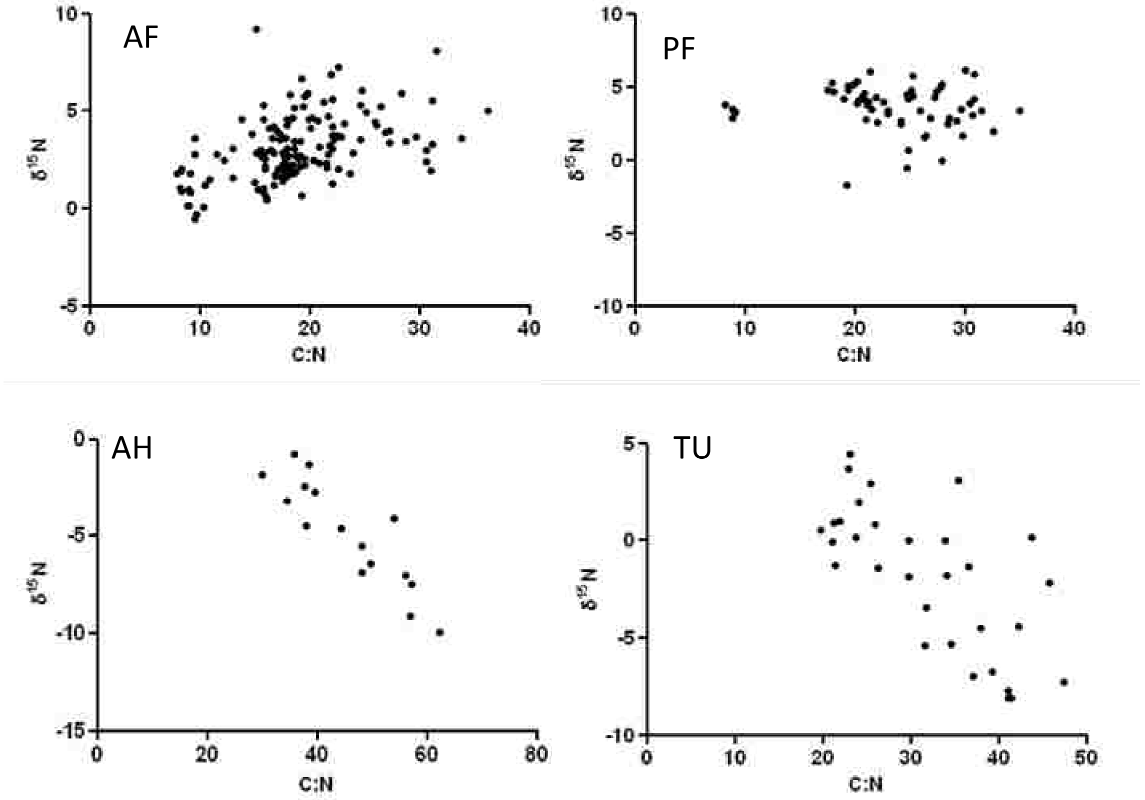

Figure 7. Correlations between foliar C:N and foliar $\delta^{15}N$ (‰) by region. AF-active floodplain, PF-passive floodplain, AH-ancient heath floodplain and TU-tundra/birch forest uplands.

	spearman r	p-value
All active floodplain	**0.52**	**<0.0001**
Alnus	0.22	0.2789
Chosenia	0.16	0.49
Salix A	0.49	0.021
Salix B	0.37	0.0219
Fillipendula	0.37	0.0246
Urtica	0.59	0.001
All passive floodplain	**-0.20**	**0.1337**
Salix	0.01	0.9797
Filipendula	-0.47	0.024
All ancient heath	**-0.87**	**<0.0001**
Vaccinium	-0.22	0.6137
Empetrum	-0.80	0.0099
All tundra and birch forest	**-0.69**	**<0.0001**
Vaccinium	-0.58	0.0373
Carex	-0.06	0.8624

Table7. Spearman rho correlations between foliar C:N and foliar $\delta^{15}N$ (‰) by region and species within each region.

significant when all species were grouped together than when any individual species was considered alone. In the active floodplain, most species' foliar δ^{15}N had greater and more significant correlation with age, soil total N and/or *Alnus* cover than foliar C:N. When all species are considered together, total soil nitrogen correlated best with foliar δ^{15}N (Table 8).

In order to test the effect of *Alnus*'s abundance on foliar δ^{15}N of co-occurring species without the confounding effects of long term changes driven by other factors, we examined a cluster of similar aged sites. Twenty-three to thirty-six year old stands were chosen because they had very similar nitrogen fertility, while *Alnus* abundance varied from 0 to 25% of total tree coverage. Younger sites tended to lack *Alnus* (relative coverage <3%) whereas *Alnus* was ubiquitous in older sites (typically 20 to 50% of total coverage). We found that there was a significant negative relationships between foliar δ^{15}N of both trees and forbs verses *Alnus* cover ($p = 0.04$, $R^2=0.10$) as well as just for trees ($p = 0.02$, $R^2=0.27$) (Figure 8). There was also a negative relationship for forbs, but it was not significant ($p=0.1$, $R^2=0.19$). Age, even within this narrow range, may still confound these relationships, because foliar δ^{15}N of trees was also significantly correlated with age ($p = 0.03$, $R^2=0.25$), although age explained less variation than did *Alnus* cover.

Discussion

Foliar C:N of the large upland-floodplain transect

We concluded that foliage in the modern floodplain, both the active (molar C:N 21) and passive (C:N 26) regions, was nitrogen-rich relative to the ancient floodplain (C:N 46) and uplands (C:N 32). Foliage in the modern floodplain was also nitrogen rich relative to the global averages for all foliage (C:N 44), and foliage in temperate broadleaf forests (C:N 35) (McGroddy et al. 2004) (Figure 3, Table 2). Floodplains are known to be nitrogen rich relative to uplands (Pinay et al. 1999), but foliar nitrogen concentrations in the Kol floodplain were considerably higher than in other temperate and boreal floodplains that do not receive significant subsidies from spawning salmon (eg. Walker and Chapin III 1986, Yarie and Van Cleve 1996, Harner and Stanford 2003, Adair et al. 2004). And, foliar nitrogen concentrations in the Kol floodplain were similar to values observed for deciduous foliage collected adjacent to other rivers with large salmon-runs (Helfield and Naiman 2001, Mathewson et al. 2003, Bartz and Naiman 2005).

The low foliar C:N values that we found were attributable to both nitrogen imported by spawning salmon and nitrogen fixed by *Alnus*, and both of these inputs occurred primarily in the active floodplain. Mixed *Alnus* stands are known to fix huge quantities of nitrogen, up to 139 kg $ha^{-1}yr^{-1}$ (Binkley et al. 1994). A simple calculation also illustrates that the quantity of salmon

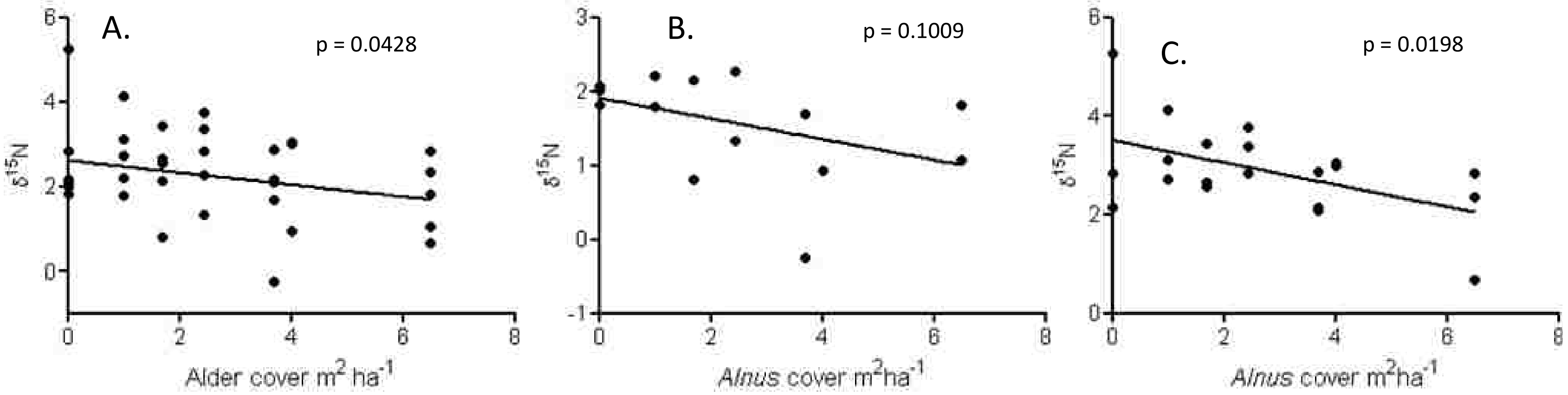

Figure 8. Linear regression relationships between foliar δ^{15}N and alder cover in forest stands aged 23 to 36 years. Graph A shows all species, Graph B shows the tall forbs *Filipendula camstchatic*a and *Urtica diocia* and Graph C shows the trees *Salix sp*. and *Chosneia arbutifolia*

	Age (years)	Soil N (min+LL) (kg-N ha^{-1})	Min. Soil N (Kg-N ha^{-1})	Alder Cover (m^{2} ha^{-1})	C:N v ^{15}N
Alnus	0.403 (0.037)	0.148 (0.490)	0.435 (0.024)	0.397 (0.045)	0.216 (0.279)
Chosenia	-0.002 (0.994)	0.031 (0.905)	0.064 (0.787)	0.003 (0.991)	0.164 (0.490)
SalixA	-0.683(<0.001)	-0.687 (0.001)	-0.712 (<0.001)	-0.609 (0.003)	0.488 (0.021)
SalixB	-0.551 (0.002)	-0.612 (0.001)	-0.586 (0.001)	-0.662 (<0.001)	0.435 (0.016)
Filipendula	-0.522 (0.005)	-0.573 (0.003)	-0.583 (0.001)	-0.558(0.003)	0.301 (0.127)
Urtica	-0.589 (0.001)	-0.583 (0.002)	-0.568 (0.001)	-0.575 (0.001)	0.586 (0.001)
Total*	-0.513(<0.001)	-0.543 (<0.001)	-0.508 (<0.001)	-0.469 (<0.001)	0.527 (<0.001)

* does not include alder

Table 8. Spearman rho correlation coefficents of foliar δ^{15}N verses age, total soil N (litter layer +10cm mineral soil), total 10cm mineral soil N, alder cover and foliar C:N for active floodplain plants only. p-values in parenthesis.

imported nitrogen that the Kol ecosystem receives would alone be sufficient to induce high nitrogen fertility. If the 150,000 kg of salmon nitrogen imported on an average year were evenly distributed across the entire active channel region (estimating that it is approximately 60 km long and 0.5 km wide) fertilization rates would average approximately 50 kg-N ha^{-1} yr^{-1}. Such a fertilization rate exceeds deposition rates known induce nitrogen saturation (Aber et al. 1989). However, this scenario is unrealistic because salmon-imported nitrogen is not evenly distributed, and much of it is exported with river flow. Furthermore, salmon imported nitrogen is delivered as organic-nitrogen which is not directly available to most plants. Nevertheless by their sheer quantity, salmon are obviously an enormous nitrogen subsidy to the Kol river ecosystem.

The differences in foliar C:N ratios that we observed among the regions of the large transect were due to both differences within the same taxa growing in different regions, as well as differences among growth forms occurring in different regions. For example, foliage from both *Salix* and *Filipendula camtschatica* were more nitrogen rich in the active than the passive floodplain, indicating that the active floodplain was the more fertile environment for these particular species. Furthermore, whereas the modern floodplain was dominated by notoriously nitrophillic species such as *Salix, Alnus*, and *Urtica diocia*, the ancient heath and tundra were dominated by nitrogen efficient taxa such as the ericaceous shrubs *Empetrum nigrum* and *Vaccinium* (Berendse and Jonnasson 1992, Michelsen et al. 1996).

Our finding that foliage in the ancient heath and tundra communities was relatively nitrogen poor is consistent with many other studies demonstrating that tundras are infertile environments. While tundra and heath soils are rich in both organic matter and total nitrogen, they typically have very low net mineralization rates, which may even be negative during the growing season (Nadelhoffer et al. 1992, Jonasson et al. 1996). However *Carex*, which was one of the dominant taxa in the tundra, had moderate foliar nitrogen concnetration, C:N 29. High variability in foliar C:N in tundra vegetation is common and is generally attributable to differences among growth forms (Michelsen et al. 1996, Michelsen et al. 1998). Despite instances in which tundra plants exhibit low foliar C:N they generally grow along with much more nitrogen poor species, and the community as a whole is nitrogen poor and slow growing. Other factors in addition to nitrogen may be also be limiting in these environments such as competition among plants and allelopathy (Nilsson 1994), harsh climatic conditions (Michelsen et al. 1996) or low availability of other nutrients such as phosphorus (Chapin III et al. 1978).

Only two sampling points along the trans-floodplain transect fell within birch forest uplands and thus we have very limited data from these sites. However, the samples we do have indicate that foliage in the birch forests was relatively nitrogen rich. Two samples of *Betula* foliage had a mean C:N ratio of 22.6 and two samples of *Filipendula camtschatica* foliage had a mean C:N ratio of 28. Thus the *Betula* foliage had very similar C:N ratios as *Salix* growing within the active floodplain and foliar C:N was only slightly higher in the birch forest for *Filipendula camtschatica* than in the passive floodplain. Despite the low foliar C:N ratios that we found in the birch forest, we observed that *Betula* trees had very small annual growth increments and *Filipendula camtschatica* in the birch forests only grew to about a third of the height that it did in the floodplain. A possible explanation for these low growth rates might be that the birch forests were phosphorus limited as upland soils of the region are commonly andisols and are known to respond to phosphorus fertilization (Sokolov 1974). Our observations confirmed that soils in the birch forest uplands adjacent to the floodplain appeared andic, and foliage was observed with purple coloration, indicative of phosphorus limitation.

Foliar C:N in floodplain primary succession

Within the active floodplain (approximately the first 100 years of succession, or stages 0-IV), we found that foliar C:N ratios were elevated for approximately the first twenty years of succession (Figure 4, Table 3). After this initial period of elevation, the ratios dropped and leveled off, and remained low until succession stage V. While we do not have direct fertilization data proving limitation, as such studies are very difficult to conduct (Aerts and Chapin IIII 2000), our results provided strong evidence that nitrogen was limiting for the first decade of two of succession.

Soil fertility measurements presented in Chapter 2 indicated that nitrogen availability should have been limiting in early succession, but abundant in later succession. For example we found that net nitrogen mineralization in young gravel bars (stage 0, or < 5 yrs old) was only 6 kg-N ha^{-1} per growing season, whereas a typical forest's annual nitrogen requirement is approximately 25 to 100 kg-N ha^{-1} yr^{-1} (Chapin III et al. 2002). In contrast, mineral soils within the active floodplain's mature forest sites (stage IV, ages 50 to 100 years) mineralized approximately 49 kg-N ha^{-1} per growing season, and the presence of a litter layer likely doubles this net mineralization rate (Stump and Binkley 1993). As has been found in other floodplain chronosequences (eg. Walker and Chapin III 1986, Adair et al. 2004), we found that changing foliar nitrogen concentrations during early succession corresponded very well with changing soil fertility during succession, and we found that foliar C:N ratios were well correlated with soil nitrogen content (Table 4).

The elevated foliar C:N ratios that we observed at the onset of succession indicated that spawning salmon did not completely alleviate nitrogen limitation as we predicted they might. Their failure to do so may have been because carcass deposition rates were simply not sufficient to satisfy the vegetation's demand; but more likely, this occurred because carcasses were only available for a brief period of time in late August and early September, and young gravel bars were poorly retentive of salmon nitrogen. In Chapter 2 we found that carcasses did create a pulse of nitrogen availability on young gravel bars in late summer, but subsequent fall and spring flooding flushed this labile nitrogen from these sites, reverting them back to their infertile states for most of the growing season. It is important to consider however, that gravel bar foliage in the Kol floodplain was still very nitrogen rich relative to young alluvial bars in floodplains that do not receive significant salmon subsidies (eg. Walker and Chapin IIII 1986, Yarie and Van Cleve 1996, Adair et al. 2004, Stanford unpublished data for Nyack floodplain, Middle Fork of the Flathead River, Montana) indicating that nitrogen limitation was much less severe in early succession on the Kol floodplain than in other systems that were not influenced by salmon.

The conclusion that nitrogen availability was not limiting in stages II through IV was based on our findings that all species were extremely nitrogen rich during this time. In the Glacier Bay chronosequence in Alaska, Hobbie et al. (1998) also found that foliar C:N ratios of *Salix sp.* were very low (approximately 10 to 13) from ages 50 to 100 years because they grew amongst nitrogen-fixing *Alnus* thickets. Hobbie et al. suggested that such low C:N ratios were due to luxury consumption and did not necessarily translate into high growth rates. However, we do not think this was the case in the Kol floodplain because cultivation experiments conducted elsewhere suggested that *Salix sp.* are much more nitrogen demanding than most other tree species, and growth remains nitrogen limited until foliar nitrogen concentrations are exceptionally high, greater than 3% or more (Rytter and Ericson 1993, Kopinga and van den Burg 1995, Labrecque et al. 1998, Jug et al. 1999). In the present study we found that the mean nitrogen concentration of foliage from *Chosenia*, *Salix A* and *Salix B* in stage 0 ranged between 2.1 and 2.4%, and concentrations increased to between 2.9 to 3.2% nitrogen in succession stages II through IV. Thus, according to the nitrogen status classifications proposed for three species of *Salix sp.* by Kopinga and van den Burg (1995), foliar nitrogen concentrations at the onset of succession in the Kol were below optimal (<2.8% to 3%) whereas they were slightly above optimal in stages II through IV. The fact that *Salix's* foliar nitrogen concentrations reached an asymptote at almost exactly the concentration in which other studies have found to be optimal for growth further suggests that they received adequate nitrogen to ameliorate limitation during mid succession.

