

Richard E. Brenner · Richard D. Boone  
Jeremy B. Jones Jr · Kate Lajtha · Roger W. Ruess

## Successional and physical controls on the retention of nitrogen in an undisturbed boreal forest ecosystem

Received: 19 August 2005 / Accepted: 13 February 2006 / Published online: 7 March 2006  
© Springer-Verlag 2006

**Abstract** Floristic succession in the boreal forest can have a dramatic influence on ecosystem nutrient cycling. We predicted that a decrease in plant and microbial demand for nitrogen (N) during the transition from mid- to late-succession forests would induce an increase in the leaching of dissolved inorganic nitrogen (DIN), relative to dissolved organic nitrogen (DON). To test this, we examined the chemistry of the soil solution collected from within and below the main rooting zones of mid- and late-succession forests, located along the Tanana River in interior Alaska. We also used a combination of hydrological and chemical analyses to investigate a key assumption of our methodology: that patterns of soil water movement did not change during this transition. Between stands, there was no difference in the proportion of DIN below the rooting zone. 84–98% of DIN at both depths consisted of nitrate, which was significantly higher in the deeper mineral soil than at the soil surface ( $0.46 \pm 0.12 \text{ mg NO}_3^- \text{ N l}^{-1}$  vs  $0.17 \pm 0.12 \text{ mg NO}_3^- \text{ N l}^{-1}$ , respectively), and 79–92% of the total dissolved N consisted of DON. Contrary to our original assumption that nutrients were primarily leached downward, out of the rooting zone, we found much evidence to suggest that the glacially-fed Tanana River (> 200 m from these stands) was contributing to the influx of water and

nutrients into the soil active layer of both stands. Soil water potentials were positively correlated with river discharge; and ionic and isotopic ( $\delta^{18}\text{O}$  of  $\text{H}_2\text{O}$ ) values of the soil solution closely matched those of river water. Thus, our ability to elucidate biological control over ecosystem N retention was confounded by riverine nutrient inputs. Climatic warming is likely to extend the season of glacial melt and increase riverine nutrient inputs to forests along glacially-fed rivers.

**Keywords** Boreal forest · Capillary flow · Nitrogen demand · Primary succession · Soil solution

### Introduction

Nitrogen (N) plays a critical role in regulating primary productivity. Thus, N inputs and losses from forest ecosystems have been the subject of much attention in ecological research (Seely et al. 1998; Sollins et al. 1980; Tietema et al. 1997; Vitousek and Field 2001). During the 1970s, it was hypothesized that N should generally be retained in aggrading, mid-succession, forests but increasingly lost from late-succession forests, as a decrease in net ecosystem productivity induces a reduction in ecosystem N demand (Gorham et al. 1979; Vitousek and Reiners 1975). A refinement of this hypothesis added that substantial losses of dissolved organic nitrogen (DON) may occur regardless of biological N demand (Hedin et al. 1995; Vitousek et al. 1998), and several studies across a wide range of forest types have shown that DON is the dominant form of N lost from many forest ecosystems (Currie et al. 1996; MacLean et al. 1999; Perakis and Hedin 2002; Sollins et al. 1980). This is probably because a substantial fraction of DON, and associated dissolved organic carbon (DOC), consist of recalcitrant, biologically unavailable forms (Qualls and Haines 1991; Stepanauskas et al. 2000; Yano et al. 2000), such that DON losses from ecosystems can occur without extensive plant or microbial utilization. Thus, while biotic N demand plays a considerable role in the

Communicated by Jim Ehleringer

R. E. Brenner (✉) · R. D. Boone · J. B. Jones Jr · R. W. Ruess  
Institute of Arctic Biology, University of Alaska Fairbanks,  
Fairbanks, AK 99775, USA

E-mail: rbrenner@berkeley.edu

Tel.: +1-510-6421054

Fax: +1-510-6421054

K. Lajtha

Department of Botany and Plant Pathology,  
Oregon State University, 2082 Cordley Hall,  
Corvallis, OR 97331-2902, USA

*Present address:* R. E. Brenner  
Department of Integrative Biology,  
University of California Berkeley, Berkeley,  
CA 94720-3140, USA

retention of N forms that are readily available to plants and soil microbes (e.g., amino acids,  $\text{NH}_4^+$  and  $\text{NO}_3^-$ ), all successional stages may have N leaching losses dominated by DON in ecosystems where anthropogenic inputs of reactive N are low.

Floodplain stands of balsam poplar (*Populus balsamifera*) and white spruce (*Picea glauca*) in Alaska's interior encompass a dramatic primary successional transition (Viereck et al. 1993a) in a region with extremely low deposition of reactive N ( $<0.3 \text{ kg N}\cdot\text{ha}^{-1}\text{ year}^{-1}$  wet + dry deposition) (EPA 2006). During the course of approximately 150 years, deciduous, mid-succession stands of balsam poplar succumb to dominance by coniferous, late-succession stands of white spruce. Net primary productivity (Ruess et al. 1996; Viereck et al. 1983), the abundance of N-fixing alder (*Alnus tenuifolia* and *A. crispa*) (Viereck et al. 1993a), as well as net soil N transformations (Klingensmith and Van Cleve 1993b; Van Cleve et al. 1993c), all decline during this transition. Furthermore, the N demand of vegetation shifts from high demand in balsam poplar stands to lower demand in white spruce stands (Van Cleve et al. 1983). Integral to the changes in composition, productivity and nutrient cycling are the development of a nearly continuous moss cover, a decline in soil temperatures and the associated occurrence of frozen soil throughout an increasing portion of the growing season in white spruce stands (Van Cleve et al. 1991). Thus, the succession of dominant overstory species induces large changes in the biological (NPP, nutrient transformations, understory species) as well as physical (soil temperature, ice formation) properties of this landscape.

Floristic succession on the boreal floodplain may also bring about an alteration of overall ecosystem N retention. Soil heterotrophs in balsam poplar stands may be N limited due to the rich supply of labile C that originates from phenolics in poplar litter (Clein and Schimel 1995; Schimel et al. 1996, 1998). In contrast, the soil and litter in white spruce stands has a host of characteristics, such as increased C:N and lignin:N ratios, that are indicative of being more recalcitrant substrates for soil microbes (Flanagan and Van Cleve 1983; Van Cleve et al. 1993c). Soil N accumulates rapidly during early succession and throughout much of the balsam poplar stage, but shows no net gain as white spruce become dominant (Van Cleve et al. 1993a; Van Cleve and Viereck 1981). The reduced rate of soil N accumulation in late succession is almost certainly linked to a decrease in the abundance of N-fixing alder. However, in keeping with successional theory, it may also indicate an acceleration of N losses. When taken together, the decline in plant productivity, reduction in soil temperatures and potential decline in organic matter quality during late succession should contribute towards a reduction in the capacity of plants and soil microbes to immobilize biologically available forms of N. Low to undetectable rates of denitrification across the entire successional sequences (Klingensmith and Van Cleve 1993a) point toward N

leaching as the primary route of N loss from these stands.

