ECOSCIENCE 15 (2): 223-230 (2008)

Soil nitrogen accretion along a floodplain terrace chronosequence in northwest Alaska: Influence of the nitrogen-fixing shrub *Shepherdia canadensis*[1]

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Abstract: Nitrogen enters terrestrial ecosystems through multiple pathways during primary succession. We measured accumulation of total soil nitrogen and changes in inorganic nitrogen (N) pools across a 300-y sequence of river terraces in northwest Alaska and assessed the contribution of the nitrogen-fixing shrub *Shepherdia canadensis*. Our work compared 5 stages of floodplain succession, progressing from a sparsely vegetated silt cap to dense shrubby vegetation, balsam poplar-dominated (*Populus balsamifera*) and white spruce-dominated (*Picea glauca*) mixed forests, and old-growth white spruce forest. Total soil N (0-30 cm depth) increased throughout the age sequence, initially by 2.4 g $N \cdot m^{-2} \cdot y^{-1}$ during the first 120 y of terrace development, then by 1.6 g $N \cdot m^{-2} \cdot y^{-1}$ during the subsequent 2 centuries. Labile soil N, measured by anaerobic incubation, increased most rapidly during the first 85 y of terrace formation, then remained relatively constant during further terrace development. On recently formed terraces, *Shepherdia* shrubs enriched soil N pools several-fold compared to soil beneath *Salix* spp. shrubs or intercanopy sites. Total and labile soil N accretion was proportional to *Shepherdia* cover during the first century of terrace development, and mineral soil $\delta^{15}N$ content indicated that newly formed river terraces receive substantial N through N-fixation. About half the 600 g total $N \cdot m^{-2}$ accumulated across the river terrace chronosequence occurred during the 120 y when *S. canadensis* was dominant. Sediment deposited by periodic flooding continued to add N to terrace soils after the decline in *Shepherdia* abundance and may have contributed 25% of the total N found in the floodplain terrace soils.
Keywords: floodplain forest, natural abundance N isotopes, primary succession, riparian biogeochemistry, sedimentation, terrestrial N cycling.

Résumé : L'azote pénètre les écosystèmes terrestres par des voies multiples au cours de la succession primaire. Nous avons mesuré l'accumulation totale d'azote dans le sol et les changements du contenu en azote inorganique (N) dans une séquence sédimentaire de 300 ans de terrasses fluviales dans le nord-ouest de l'Alaska et avons évalué la contribution de l'arbuste fixateur d'azote *Shepherdia canadensis*. Nous avons comparé 5 stades successionnels d'une plaine inondable représentant une progression allant d'un couvert vaseux avec peu de végétation à une arbustaie dense, à des forêts mixtes dominées par le peuplier baumier (*Populus balsamifera*), par l'épinette blanche (*Picea glauca*) et finalement à une pessière blanche ancienne. La quantité totale de N dans le sol (0-30 cm de profondeur) augmentait tout au long de la séquence d'âges, initialement de 2,4 g $N \cdot m^{-2} \cdot y^{-1}$ par année durant les 120 premières années de développement des terrasses, ensuite de 1,6 g $N \cdot m^{-2} \cdot y^{-1}$ par année au cours des 2 siècles suivants. Le N labile du sol, mesuré par incubation anaérobique, augmentait plus rapidement durant les 85 premières années de formation des terrasses et demeurait ensuite relativement constant au cours du développement subséquent des terrasses. Sur les terrasses récentes, les arbustes de *Shepherdia* ont fait augmenté la quantité de N dans le sol de plusieurs fois en comparaison avec le sol sous les arbustes de *Salix* spp. ou entre les arbustaies. L'accroissement de la quantité de N total et labile dans le sol était proportionnel à la couverture de *Shepherdia* au cours du premier siècle de développement des terrasses et le contenu en $\delta^{15}N$ du sol minéral indiquait que les terrasses fluviales récentes reçoivent des quantités substantielles de N grâce à la fixation. Environ la moitié du total de 600 g $N \cdot m^{-2}$ s'est accumulé dans la chronoséquence des terrasses fluviales durant les 120 années où *S. canadensis* était dominant. Les sédiments déposés par les inondations périodiques ont continué d'ajouter du N aux sols des terrasses après le déclin d'abondance de *Shepherdia* et pourraient avoir fourni 25 % du N total des sols des terrasses de la plaine inondable.
Mots-clés : abondance naturelles des isotopes de N, biogéochimie riparienne, composante terrestre du cycle de N, forêt de plaine inondable, sedimentation, succession primaire.

Nomenclature: Viereck & Little, 1986.