After the period of nitrogen abundance in succession stages II through IV we found that foliar C:N increased stepwise in stages V through VII, indicating that nitrogen availability became progressively more limiting in late succession. We are unsure of the timescale over which this occurs because these sites could not be aged with tree cores, however we estimated that stage VI sites were on the order of hundreds of years old whereas the transition to the heath community (stage VII) likely takes thousands of years.

This general decline in nitrogen fertility during the oldest succession stages is consistent with other succession chronosequences (eg. Odum 1969, Clein and Schimel 1995, Hobbie et al. 1998), and has been attributed to declining soil fertility as a result of increasing soil C:N and the accumulation of soil nitrogen in recalcitrant organic pools. Because low soil fertility promotes the growth of nitrogen efficient species, which further decrease soil fertility by depositing recalcitrant litter, a positive feedback of declining fertility may occur in late succession (Berg and MClaugherty 1989, Van Cleve et al. 1993, Schimel et al. 1996, Hobbie et al. 1998, Aerts and Chapin III 2000, Fierer et al. 2001). It is likely that these processes also drove the decline in fertility with late succession that we observed. For example, in Chapter 1 we found that total nitrogen in the mineral soil reached an asymptote at approximately 2,000 kg-N ha^{-1} between succession stages IV and V. At the same time, the tall forb communities that occurred in succession stage V are known to have some of the highest biomass accumulation rates in the world (Walter 1981). Thus while we did not measure soil organic carbon it follows logically that soil C:N ratios widened over time, and it is well documented that soil C:N ratios are negatively correlated with net mineralization rate (Flanagan and Van Cleve 1983). Furthermore, the ericaceous shrubs that dominated the ancient heath floodplain (succession stage VII) had low foliar nitrogen (C:N 36 for *Vaccinium* and C:N 55 for *Empetrum nigrum*) and these species are known to contain high concentrations of secondary compounds which retard mineralization and decomposition (Berendse and Jonnasson 1992).

Foliar $\delta^{15}N$ of large upland-floodplain transect

We found that foliar $\delta^{15}N$ in both the active and passive regions of the floodplain was high ($\delta^{15}N$ 2.2‰ and 3.3‰ respectively, Figure 5, Table 5) relative to the global average for temperate forests (-2.8‰, standard deviation = 2 (Martinelli et al. 1999)), as well as relative to vegetation samples collected in other Pacific-rim floodplains without significant salmon inputs (ranging between -1.6‰ to -8.2‰ in Kielland and Bryant (1998) and Rhoades et al. (2001)). In contrast, mean $\delta^{15}N$ of foliage collected in the tundra/birch forest uplands (-1.9‰) and ancient heath floodplain (-4.9‰) were depleted and conformed well to other tundra and heath environments. The high $\delta^{15}N$ that we observed in the modern floodplain supported our hypothesis that salmon, which are highly enriched with ^{15}N ($\delta^{15}N$ = 9‰ in the Kol floodplain, B.Ellis unpublished) were a major nitrogen source for the vegetation.

Numerous other studies conducted along small spawning streams have found that salmon were a major nitrogen source to the vegetation, but only within small spatial scales, primarily within 25 m but up to 100 m from the stream banks (Ben-David et al. 1998, Hildebrand et al. 1999, Helfield and Naiman 2002, Bilby et al. 2003). In contrast we found that foliage was enriched in ^{15}N across the entire 2.5 km wide floodplain. The fact that sites within the passive floodplain, which may be hundreds of meters away from any active channels and have not received significant salmon inputs for centuries, were also enriched in ^{15}N indicated that salmon imported nitrogen was stored in soils and recycled by these forests for centuries or more.

An alternative explanation may be that annually imported salmon nitrogen was distributed to vegetation communities throughout the entire floodplain via the alluvial aquifer (so-called hyporheic exchange-see Stanford et al. 2005). Studies in other floodplain systems commonly show that riparian zones effectively remove large quantities of nitrate from downwelling river water along hyporheic flowpaths, and it is suggested that this removal may be in part due to plant uptake (Hill 1996). However, we believe that hyporheic transported nitrogen is probably of secondary importance relative to soil derived nitrogen for most of the vegetation in the Kol Floodplain, except perhaps on young (stage 0) alluvial bars.We base this conclusion on the following arguments. First of all, despite the large nutrient subsidies from salmon, we found that river water nitrogen concentrations (see Chapter 5) and hyporheic nitrate concentrations (measured at 36 points throughout the floodplain in July-October 2004 mean= 78 μg-N L^{-1}, SD=112 μg-N, unpublished) were well within the range of typical values for large rivers (see Chapter 5), indicating that the Kol would be oligotrophic without salmon. In fact, hyporheic nitrate concentrations on the Kol River were very similar to hyporheic nitrate concentrations on another floodplain system studied by our colleagues that does not receive salmon subsidies (Reid 2007). Yet foliage in this other floodplain is nitrogen poor relative to the Kol floodplain (mean *Populus* C:N = 38, Harner and Stanford 2003, and Stanford unpublished), suggesting that these hyporheic nitrate concentrations do not explain the very nitrogen rich foliage that we observed in the present study. Rather, we found in Chapter 2 that net mineralization within the soil of stage IV forest stands was very high and could probably provide abundant nitrogen to the forest. Secondly, if salmon nitrogen delivered via hyporheic flow were the most important source of nitrogen to the vegetation then we would have expected that vegetation in stage 0 and I would have had the greatest access to nitrogen, as these sites were almost always adjacent to the mainchannel. Older sites were generally further down hyporheic flowpaths and thus would only have access to leftover salmon nitrogen that had not already been assimilated earlier in the flowpath. And, it has been demonstrated in a similar floodplain where hyporheic nitrate concentrations are within the same order of magnitude as on the Kol that 60 to 80% of hyporheic nitrate was lost, primarily by denitrification, during the first 50 m of flow paths (Cliverd et al. 2008), making it unlikely that salmon nitrogen would be transported across the entire floodplain via hyporheic flow over the short term Rather than finding that early succession sites adjacent to the mainchannels had the greatest access to nitrogen we found the opposite, that early succession vegetation actually had the lowest foliar nitrogen concentrations of all sites within the active floodplain. However, foliar C:N correlated well with soil total nitrogen for most species (Table 4) in the active floodplain. That foliar nitrogen concentrations appear to be driven by soil fertility and not hyporheic nitrogen availability is consistent with other recent studies (Schade et al 2002, Nyack Floodplain- unpublished) and is logicial, given that fine roots of nearly all plant species concentrate near the surface soil layers, and not in the hyporheic zone. Thus while the potential importance of hyporheic transport of salmon nitrogen has not been fully assessed in the Kol floodplain, our preliminary data suggests that soil nitrogen is probably the most important nitrogen source to vegetation at most sites. However, hyporheic nitrogen may be particularly important nitrogen source to vegetation growing at sites immediately adjacent to the mainchannels, as well as for vegetation growing on early succession alluvial bars where soils are very infertile, as suggested by Lisuzzo et al. 2004. Clearly, too little is known about the potential significance of hyporheically-transported nitrogen for vegetation nutrition and this mechanism warrants additional research.

Also, ammonia volatilization from decomposing salmon carcasses could also serve to transport salmon-imported nitrogen to vegetation throughout the floodplain as terrestrial plants can assimilate substantial gaseous ammonia (Pearson and Stewart 1993), however if this were the dominat mechanism whereby salmon nitrogen was delivered to vegetation we would have expected foliar $\delta^{15}N$ to be highly depleted rather than the elevated due to the large isotopic fractionation that occurs during ammonia volatilization. For example, Erskine et al. 1998 found that while penguin guano was highly enriched in ^{15}N ($\delta^{15}N = 14.6‰$) ammonia volatilized within the penguin colony was highly depleted in ^{15}N (approximate $\delta^{15}N = -10‰$). Consequently, while foliage growing directly amongst the penguin colony was enriched in ^{15}N, foliage growing downwind of the colony was highly depleted in ^{15}N to a similar extent as the volatilized ammonia. As with hyporheic flow, gaseous transport of volatilized ammonia surely accounts for for some fraction of the total salmon nitrogen transport to vegetation throughout the floodplain, but again it is probably secondary at most sites to the quantity of salmon nitrogen that is flood deposited, either as salmon carcasses or bound to fine sedimetents, and stored within soils.

Several other factors in addition to nitrogen source may influence foliar $\delta^{15}N$, notably: the form of nitrogen favored in plant assimilation, rooting depth, mycorrhizal symbiosis, plant fractionation during and after uptake and overall site fertility (Nadelhoffer et al. 1996, Högberg 1997). Under the right circumstances, each of these confounding factors alone could explain variation in foliar $\delta^{15}N$ as large as the difference between terrestrially fixed nitrogen ($\delta^{15}N$ 0‰ to -2‰) and salmon imported nitrogen ($\delta^{15}N = 9‰$).

However we accounted for these confounding effects by sampling a diversity of species of different growth forms. For example, *Salix* trees are relatively deep rooted and form ectomycorrhizal symbionts whereas *Filipendula camtschatica* are shallow rooted and would likely form VAM symbionts (Harley and Harley 1987). Despite these differences in growth forms, we found that foliar $\delta^{15}N$ in the active and passive floodplains were invariably high when all species were accounted for, indicating that this general enrichment was not due to these confounding factors.

The confounding factor with the greatest potential to cause the enrichment in ^{15}N that we observed in the modern floodplain was the influence that fertility has on foliar $\delta^{15}N$. Numerous studies have shown both experimentally through fertilization (Meints et al. 1975, Johannisson and Högberg 1994, and Högberg 1997) along natural fertility gradients (Vitousek et al. 1989a, Garten 1993, Garten and Van Miergot 1994, Kitayama and Iwamoto 2001) as well as along N-deposition gradients (Koopmans et al. 1997, Emmett et al. 1998) that foliage in high fertility sites are usually enriched with ^{15}N relative to low fertility sites. This enrichment can occur even if the nitrogen source causing the increased fertility is itself depleted, if its inputs are very large (Högberg 1997). Thus theoretically, if the fertilization effect of *Alnus* were high enough to cause extreme nitrogen losses, it alone could account for the elevated foliar $\delta^{15}N$ that we observed in the active floodplain. However, several lines of evidence indicate the ^{15}N enrichment that we observed was not due to *Alnus*. Firstly, *Alnus* was most abundant in the active floodplain, and the active floodplain was generally more fertile (based on foliar C:N) than the passive floodplain. Yet, the passive floodplain had higher foliar $\delta^{15}N$. This indicates that the effect of *Alnus*-fixed nitrogen (which itself is depleted ($\delta^{15}N$ -0.7‰) is to lower foliar $\delta^{15}N$ of co-occurring species, not increase it. This is confirmed in Figure 8 which shows that foliage at similarly aged sites with higher alder coverage generally had lower $\delta^{15}N$ than sites with lower alder coverage. Finally, if foliar $\delta^{15}N$ were elevated as a result of high fertility, we would expect a negative correlation between foliar $\delta^{15}N$ and foliar C:N, as was demonstrated in the aforementioned studies. However, we found the opposite, a significant positive correlation between foliar C:N and foliar $\delta^{15}N$ (Figure 7, Table 7). The lack of a negative correlation indicates that foliar $\delta^{15}N$ in the active floodplain was driven by inputs, and not by internal soil cycling processes associated with fertility. The observed correlation was in fact positive because, as we explain in the following section, salmon were the main nitrogen input to otherwise nitrogen poor early succession (causing elevated ^{15}N at the infertile sites), whereas *Alnus* was a nitrogen input to the older sites which were already fertile.

In the absence of significant nitrogen inputs to the passive floodplain, we expected that within site variation in foliar $\delta^{15}N$ would be driven by differences in fertility among sites. We found this to be the case for dominant species in the passive floodplain, *Filipendula camtschatica*, which showed the typical negative correlation between foliar $\delta^{15}N$ and C:N (Table 7). However, there was no correlation for *Salix* nor for all species grouped together. We conclude that the salmon inputs that built these sites caused a general elevation in foliar $\delta^{15}N$, but the variation within sampling points in the passive floodplain may have been driven by fertility and associated nitrogen losses.

In contrast to the modern floodplain, where foliar $\delta^{15}N$ was invariably high, foliage in the tundra/birch forest uplands and the ancient heath communities was, on average, depleted in ^{15}N. However, the $\delta^{15}N$ of tundra foliage was highly variable, with species mean's ranging from 1‰ all the way to -6.8‰ (Figure 5, Table 5). Such wide ranges of primarily negative $\delta^{15}N$ values are typical for tundra and heath ecosystems. For example, Michelsen et al. (1998) measured foliar $\delta^{15}N$ of different species within 4 different tundra and heath communities in Greenland, Eastern Siberia, in Northern Sweden and found the same pattern (with one exception) that foliar $\delta^{15}N$ was highest in non-mycorrhizal, intermediate in ectomycorrhizal and lowest in ericoid symbiont species. Foliage of all species ranged from approximately 2‰ to -8‰. Similarly, we found that *Carex*, which is typically non-mycorrhizal, had a foliar $\delta^{15}N$ of 1‰ whereas foliage of the other dominant species, ericaceous *Vaccinium* and *Empetrum nigrum* was highly depleted in both the ancient heath and tundra environments ($\delta^{15}N$ = -2.4‰ to -6.8‰). These consistent variations among growth forms in tundra and heath communities are generally attributable to different nitrogen acquisition strategies among growth forms competing for the very limited nitrogen supply in these infertile environments. (Nadelhoffer et al. 1996, Michelsen et al. 1996, Michelsen et al. 1998). In particular, two explanations have been proposed to explain low foliar $\delta^{15}N$ in ericaceous species: either that they assimilate ^{15}N depleted organic nitrogen (Nadelhoffer et al. 1992, Michelsen et al. 1996) or there is greater reliance of mycorrhizally assimilated nitrogen under more infertile conditions, as mycorrhizal transfer of nitrogen discriminates against the ^{15}N isotope (Hobbie et al. 2000, Hobbie and Colpaert 2003).

Thus we concluded that tundras and heaths have intrinsically different nitrogen dynamics relative to broadleaf forests, indicating that the differences in foliar $\delta^{15}N$ between the floodplain and uplands were not necessarily attributable to salmon fertilization. However, the fact that the tundra and heath communities both conformed very well to typical values, whereas the floodplain was greatly elevated in $\delta^{15}N$ relative to other temperate forests and other Pacific-rim floodplains suggests that this enrichment was due to the salmon and not due to some regional effect, such as nitrogen deposition in oceanic sea-spray (Virginia and Delwiche 1982) which would have influenced both the floodplain and uplands.

Foliar $\delta^{15}N$ in floodplain primary succession

As hypothesized, mean foliar $\delta^{15}N$ was highest during the beginning of succession (stages 0 and I), which was consistent with our finding that the flood deposition of salmon carcasses was also greatest at the beginning of succession (Figure 6, Table 6). Other studies have used linear mixing models to estimate the proportion of a plant's nitrogen that originally came from salmon, however we do not advocate the use of these models because it is well recognized that natural abundance stable isotopes are "qualitative or roughly quantitative (Hauck 1973)." Confounding fractionations and the lack of appropriate reference sites introduce large imprecision into such calculations (Morris et al. 2005). However, given that the onset of succession the foliar $\delta^{15}N$ of *Salix* species bore greater resemblance to the $\delta^{15}N$ value of a pink salmon than to either the $\delta^{15}N$ value of terrestrially fixed nitrogen or typical $\delta^{15}N$ values from temperate broadleaf forests (Martinelli et al. 1999), suggests that salmon were the most important nitrogen source to colonizing vegetation.

Pinay et al. (2003) found that denitrification, which is elevated at the soil-water interface of spawning streams, could potentially increase foliar $\delta^{15}N$ in the absence of salmon, thereby creating a false salmon signal. However, this phenomenon is unlikely to explain our results because young alluvial bars were composed of very coarse gravels and sands and had low dissolved inorganic nitrogen (see Chapter 2). And, Pinay et al. (2003) found denitrification potential was highest at sites with fine sediments and both high available nitrate and dissolved organic carbon. Foliar δ^{15}N can also be elevated it sites with high nitrification (Högberg 1997), but again, in the absence of salmon these are very infertile environments. Given that the quantity of salmon nitrogen imported annually (25 kg-N ha^{-1} on a low salmon year) by far exceeded the soil's net mineralization for the entire growing season (6 kg-N ha^{-1} to 10cm) (Chapter 2) the high foliar δ^{15}N that we observed on these young gravel bars reflected salmon imported nitrogen rather than some confounding internal soil cycle process.

Our results indicated that *Alnus* fixed their own nitrogen, because while all other species in the active and passive floodplain regions had foliar δ^{15}N values greater than 1‰ and exhibited significant changes across succession, *Alnus's* foliar δ^{15}N ranged between -0.5‰ and -0.9‰ and this did not change during succession. Furthermore, the foliar δ^{15}N values that we observed for *Alnus* conformed very well to both values documented in other forests (0.6‰ to -2.1‰; Hobbie et al. 1998, Hobbie et al. 2000, Kohls et al. 2003) as well as to *Alnus* grown on nitrogen free media (-0.3‰ to -1.9‰: Beaupied et al. 1990, Binkley et al. 1985).

