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Stable soil nitrogen accumulation and flexible organic matter stoichiometry during primary floodplain succession

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Abstract. Large increases in nitrogen (N) inputs to terrestrial ecosystems typically have small effects on immediate N outputs because most N is sequestered in soil organic matter. We hypothesized that soil organic N storage and the asynchrony between N inputs and outputs result from rapid accumulation of N in stable soil organic pools. We used a successional sequence on floodplains of the Tanana River near Fairbanks, Alaska to assess rates of stable N accumulation in soils ranging from 1 to 500+ years old. One-year laboratory incubations with repeated leaching separated total soil N into labile (defined as inorganic N leached) and stable (defined as total minus labile N) pools. Stable N pools increased faster ($\sim$2 g N m^{-2} yr^{-1}) than labile N ($\sim$0.4 g N m^{-2} yr^{-1}) pools during the first 50 years of primary succession; labile N then plateaued while stable and total N continued to increase. Soil C pools showed similar trends, and stable N was correlated with stable C (r^2 = 0.95). From 84 to 95 % of soil N was stable during our incubations. Over successional time, the labile N pool declined as a proportion of total N, but remained large on an aerial basis (up to 38 g N m^{-2}). The stoichiometry of stable soil N changed over successional time; C:N ratios increased from 10 to 22 over 275 years (r^2 = 0.69). A laboratory ^{15}N addition experiment showed that soils had the capacity to retain much more N than accumulated naturally during succession. Our results suggest that most soil N is retained in a stable organic pool that can accumulate rapidly but is not readily accessible to microbial mineralization. Because stable soil organic matter and total ecosystem organic matter have flexible stoichiometry, net ecosystem production may be a poor predictor of N retention on annual time scales.

Introduction

The accumulation of nitrogen (N) during primary succession has become paradigmatic in forest ecosystem ecology. During succession on floodplains, ecosystem N content increases rapidly during the first 50 to 100 years and then plateaus, or increases at a slower rate, over the next several centuries (Van Cleve et al. (1993a) and Boggs and Weaver (1994), Schwendenmann (2000), Adair (2001); C Rhoades, D Binkley and R Stottlemyer, unpublished data). On other substrates, the rates and timing of N accrual vary but intermediate and late successional ecosystems always

contain more N than the youngest ecosystems (deglaciation, Crocker and Major (1955); mudflows, Dickenson and Crocker (1953); sand dunes, Lichter (1998); volcanic islands, Crews et al. (1995)). Implications of N accumulation for long-term nutrient availability, species composition, and primary productivity have been studied extensively (Van Cleve et al. 1993a Chapin et al. 1994 Vitousek and Farrington 1997). The pattern may also have implications for current "N saturation" research (Agren and Bosatta 1988 Johnson 1992 Aber et al. 1998) if the rate, timing, or magnitude of N accumulation during succession reflects the capacity of ecosystems to store new N inputs.

The conventional theory relating N retention capacity to ecosystem age suggests that because inorganic N inputs are stored in organic pools, N should accumulate most rapidly when organic matter is accumulating rapidly (high net ecosystem production, NEP; Vitousek and Reiners (1975)). While the mass balance aspect of this theory (storage = inputs-outputs) must be true, some field data are inconsistent with the idea that NEP controls ecosystem N retention. Very old ecosystems (presumably, NEP = 0) in Chile efficiently retain inorganic ^{15}N (Perakis and Hedin 2001), while desorption processes unrelated to current NEP enable small, persistant losses of dissolved organic N (Perakis and Hedin 2002). In ecosystems of all ages, experimentally increasing N inputs by 10 times ambient deposition causes only small changes in N outputs on annual or decadal time scales (Ring 1995 Aber et al. 1998 Bredemeier et al. 1998 Binkley et al. 1999).

How do forests with a wide range of NEP consistently retain more than 70% of N inputs (Johnson et al. 1993 Dise and Wright 1995 Goodale et al. 2000)? How do ecosystems foster such asynchrony between N inputs and outputs? A theory parsimonious with both of these patterns is that most N inputs are rapidly incorporated into a stable soil organic pool and the rate of release from this pool controls N losses. Soil organic matter contains more than 90% of ecosystem N in many forests (Cole and Rapp 1981). This pool is a large sink for N fertilizer (Preston and Mead 1994a Nadelhoffer et al. 1999) and it may store N in stable pools that slowly release N long after episodic N inputs occur. Microbial turnover (Stark and Hart 1997) or abiotic reactions (Johnson et al. 2000 Dail et al. 2001) could incorporate inorganic N into stable organic pools even when NEP is zero.

This paper examines labile and stable soil N accumulation in a primary successional sequence on floodplains of the Tanana River in Alaska (Viereck et al. 1993a). Primary succession begins on silt and sand bars deposited by recent floods and repeated floods deposit more sediment, raising the terraces more than a meter within 200 years. Over this period, succession proceeds through shrub, deciduous forest, and coniferous forest ecosystems. These changes in plant species composition are thought to play a major role in soil development; most notably, litter from N-fixing alder trees increases soil N pools early in succession (Walker 1989). Late in succession, white spruce dominates, but effects of spruce litter on N cycling remain unclear (Binkley et al. 1997). While forest floor net N mineralization rates are lower in white spruce forests than in younger ecosystems, mineral soil net N mineralization rates do not decline (Van Cleve et al. 1993b), and soil solution inorganic N

concentrations are higher under spruce (Yarie et al. 1993), suggesting either greater N supply or lower demand.

Soils collected from the chronosequence were incubated in the laboratory for one year with repeated leaching to separate total soil N into labile (defined as leached inorganic N) and stable (defined as total minus labile N) pools. Our main objectives were to measure: 1) the amount, rate, and temporal pattern of labile and stable N accumulation during succession, and 2) whether the capacity of soils to retain ^{15}N differed from actual, observed rates of N accumulation. We were also interested in the role of white spruce trees in determining the balance between labile and stable N pools, so we incubated soils collected directly beneath white spruce canopies. These experiments suggested that stable soil organic matter had flexible stoichiometry (C:N) during succession, so we conclude with a theoretical analysis of the implications of stoichiometric changes for ecosystem N retention.

