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Long-term behaviour of ^{15}N in an alpine grassland ecosystem

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Abstract. Nitrogen dynamics in semi-natural environments is crucial for the development and ecological stability of these systems. The present paper shows the results of the reinvestigation of a ^{15}N-tracer experiment, which was established in the Grossglockner massif in Austria at 2300 m a.s.l. in 1974/1975. We show that large quantities of nitrogen introduced by a single pulse labelling (amounting to approximately 1.7% of the nitrogen in the system) into an alpine grassland remain in the soil–plant system, with only 55% being lost during 27–28 years. In the first 10 cm of the four investigated soil profiles 40% of ^{15}N was recovered, being mainly bound in organic forms. A simple site specific model was established on the basis of the results considering a biological, residual and labile N-pool, the latter being the source for N-losses. By the model a long mean residence time close to 100 years was derived for the remaining ^{15}N.

Introduction

The global nitrogen (N) cycle is increasingly influenced by industrial emissions (Nadelhoffer et al. 1999) resulting in N depositions on soils in the Alps of $10\,\mathrm{kg\,ha^{-1}\,year^{-1}}$ or more, exceeding natural net N-mineralization (Körner 1999). In contrast to intensive agricultural ecosystems, characterised by large N-input and N-losses, semi-natural environments like forests or alpine/arctic grasslands, often being deficient in plant nutrients in general, are characterised by an effective biological recycling mechanism (Hackl et al. 2000).

Productivity of alpine grasslands may be limited by the size of the available N pool, N-deposition and N-fixation by free living organisms being the only input (Körner 1999). In these ecosystems N-input through deposition might have a significant impact by altering the rate of the internal nitrogen cycle governed by turnover times of live and dead aboveground and belowground plant tissues and soil micro-organisms (Körner 1999; Lipson et al. 1999). Short and medium-term studies with ^{15}N-labelled compounds elucidated already the dynamics of competition between plants and soil micro-organisms (Jaeger et al. 1999). However, little is known about the mean residence times of N in the root zone or soil profiles in alpine ecosystems in general. Thus, predictions of the long-term effects of anthropogenic

N-deposition on alpine ecosystems and their plant communities remain to be difficult.

Haunold et al. (1980) illustrated with their $(^{15}NH_4)_2SO_4$ tracer experiment established in the years 1974 and 1975 in the Grossglockner massif that (i) plants took up between 13 and 21% of the added ^{15}N into the above ground parts during the first year, (ii) ammonium-fixation in clay mineral interlayers occurred during the first weeks after application, 13% of ^{15}N was found fixed after 49 days, but only between 1 and 7% after 1 year, (iii) the main portion of ^{15}N remained within the first 3 cm of the soil profile predominantly in organic forms, nearly no ^{15}N was recorded below 30 cm depth and (iv) 803 days after the application between 56 and 65% of ^{15}N was still present in the soil profile and plant cover. A single ^{15}N application at a later point in the vegetation period (mid August) on one plot resulted in a lower N-uptake into the aboveground plant parts (1.65% in the first year) and an even more rapid immobilisation of N in the topsoil. Here we report results from the reinvestigation of the above experiment to gain the first ^{15}N-tracer data set on the long-term behaviour of N in an alpine ecosystem.

Materials and methods

The site is located on a south-west slope in the 'Grossglockner' massif of the 'Hohe Tauern' (47°04′08″N, 12°50′18″E) at 2295 – 2305 m a.s.l. The yearly precipitation ranges from 1300 to 2000 mm, approximately 50% thereof during the vegetation period (1st of June till 31st of October) and the rest during winter. An epigeal runoff of 53.3% of the annual precipitation, especially during snow melt, was estimated (Franz 1980). The mean temperature is slightly below 0 °C (mean summer temperature: 5 °C, Weiss 1980). The site is characterised by metamorphic crystalline rocks with a high mica content (quartz phyllite), soils with a Planosol dynamic within the first 10 cm of mineral soil and a sandy loamy texture (Cambisol; horizons (averages): L: (1)–0 cm, A: 0–2 cm, AP: 2–8 cm, Bw: 8–24 cm, BwCw: >24 cm) and a short vegetation period due to a long lasting snow cover just allowing a sort of pioneer vegetation called Primulo-Caricetum curvulae ('Curvuletum') (Karrer 1980). *Carex curvula* was the dominating plant species in the year 1974 together with *Primula minima* and *Avenochloa versicolor* (Haunold et al. 1980). In the year 2002 *C. curvula* was still dominating with some abundance of *Leontodon montanum*, *Festuca ovina*, *Poa viviparia*, *P. minima*, *Homogyne alpina* and *Pulsatilla alpina*. Soils are slightly acid to acid. In the year 2002 average pH-values (measured in 0.05 M $CaCl_2$) ranged from 4.6 (plots B, D) to 5.9 (C) and 6.0 (A).