[1]Rec. 2006-10-30; acc. 2007-09-24.
Associate Editor: Alan Yeakley.
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DOI 10.2980/15-2-3027

Introduction

Plant communities dominated by nitrogen fixing species are a common component of primary succession. Research has linked soil organic matter and nitrogen (N) accretion to symbiotic N-fixation during the initial stages of ecosystem development following glacial retreat (Cooper, 1923; Crocker & Major, 1955; Bormann & Sidle, 1990; Chapin *et al.,* 1994), mudflows (Dickson & Crocker, 1953; Sollins, Spycher & Topik, 1983), volcanic eruption (Vitousek *et al.,* 1987), and floodplain terrace formation (Van Cleve, Viereck & Dyrness, 1996; Uliassi & Ruess, 2002). Symbiotic N-fixation contributes between 1 to 16 g $N \cdot m^{-2} \cdot y^{-1}$ to early successional ecosystems dominated by N-fixers (Boring *et al.,* 1988), representing the largest input of N to many areas (Galloway *et al.,* 1995). Nitrogen fixation by *Alnus tenuifolia* ranges from 3 to 16 g $N \cdot m^{-2} \cdot y^{-1}$ during the first 3 decades after river terrace formation in interior Alaska (Klingensmith & Van Cleve, 1993; Uliassi & Ruess, 2002). The net accumulation of N in mineral soil is 2–5 $g \cdot m^{-2} \cdot y^{-1}$ during that period (Walker, 1989; Kaye, Binkley & Rhoades, 2003). At Glacier Bay in southeastern Alaska, N-fixers dominate 2 distinct phases that span much of the first century following deglaciation (Chapin *et al.,* 1994). Soil N increases by 0.1 to 0.3 $g \cdot m^{-2} \cdot y^{-1}$ beneath *Dryas drummondii* Richards, a mat-forming, N-fixing pioneer for 35–45 y (Crocker & Major, 1955; Lawrence *et al.,* 1967; Chapin *et al.,* 1994), before *A. sinuata* gains dominance and accelerates the rate of soil N accretion. Soil changes induced by N-fixers have been shown to enhance growth of subsequent vegetation communities in successional landscapes (Chapin *et al.,* 1994).

The abundance of N-fixers typically declines after several decades of ecosystem development (Boring *et al.,* 1988). N-fixers may become less competitive due to light limitations following canopy closure and the high carbon cost of nodulation (Bormann & Gordon, 1984; Rastetter *et al.,* 2001; Vitousek *et al.,* 2002). Changes in soil nutrients during ecosystem development may also reduce competitive advantages associated with N-fixation. For example, N-fixation by *A. rubra*, as indexed by nodulation potential, declined with increasing soil nitrate content and lower pH in Oregon Coast Range sites (Martin, Posavatz & Myrold, 2003). Similarly, along the Tanana River in central Alaska, soil P limitation at later stages of terrace development decreases N-fixation by alder (Uliassi & Ruess, 2002).

Soil nitrogen pools continue to aggrade for centuries or millennia during the course of primary succession (Sollins, Spycher & Topik, 1983; Van Cleve *et al.,* 1993; Chapin *et al.,* 1994; Crews *et al.,* 1995; Kaye, Binkley & Rhoades, 2003; Wardle, Walker & Bardgett, 2004), long after the decline in abundance of N-fixing plants. Inorganic soil N pools build rapidly and then plateau in the early stages of succession, but growth of stable organic N pools continues much longer (Kaye, Binkley & Rhoades, 2003). This pattern indicates that most N inputs are sequestered in resistant soil pools that release N slowly. At long time scales, soil weathering alters the mineralogy and capacity of the clay exchange complex to stabilize organic matter inputs (Sollins, Spycher & Topik, 1983; Lilienfein *et al.,* 2004) and supply soil moisture and nutrients. In the absence of N-fixers, other N sources, such as periodic sediment deposition onto floodplain terraces, atmospheric deposition, and plant uptake from groundwater, supplement soil N capital (Walker, 1989; Viereck, Dyrness & Foote, 1993; Schade *et al.,* 2002; Adair, Binkley & Andersen, 2004).

Near the northern limit of the boreal forest in northwest Alaska, *Shepherdia canadensis* is the most abundant N-fixing shrub (Binkley *et al.,* 1997) on floodplain terraces. In contrast to much of interior and coastal Alaska, *Alder* spp. rarely form thickets (Viereck & Little, 1986) but are found scattered across floodplain and upland habitats (Rhoades *et al.,* 2001). Though *S. canadensis* is distributed from the Alaskan Arctic south to Arizona and New Mexico and east across northern Canada to Newfoundland (Hultén, 1968; Vierek & Little, 1986), little is known about its influence on soil N pools (Hendrickson & Burgess, 1989; Kohls *et al.,* 2003; Batzli *et al.,* 2004) or its role in ecosystem development. The objective of this study was to assess the contribution of *Shepherdia* to soil N pools along a 300-y chronosequence of floodplain terraces. We hypothesized that rates of N accretion would be greatest during the period of *Shepherdia* dominance of the shrub community, then decline during later stages of terrace ecosystem development.