Study site and methods

The floodplain ecosystems

The soils were collected from the Bonanza Creek Long-Term Ecological Research site near Fairbanks, Alaska. Mean annual temperature on the floodplains is −3.3 °C but can range from −50 to 35 °C. Mean annual precipitation is 270 mm (Viereck et al. 1993b). Atmospheric N deposition is low at this site (wet N deposition < 0.05 g N m^{-2} yr^{-1}; NADP (2000)), especially compared to N-fixation by alder (~ 15 g N m^{-2} yr^{-1} early in succession; Klingensmith and Van Cleve (1993a)). The soils and vegetation of the site have been described in detail elsewhere (Viereck et al. 1993a). Briefly, the Tanana is a glacier-fed river that floods annually in spring and summer following snowmelt. When floods deposit sediment greater than 0.5 m above the typical water level, willow (*Salix* spp.) and horsetail (*Equisetum* spp.) proliferate. The vegetation reduces flow velocity and erosion, increasing net sediment deposition and terrace height following subsequent foods. Young terrace soils are low in organic C and N and high in $CaCO_3$ and $CaSO_4$ (Marion et al. 1993). Within 5 years of vegetation establishment, balsam poplar (*Populus balsamifera* L.) and thinleaf alder (*Alnus tenuifolia* Nutt.) cover increase and after 5 to 10 years, a shrub thicket of alder and willows increases the C and N content of the soil and produces the first contiguous organic soil horizon. Balsam poplar lives longer and grows taller than alder and willow causing a transition from shrub thicket to open shrub-poplar forest to closed poplar forest. Eighty to 100 years following terrace establishment, deciduous forests are overgrown by white spruce (*Picea glauca* (Moench) Voss) forests with deep (10 – 20 cm) organic horizons and a continuous moss understory.

Patterns of succession beyond the first cohort of white spruce (~ 200 years) are unclear. Early descriptions of succession (Drury 1956 Viereck 1970) suggested that decreased soil temperatures, due to increased organic horizon thickness, lead to the

Table 1. Dominant vegetation and ages of the terraces used in this study. From Adams (1999).

Ecosystem type	LTER Name[a]	Age in 1998[b]	Age Source	Symbol[c]
Bare sand and silt deposit	Not LTER	1,1,1	Assumed	▼
Willow with alder shrubs	FP1A,B,C	18,13,18	Aerial photo	●
Young poplar – alder understory	FP2A,B,C	53,43,68	Aerial photo	■
Mature poplar – young white spruce	FP3A,B,C	123,128,98	Oldest tree	▲
Mature white spruce	FP4A,B,C	153,271,216	Oldest tree	♦
Mature black spruce	FP5A,C,D	500,500,500	Assumed	b

[a]These are long-term research terraces maintained by the Bonanza Creek LTER program. FP stands for floodplain, the number identifies the dominant vegetation, and each letter represents a unique terrace (n = 3 per ecosystem type). The bare sand and silt bars would be FP0 by LTER nomenclature, though no permanent plots exist.
[b]Each number represents a separate terrace. For LTER plots, the first second and third numbers correspond to the age of the A, B, and C terraces, respectively.
[c]Figures throughout the paper use these symbols to represent dominant vegetation.

development of permafrost, which in turn caused declines in white spruce and the emergence of black spruce (*Picea mariana* (Mill.) B.S.P.). However, recent work suggests that the transition to black spruce may result from altered hydrologic and fire regimes (Mann et al. 1995), rather than changes in organic horizon thickness alone. Well-drained stands of white spruce may or may not convert to black spruce, while poorly drained, fire prone "back swamp" stands convert to black spruce following secondary succession. Black spruce stands contain sparse tree stems and an understory dominated by *Vaccinnium* spp., *Alnus crispa*, and *Salix* spp.

Soil sampling and laboratory incubations

In August 1998, we sampled soils adjacent to permanent plots (n = 15 terraces) in the Bonanza Creek LTER floodplain chronosequence, and on bare silt and sand bars (n = 3 terraces) greater than 1 m above the river, for a total of 18 separate terraces (Table 1). The LTER terraces were stratified by dominant vegetation (n = 3 terraces × 5 vegetation types = 15 terraces). The bare sand and silt bars were devoid of vegetation and likely established during the previous flood year, though their actual age could range from < 1 year to 2 years. The exact ages of the LTER black spruce sites are unknown and could range from 500 years to several thousand years (Mann et al. 1995).

At each of the 18 terraces, we collected and then composited three mineral soil cores (each core was 4 cm in diameter × 20 cm deep) adjacent to the permanent LTER plot. On terraces with a continuous forest floor layer (30 years and older; n = 12 terraces), we also collected and then composited three 10 cm × 10 cm sections of the entire organic horizon. On the open willow terraces, we composited six, rather than three, samples because of potential heterogeneity caused by shrub islands. On terraces that contained white spruce (terrace ages 30 to 300 years; n = 9 terraces), we collected and composited an additional set of soil cores directly be-

neath the three largest white spruce near the control cores. Spruce trees ranged from 3.5 cm (diameter at breast height) on young terraces to 42 cm on older terraces.

The composited soil samples (18 mineral soil and 12 forest floor samples for the main chronosequence study, and an additional 9 mineral soil and 9 forest floor samples from directly beneath white spruce trees) were double bagged, and stored at 4 °C until the incubations were initiated one month later. The samples were weighed and sieved (4 mm mesh) and a subsample was dried at 105 °C (mineral soil) or 70 °C (forest floor) for 48 hours. Bulk density of the mineral soil was determined using the mass of the composite and the volume of three soil cores. To convert forest floor N concentrations to pool sizes per unit area, we used density (mass/area) data collected on the LTER control plots in 1989 (www.lter.alaska.edu data file BNZD00076) or from Van Cleve et al. (1983) for the black spruce sites. The 1989 forest floor sampling was extensive (10 samples per terrace) and showed no changes in mass with terrace age. We did not have bulk density data for samples collected directly under spruce trees, so these data are expressed as N concentration per gram oven dry soil. Field capacity was calculated as soil moisture content 48 hours after saturating a vertical column of soil in a plastic tube supported by cheesecloth. Total soil N and C were determined by dry combustion (LECO-1000, LECO Corporation, St. Joseph, Michigan, USA) of oven dry, ground subsamples. Inorganic soil C was determined by adding 6 N HCl with $FeCl_2$ to a dry, ground subsample, and measuring CO_2 produced using a pressure transducer (Wagner et al. 1998).

No standard method exists to separate total organic N (or C) into labile and stable pools. Previous studies have used physical (Strickland et al. 1992) and chemical (He et al. 1988) methods to fractionate soil C and N, assuming that aggregate size, organic matter density, or organic matter solubility was well correlated with C or N availability to microorganisms. We used a long-term laboratory incubation with repeated leaching to separate the total soil N pool into labile and stable pools (Stanford and Smith 1972). This biological fractionation approach, allows the "in situ microbial and microarthropod community to define ecologically relevant SOM (soil organic matter) fractions" (Robertson and Paul 1999).

A subsample (50 g mineral soil; 15 g forest floor) from each field composite was incubated at 30 °C in plastic filters (Nadelhoffer (1990); Falcon Filter model 7111, Beckton Dickenson Labware, Lincoln Park, NJ). This temperature produced the largest net N mineralization rates in short-term laboratory incubations of these soils (Klingensmith and Van Cleve 1993b). A glass fiber filter (Whatman GF/A) and an "extra thick" glass fiber pre-filter (Gelman Sciences) were placed beneath the soil and a third glass fiber filter (Whatman GF/A) was placed above the soil to prevent dispersion (Motavalli et al. 1995). The filter units were sealed in airtight 2-l jars fitted with septa. Approximately 20 ml of deionized water were placed in the bottom of each jar to sustain humidity and prevent soil drying. Every two weeks this water was changed and the soil brought to field capacity with deionized water.

