

Hydrologic controls on nitrogen availability in a high-latitude, semi-arid floodplain¹

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Abstract: Past research shows a discrepancy between apparent nitrogen supply and the annual growth requirements for early successional plant communities along the Tanana River floodplain in interior Alaska. Because previous measurements of nitrogen fixation, mineralization, and deposition can only account for approximately 26% of these communities' nitrogen requirements, other mechanisms of nitrogen supply should be operating. This study examined the potential for subsurface hydrology to supply nitrogen to the rooting zones of early successional plant communities. Three transects of ground water wells were established along the floodplain, and hydrologic characteristics and soil/water chemistry were measured for 2 y. Hydrologic measurements were then used to model the potential nitrogen contributions from advective flow and capillary rise. Ion exchange membranes and stable isotope tracers were used to identify the use of hyporheic nitrogen by vegetation. Nitrogen accumulation on ion exchange membranes showed a large input of nitrogen during a period of high water in 2003. Plants showed uptake of hyporheic ¹⁵N-labelled nitrogen at 2 of 4 locations. Models of capillary rise and advective flow estimated that nitrogen supply from subsurface water equalled or exceeded total nitrogen supply from nitrogen mineralization and nitrogen fixation combined. These findings underscore the importance of hyporheic processes in controlling nutrient supply to early successional vegetation on the Tanana River floodplain.

Keyword: advective flow, capillary fringe, hyporheic, nitrogen, riparian, Tanana River.

Resume : Des recherches precedentes ont mis en evidence une divergence entre l'apport apparent d'azote et les besoins pour la croissance annuelle des communautes vegetales de debut de succession dans la plaine inondable de la riviere Tanana II l'interieur de l'Alaska. Des mesures precedentes de la fixation, mineralisation et deposition de lazote ont demontre que ces processus ne peuvent fournir qu'approximativement 26 % des besoins en azote de ces communautes vegetales, d'autres mecanismes d'approvisionnement en azote doivent donc operer. Cette etude a examine le potentiel de l'hydrologie souterraine a fournir de lazote aux zones racinaires des communautes vegetales de debut de succession. Trois transects de puits d'eau souterraine ont ete etablis le long de la plaine inondable, les caracteristiques hydrologiques et la chimie du sol/eau ont ete mesurees durant 2 ans. Les mesures hydrologiques ont ensuite ete utilisees pour modeliser les contributions potentielles en azote du flux advectif et de la remontee capillaire. Des membranes dechanges ioniques et des traceurs d'isotopes stables ont ete utilisees pour identifier l'assimilation d'azote hyporheique par la vegetation. L'accumulation d'azote sur les membranes dechanges ioniques a mis en evidence un apport important d'azote en 2003 durant une periode de hautes eaux. Les plantes ont montre une assimilation d'azote hyporheique identifiee au ION dans 2 des 4 sites. Les modeles de remontee capillaire et de flux advectif ont evalue que l'apport en azote de l'eau souterraine etait egal ou excedait celui des processus combines de la mineralisation et de la fixation de l'azote. Ces resultats soulignent l'importance des processus hyporheiques dans le controle de l'approvisionnement en nutriments de la vegetation de debut de succession dans la plaine inondable de la riviere Tanana.

Mots-clés : azote, bordure capillaire, flux advectif, hyporheique, riverain, riviere Tanana.

Nomenclature: Hulten, 1968.

Arctic and sub-arctic ecosystem productivity is often limited by nitrogen availability (Shaver & Chapin, 1995; Atkin, 1996). The supply of inorganic nitrogen resulting from soil microbial processes has been a primary focus of research in arctic tundra and boreal forests for decades. The conventional concept of terrestrial nitrogen cycling, in the absence of nitrogen-fixers, has focused on mineralization of soil organic matter to supply plant nitrogen requirements (Vitousek & Howarth, 1991; Aerts & Chapin, 2000). One reoccurring theme has been the discrepancy between

measured rates of nitrogen mineralization and the rate of nitrogen accumulation in vegetation (Shaver, Nadelhoffer & Giblin, 1991; Ruess *et al.*, 1996). In recent years, an increasing body of evidence supports the direct uptake of organic forms of nitrogen by plants in these environments (Kielland, 1994; Persson & Nasholm, 2001; McFarland *et al.*, 2002). Because organic nitrogen can be found in much greater concentration than inorganic nitrogen in most high-latitude soils (Kielland, 2001), vegetation nitrogen demand may be met by organic forms where labile organic materials are present.

The Tanana River floodplain is a large landscape feature in interior Alaska supporting highly productive ecosystems. In the primary successional sequence that exists across the floodplain, the earliest stages are characterized by the presence of rapidly growing willow (*Salix* spp.) commu-

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nities (Van Cleve *et al.*, 1993a; Viereck, Dyrness & Foote, 1993). These communities are highly productive in spite of heavy browsing by vertebrate herbivores (McAvinchey, 1991; Kielland, Bryant & Ruess, 1997), repeated inundation from floods, and low nutrient availability (Van Cleve *et al.*, 1993b). As in other sub-arctic terrestrial ecosystems, inorganic nitrogen availability is extremely low. However, in contrast to other sub-arctic ecosystems, concentrations of organic nitrogen are also low, suggesting that this source of nitrogen does not play a major role in these environments. One characteristic of primary successional soils is the initial absence of a forest floor in the earliest stages and very low rates of nitrogen mineralization (Van Cleve *et al.*, 1993a; Klingensmith & Van Cleve, 1993a).

The Bonanza Creek Long Term Ecological Research Site (BNZ LTER) encompasses a portion of the Tanana River. Previous research within the BNZ LTER shows that the earliest stages of succession follow a general regional trend in which plant nitrogen requirements appear to outstrip the supply of nitrogen provided by mineralization, fixation, and deposition. Estimates suggest that these pathways of plant nitrogen supply can account for only 26% of the nitrogen annually accrued by vegetation in these early-successional stands (Table 1; Walker & Chapin, 1986; Klingensmith & Van Cleve, 1993b; Van Cleve *et al.*, 1993a; Viereck, Dyrness & Foote, 1993; Ruess *et al.*, 1996; Uliassi & Ruess, 2002; National Atmospheric Deposition Program, 2002-2004; Ruess *et al.*, 2004). BNZ LTER has a wealth of literature focusing on these sites, and care was taken to include the studies with the highest published values for rates of nitrogen supply from the available data to generate estimated nitrogen budgets. In addition, because these estimates of N requirements are based on standing stock (*i.e.* biomass \times concentration of N in tissue) actual N requirements are likely greater, making our estimates relatively conservative.