Methods

Site description

Research was conducted along the Kugururok River (68° 4' N, 161° 50' W), a tributary of the Noatak River. The Kugururok drains southward from the DeLong Mountains, which form the westernmost portion of the Brooks Range. The study site is situated 750 km west-northwest of the Tanana River floodplain succession sites at the Bonanza Creek Long-Term Ecological Research site (Viereck, Dyrness & Foote, 1993; Chapin *et al.,* 2006) and twice that distance from Glacier Bay in southeast Alaska (Crocker & Major, 1955; Chapin *et al.,* 1994). Annual mean air temperature and precipitation at Kotzebue, Alaska, a coastal village 175 km south of our Kugururok site, are –5.7 °C and 240 mm; growing season (May to September) air temperature averages 7.2 °C (NOAA, 2006). Summer daytime mineral soil temperature (10 cm) averages 7.3 °C ($n = 85$) beneath mature spruce forest at the Kugururok site (D. Valentine, University of Alaska, unpubl. data). The study site is located within 10 km of the northern limit of white spruce (*Picea glauca*) in this part of the Brooks Range (Edwards *et al.,* 2003).

We studied 5 stages of floodplain succession on terraces adjacent to a 6-km section of the Kugururok River. The terraces were formed by silt deposition during flood events. Silt was deposited in 5- to 20-cm increments on river cobbles that currently stand 2 to 4 m above summer base flow (C. Rhoades, pers. observ.). The silt and clay content and moss, organic layer, and mineral soil thickness all increase with terrace age to their maximum on the oldest terrace stage (Table I). The age of the 5 terraces we studied was estimated from stem cross sections taken from a subset of the dominant species ($n = 20$ except where noted; see Binkley *et al.,* 1997 for details).

The youngest terrace (open shrub; age 25 y) is covered with a thin layer of soil and scattered patches of

TABLE I. Shrub, tree seedling (< 1 cm diameter at 1.4 m height) and ground cover, soil depth (n = 20) and texture (0-30 cm depth) on Kugururok River floodplain terrace chronosequence, Noatak National Preserve, Alaska. Cover estimates were derived by point intercept at 100 points along 5 transects per terrace stage.

Terrace stage/ Age	Vegetative cover (%)									Horizon depth (cm)			Soil texture* (%)		
	Shepherdia canadensis	*Salix* spp.	Misc. shrubs**	*Populus balsamifera*	*Picea glauca*	Herb	Moss	Litter	Bare ground	Moss	Total organic	Total mineral	Clay	Silt	Sand
Open shrub/ 25 y	18.8	27.5	0.0	25.0	0.0	2.5	0.0	0.0	26.2	0.0	0.0	15.0	6.4	13.7	79.9
Willow/ 50 y	21.2	57.5	0.0	6.3	0.0	8.8	1.3	5.0	0.0	0.9	2.1	21.2	8.2	22.8	69.0
Poplar/ 85 y	40.0	33.8	0.0	10.0	1.3	3.8	1.3	10.0	0.0	0.2	2.8	26.4	4.7	11.3	84.0
Spruce-poplar/ 120 y	48.8	17.5	0.0	3.8	1.3	7.5	17.5	3.8	0.0	2.1	7.6	25.1	7.8	37.5	54.7
Old spruce/ 300 y	0.6	31.3	6.3	0.0	3.1	7.5	43.1	8.1	0.0	3.1	7.1	37.7	15.8	44.8	39.4

* Texture analysis of 15 cm silt cap.

** Shrubs include: *Betula nana*, *Vaccinium vitis-idaea*, *Vaciumim uliginosum*.

shrubs (Table I). *Shepherdia* and *Salix* spp. shrubs (chiefly *S. alaxensis* and *S. glauca*) and balsam poplar (*Populus balsamifera*) saplings cover equal areas of the open shrub terrace. Mixed willow, *Shepherdia*, and balsam poplar thickets vegetate the 50-y-old Willow stage. The third stage (Poplar; age 85 y) supports a mixture of poplar and white spruce; live poplar trees represent 70% of the canopy. Poplar and spruce trees average 9 and 13 cm diameter (at 1.4 m height) and are about 6 m tall. *Shepherdia* forms a dense understory. At 120 y, white spruce has begun to overtop the poplars; spruce stems represent 60% of the spruce–poplar stage. Forty percent of the poplars are dead. *Shepherdia* cover is slightly higher than the previous stage, but its biomass is lower (Binkley *et al.,* 1997). The most mature terrace stage supports 200-y-old white spruce (old spruce stage). Tree rings from 2 downed logs, both larger than the average stem diameter for the current stand, suggest that an early stand became established at least 100 y prior to inception of the existing stand (*i.e.,* total terrace age ≥ 300 y). *Shepherdia* and other shrubs are scarce beneath the closed-canopy spruce stand.

SAMPLING AND ANALYSIS

Mineral soil samples were collected at uniform intervals along 3 parallel transects in each of the 5 terrace ecosystems (n = 20 sample points per terrace stage). Depth of moss and organic horizons were measured prior to collecting mineral soil samples, after which these layers were removed. Mineral soil was sampled to 30 cm with a slide hammer corer (5 cm diameter), and cores were divided into 10-cm depth increments, air-dried, and passed through a 2-mm sieve to remove coarse fragments and roots.

Shrub, tree seedling (< 1 cm at 1.4 m height), and ground cover was estimated using a point intercept method along 5 transects per terrace stage. Cover was differentiated among shrub and tree species and ground cover type for 100 points located at 5-m intervals.