The objective of this study was to compare the relative biological demand for inorganic N in balsam poplar and white spruce by examining the proportion of dissolved inorganic nitrogen (DIN) versus DON in the soil solution of these successional stages. Our intention was not to determine an input/output budget of N in these stands, rather we assumed that the composition of soil solution N collected below the rooting zone (e.g.,  $\text{NO}_3^-$ ,  $\text{NH}_4^+$  and DON) will define the forms of N leached. Providing that patterns of water movement and soil solution DON leaching losses are fairly constant across this relatively brief successional transition (two critical assumptions), stands that have lower biotic N retention should also have a relatively lower ratio of DON:DIN below the rooting zone compared to stands with higher N demand. As an example, ecosystems in which biological N demand has been satiated by excess inputs of anthropogenic N have N losses with much lower ratios of DON:DIN than pristine ecosystems, even though concentrations of DON are often comparable (Perakis and Hedin 2002). Accordingly, we predicted that the soil solution below the rooting zone in late-succession white spruce stands would have a lower ratio of DON:DIN than in mid-succession balsam poplar stands. To test this prediction, we examined the chemistry (DIN, DON and dissolved ions) of the soil solution within and below the main rooting zone of these stands. We also evaluated the assumption that these stands had similar hydrological characteristics by examining patterns of water movement and comparing the ionic and  $\delta^{18}\text{O}$  isotopic composition of the soil water in these stands to its potential sources (precipitation, groundwater, and riverwater).

---

## Materials and methods

### Study sites and characteristics

This study took place at the Bonanza Creek Long Term Ecological Research Site (BNZ-LTER), approximately 30 km south of Fairbanks, Alaska, USA ( $64^\circ45'\text{N}$ ,  $148^\circ18'\text{W}$ ). Replicate research plots ( $15\times15 \text{ m}$ ;  $n=3$  per stand type) were located within stands of balsam poplar and white spruce on islands spread throughout the active portion of the Tanana River floodplain. All plots were 200+ m from the Tanana River and located on high terraces ( $>3 \text{ m}$ ) formed by the deposition of fluvial material. Mean annual precipitation in this region is low, averaging 269 mm, and is exceeded by potential evapotranspiration of approximately 466 mm. Mean annual air temperature is  $-3.7^\circ\text{C}$ , with extremely cold winters (to  $-50^\circ\text{C}$ ) and warm summers (to  $35^\circ\text{C}$ ) (Viereck et al. 1993b). All sites contained frozen soil throughout a portion of the growing season. However, balsam poplar sites generally become ice-free by August while some white spruce sites contain frozen soil until

early October (Brenner et al. 2005). Soils at these sites are alkaline due to high concentrations of calcium carbonate (Marion et al. 1993a, b) and are classified as Typic Cryofluvents (Van Cleve et al. 1993b; Viereck et al. 1983). The soil profile contains multiple buried organic layers as a result of past flooding events, with silt as the dominant mineral textural class.

Balsam poplar sites (LTER sites BP1, BP2 and BP3) consisted of mature, uneven-aged stands with some individuals exceeding 100 years of age and a dense understory of thin-leaf alder (*Alnus tenuifolia* Nutt.), rose (*Rosa acicularis*) and infrequent white spruce. White spruce sites (LTER sites 4A, 4B and 4C) consisted of mature stands 200+ years in age with an understory of alder (*A. crispa* and/or *A. tenuifolia*), rose and feather mosses (*Hylocomium splendens* and *Pleurozium schreberi*). Alder was a much smaller component of the understory in white spruce sites than in balsam poplar. A complete description of plant and soil characteristics for the floodplain can be found in Viereck et al. (1993) and on the Bonanza Creek LTER website (Bonanza Creek 2005).

#### Soil water and river sampling

Tension lysimeters (“Super Quartz” by Prenart Equipment, Frederiksberg, Denmark) were installed during late June 2000 in both stand types. Within each plot, lysimeters were installed at a 30° angle to 12 cm ( $n=5$ ) or 40 cm ( $n=4$ ) depths. In white spruce, the soil depth was measured from the base of the live moss layer, in balsam poplar it was measured from underneath the previous year’s litter. Sampling in white spruce was conducted from board walks to limit damage to the moss. Lysimeters were left undisturbed for 1 month after installation, and the first two sampling periods in 2000 were excluded from the analysis. Water samples were also collected from the adjacent Tanana River during most sampling periods.

Tensiometers (Soil Measurement Systems, Tucson, Arizona) were installed concurrent with lysimeters in arrays of 14, 32 and 50 cm depths ( $n=3$  arrays per plot). Soil water potential was measured within the head of the tensiometers using a pressure transducer. The difference in water potentials between tensiometers was used to determine the direction of vertical flux of water within the soil profile. For example, a more negative water potential at 32 cm than 50 cm indicates that water is moving up through the profile.

Upon collection, water samples were filtered with pre-leached glass fiber filters (1 µm pore diameter), and pH and conductivity were measured. Samples then were frozen until further analysis. Lysimeters were sampled 20 times during the frost-free period (late May–early October) from August 2000 until October 2001.

Nitrate and ammonium concentrations were measured on an API 300 autoanalyzer (Astoria-Pacific, Clackamas, Oregon) using standard colorimetric pro-

cedures (Bundy and Meisinger 1994). Dissolved organic N (DON) was determined by subtracting DIN (nitrate + ammonium) from total persulfate-digestible N (Cabrera and Beare 1993). Anion (chloride and sulfate) and cation (calcium, magnesium, sodium and potassium) concentrations were determined on a Dionex DX-320 ion chromatograph (Dionex, Sunnyvale, California). We also re-measured ammonium and nitrate in most samples via ion chromatography during the analysis of anions and cations. DOC was determined on a random subset of 157 samples spanning the entire experiment using a Shimadzu TOC-5000 (Shimadzu, Kyoto, Japan). The  $\delta^{18}\text{O}$  isotope ratio of water from lysimeter, rain, groundwater and river samples was conducted on a Europa PDZ 20-20 isotope ratio mass spectrometer (SerCon, Cheshire, U.K.). For this purpose, rain and groundwater samples were collected by LTER personnel at adjacent sites throughout the growing season.

