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Floodplain Succession and Soil Nitrogen Accumulation on a Salmon River in Southwestern Kamchatka

Michael R. Morris

Jack Arthur Stanford
The University of Montana, jack.stanford@umontana.edu

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Michael R. Morris and Jack A. Stanford[1]

Flathead Lake Biological Station, Division of Biological Sciences, University of Montana, 32125 Bio Station Lane, Polson, Montana 59860-6815 USA

Abstract. We documented riparian primary succession on an expansive floodplain (Kol River, Kamchatka, Russian Federation) that receives large nitrogen subsidies from spawning Pacific salmon. As is typical of primary succession, new alluvial deposits in the lower Kol floodplain were nitrogen poor (200 kg persulfate N/ha to 10 cm soil depth); however, nitrogen accumulated rapidly, and soils contained 1600 kg N/ha (to 10 cm + the litter layer) by 20 years. Soil nitrogen approached an asymptote at ~2500 kg N/ha by 80 years. Nitrogen-fixing *Alnus* trees were a minor component of the forest community during the first 20 years of succession. However, salmon carcasses were a substantial nitrogen source during this period of rapid nitrogen accumulation. Similar to other northern Pacific Rim floodplains, we found that new alluvial deposits were colonized by *Salix*, *Chosenia*, and *Alnus* trees; but, unlike other described chronosequences, the community transitioned into meadows of tall forbs (some >2.5 m in height) dominated by *Filipendula camtschatica* after ~100 years. Foliage of all the major vascular plants occurring in the modern floodplain was exceptionally nitrogen rich (i.e., mean molar C:N for each species was 12–27, and the range for all samples was 8–36); therefore we suggest that salmon allow nitrophilic vegetation to proliferate in the Kol floodplain by ameliorating nitrogen infertility during early succession and building nitrogen rich soils.

Key words: floodplain; Kamchatka, Russian Federation; Kol River; marine-derived nutrients; nitrogen; salmon; soil development; succession.

Introduction

Riparian forests of large river floodplains are often heterogeneous mosaics of forest patches in different stages of successional development caused by erosion and sedimentation as river channels migrate throughout their floodplains (Yarie et al. 1998, Stanford et al. 2005). Riparian vegetation colonizes flood-deposited alluvium, and primary succession proceeds until migrating river channels again erode away the forest patch. Stanford et al. (2005) argued that this "shifting habitat mosaic" pattern of floodplain succession promotes high biological diversity. Furthermore, the composition of floodplain forests, as determined by the patterns of successional development, controls important ecosystem functions within river systems, such as nutrient and sediment import and export and fisheries production. Understanding floodplain primary succession and its controlling factors in pristine floodplains is important not only for their high ecological value, but also because they are among the most endangered ecosystems in the world (Tockner and Stanford 2002).

Research conducted in all types of primary succession chronosequences, including floodplains, abandoned mines, glacial moraines, sand dunes, and volcanoes has widely shown that nitrogen content is very low at the onset of succession (Walker and del Moral 2003). This occurs because colonized surfaces are primarily bare rock or mineral sediments with very low organic matter content (Walker and del Moral 2003) and unlike the other plant macronutrients, most soil nitrogen is retained within organic matter (Chapin et al. 2002). Nitrogen accrues during primary succession as a result of biological nitrogen fixation, atmospheric deposition, and organic matter accumulation (Walker and del Moral 2003).

Because nitrogen is a common limiting nutrient in temperate forests and early-successional environments are so nitrogen poor, changing nitrogen fertility during succession is thought to be a primary factor controlling ecosystem development. For instance, enhanced nitrogen availability in early succession may promote the growth of non-nitrogen-fixing pioneer species (e.g., Raich et al. 1996, Sasaki et al. 2001, Adair and Binkley 2002), which in turn may hasten colonization and other successional processes, such as soil organic matter accumulation (Vitousek and Walker 1989). Likewise, symbiotic nitrogen-fixing plants may facilitate the growth of other species by building soil nitrogen pools (Marrs et al. 1983, Vitousek and Walker 1989, Fastie 1995, Walker et al. 2003). In addition to promoting growth, changes in nitrogen availability may drive species replacement in both primary (Berendse 1998) and secondary chronosequences (e.g., Tilman 1987,

[1] Corresponding author.
E-mail: jack.stanford@umontana.edu

McLendon and Redente 1991). In general, increased nitrogen availability leads to the competitive dominance of more nitrophilic species (McLendon and Redente 1992, Fenn et al. 1998, Maron et al. 2006) and may also cause an overall decline in plant diversity (Carson and Barrett 1988, Wilson and Tilman 2002). Obviously, the development of plant communities is influenced by multiple interacting factors in addition to nitrogen availability, such as abiotic conditions, the life history traits of potential colonists, and species interactions among other factors (Walker and del Moral 2003). However, many studies confirm that large changes in nitrogen fertility have important consequences for ecosystem development.

Similar patterns of succession have been documented in floodplain chronosequences throughout the northern Pacific Rim, which we define as north of 40° N latitude and south of the Arctic Circle. Primary succession of dominant overstory species generally begins with the colonization of alluvial deposits by Salicaceous trees (willows [*Salix*, *Chosenia,* and *Toisusu* sp.] and/or cottonwoods [*Populus* sp.], as well as alders [*Alnus* sp.]; Viereck 1970, Fonda 1974, Nanson and Beach 1977, Clement 1985, Viereck et al. 1993, Helm and Collins 1997, Nakamura et al. 1997, Shin and Nakamura 2005, Van Pelt et al. 2006). Deciduous trees are then replaced by or coexist with conifers, either spruce (*Picea*; Viereck 1970, Fonda 1974, Nanson and Beach 1977, Viereck et al. 1993, Helm and Collins 1997, Nakamura et al. 1997, Van Pelt et al. 2006), hemlock (*Tsuga*; Fonda 1974, Clement 1985, Van Pelt et al. 2006), fir (*Abies*; Nakamura et al. 1997), and/or cedar (*Thuja*; Clement 1985) from 100 to 200 years after initial colonization (Helm and Collins 1977, Nanson and Beach 1977, Viereck et al. 1993, Nakamura et al. 1997, Van Pelt et al. 2006). However, broadleaf deciduous trees (elm [*Ulmus*] and ash [*Fraxinus*]) dominated the oldest floodplain benches at one site on Hokkaido (Shin and Nakamura 2005).

Because new alluvial deposits are typically nitrogen poor, the growth of colonizing Salicaceae may be limited by nitrogen availability (e.g., Sasaki et al. 2001, Adair and Binkley 2002). *Alnus* species, on the other hand, fix nitrogen symbiotically, allowing them to proliferate in early succession. The quantity of nitrogen fixed by *Alnus* may be very large (50–100 kg N·ha^{-1}·yr^{-1} in mixed stands and 100 to 200 kg N·ha^{-1}·yr^{-1} in pure stands of *Alnus rubra*) and fixed nitrogen is subsequently deposited into soils as nitrogen rich litter (Binkley et al. 1994), thus ameliorating the infertility of early succession (e.g., Van Cleve et al. 1993b, Hobbie et al. 1998). Late-succession species tend to have lower nitrogen requirements or concentrations than the initial colonizers and may eventually achieve dominance because they use limiting resources more efficiently as competition intensity increases over time (Bazzaz 1979, Tilman 1985, Walker and del Moral 2003). The litter of late-succession species, especially conifers, may also contain high concentrations of recalcitrant organic compounds that, in combination with low nitrogen content, may retard soil nitrogen mineralization (Berg and McClaugherty 1987, Van Cleve et al. 1993a) and cause fertility to decline in late succession (Van Cleve et al. 1993a, Hobbie et al. 1998).

Unlike other Pacific Rim floodplains where nitrogen dynamics during primary succession have been studied, the Kol River, Kamchatka, Russian Federation, receives enormous nutrient subsidies from spawning Pacific salmon (*Oncorhynchus* spp.). An estimated five to seven million pink salmon (*O. gorbuscha*) return from the ocean to spawn and die in the Kol on years with large runs (Pavlov et al. 2009), importing up to 400,000 kg N/yr into the river ecosystem (for details on this calculation see the following *Study site* section). Recent research has suggested that Pacific salmon carcasses may fertilize riparian vegetation along spawning streams (reviewed by Naiman et al. 2002). However, this research has been conducted primarily along small streams with relatively static riparian communities, rather than in the successional forests of large river floodplains. Given that nitrogen availability is an important factor controlling floodplain primary succession, we hypothesized that if sufficient salmon-derived nitrogen is transported into the riparian zones of the Kol River, salmon could dramatically influence floodplain vegetation dynamics. The objectives of this study were to document primary plant succession on an expansive floodplain of the Kol River, to quantify soil nitrogen accumulation during succession, and to determine whether salmon represent an important nitrogen source for floodplain plants. We also compared plant community development on a floodplain of the lower Kol River to other northern Pacific Rim floodplains that do not receive substantial nutrient subsidies from salmon.

STUDY SITE

The headwaters of the Kol River are in the west-central mountains of Kamchatka and the river flows westward across a coastal plain to the Sea of Okhotsk. The Kol is a seventh-order river at its mouth and had a summer base flow of ~56 m^3/s (Kuzishchin et al. 2008). Our study site (53°49′ N, 156°04′ E) was a large (2.5–4 km wide) floodplain of the lower Kol River, ~7–10 km east of ocean confluence (Fig. 1). The entire Kol catchment is largely pristine, and in 2006 it was designated as a salmon refuge by Kamchatka Regional Administration. Our research was based on the river at a remote biological station operated by the Wild Fishes and Biodiversity Foundation of Kamchatka and the Wild Salmon Center (Portland, Oregon, USA).