Following succession stages 0 and I, foliar δ^{15}N decreased by approximately 2‰ and remained low during succession stages II, III and IV. As hypothesized, this decrease in foliar δ^{15}N corresponded with the period in which nitrogen fixing *Alnus* reached the canopy and grew rapidly. In stage II *Alnus* accounted for approximately 10% of total tree coverage and this increased to approximately 30% by stage IV (Chapter 1). In order to determine the effect that *Alnus* had on the δ^{15}N of co-occurring species without the confounding effects of other long-term processes, we compared foliar δ^{15}N within sites of a narrow age range (23 to 36 years) that had a wide range of *Alnus* coverage. These results indicated that *Alnus* did tend to decrease foliar δ^{15}N of co-occurring species (Figure 8), however the difference in foliar δ^{15}N between sites with low *Alnus* coverage and sites with higher coverage was quite small, on the order of 1‰. In contrast, the decline in foliar δ^{15}N we observed between stages I and II was approximately 2‰. Thus we conclude that on-site growth of *Alnus* could explain at most half the decline in foliar δ^{15}N that we observed between succession stage I and II.

In addition to *Alnus*, the most likely cause for the decline in foliar δ^{15}N observed between stage I and II is that the vegetation switched from assimilating nitrogen directly from decomposing salmon at the onset of succession, to nitrogen mineralized from fine sediments as they accumulated. These fine sediments originated from eroded terrestrial sites and therefore nitrogen bound to these sediments contained a mixture of both salmon imported and terrestrially-fixed nitrogen. Therefore, these sediments should have intermediate $\delta^{15}N$ values. Furthermore, mineralization and nitrification within the soil depletes the $\delta^{15}N$ of plant-available nitrogen relative to total soil nitrogen (Högberg 1997).

Another process that causes declines in foliar $\delta^{15}N$ during succession is the development of the mycorrhizal community (Hobbie et al. 2000, Hobbie and Colpaert 2003, Hobbie et al. 2005). However this cannot explain the decline we observed between stages I and II because we found that the non-mycorrhizal *Urtica diocia* (Vierheilig et al. 1996) exhibited the same patterns of change in foliar $\delta^{15}N$ across succession as *Salix*, which commonly forms ectomycorrhizal symbionts.

In contrast to our finding that foliar ^{15}N was enriched onset of succession, every other study that has quantified foliar $\delta^{15}N$ at the onset of primary succession has found the opposite, that foliage was highly depleted in ^{15}N (Hobbie et al. 1998, Hobbie et al. 2005, Kohls et al. 1994, Kohls et al. 2003, Vitousek et al. 1989a), indicating that atmospheric deposition, which is also depleted in ^{15}N, was the main nitrogen source to these infertile environments. In a chronosequence where nitrogen fixers became dominant in later stages, foliar $\delta^{15}N$ of co-occurring species then merged upon the value of the nitrogen fixer (Hobbie et al. 1998 and Kohls et al. 2003). Therefore, because soil nitrogen is so low in early primary succession relative to nitrogen inputs, foliar $\delta^{15}N$ is driven by the $\delta^{15}N$ values of the inputs to the system, which in the case of the Kol floodplain was salmon.

Following stage IV, foliar $\delta^{15}N$ increased again in stages V ($\delta^{15}N$ 4‰) and VI ($\delta^{15}N$ 3.4‰) (Figure 6, Table 6). Given that these sites were in the passive floodplain and distant from the main channel where salmon spawned, and we observed no other significant nitrogen inputs in late succession, we propose two internal cycling processes that could explain this increase in $\delta^{15}N$.

Firstly, it is possible that following the senescence of *Alnus* (which occurs between stage IV and V) foliar $\delta^{15}N$ returned to its pre *Alnus* level because there were no longer any ^{15}N depleted nitrogen inputs to drive foliar $\delta^{15}N$ down. This would indicate that *Alnus* had a much larger influence on the soil's labile nitrogen pool while they occupied a site than their influence on total soil nitrogen. This is quite possible, considering that prior to the *Alnus* canopy stages the mineral soil already had 1,500 kg-N ha^{-1} and mineral soil total nitrogen only increased to 2,000 kg-N ha^{-1} by the time *Alnus* senesced. Thus $\delta^{15}N$ of the total soil following the *Alnus* stages would bear greater resemblance to its pre-*Alnus* $\delta^{15}N$ than to the value of *Alnus* fixed N. However if a sparse *Alnus* stand fixed 30 kg-N ha^{-1} yr^{-1} and most of this nitrogen entered directly into the labile pool, which was approximately 50 kg-N ha^{-1}, then *Alnus* growing at a site would have an enormous effect on the $\delta^{15}N$ value of the labile pool. And, after *Alnus* senesced and no longer dominated the labile pool the $\delta^{15}N$ of the labile pool would increase and bear greater resemblance to the $\delta^{15}N$ of total soil nitrogen.

Such a phenomenon has been shown experimentally. Meints et al. (1975) added ^{15}N depleted fertilizer to soils that were initially enriched with ^{15}N relative to atmospheric N_2. During the fertilization period foliar δ ^{15}N declined greatly and matched the $\delta^{15}N$ value of the applied fertilizer, but the quantity of fertilizer applied was quite small relative to the total quantity of soil nitrogen and thus had negligible effect on the $\delta^{15}N$ value of the total soil. Therefore it can be assumed that once fertilization ceased, foliar $\delta^{15}N$ would increase again.

The other potential explanatory mechanism for why foliar $\delta^{15}N$ increased again between stages IV and V is the long term effect of nitrogen saturation. Based on our foliar C:N data we concluded that nitrogen was probably not limiting during succession stages II through IV, and under such nitrogen rich conditions foliar $\delta^{15}N$ would be expected to increase (Höogberg 1997). However this did not occur during stages II through IV because the tendency to increase was swamped by ^{15}N depleted *Alnus* inputs. However once *Alnus* senesced there was a period during succession where nitrogen was still very abundant yet there were no ^{15}N depleted inputs to counteract the enrichment of ^{15}N. This hypothesis is supported by the negative relationship between foliar C:N and foliar $\delta^{15}N$ exhibited by *Filipendula camtschatica* in the passive floodplain (Table 7) and is similar to an explanation proposed by Martinelli et al.(1999) whereby a long-term increase in foliar $\delta^{15}N$ in a tropical chronosequence was driven by declining nitrogen limitation due to increasing phosphorus limitation. There are also numerous experimental demonstrations that show increasingly large applications of ^{15}N depleted fertilizer initially decrease foliar $\delta^{15}N$ until nitrogen saturation, after which point foliar $\delta^{15}N$ increases (Meints et al. 1975, Högberg et al. 1992, Johannisson and Högberg 1994). Even if the 1.7‰ increase in $\delta^{15}N$ between stages IV and V were driven by this confounding mechanism this does not mean that the high foliar $\delta^{15}N$ we observed during stages V and VI were not primarily attributable to salmon, as foliage in stage IV prior to this increase in late succession were already highly enriched relative to other temperate forests (Martinelli et al. 1999).

Finally, foliage in the oldest succession stage, the ancient floodplain heath community, had very low $\delta^{15}N$ (-3 to -7‰). Such long term declines in foliar $\delta^{15}N$ are typical in chronosequences where nitrogen cycling “closes” in later succession (Hobbie et al. 1998, Hobbie et al. 1999, Chang and Handley 2000, Hobbie et al. 2005, Wang et al. 2007) and a greater proportion of the vegetation’s nitrogen is assimilated through mycorrhizae (Hobbie et al. 1999, Hobbie et al. 2005). This explanation likely explains the decline in foliar $\delta^{15}N$ between stages V, VI and VII as well, given that foliar C:N became progressively greater during these oldest succession stages and ericaceous shrubs became the dominant species in stage VII. Furthermore, we found a very strong negative correlation between foliar δ^{15}N and foliar C:N in the heath community (Figure 7, Table 7).

Based on satellite imagery and the abundance of ancient channels now turned to swales we infer that this ancient heath community was once a floodplain of the lower Kol River. However, we don't know how old this community was, perhaps on the order of thousands of years. Furthermore we do not know whether this site went through the same succession stages as the modern floodplain or whether it received salmon imported nitrogen in early succession. The very low foliar δ^{15}N we measured at this site suggests not, but after thousands of years the salmon ^{15}N signal, even if originally present, would likely fade given the high fractionation in nitrogen poor late succession. Furthermore, over thousands of years even small atmospheric nitrogen inputs (on the order of several kg-N ha^{-1} yr^{-1}) would exceed salmon inputs at the beginning of succession. Thus we conclude that foliar δ^{15}N cannot be used to determine whether this ancient floodplain ever received significant salmon fertilization, and the foliar δ^{15}N values observed today are typical for this type of heath community.

A conceptual model describing changes in foliar C:N, foliar δ^{15}N and soil nitrogen fertility during succession in the Kol River floodplain

The changes in foliar C:N and δ^{15}N that we observed during succession were complex and can only be understood in the context of the nitrogen inputs, outputs and internal soil cycling processes occurring during succession. In order to summarize these complex processes discussed above we developed a conceptual model presented in Figure 9. While none of these mechanisms are proven absolutely, the model presented here is based on the best available data and is a synthesis of our understanding of ecosystem processes to date. This model can be used as a source of future hypotheses to experimentally test the mechanisms proposed herein. This model was based on foliar δ^{15}N and C:N data over the portrayed timescale presented in this paper, as well as soil total nitrogen data for 0 to hundreds of years (presented in Chapter 1) and labile soil N data from 0 to 100 years (in Chapter 2) . All the soil carbon data, as well as total and labile soil nitrogen data for greater than 100 years are inferred from the foliar data presented in this paper, as well as other succession studies and our observations.

-0 to 20 years, the beginnings of succession. Soils in these new alluvial bars are very nitrogen-poor, both in terms of total nitrogen and the labile pool. However salmon carcasses are flooded into these sites annually and this in combination with the deposition of fine sediments and plant assimilation causes nitrogen pools to increase rapidly. Foliar C:N ratios are elevated at the onset of succession due to low nitrogen fertility. Foliar δ^{15}N values are elevated reflecting the salmon imported nitrogen

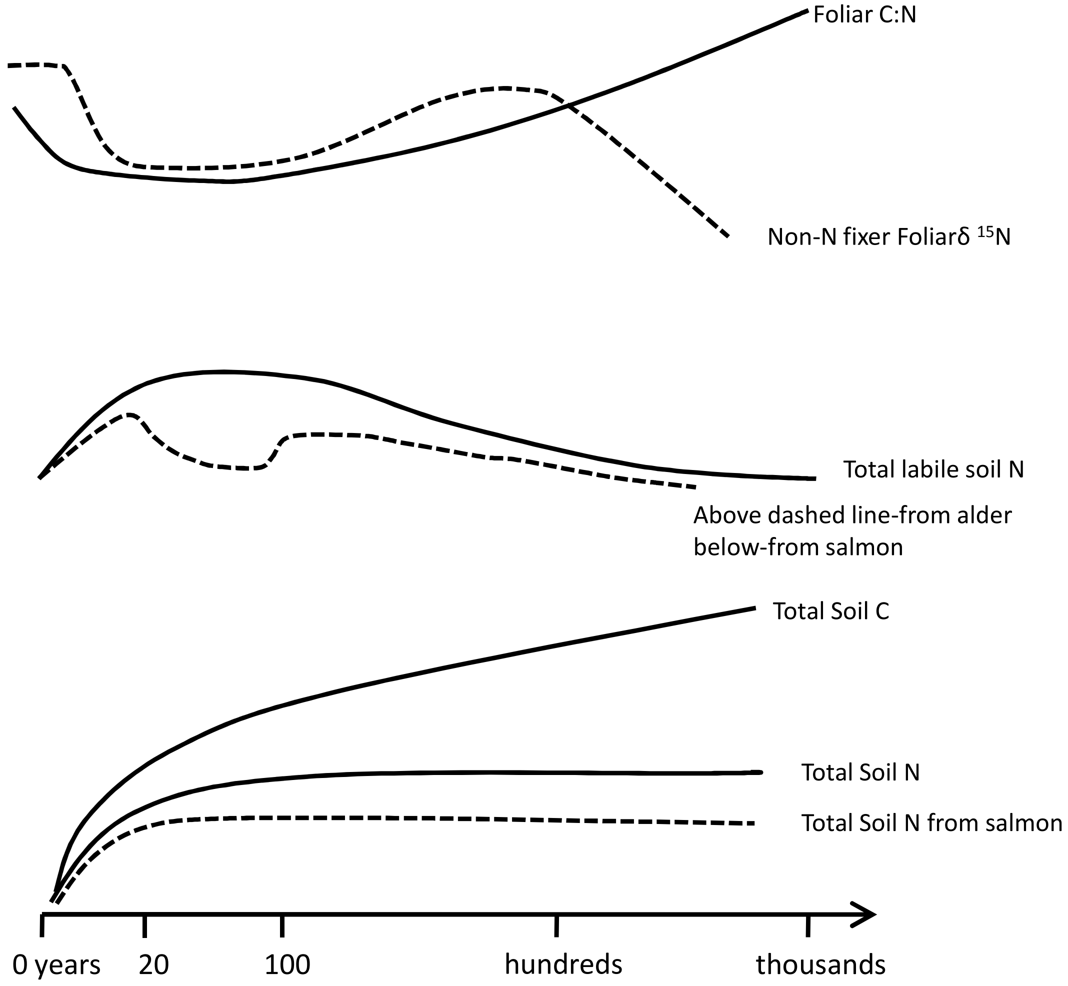

Figure 9. Summary conceptual models showing how foliar C:N and foliar δ^{15}N change during succession in relation to soil nitrogen pools.

<u>-20 to 100 years</u>. No longer adjacent to the main channel, these sites rarely receive significant salmon carcasses. Rather, nitrogen-fixing *Alnus* trees and flood deposited fine sediments are the main nitrogen inputs to these sites. Plant-available nitrogen is at its highest during this time due to rich soils from accumulated salmon inputs as well as the *Alnus* inputs. Consequently, foliar C:N ratios reach their lowest levels early in this period indicating the vegetation is no longer nitrogen limited. Because the labile soil nitrogen pool is dominated by

Alnus and nitrogen mineralized from fine sediments there is a decline in foliar $\delta^{15}N$ relative to the beginning of succession.

100 to hundreds of years. Most of the *Alnus* have senesced and there are no more major nitrogen inputs. Consequently, total soil nitrogen approaches an asymptote while soil carbon continues to accumulate rapidly, exacerbated by the tall forb meadow's enormous biomass accumulation rates (Walter 1981). This causes soil C:N ratios widen. Consequently labile soil nitrogen decreases and foliar C:N ratios increase. Foliar $\delta^{15}N$ increases from the previous time period for two potential reasons: firstly, there are no more *Alnus* inputs to dominate the labile nitrogen pool and secondly, the long term effect of nitrogen saturation (a legacy of the previous timeperiod).

Hundreds to thousands of years. Nitrogen becomes progressively more limiting due to: (1) the lack of additional nitrogen inputs, (2) soil nitrogen being tied up in recalcitrant pools, and (3) the positive feedback between soil infertility and poor litter quality. Foliar C:N ratios continue to increase and foliar $\delta^{15}N$ declines due to the "tightening" of the nitrogen cycle, as well as the development of the ericaceous mycorrhizal community.

Conclusions and Significance

We found that foliage in the modern floodplain was highly enriched in ^{15}N relative to the uplands, as well as relative to temperate forests and other Pacific-rim floodplains that did not receive significant salmon subsidies. We concluded that Pacific-salmon, which are also enriched with ^{15}N, were a major nitrogen source to the floodplain and were responsible for the high foliar nitrogen concentrations that we observed. Other studies conducted along smaller upland streams have also shown that riparian vegetation assimilates salmon imported nitrogen, but this fertilization effect was typically limited to within 25 to 100 m from the streambanks. In contrast, we found that salmon fertilized the entire 2.5 km wide modern floodplain of the lower Kol River.

Elevated foliar C:N ratios indicated that nitrogen availability may have limited vegetation growth for the first 20 years of succession, and high foliar $\delta^{15}N$ during this time indicated that salmon were a major nitrogen source to colonizing vegetation. Nitrogen did not appear to be limiting for at least the next 60 years of succession and alder-fixed nitrogen in addition to salmon-imported nitrogen stored in the soil were major nitrogen sources to vegetation during this time. Despite being distant from the mainchannel and having not received salmon-imported nitrogen for hundreds of years, old forests in the passive floodplain were still highly enriched with the ^{15}N isotope indicating that they continued to recycle salmon-imported nitrogen acquired in early succession.

One of the most well demonstrated relationships in plant ecology is that there is a strong positive relationship between foliar nitrogen concentration and photosynthesis rate (Field and Mooney 1986). Because the bare rock environments at the beginning of succession are typically very nitrogen poor, nitrogen availability usually profoundly limits vegetation growth at the onset of succession. By alleviating this infertility at the onset of succession and building nitrogen rich soils, salmon promote the proliferation of fast-growing, nitrophillic vegetation communties, and the tall forb community that dominated the passive floodplain of the Kol River is known to have some of the highest biomass accumulation rates in the world (Walter 1981).

Many of the rivers draining the Pacific-rim are inherently cold, oligotrophic and have low productivity. Because some species of Pacific-salmon grow for several years in these rivers before migrating to the ocean, it has been widely hypothesized that the fertilization effect of spawning salmon may help ensure future salmon runs (eg. Michael 1995, Schmidt et al. 1998, Griswold et al. 2003, Schindler et al. 2003, Wilson et al. 2003, Wipfli et al. 2003). Several studies have found support for this hypothesis in that both in-stream production (e.g. Wipfli et al. 1998, Wold and Hershey 1999, Chaloner and Wipfli 2002, Minikawa et al. 2002 and others) and juvenile salmon growth (Bilby et al. 1998, Wipfli et al. 2003) may increase in the presence of salmon carcasses; although whether this actually translates into increased survival across the entire lifecycle is unclear (Naiman et al. 2002, Schindler et al. 2005). A major pathway through which marine derived nutrients are assimilated by juvenile salmon in the Kol floodplain is through the riparian vegetation. Other studies conducted in the Kol floodplain have found that a large proportion of some species of juvenile salmon's diet (>60% during some seasons) was terrestrial invertebrates (Eberle 2007) and stable isotope analysis indicated that these invertebrates were enriched with salmon-derived nitrogen (B. Ellis unpublished). As robust salmon runs have disappeared and continue to decline throughout much of their historic range (Gresh et al. 2000) we urge managers to also consider the salmon's ecological role, in addition to population models and economic factors, when making management decisions.