The nitrogen dynamics of a plant community are controlled by the rate at which nitrogen is made available to plant roots (Barber, 1962). In hydrologically dynamic areas 3 mechanisms can potentially increase nitrogen supply in comparison to other terrestrial environments: 1) subsurface water can stimulate microbial activity by altering the

soil environment (*e.g.* moderating temperature, providing labile carbon), 2) the presence of subsurface water can increase nitrogen pool size via access to otherwise unavailable sources (*e.g.* dissolved nitrogen in ground water or allochthonous inputs from floods), or 3) subsurface water can accelerate the rate of supply by flowing through the rooting zone. In previous studies of nitrogen dynamics along the Tanana River, inputs from subsurface water were not accounted because mineralization studies have used water-impermeable containers (*e.g.* polyethylene bags, PVC tubes) that exclude any inputs of hydrologically transported nitrogen. If water is moving at a rate that substantially exceeds the rate of diffusion from the bulk soil to the plant roots, then a low concentration of dissolved nitrogen could equate to a significant supply for plant uptake. Another distinctive feature of the soils on the Tanana floodplain is the presence of a salt crust. This crust is created by movement of dissolved ions (*e.g.* calcium, magnesium, sulphate) from the ground water to the surface by evapotranspiration (Dyrness & Van Cleve, 1993). This process of capillary rise likely transports dissolved nitrogen, and other solutes as well, from ground water to the surface soil (Dyrness & Van Cleve, 1993).

In this study nitrogen dynamics of the early successional stage of the Tanana River floodplain were examined. The objectives of this research were threefold: 1) to identify the sources of nitrogen supply to early successional stands, 2) to quantify the relative importance of each source, and 3) to determine the controls on nitrogen availability within this system. Because the rate at which dissolved nitrogen is transported in water can greatly exceed the rates of diffusion (Barber, 1962; Nye, 1977), this study examined the primary mechanisms responsible for moving water through the rooting zone separately. Two hypotheses were tested involving hyporheic fluxes as the primary mechanisms of nitrogen supply to plants on the Tanana River floodplain:

1) the majority of plant-available nitrogen is supplied to the root matrix throughout the growing season via vertical capillary rise;

2) the majority of plant-available nitrogen is supplied horizontally by saturated subsurface flow through the rooting zone during high water.

TABLE 1. Patterns of nitrogen accumulation across 4 stages of primary succession. All data are presented as $\text{g}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$.

Total measured nitrogen inputs				
Stage	Nitrogen mineralization ¹	Nitrogen deposition ²	Nitrogen fixation ^{3,4,5}	Total N Input
III-Willow	0.25	0.08	0.10	0.43
V-Alder	1.50	0.08	6.72	8.30
VI-Poplar	1.60	0.08	2.20	3.88
VIII-White spruce	1.60	0.08	0.15	1.23
Annual plant nitrogen requirements				
Stage	Aboveground N requirements ^{6,7}	Belowground N requirements ^{6,8}	Total N requirements	% N requirements supplied
III-Willow	1.12	0.51	1.63	26
V-Alder	4.34	2.05	6.39	130
VI-Poplar	1.78	3.04	4.82	81
VIII-White spruce	1.47	1.63	3.10	40

*Constructed using data from ¹ Van Cleve *et al.*, 1993; ² National Atmospheric Deposition Program data 2002, 2003 & 2004; ³ Klingensmith & Van Cleve, 1993b; ⁴ Uliassi & Ruess, 2002; ⁵ Ruess *et al.*, 1996; ⁶ Walker & Chapin, 1986; ⁷ Viereck *et al.*, 1993; and ⁸ Ruess *et al.*, 2004.

Methods

SITE DESCRIPTION

The study was conducted at the Bonanza Creek Long Term Ecological Research (BNZ LTER) site (64°48' N, 147°52' W) about 30 km southwest of Fairbanks, Alaska and encompassed early-successional shrub communities along the Tanana River floodplain. The Tanana River originates near the border of Alaska and Canada and drains a basin with an area of 113,920 km² (Bonanza Creek LTER Website). The river follows a generally northwesterly path for approximately 850 km before flowing southwest and then north into the Yukon River. Downriver from Fairbanks, the Tanana River valley opens to 80–100 km in width, and has an active floodplain 300–2000 m across. At the study sites the Tanana River forms a series of braided channels with sandbars and islands.

The frost-free growing season is approximately 100 d, and air temperature varies from -50°C to 25°C through the year. A rain shadow created by the neighbouring Alaska Range results in the study area receiving mean annual precipitation of 269 mm, approximately 37% of which is snow (Viereck *et al.*, 1993). Potential evapotranspiration approaches twice the amount of annual precipitation (Viereck *et al.*, 1993), implying ground water and the river could act as important sources of water for biological communities along the floodplain. Floods, accompanied by the deposition of sediment, occur periodically, and aggradation as a result of river meander leads to the development of exposed alluvium. Soil particles are primarily a mix of sand and silt of glacial origin and are classified as Cryofluvents. The soil pH of these sites is typically between 7 and 8 and is directly related to high concentrations of base cations (Dyrness & Van Cleve, 1993). Among the first woody plant species to colonize are a variety of willows (*Salix interior*; *S. alaxensis*, *S. nova-angliae*, *S. branchycarpa*, *S. lasiandra*, and others) and thin-leaf alder (*Alnus tenuifolia*). In later stages of succession, balsam poplar, white spruce, and black spruce (*Populus balsamifera*, *Picea glauca*, and *P. mariana*, respectively) dominate the overstory vegetation.

Willow maintains dominance for the first 2 decades of succession until browsing pressure from mammalian herbivores (*Alces alces*, *Lepus americanus*; Kielland, Bryant & Ruess, 1997) and diminishing soil salt content, resulting from reduced evaporation beneath the developing forest floor and repeated leaching from rain events (Chapin & Walker, 1993), allow alder to colonize and assert its dominance. During alder dominance, soil nitrogen pools increase rapidly and provide much of the nitrogen found in later stages of succession.