To compare the influence of N_2-fixing and non-N_2-fixing shrubs on terrace pools and availability of soil N, a second set of mineral soil samples (0–10 cm) was collected from beneath canopies of individual *Shepherdia* and *Salix* spp. and from intercanopy open sites (n = 5 per type per terrace). Subcanopy samples were collected at the midpoint between the main shrub stem and the canopy perimeter. Open site samples were collected > 3 m from the nearest shrub, in areas without shrub litter. Because of the scarcity of *Shepherdia* in the understory of the old spruce stage, shrub comparisons were not possible for that terrace stage. *Salix* species composition varied among terraces, so it was not possible to compare individual *Salix* species.

The concentrations of total N and C of terrace (n = 20 per terrace stage per depth) and shrub soil (n = 5 per canopy location per terrace stage) were determined by dry combustion of ground samples using a LECO 1000 CHN analyzer (LECO Corporation, St. Joseph, Michigan, USA). To assess patterns of N availability across the terrace sequence, we measured instantaneously available pools of inorganic N (extractable NO_3^- and NH_4^+) as well as an anaerobic index of N availability (Waring & Bremner, 1964; Bundy & Meisinger, 1994). The waterlogged incubation measures the amount of N mineralized from dead microbial biomass. For each soil sample, an air-dried initial sample was extracted with 2 M KCl, filtered and analyzed for NO_3^- and NH_4^+ by Latchat spectrophotometry (Latchat Instruments, Milwaukee, Wisconsin, USA). A second 10-g subsample was incubated in 50 mL of de-ionized water for 7 d at 40 °C. After incubating, 50 mL of 4 M KCl was added and samples were extracted, filtered, and analyzed for NH_4^+ as above. Net production of NH_4^+ was calculated as the difference between initial and incubated subsamples and reported per unit oven-dry soil and per unit total soil N.

Total and extractable N pools were calculated for each soil depth by combining the concentration data with bulk density estimated from intact cores. Soil pH was measured in de-ionized water (1:1 air-dry soil to solution) on terrace samples (n = 20 for each depth). Soil pH readings were made while stirring samples after shaking soil solutions for 1 h on a reciprocating shaker table (Thomas, 1996).

Natural abundance $\delta^{15}N$ content of mineral soil (0-10 cm) from shrub canopy and intercanopy sites (n = 5 per

canopy location per terrace stage) and shrub foliage were analyzed on a VG Isochrom continuous flow isotope ratio mass spectrometer (VG, Middlewich, UK) coupled to a Carlo Erba NA 1500 elemental analyzer. Five current-year foliar samples were analyzed for each shrub species. The ^{15}N is expressed as $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000$ [‰], using atmospheric N_2 as a standard (Shearer & Kohl, 1989). The standard deviation of 30 replicate samples was 0.2‰.

To test the relation between terrace age and soil conditions, we used least-squares linear and non-linear regression. We also compared soil variables between the 5 terrace ecosystems using analysis of variance (ANOVA) and Tukey's least significant difference (LSD) pair-wise means comparison tests (SPSS Ver. 10.1.3, SPSS Inc., Chicago, Illinois, USA). Statistical significance is assigned for *F*-test *P* values less than $\alpha = 0.05$. Levene's statistic was used as a test of homogeneity of variance, and data were log-transformed when needed. Log transformation produced homogeneous variances. Shrub effects (shrub canopies *versus* open intercanopies) and species differences (*Shepherdia versus Salix* spp.) were compared within terrace ecosystems using ANOVA.

Results

Total soil N accumulated steadily across the terrace sequence from 49 g N·m^{-2} in the surface 10 cm of the open shrub terrace to 219 and 596 g N·m^{-2} for the upper 10 cm and the combined 30 cm profile sampled beneath old spruce (Figure 1; Table II). Across the 120-y sequence of terrace development from open shrub to mixed spruce–poplar, total soil N and C stocks increased by 2.8 and 35 g·m^{-2}·y^{-1} for the 30-cm sample depth. Nitrogen and carbon accretion slowed to 1.6 g·m^{-2}·y^{-1} and 23 g·m^{-2}·y^{-1} during the subsquent 180 y (Table II). Total N was distributed nearly evenly throughout the 30-cm sample profile; averaged across the 5 terrace ages, the upper 10 cm contained 41% of the entire total N stock, compared to 32% in the 20 to 30 cm depth.

Extractable N ($NO_3^- + NH_4^+$) increased from 0.7 g·m^{-2} on the open shrub terrace to 3.5 g·m^{-2} beneath old spruce in the 0–10 cm depth (Table II). Nitrate represented 70 to 90% of extractable soil N. Extractable NH_4^+ increased linearly across the age sequence ($y = 0.05 + 0.007$*Age; $r^2 = 0.77$). In the upper 10-cm soil layer, nitrate was 3-fold higher in the old spruce terrace compared to the other terraces (pair-wise comparisons $P < 0.001$). For the poplar terrace, in the upper 10 cm soil, nitrate was marginally lower ($P \leq 0.1$) than either the willow or spruce–poplar stages. In contrast to the uniform vertical distribution of total N, extractable NO_3^- and NH_4^+ (54 and 62%) were concentrated in the upper 10 cm of the 30-cm mineral soil profile.

