Nitrogen dynamics in grassland streams along a gradient of agricultural development

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Abstract

We examined nitrogen (N) uptake in seven grassland streams lying in catchments along a gradient (0–84%) of agricultural land use in New Zealand using a stable isotope (^{15}N) addition of NH_4^+ to quantify whole-stream uptake rates and uptake by specific compartments within the streams. Whole-stream uptake of NH_4^+ ranged from 1.2 μmol N m^{-2} min^{-1} to 7.9 μmol N m^{-2} min^{-1} and showed no evidence of strong saturation of uptake with increasing NH_4^+ availability along the land use gradient. The relatively simple pattern of increasing N uptake along the gradient occurred despite substantial shifts in uptake among community members. Uptake of NH_4^+ by epilithic biofilms followed a subsidy–stress relationship, with highest uptake rates at intermediate levels of pastoral development and lowest uptake rates at high pastoral development. At high (>60%) pastoral development, reduced uptake by epilithon was compensated for by enhanced uptake by macrophytes. Compensatory uptake can play an important role in streams when community composition is reorganized by human activity.

Intensification of agricultural land use is a global phenomenon that has degraded aquatic systems (Pimentel et al. 2004). In most cases, agricultural land use alters the physical structure and chemical characteristics of streams, which in turn affect the composition of biological communities (Townsend et al. 1997; Quinn 2000; Allan 2004). These abiotic and biotic changes contribute to alteration of ecosystem processes, including decomposition (Niyogi et al. 2003), metabolism (Young and Huryn 1999), denitrification (Inwood et al. 2005), and nutrient uptake (Niyogi et al. 2004; Bernot et al. 2006), in streams draining agricultural landscapes.

One of the most common results of agricultural intensification is the increased input of nutrients to streams (*e.g.*, Kemp and Dodds 2001). Increased nutrient delivery to streams can stimulate productivity (Quinn 2000), but excessive nutrient enrichment degrades water quality and habitat, both locally and in downstream systems, especially lakes and estuaries (*e.g.*, Carpenter et al. 1998). Streams are important transporters and transformers (Peterson et al. 2001) of nutrients, and their response to enhanced nutrient loading and other changes from agriculture will have important implications for downstream systems. The response by streams to nutrient enrichment depends on how the various organisms in streams take up, retain, and transform added nutrients. At the whole-stream level, we might expect nutrient uptake by organisms to increase as nutrient concentration rises, but uptake may ultimately saturate as other factors (light, etc.) become limiting (Dodds et al. 2002; Niyogi et al. 2004; Bernot et al. 2006). However, because agricultural land use also changes a suite of other abiotic factors and, subsequently, community structure, a more complex response may occur (Townsend and Riley 1999). For example, increased light availability resulting from clearance of riparian vegetation could increase the capacity for nutrient uptake within a stream, reducing the likelihood of nutrient saturation. On the other hand, other factors, such as sedimentation (Quinn 2000), may act as stressors that decrease the capacity for nutrient uptake, leading to rapid saturation or reduction of uptake at the whole-stream level.

Changes in whole-stream nutrient uptake associated with agricultural land use should be an integration of changes of the various components of stream communities that are responsible for nutrient uptake. In streams, primary producers such as benthic algae, moss, and macrophytes, as well as heterotrophic microbes associated

Table 1. Mean stream size (width, depth, and discharge) and temperature, transient storage (A_s : A), and the percentage of the drainage basin in pastoral land use for each stream during the 7-d study period. Values in parentheses are 1 SE for width and depth and range for temperature. For stream size and temperature, means with the same letter are not significantly different (ANOVA, $p > 0.05$).

	Width (m)		Depth (m)		Discharge (L s^{-1})		Temperature (°C)		A_s : A	% pastoral
KBN	1.62[c]	(0.09)	0.13[b]	(0.02)	12[d]	(1)	8.6[e]	(14.0)	0.15	0
KBE	2.08[bc]	(0.13)	0.09[c]	(0.01)	6[d]	(1)	8.8[e]	(5.4)	0.15	0
Stony	3.87[a]	(0.34)	0.15[b]	(0.03)	104[b]	(13)	13.2[a]	(11.6)	0.12	7
Sutton	2.86[b]	(0.27)	0.15[b]	(0.02)	44[cd]	(5)	12.4[c]	(8.0)	0.13	34
Broad	3.08[ab]	(0.12)	0.26[a]	(0.02)	190[a]	(13)	12.9[b]	(7.0)	0.25	62
Crookston	2.06[bc]	(0.10)	0.22[ab]	(0.02)	96[bc]	(25)	10.7[d]	(4.5)	0.34	72
Lovells	2.18[bc]	(0.16)	0.16[b]	(0.01)	48[cd]	(7)	10.2[d]	(5.1)	0.33	84

with detritus, are the primary drivers of whole-stream nutrient uptake (Mullholland et al. 2000). The response of individual components to land-use change may follow a variety of trajectories (Quinn 2000; Allan 2004). For example, increasing agricultural land use may produce a simple linear decline in biotic uptake resulting from stressors such as sedimentation, or uptake may follow a more complex, nonlinear trajectory. In some cases, thresholds of stress may exist, beyond which uptake rapidly changes. In other cases, a subsidy–stress response may occur in which ecosystem function is enhanced at low levels of land use, but is then reduced as land-use intensity increases (Odum 1979).

Whereas many studies have documented increases in nutrient concentration with agricultural development (*e.g.*, Harding et al. 1999), only a few (*e.g.*, Haggard et al. 2001; Niyogi et al. 2004; Bernot et al. 2006) have examined how nutrient dynamics change in response to land-use intensification. Furthermore, the latter studies examined only whole-stream changes in nutrient uptake. As a result, we know little about how nutrient fluxes among components of stream communities change or how those individual fluxes translate into altered whole-stream nutrient dynamics. The recent development of techniques using stable isotope tracers (*e.g.*, Hall et al. 1998; Mulholland et al. 2000) now enables accurate quantification of the flow of nutrients among organisms in streams and along stream reaches. We used the isotope tracer technique to examine how agricultural intensification affects nitrogen (N) uptake and retention, as NH_4^+ and NO_3^-, in seven streams in New Zealand. Our objectives were to (1) examine how whole-stream N dynamics responded to agricultural intensification, particularly whether N uptake became saturated with increasing N concentration and (2) determine how individual components within the stream community responded to pastoral development and how changes in uptake and retention by individual components within streams contributed to the whole-stream functional response.

Methods

Site descriptions—We conducted tracer additions of a stable isotope ($^{15}NH_4^+$) in seven streams found in grassland catchments along a representative gradient of agricultural development in the Otago province of the South Island of New Zealand (Table 1). In the Otago region, animal grazing on native grasslands began about 150 years ago (O'Conner 1982). Planting of European grasses and clover and fertilizing with phosphate started around 60 years ago. The conversion of pasture operations to dairy farms, which have higher stocking intensity and greater use of N and phosphorus (P) fertilizers, is yet more recent, mostly in the last 5–10 years for our catchments. We used two tributaries of the Kye Burn (KBE, KBN) that drained catchments containing relatively pristine tussock grasslands (*Chionocloa* spp.) that were ungrazed. Two other streams, Sutton and Stony Creeks, were surrounded by native tussock grass subjected to light to moderate grazing by sheep and cattle. The other three streams (Broad, Crookston, and Lovells) were in catchments containing pastures planted with exotic grasses and legumes, supplemented with phosphate fertilizer, and subject to high stocking intensity of sheep and beef cattle. The Lovells and Crookston catchments also had dairy operations upstream of our sampling reaches. For each catchment we quantified land use as the % of catchment area in pastoral use, based on data from satellite imagery in the Land Cover Database of New Zealand (Terralink International).