The Kol River has large migratory runs of all six species of Pacific salmon, but pink salmon are by far the most numerous, with up to seven million adults returning to spawn on even years. Runs are highly variable from year to year, but in general, runs on odd years are usually ~10% of even-year runs (Pavlov et al.
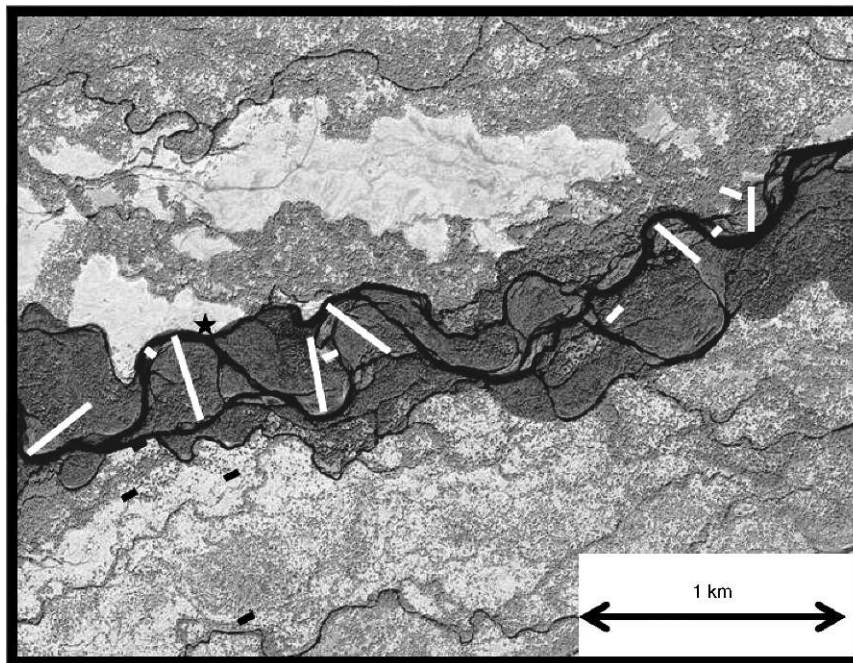
Fig. 1. Satellite image of the lower Kol floodplain in our study region of Kamchatka, Russian Federation. The Kol River originates in the central mountain ranges of Kamchatka and flows westward to the Sea of Okhotsk. Our study region is a 2.5–4 km wide floodplain located ~7–10 km east of the mouth of the river. River channels are shaded black and flow approximately east to west through the center of the image. The darkest gray shaded region surrounding the channel networks is the active floodplain (typically succession stages 0–III). Succession stage IV comprises most of the area in the passive floodplain and can be identified in the figure as the regions with a coarse gradient caused by the occurrence of sparse trees within the tall-forb meadows. Stage V grass–short forb–woody shrub meadows correspond to the areas in the passive floodplain with a smooth gradient (primarily north of the active floodplain region). The white lines indicate approximate locations of the study transects in the active floodplain. Shorter white bars indicate the additional subtransects. The short black bars show the sampling transects in the passive floodplain. The star locates the Kol biological station. The original imagery before modification (lines and shading) was from the QuickBird satellite and was provided by DigitalGlobe (Longmont, Colorado, USA) in 2004.

2009). Given that the average mass of pink salmon is ~1.7 kg at Kol (K. Kuzishchin [Moscow State University], *unpublished data*) and these fish are ~3.04% nitrogen and 0.36% phosphorus by body mass (Larkin and Slaney 1997), 400 000 kg N and 40 000 kg P may be imported into the catchment by spawning salmon on even years with very large pink salmon runs.

The coastal plain of southwestern Kamchatka has a "cold, wet, sub-oceanic climate" (Krestov 2003). 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°C and 12.2°C, respectively (Sokolov 1974). The total frost-free period is 92 days (Sokolov 1974), and annual precipitation is ~789 mm (Krestov 2003). This coastal plain is dominated by tundra with a mean peat bed thickness of ~3 m and contains horizontal layers of volcanic sands and ashes (Sokolov 1974). Tundra communities outside the study floodplain are dominated by sedges (*Carex* sp.), ericaceous shrubs (*Vaccinium* sp. and *Empetrum* sp.), and cloudberry (*Rubus chamaemorus*). Birch (*Betula ermanii*) forests with understories of forbs (*Filipendula camtschatica*, *Senecio cannibifolius*, and *Angelica ursina*), grasses, and *Vaccinium* sp. occur on

hills with andic soils where better drainage prevents formation of histosols (Sokolov 1974). Floodplains are dominated by Salicaceous trees including willows (*Salix* spp. and *Chosenia arbutifolia*) and cottonwoods (*Populus suaveolens*), as well as alder trees (*Alnus hirsuta*) (Krestov 2003). In addition, floodplains contain meadows of grasses and tall forbs (*Filipendula camtschatica*, *Senecio cannibifolius*, and *Urtica dioica*; Krestov 2003). Floodplain soils are alluvial entisols consisting of layers of sand and silt and occasionally layers of buried organic matter overlying gravel/cobble deposits.

We used the term "active floodplain" to define the region of the lower Kol floodplain bounded by primary and secondary river channels (see Fig. 1). Active floodplain sites commonly receive overland flows during annual flooding, and erosion rates are sufficiently high that forest patches are usually <100 years old. This contrasts with the "passive floodplain" that we considered to be the region between the active channels and the modern floodplain margin. We estimated that passive floodplain forests typically are >100 years old. These stands generally do not experience erosive annual flooding, but sections may be inundated during the higher flood flows, allowing fine-sediment deposition in

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

Empirical models†		Mechanistic models			
		Tree density‡		Growth§	
Linear	$Y = B0 \times X + B1$	Voropanov	$Y = B0/(X^2)$	Chapman-Richards	$Y = B0 \times [1 - B1 \times \exp(-B2 \times X)]^{1/(1-B3)}$
Logarithmic	$Y = B0 + [B1 \times \ln(X)]$	Hilmi	$Y = B0 \times \exp(-B1 \times [1 - \exp(-B2 \times X)])$	Richards	$Y = B0/[1 + B1 \times \exp(-B2 \times X)]^{1/B3}$
Inverse	$Y = B0 + B1/X$	Power	$Y = B0 \times X^{-B1}$	Von Bertalanffy	$Y = [B0^{1-B3} - B1 \times \exp(-B2 \times X)]^{1/(1-B3)}$
Quadratic	$Y = B0 + (B1 \times X) + (B2 \times X^2)$	Kayanus	$Y = (B0 + B1 \times X)/X^2$	Weibull	$Y = [B0 - B1 \times \exp(-B2 \times X^{B3})]$
Cubic	$Y = B0 + (B1 \times X) + (B2 \times X^2) + (B3 \times X^3)$			Negative exponential	$Y = B0 \times [1 - \exp(-B1 \times X)]$
Power	$Y = B0 \times X^{B1}$			Monomolecular	$Y = B0 \times [1 - B1 \times \exp(-B2 \times X)]$
Compound	$Y = B0 \times (B1^X)$			Mitcherlich	$Y = B0 - B1 \times B2^X$
S-curve	$Y = \exp(B0 + B1/X)$			Gompertz	$Y = B0 \times \exp[-B1 \times \exp(-B2 \times X)]$
Logistic	$Y = 1/[1/B0 + (B1 \times B2^X)]$			Logistic	$Y = B0/[1 + B1 \times \exp(-B2 \times X)]$

Note: $B0$, $B1$, $B2$, and $B3$ are the estimated parameters for each model.
† After SPSS (2006).
‡ After Karev (2003, 2006).
§ After Fekedulegn et al. (1999).

some cases. The passive floodplain contains numerous spring brooks (i.e., streams originating from upwelling shallow groundwater in flood channels) and tertiary river channels. We used the term "modern floodplain" to include both the active and passive floodplain regions. In contrast, an "ancient river terrace" occurs adjacent to the northern boundary of the modern floodplain and contains a heath community.

METHODS

Overview

To determine how forests developed during succession on the lower Kol floodplain, we sampled a variety of vegetation and soil variables in forest patches of a wide range of ages (i.e., a chronosequence). These variables were regressed against forest patch age, and relationships were examined for conformance to empirical and mechanistic mathematical succession models (Table 1). We used our mathematical model of nitrogen accumulation during succession and estimates of salmon carcass deposition to determine whether salmon were a significant nitrogen source during community development. Finally, we used our quantitative data to construct a conceptual model of floodplain succession.

Sampling-site selection

We selected six transects, all within 2.5 km of the Kol biological station to identify forest patches of a wide range of ages (Fig. 1). Each transect began on an alluvial deposit occurring at the inside of a main river channel bend and passed into a series of progressively older forest patches while traveling perpendicularly from the river. Transects continued until they left the active floodplain or entered a series of younger succession stages. In cases where the original transects missed older forest patches or very young alluvial deposits, five additional subtransects were established to ensure that a wide range of ages were sampled. Patches of forest containing similarly sized trees were then chosen for detailed sampling along each study transect. Patch size ranged from ~10 to >100 m in width. A total of 31 active floodplain patches were used for soil and carcass deposition analyses; however, it was later determined that in two cases, adjacent forest stands were similarly aged and therefore data for these two were combined for the subsequent analyses. We did not measure all variables in each patch (see sample sizes in Table 2). Four additional 50-m transects were established within the passive floodplain as representatives of the tall-forb community (Fig. 1).

Vegetation measurements

Vegetation and landscape measurements were completed primarily during 2005 (although some measurements were made during 2006). Diameter and density by species of trees larger than ~1 m in height above ground were measured every 5, 10, or 15 m along transects, depending on stand density. Measurements were made at 5 m for dense young patches intervals and at 15 m in the oldest patches where trees were more widely dispersed. Tree data were collected in 5 × 2 m belt transects in the dense early-succession stands and by the point-centered quarter method (Cottam and Curtis 1956) in older forests. For the point-centered quarter method, we later

TABLE 2. Summary of mathematical succession model fits to soil and vegetation variables regressed against forest patch age.