The mineral soil C:N ratio averaged 13.9 overall and had no clear relation to terrace age (Table II). The spruce–poplar terrace had the lowest soil C:N for each soil depth. The poplar terrace had the highest C:N ratio at all depths, with the exception of the surface layer of the open shrub terrace. Soil C:N changed little with depth in the early terrace stages. In contrast, soil C:N declined with depth in the spruce-dominated terraces. The anaerobic index of soil N availability increased with terrace age during the early stages of terrace development for the upper 10 cm, reached a maximum in the poplar and spruce–poplar stages, then declined in the old spruce stage (Table II). As a percent of the total soil N pool, mineral N production was also highest beneath the poplar (2.5%) in the upper soil layer, declining toward younger and older terraces.

The pH of the upper 10 cm of mineral soil declined linearly from 8.1 to 6.6 across the terrace age sequence (Table II). Soil acidity increased 0.45 pH units during the first century of terrace development, then by 1 pH unit during the subsequent 2 centuries; surface soil and composite profile pH of the old spruce terrace were significantly higher (pair-wise comparisons: $P < 0.001$) than all other terraces stages. Soil pH increased with depth in all stages, but upper and lower soils differed more in the older terraces. On the willow and poplar–spruce terraces, pH of the top 10 cm of mineral soil and the 20-30 cm depth differed by 0.1 pH units, compared to a 1 pH unit difference on the old spruce terrace.

Overall, extractable and total soil N pools and the N availability index were greater beneath shrub canopies relative to intercanopy sites, though the effects of both *Shepherdia* and *Salix* spp. varied among terrace stages (Table III). The most pronounced *Shepherdia* effect occurred during the open shrub stage, where all soil N parameters were significantly higher beneath *Shepherdia* canopies compared to intercanopy sites. Averaged across all terrace ages, extractable NO_3^- and NH_4^+ and total N were 78, 44, and 25% higher beneath shrub canopies compared to inter-

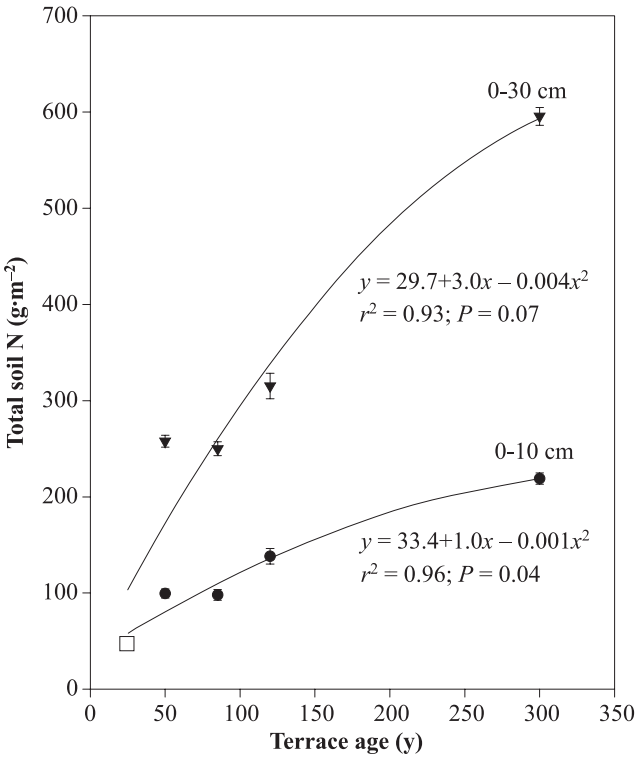

FIGURE 1. Soil N in Kugururok River terraces (0-10 cm and 0-30 cm depths) and the non-linear relations for mean total soil N and terrace age. Bars (1 SE of terrace mean; $n = 20$) do not contribute to goodness of fit estimates. Both models incorporate the hollow symbol denoting the open shrub terrace.

TABLE II. Soil C and N pools, N availability and pH (n = 20; means with SE in parentheses). Whole profile data (0-30 cm) report the sum of total C and N pools and the mean of all other variables. Least squares linear relations are between soil properties and terrace age.