^{15}N *tracer addition*—We used battery-powered fluid metering pumps (Model QBG, FMI) to deliver solutions of ^{15}N-NH_4^+ (99% ^{15}N) to the top of each study reach at a constant rate (4.5 mL min^{-1}) for a 7-d period. ^{15}N was added to the streams at rates calculated to create about an 800‰ increase in stream water $\delta^{15}NH_4$, based on discharge and NH_4^+ concentration measured before the additions. The total NH_4^+ concentration in each stream increased <1%, so our additions were true tracer experiments. The additions were started at different dates between 09 February and 18 April 2002 (late summer to early autumn in New Zealand) to facilitate sampling.

During the additions we monitored pump rate and measured discharge and NH_4^+, NO_3^-, and soluble reactive phosphorus (SRP) concentrations every second day. Discharge at the addition point was calculated by measuring the cross-sectional area of the stream and mean water velocity with an electronic flow meter (Flo-Mate, Marsh-McBirney). Duplicate water samples for nutrient analysis were collected slightly upstream of the addition point, filtered through glass fiber filters (Whatman GF/F),

frozen until the end of the experiments, and analyzed on a Skalar SANplus segmented flow analyzer (Breda) to determine NH_4^+, NO_3^-, and SRP concentrations using the phenate, cadmium reduction, and ascorbic acid reduction methods, respectively (APHA, 1999). In each stream, temperature was measured at 15-min intervals during the additions, using data loggers (HOBO, Onset Computer) placed in the stream at the addition point.

^{15}N sampling and analysis—We quantified tracer ^{15}N uptake and retention from samples of water, primary producers, detritus, and invertebrates collected at five stations downstream from the addition point in each stream. The distance between stations varied among streams from 10 m to 200 m and was chosen based on preliminary additions of $^{14}NH_4^+$. Each sampling station consisted of a riffle (<15-cm deep) with turbulent water.

To measure whole-stream uptake of N, water for $^{15}NH_4^+$ and $^{15}NO_3^-$ analysis was collected at each station 24 h and 7 d after starting the ^{15}N additions. On each date we added a conservative tracer (Cl^- as NaCl) at a constant rate to the stream to account for groundwater dilution and to measure transient storage ($A_s : A$, the area of relatively slow moving water in the channel and hyporheic zone). Chloride concentration was monitored at the bottom station with a conductivity meter (YSI Model 85, Yellow Springs Instruments), and once Cl^- reached a plateau, water was collected at each station. A battery-powered diaphragm pump and an in-line glass fiber filter (preashed, GF/F) were used to collect 5-liter samples for $^{15}NH_4^+$ and $^{15}NO_3^-$ analysis. The samples for $^{15}NH_4^+$ were processed in the field and returned to the laboratory. Water for $^{15}NO_3^-$ analysis was returned to the laboratory on ice and processed. We followed the methods of Holmes et al. (1998) and Sigman et al. (1997) for $^{15}NH_4^+$ and $^{15}NO_3^-$ analysis, respectively. Briefly, NH_4^+ samples were treated with magnesium oxide (MgO) to convert NH_4^+ to ammonia (NH_3^+), which was collected on an acidified filter packet sealed in the sample bottle. Samples for NO_3^- were boiled under alkaline conditions to concentrate NO_3^- and to remove NH_4^+. The samples were then treated with DeVarda's alloy and MgO to convert NO_3^- to NH_3^+, which was collected on a filter packet. $^{15}NH_4^+$ and $^{15}NO_3^-$ samples were shaken in sealed containers for 3 weeks at $\sim 28°C$, after which the filter packs were removed for analysis. The samples for day 7 at Sutton, Broad, and Crookston were accidentally destroyed during isotope analysis, so only data for the 24-h samples are given for those streams.

Samples of benthic compartments (epilithon, moss [*Achrophyllum* sp.], filamentous algae, macrophytes [*Nasturtium officinale*], and coarse and fine benthic organic matter [CBOM and FBOM, respectively]) were collected 1, 3, and 5 days after starting the additions at the second station below the pump and again at all stations after 7 days. These compartments are responsible for the bulk of the uptake in grassland streams of this region (Simon et al. 2004). We also sampled a mayfly (*Deleatidium* spp.) that was the dominant grazing insect in all of the streams. Epilithon was sampled by gently rinsing 3–5 rocks to

remove loosely adhered detritus. The rocks were scrubbed in a small amount of stream water, and any invertebrates and detritus were removed from the epilithon slurry in the field. The epilithon slurry was returned to the laboratory, centrifuged, decanted, resuspended with deionized water, and centrifuged to a pellet that was placed in a glass vial. Moss was collected manually from the stream, rinsed gently to remove detritus and invertebrates, and returned to the laboratory. Macrophytes were clipped at their bases and frozen until processing. FBOM was collected by suctioning material from the top 5 cm of the stream bed with a turkey baster. The FBOM slurry was passed through a 1-mm sieve, returned to the laboratory, and processed as described for epilithon. CBOM and *Deleatidium* were collected using a hand net and sorted in the field. *Deleatidium* were suspended on a small piece of plastic mesh in 50-mL tubes containing stream water. The animals were allowed to clear their guts overnight at 10°C, and 3–10 individuals were composited for each sample.

All organic samples were dried at 60°C for 24–48 h, ground into a fine powder, and packaged in tin capsules. Samples were analyzed for $^{13}C : ^{12}C$ and $^{15}N : ^{14}N$ ratios on a Europa 20-20 Update mass spectrometer interfaced to a Carlo-Erba NA1500 elemental analyzer. All ratios were expressed as δ units (‰) relative to standards (Pee-Dee Beleminite for ^{13}C and air for ^{15}N). We calculated the amount of tracer δ^{15}N in each compartment by subtracting the δ^{15}N of samples collected just before starting the additions at each station from the samples collected after the additions were started.

N biomass—Immediately after completing the ^{15}N additions, we measured the N biomass of each compartment in each stream. After collection and processing, samples were dried at 60°C and weighed to determine dry mass (DM). Dry mass standing stock was converted to N standing stock using the C : N ratio of each compartment determined from samples processed for stable isotope analysis.