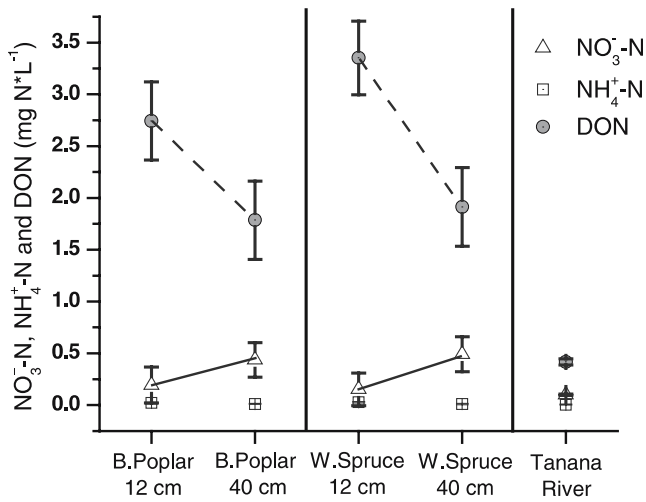
#### Statistical analyses

The concentrations of elements collected within each plot  $\times$  depth combination were averaged such that each plot represented a single replicate ( $n=3$  plots per stand type). Data were analyzed with a split-plot ANOVA design using PROC MIXED in SAS (SAS 1999). Stand type was used as the between-subject (whole plot) factor, and depth was the within-subject (split-plot) factor. Season (spring: 15 May–15 June; summer: 16 June–15 August; fall: 16 August–15 October) was also included in the model as a repeated measures factor. Significant effects were further analyzed using paired contrasts. A Kenward and Roger correction (Littell et al. 2002) was implemented because exact  $F$ -tests were generally not possible. For all analyses, the homogeneity of variance assumption was tested using Levene’s test. Data were square-root transformed when the assumptions of homogeneity of variance were violated (Zar 1999), and an additional analysis was performed. Principal components analysis (PCA) was used to investigate the relationship between dissolved ions in the Tanana River with those from the soil solution. The first two factor scores from the PCA were further analyzed using a MANOVA and, when there were significant effects, paired contrasts were used to determine significant differences between groups. Data presented in tables and figures are means ( $\pm 1\text{SE}$ ) from untransformed data.

---

## Results

The largest portion (79–92%) of total dissolved nitrogen (TDN) in the soil solution at all stands and depths was comprised of DON (Fig. 1, Table 1). In addition, DON concentrations across stand types were significantly higher at the 12 cm, than 40 cm, depth ( $3.05 \pm 0.27$  for 12 cm vs  $1.85 \pm 0.27$  for 40 cm;  $P=0.01$ ). This difference



**Fig. 1** The concentrations of soil solution  $\text{NO}_3^-$ -N,  $\text{NH}_4^+$ -N and DON from floodplain stands of balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*) and the Tanana River. Values are means obtained from a repeated-measures ANOVA of the soil solution and stream water over time. Samples were collected 20 times from August 2000 to October 2001 ( $n=3$  for each stand $\times$ depth combination)

between depths was significant for white spruce ( $P=0.02$ ) but only marginally significant for balsam poplar ( $P=0.10$ ). The ratio of DON:DIN was not significantly different between stand types but was significantly higher at the 12 cm than 40 cm depth (Table 1). Averaged across stands, DON concentrations at the 12 cm depth were significantly higher during the summer period compared to the fall ( $P=0.05$ ; Fig. 2). The summer was also the period when soil moisture content was lowest (see below), suggesting that DON concentration was influenced by dilution from snowmelt during the spring and precipitation in autumn.

Nitrate accounted for the largest fraction (84–98%) of the DIN pool with ammonium concentrations low throughout the study, averaging  $<0.03 \text{ mg NH}_4^+ - \text{N} \cdot \text{l}^{-1}$  (Fig. 1). Soil solution nitrate concentration was significantly higher ( $P=0.05$ ) at the 40 cm depth ( $0.46 \pm 0.12 \text{ mg NO}_3^- - \text{N} \cdot \text{l}^{-1}$ ) compared to the 12 cm depth ( $0.17 \pm 0.12 \text{ mg NO}_3^- - \text{N} \cdot \text{l}^{-1}$ ) when averaged across stands (Figs. 1, 2). However, within stands, the difference between depths was only marginally signifi-

cant for white spruce ( $P=0.08$ ) and was not significant for balsam poplar ( $P=0.19$ ). Nitrate concentration did not change significantly across seasons ( $P=0.31$ ), although the highest mean nitrate concentration observed in the study was from the 40 cm depth of white spruce during the fall (mean nitrate =  $0.61 \text{ mg NO}_3^- - \text{N} \cdot \text{l}^{-1}$ ; Fig. 2).

Averaged across both stands, soil solution DOC was significantly higher at 12 cm than 40 cm ( $P=0.03$ ; Table 1) but, as with other solutes, this difference was only significant for white spruce ( $P=0.04$ ) and not for balsam poplar ( $P=0.14$ ). DON and DOC concentrations were positively correlated across all sampling periods and sites (adj.- $R^2=0.82$ ,  $P<0.001$ ; data not shown). As such, the ratio of DOC:DON was fairly consistent across all depths and stand types, ranging from 34.7 in the 12 cm depth of balsam poplar to 40.5 in the Tanana River (Table 1).

Of the cations and anions measured, only potassium and chloride concentrations exhibited consistent depth-wise patterns, with highest concentrations at the 12 cm depth for both stand types ( $P<0.01$ ; Table 2). Although there were some exceptions, cation concentrations in soil solution and river samples generally followed the pattern of  $\text{Ca} > \text{Mg} > \text{K} > \text{Na} > \text{Li}$ , and for anions  $\text{SO}_4 > \text{Cl}$ . Factor scores generated from a PCA of ion concentrations generally show ions from the Tanana River and 40 cm soil solution to be grouped much more tightly on the factor plane than those from the 12 cm soil solution (Fig. 3). The first two PCA-generated factors explained  $>83\%$  of the total variance. Factor 1 was highly correlated with  $\text{SO}_4$ , Ca, Na, and Mg and factor 2 was highly correlated with Cl and K. A MANOVA of the factor scores yielded a highly significant site effect ( $P<0.0001$ ; data not shown). For factor 1, pair contrasts indicate significant differences ( $P<0.02$ ) between ions in the Tanana River and those in the soil solution at all depths except white spruce 40 cm (Table 3). For factor 2, paired contrasts only yielded significant contrasts between ions in the Tanana River and the soil solution at the 12 cm depth of balsam poplar (Table 3).

The mean  $\delta^{18}\text{O}$  isotopic signature of rainwater was significantly more enriched (by 4–6‰) than the soil solution from any of the plots ( $P<0.001$ ; Fig. 4). In contrast, the mean  $\delta^{18}\text{O}$  isotopic signature of Tanana River water was 1.5–3‰ more depleted than that from

**Table 1** Select water characteristics for the Tanana River and the soil solution from stands of balsam poplar (*Populus balsamifera*) and white spruce (*Picea glauca*)