HYPORHEIC MEASUREMENTS

Transects of ground water wells were established at 3 early-successional sites, separated by up to 10 river km (Figure 1). Wells consisted of 4-cm PVC pipes, 3 m in length, with the lower 1.5 m being perforated and wrapped in Geotextile® cloth to prevent filling of wells with sediment. Transects ranged from 500 to 1000 m in length. A total of 35 wells were installed to a depth of 2 m at intervals along the transects, with approximately 80 m between wells. Water levels in wells were measured every 2 weeks

from early June to mid-September throughout the summers of 2003 and 2004. Soil cores were taken at 3 locations along each transect to a depth of 120 cm and analyzed for hydraulic conductivity in the lab using a falling head permeameter (Scott, 2000). Particle size analysis was also performed on these soils, using the buoyous method (Elliot *et al.*, 1999). Subsurface flow rates were taken from ongoing research at the same locations (BNZ LTER, unpubl. data).

On each sampling date, 100 mL of water from each well was collected in polyethylene bottles. Prior to collection, bottles were acid washed and then triple rinsed with sample water from each well in the field. Samples were stored in a cooler and immediately returned to the lab, refrigerated, and filtered within 24 h. Samples were analyzed by ion chromatography (Dionex Corporation, Sunnyvale, California, USA) for nitrate and nitrite concentrations, and sub-samples were frozen and analyzed for ammonium at a later date. Total dissolved nitrogen (TDN) was determined using a Shimadzu 5000 total organic carbon analyzer (Shimadzu Scientific, Kyoto, Japan) plumbed to an Antek 7050 nitrous oxide chemoluminescent detector (Antek Instruments, Houston, Texas, USA). Dissolved organic nitrogen (DON) was calculated as TDN minus the sum of nitrate, nitrite, and ammonium in each sample.

Data from the United States Geological Survey (USGS) gauging station (#15485500) located on the Tanana River 30 km upriver in Fairbanks, Alaska were used to create a relationship between river discharge (m³·s⁻¹) and the depth to water measured in wells at the sites for the 2 study years. This relationship was then used to calculate seasonal fluctuations in the water table over the past 3 decades using archived river discharge data (Table II). This allowed the hydrologic regime of the 2 study years to be compared and placed in longer-term context and increased our confidence that data presented are representative of a typical year. Potential evapotranspiration rates were calculated using the Thornthwaite Method, which incorporates temperature, length of day, and periodic heat indexes (Thornthwaite & Mather, 1955; Sellinger, 1996).

ION EXCHANGE MEMBRANES

Ion exchange membranes (CMJ 7000 & AMI 7001, Membranes International, Glen Rock, New Jersey, USA)

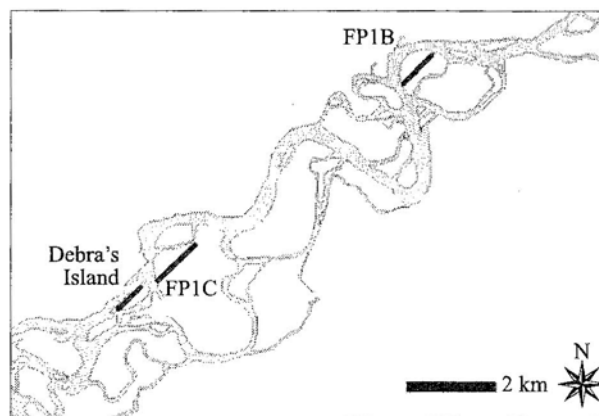


FIGURE 1. Location of ground water well transects along the Tanana River floodplain.

TABLE II. Summary of UPFLOW model parameters used to estimate nitrogen inputs from capillary rise. Data shown are means taken over 15- or 16-d periods. PET: Potential Evapotranspiration.

Year	Soil moisture (%)	Conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$)	Water depth (cm)	PET ($\text{mm}\cdot\text{d}^{-1}$)	Soil texture (0–50 cm soil layer)	Soil texture (50–100 cm soil layer)	Annual salt load ($\text{t}\cdot\text{ha}^{-1}$)	14-d nitrogen load ($\text{g}\cdot\text{m}^{-2}$)
2003								
Jun 1 to Jun 15	11.2	0.8	151.0	3.8	sandy loam	loamy sand	0.7	0.002
Jun 15 to Jun 30	11.2	0.8	145.9	3.8	sandy loam	loamy sand	0.8	0.003
Jul 1 to Jul 15	13.8	0.8	129.9	4.2	sandy loam	loamy sand	1.1	0.003
Jul 16 to Jul 31	34.0	0.9	19.4	4.2	sandy loam	loamy sand	8.8	0.018
Aug 1 to Aug 15	17.3	1.0	58.1	3.1	sandy loam	loamy sand	7.2	0.014
Aug 15 to Aug 31	13.8	0.9	95.8	3.1	sandy loam	loamy sand	3.2	0.006
2004								
Jun 1 to Jun 15	13.8	0.8	85.8	3.8	sandy loam	loamy sand	3.9	0.01
Jun 15 to Jun 30	13.8	0.8	94.6	3.8	sandy loam	loamy sand	3.0	0.012
Jul 1 to Jul 15	34.0	0.8	18.4	4.2	sandy loam	loamy sand	7.8	0.023
Jul 16 to Jul 31	21.7	0.9	41.5	4.2	sandy loam	loamy sand	8.8	0.018
Aug 1 to Aug 15	21.7	1.0	66.7	3.1	sandy loam	loamy sand	7.2	0.014
Aug 15 to Aug 31	21.7	0.9	42.4	3.1	sandy loam	loamy sand	6.5	0.012
30-YEAR MEAN								
Jun 1 to Jun 15	13.8	0.8	118.1	3.8	sandy loam	loamy sand	1.6	0.004
Jun 15 to Jun 30	13.8	0.8	81.4	3.8	sandy loam	loamy sand	4.5	0.017
Jul 1 to Jul 15	17.3	0.8	57.3	4.2	sandy loam	loamy sand	8.4	0.024
Jul 16 to Jul 31	21.7	0.9	40.2	4.2	sandy loam	loamy sand	8.8	0.018
Aug 1 to Aug 15	21.7	1.0	46.6	3.1	sandy loam	loamy sand	7.2	0.014
Aug 15 to Aug 31	21.7	0.9	70.5	3.1	sandy loam	loamy sand	6.5	0.012