We estimated epilithon biomass in each stream from 10 cobbles that were collected along each study reach. A 5-cm-diameter tube was sealed to the surface of each cobble, and the area within the tube was scrubbed using a nylon brush. The resultant slurry was collected, returned to the laboratory, and filtered onto a glass fiber filter (Whatman GF/F) that was then processed for DM. CBOM and grazers were collected from 10 locations in each reach using a Surber sampler (0.06 m², 250-μm mesh net), returned to the laboratory, and frozen until they could be further processed. Invertebrates in the Surber sample were sorted, and *Deleatidium* were processed for DM. The remaining material from each Surber sample was collected on a 1-mm sieve and processed to measure DM of CBOM. FBOM was collected by sealing a pipe (0.07 m²) to the stream bed, mixing the top 5 cm of the sediment and water in the pipe, and then pumping the slurry from the pipe into a bucket where the total volume was noted. The slurry was mixed in the bucket, and a 100-mL subsample was collected and returned to the laboratory. The FBOM slurry was passed through a 1-mm sieve, filtered onto preashed glass fiber

filters (GF/F), and processed for DM. The percent covers of moss, filamentous algae, and macrophytes were determined from 10 transects across each reach. Samples of moss, filamentous algae, and macrophytes from three areas of 100% coverage were collected and processed for DM to convert percent cover to DM.

^{15}N calculations from water and biomass samples—We calculated three metrics that describe whole-reach N uptake in streams: (1) uptake length (S_w, m), the average distance a nutrient atom travels downstream in inorganic form before uptake; (2) uptake rate (U, mmol N m^{-2} h^{-1}), the mass of N moved from the water column to the benthos per unit area and time, and (3) uptake velocity (v_f, m s^{-1}), a measure of nutrient uptake efficiency (i.e., v_f is the ratio of U to ambient nutrient concentration) that corrects for differences in depth and velocity among streams (Stream Solute Workshop 1990, Davis and Minshall 1999). NH_4^+ and NO_3^- S_w, U, v_f, and nitrification rates were calculated as described by Mulholland et al. (2000).

Areal NH_4^+ uptake rates and N-specific NH_4^+ uptake rates (areal uptake rates weighted by compartment N biomass) of each compartment were calculated following the methods of Mulholland et al. (2000). Briefly, mass of ^{15}N associated with each compartment was calculated as:

$$^{15}N_{biomass}(mmol\ m^{-2}) = (\delta^{15}N_{biomass}/1000) \times 0.003663 \times TN_{biomass} \tag{1}$$

where $\delta^{15}N_{biomass}$ is the δ^{15}N value of the compartment, and $TN_{biomass}$ is the N standing stock of that compartment (mmol N m^{-2}). The compartment-specific uptake rates were calculated as:

$$NH_4^+\ uptake\ rate\ (mmol\ N\ m^{-2}d^{-1}) = (^{15}N_{biomass}/^{15}N_{water})/d \tag{2}$$

where $^{15}N_{biomass}$ is the biomass of ^{15}N, $^{15}N_{water}$ was calculated as $(\delta^{15}NH_4/1000) \times 0.003663$, and d is the number of days after starting the additions from which data were used in the calculations. For each compartment, we used the latest day, usually day 7, on which δ^{15}N was still increasing linearly. We applied correction factors suggested by Mulholland et al. (2000) to avoid error caused by uptake of regenerated ^{15}N. Calculations were made for each of the top three stations and averaged. We calculated N turnover times of each compartment as the inverse of N-specific NH_4^+ uptake rates.

At the end of the additions, we constructed a mass balance of ^{15}N added, retained, and exported during the 7-d additions. ^{15}N retained in each compartment was calculated by integrating ^{15}N in each compartment over distance on the final day of the additions (Mulholland et al. 2000). Tracer loss as NH_4^+ and NO_3^- during the entire addition period was determined using the average flux of ^{15}N out of the reach on days 1 and 7.

Table 2. Mean concentrations of NH_4^+, NO_3^-, and soluble reactive phosphorus (SRP) in each stream during the 7-d study period. Values in parentheses are 1 SE. For each nutrient, means with the same letter are not significantly different (ANOVA, $p > 0.05$).

	NH_4^+ (μmol N L^{-1})		NO_3^- (μmol N L^{-1})		SRP (μmol P L^{-1})	
KBN	0.17[c]	(0.07)	0.10[d]	(0.01)	0.04[d]	(0.003)
KBE	0.22[c]	(0.06)	0.23[d]	(0.01)	0.03[d]	(0.003)
Stony	0.52[b]	(0.05)	0.07[d]	(0.01)	0.05[d]	(0.003)
Sutton	0.41[b]	(0.04)	0.47[d]	(0.05)	0.07[d]	(0.010)
Broad	0.88[a]	(0.02)	5.90[c]	(0.41)	0.44[b]	(0.019)
Crookston	0.89[a]	(0.03)	59.78[a]	(3.87)	0.60[a]	(0.006)
Lovells	0.96[a]	(0.03)	15.12[b]	(16.92)	0.33[c]	(0.010)

Statistical analyses—Stream size, chemistry, and N biomass, uptake rate, and turnover time of individual compartments were compared among streams using one-way analysis of variance (ANOVA) followed by post-hoc tests (Tukey) using SAS release 8.00 (SAS Institute). Data were transformed (ln) as needed to meet assumptions of normality before analysis. The relationship between the uptake rate and NH_4^+ concentration was examined using linear regression and saturation kinetics (Michaelis-Menten) models using SigmaPlot software (SPSS). We assumed statistical significance at $\alpha = 0.05$.

Results

Stream size, chemistry, and N standing stocks—Agricultural development, as percent of catchment area in pastoral use, ranged from 0% in the pristine sites (KBE, KBN) to 84% in the most highly developed catchment (Lovells) (Table 1). The streams in pristine catchments were smaller (width, depth, Q) and slightly cooler than the streams in the highly pastoral catchments (Table 1). However, Stony Creek, which had low pastoral land use (7%), was one of the largest and warmest streams in the study. Transient storage was roughly twice as high in the most developed streams (Broad, Lovells, Crookston) as in the other streams (Table 1). Streams in catchments with agricultural development had high N and P concentrations, with NH_4^+, NO_3^-, dissolved inorganic nitrogen (DIN), and SRP concentrations up to 5, 598, 141, and 23 times higher, respectively, than in the pristine streams (Table 2). The amount of pastoral development in the catchments was strongly correlated with lnNH_4^+ ($p = 0.007$, $r = 0.89$), lnSRP ($p = 0.001$, $r = 0.94$), and lnNO_3^- ($p = 0.001$, $r = 0.95$) concentrations in the streams.