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CHAPTER 4:
ANALYSIS OF FOLIAR δ^{15}N ACROSS A WIDE RANGE OF SALMON FERTILIZATION RATES IN RIPARIAN FORESTS THROUGHOUT THE PACIFIC-RIM.

Abstract

Adult Pacific-salmon migrate to their natal rivers to spawn and subsequently die. In doing so, they may import large quantities of labile nutrients into these freshwaters. Numerous studies employing the ^{15}N stable isotope as a natural tracer of salmon-nitrogen have concluded that riparian vegetation growing along spawning streams assimilates large quantities of salmon-imported nitrogen when available. However, several recent papers have questioned the reliability of these results because isotopic fractionation errors could lead to large overestimates of the importance of salmon-nitrogen in vegetation nutrition. The purpose of this study was to determine the reliability and resolution of foliar δ^{15}N as an indicator of salmon-nitrogen loading rates at a diversity of sites around the Pacific-rim. We answered this question by compiling published and unpublished data from 19 rivers throughout the Pacific-rim, and regressing riparian foliar δ^{15}N as a function of the quantity of salmon-nitrogen imported per stream kilometer at each site. We found a highly significant, positive-relationship between foliar δ^{15}N and salmon nitrogen loading rate ($p<0.0001$ and $R^2=0.55$) among all these sites, but this relationship was nonlinear. Each per-unit increase in salmon subsidy became progressively less influential on foliar δ^{15}N, resulting in an asymptote at the highest fertilization levels. However, we also observed a wide range in foliar δ^{15}N values among species within each site (commonly 5‰), and this was not clearly related to either mycorrhizal status or general growth form. Therefore, numerous species of non-nitrogen-fixing, terrestrial vascular plants should be sampled in order to effectively compare foliar δ^{15}N among sites. Furthermore, we found that foliage collected at our study site, the Kol River (Kamchatka, Russian Federation), conformed well to the regression, and was third highest in both salmon nitrogen loading rate and foliar δ^{15}N when compared with the other sites. We concluded that foliar δ^{15}N can be used to distinguish between very high (>1,000 kg-N km), moderate (100 to 1,000 kg-N km) and low (<100 kg-N km) salmon nitrogen loading rates, and thus can serve as a valuable tool indicating the general extent to which salmon fertilize vegetation, but only if numerous taxa are sampled. This result will allow foliar δ^{15}N to be used as evidence of salmon fertilization in study areas that do not have appropriate non-salmon reference sites, as was the case with our study site on the Kol River floodplain.

Introduction

Pacific salmon mature in the ocean and then return to their natal streams to spawn and then die, thereby contributing high quality nutrients and production to these otherwise oligotrophic freshwaters. Recent studies have found that salmon imported nitrogen (SN) may also be assimilated by riparian vegetation. This discovery is important because riparian forests have a much greater capacity to retain and recycle nitrogen than in-stream processes. And, as riparian forests are production sources for both aquatic and terrestrial food webs, assimilation by riparian vegetation may be an important pathway through which SN are reallocated back to juvenile salmon, which often spend several years rearing in freshwaters before migrating to the ocean (Naiman et al. 2002).

Because salmon are enriched in ^{15}N ($\delta^{15}N$ = 9‰ to 14.1‰; Naiman et al. 2002, Morris et al. 2005, B. Ellis FLBS unpublished data) relative to foliage from high latitude forests (mean $\delta^{15}N$ = -2.8‰, SD = 2.0‰ Martinelli et al. 1999) the natural abundance of the ^{15}N isotope has been used as a tracer of SN (Bilby et al. 1996, Ben-David et al. 1998, Hildebrand et al. 1999, Helfield and Naiman 2001, Helfield and Naiman 2002, Mathewson et al. 2003, Bilby et al. 2003, Bartz and Naiman 2005). Using isotope mixing models that compare riparian foliage along spawning streams to foliage at non-salmon reference sites, these studies have concluded that non-nitrogen fixing plants have acquired between 16 to 63% of their nitrogen from salmon (Bilby et al. 1996, Hildebrand et al. 1999, Helfield and Naiman 2001, Helfield and Naiman 2002, Mathewson et al. 2003, and Bilby et al. 2003). However these results have recently been questioned because non-salmon reference sites may be fundamentally different than spawning sites in ways that could cause defferences in background ^{15}N abundance even without salmon. For example, spawning sites may have finer sediments (Pinay et al. 2003) or better soil drainage (Kirchoff 2003) than reference sites, and both of these factors could influence denitrification rates, and denitrification is known to elevate foliar $\delta^{15}N$. Also, confounding isotope fractionations occurring during decomposition, mineralization and and processing of SN in the soil prior to to plant assimilation could cause large overestimates of the importance of SN (Morris et al. 2005).

Because $\delta^{15}N$ values are influenced by many factors in addition to SN, most research to date has been limited to riparian forests with nearby non-salmon reference sites that are used to establish background $\delta^{15}N$ (see Appendix). Some studies have used reference sites that were upstream of barriers to migrating salmon. Other studies have compared small streams in catchments where some of the streams lacked salmon runs. Prior to this dissertation, SN cycling in large river floodplains was virtually unstudied because there are generally no barriers to migrating salmon in these systems, and consequently, they have no appropriate reference sites.

Even sites that are distant from the mainchannel cannot be used as references because the processes of flooding, hyporheic flow, and channel migration may deliver SN throughout the entire floodplain (see Chapter 3). Without appropriate references or a clear demonstration that δ^{15}N can reliably indicate degree of SN fertilization at diverse sites, it could be argued that observations of elevated δ^{15}N at spawning sites may be due to factors other than SN fertilization. It is unfortunate that SN cycling in large river floodplains has not been studied as these sites often have the greatest concentrations of spawning salmon and they function to retain nutrients (Junk et al. 1989, Stanford et al. 2005). In contrast, the small streams where SN cycling has been studied primarily export nutrients from the riparia downstream.

Herein we examined the potential relationship between riparian foliar δ^{15}N and the SN loading rate for rivers around the Pacific-rim. If there is no relationship between SN loading rate and foliar δ^{15}N, then it can be concluded that δ^{15}N is not a reliable indicator of salmon fertilization, and differences between spawning and reference sites observed in studies to date could be due to confounding factors rather than SN, as suggested by Pinay et al. (2003). Conversely, if there is a significant relationship between foliar δ^{15}N and SN loading rate, then it can be concluded that foliar δ^{15}N can be used as a relative indicator of salmon-fertilization among diverse sites. For this analysis we compiled previously published foliar δ^{15}N data, and we also added new data from sites in the Salmonid Rivers Observatory Network (SaRON) (See http://www.umt.edu/flbs/Research/SaRON.htm).

We observed a strong positive relationship between foliar δ^{15}N and salmon run size and this relationship was strong enough to allow the use of foliar δ^{15}N values to distinguish between sites receiving low (<100 kg-N km^{-1} yr^{-1}) moderate (100 to 1,000 kg-N km^{-1} yr^{-1}) and high SN loading rates (>1,000 kg-N km^{-1} yr^{-1}). We also found that our study site, an expansive floodplain of the Kol River, Kamchatka (Russian Federation N53°49.506’ E156°3.716’) conformed well to the relationship established by the other sites, and was third highest in foliar δ^{15}N and fourth highest in SN loading rate among the 19 study sites.

Methods

Foliar δ^{15}N data, along with data on salmon run sizes were compiled from 19 rivers around the Pacific-rim (see Figure 1). Raw data and sources are given in the Appendix.Where raw data was not given directly in the papers it was estimated from graphs. These rivers encompassed a wide range of geomorphic domains from small creeks with constrained channels to large rivers with expansive floodplains. Only foliage of vascular, non nitrogen-fixing terrestrial species collected immediately adjacent to the streams were included in the analysis. We plotted the mean foliar $\delta^{15}N$ value for each species as a function of the SN loading rates that these sites received (measured as kg-N stream km^{-1} yr^{-1}). Where estimates of SN loading rate were not included in original sources, values were calculated by multiplying run sizes (averaged from recent years) by the typical mass for each salmon species (Bigler et al. 1996) and then

Figure 1. Map showing riparian sites along salmon rivers where foliar $\delta^{15}N$ has been quantified. Green shading shows the range of salmon rivers. Original map (without numbers or site names) from the State of the Salmon Consortium, available at http://www.stateofthesalmon.org/page.php?pgID=19. See also "http://creativecommons.org/licenses/by-nc-sa/2.0/" for information on map use.

multiplying this biomass by 3%, the average nitrogen concentration of salmon (Larkin and Slaney 1997). This total quantity of nitrogen was then divided by the length of the mainchannel. While these estimates of SN km^{-1} are admittedly rough, they were adequate for the proposed analysis given the enormous range of run sizes among sites. Data were fitted with both linear and non-linear regression in the Graphpad Prism 5 computer program. A similar analysis by Nagasaka et al.(2006) used some of the same data presented in this study, however they only included *Salix* foliage from 12 sites.

Results and Discussion

Riparian foliar $\delta^{15}N$ is positively related to salmon run size in Pacific-rim rivers

We found a highly significant, positive relationship between foliar $\delta^{15}N$ and SN loading rate (as kg-N km^{-1}) for 19 rivers occurring at distant sites throughout the Pacific-rim (Figure 2). Foliar $\delta^{15}N$ values from the non-salmon reference sites were on average slightly enriched (mean $\delta^{15}N = -1.4‰$) relative to the global average for foliar $\delta^{15}N$ in temperate forests (-2.8‰; Martinelli et al. 1999), but were well within the range of typical values for plant tissues (-5 to 2‰; Fry 1991). In contrast, foliage at sites with the largest salmon runs (exceeding 1,000 kg-N km^{-1}) always had positive $\delta^{15}N$ values, ranging from 2‰ to 7‰, and with a mean of about 5‰. When the x-axis was log-transformed, the relationship was approximately linear, and SN loading rate could explain 55% of the total variation in foliar $\delta^{15}N$ (Figure 2). Thus we concluded that foliar $\delta^{15}N$ was well correlated with SN loading rate, and was surprisingly robust to the wide array of confounding factors that potentially occur among distant and ecologically diverse rivers.

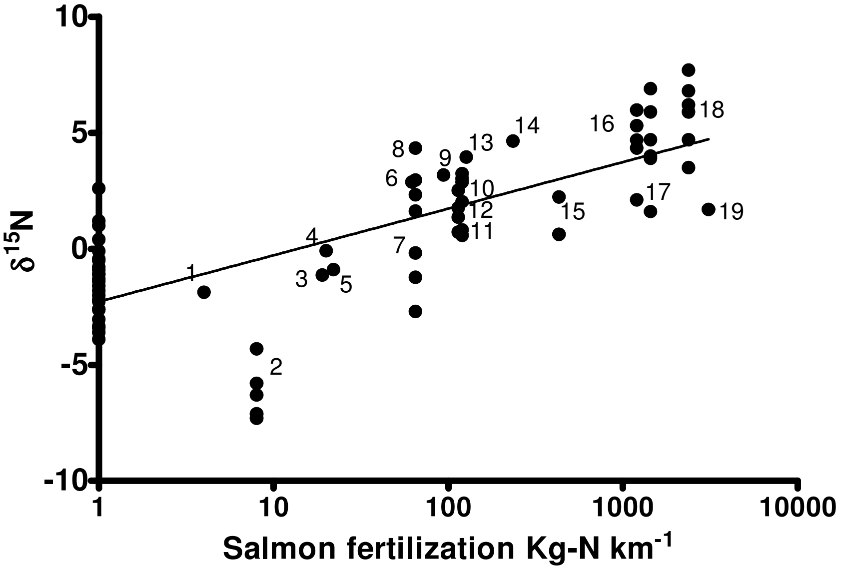

Figure 2. Riparian foliar $\delta^{15}N$ (‰) regressed against salmon nitrogen loading rate for rivers throughout the Pacific-rim. Means were plotted for all terrestrial, non nitrogen-fixing vascular species that were sampled at each site. See the original data with citations for each study in the appendix). Note that the x-axis was log-transformed. Numbers correspond to sites shown in Figure 1.

The observed relationship between foliar δ^{15}N and run size among Pacific-rim rivers is nonlinear

Foliar δ^{15}N increased most rapidly at lowest fertilization rates, and at the highest fertilization levels (above 1,000 kg-N km^{-1}) increasing run size had little effect on foliar δ^{15}N relative to the variation among species (Figure 3).

In an attempt to explain the shape of this curve, we constructed a conceptual model describing a closed system where salmon are the only nitrogen input to a pre-existing (background) nitrogen pool. Furthermore we assumed there were no isotopic fractionations within this system. Under these conditions, the expected change in foliar δ^{15}N with increasing SN can be described as:

$$\delta^{15}N_F = (\delta^{15}N_T * P_0 + \delta^{15}N_S * P_S) / (P_0 + P_S)$$

where $\delta^{15}N_F$ is the calculated value of the total pool after the SN addition, $\delta^{15}N_T$ is the δ^{15}N value of the pool prior to any SN (-1.4‰), P_0 is the size of the nitrogen pool prior to any SN, $\delta^{15}N_S$ is the δ^{15}N of the added SN (9‰ to 14‰), and P_S is size of the SN input. We set P_0 to an arbitrary value of 1 and P_S was varied on the x-axis as multiples of P_0.

Figure 4 shows that this equation produces the same general behavior as seen in the empirical data. $\delta^{15}N_F$ is initially highly responsive to SN at the lowest fertilization levels, but the response becomes decreases with each per unit increase in fertilization. This occurs because each unit of SN addition becomes a progressively smaller fraction of the total nitrogen in the system as the total nitrogen pool grows. Furthermore, even with infinite SN the highest value that $\delta^{15}N_F$ could achieve would be the δ^{15}N value of the salmon itself.

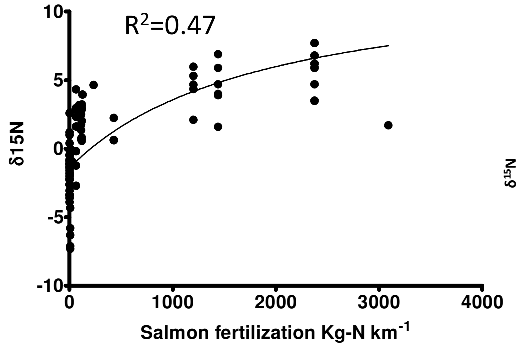

Figure 3. The conceptual model fit to the empirical data for all plant species sampled at each site. Note that this is the same data presented in Figure 2, the only difference is that the X-axis is not log transformed as it was is Figure 2.

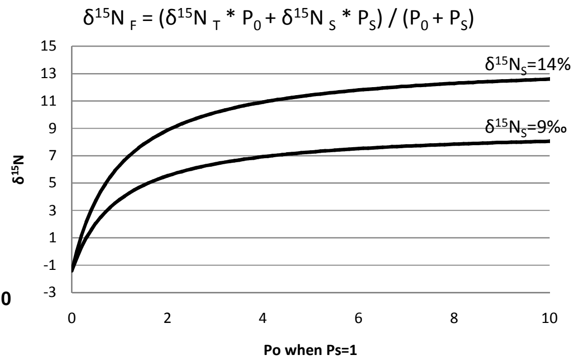

Figure 4. Conceptual model showing the effect of increasing salmon subsidies on foliar δ^{15}N.

However, nonlinear regression of the conceptual model produced a poorer fit (Figure 3) to the empirical data (R^2=0.47) than the simple log transformed linear relationship (R^2=0.55) (Figure 2). There are several potential explanations for this. Firstly, the model is a gross over-simplification given that it treats all sites as identical, aside from the magnitude of the SN. It also assumes that there are no losses or confounding fractionations within the system. In reality, confounding fractionations and losses are considerable, and they would also vary with the magnitude of the SN inputs.

We were surprised that the mean foliar $\delta^{15}N$ was not closer to the value of salmon (9 to 14‰) at the highest SN loading rates, considering the enormous quantities of nitrogen imported to these sites. This may have occurred if the vegetation still obtained a large proportion of their nitrogen from terrestrial sources even at the highest SN loadings, perhaps because decomposing salmon are often only available for brief periods during the growing season, as well as that much of the annually imported SN is exported with river flow (Moore et al. 2007). Alternatively, vegetation at sites with the highest SN loading rates may have received the vast majority of their nitrogen from SN, but foliar $\delta^{15}N$ was still depleted several ‰ relative to SN because of confounding isotopic fractionations. This may have occurred if vegetation assimilated SN that was stored in the soil and subsequently mineralized, or SN was delivered to the vegetation as nitrate via hyporheic flow, given that typically sediment-$\delta^{15}N$ > NH_4-$\delta^{15}N$ >NO_3-δ^{15} (Högberg 1997). Also, foliar $\delta^{15}N$ may have been depleted several ‰ if nitrogen was not limiting at these sites, as plants fractionate against ^{15}N during uptake under nitrogen saturated conditions (Högberg 1997). Therefore, we are unsure whether vegetation could have incorporated an even greater proportion of their total nitrogen from SN, or whether this depletion reflected an isotopic fractionation process.

Within site variation among species.

Clearly, a large proportion of the variance in this dataset was attributable to within site variation among the different plant species sampled at each site. Indeed, mean foliar $\delta^{15}N$ among species within a single site was as much as 5‰, which is only slightly less than the difference in mean $\delta^{15}N$ of foliage at spawning and reference sites (about 6 to 7‰) (Figure 2). Such wide variation among species is common in most forests and is attributable to numerous factors including different preferences for nitrogen sources, variation in rooting depth, differences in mycorrhizal associations, and isotopic fractionation occurring during and after nitrogen uptake (Nadelhoffer et al. 1996).