Terrace stage	Soil depth cm	Total C g·m^{-2}	Total N g·m^{-2}	N Availability index g N·m^{-2}·7d^{-1}	Extractable soil N NH_4^+ g·m^{-2}	Extractable soil N NO_3^- g·m^{-2}	Soil C:N	Soil pH
Open Shrub	0-10	729.32 (39.2)	48.9 (3.9)	–0.02 (0.01)	0.01 (0.01)	0.72 (0.20)	14.9 (0.57)	8.1 (0.07)
Willow	0-10	1387.13 (60.9)	99.4 (4.7)	1.89 (0.17)	0.09 (0.01)	0.97 (0.19)	14.0 (0.20)	7.9 (0.05)
	10-20	1126.91 (137.5)	79.3 (8.9)	0.58 (0.11)	0.08 (0.02)	0.34 (0.08)	14.2 (0.27)	8.0 (0.06)
	20-30	1141.58 (78.4)	79.0 (5.1)	0.50 (0.15)	0.08 (0.01)	0.30 (0.07)	14.4 (0.24)	8.0 (0.10)
	0-30	3655.62 (92.3)	257.7 (6.2)	0.99 (0.14)	0.08 (0.01)	0.53 (0.11)	14.2 (0.24)	8.0 (0.07)
Poplar	0-10	1448.27 (88.4)	98.1 (5.6)	2.48 (0.30)	0.16 (0.02)	0.36 (0.08)	14.8 (0.29)	7.8 (0.05)
	10-20	1037.17 (116.1)	70.4 (7.7)	0.79 (0.22)	0.05 (0.01)	0.23 (0.07)	14.7 (0.31)	7.9 (0.04)
	20-30	1302.65 (146.5)	81.4 (8.4)	0.52 (0.11)	0.05 (0.01)	0.30 (0.10)	16.0 (0.60)	7.9 (0.04)
	0-30	3788.09 (117.0)	249.9 (7.2)	1.26 (0.21)	0.09 (0.01)	0.30 (0.08)	15.2 (0.40)	7.9 (0.04)
Spruce - Poplar	0-10	1861.0 (116.1)	138.2 (8.0)	2.00 (0.18)	0.16 (0.03)	0.90 (0.28)	13.5 (0.31)	7.7 (0.06)
	10-20	1174.0 (134.8)	91.5 (12.3)	0.65 (0.14)	0.04 (0.01)	0.41 (0.10)	12.8 (0.43)	7.9 (0.05)
	20-30	999.87 (177.3)	85.5 (19.7)	0.21 (0.05)	0.02 (0.01)	0.23 (0.05)	11.7 (0.65)	7.9 (0.07)
	0-30	4034.77 (142.7)	315.2 (13.3)	0.95 (0.12)	0.07 (0.02)	0.51 (0.14)	12.7 (0.46)	7.8 (0.06)
Old Spruce	0-10	3210.53 (114.7)	219.0 (5.9)	1.51 (0.09)	0.24 (0.07)	3.27 (0.20)	14.6 (0.17)	6.6 (0.09)
	10-20	2846.82 (128.3)	212.2 (8.6)	1.05 (0.10)	0.08 (0.02)	1.52 (0.10)	13.4 (0.17)	7.3 (0.10)
	20-30	2091.37 (180.5)	164.3 (13.5)	0.52 (0.07)	0.04 (0.01)	0.86 (0.13)	12.7 (0.16)	7.6 (0.11)
	0-30	8148.72 (141.2)	595.5 (9.3)	1.03 (0.09)	0.12 (0.03)	1.88 (0.14)	13.6 (0.17)	7.2 (0.10)
Linear Trends	0-10	P = 0.003	0.006	NS	0.051	0.026	NS	0.001
		r^2 = 0.97	0.94		0.77	0.85		0.99
	0-30	P = 0.015	0.012	NS	NS	NS	NS	0.001
		r^2 = 0.89	0.91					0.99

TABLE III. Shrub effects on mineral soil N pools and N availability index (mean and SE for 0-10 cm depth; n = 5). Within a terrace stage, means followed by a similar letter are not different (α = 0.05).

Terrace Stage	Extractable N ($NH_4^+ + NO_3^-$) (g·m^{-2})			Total N (g·m^{-2})			N Availability index (g N·m^{-2}·7d^{-1})		
	Open intercanopy	*Shepherdia* canopy	*Salix* canopy	Open intercanopy	*Shepherdia* canopy	*Salix* canopy	Open intercanopy	*Shepherdia* canopy	*Salix* canopy
Open shrub	0.73 (0.16)^{b}	8.07 (1.29)^{a}	1.69 (0.60)^{b}	48.9 (3.9)^{b}	113.3 (11.0)^{a}	70.6 (6.7)^{b}	–0.01 (0.01)^{b}	1.17 (0.37)^{a}	0.07 (0.27)^{ab}
Willow	1.24 (0.31)^{a}	0.79 (0.27)^{a}	1.23 (0.44)^{a}	79.4 (9.9)^{a}	77.9 (6.9)^{a}	94.0 (7.2)^{a}	1.39 (0.30)^{a}	1.69 (0.41)^{a}	2.03 (0.28)^{a}
Poplar	2.55 (0.36)^{b}	3.75 (0.40)^{a}	3.00 (0.34)^{ab}	87.0 (10.4)^{a}	107.4 (15.9)^{a}	111.7 (7.0)^{a}	2.00 (0.56)^{a}	2.04 (0.29)^{a}	2.50 (0.82)^{a}
Spruce - Poplar	1.41 (0.37)^{ab}	0.51 (0.26)^{b}	1.93 (0.65)^{a}	126.4 (11.9)^{a}	145.6 (8.9)^{a}	131.2 (7.5)^{a}	2.65 (0.39)^{b}	3.76 (0.33)^{a}	2.37 (0.35)^{b}

canopy sites (pair-wise comparisons: $P < 0.06$; $P < 0.10$, $P < 0.01$, respectively). On average, pH was 0.3 units higher beneath *Shepherdia* compared to open soil (data not shown). On both the open shrub and spruce–poplar terraces, soil beneath *Shepherdia* canopies was 0.6 pH units lower than adjacent intercanopy soil. In contrast, *Salix* had no effect on soil pH at any terrace stage.