were deployed to assess nitrogen supply at 8 points along each transect. Membranes were deployed once per month throughout the growing season in 2003 and twice per month in 2004 for 15-d incubation periods. Although ion exchange membranes can be deployed for up to 1 month *in situ* (Qian & Schoenau, 2002), a shorter deployment length was chosen to ensure that saturated adsorption dynamics did not occur during the experiment as a result of the large concentration of solutes. Prior to deployment in the field, membranes were shaken in 3% concentrated HCl for 1 h. Membranes were then placed in 0.5 M $\text{Na}(\text{CO}_3)_2$ and shaken for 1 h. The solution was then poured off, replaced, and shaken for a total of 3 times. Following the third $\text{Na}(\text{CO}_3)_2$ treatment, membranes were briefly rinsed with de-ionized water and stored moist until deployment the following day. This system of preparing the membranes ensures that they are stripped of any residual nitrogen and saturated with exchangeable salts before deployment (Qian & Schoenau, 2002). At each location, 2 intact, replicate soil cores 10 cm in diameter and 15 cm in length were taken. Each core was cut in half vertically, and a cation and an anion exchange membrane were placed in between the halves. A paired sample design was used such that at each location there were two replicate cores receiving different treatments for each sample date. One treatment consisted of cores being reassembled and placed into a water impermeable polyethylene bag, typically used for buried bag incubations, and open to nitrogen inputs from both mineralization and free-living nitrogen fixers. The second treatment consisted of a water-permeable nylon mesh bag that was open to inputs from soil microbial processes and both capillary rise and saturated subsurface flow. Both cores were then placed back into the ground so that membranes were 25 cm beneath the soil surface. This procedure provided a directly comparable index of *in situ* nitrogen availability in the presence (water

permeable) and absence (water impermeable) of hydrologic nitrogen sources. Following incubation, membranes were extracted in 0.5 M K_2SO_4 for 1 h and analyzed with a Bran-Lubbe auto-analyzer (SPX Corporation, Delavan, Wisconsin, USA) using the phenol-hypochlorite method for NH_4^+ and the sodium nitroferrocyanide-cadmium reduction method for NO_3^- (Page, 1982).

NITROGEN MINERALIZATION

In the summer of 2003 standard buried bag incubations (Eno, 1960; Binkley & Hart, 1989) were used to measure rates of net nitrogen mineralization along each transect using native soil and 10-cm soil cores. Buried bags were placed adjacent to ion exchange membranes at each of the 8 locations along each transect at depths of 25 and 50 cm and incubated *in situ* for 15 d at 3 dates during the summer. Initial and final soil cores were returned to the lab, passed through a 2-mm sieve, and homogenized. Sub-samples were collected and dried at 105°C to establish fresh weight to dry weight ratios. A 10-g subsample of each soil sample was then extracted with 25 mL of 0.5 M K_2SO_4 and nitrogen concentrations in the soil extracts were determined using the methods described above for ion exchange membrane extracts.

CAPILLARY RISE AND SATURATED FLOW

Hyporheic nitrogen supply was calculated as a function of subsurface water flux via 2 mechanisms, either vertical, capillary rise under unsaturated conditions or lateral, saturated flow through the rooting matrix under high water conditions. Separate mathematical models were applied to calculate rates of nitrogen supply for both mechanisms. Nitrogen data from well water samples and soil-hydraulic properties were used to estimate capillary (vertical) rise using the model UPFLOW (Raes & Deproost, 2003; Raes,

2004). UPFLOW is a mathematical model that uses soil and environmental characteristics to predict vertical solute transport based on Richard's equation for unsaturated flow. The parameters used in the UPFLOW model can be found in Table II. Total nitrogen flux from capillary rise was then calculated by multiplying the ratio of total dissolved nitrogen to total dissolved solutes by the total salt flux. Because UPFLOW was developed for agricultural settings, no suitable vegetation class was available to represent floodplain vegetation. Hence, we conservatively estimated vertical fluxes based on barren soil.

Average rooting depth was measured for the dominant species of willow (*S. interior* and *S. alaxensis*) along river cut-banks during a period of low water level for the Tanana River in August 2004. These cut-banks created areas resembling large soil pits several metres deep. Using shovels and metre sticks at several locations, the soil profile was exposed and average rooting depth was measured. Rooting depth for this study was defined as the point where roots were no longer obviously visible to the eye. Soil porosity was calculated using bulk density measurements from Van Cleve *et al.* (1993b) and was corroborated by measuring a subset of the soils from hydraulic conductivity measurements in the laboratory. The saturated area of the rooting zone was calculated using the average rooting depth and the water level from well measurements. Subsurface (horizontal) flux was calculated as

$$Q = v \cdot \Phi \cdot A \quad [1]$$

where Q = subsurface flux ($\text{m}^3 \cdot \text{d}^{-1}$), v = subsurface flow rate ($\text{m} \cdot \text{d}^{-1}$), Φ = porosity, and A = cross-sectional area of rooting zone saturated (m^2).

The rate of hyporheic nitrogen flux from saturated flow was then calculated by multiplying sub-surface flux by the nitrogen concentration measured in the ground water wells.

Estimates for advective nitrogen flux and capillary rise based on 30-y daily means for water table height were calculated using mean values for hyporheic chemistry measured in this study. The growing season was divided into 7 periods, 15 to 16 d in length, to facilitate comparisons with ion exchange membrane and buried bag mineralization measurements, and fluxes were calculated using mean values pooled across sites for the input variables during each time period.

PLANT USE OF HYPORHEIC NITROGEN

To evaluate the importance of plant uptake of hyporheic-derived N, ^{15}N isotopes were used to track nitrogen flow from the hyporheic zone to the vegetation. At 2 of the study sites (FP1B and Debra's Island), 2 hollow flow-boxes were installed next to the well transects. Each flowbox was constructed of perforated PVC sheets 3 m long, 0.4 m tall, and 0.04 m thick and had an internal volume of approximately 30 L. The flowboxes were installed to a depth of 1.3 m, with the top buried below the rooting zone. Hyporheic water within each box was labelled by adding 500 mL of a solution containing 9.0 mM $^{15}\text{NH}_4\text{Cl}$ and 5.0 mM K^{15}NO_3 (99% atom, Icon Isotopes, Summit, New Jersey, USA) to 2 flow-boxes (Debra's Island) on 1 July 2004 and to 2 flow-boxes (FP1B) on 13 July 2004. Water in the flow-boxes was then circulated using a peristaltic pump for 2 h to ensure