To determine the labile N pool size, we leached the soil at 1, 14, 29, 43, 84, 111, 179, 238, 295, and 356 days with a solution containing all essential nutrients except N (Nadelhoffer 1990). At each leaching, 100 ml of the N-free leaching solu-

tion was added to the top of the filter, allowed to equilibrate with the soil for 1 hour, and then drawn through the filter with a weak vacuum (−0.05 MPa). The vacuum was applied until leachate ceased to drip from the filter (< 10 min). Leachates were frozen until analysis for NH_4^+ and (NO_2^- + NO_3^-) by flow injection colorimetry and converted to g N m^{-2} using leachate (plus soil water) volume, initial dry mass of the incubated soil, and bulk density. At the end of the incubation, a subsample (20 g) of the residual soil was extracted with 100 ml of 0.5 M K_2SO_4 to account for unleached inorganic N. We defined the labile N pool as the sum of all leached inorganic N (NO_2^- + NO_3^- + NH_4^+) plus inorganic N extracted with K_2SO_4 immediately after the last leaching. Stable N was defined as total N minus labile N.

Labile C pools were determined by capturing CO_2 in the headspace of the incubation jars. Before the jars were sealed, they were fanned with ambient air for 1 hour to provide a uniform background CO_2 concentration. Then the jars were sealed for periods from 2 days (beginning of the incubation) to 3 weeks (end of the incubation) after which the concentration of CO_2 in the headspace was determined using an infrared gas analyzer (LICOR-6200). The headspace was sampled by first mixing with a 35 ml syringe and then sampling 2 ml with a 10 ml syringe. Ten sealed jars without soil were used as blanks to correct for ambient CO_2. Atmospheric pressure, air temperature, the volume of the jars, the volume of gas sampled, oven dry mass, and bulk density were used to convert headspace concentration to g C m^{-2}.

An ^{15}N addition experiment was conducted on soils from young poplar forests (n = 3 terraces; FP2 sites in Table 1) and mature white spruce forests (n = 3 terraces; FP4 sites). We added 18, 25, 50, and 150 mg N to ~50 g soil (equivalent to ~ 65, 80, 160, and 500 g N m^{-2}) as 99, 79,79, and 25% (atom percent enrichment) $^{15}NH_4Cl$ in the solutions used to bring the soil to field capacity (typically ~5 ml). The lowest addition was intended to double the labile organic N pool and the larger additions were intended to identify thresholds for the capacity of the soil to retain N. After the ^{15}N addition, the soils were incubated for 3 weeks, and then leached on the same schedule described above. At the end of the incubation, a 5 g subsample was extracted three times each with 25 ml of 0.5 M K_2SO_4 and 25 ml of water to remove residual inorganic ^{15}N. We shook the sample with extractant for 0.5 hours, added several drops of 0.25 M $CaCl_2$ (to flocculate clay), centrifuged at 10000 rpm for 10 minutes, and then discarded the supernatant. The soil and added $^{15}NH_4Cl$ solutions were analyzed for total N and ^{15}N at the Stable Isotope Laboratory, Utah State University, USA The mass of ^{15}N retained in the soil was calculated from the mass of N in the sample at the end of the experiment (post washing), the ^{15}N enrichment of the sample at the end of the experiment (from 5 to 25 atom percent ^{15}N), the measured ^{15}N enrichment of the added N, and the ^{15}N enrichment of soil not receiving N additions (assumed 0.3663 atom percent ^{15}N).

We used linear and non-linear regression with terrace age as the independent variable to determine the effect of ecosystem age on N and C response variables. The regression model that produced the lowest sum of squares was used. We did not include black spruce sites in regression analyses because the age of black spruce

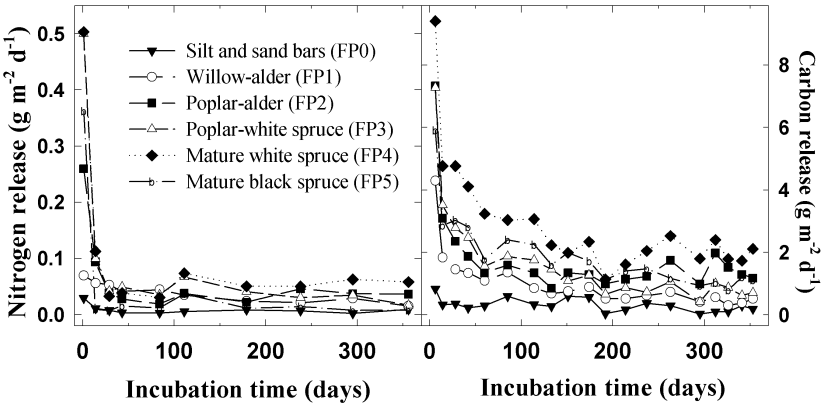

Figure 1. Left panel: Nitrogen (N) release during long-term laboratory incubations of soils (forest floor + 0 to 20 cm mineral soil) from the Tanana River floodplain successional sequence. *Right panel*: Carbon (C) release during the incubation. Each point is the mean of 3 terraces grouped by terrace age and dominant vegetation (Table 1): silt and sand bars (▼), willow-alder (●), poplar-alder (■), poplar-white spruce (▲), mature white spruce (♦), and black spruce (b)

forests was unknown and because the transition to black spruce may relate more to stochastic disturbance events than predictable vegetation changes. We compared black spruce sites to other stages using one-way ANOVA's with dominant vegetation as the main effect. We compared samples collected under white spruce trees to controls using a nested ANOVA with successional stage, replicate within stage (error term for stage), spruce presence, spruce × stage interaction, and stand × spruce within stage (error term for spruce and spruce × stage) as model effects. A similar nested ANOVA was used to assess the effect of vegetation type and N addition level on ^{15}N retention. Data were log-transformed before ANOVA tests when residual plots revealed unequal variance.

Results

Both N and C release were most rapid during the first month of the incubation, then rates declined (Figure 1). For vegetated terrace soils, N and C release rates at the end of the incubation were less than 10 and 20% of initial rates, respectively. The bare silt and sand bars released little N and C throughout the incubation.