We did not find clear evidence that either mycorrhizal status or broad taxonomic groupings consistently explained the variance that we observed among species. When species were grouped according to their potential mycorhizal associations (non/VAM, ecto and eriocoid- according to Newman and Reddell 1987, Harley and Harley 1987), and regressed against SN loading rates, the best fit lines for each mycorrhizal group had nearly identical slopes (p=0.84) and differences among intercepts were insignificant (p=0.088) (data not presented). We also grouped the species according to whether they were forbs, ericaceous shrubs, evergreen trees or broadleaf deciduous shrubs/ trees, but again, neither slopes (p=0.81) nor intercepts (p=0.11) were significantly different among groups. Given that neither mycorrhizal status nor broad growth form explained the differences that we observed among species, we hypothesize that intra-species variation may be better explained by preferences for nitrogen source, or differences in rooting depth, or combinations of all of these factors.

In order to control for some of the variation that occurred among taxa we also regressed data for just *Salix* foliar δ^{15}N versus SN loading rate because *Salix* is ubiquitous throughout the Pacific-rim and was sampled at many of these sites. When SN loading rate was log transformed the linear regression model for just *Salix* explained slightly more variation in the data ($R^2 = 0.61$, Figure 5) than for when all species were combined ($R^2 = 0.55$, Figure 2). We reccommend that all future studies of this type consider sampling *Salix* in addition to other species to allow better comparisons among sites.

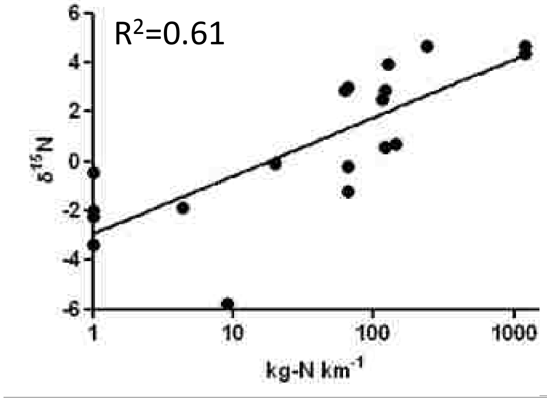

Figure 5. Linear relationship between foliar δ^{15}N and salmon-N loading rate for *Salix* only. Note that the X-axis was log transformed.

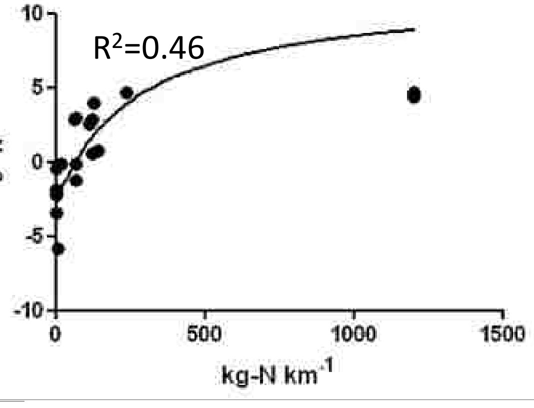

Figure 6: The conceptual model fit to *Salix* data only.

How does foliar $\delta^{15}N$ in the Kol River floodplain fit this relationship?

The Kol River floodplain ranked third highest for mean foliar $\delta^{15}N$ and fourth highest for SN loading rate and conformed very well to the best fit curve (Figure 2), despite that most of these other sites were along small streams without expansive floodplains. This good conformance provides very strong evidence that the elevated foliar $\delta^{15}N$ values that we observed in the Kol floodplain were in fact due to SN, and not some other confounding factor. This finding is crucial to this dissertation because as we explained in the introduction, there are no suitable non-salmon reference sites in expansive floodplains.

Only one study site, the Kitlope River in British Columbia, produced a very poor fit relative to the general pattern established by the other sites (Figure 2). As a result of overharvest for more than 100 years this site had very low salmon runs (Hill 2007). Also, this site had exceptionally low foliar $\delta^{15}N$. The very low foliar $\delta^{15}N$ observed in the Kitlope floodplain probably reflected that the Kitlope River was extremely oligotrophic and was in close proximity to glacial mountains (Hill 2007), as highly negative $\delta^{15}N$ values have also been found in other recently deglaciated forests (Kohls et al. 1994, Hobbie et al. 1998). High depletions in these systems have been attributed to the heavy reliance on mycorrhizally-assimilated and atmospherically-deposited nitrogen under very infertile conditions. The extremely low foliar $\delta^{15}N$ measured in this system also attests to minimal influnece of the low numbers of salmon that this river receives, given that Figure 4 suggests under such infertile conditions even minor SN would greatly increase foliar $\delta^{15}N$.

Conclusions and implications

We conclude that there is a clear positive relationship between riparian foliar $\delta^{15}N$ and the SN loading rate amongst a diversity of rivers throughout the Pacific-rim. However, the observed relationship is nonlinear and foliar $\delta^{15}N$ becomes progressively less sensitive to each per unit increase in SN loading rate.

Based on Figure 2 and Table 1 we propose that the relationship between foliar $\delta^{15}N$ and SN loading rate has sufficient resolution to allow foliar $\delta^{15}N$ to be used to distinguish between low, medium and high SN loading rates, but only if foliage from numerous non nitrogen fixing, terrestrial, vascular plant species are sampled. We propose the following groupings:

	<100 kg-N km^{-1}	100 to 1000	>1000
n	43	15	18
Minimum	-7.3	0.58	1.6
25%	-2.7	0.72	3.8
mean	-1.3	2.1	4.8
75%	-0.09	3	6
Maximum	4.3	4.7	7.7

Table 1. summary of mean foliar $\delta^{15}N$ (‰) values as well as ranges and quartiles for each vascular plant species sampled at each salmon river (see appendix) grouped according to the size of the salmon nitrogen loading rate that each river recieves. <100 kg-N km^{-1} includes non-salmon reference sites used in the study. Symbiotic nitrogen fixing species were not included in this analysis

(1) 0 to low SN loading rate (<100 kg-N km^{-1} yr^{-1}): mean foliar $\delta^{15}N$ value for all species together around -1‰ and individual species means typically ranging between -3‰ to 0‰ (based on 25th and 75th percentile respectively).

(2) Moderate SN loading rate (100 to 1,000 kg-N km^{-1} yr^{-1}): mean foliar $\delta^{15}N$ value for all species around 2‰ and with individual species means typically ranging between 1 to 3‰

(3) High SN loading rate (>1000 kg-N km^{-1} yr^{-1}): mean foliar $\delta^{15}N$ values for all species around 5‰ and with individual species means typically ranging between 4 and 6‰ and multiple species means exceeding 5‰.

As numerous factors can influence $\delta^{15}N$ values in addition to SN there will undoubtedly be exceptions to these proposed rules, particularly at sites that are influenced by anthropogenic pollution or sites that have other unique nitrogen sources. Therefore, the presence of significantly elevated foliar $\delta^{15}N$ values alone does not prove unequivocally that a site is influenced by salmon. But, given the strong relationship between foliar $\delta^{15}N$ and SN loading rate that we observed, abnormally high foliar $\delta^{15}N$ could provide strong supporting evidence that this were the case. The ability to compare foliar $\delta^{15}N$ values to typical values from sites with low, moderate and high SN loading rates will be especially useful for the study of sites that do not have appropriate references, such as in expansive floodplains of large rivers.

Considering that SN loading rate explained slightly more than half of the variance in this dataset we do not advocate the use of quantitative isotope mixing models to estimate the % contribution of SN to total foliar nitrogen, as has been done in most of the studies that we reviewed. Instead we suggest that future studies use the guidelines given above, as well as correlation to make broad comparisons among sites with wide ranges of salmon abundances. For example, natural abundance isotopes do not have the resolution to claim that foliage at one site receives 20% of its nitrogen from salmon while another receives 30% of its nitrogen from salmon. But this study indicates that there is enough resolution to claim that a site has foliar δ^{15}N values that are consistent with high SN loading rates (>100kg-N km^{-1} yr^{-1}) while another site has foliar δ^{15}N values consistent with low/no SN loading rates (<100 kg-N km^{-1} yr^{-1}).We agree with Hauck (1973) that ^{15}N natural abundance as an indicator of nitrogen source is “qualitative or roughly quantitative.”

The highly significant, positive relationship between foliar δ^{15}N and SN loading rate that we observed clearly indicates that riparian vegetation growing along spawning streams assimilates large quantities of SN when available. And because temperate and boreal forests are typically nitrogen limited, it is likely that SN influences the growth and composition of these riparian communities. Given the growing recognition that salmon are valuable nutrient and production resources to freshwater ecosystems, we urge that salmon managers begin to consider the ecological role of salmon when setting escapement goals.

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Appendix page 1

			salmon sites Foliar δ^{15}N ‰	reference sites Foliar δ^{15}N ‰	salmon-N import Kg-N/stream km
Mathewson et al. 2003[1,2]	**Common name**	**Scientific name**			**1440**
Claste, BC	Deerfern	*Blechnum spicant*	4	2.6	
	Alaskan blueberry	*Vaccinum alaskaense*	5.9	1	
	Red huckleberry	*Vaccinium parvifolium*	4.7	-0.1	
	False azalea	*Menziesii ferruginea*	3.9	0.4	
	Salmonberry	*Rubus spectabilis*	6.9	1.2	
	Western hemlock	*Tsuga heterophylla*	1.6	-1.4	
		mean:	**4.5**	**0.6**	
Neekas, BC	Deerfern	*Blechnum spicant*	6.2	-2.6	**2375**
	Alaskan blueberry	*Vaccinum alaskaense*	7.7	-1.6	
	False azalea	*Menziesii ferruginea*	4.7	-3.6	
	Devil's club	*Oplopanax horridus*	5.9	-1.1	
	Salmonberry	*Rubus spectabilis*	6.8	-0.8	
	Western hemlock	*Tsuga heterophylla*	3.5	-3.9	
		mean:	**5.8**	**-2.3**	

article states: 1990-1999: Clatse annual average runs: 17,000 pink and 5,000 chum. Impassable waterfalls at 1km upstream.
paper states: 1990-1999: Neekas annual average runs: 18,000 pink and 30,000 chum. Impassable waterfalls at 2.1km upstream.

			salmon sites Foliar δ^{15}N ‰	reference sites Foliar δ^{15}N ‰	salmon-N import Kg-N/stream km
Helfield and Naiman 2001					
Chichagof, SE AK	Sitka spruce	*Picea sitchensis*	0.63	-3.34	**430**
averaged from sites on the Kadashan and Indian Rivers	Devils club	*Oplopanax horridus*	2.24	-0.91	
	Fern	*Dryopteris dilatata*	0.62	-3.05	
	Red alder	*Alnus rubra*	-0.91	-1.04	
		mean:	**1.16**	**-2.43**	

article states annual escapement of pink salmon = 30,000 to 125,000 spawners in Kadashan and 200 to 45,000 spawners in Indian river. Pink salmon about 65g of N in body tissue.
kadashan: 5,037kg-N/ approximately 20km of stream length
Indian : 1,469 kg-N/2.4 km stream length (to impassible falls)

			salmon sites Foliar δ^{15}N ‰	reference sites Foliar δ^{15}N ‰	salmon-N import Kg-N/stream km
Bilby et al. 2003[1]					
Griffin Creek, WA	Salmonberry	*Rubus spectabilis*	**-0.9**	**-0.5**	**22**given directly in article
Kennedy Creek, WA	Salmonberry	*Rubus spectabilis*	**1.7**	**-1.1**	**3090**given directly in article
Bilby 1996[3]					
Stream 0372, WA	Various terrestrial vegetation	Not specified		**-2.2**	
Grizzly creek, WA	Various terrestrial vegetation	Not specified	**0.7**		**30**

article: adult coho for 2 years during study was 240 and 475 fish per km

Appendix page 2	Common name	Scientific name	salmon sites Foliar $\delta^{15}N$ ‰	reference sites Foliar $\delta^{15}N$ ‰	salmon-N import Kg-N/stream km	
Helfield and Naiman 2002[1,4]						
Wood river Lakes system SW, AK: following data are means for each species taken at multiple streams	White Spruce	*Picea glauca*	1.77	-1.8		
	Balsam poplar	*Populus balsamifera*	1.36	-2.2	150	Hanset Creek
	Feltleaf willow	*Salix alaxensis*	0.72	-3.4	65	Happy Creek
		mean:	**1.28**	**-2.47**	40	Ice Creek
All following for sockeye					100	Lynx Creek
Hansent Creek: stream length: 2.1km, mean escapement 1957- 1997: 3986					215	Pick Creek
Happy Creek: stream length: 6.45 km, mean escapement 1957- 1997: 5165					**114**	mean
Ice Creek: stream length: 16.13km, mean escapement 1957- 1997: 8622						
Lynx Creek: stream length: 2.26km, mean escapement 1957- 1997: 2921						
Pick Creek: stream length: 4.03km, mean escapement 1957- 1997: 10776						
Bartz and Naiman 2005						
Bristol Bay System: the following data are means for each species taken at multiple streams	White Spruce	*Picea glauca*	0.81	-2.63		rivers, kg-N/km givenin article
	Feltleaf willow	*Salix alaxensis*	0.58	-2.01	33	Kijk
	polar grass	*Arctagrostis latifolia*	2.03	-1.3	13	Elva
		mean:	**1.14**	**-1.98**	80	Kakhonak
					48	Grant
					40	Fenno
					95	Margot
					268	Tazimina
					182	Chinkelyes
					107	Southeast
					337	Copper
					120	
SARON Unpublished						
Kwethluk River, AK	Arctic blackberry (marsh 3-finger)	*Rubus arcticus*	-2.70		**65**	SARON estimates
	Marsh cinquefoil	*Potentilla palustris*	2.33			
	Red top grass	Poaceae sp.	1.62			
	Horsetails spp.	*Equisetum sp.*	4.34			
	Diamond-leaf willow	*Salix pulchra*	-1.23			
	Felt leaf willow	*Salix alaxensis*	2.96			
	Little tree willow	*Salix arbusculoides*	-0.18			
		mean:	**1.02**			
Kitlope River, BC						
	Cottonwood	*Populus sp.*	-7.3		**8**	SARON estimates
	Grass	Poaceae sp.	-4.31			
	Salmonberry	*Rubus spectabilis*	-6.3			
	Thimbleberry	*Rubus parviflorus*	-7.11			
	Willow	*Salix sp.*	-5.8			
		mean:	**-6.16**			

Appendix page 3	**Common name**	**Scientific name**	**salmon sites Foliar δ^{15}N ‰**	**reference sites Foliar δ^{15}N ‰**	**salmon-N import Kg-N/stream km**	
Utkholok River, RU	Grass	Poaceae sp.	3.24		**120**	SARON estimates
	Filipendula kamschatka	*Filipendula kamschatka*	3.03			
	Willow	*Salix sp.*	2.87			
		mean:	**3.05**			
Kol River, RU	Chosenia tree	*Chosenia arbutifolia*	5.98		**1200**	SARON estimates
	Stinging nettle	*Urtica dioica*	5.31			
	Unidentified willow A	*Salix sp.*	4.68			
	Unidentified willow B	*Salix sp.*	4.35			
	Filipendula kamschatka	*Filipendula kamschatka*	2.11			
		mean:	**4.49**			
Nagasaka et al. 2006						
Shibetoro River, Northern Territory	Willow	*Salix sp.*	4.65		235	chum/pink 5450 fish per km---used pink data
Lower Piraito River, Northern Territory	Willow	*Salix sp.*	2.88		62	chum/pink 1443 fish/km---used pink data
Rusha River, Hokkaido	Willow	*Salix sp.*	-1.87		4	pink 100 fish/km
Nodaoi, Hokkaido	Willow	*Salix sp.*		-0.44		
Subetsu River, Hokkaido	Willow	*Salix sp.*		-2.27		
Johnston et al. 1997---cited in Nagasaka et al. 2006						
Bivouac Creek, BC	Willow	*Salix sp.*	-0.09		20	Sockeye 254 fish/km
Forfar Creek, BC	Willow	*Salix sp.*	3.95		127	Sockeye 1634 fish/km
O'Ne-eil Creek, BC	Willow	*Salix sp.*	2.52		113	Sockeye 1457 fish/km
Reimchen et al. 2003---cited in Nagasaka et al. 2006						
Warn Bay Creek, Vancouver Island, BC	Salmonberry	*Rubus spectabilis*	3.18		94	chum 728 fish/km
Sydney River, Vancouver island BC, Canada	Salmonberry	*Rubus spectabilis*	-1.13		19	chum 147 fish/km

Appendix page 4

[1] Notes: these studies did not provide the original δ15N raw data. Thus δ15N was estimated from graphs provided in the original publications using the XYDIGZ graph reading program, downloaded from http://www.esg.montana.edu/.

[2] Assumed average BC pink salmon is 1.43kg and chum is 4.63kg (Bigler et al. 1996), salmon are approximately 3.03%N by mass (Larkin and Slanely 1997)

[3] Assumed average WA coho salmon is about 2.83kg (Bigler et al. 1996) andapproximately 3.03%N by mass (Larkin and Slanely 1997)

[4] Assumed average Bristol Bay Sockeye is 2.66kg (Bigler et al. 1996) and approximately 3.03%N by mass (Larkin and Slanely 1997)

*Foliar δ15N, ppm- per mil deviation from atomospheric 15N:14N ratio

-Note: in many cases salmon N-import in kg/km was not reported in the original source

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We also used data reported in Nagasaka et al. 2006 that was compiled from the following studies

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Johnston, N.T., J.S. Macdonald, K.J. Hall, P.J Tschaplinski. 1997. A preliminary study of the role of sockeye salmon *(Oncorhynchus nerka)* carcasses as carbon and nitrogen sources for benthic insects and fishes in the "Early Stuart" stock spawning streams, 1050 km from the ocean. British Columbia Ministry of Environment, Land and Parks Fisheries Project Report No. RD55, p24.