uniform mixing. At the start of both injections the water was approximately 10 cm below the top of the flowboxes and thus 20-30 cm below the mean rooting depth. The area "downriver" from the injection point was divided into sections 1 m long and 3 m wide for 10 m. Every 7 d after the addition, 6 soil cores 3 cm in diameter were collected to depths of 30, 60, and 90 cm from each section and composited by depth. After 3 weeks (July) or 4 weeks (August) shoot and leaf tissues in the form of 1 randomly selected intact branch with foliage from each plant were collected in addition to the soil samples. Six cores 10 cm in diameter and 25 cm long were also taken on the last sampling date from each section. The roots were sampled from these cores *in situ* by washing cores through a 0.5-mm sieve using river water. As willows were the only woody species in these sampling areas, their larger roots could be identified. Non-woody roots (primarily from *Equisetum fluviatile*) > 1 mm in diameter were removed and discarded; roots < 1 mm in diameter could not be reliably sorted as woody or non-woody and were left in the sample. Control samples were collected 2 m upriver from the injection point on the same sampling schedule. Plant tissues (leaf, root, and shoot) and soils were dried at 65°C for 48 h. All samples were ground in a ball mill or using a Wiggle-bug® and analyzed for $\delta^{15}\text{N}$ using a continuous flow mass spectrometer (PDZ Europa Inc., Cheshire, UK).

STATISTICS

Statistical analyses were performed using Statistix 8 (Analytical Software, Tallahassee, Florida, USA). Significant differences in ion exchange membrane nitrogen accumulation for the various treatments and incubation dates were tested using 2-way analysis of variance (ANOVA); where significant differences were found Tukey's multiple comparisons tests were also performed.

Results

ANNUAL VARIATION IN FLUVIAL DYNAMICS

Surface soils ranged from being dry and cracked to being completely saturated both years. Water levels along all 3 transects varied by more than 1.5 m throughout both summers and were closely correlated with river level and discharge ($y = 145.561 \ln[x] - 1103.4$, $R^2 = 0.98$, river data provided by USGS Gauging Station #15485500, located on the Tanana River in Fairbanks, Alaska).

Over the 30-y record for discharge, stream flow on average increased through the summer, peaking in early August and declining into September (Figure 2). During the 2 study years the sites experienced different seasonal patterns in discharge. Discharge in 2003 was variable in mid to late summer, twice exceeding $2300 \text{ m}^3 \cdot \text{s}^{-1}$, which resulted in floods that submerged the sites in up to 1 m of water. These floods occurred following storms and coincided with the peak flow of glacial melt from the Alaska Range in mid-summer. During the summer period of 2003, approximately 1-4 cm of sediment was deposited on the study sites. In contrast, 2004 was characterized by relatively high discharge throughout the summer, from late May until mid-August. Although surface soils approached saturation

during mid-June, no flooding occurred. A summary of soil and hyporheic properties is presented in Table III.

ION EXCHANGE MEMBRANES AND NITROGEN MINERALIZATION

In the summer of 2003 ion exchange membranes showed differences in total nitrogen accumulation both by location and by incubation date (Table IV). Nitrogen accumulation increased marginally in the water permeable treatment compared to the water-impermeable treatment. Patterns in total nitrogen accumulation were largely driven by an approximately 400% increase in nitrogen supply during the incubation period that began between the 2 floods that occurred in July 2003 (Figure 3a).

In the summer of 2004 ion exchange membranes showed a difference in total nitrogen accumulation only by date (Table IV). Nitrogen supply did not differ between the water-permeable and water-impermeable treatments or among locations along the transects. Higher rates of accumulation were observed early in June and at the end of the summer in September 2004 (Figure 3b). Accumulation rates for most of the growing season were similar to those found during 2003 with the exception of during floods.

Nitrogen mineralization rate throughout the summer of 2003 was very low (Figure 4) and did not vary significantly with depth (ANOVA, $n = 106$, $\alpha = 0.5$).

CAPILLARY RISE AND SATURATED FLOW

Based on the UPFLOW model output, capillary rise was predicted to occur during every incubation period for both years of the study (Figure 5). In the summer of 2003 capillary rise was extremely low until the mid-summer

Storms. Following the periods of high rainfall, capillary rise became comparable to both the 2004 growing season and the 30-y average. The total flux of nitrogen for 2004 and the 30-y average were fairly consistent throughout the growing season. Seasonal totals of nitrogen flux from capillary rise were between 2 and 6% of the annual nitrogen requirements for the willow communities (Table V; Figure 5). These results lead us to reject our first hypothesis, which was that capillary rise is supplying the majority of the plant-available nitrogen to these sites.

The average rooting depth measured for these sites was between 70 and 80 cm. Saturated subsurface flow occurred in the rooting zone during a 4-week period in 2003 and an 8-week period in 2004 (Figure 6). Model predictions based on the 30-y mean showed subsurface flow occurring in the rooting zone for 11 weeks of the summer. The supply of nitrogen to the rooting zone was approximately 20-50% of the annual nitrogen requirements for the willow communities (Table V; Figure 6). Although these results do not support our second hypothesis - that saturated subsurface flow provides the majority of nitrogen - they do strongly suggest that this mechanism is an important component of nitrogen availability to these sites.

PLANT USE OF HYPORHEIC NITROGEN

Uptake of hyporheic ^{15}N was observed in foliage and stem tissue at 2 of the 4 flow-box locations in 2004 (Figure 7), with enrichment in foliar $\delta^{15}\text{N}$ values of approximately 7 and 10‰ at flow-boxes located at the upriver ends of FP1B and Debra's Island, respectively; the other 2 flow-box sites showed no sign of isotopic enrichment. We did not detect isotopic enrichment of either soil and root tissue in any of the sites.