From 85 to 94% of the total soil N (forest floor plus top 20 cm of mineral soil) was stable during the incubations. Stable N pools increased from 50 g N m^{-2} on bare silt and sand bars to over 300 g N m^{-2} in white spruce forests (Figure 2). Labile N pools ranged from 10 to 38 g N m^{-2} on forested terraces (Figure 2). Both labile ($r^2 = 0.77$) and stable ($r^2 = 0.76$) N pools were best described by a negative exponential curve with a non-zero y-intercept. Labile (0.6 to 0.2 g N m^{-2} yr^{-1}) and stable ($\sim$3 to 2 g N m^{-2} yr^{-1}) pools accumulated most rapidly during the first 50 years, then labile pools leveled off while stable N continued to accumulate with

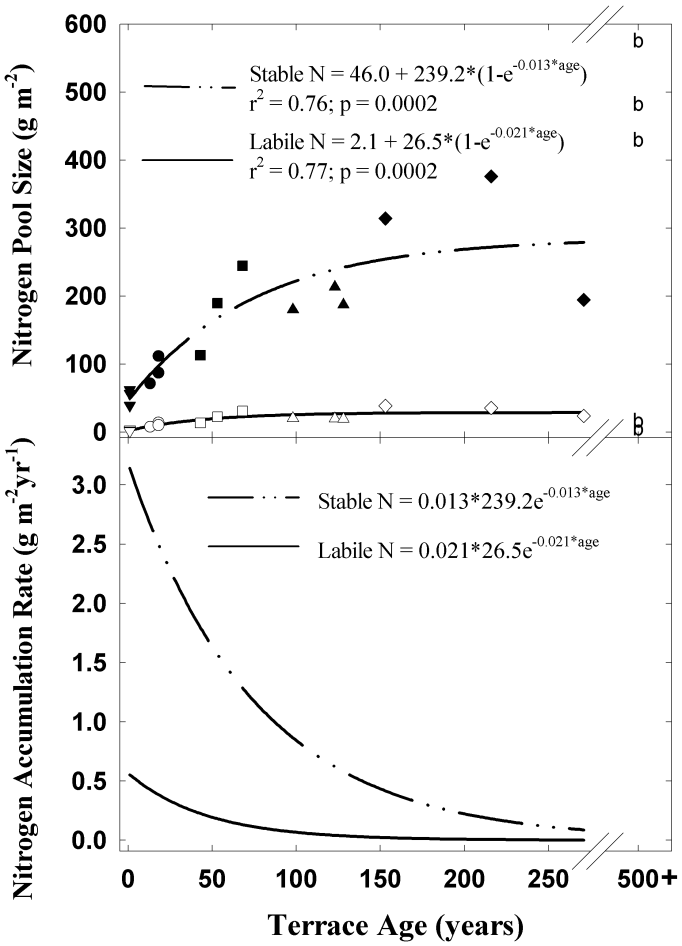

Figure 2. Top panel: Stable and labile soil (forest floor + 0 to 20 cm mineral soil) nitrogen (N) pool sizes in relation to terrace age. *Bottom panel*: Accumulation rates of N pools calculated from the first derivative of the best-fit curve through pool sizes. Symbols denote labile (open) and stable (closed) pools and dominant vegetation (Table 1): silt and sand bars (▼), willow-alder (●), poplar-alder (■), poplar-white spruce (▲), mature white spruce (◆), and black spruce (b). Black spruce sites were not included in regression analyses.

time (Figure 2). Soil C followed similar trends (Figure 3) and labile C and N pools [Labile C = 58 + 21*(Labile N); $r^2 = 0.91$; $p < 0.001$] and stable C and N pools [Stable C = -452 + 16*(Stable N); $r^2 = 0.95$; $p < 0.001$) were strongly correlated when black spruce sites were excluded. The C:N ratio of stable organic matter increased with terrace age ($r^2 = 0.69$), from 10 early in succession to 20 in white spruce stands (Figure 4). Labile C:N ratios (from 20 to 134) were generally higher than stable C:N ratios, but did not vary predictably with terrace age (Figure 4).

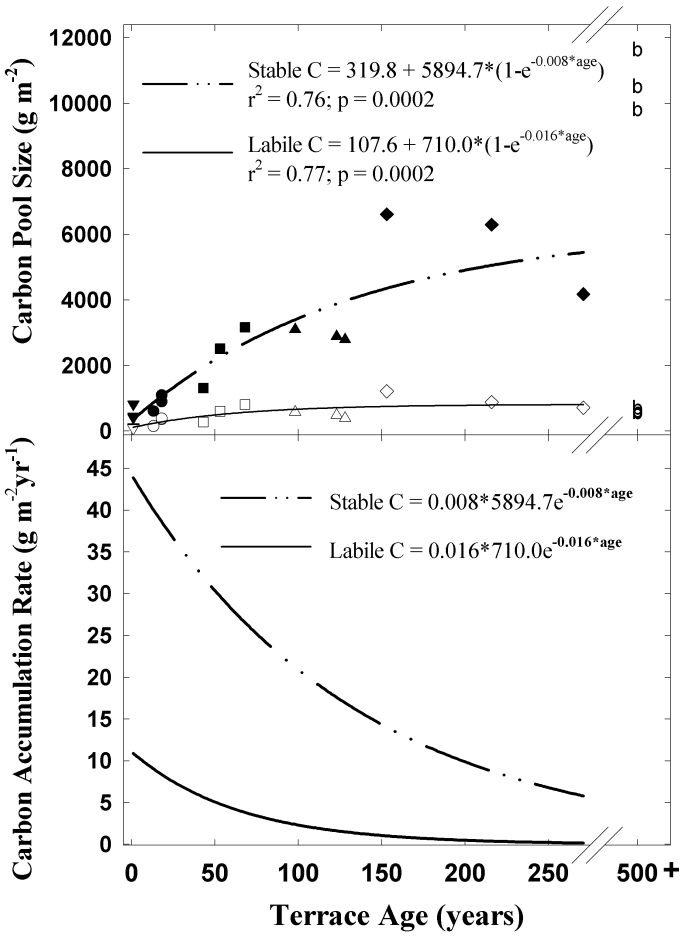

Figure 3. Top panel: Stable and labile soil (forest floor + 0 to 20 cm mineral soil) carbon (C) pool sizes in relation to terrace age. *Bottom panel*: Accumulation rates of C pools calculated from the first derivative of the best-fit curve through pool sizes. Symbols denote labile (open) and stable (closed) pools and dominant vegetation (Table 1): silt and sand bars (▼), willow-alder (●), poplar-alder (■), poplar-white spruce (▲), mature white spruce (♦), and black spruce (b). Black spruce sites were not included in regression analyses.

Black spruce soils had less labile N (Figure 2) than all other vegetated ecosystems ($p < 0.03$ for all systems except willow-alder: $p = 0.052$). Conversely, stable N was greater in black spruce mineral soils ($\sim$ 450 g N m^{-2}) than in any other successional stage ($p < 0.01$). Only about 1% of the N in the mineral soil and 3% of the N in the forest floor were labile from the black spruce soils during the incubation. We did not detect differences in labile N concentrations (per gram oven dry soil) between controls and soil sampled directly beneath white spruce trees (Figure 5).