Succession variable	Model type	Equation	Applicable age range (years)	Parameter SE				R^2	N
				First	Second	Third	Fourth		
Tree density(trees/ha)									
All trees	Hilmi†	density = 700 000 × exp(−8.3 × (1 − exp(−0.028 × age)))	7–81	500 000	0.6	0.008		0.83	22
Salix A	Voropanov†‡	density = 3 300 000/(age²)	7–81	900 000				0.37	11
Salix B	compound†	density = 31 000 × (0.941ᵃᵍᵉ)	7–81	9000	0.006			0.70	11
Alnus	Voropanov†	density = 500 000/(age²)	7–81	100 000				0.36	22
Chosenia	Hilmi†	density = 30 000 × exp(−10 × (1 − exp(−0.01 × age)))	7–81	50 000	10	0.02		0.40	22
Tree absolute cover (m²/ha)									
All trees	compound	abs.cov. = 14 × (1.014ᵃᵍᵉ)	7–81	2	0.002			0.64	22
Salix A	linear	abs.cov. = −0.11 × age + 10	7–81	0.04	2			0.45	11
Salix B	compound	abs.cov. = 3 × (1.030ᵃᵍᵉ)	7–81	1	0.007			0.78	11
Alnus	power	abs.cov. = 0.006 × age¹·⁸	7–81	0.01	0.4			0.72	22
Chosenia	negative exponential	abs.cov. = 3 × (1 − exp(−0.09 × age))	7–81	1	0.2			0.02	22
Herbaceous layer coverage (%)									
Filipendula	Weibull	h.cov. = (45 − 41 × exp(−4 × 10⁻¹⁶ × age⁹))	3–81	1	2	1×10^{-14}	8	0.91	23
Urtica	S-curve	h.cov. = exp(3.8 + −40/age)	3–81	0.3	10			0.44	23
Grass	linear	h.cov. = −0.33 × age + 26	3–81	0.09	4			0.38	23
Soil variables									
Surface soil bulk density (g/cm³)	cubic	bulk.dens. = 2.2 + −0.11 × age + 0.0024 × age² + −0.000016 × age³	1–81	0.1	0.01	0.0004	0.000003	0.88	30
Surface soil total N (kg/ha, to 10cm)	S-curve	total.N. = exp(7.96 + −13/age)	1–81	0.06	2			0.88	30
Surface soil total N, to 10 cm (mg/g)	S-curve	total.N. = exp(1.7 + −16/age)	1–81	0.1	3			0.77	30
Mass litter layer (Mg/ha)	logarithmic	LL = 1 + (1.0 × ln(age))	7–81	2	0.7			0.08	25
Litter layer total N (kg N/ha)	S-curve	LL.N = exp(4.5 + −8/age)	7–81	0.2	5			0.15	24
Total surface soil + litter layer N (kg N/ha)	S-curve	total.N. = exp(7.99 + −12/age)	1–81	0.06	2			0.88	29
Carcass deposition (kg N/ha)	Power	Carc.N. = 90 × age⁻¹·⁸	1–82	3	0.1			0.97	30

Note: Parameter standard errors (SE) are listed in order of their sequence in the models.

† Used $1/Y^2$ rather than ordinary least-squares weighting. Weighted R^2 was calculated as 1 − [sum of squares weighted model/sum of squares weighted horizontal line] (Graphpad Software 2007).

‡ This variable showed poor conformance to the model for sites >40 years old.

added the radius of each stem (Dahdouh-Guebas and Koedam 2006), or in the case of multiple stems, the average diameter of the stems, to calculate the approximate distance to the center of the tree. Where the same tree was sampled twice, the data were kept and treated as regular samples. Because trees often colonized narrow bands on the youngest alluvial deposits, we ensured that one belt transect fell within the most prominent band of trees at these sites. Final density and coverage estimates were calculated as trees/ha and m²/ha at ~1 m tree height, respectively. Relative density and relative cover were calculated as the percentage contribution that each

tree taxa made to the total value for these variables. After completion of three initial transects, we realized that two species of Salix were present on the floodplain. Therefore, only half of the sites were used for analyses that distinguished between these two Salix species. Percent herbaceous cover was also estimated visually in roughly 5 × 2 m plots located at 5- or 10-m intervals along the main sampling transects.

A rough estimate of forest patch age was determined by counting growth rings from two (and at one site, one) or more trees that appeared to have above average trunk width near our transects. Trees were cross-sectioned

near the base in young stands, whereas older trees were cored at ~1 m height. The oldest age estimate from ring counts was used as the age for each patch. Four years were added to the age of the older cored trees to account for the approximate time that it takes trees to reach ~1 m height after germination. We emphasize that patch age estimates are approximate because there is a window of time on the order 10 years in which trees fully colonize a new alluvial deposit. Moreover, older forest patches are formed by coalescence of similarly aged alluvial deposits as channels separating them fill with fine sediments and thus, age variation within a patch increases with patch age. Furthermore, age was difficult to determine on some patches (especially those >60 years old) because trunks were often rotted, and piths were not obtained in all cases. Therefore, a general bias towards patch age underestimates was expected. Better estimates of patch age could have been obtained with more extensive sampling; however, we sought only to determine successional changes on the scale of decades, rather than exact dates.

Soil measurements

The depth of fine sediments to the gravel/cobble interface was measured every ~5 m along our six study transects using a 80 cm long soil probe. Additional points were measured at the banks and deepest points of seasonally-flooded channels, and the regular interval point was skipped where these additional points were proximate; in that case, the closest point to the regular 5-m interval was used to calculate mean fine-sediment depth for each forest patch. Soil samples were collected for nitrogen analysis during August 2005, within forest patches that were ≥7 years old along our study transects. Within each patch, five points were randomly chosen along 50-m transects (or multiple parallel transects summed to ~50 m) and the litter layer, defined here as all visually identifiable plant detritus on the soil surface, was excavated within a 100-cm^2 frame at each point (sticks larger than ~1 cm diameter were excluded). Surface soil samples (i.e., the soil immediately beneath the litter layer and including O3, A, and other underlying layers) were extracted using a 10.16 cm (4 inches) long by 4.83 cm (1.9 inches) diameter corer, referred to hereafter as to 10 cm deep soil cores. The corer was driven to a depth slightly deeper than the soil surface to account for compression. In cases where the soil core sampler was obstructed by large roots, the sample was taken at an unobstructed adjacent spot. In cases where the depth of fine sediments overlying the gravel layer was <10 cm, we attempted to drive the corer into the gravel layer with a rocking motion. Where this was not possible, additional sediments that were smaller sized than the diameter of the corer (4.83 cm) were scooped from the gravel layer to make up the unfilled volume of the corer (Note: cores taken later at some of the same sites suggest that using less aggressive coring techniques may collect ~10% less fine sediment on

average at older forest sites and 20% less at younger sites, though with a maximum likely average bias of 30% after correcting for different size fractions sampled. Bias likely occurred to a lesser degree than these values suggest because the more conservative cores likely under-collected sediment.) Sediments were too coarse to use the corer at sites <5 years old, so during August 2006, surface soil was collected by excavating sediments within a 26 cm diameter circular frame to 10 cm depth and at three points randomly chosen along transects within these sites. Litter samples were not collected at these sites because litter was very sparse due to frequent flooding. The volume of each excavation was determined by lining the holes with thin plastic sheeting and measuring the volumes of water required to fill the holes. All litter layer and/or surface soil samples collected within forest patches were combined to make one sample per site.

Surface soils were refrigerated <3 days and dried at ~40–60°C, and total bulk density was determined by dividing total sediment dry mass by the volume sampled. The coarse and fine fractions of surface soils were then separated using a 2-mm sieve. A subsample with fine roots removed was taken from the fine fraction and pulverized to a fine powder with a mortar and pestle. Approximately 50 mg of this fine fraction was digested with persulfate and the resulting ammonium was measured colorimetrically with a Perkin-Elmer (Waltham, Massachusetts, USA) Lambda-1 spectrophotometer using salicylate (adapted from Raveh and Avnimelech 1979 and Mulvaney 1996) to determine total persulfate nitrogen (referred to as total nitrogen throughout, although persulfate nitrogen probably underestimates total nitrogen due to incomplete digestion of recalcitrant soil organic matter; see Martin et al. 1981). Mean relative percentage difference for nitrogen concentration per gram of soil determined with seven pairs of separately digested replicates was 18%. The total quantity of nitrogen (kg N/ha to 10 cm depth) in the soil was then calculated by multiplying the nitrogen concentration of the soil by the estimated mass of fine fraction per hectare. Because large roots were avoided when sampling the soil, the final values reflect the mass of nitrogen per hectare of soil devoid of large tree roots. While this means that our estimates of total persulfate nitrogen per hectare of forest are slightly overestimated, our results are comparable to other studies because correction for the volume of soil occupied by large roots was not reported in other studies that we compare our results to (see Kaye et al. 2003). Moreover, researchers that sampled with soil pits probably chose not to dig pits amongst tree root wads (see Luken and Fonda 1983). Unwashed litter samples were refrigerated <2 weeks and dried at 60–80°C. Dried samples were ground to a powder using a hand mill, subsampled, redried, ground further in a Spex SamplePrep 5100 mixer mill (Spex CertiPrep, Metuchen, New Jersey, USA) and analyzed for total nitrogen using a Fisons (Beverly, Massachu-

setts, USA) NA1500 elemental analyzer. Total litter nitrogen was determined by multiplying the mass of the litter layer per hectare by the concentration of nitrogen in the litter.