CHAPTER 5:
SEASONAL INFLUENCE OF DECOMPOSING SALMON ON NITROGEN ASSIMILATION DYNAMICS OF GRAVEL-BAR WILLOWS.

Abstract

Primary succession on the lower Kol River floodplain (Kamchatka, Russian Federation N53 49.506 E15603712) begins with the colonization of flood-deposited alluvial bars by three species of willow trees *(2 Salix sp. and Chosenia arbutifolia)*. Because these new alluvial bars are composed of coarse sands and gravels, they have very low nitrogen fertility. However, annual runs of spawning salmon import large quantities of labile nutrients to the Kol River, causing mainchannel total nitrogen concentrations to increase three times, and nitrate ten times, from their pre salmon levels. And, late season flooding deposits decomposing salmon carcasses onto these young gravel bars, causing a pulse of nitrogen availability in these otherwise infertile environments. However, this pulse is brief, generally less than three weeks during late August and early September because these gravel bars are poorly retentive of salmon-imported nitrogen and subsequent fall flooding flushes these sites, reverting them back to their infertile states for most of the growing season.

The purpose of this study was to determine whether colonizing willows *(Salix sp.)* were able to capitalize on this brief nitrogen pulse given that it occurred so late in the growing season. We used sequential whole-willow harvests to quantify seasonal growth and nitrogen uptake during 2006, and we also used the ^{15}N isotope as a natural tracer of salmon-derived nitrogen. As expected, we found that early season growth of young willows was fueled by remobilization of nitrogen stored in root tissue, and high $\delta^{15}N$ during this time indicated that this nitrogen was originally acquired from salmon during the previous growing season. These plants then assimilated nitrogen mineralized from sediments throughout the early summer and intermediate $\delta^{15}N$ values during this time indicated that this nitrogen was a mixture of salmon and non-salmon derived nitrogen.

Young willows grew and assimilated nitrogen most rapidly during the main period of salmon decomposition. However, there was only a minor increase in whole plant $\delta^{15}N$ during this time indicating that this accelerated late season growth may not have been due to the fertilization effect of salmon carcass decomposition. This probably occurred because salmon-runs were highly depressed; approximately 1/10th their normal abundance during the 2006 season. Furthermore, there was little late season flooding during 2006 and no carcasses were deposited directly amongst this willow stand. Therefore, we conclude that colonizing willows certainly have the

ability to assimilate nitrogen during the time when carcasses are available, despite that this occurs so late in the growing season. However, assimilation of nitrogen directly from carcasses may be minor if salmon runs are greatly depressed and/or there is little late season flooding as occurred during 2006. Because these alluvial bars are nitrogen-poor both before and after carcass decomposition, the ability to capitalize on this brief nitrogen-pulse may help the willows maintain high growth rates on these otherwise nitrogen-poor alluvial bars.

Introduction

Plant growth is usually strongly nitrogen limited in early floodplain succession because vegetation colonizes bare alluvial bars that are very low in organic matter. Soil fertility then increases as succession proceeds due to the accumulation of fine sediments, forest litter and biologically-fixed nitrogen (Van Cleve et al. 1993, Sasaki et al. 2001, Walker and del Moral 2003, Adair and Binkley 2002, Adair et al. 2004). We showed elsewhere (Chapters 1, 2 and 3) that newly formed gravel bars in the floodplain of the lower Kol River were, in fact, nitrogen poor, and net nitrogen mineralization within these soils could only provide a small fraction of the colonizing willow's *(Salix sp.)* annual nitrogen requirement. However soil nitrogen accumulated extremely rapidly during succession, increasing an order of magnitude by the time willow stands were 30 years old. We also found that willows responded to changing soil fertility during succession as their foliar nitrogen concentrations were lower during the first 20 years of stand development but increased to optimal foliar nitrogen concentrations after this time (Chapter 3).

The Kol river floodplain is unique relative to other primary succession chronosequences studied to date in that it receives large annual nitrogen subsidies from Pacific-salmon, which mature in the ocean and spawn and die in the river. While the Kol receives runs of all 6 species of Pacific-salmon, pink salmon (*Oncorhynchus gorbuscha*) are by far the dominant species with up to five million adults returning to spawn per year, importing up to 270,000 kg-N yr^{-1} into the river. We found that flooding driven by fall rains washed decomposing salmon carcasses amongst young alluvial bar willow stands because they were adjacent to the mainchannel and flooded regularly. In contrast, mature forest sites received few carcasses (Chapter 1).

Using the ^{15}N isotope as a natural tracer, we confirmed that salmon were in fact a major nitrogen source to colonizing willows. However these subsidies were apparently not strong enough to completely alleviate nitrogen limitation. This likely occurred because salmon carcasses were: 1) not available until late in the growing season (late August and September), 2) decomposed very rapidly (within weeks) and 3) subsequent fall and spring flooding flushed salmon nitrogen from the coarse soils of the gravel bars. We found that gravel bars were nitrogen poor again in the late fall and following spring, despite having received large salmon nitrogen subsidies in late summer.

The purpose of this study was to determine whether colonizing willows do in fact assimilate salmon nitrogen during the brief period of carcass availability, given that it is very late in the growing season. If young willows are unable to capitalize on this brief nitrogen pulse then salmon may have limited influence on vegetation growth. However if they are able to assimilate and store large quantities of nitrogen when salmon are available, then this pulse may sustain growth through the infertile periods.

In this study we used sequential, whole-willow harvests to quantify seasonal growth and nitrogen uptake in relation to salmon nitrogen availability. We also measured nitrogen content in the roots, stems and leaves in order to determine how nitrogen was stored and allocated. Finally, because salmon are highly enriched in the ^{15}N isotope relative to terrestrial sources (Naiman et al. 2002) we used $\delta^{15}N$ as a natural tracer of salmon imported nitrogen.

Study site

The headwaters of the Kol River (Kamchatka, Russian Federation) originate in the central Kamchatka mountain range and the river flows westward (see Figure 1). By the time it reaches the Sea of Okhotsk the Kol is a seventh order river. Our study site was within a large flood plain (N53°49.506’ E156°3.716’) of the lower Kol River and was approximately 12 km upstream of the Kol’s mouth. This floodplain was largely pristine with no roads or year-round inhabitants and the entire Kol catchment was recently designated as a salmon conservation area by the Russian government. Research was based out of a biological station operated by The Wild Fishes and Biodiversity Foundation (Kamchatksky, Russian Federation) and The Wild Salmon Center (Portland, OR).

The climate of the south-western Kamchatka is cold, wet, sub-oceanic (Krestov 2003). According to weather data collected in the town of Sobolevo, approximately 50 km north of the Kol River, the mean annual temperature of the region is -0.9 °C. The mean temperatures of the coldest and warmest months are -14.9 and 12.2 °C respectively. The total frost-free period is 92 days (Sokolov 1974), and annual precipitation is approximately 789 mm. (Krestov 2003).

Morris et al. (Chapter 1) modeled the dominant vegetation succession pathway in the lower Kol floodplain. In the active floodplain, primary succession began with the colonization of alluvial bars by willows and fewer *Chosenia arbutifolia* trees. These willows grew rapidly into dense pole-stands and formed a canopy within 20 years. Alders emerged beneath this

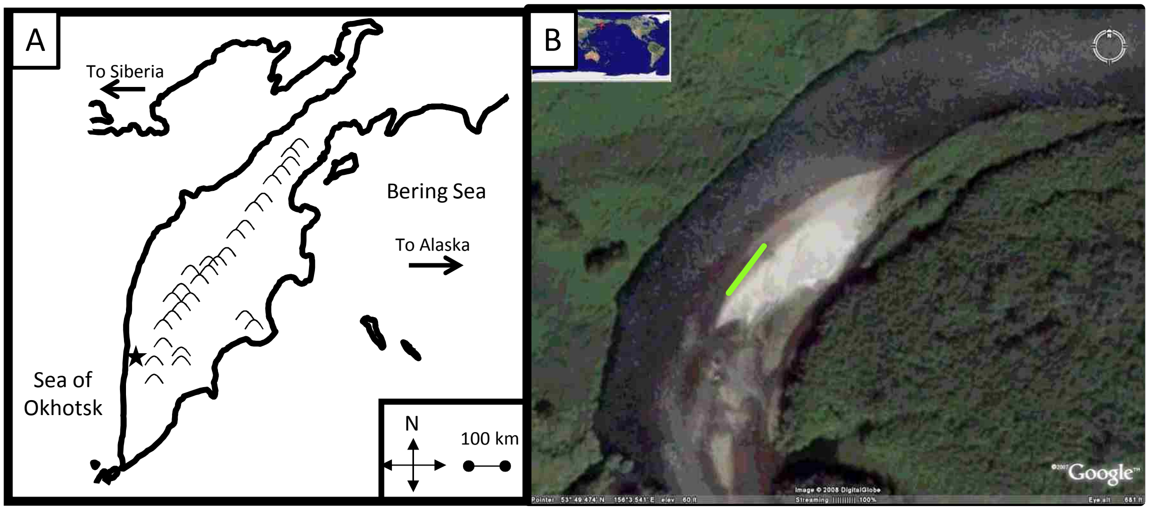

Figure 1. Study site.The star in map A shows the location of the Kol river in southwestern Kamchatka, RU. The green line in map B: shows the location of the study band of 3yr old willows growing on the outer margin of the young alluvial bar. This bar is on the inside of of a river bend and the river flows from the upper right hand corner to the lower left corner of the picture. For perspective, the length of the green line is approximately 20m. Map B is from "Google Earth 2007".

canopy and for the next sixty years a mixed willow, alder and *Chosenia* canopy forest occupied these sites. By about 100 years these trees senesced and were replaced by a nitrophillic-tall forb community. Outside of the floodplain, roughly seventy percent of the catchment was tundra-dominated coastal plain below 150 m although birch *(Betula sp.)* forests are present on hills within the tundra landscape.

This paper addressed a single patch of three year old willows (2 *Salix sp*.) that formed a band on the outer margin of a young gravel bar (see Figure 1). The mainchannel adjacent to this gravel bar had a minimum summer baseflow of approximately 20 to 30 $m^3 s^{-1}$. Table 1 shows the soil properties (see Chapter 2) determined from a transect across this entire gravel bar, not just amongst this band of willows. It is clear from these soil data that that this gravel bar had very low nitrogen fertility. There was less than 200 kg total-N ha^{-1} in the top 10 cm of soil and the standing stock of plant available dissolved inorganic nitrogen was less than 1kg-N ha^{-1}. Net N-mineralization rate (averaged from the spring and late summer samplings during 2006) was only 0.02 kg-N ha^{-1} d^{-1}. Given that there are approximately 92 frost-free days in the growing season of this region (Sokolov 1974) net mineralization within the top 10 cm of soil on this gravel bar was less than 2 kg-N ha^{-1} for the entire growing season. In contrast forests typically assimilate 25 to 100 kg-N ha^{-1} yr^{-1} (Chapin III et al. 2002).

Bulk Density	2.1 g cm^{-3}
Total Soil N	180 kg-N ha^{-1}
PMN	7 kg-N ha^{-1}
DIN	1 kg-N ha^{-1}
Net mineralization	0.02 kg-N ha^{-1} d^{-1}
2006 salmon carcass deposition	6 kg-N ha^{-1}

Table 1. Soil properties (to 10 cm) of the alluvial bar upon which our study willow stand occurred. These data are from Chapters 1 and 2. PMN is potentially mineralizeable nitrogen pool (7-day water-logged net ammonification at 40°C); DIN is KCl-extractable dissolved inorganic nitrogen.

Methods

In order to determine the timing and extent of the salmon fertilization, mainchannel water samples were collected throughout the 2005 and 2006 growing seasons (late May until late September). Whole water samples were frozen after collection and then thawed and analyzed for total nitrogen using the persulfate digest method followed by cadmium reduction. Water filtered through Millipore 0.45 µm membrane filters (HAWP02500) was frozen, thawed and then analyzed for nitrate according to the cadmium reduction method (Clescerl et al. 1999). To ensure the accuracy of our results, all calibrants and standards were made by diluting NIST standard stock solutions and all standards and reagents were made with ultrapure DI water and analytical grade chemicals. To evaluate precision, nine duplicates were run during the total nitrogen analyses and twenty five duplicates were run during the nitrate analyses. The mean difference between total nitrogen replicates (with one outlier removed) was within 19 µg-N L^{-1} (+/-SD = 11). The mean difference between the 25 nitrate replicates was 6 µg-N L^{-1}(+/-SD = 4). Considering that typical total nitrogen values ranged between 100 to 500 µg-N L^{-1} and nitrate ranged from 20 to 300 µg-N L^{-1} this precision was more than adequate to demonstrate differences in mainchannel nitrogen concentrations among seasons.

Whole willows were harvested six times throughout the growing season during 2006. The collections began soon after bud break, and ended prior to fall leaf senescence. Eight to ten replicates were haphazardly chosen along the length of the willow band. The roots of these willows were carefully excavated by hand while simultaneously rinsing away fine sediments with buckets of river water. We tried to retain as much of the fine root mass as possible, although some fine roots were of course lost. The whole willows were refrigerated in the laboratory at the Kol camp for up to 48 hours, although they were usually processed within 24 hours. In the laboratory, the willow were rinsed briefly (several minutes) with deionized water to remove any adhering fine sediments. The roots were also picked clean of detritus and visibly dead roots. Root and shoot lengths were recorded and each plant was dissected into roots, stems and leaves. These parts were then dried at 70°C. After drying, the plant parts were weighed and stored in for several months in Ziploc bags and then exported by permit to the Flathead Lake Biological Station. Dried parts were then homogenized using a coffee grinder and the resultant powder was subsampled and re-ground in a Spex Mill. This fine powder was then re-dried at 60 to 80° C and sent to the University of Georgia Stable Isotope Laboratory where it was analyzed for total carbon and nitrogen as well as the ratio of ^{15}N to ^{14}N isotopes using a combustion GC/MS system. ^{15}N concentration was reported in $\delta^{15}N$ units which is the parts per thousand deviation of the sample's ^{15}N:^{14}N from atmospheric N_2's ^{15}N:^{14}N which is 0.003675. Therefore $\delta^{15}N = ((R_{sample}R_{N2})/(R_{N2}))*1000$.

Statistical analyses were conducted using the Graphpad Prism 5 program. One-way ANOVA followed by the Tukey-test was used to test for differences among sampling dates. Differences were considered significant when $p<0.05$. Variables were log-transfromed in cases where variables were not normally distributed according to the D'Agostino and Pearson omnibus test or where groupings had significantly different variances according to Bartlett's Test for Equal Variances. The equality of variance assumption was accepted when at least five out of the six sampling dates were not rejected as normal for each variable.

Results

Mainchannel nitrogen concentrations were elevated (400-600 μg-N L^{-1}) during spring flooding (through June) and then declined as flooding receded (Figure 2). They were at their lowest levels (100 to 200 μg-N L^{-1}) during baseflow in July and then increased as the pink salmon entered the river in August. Nitrogen concentration then peaked (500-600ug-N L^{-1}) during the main period of spawning and death in late August and early September and then decreased with fall flooding. The main salmon run and resulting nitrogen pulse were approximately 2 weeks later in 2006 than 2005. During spring flooding the majority of the river water nitrogen was NO_x-N, whereas NO_x-N comprised a smaller fraction of total nitrogen when salmon were in the river.

On average, the juvenile willows weighed less than 1 g during the first harvest and grew to 11 g by the last harvest (Figure 3). Growth rate was not uniform across the seasons, and mass actually decreased significantly (Table 2) by approximately 0.5 g from the first to the second sampling period (June 6 to June 25). Furthermore, there was no statistically significant growth between July 28 and August 24 (Figure 3, Table 2). Willows grew the fastest from August 24 until September 12 and this corresponded to the period of salmon carcass decomposition. Roots and stems followed the same growth pattern as the whole plant and these parts were each approximately one-third of the total mass after the leaves fully developed, from July 28 through August 24 (Table 3). However the roots grew disproportionately after this time, increasing to approximately 43% of the total mass. Leaf growth also followed a similar pattern as the other plant parts with the exception that it did not decrease during the first two sampling dates nor did leaf mass increase significantly between the last two sampling dates.

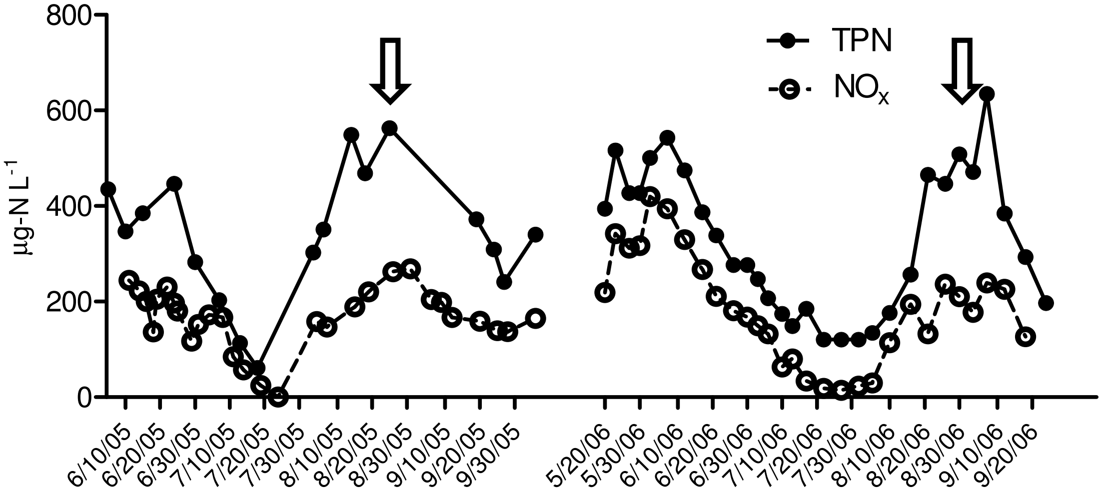

Figure 2: mainchannel nitrogen concentrations during the 2005 and 2006 growing seasons. TPN is total persulfate nitrogen and NO_x is nitrate (+nitrite). The pink salmon run began in late July in 2005 and early August in 2006. The maximum periods of spawning and death are shown with the arrows. Spring flooding/high flows persisted through mid to late June.