The isotopic composition of *Shepherdia* foliage ($\delta^{15}N$ of –0.4‰; n = 5; data not shown) suggests that the shrub species accesses atmospheric N through symbiotic fixation. Leaf tissue $\delta^{15}N$ of *Shepherdia* growing in deglaciated portions of Glacier Bay also indicated that the shrub relied little on soil N pools (Kohls *et al.,* 2003). In contrast, the isotopic composition of Kugururok willow foliage (–5.5‰) reflects either a soil N source that is depleted relative to atmospheric N or fractionation within the plant. Soil $\delta^{15}N$ (Figure 2) was similar between intercanopy and *Shepherdia* canopy locations averaged across the Kugururok terrace sequence (–0.7‰; n = 20 per location). In contrast, *Salix* canopy soils were significantly depleted in ^{15}N relative to intercanopy and *Shepherdia* canopy locations ($P < 0.001$).

Discussion

SOIL N ACCRETION ON FLOODPLAIN TERRACES

The accumulation of total mineral soil N and increase in available N progressed most rapidly during the initial decades of development on the Kugururok terraces (Table II). The inventory of total soil N doubled during the 25-y interval between the open shrub and willow stages, an increase of 2.0 g N·m^{-2}·y^{-1} for the 0-10 cm depth (Figure 1). Total soil N continued to increase across the Kugururok terrace sequence, although subsequent doubling of the N inventory in the upper 10 and 30 cm required an additional 200 y. The pattern and rates of N accretion on the Kugururok were consistent with studies of N accretion on Tanana River terraces in central Alaska (Walker, 1989; Van Cleve *et al.,* 1993; Kaye, Binkley & Rhoades, 2003), where the highest rates of N accretion occurred within 30 to 50 y of terrace formation and N increment continued for several centuries. Similarly, floodplain terraces along 2 rivers in northwestern Colorado added total soil N at 7 g·m^{-2}y^{-1} during the first 80 y of floodplain development and then

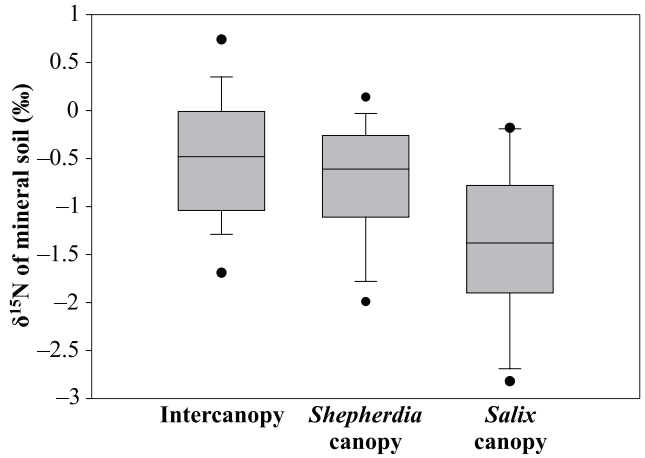

FIGURE 2. Soil $\delta^{15}N$ of intercanopy and *Shepherdia* and *Salix* spp. canopy sites (0–10 cm; $n = 20$ per location). Plots indicate median and 25, 75, 10, and 90 percentiles with boxes and error bars; dots denote 5th and 95th percentiles for the 4 initial terrace stages along the Kugururok River when *Shepherdia* was common.

slowed to 3 g $N \cdot m^{-2} \cdot y^{-1}$ for the next 90 y (Adair, Binkley & Andersen, 2004).

On the Kugururok terraces, plant-available N increased rapidly during the first 85 y of development and then reached a plateau (Table II). A previous study of the same Kugururok River terraces (excluding the open shrub stage; Binkley *et al.,* 1997) found that N availability as assessed by ion exchange resins increased 3-fold between the willow and poplar stages and remained unchanged throughout later spruce-dominated stages. Similarly, on the Tanana River, labile N increased annually by 0.2 to 0.6 g $\cdot m^{-2}$ during the first 50 y of terrace formation but was unchanged during the later terrace phases (Kaye, Binkley & Rhoades, 2003). The continued accumulation of total soil N after the plateau of labile N pools suggests that the majority of soil N is retained in stable N forms that are unavailable for either microbial metabolism or plant uptake (Kaye, Binkley & Rhoades, 2003).