Salmon carcass measurements

In 2006 we quantified terrestrially deposited carcasses approximately two weeks after the main pink salmon die-off and after fall flooding washed carcasses into the riparian zones. Carcasses were counted within 5 m of either side of the site transects. At young alluvial bar sites carcasses were counted as terrestrial even when occurring along the regularly inundated shorelines because we observed high concentrations of carcasses among colonizing seedlings in these areas. Total carcass nitrogen per site was determined by multiplying the number of distinct carcasses or carcass remnants by the average adult wet mass for Kol River fish (during 2006, 1.8 ± 0.4 kg for pink salmon [mean ± SD; $n = 122$] and 3.4 ± 0.7 kg for chum salmon [*O. keta*; $n = 113$]; K. Kuzishchin, *unpublished data*), and then multiplying by 3.04%, which is the average percentage nitrogen content for salmon (Larkin and Slaney 1997). Forty percent of the calculated nitrogen was then subtracted from the totals to account for metabolic/spawning losses occurring prior to salmon death (averaged from losses for pink and chum salmon values reported by Gende et al. 2004).

Foliar nitrogen concentrations

More than 200 foliage samples were collected during July and August 2006, at the forest patches where soil was sampled, as well as along one long transect that spanned the entire floodplain perpendicular to the river and into the uplands on either side. Where present, whole, fully developed leaves of the two *Salix* species, *Chosenia*, *Alnus*, *Filipendula*, and *Urtica* were collected near the tops of plants at our regular study patches. Where dominant, whole leaves of *Salix*, *Filipendula*, and *Vaccinium*, as well as samples of grass and *Carex*, were collected approximately every 200 m and 0, 10, and 50 m from each of the flowing channels encountered along this long transect. Samples from multiple (usually three to five) different aboveground stems of the same species were combined to make one sample per site. Samples were refrigerated ≤2 d, dried at ~60–80°C until brittle, and ground in a coffee grinder. This homogenate was then ground further in a Spex SamplePrep 5100 mixer mill (Spex CertiPrep, Metuchen, New Jersey, USA) and redried. Molar C:N ratios were determined in subsamples using a micro-Dumas combustion elemental analyzer at the Stable Isotope and Soil Biology Laboratory of the University of Georgia (Athens, Georgia, USA). Accuracy was confirmed with known standards, and with one outlier excluded (most likely a labeling error) mean relative percent difference in molar C:N ratios of 9 duplicate pairs was <1%.

Statistical analysis

In order to quantify successional changes, vegetation and soil variables were regressed against succession age. Models were fit to data sets using ordinary least-squares regression, except that $1/Y^2$ weighting (minimization of relative distances squared) was used when modeling tree density because ordinary least squares generally produced poor fits because of much higher variance among sites with high tree densities relative to sites with low tree densities. All variables were tested for conformance to the empirical models available in SPSS 15 (Table 1; SPSS 2006). Tree density data also were tested for conformance to mechanistic stand thinning models presented in Karev (2003, 2006). Absolute tree coverage, herbaceous coverage, litter layer mass/nitrogen content, and soil nitrogen content are attributes of successional growth; therefore, these variables were tested for conformance to the growth models reviewed by Fekedulegn et al. (1999) as well. Akaike information criteria (corrected for small sample size) were used to select the best model for each data set. (Note: least-squares regression assumes residuals are Gaussian and homoscedastic, Y values are independent, and X values are known exactly (Graphpad Prism 5 [2007]); the first two assumptions were sometimes violated for the selected model; the second two assumptions were always violated in our analyses.) All analyses were conducted using the Graphpad Prism 5 (2007) software program.

RESULTS

Variables regressed against age

Mathematical succession models produced R^2 values >0.5 for 11 of 20 riparian variables regressed against age within the active floodplain (Table 2). In particular, density of all trees, coverage of *Salix* B, coverage of *Filipendula*, all surface soil nitrogen variables, and carcass deposition were well explained by succession models ($R^2 > 0.75$).

Soil development

We observed that newly deposited alluvial bars at Kol were composed primarily of cobble and gravel with sand filling the interstitial spaces of this matrix. Fine sediment (sand and smaller) deposits on gravel bar surfaces averaged only 4 cm deep at sites <5 years old and fine sediments accumulated during succession (Fig. 2). Bulk density was highly related to succession age ($R^2 = 0.88$; Table 2, Fig. 2). Total sediments (to 10 cm) occurring at the onset of succession (<5 years) had very high bulk density ranging from 1.9–2.2 g/cm^3, and bulk density declined rapidly to ~0.6 g/cm^3 by 30 years. From 30 to 80 years, surface soil bulk density declined more slowly and leveled off at ~0.5 g/cm^3 (Fig. 2).

The youngest alluvial bars had very low surface soil total nitrogen content: ~200 kg persulfate N/ha (to 10 cm) at sites ≤5 years old (Fig. 3). However, total soil nitrogen (i.e., in the top 10 cm of surface soil/sediment
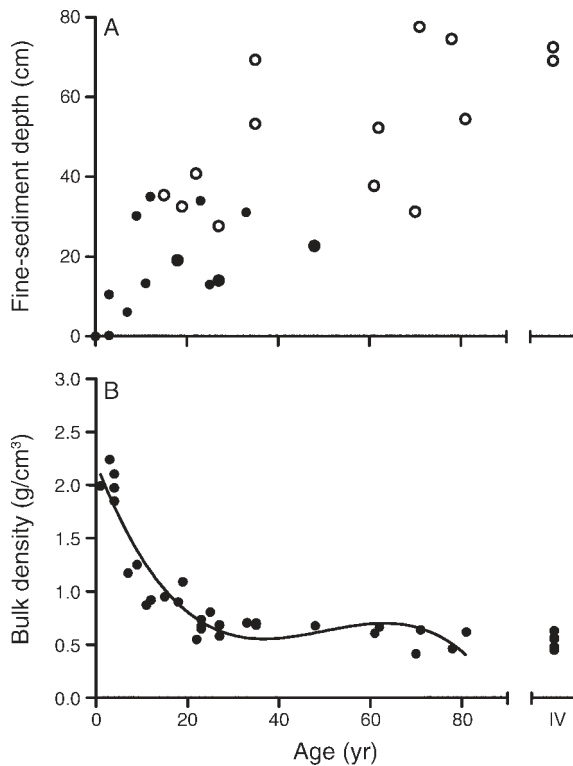
FIG. 2. Soil development in the Kol River floodplain. (A) Average depth of fine sediments to the gravel/cobble layer. Our soil probe had a maximum depth of ~80 cm; therefore, averages represented by open circles are underestimates because fine sediments were deeper than 80 cm at some points. (B) Bulk density of the surface soil to 10 cm depth (see Table 2 for regression curve). "IV" represents the tall-forb meadow sites in the passive region of the floodplain; these were not aged and therefore were not used in the analysis. Sediment deposits at early-succession sites were composed primarily of a coarse cobble and gravel matrix with some fine sediments in the interstitial spaces and therefore had high bulk density. Surface layers of fine sediments accumulated rapidly during succession, resulting in a rapid decrease in bulk density. While AIC analysis indicated that the cubic equation was the best model, we suspect the true relationship is more simple than this. The model's indication that bulk density increased again from 40 to 60 years may be due to sampling error, too few data points in that region of the curve, or use of unweighted least-squares regression.

plus the litter layer) accumulated rapidly for the first 30 years of succession, reaching 2000 kg N/ha. Total soil nitrogen content increased more slowly from 30 to 80 years, gaining an additional 500 kg N/ha, and sites in the passive floodplain contained about the same quantity of total soil nitrogen as the oldest sites in the active floodplain. Our site age model accounted for the vast majority of the variation in the surface soil total nitrogen ($R^2 = 0.88$); however, litter layer total nitrogen, which was typically a small fraction (<10%) of total soil nitrogen, was not as well explained by our model ($R^2 = 0.15$; Table 2). Total persulfate nitrogen concentration of the <2 mm fraction of the top 10 cm of surface soil (expressed in mg/g) was well predicted by the total bulk

density of the soil ($R^2 = 0.89$; Fig. 3). Soils with high bulk density had low nitrogen concentrations.

Salmon nitrogen deposition

Nitrogen deposition from salmon carcasses was greatest during very early succession (Fig. 4; see Plate 1). During the September 2006, salmon die-off, an average of 21 kg N/ha was deposited at sites ≤10 years old; but, deposition rates were highly variable, ranging from 91 kg N/ha to 0 kg N/ha. Nitrogen inputs to sites >30 years old were consistently low (≤2 kg N/ha).

Vegetation chronosequence

Four tree species commonly occurred on the floodplain transects: two unidentified species of *Salix* (which we refer to as A and B), *Chosenia arbutifolia* and *Alnus hirsuta*. (Many species of *Salix* occur in Kamchatka, and *Salix* identification is notoriously difficult. Based on leaf morphology we identified two species that commonly occurred on the floodplain; however, we were not able to confirm the taxonomy. *Salix* A has long, slender leaves with hairy undersides, and the *Salix* B has more oval-shaped leaves without hair.) Between 10 and 20 years after colonization, these trees formed dense stands with an average density of 6.6 trees/m^2 and a mean total coverage of ~20 m^2/ha (Fig. 5). Tree density declined during succession, while coverage increased to 36 m^2/ha at the mature forest sites (~50 to 80 years). Based upon relative density and coverage, *Salix* A was the dominant species during the first 30 years of succession, while *Salix* B and then *Alnus* were the dominant tree species in later succession (40 to 80 years). The importance of *Alnus* was low in early succession, but increased over time, with *Alnus* comprising ~36% of the total density and ~31% of the total coverage at sites >60 years old. In contrast with the other species, the relative density and coverage of *Chosenia* density was poorly related to succession.