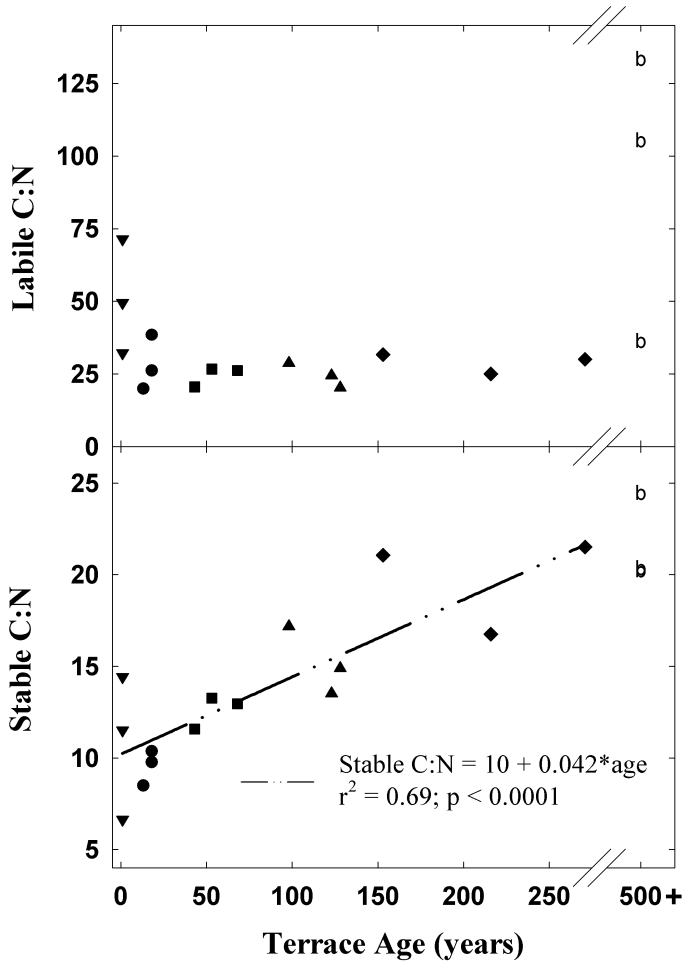

Figure 4. Top panel: The carbon (C) to nitrogen (N) ratio of labile soil (forest floor + 0 to 20 cm mineral soil) organic matter in relation to terrace age. *Bottom panel*: The C:N ratio of stable soil organic matter in relation to terrace age. Symbols denote dominant vegetation (Table 1): silt and sand bars (▼), willow-alder (●), poplar-alder (■), poplar-white spruce (▲), mature white spruce (♦), and black spruce (b). Black spruce sites were not included in regression analyses.

Up to 35% of the ^{15}N labeled N added 3 weeks prior to the incubations was in the stable pool after a year of repeated leaching. Total stable N retention in both white spruce and poplar-alder soils ranged from 7 to 78 g N m^{-2} (Figure 5). White spruce soil retained about 40% less ^{15}N per gram soil C than poplar-alder soil ($p = 0.01$; data not shown). Increasing the mass of ^{15}N added to the soil increased the amount of stable ^{15}N ($r^2 = 0.39$; Figure 6), but decreased the percentage of ^{15}N retained. Labile C pools did not correlate with the amount of ^{15}N added (Figure 6) or retained ($p > 0.16$, data not shown).

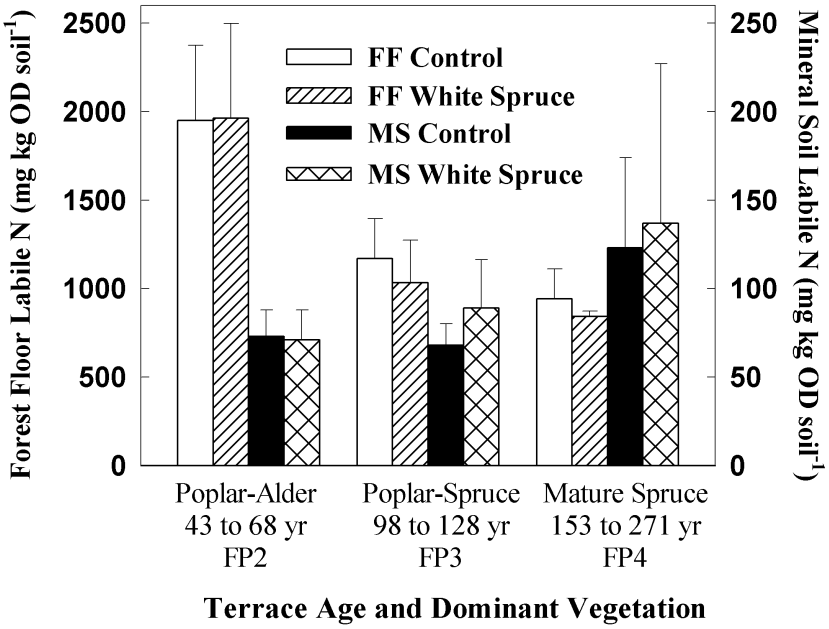

Figure 5. Labile nitrogen concentrations [per kilogram oven dry (OD) soil] from forest floor (FF) and mineral soil (MS; 0 to 20 cm depth) samples collected at the base of white spruce trees and control samples that were collected without respect to canopy type. The x-axis is dominant vegetation type (top line), range of terrace ages (middle line), and LTER name (bottom line). See Table 1 for details. We did not detect differences between control and spruce-biased samples ($p > 0.17$). Bars are means ($n = 3$) plus one standard error.

Discussion

Our results demonstrate that stable soil pools are rapid and large sinks for N during primary succession. Rates calculated here (Figure 2) corroborate Walker (1989) estimate that Tanana River floodplains accumulate 2 to 5 g N m^{-2} yr^{-1} of surface soil N during the first 50 years of succession. Most of this early N accumulation occurred in stable pools that were larger and grew faster than labile pools (Figure 2). Later in succession, labile pools approached steady state, while stable N continued to accumulate for at least 200 years. How does stable N accumulation compare to non-soil ecosystem N sinks? Gaseous N losses are below detection limits at this site (Klingensmith and Van Cleve 1993a). Inorganic N leaching is also small; deep soil inorganic N concentrations (maximum of $\sim$0.4 mg N l^{-1} at 50 cm depth; Yarie et al. (1993)) combined with a crude water budget (precipitation = 270 mm yr^{-1} and PET > 400 mm yr^{-1}, suggesting minimal leaching, but we conservatively assume 100 l m^{-2}) suggest losses < 0.04 g N m^{-2} yr^{-1}. Plant biomass is an important N sink during the first 25 years of succession ($\sim$3 g N m^{-2} yr^{-1} when alders are proliferating; Van Cleve et al. (1971)), but plants are always a smaller sink than