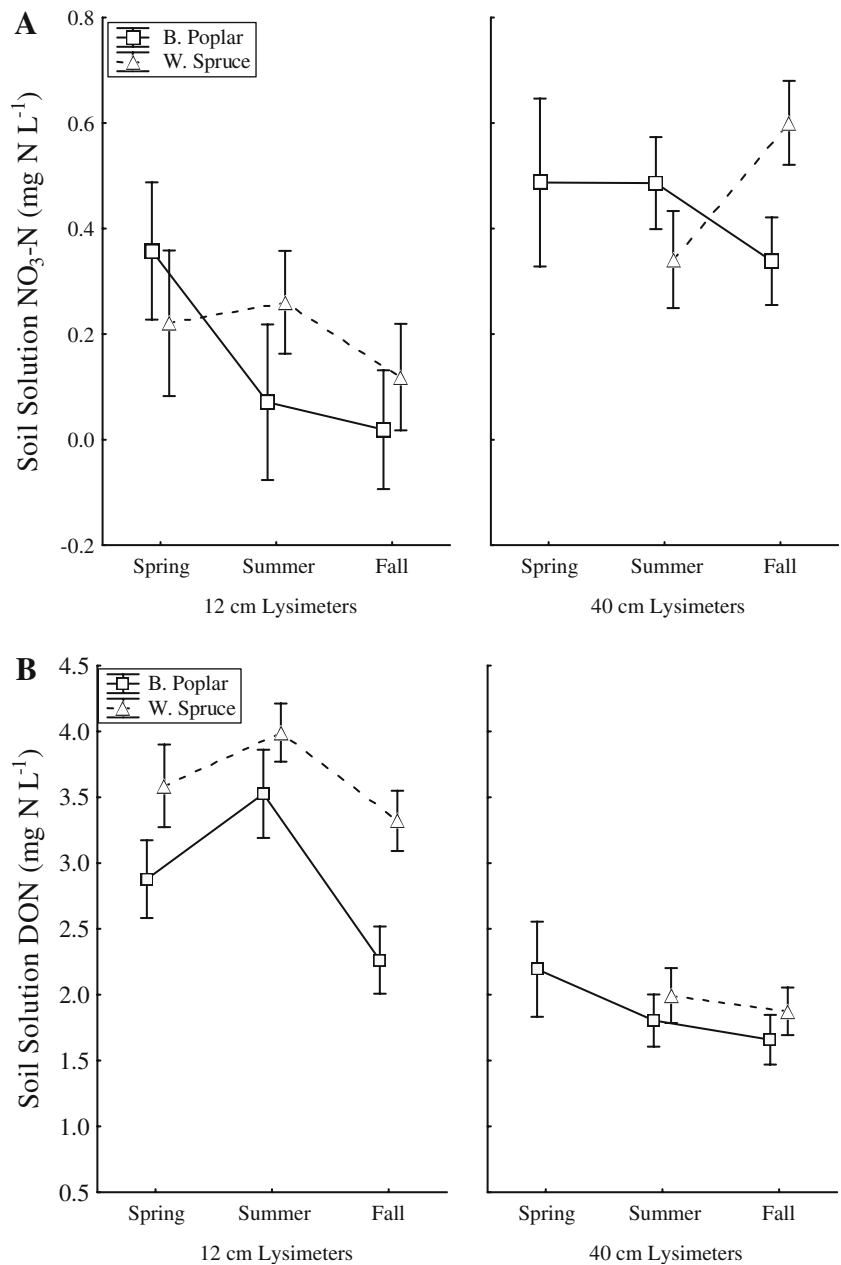
	BP 12 cm	BP 40 cm	WS 12 cm	WS 40 cm	Tanana River
pH	8.50 <sup>a</sup> (0.07)	8.37 <sup>a</sup> (0.11)	8.20 <sup>a</sup> (0.10)	8.30 <sup>a</sup> (0.09)	8.41 <sup>a</sup> (0.12)
Electrical conductivity ( $\mu\text{S} \cdot \text{cm}^{-1}$ )	283.5 <sup>ab</sup> (86.8)	539.2 <sup>b</sup> (204.1)	394.8 <sup>ab</sup> (232.1)	335.2 <sup>ab</sup> (92.4)	164.5 <sup>a</sup> (10.6)
DON:DIN*	27.6 <sup>a</sup> (16.9)	5.7 <sup>b</sup> (2.5)	24.0 <sup>a</sup> (9.5)	6.6 <sup>b</sup> (4.2)	4.3 <sup>b</sup> (0.5)
DOC	95.2 <sup>ab</sup> (6.6)	68.2 <sup>b</sup> (2.3)	127.7 <sup>a</sup> (25.6)	76.7 <sup>b</sup> (11.2)	16.8 <sup>c</sup> (1.2)
DOC:DON	34.7 <sup>a</sup> (3.4)	38.2 <sup>a</sup> (2.8)	38.1 <sup>a</sup> (1.9)	40.1 <sup>a</sup> (0.6)	40.5 <sup>a</sup> (6.7)

Values are means ( $\pm$  ISE) and all concentrations are in  $\text{mg l}^{-1}$

Superscript with the same letters are not significantly different ( $P>0.05$ )

\*Means were transformed prior to analysis

**Fig. 2** Mean ( $\pm$  1SE) seasonal soil solution concentrations of **a**  $\text{NO}_3^-$ -N and **b** DON averaged across 2000–2001. Means were determined in a repeated measures ANOVA with  $n=3$  replicate plots per stand $\times$ depth combination. There were no significant seasonal trends for nitrate ( $P>0.05$ ). Across stands the concentration of DON was significantly lower at the 12 cm depth during the fall compared to the summer period. Spring: 15 May–15 June; summer 16 June–15 August; fall: 16 August–15 October



the soil solution, but this difference was not significant for all research plots. Electrical conductivity did not differ significantly between stand types or depths but, like all the elements measured, it was lower in river water than the soil solution (Table 1). The pH of the soil solution did not vary significantly by stand type, soil depth, or season ( $P>0.10$ ) and ranged from 8.2 to 8.5 (Table 1).

At all depths, the soil water potentials were highest, and often positive (saturated), during the spring (Fig. 5). These high values were the result of snowmelt which saturated soil and, in some cases, pooled water on top of frozen soil during the spring flush. Standing water was most evident at the 50 cm depth of both stands, where water potentials remained positive until late June or early July. Water potentials at all depths

dropped sharply in late June and early July as soil surfaces dried out. Water potential increased in late July as the discharge of the Tanana River increased and rains began, and decreased in the fall as the river level fell. There was a significant correlation between discharge of the Tanana River and soil water potential ( $R^2=0.92$ ,  $P<0.0001$  for white spruce, and  $R^2=0.56$ ,  $P=0.01$  for balsam poplar), but only for the period after 10 July (Fig. 6), when surface horizons had begun to dry following the spring flush. Based on differences in water potentials between depths, we determined that the downward infiltration of water roughly tracked precipitation events in white spruce plots (Fig. 7). In contrast, only during the spring flush was downward infiltration of water observed in balsam poplar.