The actual nitrogen deposition at the site is not known. Smidt and Mutsch (1993) suggested a range of 8–13 kg N kg N ha^{-1} $year^{-1}$ deposited above the climatic treeline for the Tyrolean Alps.

The four 1 m^2 plots were treated with an equivalent of 100 kg N ha^{-1} (10 g $(^{15}NH_4)_2SO_4$- N m^{-2}) on 11 August 1974 (plot A) and 29 June 1975 (plots B, C, D) after harvesting the plant cover to allow an exact distribution of the fertilizer

(Haunold et al. 1980). The labelled fertilizer was mixed with quartz sand and applied in equal amounts to 16 subplots of 0.0625 m^2. The ^{15}N enrichment of the labelled fertilizer was 33.6/26.12/27.13/26.83 atom%^{15}N in plot A/B/C/D, respectively. The amount of N applied was a compromise between a minimum impact on the N dynamics of the system and the detection limits of the instrumentation at that time. Soil (down to 50 cm depth) and plant samples were taken 49 (29 September 1974), 322 (6 June 1975), 698 (7 July 1976) days after application on plot A and 48 (16 August 1975), 78 (15 September 1975), 376 (6 July 1976) and 803 (11 September 1977) days after application on plots B, C and D. 0.25 m^2 sub-plots remained completely untouched in the 1970s and were used for the final sampling on 11 July 2002. A 30 cm times 30 cm large soil monolith was excavated down to 20/25 cm at all plots after harvesting the plant cover. On plots C and D additional soil samples were taken down to 90 cm with an auger of 8 cm diameter. Soil monoliths were subdivided into 1–5 cm thick layers. Soil was sieved to 2 mm. Fresh samples were used for microbiological and mineral-N measurements, air dried samples for all other investigations. Soil bulk density and skeleton contents were determined. Plant samples were dried at 70 °C and milled to powder. Humic substances were extracted by using a 0.02 M tetrasodium diphosphate solution. Humic acids were precipitated with 0.1 M hydrochloric acid. Fulvic acids remained in the supernatant (Gerzabek et al. 1996). Nitrogen content was analysed using a dry combustion elemental analyser (Carlo Erba NA 1500, Milano, Italy). ^{15}N abundance was measured using the same elemental analyser coupled to an isotope ratio mass spectrometer (Finnigan MAT 251, Bremen, Germany). At five spots not having received the labelled fertilizer control samples were taken. All of them showed very small deviations from the natural $^{15}N/^{14}N$ ratio of air (= 0.368 atom%^{15}N) in the range of a few per mill of this value, which is irrelevant for our purposes.

NO_3-N and NH_4-N and their isotopic composition were measured after extraction with 2 M KCl and removing NH_4 by alkalinisation or destillation of NH_4, respectively.

Microbial N was determined by applying chloroform fumigation and subsequent extraction of organic N (Brookes et al. 1985; Vance et al. 1987).