Discussion

RIPARIAN SOIL NITROGEN DYNAMICS

Nitrogen cycling in riparian ecosystems operates under additional controls compared to other terrestrial ecosystems, and traditional methods for quantifying soil nitrogen availability may fail to explain rates of accumulation in vegetation (Adair & Binkley, 2002; Andersen, Nelson & Binkley, 2003). Surface and subsurface hydrology exert strong control over biogeochemical processes in riparian ecosystems, but previously these have not been adequately quantified along the Tanana River. Recent studies in other riparian areas have focused more attention on fluvial processes, primarily in regard to changes in nitrogen availability in the soil environment following floods and changes in rates of microbial processing of nitrogen as result of inundation magnitude and duration (Andersen, Nelson & Binkley,

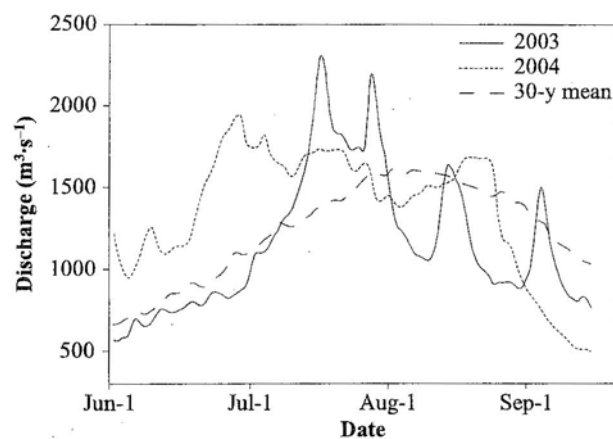


FIGURE 2. Seasonal fluctuations in discharge. Mean daily discharge for the Tanana River for the 2003 and 2004 growing seasons and the average calculated for the period from 1971 to 2001.

TABLE III. Summary of soil and hyporheic properties along the early successional stands of the Tanana River. Hydraulic conductivity, velocity, and nitrogen concentrations are means \pm SE.

Transect	% sand	Hydraulic conductivity (m·d ⁻¹)	Velocity of hyporheic water (m·d ⁻¹)	Concentration of nitrogen in hyporheic water (µg·L ⁻¹)	Ratio of organic to inorganic nitrogen in hyporheic water	Solute concentration of hyporheic water (µS·cm ⁻¹)
FP1B	59	9.2 \pm 3.4	0.39 \pm 0.06	148.8 \pm 16.1	2.0	814.4 \pm 30.5
FP1C	60	25.0 \pm 6.2	NA	743.5 \pm 113.6	5.8	1015.3 \pm 52.6
Debra's Island	60	14.0 \pm 3.7	0.37 \pm 0.07	181.1 \pm 13.1	5.9	673.4 \pm 16.7

2003; Andersen & Nelson, 2003; Sabater *et al.*, 2003). For example, nitrogen accumulation for the Yampa and Green Rivers in northwestern Colorado was recently attributed to nutrients stored in the sediments deposited during floods

TABLE IV. Two-way ANOVA results for the total nitrogen accumulation on ion exchange membranes. Data represents 15-d deployment periods as measured by membranes for the a) 2003 and b) 2004 growing seasons.

	Variable	df	MSE	F	P
a) 2003	Treatment	1	1.21	3.15	0.07
	Deployment date	2	11.49	29.99	< 0.001
	Location	24	0.6	1.57	0.05
	Error	192			
b) 2004	Treatment	1	0.19	0.64	0.43
	Deployment date	6	3.69	12.71	< 0.001
	Location	13	0.19	0.66	0.8
	Error	218			

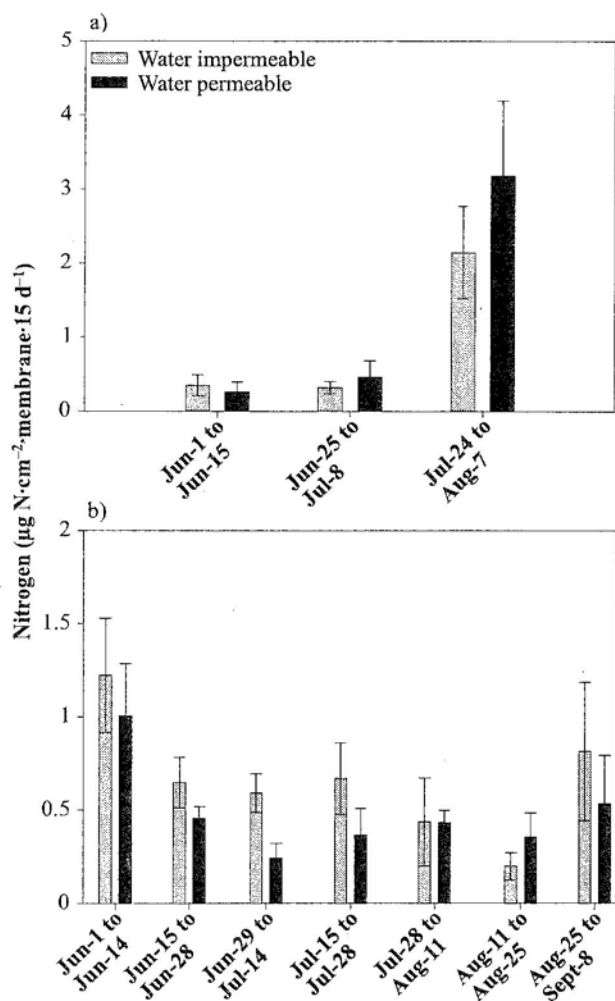


FIGURE 3. Seasonal variation in total nitrogen accumulated on ion exchange membranes. Calculated over 15-d incubations during a) the 2003 and b) the 2004 growing seasons. Data presented for both water-impermeable and -permeable treatments as means \pm SE.

(Adair, Binkley & Andersen, 2004). Although total accumulation of soil nitrogen during succession may be explained by sedimentation in some ecosystems, this process likely does not explain the discrepancy observed in early succession along the Tanana. Sedimentation is sporadic and occurs only in years with very high water levels. Recent research has also shown that rates of both decomposition and nitrogen mineralization decrease exponentially as the rate of sedimentation increases (Lockaby *et al.*, 2005). Finally, if 80% of soil nitrogen in the semi-arid riparian zone is ecologically "stable", *i.e.*, not available for uptake, as suggested by Kaye, Binkley, and Rhoades (2003), then the floodplain soils only contain enough nitrogen for a single year of growth throughout the first decade of succession. This implies that alluvial stores of nitrogen alone would not explain the discrepancies between rates of nitrogen supply and plant nitrogen uptake in the Tanana River's floodplain willow communities.