Total plant nitrogen increased from 27 mg to 116 mg from the first to the last harvest, but again, net nitrogen increase rates were not uniform (Figure 3). On average, juvenile willows lost 11 mg of nitrogen from the first to second sampling date, but then total nitrogen increased over the next two sampling dates. As with total mass, total nitrogen also did not change significantly between July 28 and August 24, and total nitrogen increased most rapidly between August 24 and September 12. Total leaf nitrogen across the growing season followed the same pattern as total plant nitrogen, except that it did not have an initial decline at the beginning of the growing season. Once leaves fully developed they contained the majority of total plant nitrogen, more than 60% of the total from July 8 until August 24. Total nitrogen content of the roots decreased from June 6 until June 25, increased very gradually from June 25 until July 28, and then increased most rapidly between August 24 and September 12, again corresponding to the main period of salmon decomposition. Stem nitrogen followed the same pattern as the roots, except that there was no initial decline in total nitrogen (Figure 3, Table 2).

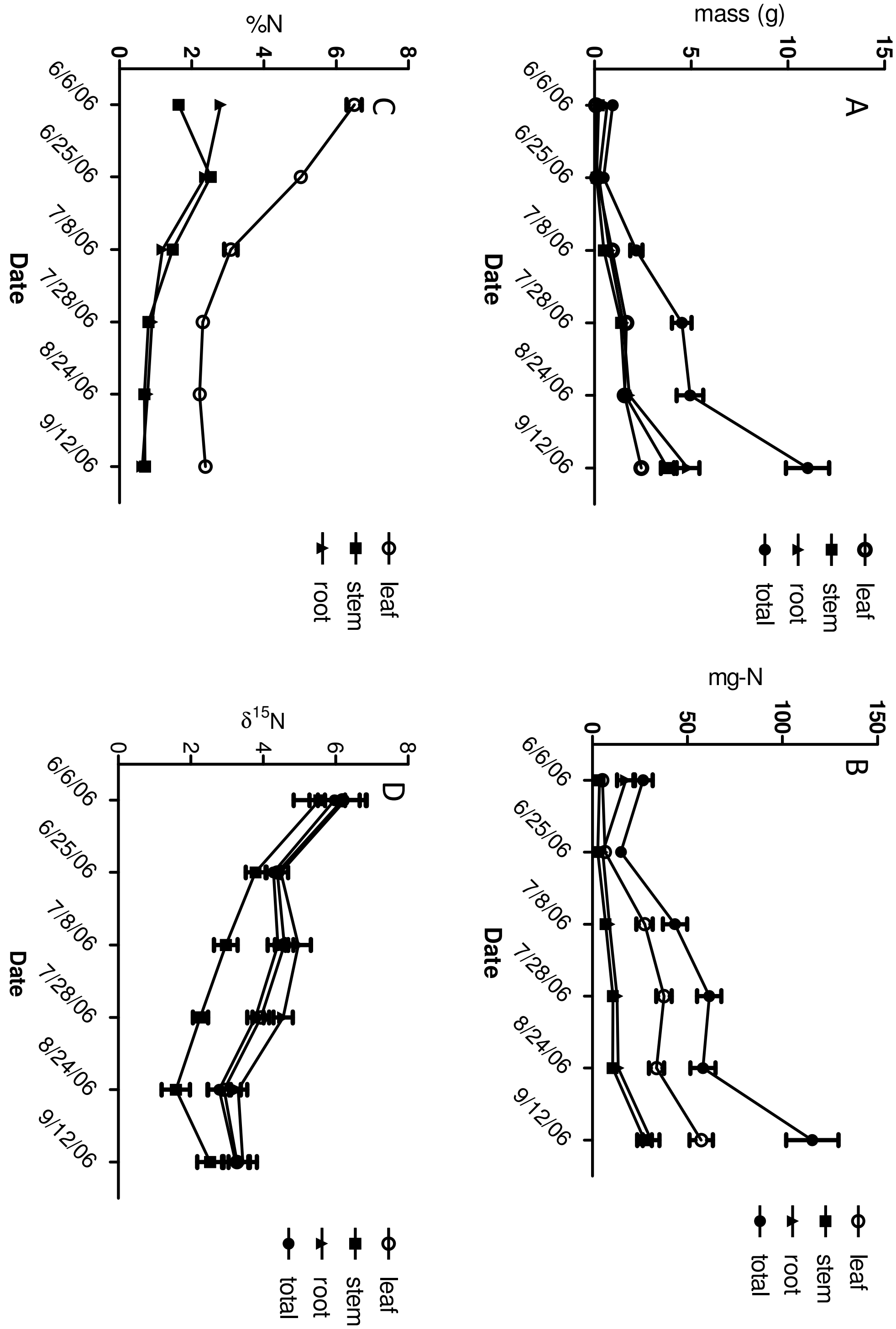

Figure 3: Seasonal change in willow growth and nitrogen nutrition. Graph A: willow mass; Graph B: nitrogen content; Graph C: nitrogen concentration and graph D: $\delta^{15}N$ (‰). Error bars show standard error and there were 8 to 10 replicates for each plant part per date. The main period of salmon death and terrestrial deposition of carcasses occurred between 8/24 and 9/12/06.

		T2	T3	T4	T5	T6
Mass	total	-	+	+	n	+
	roots	-	+	+	n	+
	stems	-	+	+	n	+
	leaves	n	+	+	n	n
N-content	total	-	+	n	n	+
	roots	-	n	n	n	+
	stems	n	+	n	n	+
	leaves	n	+	n	n	+
%N	roots	-	-	-	n	n
	stems	+	-	-	n	n
	leaves	-	-	-	n	n
δ^{15}N	total	-	n	n	n	n
	roots	-	n	n	n	n
	stems	n	n	n	n	n
	leaves	-	n	n	n	n

Table 2. Results of one way ANOVA and Tukey post-hoc testing whether each mean on a given date was significantly different than the previous date only. "+" indicates there was a significant increase ($p<0.05$), "-" indicates there was a significantly decline and "n" indicates there was no significant change. These statistics correspond to the results presented in Figure 3.

	T1	T2	T3	T4	T5	T6
%root	64	50	36	33	36	43
95%CI	56 to 72	43 to 55	32 to 40	30 to 35	33 to 39	39 to 47
%stem	26	23	22	30	33	35
	19 to 33	20 to 27	19 to 25	27 to 33	30 to 35	32 to 38
%leaves	10	28	41	37	31	22
	7 to 12	23 to 33	40 to 44	35 to 39	28 to 35	19 to 25
stem length	16	12	17	31	32	43
	13 to 18	10 to 13	15 to 20	26 to 37	28 to 39	39 to 47
taproot length	nm	nm	21	20	35	39
			16 to 25	16 to 23	24 to 46	26 to 51
longest root	nm	23	40	48	65	84
		19 to 27	28 to 53	39 to 57	48 to 85	70 to 98

Table 3. Summary table of the morphometric characteristics of the 3 year old willows and how they changed during the growing season. The upper values show the % (by mass) of the whole willow that each part comprised and the lower values are length in cm. nm=not measured.

Both leaves and roots were most nitrogen rich during the first harvest and then % nitrogen declined stepwise until July 28, after which there was no additional change in nitrogen concentration (Figure 3). Stems followed a similar pattern except that there was an initial increase in stem nitrogen concentration between June 6 and June 25. While all of the other variables showed considerable variation, there was very little variance in % nitrogen among replicates.

Mean whole plant $\delta^{15}N$ decreased by 2‰ over the entire growing season, from 6‰ at the beginning of the harvests to slightly less than 4‰ by September 12 (Figure 3). Leaf $\delta^{15}N$ was nearly identical to whole plant $\delta^{15}N$. At the first harvest all tissues had very similar $\delta^{15}N$ and were less than 1‰ apart. All tissues exhibited a rapid decline in foliar $\delta^{15}N$ between the first two sampling periods, June 6 to June 25 and after this date foliar $\delta^{15}N$ among parts diverged. Stem $\delta^{15}N$ declined until August 24 whereas leaf and root $\delta^{15}N$ showed little change between June 25 and July 8 but then decreased by approximately 1‰ by August 24. Between August 24 and September 12 (when salmon carcasses were available) all plant parts increased in $\delta^{15}N$, although this was slight, <1‰. While the plant parts exhibited similar trends, changes in $\delta^{15}N$ were largely not significant between consecutive sampling dates (Table 2) due to the small sample sizes (usually 10) relative to the variation among replicates.

Discussion

As has been found in other studies (eg. Jauquet et al. 2003, O'Keefe and Edwards 2003), spawning salmon increased river water nitrogen concentrations substantially. Prior to the pink salmon run, mainchannel total nitrogen was elevated during spring flooding and then declined greatly as the river approached baseflow in the summer (Figure 2). This pattern is typical for snowmelt driven-alluvial rivers and is due to the flushing of nitrogen from soils and aquifers in the spring, as well as increased nitrogen assimilation by primary producers in the summer (Wetzel 2001). The main runs of pink and chum salmon then entered the river in midsummer and their metabolic excretion caused nitrogen to increase. That the salmon caused this increase is proven by the fact that the main salmon runs and the associated nitrogen increases were both two weeks later in 2006 than 2005. During both of these years nitrogen concentrations peaked during the main period of spawning and death, as decomposing carcasses accumulated in the river. Whereas nitrate was the predominant mainchannel nitrogen species during spring flooding, reduced nitrogen forms, the direct products of carcass decomposition, were the main nitrogen species when salmon were in the river, although nitrate concentrations also increased about 10X after salmon entered the river. Nitrogen concentrations then declined in the fall as flooding flushed carcasses from the mainchannel.

Despite this enormous nitrogen subsidy, nitrogen concentrations in the mainchannel of the Kol were well within the range of typical values for unpolluted rivers. During the growing season mean total nitrogen (330-340 μg-N L^{-1}) and nitrate (170-180 μg-N L^{-1}) were about the same in both 2005 and 2006. And, although not measured, whole-year means should be much lower due to the lack of flooding and salmon during the winter base-flow period. In comparison, the mean value for nitrate in unpolluted rivers is about 100 µg-N L^{-1} and ranges between 50-200 µg-N L^{-1} (Meybeck 1982, Wetzel 2001). Total nitrogen was less commonly reported in the literature, but total dissolved nitrogen averaged 380 µg-N L^{-1} (Wetzel 2001), which is greater than mean total nitrogen of the Kol during the growing season. Even during the height of salmon death, total nitrogen in the Kol River (600 µg-N L^{-1}) was well below typical values for streams in polluted regions, where nitrogen concentrations are often several thousand µg-N L^{-1} or more (Meybeck 1982). That the Kol River maintains moderate nitrogen concentrations despite these enormous subsidies attests to the very low background fertility of this system (specific conductance = 50 to 60 µS cm^{-1}), and the Kol clearly would be a very oligotrophic ecosystem if not for salmon. The low background fertility of the Kol may be due to its glacial/snowmelt inputs in its headwaters, as well as that tundra, which comprised most of the land area in the catchment, typically has very low nitrogen fertility (eg. Meybeck 1982, Nadelhoffer et al. 1992, Jonasson et al. 1996). This is confirmed by our findings that two tributaries of the Kol that drained the tundra had very low NO_X concentrations, ranging from <25 to 36 µg-N L^{-1} (FLBS unpublished data).

Despite the very low soil nitrogen fertility that we measured on this gravel bar (Table 1), our study population of young willows grew rapidly, with their mass increasing more than 10X during the growing season (Figure 3). This rapid growth was in part fueled by high foliar nitrogen concentrations (>2% N), as foliar nitrogen concentration is strongly positively correlated with photosynthesis rate (Field and Mooney 1986, Aerts and Chapin III 2000). While still nitrogen limited (Chapter 3), the moderate foliar nitrogen concentrations of these young willows indicates that nitrogen limitation was considerably less severe at our study site than occurs on young alluvial bars in other floodplains that did not have significant salmon subsidies (eg. Walker and Chapin IIII 1986, Adair et al. 2004, Stanford unpublished data for Nyack floodplain, Middle Fork of the Flathead River, Montana).

As expected, whole plant $\delta^{15}N$ was very high at the beginning of the growing season, indicating that these willows assimilated large quantities of salmon-imported nitrogen during the previous growing season, and this nitrogen was retained over the winter (Figure 3). To illustrate how high $\delta^{15}N$ was, consider that whole plant $\delta^{15}N$ was approximately 6‰, whereas the pink salmon nitrogen was about 9‰ (B.Ellis; FLBS unpublished). In contrast, foliage from temperate broadleaf forests averages -2.8‰, with a standard deviation of about 2 (Martinelli et al. 1999). Therefore the $\delta^{15}N$ values of these young willows bore greater resemblance to salmon than terrestrially-fixed nitrogen. Some willows had $\delta^{15}N$ values of 7 to 9 ‰ which is practically unheard of in unpolluted terrestrial ecosystems, except at sites fertilized with salmon nitrogen or bird guano (Mizutani and Wada 1988, Nadelhoffer and Fry 1994, Högberg 1997, Mathewson et al. 2003, Erskine et al. 1998).

As is typical of broadleaf deciduous vegetation during the spring flush (Chapin III 1980, Bollmark et al. 1999, Kolb and Evans 2002), our study plants appeared to reallocate nitrogen stored in their roots to developing foliage during early season growth. This conclusion was based on our findings that there was no net uptake of nitrogen between our first and second sampling dates (June 6 through 25), and root nitrogen decreased while leaf nitrogen increased during this period (Figure 3). Interestingly, the roots lost much more nitrogen than the leaves gained, and there was a large loss in whole-plant nitrogen during this time. This finding was surprising and we initially thought it may have been due to a sampling effect, as our measurements of previous year's stem length indicated that smaller willows on average were sampled on the second date (Table 3). In order to test how this sampling error influenced our results, we re-analyzed the data by excluding all replicates with previous year's stems <10 cm and >15 cm, but again, we found the same result, that roots lost 6 to 15X more nitrogen than the developing leaves gained. Furthermore, whole plant $\delta^{15}N$ declined greatly over this period, and due to conservation of mass this could only occur if there were gains or losses of nitrogen.

The most likely explanation for this nitrogen loss between the first two sampling periods is root senescence, as root mass decreased greatly during this time and we did not observe any obvious loss of leaf or stem tissue. This root loss may have been associated with the disturbance effect of spring flooding, as other studies have found that flooding can cause root death (eg. Cao and Conner 1999). Because reallocation of nitrogen discriminates against the ^{15}N isotope (Gebauer and Schulze 1991, Kolb and Evans 2002, Choi et al. 2005 and others) whole plant $\delta^{15}N$ should decline if root nitrogen were reallocated to other organs prior to root senescence. We found that the whole plant $\delta^{15}N$ decreased by approximately 2‰ during this time (Figure 3). If the decline were driven solely by losses, the lost nitrogen would have to be enriched 2‰ relative to the whole plant, which is very feasible as a 2‰ discrepancy among plant organs is well within the normal range of intra-plant variation (Evans 2001).

After the initial nitrogen loss at the beginning of the growing season the willows assimilated nitrogen through July (Figure 3). Most of this nitrogen was invested in the developing foliage as total nitrogen content of the roots and stem only increased slightly until this point. Despite that whole plant nitrogen content increased several times over, we found that the willow's $\delta^{15}N$ did not change significantly. Assuming that whole plant $\delta^{15}N$ reflected the large quantity of assimilated nitrogen and there is minimal fractionation during uptake when nitrogen is limiting (Högberg 1997), we calculated that the $\delta^{15}N$ of assimilated nitrogen ranged from 2 to

4‰. As there were no salmon carcasses available yet, nitrogen assimilated early in the growing season likely originated primarily from mineralization within the sediments. Given that this mineralized nitrogen was depleted with respect to salmon nitrogen, but highly enriched relative to typical values in temperate forests, we conclude that soil nitrogen was a mixture of salmon-imported and non-salmon nitrogen. We cannot quantify the fraction of soil nitrogen that originated from salmon, because even if the nitrogen mineralized from the soil originated solely from the salmon, the plant available fraction should be depleted with respect to the original salmon nitrogen due to the fractionations associated with mineralization and nitrification (Högberg 1997).

Following the growth that we measured in early summer we found that there was no significant growth during the midsummer sampling period (7/28 until 8/24) and total nitrogen actually declined slightly (although insignificantly) during this time (Figure 3). We suspect that this was due to poor water availability at this site, as 2006 was the driest year that we observed in five years of working on this river and gravel bars are especially susceptible to desiccation due to their coarse sediments.

Given that there was no significant net change in willow nitrogen content between 7/28 and 8/24, we were surprised to find that whole plant δ^{15}N decreased during this time (although insignificantly due to low sample sizes) (Figure 3). For this to have occurred there would either have to be 1) large gross gains and losses in nitrogen over this very short timescale, 2) the very small accumulation of a highly ^{15}N-depleted nitrogen source, or 3) the very small loss of a highly ^{15}N enriched nitrogen pool. We feel that the first option is infeasible because we do not know of any mechanism that would cause such a high nitrogen turnover rates on the scale of less than one-month. Even fine roots, which possess some of the highest tissue turnover rates had mean life spans of ranging between 52 and 108 days in a similar Alaskan floodplain (Ruess et al. 2006). The second option may be possible if the vegetation assimilated very small quantities of ammonia volatilized from the salmon, as volatilized ammonia is highly depleted in ^{15}N (Erskine et al. 1998). However, we also think that this is unlikely, because this sampling period was prior to spawning and death and we suspect that this factor would have been greater when decomposing carcasses were available between the last two sampling periods.