The total N standing stock of the primary uptake compartments ranged from 24.6 mmol N m^{-2} to 862.6 mmol N m^{-2}, with an increased N standing stock associated with greater pastoral development ($p = 0.042$, $r = 0.77$). Epilithic biomass was 3–11 times higher in Lovells Stream, the stream with the largest percent pastoral land use, than in the other streams, which had similar standing stocks of epilithic N (Table 3). Epilithon accounted for 23–44% of the total benthic N in the four streams with the

Table 3. Mean standing stocks of N (mmol N m^{-2}) in benthic compartments in each stream. Values in parentheses are 1 SE. For each compartment, values with the same letter are not significantly different (ANOVA, $p > 0.05$).*

Stream	Epilithon		Filamentous algae		Moss		Macrophytes		FBOM		CBOM		*Deleatidium*	
KBN	18.5[b]	(3.2)	0[b]	(0)	2.5[b]	(1.2)	0[d]	(0)	48.7[b]	(10.1)	7.5[b]	(4.0)	3.6[bc]	(1.3)
KBE	7.6[b]	(0.6)	0[b]	(0)	0.8[b]	(0.3)	0[d]	(0)	14.1[b]	(3.5)	2.2[b]	(1.7)	1.2[c]	(0.6)
Stony	13.5[b]	(1.1)	0[b]	(0)	1.0[b]	(0.3)	0[d]	(0)	13.8[b]	(4.4)	0.8[b]	(0.2)	1.4[c]	(0.2)
Sutton	30.8[b]	(3.9)	0.2[b]	(0.1)	0.6[b]	(0.2)	0[d]	(0)	73.8[b]	(27.2)	0.8[b]	(0.3)	3.6[bc]	(1.3)
Broad	8.9[b]	(1.8)	0[b]	(0)	7.4[a]	(3.6)	3.8[c]	(1.9)	75.8[b]	(10.6)	3.4[b]	(0.7)	6.5[b]	(1.7)
Crookston	21.3[b]	(4.7)	0[b]	(0)	0[b]	(0)	400.4[a]	(114.4)	438.5[a]	(51.6)	2.5[b]	(0.3)	12.5[a]	(0.8)
Lovells	86.5[a]	(14.3)	22.4[a]	(11.1)	0[b]	(0)	111.0[b]	(50.8)	304.7[a]	(97.2)	51.4[a]	(26.5)	6.5[b]	(2.1)

* FBOM, fine benthic organic matter; CBOM, coarse benthic organic matter.

lowest pastoral development, but only 2–15% of benthic N in the three most pastoral streams. Moss was absent from the streams with the highest pastoral development (Lovells and Crookston), and only Sutton and Lovells Streams contained filamentous algae. The three streams with the highest pastoral development all contained macrophytes, which comprised a large proportion of the N standing stock, particularly in Lovells (19%) and Crookston (46%) Streams. FBOM comprised more than half of the standing stock of N in all streams; however, Lovells and Crookston had 4–32 times more N as FBOM than the other streams with less pastoral development. Lovells also had 7–67 times more CBOM than the other streams, which contained similar amounts of CBOM. The type of CBOM was not the same in each stream; more pristine sites generally contained tussock grass, whereas the more developed streams contained exotic pasture grasses or dead macrophytes (Niyogi and Simon, pers. obs.). Moss and filamentous algae were absent from most streams and accounted for only a small proportion (<7%) of the total benthic N in streams where they were present. *Deleatidium* mayflies were most abundant in the streams with the highest agricultural land use, but accounted for <6% of the total N measured in all streams (Table 3).

Whole-stream uptake—Uptake lengths of NH_4^+ ranged from 17 m to 510 m among sites (Table 4) and were not related to pastoral development ($p = 0.157$, $r^2 = 0.23$). Most of the variation in uptake length among streams was explained by discharge ($p < 0.001$, $r^2 = 0.88$, $S_w = 1.62Q^{1.13}$). The uptake velocity of NH_4^+ declined with increasing NH_4^+ concentration ($p = 0.001$, $r^2 = 0.67$; Fig. 1) and pastoral land use ($p = 0.020$, $r^2 = 0.63$; Fig. 2). The uptake rate of NH_4^+ was generally well fitted by linear ($p = 0.002$, $r^2 = 0.77$) and Michaelis Menten models ($p = 0.005$, $r^2 = 0.74$, $k_s = 1.12$ μmol N L^{-1}), although Broad Stream had a relatively low U considering its high concentration of NH_4^+ (Fig. 3). With Broad Stream removed, saturation kinetics strongly fitted the remaining data ($p < 0.001$, $r^2 = 0.93$, $k_s = 1.21$ μmol N L^{-1}). The uptake rate of NH_4^+ increased with increasing pastoral development ($p = 0.043$, $r^2 = 0.51$; Fig. 2).

In the agricultural streams with high background NO_3^- concentrations, we did not detect production of $^{15}NO_3^-$ (Broad and Crookston) or only measured a very small enrichment (Lovells, $\delta^{15}NO_3^- < 1.5$‰ above background). In Lovells Stream, our calculated nitrification rates exceeded total NH_4^+ U calculated from the decline in $^{15}NH_4^+$. Considering the very low enrichment of $^{15}NO_3^-$ in

Table 4. Ammonium, nitrate, and dissolved inorganic nitrogen (DIN) uptake parameters for each stream after 1 and 7 days.*

	KBN		KBE		Stony		Sutton		Broad		Crookston		Lovells	
	1	7	1	7	1	7	1	7	1	7	1	7	1	7
NH_4^+														
S_w (m)	38	34	17	17	134	200	101	nd	1198	nd	510	nd	269	188
v_f ($\times 10^{-4}$ m s^{-1})	2.5	2.3	2.5	1.9	1.9	1.3	1.5	nd	0.6	nd	1.2	nd	1.4	1.1
U (μmol N m^{-2} min^{-1})	1.4	1.2	1.8	2.5	4.2	3.6	3.1	nd	2.7	nd	5.6	nd	7.9	6.6
Nitrification rate (μmol N m^{-2} min^{-1})	0.1	0.1	0.5	0.4	0.4	0.1	1.4	nd	–	nd	–	nd	18.0	9.0
Assimilatory U (μmol N m^{-2} min^{-1})	1.3	1.1	1.3	2.1	3.8	3.5	1.7	nd	2.7	nd	5.6	nd	−10.1	−2.4
NO_3^-														
S_w (m)	50	113	177	287	nd	1121	34	nd	–	nd	–	nd	608	3104
v_f ($\times 10^{-4}$ m s^{-1})	1.9	0.7	0.3	0.1	nd	0.2	4.3	nd	–	nd	–	nd	0.6	0.1
U (μmol N m^{-2} min^{-1})	1.1	0.4	0.4	0.1	nd	0.1	10.3	nd	–	nd	–	nd	69.8	4.1
DIN														
U (μmol N m^{-2} min^{-1})	2.5	1.6	2.2	2.6	4.2	3.7	13.4	nd	2.7	nd	5.6	nd	77.7	10.7
Assimilatory U (μmol N m^{-2} min^{-1})	2.4	1.4	1.7	2.2	3.8	3.6	12.0	nd	2.7	nd	5.6	nd	59.7	1.7

* S_w, uptake length; v_f, uptake velocity; U, uptake rate; nd, no data; –, below detection.
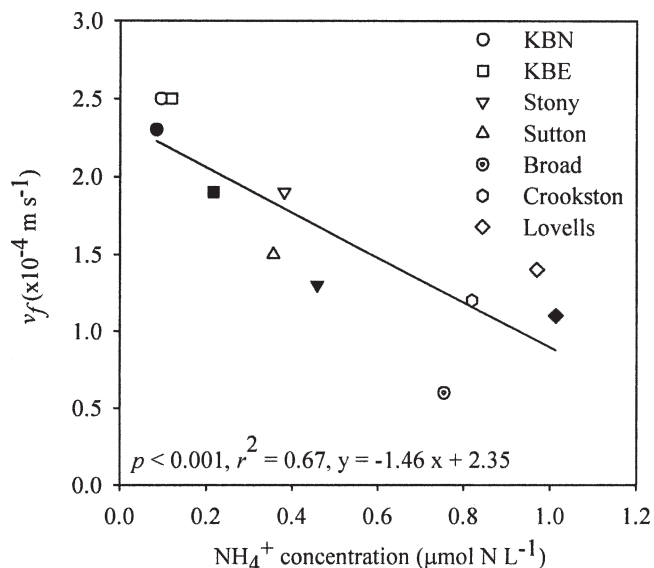
Fig. 1. Relationship between NH_4^+ uptake velocity (v_f) and NH_4^+ concentration across streams. Open symbols are values after 1 d and closed symbols are values after 7 d of $^{15}NH_4^+$ addition. Only data for 1 d are available for three streams (Sutton, Broad, and Crookston).