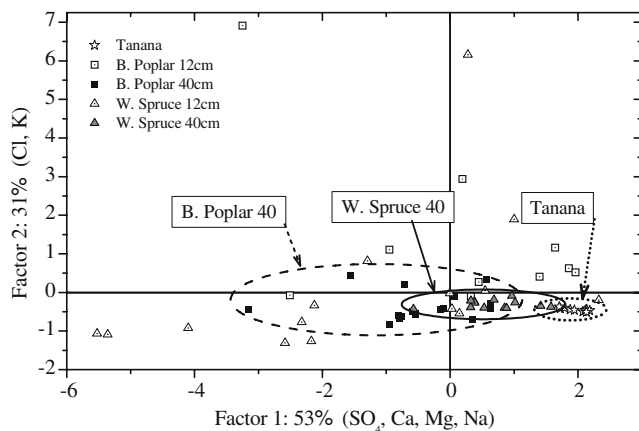
**Table 2** The concentration ( $\text{mg l}^{-1}$ ) of major ions from the Tanana River and the soil solution of balsam poplar and white spruce stands

	BP 12 cm	BP 40 cm	WS 12 cm	WS 40 cm	Tanana River
<b>Cations</b>					
Ca	31.28 (7.73)	42.89 (7.61)	31.47 (10.42)	37.83 (6.17)	18.57 (1.63)
Mg	14.24 (6.47)	35.87 (13.75)	22.55 (13.53)	22.87 (7.81)	6.67 (1.51)
K	20.35 (4.08)	8.36 (0.37)	17.59 (2.77)	6.05 (1.81)	2.64 (0.26)
Na	5.74 (3.38)	13.50 (7.24)	12.31 (7.98)	7.93 (3.41)	3.34 (0.39)
Li	0.01 (0.01)	0.001 (0.002)	0.02 (0.01)	0.003 (0.001)	0.001 (0.0003)
<b>Anions</b>					
SO <sub>4</sub>	35.99 (19.07)	127.58 (92.61)	134.98 (113.93)	49.86 (27.59)	35.80 (4.06)
Cl	21.03 (3.22)	5.49 (1.09)	11.81 (5.05)	2.80 (0.71)	1.18 (0.12)

All values are means ( $\pm 1$  SE)

## Discussion

We did not find evidence to support our hypothesis that mid-succession stands would have a higher demand for N than late-succession stands. Mid- and late-succession stands had similar concentrations of soil solution DIN and similar ratios of DON:DIN below the rooting zone (Fig. 1). The largest portion, 85–87%, of the soluble N in the soil solution was comprised of DON. While the bioavailability of the soil solution DON is unknown, DON from streams draining boreal forest ecosystems has been shown to have a high proportion (81–72% at baseflow) of biologically unavailable constituents (Stepanuskas et al. 2000). The same is likely true in these stands where there was a relatively high ratio of DOC:DON in the soil solution at all depths (DOC:DON=34–41; Table 1). This ratio exceeds by several fold the C:N ratio of substances such as amino acids, which are known to be a direct sources for plant N uptake in the boreal forest (McFarland et al. 2002; Nasholm et al. 1998; Persson and Nasholm 2001). We do not discount the possibility that there is some



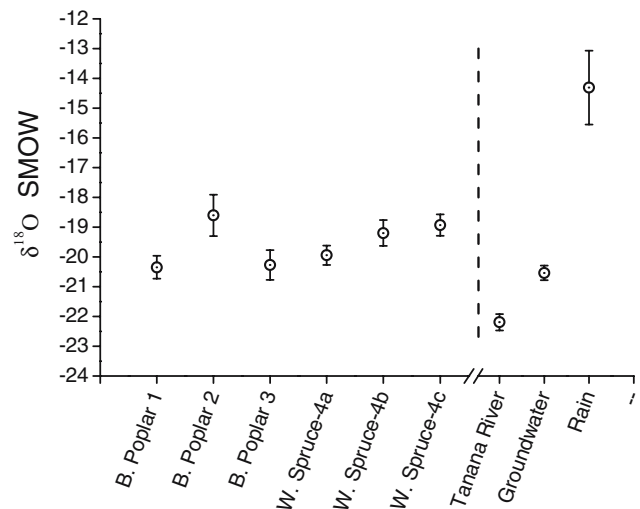
**Fig. 3** The grouping of the two principle factors from a principle component analysis of major ions in the Tanana River and the soil solution. Factor 1 explained 52.71% of the total variance and was highly correlated with SO<sub>4</sub>, Ca, Mg and Na; factor 2 explained 30.64% of the total variance and was highly correlated with Cl and K

**Table 3** *P*-values from planned contrasts between ions in Tanana River water and the soil solution

	Wilks multivariate test	Factor 1 (SO <sub>4</sub> , Ca, Mg, Na)	Factor 2 (Cl, K)
BP 12 cm	< 0.0001	0.02	0.0006
BP 40 cm	0.002	0.0008	0.86
WS 12 cm	< 0.0001	< 0.0001	0.64
WS 40 cm	0.21	0.11	0.68

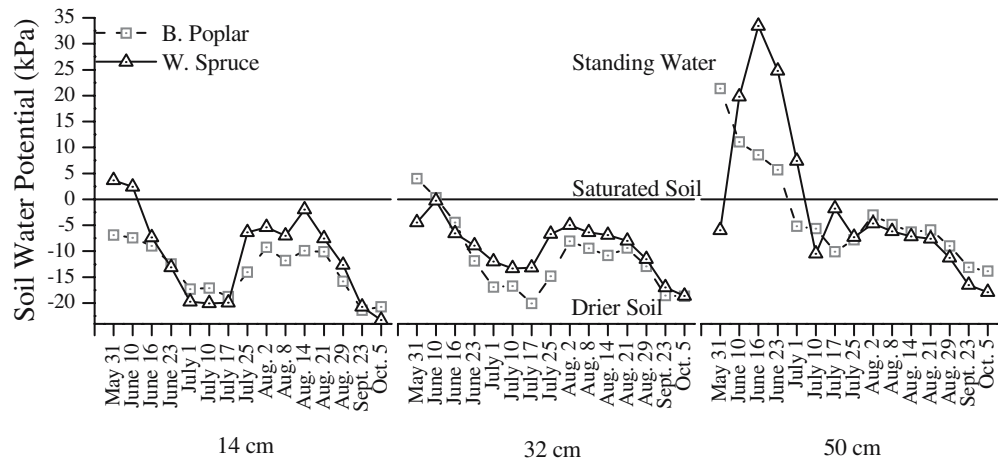
The contrasts follow a MANOVA of the first two factor scores taken from a principle component analysis. The factor scores were square-root transformed prior to the MANOVA and were highly correlated (> 76% correlation) with the ions listed beneath them

microbial utilization of this dissolved organic material. However, we believe the high C:N ratios alone indicate that it is generally not of high quality, and therefore lends support to the idea that a sizeable fraction of DON losses in this system are not necessarily controlled by biological N demand (Vitousek et al. 1998). Overall, our study reaffirms that “pristine” ecosystems, with



**Fig. 4** Mean  $\delta^{18}\text{O}$  ( $\pm 95\%$  CI) of water from lysimeters, rain, groundwater and the Tanana River collected during 2000–2001. Lysimeter data from the 12 and 40 cm depths were combined in the analysis. Evaporative losses should cause the  $\delta^{18}\text{O}$  signature of water sources to become progressively more enriched

**Fig. 5** Mean soil water potentials (kPa) for stands of balsam poplar (*dashed line*) and white spruce (*solid line*) during 2001 ( $n=3$  stands)