The portion of nitrogen remaining from the originally applied N mass within each soil layer was obtained as follows:

$$\text{N\_applied} = \text{N}_t X \tag{1}$$

where N_t is the total amount of N (g m^{-2}) per layer and X is calculated as follows:

$$X = 1 - \left[\frac{\text{atom\%}^{15}\text{N}_{\text{soil\_layer}} - \text{atom\%}^{15}\text{N}_{\text{labelled\_N\_applied}}}{\text{atom\%}^{15}\text{N}_{\text{non\_labelled\_soil}} - \text{atom\%}^{15}\text{N}_{\text{labelled\_N\_applied}}} \right] \tag{2}$$

where atom%$^{15}N_{\text{soil\_layer}}$ is the atom%^{15}N value of the respective soil layer, atom%$^{15}N_{\text{labelled\_N\_applied}}$ is the atom%^{15}N value of the ^{15}N labelled nitrogen added and atom%$^{15}N_{\text{non\_labelled\_soil}}$ is 0.3684. This is the atom%^{15}N value of the soil samples, which were taken in 2002 from the same site, having received no ^{15}N labelled material.

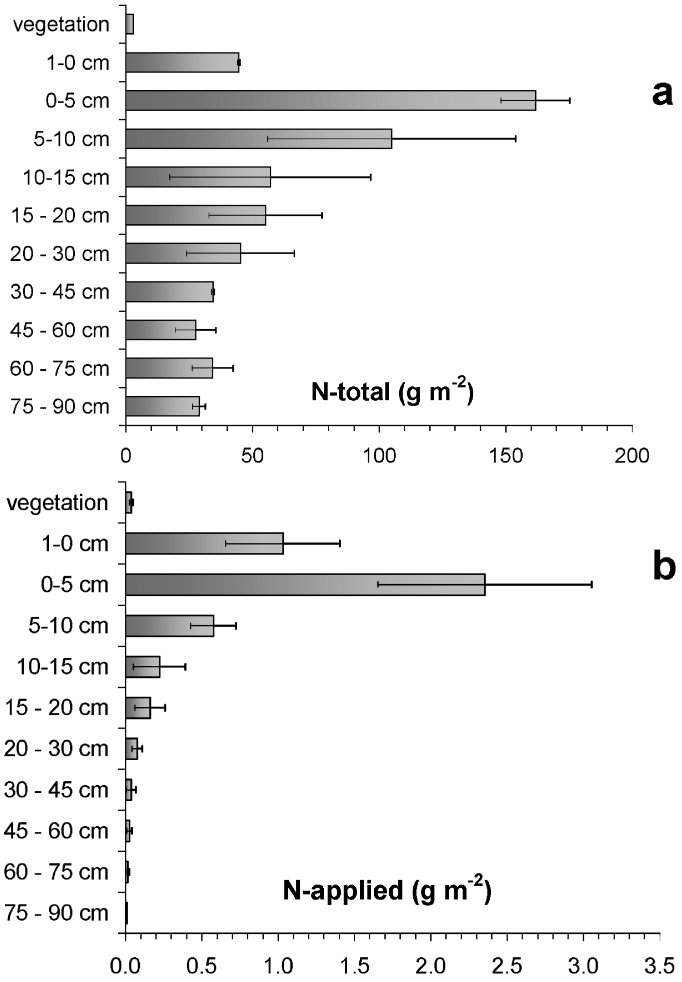

Figure 1. Nitrogen distribution within the soil profiles. Mean values of four plots plus standard deviations of nitrogen distribution within the soil profiles sampled in 2002. (a) Total nitrogen content in g m^{-2}; data were obtained by multiplying the %N content with the weight of the <2 mm soil fractions of the respective volume. (b) Gram of nitrogen of the initially 10 g applied which is recovered in soil after 27–28 years.

Mathematical calculations based on three N-compartments were performed (Figure 2(b)) relying on a simple model structure with a limited number of pools comparable to models used for N-mass balances (Amundson et al. 2003). The purpose was to better visualise the processes and not to develop a generic model for N behaviour in alpine ecosystems. Input data were the historical data set as presented in Haunold et al. (1980) and the results of the sampling in the year 2002. Rate constants (k) were fitted based on the following recovery of applied ^{15}N mass in the soil profile (0–90 cm): 0.13 years: 83.9%; 0.21 years: 88.9%; 1.03 years:

79.3%; 2.2 years: 60.9%; 28 years: 44.9%. The N-labile pool represents all mineral forms of N – mainly ammonia and nitrate – and DON (dissolved organic nitrogen), the N-biological represents N in plants, roots and all other living biomass, and the N-residual pool contains all N bound in litter and soil organic matter. All three compartments were fully reversibly connected. The outflow of nitrogen from each pool depends on a fitted rate constant and the size of the pool (= first order kinetics), inflow into each pool is also modelled as a first order reaction in dependency of the size of the respective neighbouring pool(s). Nitrogen-loss is considered to occur only through the N-labile pool.