Based on the finding of other studies, nitrate efflux provides a very plausible explanation for the ^{15}N depletion that occurred between 7/28 and 8/24. Given the very small net nitrogen loss occurring during this time we calculate that the lost nitrogen would have to be highly enriched (roughly δ^{15}N about 20‰) to cause this whole-plant depletion, and nitrate efflux has been shown to cause such small losses of highly enriched nitrogen (Robinson et al. 1998). Because nitrate reductase discriminates against the ^{15}N isotope, the small pool of free nitrate remaining in the plant is highly enriched in ^{15}N. If nitrate efflux is negligible, then whole plant δ^{15}N should largely resemble the δ^{15}N value of the nitrate source, but whole plant δ^{15}N may decline if nitrate efflux becomes enhanced. This may have occurred if water rather than nitrogen became limiting during this dry spell as osmotic stress can retard nitrate reduction even while nitrate uptake remains high (Larsson 1992).

Nitrate reduction may also be responsible for the discrepancies in δ^{15}N among plant parts that we measured (Figure 3), because highly ^{15}N enriched free-nitrate accumulates at the site of reduction, whereas slightly depleted assimilated nitrate-nitrogen is exported to other tissues (Robinson et al 1998, Evans 2001). Our finding that the roots and leaves were consistently enriched relative to the stem tissue indicates that the roots and leaves were the main sites of nitrate reduction and the stems were a sink for assimilated nitrate-nitrogen. This finding is consistent with other studies that have shown that nitrate assimilation occurs both in the roots and leaves of related *Populus* trees (Min et al. 1998, Black et al. 2002). The differences among plant parts that we observed may have also been due to reallocation of N-compounds as remobilized nitrogen tends to be depleted in ^{15}N (Kolb and Evans 2002, Choi et al. 2005).

Finally we conclude that willows not only grew late in the season when salmon were available, they actually grew fastest and assimilated nitrogen most rapidly between our last two sampling dates (Figure 3). All parts of these young willows assimilated nitrogen, and this nitrogen supported growth rather than luxury consumption as tissue nitrogen concentrations did not increase significantly. We were especially surprised that these young willows grew additional leaf biomass during September because leaves senesced in October. While these results indicate that willows have the potential to assimilate nitrogen directly from decomposing salmon carcasses, we found that whole plant δ^{15}N increased only slightly (and this was insignificant) between the last two sampling dates. δ^{15}N did not come close to approaching the levels that we observed on our first sampling date as we predicted they would. Given that these willows were still growing during our final harvest it possible that they continued to assimilate that year's salmon-imported nitrogen, however, we suspect that the main fertilization effect was over as most carcasses had decomposed completely and fall flooding had flushed this site by our last sampling date. These results suggest that decomposing salmon carcasses may not have been responsible for this late-season burst of growth and nitrogen assimilation that we observed. Rather, these effects may have been due increased water availability associated with late summer rains following the mid-summer dry spell.

We suspect the lack of a large increase in $\delta^{15}N$ at the end of the growing season accurately reflected the very low salmon-fertilization rate that occurred in 2006. In Western-Kamchatkan rivers, even year pink salmon runs are typically about 10x higher than odd year runs due to density dependent population dynamics in the oceans (Quinn 2005), and we designed this study to take place on a high salmon year. However, pink-salmon runs were extremely depressed in 2006 for all of Western Kamchatka, and were about the same size or smaller than odd year runs. Furthermore, there was very little late season flooding in 2006. Between these two factors, very few salmon carcasses were deposited amongst riparian vegetation. We estimated that the entire alluvial bar where our study willow stand occurred received <2kg-N ha^{-1} from salmon carcasses during 2006, and none of these carcasses were deposited directly amongst our willow stand. Based on carcass deposition rates at nearby sites on other years, we estimate that deposition rates were roughly 3X higher on low salmon years when flooding was more extensive, and up to 30x higher on abundant salmon years with typical flooding. As this study was designed to document the annual change in willow nitrogen under natural conditions, we did not add any carcasses to this site. We suggest that future studies use sequential harvests under natural conditions in addition to adding carcasses at low and high deposition rates.

It may be possible that salmon were still responsible for this late-season pulse of willow growth and nitrogen assimilation, but this was not reflected by large increases in $\delta^{15}N$. This could occur if there were large fractionations associated with the mineralization of salmon nitrogen during decomposition. However, we suspect that this is unlikely for carcasses decomposing on-site because they were fully decomposed over a short period of time, and due to conservation of mass, salmon derived ammonium should have roughly the same $\delta^{15}N$ as the original salmon nitrogen once fully decomposed. Rather, salmon-derived ammonium remaining in the soil would probably be slightly enriched in ^{15}N relative to the original salmon due to the fractionations associated with ammonia volatilization and gull metabolism, as these birds consumed a huge proportion of these carcasses and redeposited their nitrogen on-site as uric-acid (Mizutani and Wada 1988).

A much more likely scenario for that lack of ^{15}N enrichment may be that these willows assimilated salmon-imported nitrogen via hyporheically delivered nitrate. Salmon-derived nitrate would be expected to be quite depleted in ^{15}N relative to the original salmon because there is a large fractionation associated with nitrification (Nadelhoffer and Fry 1994, Högberg 1997), and only a small proportion of salmon-imported nitrogen was nitrified during the growing season. We found that mainchannel nitrate did increase about 10X when the salmon entered the river, and this young alluvial bar actively exchanged hyporheic water with the mainchannel. As nitrate is very mobile in sediments whereas reduced nitrogen is very immobile, we expect that nitrate was preferentially conducted along hyporheic flow paths.

We are unsure as to the extent to which these young willows have access to this hyporheic nitrate given that their roots did not extend into the saturated zone except during flooding, and the vast majority of their fine roots occurred in the upper sediment layers. A recent study in another floodplain has found that young alluvial bar willows did assimilate a nitrate tracer injected into the hyporheic zone and they concluded that hyporheic nitrate may be a more important nitrogen source than soil mineralization on infertile alluvial bars (Lisuzzso et al. 2004). If hyporheic nitrate were the sole delivery pathway of salmon-derived nitrogen, we would expect that salmon to be a relatively minor nitrogen source to these willows relative to the potential effect of on-site carcass decomposition. While salmon do increase mainchannel nitrate concentrations 10X, they are still not that high relative to nitrogen concentrations typical of soil solutions, or relative to nitrate concentrations in rivers without salmon. For example, the Kol River's nitrate concentrations were similar to levels measured at one of our other study sites that does not receive salmon nutrient subsidies, the Middle Fork of the Flathead River in the Nyack Floodplain (Montana, USA) (Reid 2007) and foliage in this floodplain is nitrogen poor (Harner and Stanford 2003). However, we only have data from low salmon years and it is likely that mainchannel nitrate concentrations are considerably higher on abundant salmon years. Clearly, too little is known about the potential significance of hyporheic-transported nitrogen for vegetation nutrition and this mechanism warrants additional research.

As explained previously, $\delta^{15}N$ may have not increased if the willows assimilated salmon-derived nitrogen via ammonia volatilized from carcasses, given that volatilized ammonia is highly depleted in ^{15}N (Erskine et al. 1998). Pearson and Stewart (1993) reviewed numerous studies of plants grown under elevated atmospheric ammonia concentrations and concluded that foliage can assimilate substantial proportions of their total nitrogen from ammonia when concentrations are well below the human odor threshold. And, we observed a strong foul odor throughout the river when carcasses were decomposing, suggesting that atmospheric ammonia concentrations may have been substantial. However, it is unlikely that volatilized ammonia accounted for most the nitrogen assimilated between our last two sampling dates as there would almost assuredly have been a large depletion in whole plant ^{15}N if this were the case. Without knowing how highly ammonia concentrations were elevated and for how long we cannot assess the significance of this pathway. Foliar assimilation of atmospheric ammonia derived from salmon warrants further research as well.

Conclusions

We found that migrating salmon caused mainchannel nitrogen to increase as they entered the river in early August. During the period of spawning and death (early September) total nitrogen and nitrate peaked at about 3x and 10x (respectively) the pre-salmon baseflow levels. However, despite these subsidies, mainchannel nitrogen concentrations were still well within the range of values typical for unpolluted rivers, indicating that mainchannel nitrogen would be extremely low if not for salmon.

Initial willow growth in the spring was fueled by remobilization of nitrogen stored in the roots, and high $\delta^{15}N$ at this time indicated that recycled nitrogen originated from spawning salmon in the previous year. The willows then assimilated nitrogen mineralized from sediments in early summer. The relatively high $\delta^{15}N$ of plant-available nitrogen during this time indicated that some fraction of this nitrogen was salmon-derived. We found that these young willows grew and assimilated nitrogen most rapidly during the main period of salmon death in late August to early September. However, the lack of large increase in whole-plant $\delta^{15}N$ during this time indicated that most of this assimilated nitrogen was not acquired directly from decomposing carcasses. This is probably due to that salmon runs were depressed during this year and carcass deposition was approximately 1/10th to 1/30th of their typical value. Furthermore no carcasses were deposited directly amongst the willow stand that we studied.

Therefore, we conclude that colonizing willows certainly have the ability to assimilate nitrogen when carcasses are available, despite that this occurs so late in the growing season. Because these alluvial bars are extremely nitrogen poor both before and after carcass decomposition, the ability to capitalize on this brief nitrogen pulse may help the willows maintain high growth rates on these otherwise nitrogen poor alluvial bars. Given that riparian vegetation forms the base of both the terrestrial and aquatic food webs, and it also controls a wide range of floodplain processes, such as nutrient and sediment transport, water dynamics etc., salmon may indirectly influence nearly every aspect of floodplain ecosystem function by alleviating strong nitrogen limitation in early succession.

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MAJOR CONCLUSIONS FROM EACH CHAPTER

Chapter 1: Primary vegetative succession and soil nitrogen accumulation on an expansive floodplain of a large salmon river.

- The succession chronosequence concept was a good organizing principle for understanding the range of variation in many soil and vegetation variables in the Kol floodplain. Our succession models were able to explain at least half the variance in over half the vegetation and soil variables that we measured.

- As in all types of primary succession, the Kol's floodplain soils were nitrogen poor (200 kg-N ha^{-1} to 10cm) at the onset of succession. However these soils accumulated more nitrogen, more rapidly during succession than has been shown in other primary succession chronosequences, and by 30 years these soils contained approximately 2,300 kg-N ha^{-1} (to 10 cm + litter layer).

- Unlike other Pacific-rim chronosequences, nitrogen-fixing alder was not the primary source of this accumulated nitrogen. Rather, the rapid accumulation of nitrogen in early succession could be explained by the import of salmon nitrogen, and the incorporation of this salmon nitrogen in rapidly accumulating fine sediments and forest biomass.

- The early succession vegetation community on the Kol floodplain was similar to what has been described in other Pacific-rim chronosequences in that willows and alders colonized young alluvial bars and formed canopy forests. However early succession on the Kol floodplain was different from these other chronosequences in that tree willows persisted for more than 100 years and alders were a relatively minor component of the community.

- Late succession on the Kol floodplain was very unique relative to other chronosequences described to date in that the community transitioned from a willow/alder forest to a nitrophillic-tall forb community at approximately 100 years. Approximately 80% of total coverage was dominated by one species, *Filipendula* *camtschatica*. We observed that these nitrophillic tall forb meadows were eventually replaced by grass meadows, which were eventually replaced by a heath community that only occurred in an ancient floodplain terrace.

- Finally, our study chronosequence was also unique in that all the dominant species occurring during the first several hundred years of succession had very high foliar nitrogen concentrations, with C:N ratios ranging from 12 to 22.

Chapter 2: The contribution of spawning Pacific-salmon to soil nitrogen fertility during primary succession in a large-river floodplain

- In the absence of salmon, early succession soils had very low total nitrogen, potentially mineralizeable nitrogen, and KCl extractable dissolved inorganic nitrogen. Net-mineralization in early succession soils could only provide a small fraction of the forest's annual nitrogen requirement.

- In contrast, soils in mature forests were nitrogen rich and net-mineralization could provide the majority of the vegetation's nitrogen requirement.

- However, the nitrogen infertility of early succession may be temporarily alleviated by a late season pulse of labile nitrogen entering the soils from decomposing salmon carcasses. The quantity of labile nitrogen imported to gravel bars from decomposing salmon carcasses averaged 25 kg-N ha^{-1} growing $season^{-1}$ on a low salmon year, but was approximately 10 to 30 times higher on high salmon years. Even on this low salmon year the quantity of nitrogen imported by the salmon exceeded net-mineralization within the top 10 cm of soil indicating that salmon were the most important nitrogen source to colonizing vegetation.

- However, this fertilization effect lasted several weeks at most, as carcasses decomposed rapidly and subsequent fall flooding flushed young gravel bars, reverting them back to their infertile states.

Chapter 3: The contribution of spawning salmon to foliar nitrogen nutrition during floodplain primary succession

- Foliage in both the active and passive floodplain regions was nitrogen-rich (mean molar C:N 21 and 26 respectively) relative to the uplands (C:N 32), other Pacific-rim floodplains, as well as the global average for temperate broadleaf forests.

- Foliage in the modern floodplain was highly enriched in ^{15}N relative to the uplands, as well as relative to temperate forests and other Pacific-rim floodplains that did not receive significant salmon subsidies, indicating that Pacific-salmon, which are also enriched with ^{15}N, were a major nitrogen source to the floodplain.

- Other studies conducted along smaller upland streams have also shown that riparian vegetation assimilates salmon imported nitrogen, but this fertilization effect was typically limited to within 100 m from the streambanks. In contrast, we found that salmon fertilized the entire 2.5k m wide modern floodplain of the lower Kol River.

- Elevated foliar C:N ratios indicated that nitrogen availability may have limited vegetation growth for the first 20 years of succession, and high foliar $\delta^{15}N$ during this time indicated that salmon were a major nitrogen source to colonizing vegetation.

- Low foliar C:N suggested that nitrogen was not likely limiting for at least the next 60 years of succession and alder-fixed nitrogen in addition to salmon-imported nitrogen stored in the soil were nitrogen sources to vegetation during this time.

- Despite being distant from the mainchannel and having not received salmon carcasses for hundreds of years, old forests in the passive floodplain were still enriched with the ^{15}N isotope indicating that they continued to recycle salmon-imported nitrogen acquired in early succession.

Chapter 4: Analysis of foliar $\delta^{15}N$ across a wide range of salmon fertilization rates in riparian forests throughout the Pacific-rim.

- There was a highly significant, positive relationship between riparian foliar $\delta^{15}N$ and the quantity of salmon nitrogen imported per stream kilometer amongst a diversity of rivers throughout the Pacific-rim. However, the observed relationship was nonlinear and foliar $\delta^{15}N$ becomes progressively less sensitive to each per unit increase in salmon nitrogen loading rate.

- The positive relationship between foliar $\delta^{15}N$ and salmon nitrogen loading rate that we observed clearly indicates that riparian vegetation growing along spawning streams assimilates large quantities of salmon imported nitrogen when available.

- The relationship between foliar $\delta^{15}N$ and salmon nitrogen loading rate has sufficient resolution to allow foliar $\delta^{15}N$ to be used to distinguish between low, medium and high salmon nitrogen loading rates, but only if foliage from numerous non nitrogen fixing, terrestrial, vascular plant species are sampled. We propose the following groupings:

    1. 0 to low salmon nitrogen loading rate (<100 kg-N km^{-1} yr^{-1}): mean foliar $\delta^{15}N$ value for all species together around -1‰ and individual species means typically ranging between -3‰ to 0‰ (based on 25th and 75th percentile respectively).
    2. Moderate salmon nitrogen loading rate (100 to 1,000 kg-N km^{-1} yr^{-1}): mean foliar $\delta^{15}N$ value for all species around 2‰ and with individual species means typically ranging between 1 to 3‰
    3. High salmon nitrogen loading rate (>1000 kg-N km^{-1} yr^{-1}): mean foliar $\delta^{15}N$ values for all species around 5‰ and with individual species means typically ranging between 4 and 6‰ and multiple species means exceeding 5‰.

Chapter 5: Seasonal influence of decomposing salmon on nitrogen assimilation dynamics of gravel-bar willows.

- Migrating salmon caused mainchannel nitrogen to increase as they entered the river in early August. During the period of spawning and death (early September) total nitrogen and nitrate peaked at about 3x and 10x (respectively) the pre-salmon baseflow levels.

- However, despite these subsidies, mainchannel nitrogen concentrations were still well within the range of values typical for unpolluted rivers, indicating that mainchannel nitrogen would be very low if not for salmon.

- Initial willow growth in the spring was fueled by remobilization of nitrogen stored in the roots, and high $\delta^{15}N$ at this time indicated that recycled nitrogen originated from spawning salmon in the previous year.

- The willows then assimilated nitrogen mineralized from sediments in early summer. The relatively high $\delta^{15}N$ of plant-available nitrogen during this time indicated that some fraction of this nitrogen was salmon-derived.

- Young willows grew and assimilated nitrogen most rapidly during the main period of salmon death in late August to early September. However, the lack of large increase in whole-plant $\delta^{15}N$ during this time indicated that most of this assimilated nitrogen was not acquired directly from decomposing carcasses. This is probably due to that salmon runs were depressed during this year and carcass deposition was approximately 1/10th to 1/30th of their typical value. No carcasses were deposited directly amongst the willow stand that we studied.

- Therefore, we conclude that colonizing willows have the ability to assimilate nitrogen when carcasses are available, despite that this occurs so late in the growing season.

Synthesis

Spawning Pacific-salmon functioned to fertilize otherwise nitrogen poor early succession in the Kol floodplain. Over the long term, salmon nitrogen inputs in early succession built soil and biomass nitrogen pools, as nitrogen retention capacity increased during succession. Consequently all vegetation species occurring during the first several hundred years of succession were nitrophillic.