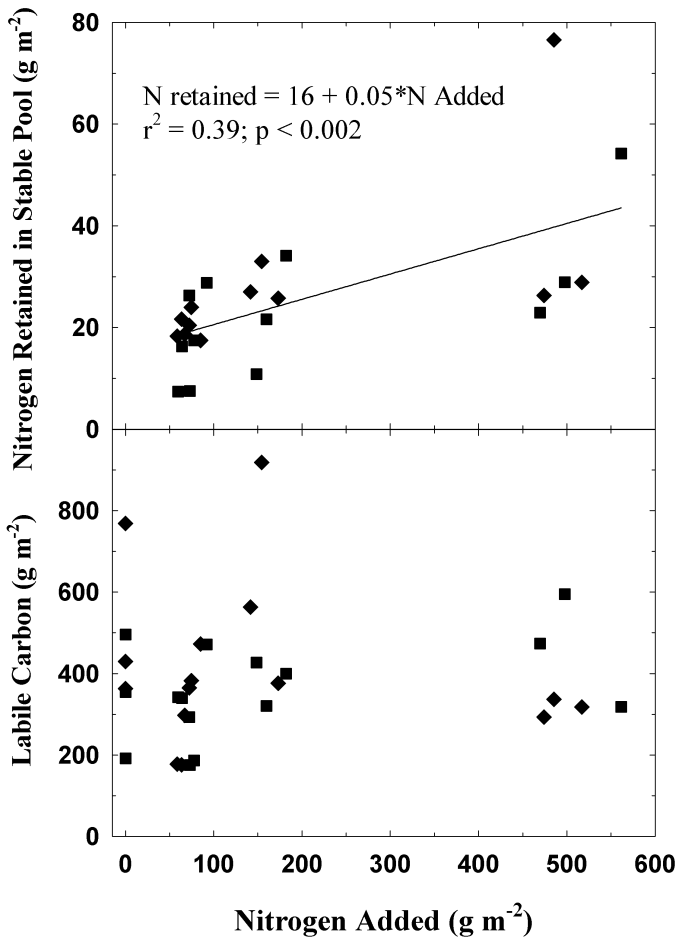

Figure 6. Top panel: The relationship between the amount of ^{15}N labeled N added to mineral soil (0 to 20 cm depth) three weeks prior to the incubation, and the amount of ^{15}N labeled N retained in the stable pool after a one year incubation with repeated leaching. *Bottom panel*: The relationship between added N and the labile C pool size. Added N and labile C were not correlated ($p = 0.27$). Symbols denote dominant vegetation: poplar-alder (■) and mature white spruce (♦).

soils, and after 25 years plant biomass N declines (Van Cleve et al. 1983) while the soil continues to accumulate N.

The stable N that accumulated in surface soils of this chronosequence came from a combination of mostly stable N deposited with sediments (e.g. silt and sand bars in Figure 2) and more labile organic N derived from plant tissues (mainly alder, but also trees using deep soil or groundwater N). New inputs of N to many forests are neither organic nor stable; they come from inorganic N fertilizer or atmospheric N deposition. Our laboratory ^{15}N experiment showed that, like alder-derived N, inorganic N is incorporated into the stable organic pool quickly; up to 35% of the ^{15}N

we added 3 weeks prior to incubation was stable. The amount of retained ^{15}N (up to 78 g N m^{-2}) was 10 to 20 times greater than measured annual stable N accumulation (Figure 2), indicating that soils in both early and late successional stages had the capacity to retain far more N than occurred during succession. These ^{15}N additions were very large. The lowest addition was about as large as the labile N pool and comparable to the amount of fertilizer added to some N saturation experiments over a decade (Aber et al. 1998). Our larger N additions were ecologically unrealistic, but were chemically intriguing as a test of soil N retention capacity (analogous to a phosphorus adsorption isotherm). Even in the largest N addition ($\sim$ 0.5 kg N m^{-2}), soil N retention capacity did not appear saturated; there was a linear relationship between N added and N retained in the stable pool (Figure 6).

There are several mechanisms by which organic N from plant litter and inorganic N inputs could be incorporated into stable soil organic matter quickly. Fine textured soils may promote stable N formation through NH_4^+ fixation in clay lattices (Nommik and Vahtras 1982), or chemical interactions between organic N, cations, and clay surfaces (Oades 1988). These mechanisms were likely unimportant in our experiment because the soils have low clay content (mean = 3.7% clay). Organic N, NH_4^+, and NO_2^- react directly with soil organic C to form complex molecules (humus) that are thermodynamically costly for heterotrophs to decompose (Burge and Broadbent 1961 Mortland and Wolcott 1965 Johnson et al. 2000 Dail et al. 2001). Microbial N turnover may promote humus-forming reactions or directly assimilate N and C into stable tissues (He et al. 1988 Kaye et al. 2002 (in press)). While both of these processes (abiotic reactions with organic C and microbial turnover) likely contributed to the conversion of alder litter to stable soil N, microbial turnover cannot account for the large ^{15}N retention observed in our laboratory addition. If the retained ^{15}N had been incorporated into microbial biomass and then into stable organic matter following microbial death or exudation, we would have easily detected a large pulse of microbial respiration. Using conservative estimates of microbial C:N ratios (6) and growth efficiency [(biomass C/(biomass C + respired C)] = 0.6, Hart et al. (1994)], assimilation of 1 g of N would have respired 4 g of C. Nitrogen additions did not increase CO_2 production relative to control samples in our experiment (Figure 6).

Given the low clay content and lack of a respiration response to N additions in our soils, we suggest that stable ^{15}N retention resulted from chemical reactions between added NH_4^+ and organic matter. Increased N retention with increasing N inputs (Nommik 1970 Axelsson and Berg 1988) implies that these reactions are, to some extent, substrate (N) limited. Whether or not atmospheric N deposition reacts with organic matter in the same manner as our large laboratory N additions is unclear (Johnson 1992). Low and high N additions produce different NMR spectra (Preston et al. 1982 Thorn and Mikita 1992 Clinton et al. 1995), suggesting that the chemical nature of retained N is dose dependent. In addition, the low pH of many forest soils may inhibit NH_4^+-organic matter reactions, though several studies have observed abiotic fixation in acidic soils (Axelsson and Berg 1988 Johnson et al. 2000 Dail et al. 2001). Clearly, we are far from understanding the importance of organic matter-N reactions under field conditions. Future research should focus on

low-dose field studies across a range of sites to assess the real-world importance of abiotic N retention.

All of the mechanisms described above cause stable N to accumulate by actively transferring N from labile to stable pools. Ecosystems could also develop a high concentration of stable N through losses of mineralized labile N. While mineral N losses are certainly one factor affecting the labile N pool size, they do not fully explain the observed patterns of labile and stable N accumulation during succession. Labile N losses from the terraces (external sinks of denitrification and leaching < 0.04 g N m^{-2} yr^{-1}) are 100 to 1000 times smaller than labile N pool sizes (on vegetated terraces > 10 g N m^{-2}; Figure 2) and alder N inputs. Thus, external losses of N do not necessarily constrain the labile N pool to be small. Internal sinks for labile soil N (eg. plant uptake and stable soil N pool accumulation) are much larger than external losses, and these internal fluxes impose the most important constraints on the size of the labile N pool. Over centuries or millenia, even small losses of mineral N could increase the *concentration* of stable N in soils, but this long-term process can not explain the accumulation of large *amounts* of stable (or labile) N over weeks to years.