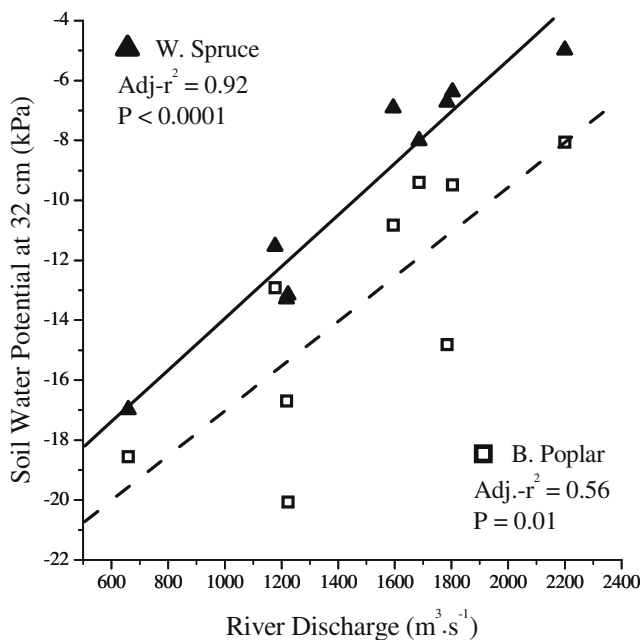


extremely low rates of N deposition, generally have soil solution and stream N pools consisting primarily of DON (MacLean et al. 1999; Sollins et al. 1980; Hedin et al. 1995; Stepanauskas et al. 2000).

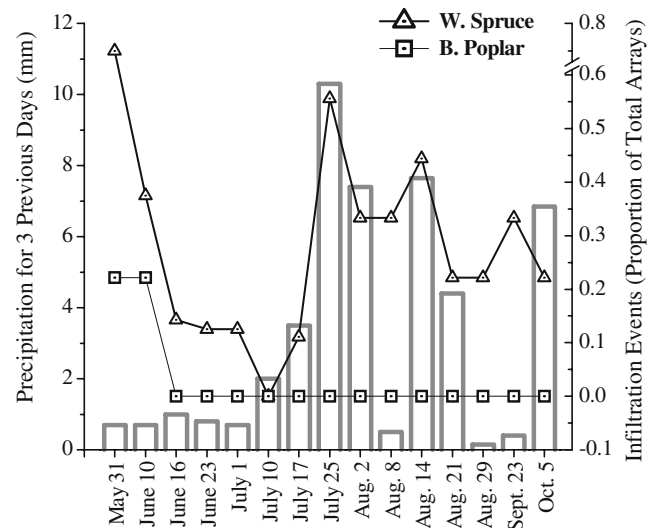
Successional stage did have a large control on the infiltration of rain water to deeper soil horizons. Following snowmelt, the downward infiltration of water to the 50 cm depth was never evident after rain events in balsam poplar, but was often observed in white spruce stands (Fig. 7). This apparent difference between stand types might be partially explained by higher stand-level transpirational water loss by the deciduous plants (e.g., poplar, alder, rose) found in mid-succession stands,

which could prevent the downward infiltration of rain water. Therefore, despite the similar composition of N forms in the soil solution in both stand types, a larger amount of infiltration into the deeper mineral soil following rain events in white spruce stands should result in greater N leaching. This result renders invalid our methodology for examining N demand between these stands, which was based on the assumption that patterns of soil water movement were similar throughout the transition from mid to late succession. Nitrogen losses due to downward infiltration are also complicated by the greater prevalence of frozen soil in white spruce (Brenner et al. 2005), which could prevent precipitation or snowmelt from infiltrating to groundwater.

The amount of soluble N lost from these stands via leaching is difficult to estimate due to the unpredictable nature of water movement through seasonally frozen soil (Kane and Chacho 1990), as well as uncertainty in



**Fig. 6** Mean soil water potential (kPa) versus discharge of the Tanana River ( $m^3 s^{-1}$ ) at the 32 cm depth of soil in stands of balsam poplar and white spruce from 10 July to 5 October during 2001. Soil water potential values are the mean taken from  $n=3$  plots per stand type. The *dashed regression line* is for balsam poplar and the *solid line* for white spruce



**Fig. 7** The proportion of tensiometer arrays per stand showing downward infiltration of water (*line + symbol*) and the cumulative precipitation (mm) for 3 days prior to sampling (*bars*) on each sampling day during 2001

estimating soluble N concentrations in the mineral soil during the early spring (late April–May) and early winter (October–November). During these periods, it is difficult to collect the soil solution with lysimeters due to the freezing of lysimeter tubing. Moreover, we could not access these research plots during the process of river freeze-up in October when travel by boat was not possible. However, three main factors suggest that N leaching losses likely occur during the early winter in this ecosystem: (1) much of the upper 1 m of mineral soil remains unfrozen for two or more months after surface horizons freeze, making infiltration to groundwater possible; (2) plant N demand is probably much reduced during early winter as photosynthetic activity stops, and N immobilization by soil microbes is likely much diminished relative to the summer period due to low soil temperature; and (3) reduced evapotranspiration following leaf-fall (balsam poplar) and the onset of near freezing conditions should increase the possibility of downward infiltration of water.

As a result of snowmelt, soil water potentials at all depths were quite high (wet soil) in May and June, and then became progressively more negative (drier soil) until mid-July (Fig. 5). Post-snowmelt, soil water potentials were significantly correlated with the rate of discharge from the Tanana River (Fig. 6). Despite the continuation of rain events, soil water potentials at all depths actually decreased during mid-August, as did the discharge from the Tanana River. This indicates that the height of the river is more important than rain events in controlling the moisture of the active layer during the growing season. The rise of the Tanana River during the growing season extends the lateral hyporheic zone 200 m or more away from the river edge. This water then enters the unsaturated zone via capillary flow (Viereck et al. 1993b). This process explains how soil water status can remain favorable to plants (generally  $> -20$  kPa) in an ecosystem which has annual losses from evapotranspiration (466 mm) that are considerably higher than precipitation inputs (269 mm).

Several lines of evidence from the chemical analysis of the soil solution also point toward capillary movement as a major factor controlling inputs of dissolved substances into the unsaturated zone. The ratios of major ions (excluding sulfate) in the 40 cm soil solution to those of the same ion in the Tanana River (e.g.,  $\text{Ca}_{40\text{ cm}}:\text{Ca}_{\text{RIVER}}$ ) were fairly constant in both stand types (2.3–5.4 in balsam poplar and 2.0–3.4 in white spruce), suggesting that the soil water originated from a common source (Table 2). Similarly, Yarie et al. (1993) also found significant positive correlations between many individual ions in Tanana River water and those collected from tension lysimeters in these stand types. A PCA of major ions also shows that ions in the Tanana River (particularly K and Cl) are closely associated with those in the 40 cm soil solution (Fig. 3, Table 3). Last, and perhaps most persuasive, the substantially more enriched  $\delta^{18}\text{O}$  signatures of rainwater than the soil solution (Fig. 4) suggests that rain does not make a

significant contribution to the soil solution. This is because a given pool of water will only get more enriched over time as lighter isotopes preferentially evaporate. That river and groundwater are more depleted than the soil solution indicates they are its primary source during much of the growing season.