Three different vegetation types dominated the herbaceous layer in the active floodplain (Fig. 6). Sequentially, grasses were the dominant herbaceous species during the first 30 years of succession, followed by *Urtica* from about 30 to 50 years, and *Filipendula* at sites >60 years old. Occasional *Filipendula* plants were observed colonizing the initial succession stages, but this plant was sparsely distributed among the dense stands of young trees. We observed that *Filipendula* spread by seeding and sending up new shoots from large, spreading rhizomes. From around 60 to 80 years, *Filipendula* covered on average ~45% of the land area in the understory. Once most of the trees had senesced in the passive floodplain, *Filipendula* coverage increased to 63–88%, and the remaining area was largely covered by *Urtica* (5–11%). These tall-forb meadows had only occasional *Salix* B or *Alnus* trees that we often observed sprouting from fallen boles of old, senescent trees. Tree data were not collected at these sites as trees were very sparse.
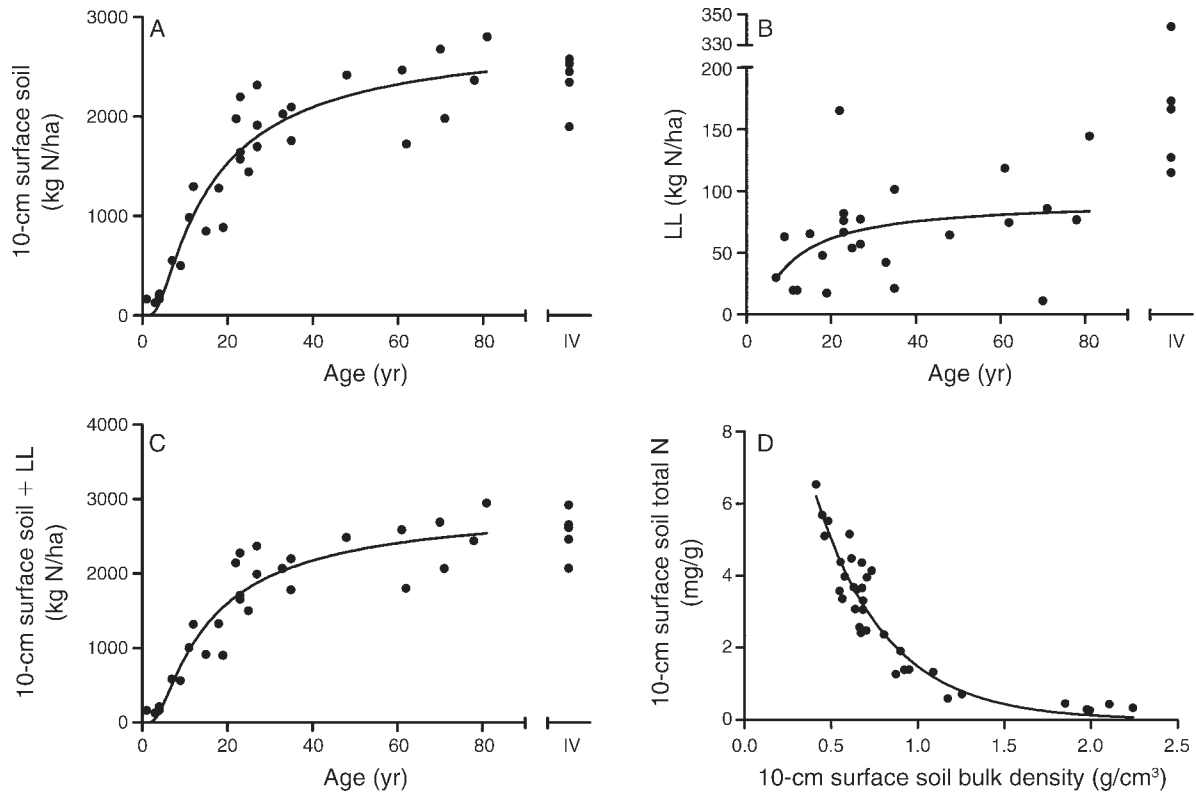
FIG. 3. Soil nitrogen accumulation during succession. (A) Accumulation of surface soil total persulfate nitrogen (to 10 cm depth). (B) Accumulation of litter layer (LL) nitrogen. (C) Accumulation of total (10-cm surface soil + litter layer) nitrogen (note that data from Fig. 3A and B were summed to produce this panel). (D) Relationship between surface soil nitrogen concentration and soil bulk density, BD. Surface soil total $N = 17 \times 0.09^{BD}$, $R^2 = 0.89$. "IV" represents the tall-forb meadow sites. These sites were not aged and therefore not fitted to the models. The nitrogen content of surface soils increased rapidly during the first 30 years of succession, and surface soils at the passive floodplain sites contained a similar quantity of nitrogen as the oldest sites in the active floodplain. The strong relationship between soil nitrogen concentration and bulk density suggests that nitrogen accumulation may be influenced by fine-sediment deposition. See Table 2 for regression statistics.

All plant species occurring in the modern floodplain had high foliar nitrogen concentrations with mean molar C:N ratios ranging from 12 to 27 depending on the species. When all species were considered together, foliar C:N ratios ranged from 8 to 36. *Salix* A ($n = 26$), *Salix* B ($n = 51$), and *Chosenia* ($n = 17$), as well as the tall forb, *Filipendula* ($n = 54$), all had very similar mean foliar C:N ratios ranging from 19 to 22, whereas *Alnus* ($n = 28$) and *Urtica* ($n = 30$) foliage was more nitrogen rich on average (i.e., C:N = 17 and 12, respectively) than the other plant species. *Vaccinium* ($n = 3$), *Carex* ($n = 4$), and grass ($n = 5$) had the least N-rich foliage (C:N 25 to 27).

Conceptual model of floodplain succession

We simplified and conceptualized succession on the floodplain by defining six stages named for the dominant vegetation types (Figs. 7 and 8, Tables 3 and 4): Stage 0, alluvial bars either sparsely or unvegetated (0 to 10 years); Stage I, dense alluvial bar *Salix–Chosenia* stands (10 to 20 years); Stage II, *Salix–Alnus–Chosenia* forest canopy (20 to 50 years); Stage III, declining *Salix* and
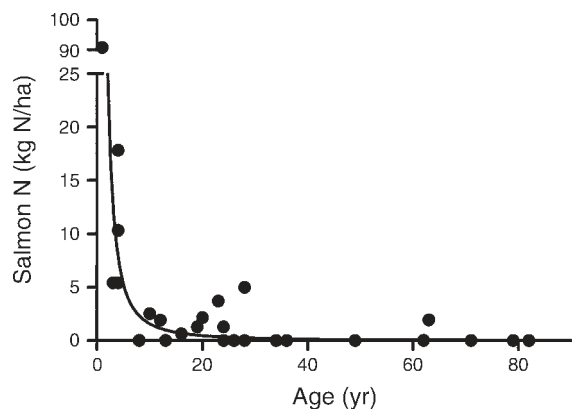

FIG. 4. Nitrogen inputs from flood-deposited salmon carcasses during September 2006 in the active floodplain. Salmon nitrogen inputs were greatest at early-succession sites because they were adjacent to the river channels and flooded regularly. Preliminary data from previous years suggest that the magnitude of salmon nitrogen inputs to early succession varies greatly from year to year and in some cases may be substantially higher than the values observed during 2006. See Table 2 for regression statistics.
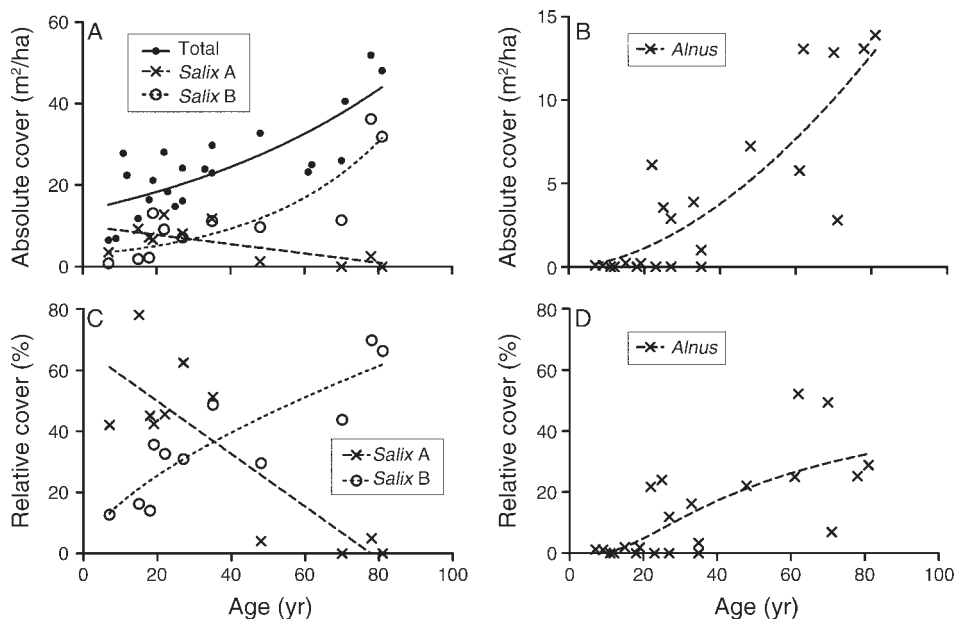
FIG. 5. Changes in tree coverage during succession. (A, B) Absolute coverage at ~1 m height. See Table 2 for regression curves. (C, D) Relative coverage at ~1 m height: *Salix* A relative cover $= -0.9 \times \text{age} + 67$, $R^2 = 0.71$; *Salix* B relative cover $= 4 \times \text{age}^{0.6}$, $R^2 = 0.76$; *Alnus* relative cover $= \exp(4.1 - 50/\text{age})$, $R^2 = 0.51$; *Chosenia* relative cover $= -0.2 \times \text{age} + 19$, $R^2 = 0.07$ (not shown). *Salix* A was the dominant tree species during the 30 years of succession, whereas *Salix* B, and then *Alnus* were the dominant tree species from 40 to 80 years. See Table 2 for additional regression statistics.

mature *Alnus* canopy (50 to at least 80, but probably 100 or more years); Stage IV, tall-forb meadows; and, Stage V, grassy, short-forb meadows with some woody shrubs. These stages (0–V) are used hereafter.