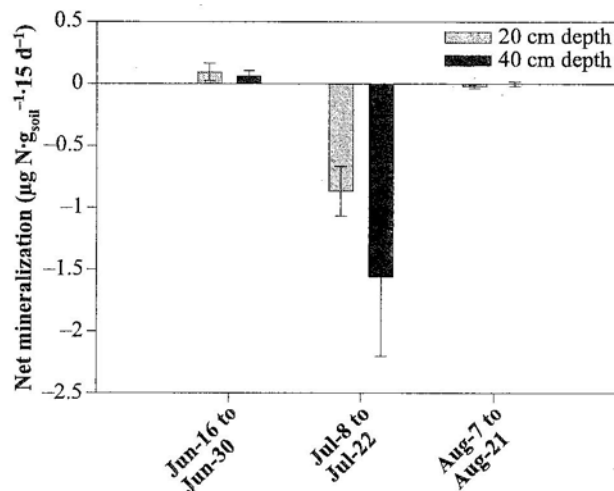


FIGURE 4. Net nitrogen mineralization rates for the 2003 growing season. Data are means \pm SE.

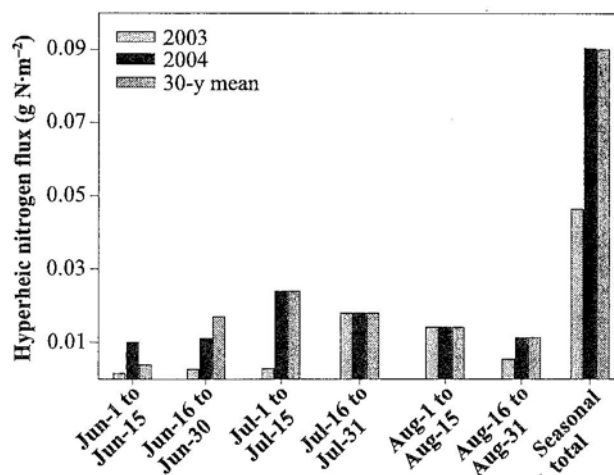


FIGURE 5. Predicted supply of nitrogen from capillary rise. Presented as total dissolved nitrogen transported to the rooting zone over periods of 15 d. Data are means for 2003, 2004, and estimates based on the 30-y daily mean river discharge.

TABLE V. Summary of estimated patterns of nitrogen accumulation. Nitrogen mineralization, deposition, fixation data, and total nitrogen requirements reproduced from Table I. Capillary rise and saturated flow data are means based on both years of this study.

Stage III-Willow	Nitrogen mineralization	Nitrogen deposition	Nitrogen fixation	Capillary rise	Saturated flow	Total N input	Total N requirement
Nitrogen input and requirements ($\text{g}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$)	0.25	0.08	0.1	$0.06 (\pm 0.03)$	$0.54 (\pm 0.24)$	0.43	1.63
Nitrogen input as % of annual plant nitrogen requirements	15	5	6	$4 (\pm 2)$	$33 (\pm 15)$	$63 (\pm 17)$	

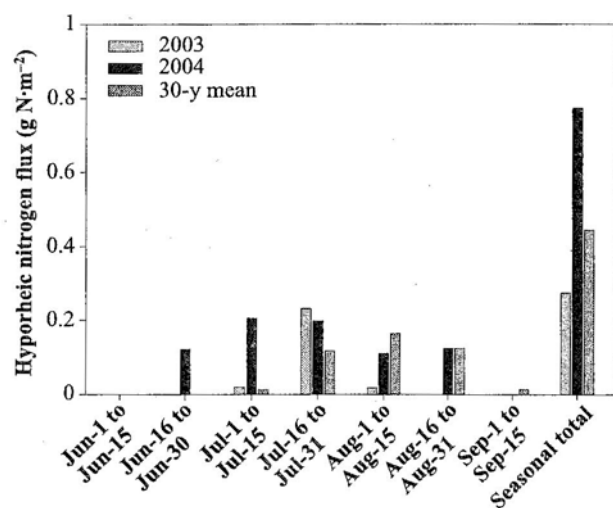
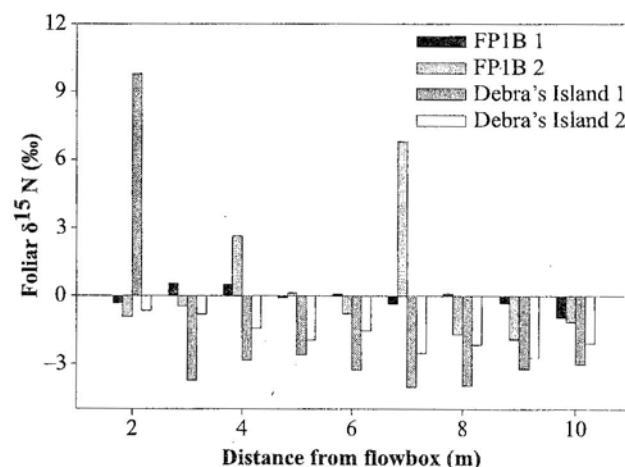


FIGURE 6. Predicted supply of nitrogen from saturated flow. Presented as total dissolved nitrogen transported to the rooting zone over periods of 15 d. Data are means for 2003, 2004, and estimates based on the 30-y daily mean river discharge.

HYPORHEIC CONTROL OF NITROGEN FLUX

Riparian ecosystems have long been recognized as having important influences on nitrogen cycling as a result of interactions between the terrestrial and aquatic environments. Changes in water table depth can directly control soil microbial processes, with the dominant pathway of nitrogen transformation shifting between net nitrogen mineralization, nitrification, and denitrification with fluctuations in the water table of less than 0.5 m (Hefting *et al.*, 2004). Nitrate removal as a result of plant uptake and denitrification is also typical of riparian areas (Peterjohn & Correll, 1984; Schade *et al.*, 2001; Sabater *et al.*, 2003). In particular, floods have been suggested as a mechanism for increases in nitrogen supply via deposition of organic matter with sediment or direct supply from floodwater (Schade *et al.*, 2002; Adair, Binkley & Andersen, 2004).