We also believe that the capillary rise of hyporheic water into the unsaturated zone helps to explain why, in both stands, there was a higher concentration of nitrate in the deeper mineral soil than the surface (Yarie et al. 1993; Fig. 1). The river–groundwater interface is known to be a significant source of  $\text{NO}_3^-$  when oxygen-rich river water, with low bio-available DOC, creates conditions favorable for nitrification (Jones and Holmes 1996). The capillary rise of groundwater would bring this  $\text{NO}_3^-$  to the surface horizons. We speculate that the concentration of  $\text{NO}_3^-$  decreased between 40 and 12 cm as a result of microbial immobilization, fueled by labile C from root exudates and litter, and plant uptake. Thus, the concentration of  $\text{NO}_3^-$  in the soil solution results from the complex interaction of riverine inputs, leaching and biological demand.

It is our view that both capillary inputs and the downward leaching of the soil solution are important processes in the biogeochemistry of the floodplain and do not represent mutually exclusive mechanisms for the movement of N and other dissolved solutes in this ecosystem. For example, experimental additions of  $\text{NH}_4\text{NO}_3$  applied to adjacent plots of balsam poplar and white spruce stands leached below the rooting zone within a year (Brenner et al. 2005). Downward leaching (and runoff) might be more prevalent following snowmelt and during the late fall when river level is relatively low, precipitation inputs are relatively high and surface soils are wettest. In contrast, capillary inputs to the unsaturated zone is likely the dominant process during July and early August as frozen soil dissipates, soil and air temperatures are near their maximum, and glacial melt increases river discharge, elevating groundwater closer to the soil surface (Viereck et al. 1993b; Fig. 5). High-latitude climatic warming (Houghton et al. 1996; Overland et al. 2004; Serreze et al. 2000) is almost certain to increase glacial melt (Arnedt et al. 2002) and river discharge, which would expand the temporal and spatial range of riverine inputs to these stands during the growing season.

In summary, the goal of this study was to compare the relative biological demand for inorganic N in mid-versus late-succession stands by examining the ratio of soil solution DON:DIN below the rooting zone. Our method relied on two key assumptions: (1) that the concentration of DON within the soil solution was fairly constant throughout this successional transition, and (2) that patterns of soil water movement were similar within mid- and late-succession stands. The concentrations of soil solution DON were similar between stands (Fig. 1) and validate our first assumption. However, patterns of water movement were not similar between stands. Downward leaching was often evident following rain

events in white spruce stands but not in balsam poplar stands (Fig. 7). Moreover, we also found much evidence to suggest that the capillary rise of Tanana River water within these forests is responsible for inputs of water and dissolved ions to the soil active layer during the growing season. The different patterns of water movement across this successional transition, and the riverine inputs of water (and associated nutrients) into the soil active layer, greatly confounded our attempt to evaluate the potential change in stand-level N demand. Downward leaching and the capillary rise of water are both important processes influencing the availability of N in this ecosystem. However, the degree to which these processes control N inputs and losses across seasons and throughout succession remains to be determined.

**Acknowledgments** This research was supported with core NSF and USFS funds to the Bonanza Creek LTER (BNZ-LTER) program (NSF DEB 0080609 and USFS PNW01-JV11261592–231). Additional funding came from the Center for Global Change and the UAF Graduate School. We thank J. Garron and L. Oliver for stable isotope analysis, J. McFarland, A. Lecis and M. Helfrich for assistance in the field and D. Masiak for advice and assistance in the laboratory. K. Petrone and T. Dawson provided suggestions on nutrient chemistry and isotopic analysis. We would also like to thank two anonymous reviewers for their helpful suggestions.