DISCUSSION

Previous studies of Pacific Rim floodplains have documented similar patterns of primary succession: Nitrogen poor alluvial deposits are colonized by Salicaceous and *Alnus* trees, and these communities then transition into coniferous forests after one or more centuries (reviewed in the *Introduction*). Our results indicate that succession on the lower Kol River floodplain is unique from what has been described previously in that nitrogen inputs from spawning Pacific salmon rapidly build soil nitrogen pools during early succession and the riparian communities are dominated by plant species with exceptionally nitrogen-rich foliage. Because nitrogen accumulation is an important controlling factor in community development, we speculate that salmon-imported nitrogen may allow nitrophilic species to proliferate in this floodplain, although experimentation would be required for verification.

The relationships between patch age and riparian variables

Prior to constructing a chronosequence model, we examined the relationships between riparian variables and site age. Our finding that succession models (both empirical and mechanistic) produced R^2 values >0.5 in over half of the vegetation and soil variables that we measured (Table 2) indicates that stand age is a primary
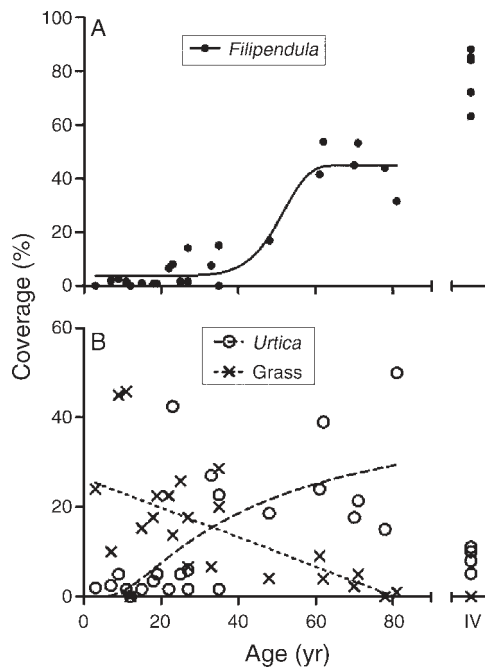

FIG. 6. Changes in percent coverage of herbaceous species during succession. "IV" represents the tall-forb meadow sites that were not aged and therefore not fitted to the model. Sequentially, grasses were the dominant herbaceous species during the first 30 years of succession, followed by *Urtica* from about 30 to 50 years and *Filipendula* at sites greater than 60 years old. See Table 2 for regression statistics.
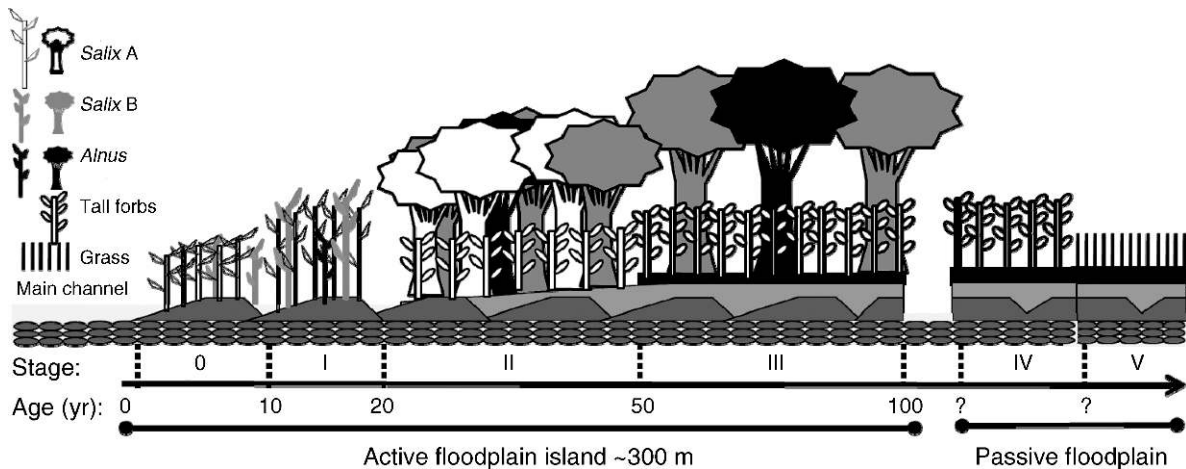
Fig. 7. Conceptual model of primary succession in the lower Kol floodplain. This model depicts the six succession stages in relation to age. The age ranges shown on the *x*-axis are approximate. A question mark indicates that only relative age, rather than exact age, was determined for stages IV and V. This conceptual model was constructed from data presented in the previous figures in order to present a comprehensive model of succession. For the sediment layers, dark gray signifies cobble/gravel, light gray is fine sediments (sand and silt), and black is surface soils with high organic matter content.

factor in explaining the properties of riparian forests on the lower Kol floodplain. In particular, surface soil variables, such as total nitrogen ($R^2 = 0.88$) and bulk density ($R^2 = 0.89$), and variables describing the dominant species, *Salix* B and *Filipendula,* conformed very well to the succession models. On the other hand, variables associated with the litter layer and rarer species, such as *Chosenia*, did not. Litter layer variables were probably confounded by localized flooding because litter was nearly absent from the most heavily flooded sites. The occurrence of rare species may be better described by multivariate succession models that also take into account the distribution of specific microhabitats. For example, we observed, and it has been documented elsewhere (Ishikawa 1987, 1994), that *Chosenia* was usually limited to sites with coarse alluvia. The extent to which successional changes are consistent and generalizable with age has been debated extensively (see Walker and del Moral 2003), but our results confirm that constructing a chronosequence model is appropriate for portraying complex riparian communities of the lower Kol floodplain.

Soil nitrogen accumulation during succession

As is generally the case in primary succession (Walker and del Moral 2003), soil nitrogen was low during early succession (200 kg persulfate N/ha [to 10 cm]; Fig. 3) and accumulated over time. Soil nitrogen increased rapidly to 1600 kg N/ha (to 10 cm + litter layer) by 20 years, and then increased more slowly to ~2500 kg N/ha by 80 years within the active region of the floodplain (Fig. 3). Because surface soils in the older passive floodplain sites (Stage IV; Fig. 3), contained about the same amount of persulfate nitrogen as the 60- to 80-year-old sites in the active floodplain, we conclude that nitrogen accumulation during early succession controls

long-term soil fertility. Similar patterns of rapid nitrogen accumulation have been demonstrated in other Pacific Rim floodplain chronosequences. In a floodplain of the Tanana River, Alaska, Kaye et al. (2003) also found that young alluvial deposits initially contained low quantities of nitrogen (500 kg N/ha to 20 cm + litter layer [<4 mm fraction]) and total nitrogen accumulated to 1100 kg N/ha by 20 years and 2200 kg N/ha by 80 years. Luken and Fonda (1983) found that new alluvial deposits on a floodplain of the Hoh River, Washington, contained about 300 kg N/ha (to 15 cm) and by 65 years, soil nitrogen had accumulated to 1700 kg N/ha (to 15 cm + detritus [size fraction unspecified]). While the differences among these sites are not large, the results suggest that surface soil nitrogen accumulated more rapidly and to higher levels within the lower Kol floodplain than at these other sites. In fact, the differences between the soils of the Kol floodplain and these other sites are likely even greater than the previous comparisons suggest, especially considering that our sampling depth was shallower, and we measured persulfate nitrogen in surface soils (whereas Kaye et al. [2003] measured dry combustion nitrogen, and Luken and Fonda [1983] measured Kjeldahl nitrogen), which may substantially underestimate total nitrogen, especially at older sites, because some highly recalcitrant soil organic compounds may not be digested using persulfate (Martin et al. 1981).

Sources of nitrogen accumulation during succession

Nitrogen-fixing *Alnus* trees often dominate early-successional forests of the northern Pacific Rim and add large quantities of nitrogen to developing soils (Binkley et al. 1994). Both Walker (1989) and Luken and Fonda (1983) suggested that *Alnus* was a major nitrogen source during succession in the floodplains of the Tanana and Hoh Rivers. However, our results

PLATE 1. Salmon carcasses deposited on a stage-0 alluvial bar during the fall of 2006. This particular location received exceptionally high carcass deposition rates. Over the short term, nutrients released from decomposing salmon carcasses are likely taken up by the vegetation that colonizes these otherwise nitrogen-poor alluvial bars. However, these carcasses are eaten by gulls and decompose rapidly, and subsequent flooding washes much of the remaining tissue away. We hypothesize however that through binding to fine sediments and organic matter (which accumulate during early succession) and by being assimilated by plants, salmon-imported nutrients may accumulate during early succession and promote long-term fertility. Photo credit: Josh Epstein.

suggest that *Alnus* was not responsible for the rapid persulfate nitrogen accumulation that we measured in early succession. About 60% of total surface soil persulfate nitrogen that accumulated (to 10 cm) during succession originated during the first 20 years, and *Alnus* was a minor component of the forest community during this period, comprising <1% of total tree coverage on average (Fig. 5, Table 3). *Alnus* trees did become a major component of the forest community by succession stage III (50–80 years), comprising >30% of the total coverage on average. However, soil nitrogen accumulation in the surface layers was much slower from 30 to 80 years, gaining only an additional 600 kg N/ha (10 cm + litter layer). (Note however, persulfate nitrogen may disproportionately underestimate total nitrogen at the older succession stages if a greater fraction of soil nitrogen occurs as recalcitrant soil compounds; see Martin et al. 1981.)