CONTROLS ON N ACCRETION

Of the 600 g total $N \cdot m^{-2}$ that accumulated during 300 y of river terrace development, slightly over half occurred during the initial 120 y when *Shepherdia canadensis* was a dominant shrub (Tables I, II). *Shepherdia* cover increased steadily during the early stages of succession, attained its maximum (~50% cover) during the spruce–poplar stage (120 y), and was rare in the understory of the old spruce stage. Total soil N accretion was well correlated to *Shepherdia* cover ($r^2 = 0.66$) during the initial century of terrace succession, and the highest anaerobic N mineralization occurred where *Shepherdia* cover was highest. During the open shrub stage, greater soil N pools and N availability beneath *Shepherdia* canopies relative to intercanopy and *Salix* canopy soil suggest that the N_2-fixing shrub may facilitate soil development during the initial stages of floodplain succession (Table II). Discrete zones of soil N enrichment were not evident during latter stages of terrace development, when both total shrub cover and intercanopy soil N pools were higher, though the soil legacy of *Shepherdia* most likely persisted. Similarly, along another tributary of the Noatak River, isolated alder shrubs (*A. crispa*) increased N availability to the greatest degree on low N floodplain terraces as compared to adjacent hillslope and tundra landscapes where intercanopy soil N was higher (Rhoades *et al.,* 2001).

Soil N continued to increase for more than a century following the decline of *Shepherdia* from Kugururok River terraces. Nitrogen capital has been shown to grow for 500 to 1000 y during floodplain primary succession (Van Cleve, Viereck & Dyrness, 1996; Kaye, Binkley & Rhoades, 2003), long after the decline in the abundance of N-fixers. Much as they do on the Tanana River (Walker, 1989), sediments deposited by periodic flooding may supplement soil N levels throughout floodplain succession on the Kugururok River. Silt content and the depth of the silt cap both increase along the Kugururok age sequence (Table I). We observed episodic silt deposition on the surface of Kugururok terraces and banded silt stratigraphy in terrace soil profiles.

Silt content and depth explain much of the variation in total soil N across the 300-y terrace series (silt content: $r^2 = 0.81$; $P = 0.04$; silt cap depth: $r^2 = 0.91$; $P = 0.01$), and sedimentation is a likely source of N to Kugururok terraces. The total N contained in intercanopy soils of the 25-y-old open shrub stage provides our best estimate of the N deposited with Kugururok flood sediments (49 g $\cdot m^{-2}$ to the top 10 cm). Initial sediment deposited during the formation of Tanana River terraces introduces a comparable amount of N (40 g total $N \cdot m^{-2}$; Walker, 1989). If the sediment added to Kugururok terraces contributes a uniform amount of N with depth (*e.g.,* ~ 5 g $N \cdot m^{-2} \cdot cm^{-1}$ of sediment), the upper 30 cm of mineral soil would contain 150 g $N \cdot m^{-2}$ of sediment-derived N. This N source could account for an annual accumulation of 0.5 g $\cdot m^{-2}$ during the 300 y terrace age sequence, and represent 25% of the soil total N inventory of the old spruce terrace.

Nitrogen accumulated through sediment deposition represents a source of N to Kugururok floodplain terraces that likely exceeds precipitation N inputs to the region by more than an order of magnitude (0.03 g $\cdot m^{-2} \cdot y^{-1}$ in the Noatak National Preserve [R. Stottlemyer, unpubl. data] and Poker Creek, Fairbanks, Alaska [NADP, 2006]). Nitrogen input by sedimentation has been shown to contribute 1-5 g $\cdot m^{-2}$ in individual flood events on Dutch floodplains (Olde Venterink *et al.,* 2006) and 3.5 to 134 g $\cdot m^{-2}$ annually to floodplains on the Atlantic Coastal Plain of North America (Noe & Hupp, 2005). Floodwater sediments have been credited with contributing 70 to 100% of the N accumulated on terraces along the Yampa and Green Rivers in northwestern Colorado (Adair, Binkley & Andersen, 2004). Sedimentation may also contribute to greater stabilization of organic matter and N inputs to terrace soils. For example, in floodplain forests of southeastern North America, organic matter and N turnover rates declined sharply when annual sedimentation inputs exceeded 25 mm (Lockaby *et al.,* 2005).

On the Kugururok River terraces, the influence of N-fixing shrubs was substantial. In agreement with our expectations, rates of N accretion were greatest during the period when *Shepherdia* dominated the shrub community, then declined during later stages of terrace ecosystem develop-

ment. About half the 600 g total $N \cdot m^{-2}$ accumulated across the river terrace chronosequence aggraded during the 120 y when *Shepherdia* was most abundant. Moss cover increased with terrace age on the Kugururok terraces, and N-fixation associated with the cyanobacterium *Nostoc* sp. may have contributed N (DeLuca *et al.,* 2002) in the absence of *Shepherdia*. During later stages of succession, periodic sedimentation appears to become a major pathway for N inputs, altering both total N capital and the capacity of terrace soils to cycle and retain soil N.

Acknowledgements

Thanks to L. Dalle-Molle of the National Park Service and J. Rood and J. St. Germaine of Northwestern Aviation for aviation support. Thanks to R. King for statistical direction, D. Reuss for mass spectrometry assistance, and H. Steltzer and G. Kelly for assistance in the field. Comments from A. Yeakley, R. Ruess, and an anonymous reviewer greatly improved the manuscript. This work was funded by EPA and USGS grants to R. Stottlemyer.

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