This study suggests that a substantial amount of nitrogen could be supplied directly from flowing water. The greatest flux of nitrogen from subsurface flow in the rooting zone coincided with the ion exchange membrane deployment that accumulated the greatest amount of nitrogen throughout the summer of 2003. For example, during this period of high subsurface flux the membranes accumulated nitrogen at rates comparable to membranes in stands of *Lupinus* spp. in Sweden (Myrold & Huss-Danell, 2003). These stands of *Lupinus* had mean rates of nitrogen miner-

FIGURE 7. Plant use of hyporheic nitrogen. Isotopic signature of willow foliage 4 weeks (FP1B) and 3 weeks (Debra's Island) after injection of ^{15}N -labelled nitrogen into ground water at a depth of 1.3 m.

alization 18-fold greater than the highest rates of mineralization recorded for the Tanana willow communities (Van Cleve *et al.*, 1993a). Other than during the flood of 2003, rates of nitrogen accumulation for membranes in our study were in the lower range of values reported from literature for ecosystems without nitrogen-fixers (Huang & Schoenau, 1997; Hanks, Greer & Sulewski, 2004). Ion exchange membrane data from 2004 did not show the same connection to predictions of advective flow, potentially due to the fact that ion exchange membranes were buried at 25 cm, while advective flow predictions were based on a 75-cm-deep rooting zone. Membranes buried 25 cm deep were saturated only during times when river discharge exceeded $1800 \text{ m}^3\cdot\text{s}^{-1}$. This occurred for relatively short periods of each summer (Figure 2). During most of the summers the ion exchange membrane treatments could effectively compare nitrogen inputs from capillary rise under these circumstances. However, relatively few of our ion exchange membranes actually represent a true comparison of nitrogen supply from saturated flow *versus* membranes cut-off from saturated flow. This factor may account for the discrepancies between our estimates of relatively large nitrogen supply from subsurface flow and the apparent accumulation of more nitrogen on membranes in the non-permeable treatment. Most of the nitrogen supplied to these ecosystems from hydrologic processes was predicted to occur during periods of high water that would not typically be considered floods and at depths greater than the top 25 cm of mineral soil often used in nitrogen cycling studies.

Although we found capillary rise to contribute a relatively small amount of nitrogen to the rooting zone, the UPFLOW program used in this study was an admittedly coarse model. As with all modeling there is a trade-off between the details of information required, the resources needed to acquire that detail, and the accuracy of the prediction. Because UPFLOW was designed and tested in temperate agricultural ecosystems, undoubtedly inherent differences exist between calibration sites and our study sites. UPFLOW's options are limited parameters that represent ecosystems such as orchards, grasslands, and crop fields. With this in mind we used UPFLOW to predict capillary rise under other vegetation scenarios. We found that capillary rise increased between 4 and 15% under the different available vegetation types when compared to barren soil. Thus, our choice of using no cover likely underestimates actual capillary rise by excluding the influence of plants.

The stable isotope experiment demonstrated that willows assimilated hyporheic nitrogen at times during the growing season. Although the relative importance of hyporheic supply to annual nitrogen budgets was difficult to assess based on the isotope data, a recent study using a similar technique estimated plant uptake of 1 g N m^{-2} over a 40-d period in a semi-arid floodplain located in the Sonoran desert (Schade *et al.*, 2005). The uptake of ^{15}N at some sites in this study but not at other sites along the Tanana River suggests that a spatial threshold exists that dictates the availability of hyporheic nitrogen to plants. Both water level and micro-topography appear to interact to create a zone where hyporheic water must flow before fine root density is high enough for plants to access significant amounts of nitrogen. Regardless, our data show that not only do significant fluxes of hyporheic nitrogen exist within the plant rooting depth along the Tanana River's riparian zone, but also the dominant plant communities are capable of readily assimilating that nitrogen. Establishing nitrogen absorption dynamics for roots at different depths in the soil profile may be critical to improving our understanding of the thresholds that regulate how and when plants can use substantial hyporheic fluxes of nutrients.

ALTERNATE SOURCES OF NITROGEN

Large inter-annual variation in water level makes it difficult to assess exactly how much nitrogen is supplied from the hyporheic zone. Microbial processes coupled with hydrologic supply of nitrogen still may not account for all nitrogen uptake by plants at these sites, suggesting that there still could be unaccounted sources of nitrogen. Sediment and litter deposited during years when substantial flooding occurs undoubtedly supply nitrogen for mineralization by microbial communities. The alkalinity of these soils also presents another possible nitrogen source in the form of stomatal uptake of atmospheric nitrogen gas. The combination of large pools of soil nitrogen and high pH could create significant fluxes of volatilized ammonia under stands of thin-leaf alder that dominate mid succession (Sharpe & Harper, 1995). This gaseous nitrogen could potentially be carried by local air currents and absorbed via the stomata of nitrogen-limited willow communities (Hutchinson *et al.*, 1972).

Finally, the period of saturated flow in the rooting zone calculated in this study may represent only a portion of the

growing season when water is flowing through the rooting zone. In late spring, surface soils are saturated with flowing water resulting from snowmelt. Freeze-thaw cycles and snowmelt are known to release and transport large amounts of nitrogen. For example, at Hubbard Brook Experimental Forest, 69% of annual stream export of nitrate occurs during snowmelt (Likens & Bormann, 1995) and freeze-thaw events were found to result in as much as a 400% increase in DON export (Fitzhugh *et al.*, 2001). Thus, the tail-end of seasonal snowmelt may coincide with the period when plant requirements of nitrogen are large.

Conclusion

Our original hypotheses were designed to test 2 possible mechanisms that could potentially explain the discrepancies found in the nitrogen budgets of these sites. Although neither of our hypotheses was completely supported by our results, there is strong evidence that subsurface hydrology directly affects nitrogen availability in our study areas. As can be expected in most complex ecosystems, there was no single mechanism of nitrogen supply that accounted for the majority of plant-available nitrogen. Saturated flow in the rooting zone and capillary rise together supply an estimated 0.35 to $0.91 \text{ g N m}^{-2} \text{ y}^{-1}$ to the rooting zone in early successional stands of the Tanana River floodplain. Combined with previously measured inputs from nitrogen mineralization and fixation studies of approximately $0.43 \text{ g N m}^{-2} \text{ y}^{-1}$, these inputs explain between 50 and 80% of annual nitrogen requirements (Table V). Although hydrologic nitrogen supply displayed large inter-annual variation, these hyporheic fluxes likely represent one of the major mechanisms of nitrogen supply in this ecosystem, equalling rates of nitrogen mineralization or potentially exceeding them, making up to twice the amount of nitrogen available. Incorporation of periodic sedimentation, nutrient fluxes following snow melt, and potential contributions from other sources is likely to be the key to closing the nitrogen budgets of early successional communities along the Tanana River. These hydrologic processes appear critical to the transition from bare silt to forests, not just by regulating water supply and the physical structure of the environment, but also by supplying a vital source of nutrients to these nitrogen-limited systems.

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