Tree species may affect labile soil N pools on the Tanana floodplains (Flanagan and Van Cleve 1983 Van Cleve et al. 1993b Schimel et al. 1998). Previous research at this site showed that forest floor net N mineralization decreased in spruce stands and the decline was mainly attributed to the poor quality of white spruce litter relative to litter of willow, alder, and poplar (Flanagan and Van Cleve 1983 Van Cleve et al. 1993b). However, spruce stands also had higher mineral soil N mineralization rates (Van Cleve et al. 1993b) and deep soil solution N concentrations (Yarie et al. 1993), suggesting either higher N availability or lower N demand compared to younger ecosystems (Binkley et al. 1997). In these previous studies, the effect of individual species was confounded by changes in terrace age. When we controlled for terrace age by sampling beneath and outside of spruce canopies on the same terrace, we found no evidence for spruce-induced changes in labile N concentrations of the forest floor or mineral soil (Figure 5). In addition, we did not detect a decline in the labile N pool size (forest floor plus 0 to 20 cm mineral soil) with time (Figure 2).

Implications for N retention in forest ecosystems

On all time scales observed in this study, stable N pools were important sinks for N. Our lab experiment showed that inorganic ^{15}N was shunted into stable pools after a three-week exposure to soil (Figure 6), and data from the entire successional sequence showed that on annual, decadal, and centennial time scales, stable N pools were larger and grew faster than more labile pools (Figure 2). Other lab and field ^{15}N addition experiments, using a wide range of fractionation techniques, have shown that 25 to > 50% of added N is stable weeks to months after application (Stanford et al. 1970 He et al. 1988 Strickland et al. 1992 Chang et al. 1999). In addition, many studies have shown or simulated rapid incorporation of ^{15}N into

soil without determining the lability of the ^{15}N (Currie and Nadelhoffer 1999 Nadelhoffer et al. 1999 Johnson et al. 2000 Dail et al. 2001).

If stable soil organic matter in a wide range of ecosystems accumulates N rapidly but releases it slowly (our stable pool has a non-zero turnover time; Figure 1), then current annual NEP may be a poor predictor of fertilizer or deposition N retention. The mechanisms that control N incorporation into stable soil pools, microbial turnover and abiotic reactions, operate even when NEP is small or zero. Thus, in both aggrading and mature ecosystems, N inputs and outputs should be asynchronous as the stable soil N pool sequesters pulse N additions and releases them either slowly over long time scales (perhaps as dissolved organic N; Perakis and Hedin (2002)) or episodically after a disturbance. A key feature of N retention in stable soil pools is flexible organic matter stoichiometry: the organic matter (OM) to N ratio changes (Vitousek and Reiners 1975 Reiners 1986 Vitousek et al. 1988). For example in our ^{15}N addition experiment 7 to 78 g N m^{-2} were retained without new OM inputs (Figure 6). Across the entire successional sequence, the C:N ratio of stable soil OM increased from 10 to 20 over 275 years (Figure 4).

We compared the roles of NEP and ecosystem stoichiometry in N accumulation on the Tanana floodplains by synthesizing published values for soil (Van Cleve et al. 1993a), root (Van Cleve et al. 1971 Reuss et al. 1996), and aboveground plant (Viereck et al. 1993a) OM and N stocks. In this analysis, we included black spruce forests with the caveat that some, but not all white spruce stands follow this successional pathway. We converted ecosystem OM values to C (by dividing by 2) for comparison with soils data in this and other studies. Total ecosystem C and N pools (forest floor plus mineral soil to 60 cm, roots, and aboveground tree biomass) were lowest early in succession and reached maxima after 100 to 200 years (Figure 7). Organic matter accumulation rate (NEP = change in ecosystem C/time interval) and nitrogen accumulation rate were highest early in succession and approached zero after 200 years.

While NEP and net N increment were clearly correlated, changes in NEP did not fully explain changes in N accumulation rate. Ecosystem stoichiometry varied greatly throughout succession with C:N ratios ranging from 12 during the first 4 years to 36 in white spruce stands (Figure 7). If NEP throughout succession maintained the same stoichiometry as the early successional ecosystems (assume C:N = 15 for all ages), the floodplains would have accumulated 1300 g N m^{-2} over 200 years; a 140% increase over actual N accumulation (Figure 7). Conversely, if NEP throughout succession maintained the same stoichiometry as 200 year-old terraces (assume C:N = 36 for all ages), the floodplains would have accumulated only 200 g N m^{-2} during the first 25 years; about half the actual value of 400 g N m^{-2}.

Changes in ecosystem and soil stoichiometry during succession are not unique to our study. Stable soil N pools (defined by density fractionation) were the largest sink for N and had C:N ratios ranging from 10 to 20 on a 1000-year mudflow chronosequence (Sollins et al. 1983). To examine the generality of variable ecosystem stoichiometry, we synthesized mineral soil C:N data (the only data available for a large number of sites) from seven other chronosequence studies spanning approximately the same time period as the Tanana floodplains, and one very long chro-