## References

- Arndt AA, Echelmeyer KA, Harrison WD, Lingle CS, Valentine VB (2002) Rapid wastage of Alaska glaciers and their contribution to rising sea level. *Science* 297:382–386
- Bonanza Creek (2005) Bonanza creek long-term ecological research site website [http://www.lter.uaf.edu/BCEF\\_index.htm](http://www.lter.uaf.edu/BCEF_index.htm). Cited 15 Dec 2005
- Brenner RE, Boone RD, Ruess RW (2005) Nitrogen additions to pristine, high-latitude, forest ecosystems: consequences for soil nitrogen transformations and retention in mid and late succession. *Biogeochemistry* 72:257–282
- Bundy LG, Meisinger JJ (1994) Nitrogen availability indices In: Weaver RW, (ed) *Methods of soil analysis, Part 2. Microbiological and biochemical properties*, vol 5. Soil Science Society of America, Madison, pp 951–984
- Cabrera ML, Beare MH (1993) Alkaline persulfate oxidation for determining total nitrogen in microbial biomass extracts. *Soil Sci Soc Am J* 57:1007–1012
- Clein JS, Schimel JP (1995) Nitrogen turnover and availability during succession from alder to poplar in alaskan taiga forests. *Soil Biol Biochem* 27:743–752
- Currie WS, Aber JD, McDowell WH, Boone RD, Magill AH (1996) Vertical transport of dissolved organic C and N under long-term N amendments in pine and hardwood forests. *Biogeochemistry* 35:471–505
- EPA (2006) Environmental Protection Agency website <http://www.epa.gov/castnet/sites/den417.html>. Cited 2 Jan 2006
- Flanagan PW, Van Cleve K (1983) Nutrient cycling in relation to decomposition and organic-matter quality in taiga ecosystems. *Can J For Res* 13:795–817
- Gorham E, Vitousek PM, Reiners WA (1979) The regulation of chemical budgets over the course of terrestrial ecosystem succession. *Annu Rev Ecol Syst* 10:53–84
- Hedin LO, Armesto JJ, Johnson AH (1995) Patterns of nutrient loss from unpolluted, old-growth temperate forests: evaluation of biogeochemical theory. *Ecology* 76:493–509
- Houghton JJ, Meiro Filho LG, Callander BA, Harris N, Kattenberg A, Maskell K (1996) The science of climate change, contribution of working group I to the second assessment report of the intergovernmental panel on climate change (IPCC), vol. 1, *Climate change 1995*. Cambridge University Press, Cambridge
- Jones JB Jr, Holmes RM (1996) Surface-subsurface interactions in stream ecosystems. *Trends Ecol Evol* 11:239–242
- Kane DL, Chacho EF Jr (1990) Frozen ground effects on infiltration and runoff In: Ryan WL, Crissman RD (eds) *Cold regions hydrology and hydraulics*. Technical council on cold regions engineering monograph American Society of Civil Engineers, New York, pp 259–300
- Klingensmith KM, Van Cleve K (1993a) Denitrification and nitrogen fixation in floodplain successional soils along the Tanana River, interior Alaska. *Can J For Res* 23:956–963
- Klingensmith KM, Van Cleve K (1993b) Patterns of nitrogen mineralization and nitrification in floodplain successional soils along the Tanana River, interior Alaska. *Can J For Res* 23:964–969
- Littell RC, Stroup WW, Freund RJ (2002) *SAS for linear models*, 4th edn. SAS Institute, Cary
- MacLean R, Oswood MW, Irons JG III, McDowell HW (1999) The effect of permafrost on stream biogeochemistry: a case study of two streams in the Alaskan (U.S.A) taiga. *Biogeochemistry* 47:239–267
- Marion GM, Van Cleve K, Dyrness CT (1993a) Calcium carbonate precipitation-dissolution along a forest primary successional sequence on the Tanana River floodplain, interior Alaska. *Can J For Res* 23:923–927
- Marion GM, Van Cleve K, Dyrness CT, Black CH (1993b) The soil chemical environment along a forest primary successional sequence on the Tanana River floodplain, interior Alaska. *Can J For Res* 23:914–922
- McFarland JW, Ruess RW, Kielland K, Doyle AP (2002) Cycling dynamics of NH<sub>4</sub><sup>+</sup> and amino acid nitrogen in soils of a deciduous boreal forest ecosystem. *Ecosystems* 5:775–788
- Nasholm T, Ekblad A, Nordin A, Giesler R, Hogberg M, Hogberg P (1998) Boreal forest plants take up organic nitrogen. *Nature* 392:914–916
- Overland JE, Spillane MC, Soreide NN (2004) Integrated analysis of physical and biological pan-Arctic change. *Clim Change* 63:291–322
- Perakis SS, Hedin LO (2002) Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds. *Nature* 415:416–419
- Persson J, Nasholm T (2001) Amino acid uptake: a widespread ability among boreal forest plants. *Ecol Lett* 4:434–438
- Qualls RG, Haines BL (1991) Geochemistry of dissolved organic nutrients in water percolating through a forest ecosystem. *Soil Sci Soc Am J* 55:1112–1123
- Ruess RW, Van Cleve K, Yarie J, Viereck LA (1996) Contributions of fine root production and turnover to the carbon and nitrogen cycling in taiga forests of the Alaskan interior. *Can J For Res* 26:1326–1336
- SAS (1999) *The SAS system for Windows*, Release 8.02. SAS, Cary
- Schimel JP, Cates RG, Ruess RW, (1998) The role of balsam poplar secondary chemicals in controlling soil nutrient dynamics through succession in the Alaskan taiga. *Biogeochemistry* 42:221–234
- Schimel JP, Van Cleve K, Cates RG, Clausen TP, Reichardt PB (1996) Effects of balsam poplar (*Populus balsamifera*) tannins and low molecular weight phenolics on microbial activity in taiga floodplain soil: implications for changes in N cycling during succession. *Can J Bot* 74:84–90
- Seely B, Lajtha K, Salvucci GD (1998) Transformation and retention of nitrogen in a coastal forest ecosystem. *Biogeochemistry* 42:325–343
- Serreze MC, Walsh JE, Chapin FS III (2000) Observational evidence of recent change in the northern high-latitude environment. *Clim Change* 46:159–207

- Sollins P, Grier CC, McCorison FM, Cromack Jr. K, Fogel R, Fredriksen RL (1980) The internal element cycles of an old-growth Douglas-fir ecosystem in Western Oregon. *Ecol Monogr* 50:261–285
- Stepanauskas R, Laudon H, Jorgensen NOG (2000) High DON bioavailability in boreal streams during a spring flood. *Limnol Oceanogr* 45:1298–1307
- Tietema A et al (1997) Nitrate leaching in coniferous forest ecosystems: the European field-scale manipulation experiment NITREX (nitrogen saturation experiments) and EXMAN (experimental manipulation of forest ecosystems). *Global Biogeochem Cycles* 11:617–626
- Van Cleve K, Chapin FS III, Dyrness CT, Viereck LA (1991) Element cycling in taiga forest: state-factor control. A framework for experimental studies of ecosystem processes. *BioScience* 41:78–83
- Van Cleve K, Dyrness CT, Marion GM, Erickson R (1993a) Control of soil development on the Tanana river floodplain, interior Alaska. *Can J For Res* 23:941–955
- Van Cleve K, Oliver L, Schlentner R, Viereck LA, Dyrness CT (1983) Productivity and nutrient cycling in taiga forest ecosystems. *Can J For Res* 13:747–766
- Van Cleve K, Viereck LA (1981) Forest succession in relation to nutrient cycling in the boreal forest of Alaska. In: West DC, Shugart H, Botkin DB, (eds) *Forest succession: concepts and applications*. Springer, Berlin Heidelberg New York, pp 185–211
- Van Cleve K, Viereck LA, Marion GM (1993b) Introduction and overview of a study dealing with the role of salt-affected soils in primary succession on the Tanana River floodplain, interior Alaska. *Can J For Res* 23:879–888
- Van Cleve K, Yarie J, Erickson R (1993c) Nitrogen mineralization and nitrification in successional ecosystems on the Tanana River floodplain, interior Alaska. *Can J For Res* 23:970–978
- Viereck LA, Dyrness CT, Foote MJ (1993a) An overview of the vegetation and soils of the floodplain ecosystems of the Tanana River, interior Alaska. *Can J For Res* 23:889–898
- Viereck LA, Dyrness CT, Van Cleve K, Foote MJ (1983) Vegetation, soils, and forest productivity in selected forest types in interior Alaska. *Can J For Res* 13:703–720
- Viereck LA, Van Cleve K, Adams PC, Schlentner RE (1993b) Climate of the Tanana River floodplain near Fairbanks, Alaska. *Can J For Res* 23:899–913
- Vitousek PM, Field CB (2001) Input/output balances and nitrogen limitation in terrestrial ecosystems. In: Schulze E-D, et al., (eds) *Global biogeochemical cycles in the climate system*. Academic, San Diego, pp 217–223
- Vitousek PM, Hedin LO, Matson PA, Fownes JH, Neff JC (1998) Within-system element cycles, input–output budgets, and nutrient limitation. In: Pace ML, Groffman PM (eds) *Successes, limitations, and frontiers in ecosystem science*. Springer, Berlin Heidelberg New York, pp 433–451
- Vitousek PM, Reiners WA (1975) Ecosystem succession and nutrient retention: a hypothesis. *Bioscience* 25:376–381
- Yano Y, McDowell HW, Aber JD (2000) Biodegradable dissolved organic carbon in forest soil solution and effects of chronic nitrogen deposition. *Soil Biol Biochem* 32:1743–1751
- Yarie J, Van Cleve K, Dyrness CT, Oliver L, Levison J, Erickson R (1993) Soil-solution chemistry in relation to forest succession on the Tanana River floodplain, interior Alaska. *Can J For Res* 23:928–940
- Zar JH (1999) *Biostatistical analysis*, 4th edn. Prentice Hall, Upper Saddle River