Lovells, these data probably reflect slight errors in the very small enrichment values and are therefore not reliable. For the remaining streams in which we detected $^{15}NO_3^-$ production, nitrification accounted for 1–45% of whole-stream NH_4^+ uptake among streams.

Compartment uptake—Uptake rates of NH_4^+ by epilithon were 2–9 times higher in the streams with moderate agricultural land use (Sutton and Stony) than in streams on either extreme of pastoral development (Table 5, Fig. 2). This higher uptake was not because of higher standing stocks of epilithon (Table 3); rather, epilithic biofilms were much more metabolically active in Sutton and Stony Streams. The turnover times of epilithon in these streams were 2.3–4.5 times faster than in the pristine streams and 3.2–11.5 times faster than in highly pastoral streams (Table 6, Fig. 4). This trend also held for moss, FBOM, CBOM, and *Deleatidium*, which had 1.4–57.4 times faster turnover times in Sutton and Stony than in the other streams (Table 6, Fig. 4).

Epilithon accounted for a large percentage (66–74%) of total uptake by compartments in the four streams with the lowest pastoral development, but only 19–33% in the three most pastoral streams (Table 5). In the more pastoral streams, FBOM and macrophytes accounted for much of the total NH_4^+ uptake by compartments. Uptake rates by FBOM generally increased with increasing pastoral development (Fig. 2), with the exception of Broad Stream, which had a relatively low standing stock of FBOM as compared to the more pastoral streams (Table 3). Although FBOM was abundant in the pastoral streams, it was relatively inactive, as indicated by slow turnover times (Table 6). Uptake rates of NH_4^+ by macrophytes were very high (Table 4) in Crookston and Lovells Streams, where they were abundant. In Crookston,

macrophytes accounted for 77% of the total compartmental uptake in the stream.

Filamentous algae had very fast turnover times, but were only important in Lovells and Sutton Streams where they were present. In Lovells Stream, filamentous algae were abundant and accounted for the largest (32%) portion of total NH_4^+ uptake by compartments. CBOM and *Deleatidium* had relatively low values for U compared to other compartments (Table 5), largely because of their low biomass. There was little difference in uptake by CBOM among streams. Uptake rates by *Deleatidium* were generally highest in streams of intermediate pastoral development (Table 4, Fig. 2).

The sum of uptake by individual compartments accounted for 73% to 315% of the whole-stream estimate of NH_4^+ U based on $\delta^{15}NH_4^+$ decline with distance along each reach. Total compartment U was not well explained by linear ($p = 0.132$) or Michaelis-Menten ($p = 0.117$) models. As with whole-stream U based on $\delta^{15}NH_4^+$, Broad Stream had a relatively low compartment U, considering its NH_4^+ concentration (Fig. 3). With Broad stream excluded, total compartmental U was fitted well by linear ($p = 0.005$, $r^2 = 0.87$) and Michaelis-Menten ($p = 0.004$, $r^2 = 0.88$, $k_s = 3.91$ μmol N L^{-1}) models (Fig. 3).

N retention and export—At the end of 7 days, we accounted for 27–111% of the ^{15}N added to the streams (Table 7). In the four streams with lowest pastoral development, epilithic biofilms accounted for most (>66%) of the N retained in the stream. In Broad Stream, only 7.5% of the ^{15}N added was retained in the stream, whereas 17% was exported as NH_4^+. In the two streams with the highest pastoral development, macrophytes were responsible for the largest portion of N retention in the streams.

Discussion

Physical and chemical response to land use—In forested systems, pastoral development typically leads to increased temperature and reduced CBOM biomass in streams (Allan 2004). In contrast, neither temperature nor CBOM biomass changed along the land-use gradient in our study. The lack of a temperature and CBOM response to pastoral development is typical of grassland streams in New Zealand, which lack heavy canopy shading even in pristine catchments (Riley et al. 2003). The delivery of fine sediments commonly results from bank failure and stock trampling in agricultural streams of forested and grassland catchments (Quinn 2000; Allan 2004). Increasing FBOM biomass along the gradient of pastoral development suggests this was the case in our streams as well, and the fine sediments probably contributed to macrophyte rooting. As in other systems (Johnson et al. 1997; Bernot et al. 2006), agricultural intensification led to increased nutrient concentration in our streams. Maximum values for NH_4^+, NO_3^-, and SRP in our streams were similar to median values seen in agricultural streams across New Zealand (Larned et al. 2004) and in the low to moderate range of North American and European streams in
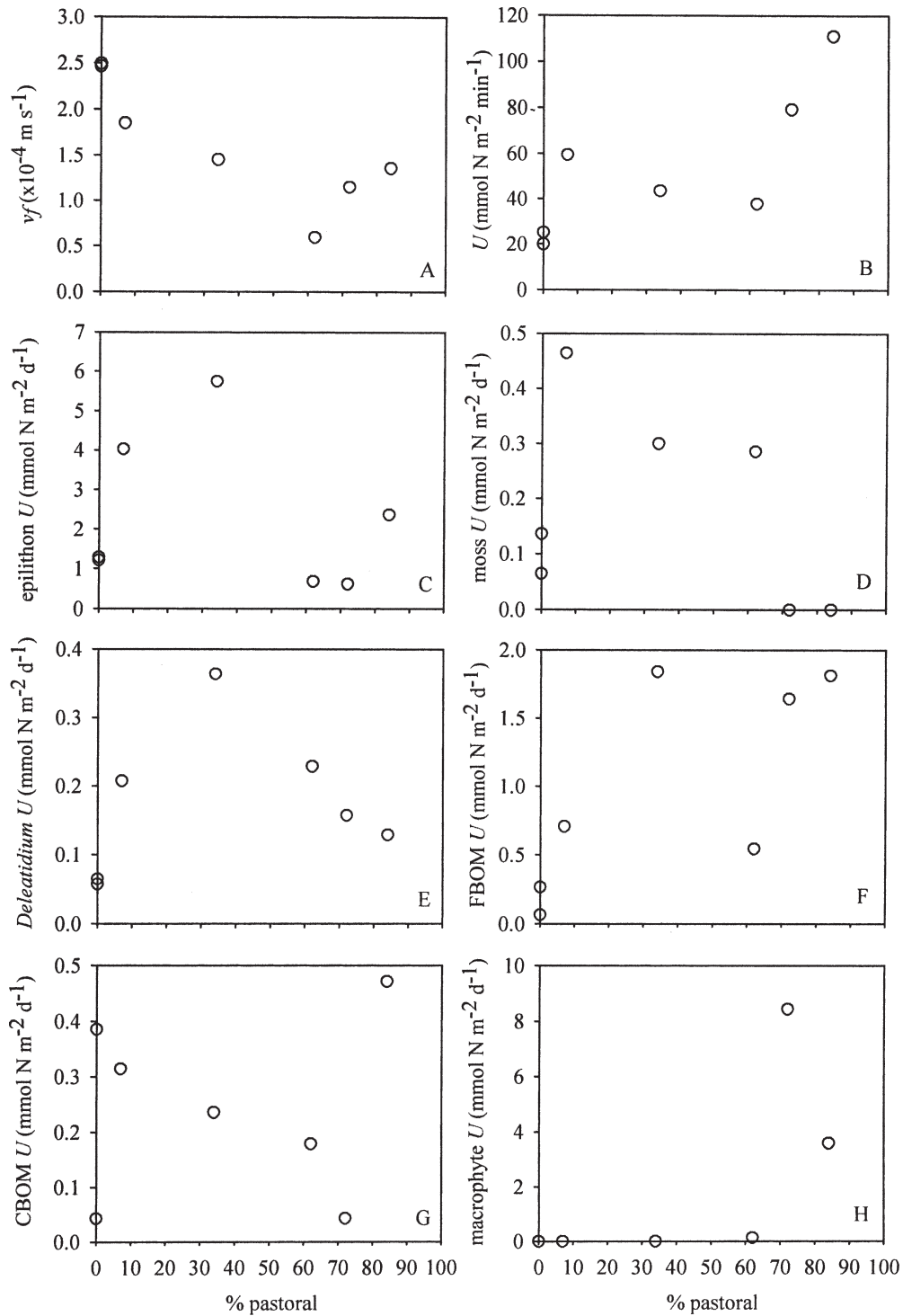
Fig. 2.   (A) Relationship between the amount of pastoral development in each catchment and uptake velocity (v_f), (B) whole-stream uptake rate (U), and (C, D, E, F, G, H) uptake rates of individual compartments across streams.