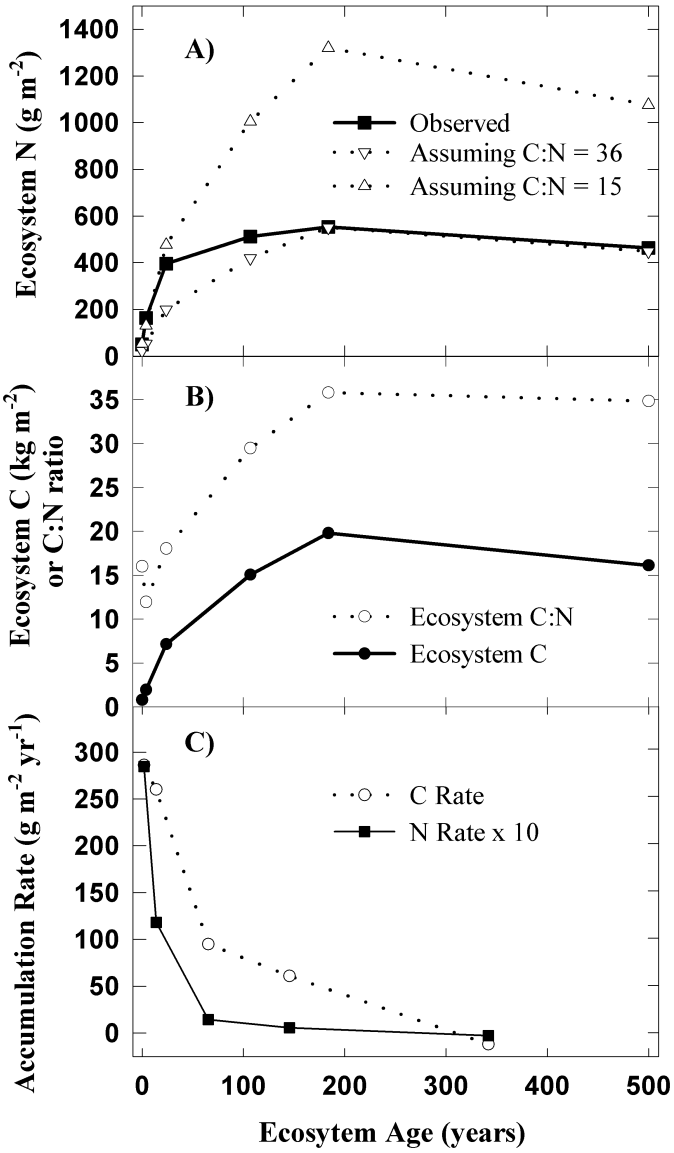

Figure 7. Panel A: Total ecosystem nitrogen (N) accumulation under observed or hypothetical ecosystem stoichiometry during primary succession on the Tanana River floodplains. *Panel B*: Total ecosystem carbon (C) or C:N ratio during succession. *Panel C:* Net ecosystem production (C accumulation rate) or net nitrogen accumulation rate (× 10) during succession. Divide the y-axis by 10 for actual N accumulation rates.

nosequence (Crews et al. 1995). Soils within a given chronosequence show highly variable stoichiometry, often increasing or decreasing by a factor of 5 during the

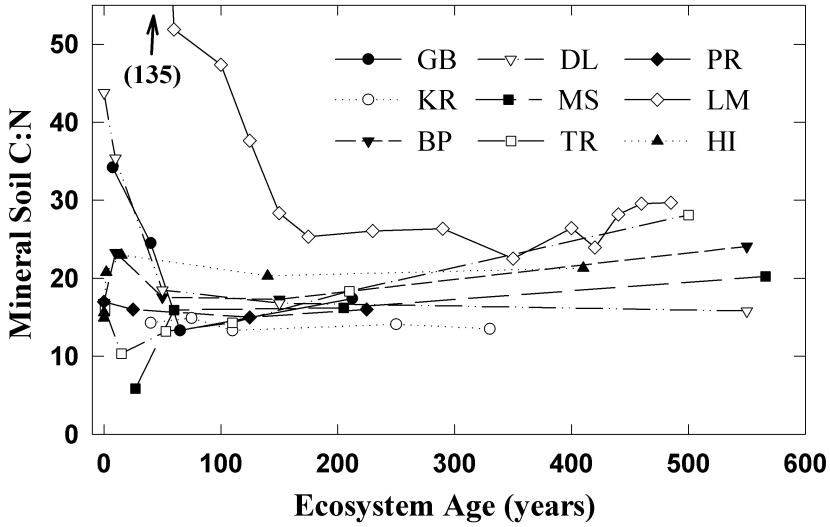

Figure 8. The relationship between the mineral soil C:N ratio and ecosystem age in a variety of chronosequences. Ages of the HI sequence are 10000 times values shown here. The ages of the oldest BP and DL terraces are unknown; we arbitrarily assigned an age of 550 years. GB: Glacier Bay deglaciation, A + B horizons (Chapin et al. 1994). KR: Kugarurok River floodplains, 0 to 40 cm (Rhoades C, Binkley D, & Stottylemyer R, unpublished data. BP: Browns Park floodplains, 0 to 20 cm (Adair 2001). DL: Deer Lodge Park floodplains, 0 to 20 cm (Adair 2001). MS: Mt. Shasta mudflows, 0 to 91 cm depth (Dickenson and Crocker 1953). TR: Tanana River floodplains, 0 to 60 cm (this study; Van Cleve et al. (1993a)). PR: Peace River floodplains, 0 to 20 cm (Schwendenmann 2000). LM: Lake Michigan sand dunes, 0 to 20 cm (Lichter 1998). HI: Hawaii volcanic islands, 0 to 50 cm (Crews et al. 1995).

first 200 years of succession (Figure 8). After 200 years, C:N ratios changed less over time, but values double in some chronosequences. In the Hawaiian chronosequence, soil C:N ratios increased from 16 to 23 over the first 150,000 years then declined to 20 or 21 over the next 4 million years. Soils should provide a conservative estimate of stoichiometric flexibility because forest floor and plant stoichiometry are more variable over time.

Changes in soil stoichiometry are also not unique to primary succession, mixtures of N-fixing trees have lower soil (and ecosystem) C:N ratios than plots without N fixers (Kaye et al. 2000). Forests with high N deposition often have lower soil C:N ratios than sites with lower atmospheric N deposition (McNulty et al. 1991 Van Miegroet et al. 1992 Nohrstedt et al. 1996 Emmett et al. 1998). If changing stoichiometry is an important mechanism for N retention in soils, then soils with wide C:N ratios may retain more N than those with narrow C:N ratios. In our ^{15}N experiment, initial soil C:N ratios did not predict N retention capacity (Figure 6); poplar-alder soils (narrow C:N) retained as much ^{15}N as white spruce soils (wide C:N). Our lab results may differ from field data if, as we suspect, abiotic mechanisms were responsible for retention of our large ^{15}N additions. Johnson et al. (2000) showed that for a wide range of soils biotic N retention was correlated with soil C:N ratios, but abiotic retention was not.

Conclusions

Stable soil N pools were large and rapid sinks for N during primary succession and in a laboratory ^{15}N experiment. Nitrogen accumulation rates could not be predicted from NEP alone because ecosystem stoichiometry changed during the course of succession. Flexible soil stoichiometry appears to be a characteristic of a wide range of ecosystems, though there is no clear pattern over time (Figure 8). Changes in ecosystem stoichiometry also result from changes in biomass stoichiometry (Vitousek et al. 1988), but plant and microbial biomass N are always small fractions of total ecosystem N (Cole and Rapp 1981 Smith and Paul 1990). On the Tanana floodplains for example, white spruce and poplar forests have 300–600 g N m^{-2} in soil (to 0.8 m) and about 27 g N m^{-2} in aboveground biomass (Van Cleve et al. 1983). Over decades or centuries, the vast majority of N inputs will either be lost or retained in soil.

The mechanisms that incorporate N into soil OM have not been completely elucidated, but all of those currently being considered (microbial turnover, mycorrhizal enzyme production, and abiotic fixation; Stark and Hart (1997) and Aber et al. (1998), Johnson et al. (2000), Dail et al. (2001)) would operate even when NEP is zero. Rapid incorporation of N into soil pools that release N slowly (our stable pool) is consistent with observations that: 1) forests with a wide range of NEP efficiently retain N in soils, and 2) most forests display asynchrony between N inputs and outputs. Conceptual models of N retention that include stable OM pools and their stoichiometry should complement existing models that focus on actively cycling plant and microbial pools (Reiners 1986 Aber et al. 1998)

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