Rather than *Alnus*, our data suggest that the rapid accumulation of nitrogen observed in early succession at Kol was associated with the flood deposition of fine sediments, as well as the import of salmon nitrogen. In

gravel–cobble-bedded rivers like the Kol, high velocity flows during flooding either minimize accumulation of fine sediments on new gravel bar deposits or the distribution of fines is very patchy. Over time, channel migration away from these sites and establishment of vegetation reduces water velocity and promotes fine-sediment deposition during flooding. We found that fine sediments accumulated rapidly during early succession (Fig. 2), and the importance of fine sediment deposition in nitrogen accumulation is inferred from the very strong relationship between bulk density and surface soil nitrogen concentration ($R^2 = 0.84$; Fig. 3). Likewise, Adair et al. (2004) found that fine-sediment deposition could account for the vast majority, if not all, of the nitrogen accumulated during primary succession on floodplains of the Green and Yampa Rivers, Colorado. In addition to being a source of nitrogen, fine-sediment accumulation likely increases capacity to bind and retain nitrogen and organic matter imported from other sources, at least relative to the very coarse soils occurring at the onset of succession.

FIG. 8. Photographs of the six succession stages corresponding to the model presented in Fig. 7. The first photograph (stage 0) shows a recently deposited alluvial bar that is just beginning to be colonized by *Salix* trees. From 10 to 20 years later (stage I) the sites are fully colonized by dense *Salix* stands, and from 20 to 50 years (stage II) *Salix* and *Alnus* trees form a canopy, and stands of tall forbs dominated by *Urtica dioica* and *Filipendula camtschatica* develop in the understory. From 50 to 80+ years (stage III), the canopy opens, and the stands of tall forbs proliferate. Sites in the passive floodplain are dominated by stands of *Filipendula camtschatica*, which may grow >3 m in height from snowmelt until early July and in densities exceeding 12 shoots/m² (stage IV). The oldest recognized sites (stage V) in the passive floodplain are dominated by grass–short forb–woody shrub meadows. The lead author of the study (M. R. Morris) appears in the photograph for stage IV, and his assistant (Lorri Eberle) appears in the photograph for stage II. Photo credits: M. Morris and Michelle Anderson.

In addition to fine-sediment deposition, the massive numbers of salmon that die after spawning may be another major source of nitrogen during early succession at Kol. Salmon carcasses were deposited on alluvial bars (Fig. 4) during flooding that regularly occurs in late summer and fall in western Kamchatka after the peak of spawning. Early-succession sites received the most salmon carcasses because they were usually adjacent to main channels and regularly inundated with floodwaters. Salmon carcasses accounted for an average of 21 kg N/ha, but up to 91 kg N/ha, on stage 0 alluvial bars

during 2006, even though salmon densities were unusually low and flood levels were below normal that year. Most of these carcasses were found lining the margins of these alluvial bars along the water's edge, but among colonizing seedlings. Very few carcasses were found further inland amongst the young alluvial bar's older vegetation patches, probably due to limited flooding during 2006. Preliminary carcass deposition data were also collected during 2004 at two sites that were near two of the 2006 study sites. While carcass deposition translated to 9 and 30 kg N/ha in 2004, no

TABLE 3. Means, followed by range in parentheses, and sample size (N) of vegetation variables measured at succession stages.

Stage	N	Total tree density (trees/ha)	Contribution to total tree density (%)			Total tree coverage (m^2/ha)	Contribution to total tree coverage (%)	
			Salix	Alnus	Chosenia		Salix	Alnus
I	5	66 000 (41 000–120 000)	86 (62–100)	2 (0–7)	12 (0–38)	20 (12–28)	86 (59–100)	1 (0–2)
II	9	6400 (2000–20 000)	83 (50–100)	10 (0–27)	7 (0–23)	23 (15–33)	73 (34–100)	11 (0–24)
III	6	500 (270–870)	63 (40–93)	36 (8–57)	1 (0–3)	36 (23–52)	67 (44–93)	31 (7–52)
IV	5	...	...	...	...	...	...	...

Note: Ellipses indicate that a variable was not measured.

carcasses were observed at the nearby sites in 2006 (note however, the preliminary 2004 data were collected at different locations that may naturally receive higher carcass deposition rates). Furthermore, spawner abundance was considerably greater during 2008 relative to 2004 and 2006 (K. Kuzishchin, *unpublished data*). Therefore, carcass deposition rates undoubtedly exceed the values that we recorded during 2006 during some years. In any case, we observed that relatively few salmon carcasses were usually deposited in the >30-year-old sites regardless of run size or flood extent because these sites were higher in elevation and farther from the main channel. Whereas *Alnus* occurred later in succession, both maximal nitrogen accumulation and maximal carcass deposition rates occurred during very early succession at Kol.

Considering that temperate and boreal forests typically assimilate 25 to 100 kg N·ha^{-1}·yr^{-1} (Chapin et al. 2002), we conclude that salmon had the potential to provide a very large proportion, if not all, of the nitrogen required annually by the vegetation colonizing some of these young alluvial bars at Kol, especially during years of high salmon runs. Indeed, in 2006 at some sites carcass nitrogen deposition rates were comparable to anthropogenic nitrogen addition rates that may result in nitrogen saturation (Högberg et al. 1992, Kuylenstierna et al. 1998). In actuality, our estimates of carcass nitrogen deposition rates must underestimate the total quantity of salmon nitrogen imported into early-succession sites because other translocation processes undoubtedly occurred in concert with flood deposition of carcasses including: hyporheic flux of salmon enriched river water into the root zone

(O'Keefe and Edwards 2003, Helfield and Naiman 2006), physical transport of salmon nitrogen by bears and other animals that feed upon salmon (Ben-David et al. 1998, Hilderbrand et al. 1999, Helfield and Naiman 2006), and especially, flood deposition of fine sediments that bind salmon nitrogen during transport in the river channels (Bilby et al. 1996).

Salmon flesh is very labile and does not persist in the environment. The major pink salmon die-off occurred in early September, and many carcasses deposited on young alluvial bars were consumed on site by seagulls, which then redeposited salmon nitrogen as uric acid. In fact, some alluvial bars accumulated so much excretia from seagulls that the bars appeared speckled white. In addition, some carcasses were consumed by maggots and/or decomposed microbially within about a month. Given that carcasses decomposed rapidly and that retention of salmon nitrogen probably is low in the gravel substrata of newly formed bars, the accumulation of fine sediments and biomass during succession is likely crucial in retaining salmon-imported nitrogen. It has been shown experimentally that sediments assimilate salmon-imported nitrogen through both biotic and abiotic processes (Bilby et al. 1996, Rex and Petticrew 2008) and binding capacity should increase with decreasing sediment size. Also, *Salix* stands commonly assimilate 50 to 100 or more kg N·ha^{-1}·yr^{-1} (e.g., Perttu and Kowalik 1997, Adegbidi et al. 2001, Sasaki and Nakatsubo 2007). Given these rates, it could require 20–50 years for the developing forest to assimilate as much nitrogen as accumulated in surface soils during early succession. Plant uptake likely functions in retaining

TABLE 4. Means, followed by range in parentheses, and sample size (N) of soil variables measured at succession stages.

Stage	Litter layer (Mg/ha) Mean	N	Litter layer (kg N/ha) Mean	N	Surface soil bulk density (g/cm^3) Mean	N	Fine-sediment depth (cm) Mean	N	Surface soil total N (mg/g) Mean	N
0					1.8 (1.2–2.2)	7	9 (0–30)	5	0.4 (0.3–0.7)	7
I	3 (1–7)	5	30 (20–70)	5	0.9 (0.9–1.1)	5	>27 (13 to >35)	5	1.5 (1.3–1.9)	5
II	5 (2–10)	12	70 (20–170)	11	0.7 (0.5–0.8)	12	>34 (13 to >69)	9	3.4 (2.4–4.4)	12
III	6 (1–9)	6	90 (10–140)	6	0.6 (0.4–0.7)	6	>55 (>31 to >78)	6	4.5 (2.6–6.5)	6
IV	12 (10–18)	5	180 (120–340)	5	0.5 (0.4–0.6)	5	>71 (>69 to >73)	2	4.5 (3.4–5.7)	5

Note: Ellipses indicate that a variable was not measured.

TABLE 3. Extended.

Contribution to total tree coverage (%)	Understory cover (%)		
Chosenia	Grass	*Urtica*	*Filk*
13 (0–41)	20 (0–46)	2 (0–5)	1 (0–2)
16 (0–52)	16 (4–29)	14 (2–43)	8 (0–17)
2 (0–7)	4 (0–9)	28 (15–50)	45 (32–54)
...	0 (0–0)	9 (5–11)	78 (63–88)

salmon nitrogen by redepositing it in more recalcitrant plant litter compounds.

Vegetation changes during succession

Similar to other floodplain chronosequences of the northern Pacific Rim (see *Introduction*), early-succession sites on the lower Kol floodplain were characterized by *Salix*, *Chosenia*, and *Alnus* colonizing alluvial bars. However, in contrast with other studies, *Alnus* was of comparatively minor significance in the lower Kol floodplain, never achieving dominance. For example, we found that *Alnus* coverage reached its maximum during succession stage III, with an average coverage of ~10 m^2/ha and a mean relative cover of 31% (Table 3). In comparison, maximum *Alnus* coverage during *Alnus*-dominated stages was approximately two times that of the lower Kol floodplain on a floodplain of the Tanana River, Alaska (range 15–27 m^2/ha; Viereck et al. 1993), three times greater at the Queets River, Washington, (~28 m^2/ha; Balian and Naiman 2005), and four times greater at the Hoh River also in Washington (~44 m^2/ha; Luken and Fonda 1983). However, the most striking difference between succession in the lower Kol floodplain and other published studies is that rather than transitioning to conifers or other deciduous trees, the pioneer tree species eventually senesced altogether, leaving meadows of tall forbs composed primarily of *Filipendula* and *Urtica*, which were the dominant community type in the passive floodplain. We are unaware of any other study describing a successional transition from a forest to a similar tall-forb community.