agricultural catchments (*e.g.*, Bernot et al. 2006; Gücker and Pusch 2006).

Whole-stream response to land-use intensification—If the additional nutrients had saturated uptake along the land-use gradient in our study, S_w would have lengthened,

uptake velocity (v_f) would have declined, and uptake rate (U) would have followed saturation kinetics (Dodds et al. 2002; Niyogi et al. 2004). Whereas the longest S_w of NH_4^+ and NO_3^- occurred in the most pastoral streams in our study, the amount of pastoral land use within a catchment was a poor overall predictor of S_w. Rather, stream size
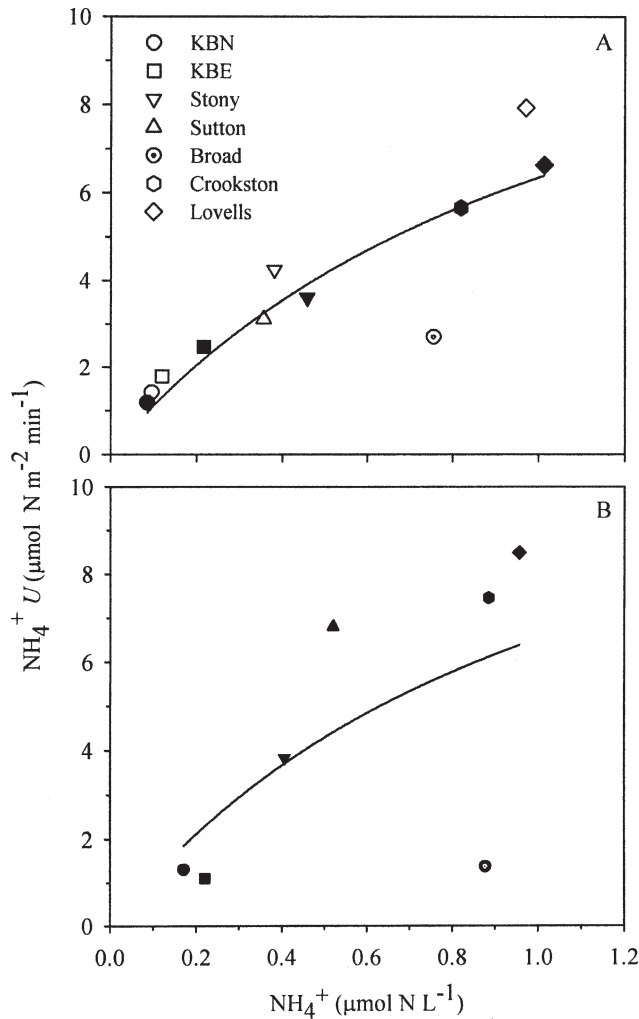
Fig. 3. (A) Relationship between streamwater NH_4^+ concentration and whole-stream uptake rate and (B) total uptake by benthic compartments measured during the experiments. Open symbols are values after 1 d, and closed symbols are values after 7 d of $^{15}NH_4^+$ addition. Only data for 1 d are available for whole-stream U for three streams (Sutton, Broad, and Crookston). Total U by benthic compartments was calculated only after 7 d. Lines are fits of Michaelis-Menten models including all streams.

Uptake velocity and uptake rate, which compensate for differences in stream size, should be better indicators of changes in biotic uptake resulting from land-use change. As agricultural land use increased, the communities in our streams became less efficient at removing NH_4^+ and NO_3^- from the water column. For example, the communities in the most pristine streams were 1.7–4 times more efficient at removing available NH_4^+ from the water column than the communities in the most pastoral streams. In addition, Michaelis-Menten kinetics fit the relationship between NH_4^+ uptake rate and concentration quite well, suggesting that our streams followed the saturation kinetics model along the pastoral gradient. However, the facts that a linear model also fit our uptake rate data well and NH_4^+ concentration in all of our streams was less than the calculated half-saturation coefficient ($k_s = 1.12$ μmol N L^{-1}) for the Michaelis-Menten model indicate that even the streams in the most pastoral catchments were only in the early stages of NH_4^+ saturation. In a similar way, Niyogi et al. (2004) found that uptake of NO_3^- and SRP did not strongly saturate along a land-use gradient in New Zealand streams (some of which were used in the present study). Bernot et al. (2006) also found NH_4^+ uptake did not saturate in North American streams subjected to agricultural land use, leading to NH_4^+ concentrations up to 14 times higher than in our streams.

Agricultural land use typically adds substantial amounts of NO_3^- to streams, which can lead to saturation of uptake (Bernot et al. 2006). NO_3^- was a large N subsidy in our streams, but unfortunately we could not make a detailed examination of how NO_3^- uptake responded to pastoral development. The $^{15}NH_4^+$ method relies on nitrification to produce $^{15}NO_3^-$, and in Broad and Crookston Streams that rate was apparently too low to produce enough $^{15}NO_3^-$ relative to ambient NO_3^- concentration for us to measure whole-stream NO_3^- uptake. Among the streams for which we have data, NO_3^- uptake generally increased with increasing NO_3^- availability, and NO_3^- uptake was a substantial component of DIN uptake. In a study that included some of our streams, Niyogi et al. (2004) found that NO_3^- uptake did not saturate up to concentrations (264 μg L^{-1}) above all but one of our streams.

Linking whole-stream uptake to community components— The lack of strong saturation of nutrient uptake in New Zealand (this study; Niyogi et al. 2004), North American (Bernot et al. 2006), and European (Gücker and Pusch

explained most of the differences in S_w among our streams. This is a typical response that results from reduced contact time between nutrients and the stream bottom in deep, fast streams (Wollheim et al. 2001).

Table 5. Mean uptake rates of N (mmol N m^{-2} d^{-1}) by benthic compartments in each stream. Values in parentheses are 1 SE. For each compartment, values with the same letter are not significantly different (ANOVA, $p > 0.05$).*

Stream	Epilithon		Filamentous algae		Moss		Macrophytes		FBOM		CBOM		*Deleatidium*	
KBN	1.29cd	(0.13)	np		0.14ab	(0.02)	np		0.06c	(0.01)	0.39a	(0.06)	0.06d	(0.01)
KBE	1.21d	(0.34)	np		0.06ab	(0.01)	np		0.26bc	(0.04)	0.04a	(0.01)	0.06d	(0.01)
Stony	4.03b	(0.15)	np		0.46a	(0.09)	np		0.71abc	(0.14)	0.31a	(0.04)	0.21bc	(0.03)
Sutton	5.75a	(0.57)	0.20b	(0.01)	0.30a	(0.05)	np		1.84a	(0.37)	0.24a	(0.09)	0.36a	(0.01)
Broad	0.68d	(0.01)	np		0.29ab	(0.29)	0.13b	(0.13)	0.54abc	(0.10)	0.18a	(0.06)	0.23b	(0.01)
Crookston	0.61d	(0.06)	np		np		8.44a	(2.44)	1.64ab	(0.56)	0.04a	(0.02)	0.16bc	(0.01)
Lovells	2.36c	(0.31)	3.99a	(1.01)	np		3.58a	(0.38)	1.81a	(0.43)	0.47a	(0.19)	0.13cd	(0.01)

* FBOM, fine benthic organic matter; CBOM, coarse benthic organic matter; np, not present in the stream.

Table 6.   Nitrogen turnover times (d) of benthic compartments in each stream. Values in parentheses are 1 SE. For each compartment, values with the same letter are not significantly different (ANOVA, $p > 0.05$).*

Stream	Epilithon		Filamentous algae		Moss		Macrophytes		FBOM		CBOM		*Deleatidium*	
KBN	14.7cd	(1.5)	np		19.0b	(2.3)	np		121.8b	(21.5)	25.4b	(3.8)	61.9c	(7.4)
KBE	7.6bc	(2.6)	np		11.8b	(0.7)	np		56.3ab	(8.7)	74.7b	(35.3)	19.2bc	(3.1)
Stony	3.3a	(0.1)	np		2.3a	(0.4)	np		39.7a	(7.0)	2.5a	(0.3)	7.4a	(1.3)
Sutton	4.9b	(0.6)	1.0a	(0.1)	1.9a	(0.3)	np		31.5a	(6.7)	5.4a	(1.5)	10.1ab	(0.8)
Broad	10.7cd	(4.7)	np		25.6b	(12.8)	47.6a	(29.4)	151.8b	(32.7)	26.9b	(12.8)	28.1c	(0.6)
Crookston	35.2d	(3.2)	np		np		58.2a	(19.3)	325.1b	(87.1)	38.0b	(5.1)	80.3c	(3.2)
Lovells	37.9d	(4.9)	6.8b	(2.3)	np		31.6a	(3.4)	185.1b	(36.3)	143.4b	(41.9)	50.0c	(3.8)

* FBOM, fine benthic organic matter; CBOM, coarse benthic organic matter; np, not present in the stream.

2006) streams in agricultural catchments indicates that the communities in those streams were able to take advantage of increased nutrient availability to some extent. Indeed, total uptake by biotic components in our streams increased with pastoral development. However, the increased uptake required a significant reshuffling of uptake among community members. At low to moderate pastoral development, epilithic biofilms accounted for most (>66%) of the uptake of NH_4^+ by primary uptake compartments. In contrast, epilithon in the three most pastoral streams
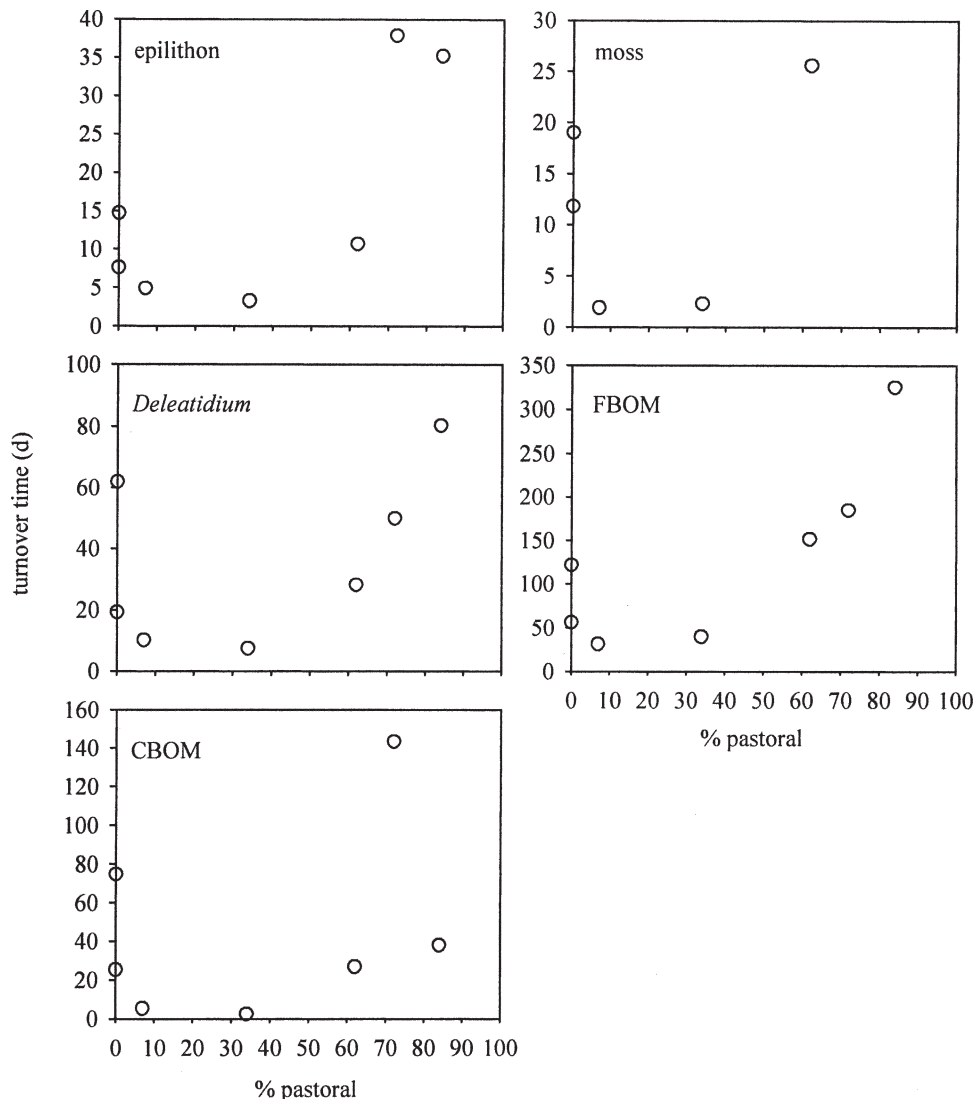

Fig. 4.   Relationship between the amount of pastoral development in each catchment and N turnover times of individual compartments across streams.