These tall-forb meadows may eventually transition into grassy, short-forb meadows with some woody shrubs (stage V) that occurred in the oldest region of the passive floodplain. Dominant plants of the stage V

TABLE 4. Extended.

Surface soil total N (kg/ha)		Total soil N (surface + litter layer; kg N/ha)		2006 carcass deposition (kg N/ha)	
Mean	N	Mean	N	Mean	N
300 (100–600)	7	300 (100–600)	7	21 (0–91)	6
1100 (800–1300)	5	1100 (900–1300)	5	1 (0–3)	5
1900 (1400–2400)	12	2000 (1500–2500)	11	1 (0–5)	13
2300 (1700–2800)	6	2400 (1800–3000)	6	0.3 (0–2)	6
2400 (1900–2600)	5	2500 (2100–2900)	5	. . .	

community included grasses, fireweed (*Epilobium agustifolium*), an array of small forbs, and occasional woody shrubs, particularly *Vaccinium* sp. and *Rosa* sp. We hypothesize that this community type is older than stage IV because remnant trees or decaying logs were not present and these areas contained few flood channels and spring brooks. They did, however, have an abundance of swales, which can be interpreted in a floodplain context as old river channels that long ago filled with fine sediments (Ward 1997). We also observed that a heath community (stage VI) dominated by *Empetrum nigrum* and *Vaccinium* sp. occurred on what appeared to be an ancient river terrace or abandoned floodplain area adjacent to the modern floodplain. We hypothesize that this heath community develops over very long periods of time only after the river channels move into a new floodplain because site turnover time is short enough in the modern floodplain to prevent this community from forming.

A major assumption of the "space for time substitution" (Pickett 1989) used in succession chronosequence studies is that existing stands of different ages underwent the same developmental patterns, although this may not always be true (Fastie 1995). Theoretically, no two site histories will be exactly the same. At Kol, when all forest patches are considered together, the gradual transition between *Salix* trees and the tall forbs *Urtica* and *Filipendula* is obvious and we are confident that this has been the dominant sere in the active floodplain for at least the last century. Within this chronosequence, however, the occurrence of less abundant species, notably *Chosenia* trees, was less consistent. And, we emphasize that the histories of stages V and VI are inferred at best. Considering their hypothesized ages (hundreds to thousands of years), it is possible a different course of succession than is described by our model generated these distinct communities.

Another unique feature of the lower Kol floodplain is that all the major vegetation species occurring in the modern floodplain had very high foliar nitrogen concentrations, with mean molar foliar C:N ranging between 12 and 27. In contrast, the average foliar C:N ratio in temperate forests is 35.1 with a standard deviation of 19.9 (McGroddy et al. 2004). For contrasting Kol with temperate forests it is appropriate to consider the range of values, as C:N varied significantly between the active and passive floodplain regions (M. R. Morris, *unpublished data*), and the two regions were not sampled proportional to area. In any case, we concluded that foliage in the modern floodplain was exceptionally nitrogen rich because the highest foliar C:N ratio that we observed was 36 and most samples were well below this value, with some as low as 8 to 12. We suggest that such high foliar nitrogen concentrations likely reflect high soil fertility resulting from salmon-imported nitrogen, and to a lesser extent, *Alnus*-fixed nitrogen.

*Implications: how could salmon subsidies influence
vegetation dynamics?*

Our results demonstrate that, while new alluvial deposits are initially nitrogen poor, soil nitrogen accumulates very rapidly during early succession and salmon are an important nitrogen source during this time. Hence, salmon nitrogen accumulation during early succession may control long-term fertility in this ecosystem. Other salmon-derived nutrient studies conducted in small-river systems have more directly interpreted the ecological implications of these subsidies by comparing stream reaches with and without salmon. However, natural migration barriers do not exist in the lower Kol River, and salmon spawn so densely throughout the channel network that no suitable fishless control sites existed. Thus, in the following discussion we use inference from the data presented in this study in addition to empirical knowledge of the effects of enhanced nitrogen fertility in other systems to hypothesize how salmon nitrogen subsidies likely influence vegetation dynamics in the lower Kol floodplain.

Most obviously, salmon likely increase the growth rates of vegetation. The riparian plants at Kol were exceptionally nitrogen rich, and it is well documented that photosynthesis rate is strongly positively correlated with foliar nitrogen concentrations (Field and Mooney 1986). We have observed that Kol floodplain vegetation grows very rapidly and forms dense stands. For instance, stands of the tall forb, *Filipendula*, may contain more than 12 shoots/m^2, and individual shoots may grow 3 m in height between snowmelt (around late May to early June) and early July. Furthermore, Walter (1981) stated that similar tall-forb communities of floodplains in northeast Asia had among the highest biomass accumulation rates of natural vegetation in the world. In contrast, we have observed, and it has been documented elsewhere (Walter 1981), that the growth of these tall-forb species is greatly reduced in the uplands outside of the floodplains where there are no salmon nutrient subsidies. The nitrogen-rich floodplain foliage of the Kol is especially remarkable considering that prior to the annual salmon runs the river is oligotrophic. Total ion content of the water is consistently low (average specific conductance ~40–60 μS/cm), and total persulfate nitrogen concentrations were approximately 100–200 μg N/L near base flow prior to the salmon runs (M. R. Morris and J. A. Stanford, *unpublished data*). Nitrogen concentrations did however increase to 500 μg N/L when pink salmon were spawning and dying (M. R. Morris and J. A. Stanford, *unpublished data.*)

Nitrogen availability often strongly limits vegetation growth on young alluvial bars (Walker and Chapin 1986, Sasaki et al. 2001, Adair and Binkley 2002), but we found that salmon fertilized these early-successional stages on the lower Kol floodplain and built nitrogen-rich soils during this time. Because primary succession may occur more quickly under higher fertility conditions

(e.g., Marrs et al. 1983), the loss of salmon runs in the Kol may be expected to increase nitrogen limitation in early succession, thereby slowing establishment and forest development. Furthermore, future mature forest sites would also be expected to be less fertile if their soils did not accumulate large quantities of salmon nitrogen during early succession.

In addition to growth rate, nitrogen fertility also influences community composition. Theoretically, increased nitrogen richness should favor the dominance of more nitrophilic species (Tilman 1985, 1987, Aerts and Chapin 2000), and prior studies indicate that salmon nitrogen subsidies may have this effect in riparian communities (Mathewson et al. 2003, Bartz and Naiman 2005). We suspect that the tall forbs that dominate the passive floodplain of the Kol are nitrophilic for several reasons. Firstly, one of the forbs that commonly occurs, *Urtica dioica*, is widely recognized as being highly nitrophilic (e.g., Ivins 1952, Diekmann and Falkeng- ren-Grerup 1998), although its occurrence may better explained by phosphorus availability in some cases (Pigott and Taylor 1964). Also, as is typical of species adapted to nitrogen-rich habitats (Chapin 1980), we found that both *Urtica* and *Filipendula* had exceptionally high foliar nitrogen concentrations in combination with high growth rates (also see Walter 1981). Based on other written accounts describing floodplain forests and our own experience in western Kamchatka, 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 are well known as major salmon producers.

Without salmon, we suspect that the vegetation community may shift from *Salix–Alnus*-dominated forests to a less nitrophilic community after the first century of succession, as was the case for the conifer-dominated mature forests of the North American floodplains of the Pacific Rim (reviewed in the *Introduction*). However, even without salmon, the passive floodplain would probably not be conifer dominated, as we have observed that these trees do not occur at low elevations in the region of the lower Kol floodplain. Rather, without salmon, the community might transition to *Betula* forests rather than the tall-forb community, because *Betula* trees are abundant outside of the floodplain and occasionally occur in the oldest regions of the floodplain. *Betula* trees also dominate Kamchatkan volcano seres (Grishin et al. 1996). Alternatively, without salmon the vegetation community might shift directly from the stage III *Salix–Alnus* forests to vegetation types found in the stage V grassy meadows (which we suspect are less nitrophilic) after the first century, thus bypassing the tall-forb communities that currently dominate the floodplain.

Another expected change in the vegetation communities with the loss of salmon would be increased *Alnus*

abundance, as nitrogen fixation, which is energetically costly (Gutschick 1981), would become progressively more profitable as fertility declined (see also Helfield and Naiman 2002). We have observed that while both *Alnus* and *Salix* colonized during early succession, the growth of *Alnus* trees was suppressed in dense *Salix* stands, suggesting that *Salix* growth may have limited *Alnus* abundance. While increased *Alnus*-fixed nitrogen may compensate for the loss of salmon-imported nitrogen if salmon returns declined, it should be considered that salmon import an array of other nutrients to riparian forests in addition to just nitrogen. Furthermore, additional nitrogen fixation by *Alnus* would incur additional energetic costs and thus perhaps decreased forest growth rates. Also, increased *Alnus* abundance may cause other unforeseen changes to the composition of riparian communities.

The present study demonstrates that salmon are a major nitrogen source to this floodplain and other findings at Kol, notably that feeding and growth of some juvenile salmon species are substantially tied to allochthonous arthropod forage (Eberle and Stanford 2010), suggest that riparian recycling of salmon nitrogen may support the production of salmon species that initially rear in freshwater prior to migrating to the ocean. Research elucidating the speculative relationships that we propose will be difficult, due to the long temporal scale at which primary succession processes occur, as well as the lack of local reference (fishless) sites. We also point out that, while we chose to focus solely on nitrogen availability in the present study, the unique characteristics of the riparian communities at Kol are certainly influenced by many additional factors, such as the regional geology and climate, the life history characteristics of plant species, and the interactions among species within the community. Nonetheless, prior research demonstrating the ubiquity of nitrogen limitation in primary succession, as well as the dramatic influences that nitrogen fertilization has on community development (reviewed in the *Introduction*), suggests that the large marine nutrient subsidies from salmon are likely a key factor influencing ecosystem structure and function in this floodplain and others like it.

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