Table 7. Mass balance of tracer ¹⁵N retained and exported after 7 days in each stream. Values are mmol ¹⁵N retained or exported and the % of total ¹⁵N added during the additions accounted for by each compartment.*

	KBN		KBE		Stony		Sutton		Broad		Crookston		Lovells	
	mmol	%	mmol	%	mmol	%	mmol	%	mmol	%	mmol	%	mmol	%
Retention														
Epilithon	5.52	20.9	4.20	13.1	5.66	10.8	6.66	19.5	3.99	2.0	5.83	3.5	12.63	19.2
Filamentous algae	–	–	–	–	–	–	0.24	0.7	–	–	–	–	17.35	26.4
Moss	0.46	1.8	0.28	0.9	0.66	2.3	0.33	1.0	4.44	2.2	–	–	–	–
Macrophytes	–	–	–	–	–	–	–	–	1.79	0.9	87.29	52.5	19.55	29.8
FBOM	0.29	1.1	1.09	3.4	1.39	1.7	2.25	6.6	2.54	1.3	12.92	7.8	10.39	15.8
CBOM	1.61	6.1	0.28	0.9	0.46	0.9	0.22	0.7	1.29	0.6	0.65	0.4	2.22	3.4
Deleatidium	0.26	1.0	0.27	0.8	0.32	0.6	0.39	1.1	1.04	0.5	1.35	0.8	0.63	1.0
Export														
¹⁵NH₄⁺	1.00	3.8	0.04	0.1	3.19	6.1	0.66	2.0	34.05	17.1	53.45	32.1	4.33	6.6
¹⁵NO₃⁻	1.16	4.4	3.02	9.4	6.97	13.4	0.66	1.9	0.0	0.0	0.0	0.0	5.62	8.5
Total ¹⁵N accounted	10.29	39.0	9.17	28.7	18.65	35.7	11.41	33.5	49.15	24.6	161.49	97.0	73.14	111.3
Total ¹⁵N added	26.34	100.0	31.98	100.0	52.19	100.0	34.13	100.0	199.69	100.0	166.69	100.0	65.68	100.0

* –, compartment not present in the stream.

accounted for <33% of total N and had uptake rates up to nine times lower than the epilithon in the streams with moderate pastoral development.

Across all streams, the uptake rate of epilithon, moss, and *Deleatidium*, which feeds on epilithic biofilms (Simon et al. 2004), followed a subsidy–stress relationship with increasing land use. These results are consistent with those of Young and Huryn (1999) who found that a moderately agricultural stream was more autotrophic than both an ungrazed grassland stream and a highly pastoral stream in the same area of New Zealand. Whereas epilithic standing stocks sometimes increase in response to agricultural development except at heavily impacted sites (Harding et al. 1999), epilithic biomass in our streams changed little along the pastoral gradient. Instead, the subsidy–stress relationship was driven by changing productivity of epilithic biofilms, as evidenced in turnover times that also followed a subsidy–stress relationship with very rapid turnover in streams of intermediate pastoral development. This boost in productivity at intermediate levels of pastoral development held across all community compartments that were ubiquitous in the streams.

Enhanced productivity and N uptake at moderate pastoral development was likely caused by increased nutrient availability with little sedimentation stress. The addition of fine sediments to streams is a common result of agricultural development in general and in our study area (Matthaei et al. 2006). Experimental additions of fine sediment to streams similar to ours reduced moss coverage, apparently through smothering and reduction in the amount of hard substrate on the stream bed (Matthaei et al. 2006). Such smothering probably led to reduced epilithic uptake and the importance of moss in the highly pastoral catchments of our study. Considering the importance of epilithic biofilms in N uptake and their reduced role in highly pastoral streams, whole-stream uptake of NH₄⁺ should have shown a stronger saturating relationship or even have been severely reduced at

high pastoral development. However, the loss of uptake capacity by epilithon was compensated for by macrophytes, which demonstrated a threshold response in which they were absent from streams with <60% pastoral development and therefore made no contribution to N uptake. Among the highly pastoral streams, macrophytes accounted for substantial N uptake only in the two most pastoral streams (Crookston and Lovells), where they were very abundant. The high uptake rate by macrophytes in Crookston and Lovells Streams was caused by both macrophyte abundance and reasonably fast N turnover. Macrophytes also have large surface areas and probably contributed to the increased transient storage in the three most pastoral streams by slowing water velocity through macrophyte beds (Dodds and Biggs 2002). Abundant macrophyte growth is common in highly pastoral streams of New Zealand (Collier 2004) and is probably a response to the accumulation of fine sediments that macrophytes require for rooting. It appears that although the addition of fine sediment may be a stressor for some community components (epilithon, moss), it may be a subsidy for others (macrophytes).

Unlike the two most pastoral streams, Broad Stream had reasonably high land use and N availability, but low whole-stream NH₄⁺ uptake, indicative of strong N saturation. The reason for this appears to be the low abundance and uptake by macrophytes and FBOM. Broad Stream was characterized by several bedrock outcrops and lacked the typical channel incision and fine sediment deposition common in the most pastoral streams we studied (Niyogi and Simon, pers. obs.). Unlike the other highly pastoral streams, Broad Stream also did not have high transient storage. It is not clear whether this was because of local geology, influencing channel geomorphology, or specific land-use practices in this drainage basin. Our index of land use, total percent pastoral development in the catchment, is a coarse metric of land use, and site-specific factors have been shown to be

important in other studies (Harding et al. 1999; Young and Huryn 1999). The case of Broad Stream suggests that such site-specific factors may substantially alter community structure and, subsequently, N uptake.

The response of whole-stream nutrient uptake to land-use change is an integration of a variety of response types (linear, threshold, subsidy–stress) by individual members of the stream community. Shifts in the relative importance of community members, in terms of nutrient uptake, are apparently an important component driving whole-stream nutrient uptake. For example, Webster et al. (2003) suggested that relatively constant N uptake rate among streams in differing biomes could be explained by metabolic compensation as autotrophs and heterotrophs traded importance in uptake among streams. Webster et al. (2003) questioned whether such compensation would continue to occur as anthropogenic influence increased. Our results indicate that compensation occurs in agriculturally influenced streams, but among the autotrophs (epilithic algae and macrophytes) rather than between autotrophs and heterotrophs. This may be a unique feature of grassland systems in which autotrophs play a large role in pristine streams that are unshaded. Such compensatory uptake, perhaps between heterotrophs and autotrophs, may explain the lack of saturation of nutrient uptake seen in studies of forested streams that have been influenced by agriculture. It is apparent, though, that compensatory uptake in the face of land-use change can break down when factors prevent community restructuring. The next challenges will be to determine the factors that govern when compensation will occur and how to best manage for that situation.

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