The schema of mathematical calculations is represented in Figure 2(b). Accordingly the following set of ordinary differential equations (ODEs) is needed:

$$\frac{\mathrm{dN}_{\mathrm{labile}}(t)}{\mathrm{d}t} = -(k_1 + k_{\mathrm{N-loss}})\mathrm{N}_{\mathrm{labile}}(t) + k_2\mathrm{N}_{\mathrm{biological}}(t) \tag{3}$$

$$\frac{\mathrm{dN}_{\mathrm{biological}}(t)}{\mathrm{d}t} = -(k_2 + k_3)\mathrm{N}_{\mathrm{biological}}(t) + k_1\mathrm{N}_{\mathrm{labile}}(t) + k_4\mathrm{N}_{\mathrm{residual}}(t) \tag{4}$$

$$\frac{\mathrm{dN}_{\mathrm{residual}}(t)}{\mathrm{d}t} = -k_4\mathrm{N}_{\mathrm{residual}}(t) + k_3\mathrm{N}_{\mathrm{biological}}(t) \tag{5}$$

The k-values are described in Figure 2. The ODEs were solved analytically with the software Maple 8.00 Student Edition (Maple 2002). The ‘LinearAlgebra’ package and ‘Linsolve’ function were applied to solve the linear system after Laplace transformation of the original equations. The integral transforms were calculated with the ‘inttrans’ package and the function ‘invlaplace’. For comparison with these results the differential equations were directly solved using the Maple ‘dsolve’ command for exact and numerical ODE solutions. Analytical solutions of the ODEs can be obtained from the authors. The mean residence time is defined by the area under the first moment of the concentration–time curve ($t\mathrm{N}_t$) of N_t from $t = 0$ to infinity divided by the area under the concentration–time curve of N_t from $t = 0$ to infinity.

Results

Table 1 presents data of the sampling 27–28 years after start of the experiment. It is interesting to note that even after this long period the highest ^{15}N-enrichment above the natural ^{15}N abundance of 0.368 atom% is observed in the litter layer (1.03 atom%). From there we can observe a steady decrease with depth, meeting the natural ^{15}N abundance below 75 cm.

When quantifying the amount of ^{15}N still present in the profiles (g m^{-2}, Figure 1(b)) we can observe the following. The largest amount (2.35 g N m^{-2} of 10 g N m^{-2} originally applied) is located in the first mineral soil horizon (0–5 cm), followed by the litter layer (1.03 g N m^{-2}) and the deeper mineral soil horizons. Total ^{15}N recovered in the soil profiles ranges from 33.6% (plot A) to 60.9% (plot B). The mean ^{15}N recovery is 45 ± 13%. Profiles B and D have lower pH values (0–

Table 1. Characterisation of soil profiles 27–28 years after ^{15}N application (sampled in 2002). All values are mean values of the four plots, standard deviations are given in parentheses (N_t = total nitrogen, C_{org} = organic carbon, C/N ratio, FA/HA = fulvic acids to humic acids ratio, HS = extractable humic substances).

Depth	N_t (%)	C_{org} (%)	C/N ratio	Bulk density (<2 mm) (kg m^{-3})	FA/HA ratio	N_{HS} (% of N_t)	$N_{Biomass}$ (% of N_t)	Atom%^{15}N in soil (%)	Atom%^{15}N in HS (%)
Vegetation	2.34 (0.34)							0.71 (0.04)	
1–0 cm	1.56 (0.21)	9.25 (0.96)	5.9	0.28 (0.06)			4.96 (2.13)	1.03 (0.21)	
0–5 cm	0.67 (0.12)	3.04 (0.68)	4.6	0.48 (0.08)	0.34	17 (8)	6.74 (0.70)	0.80 (0.15)	0.81 (0.15)
5–10 cm	0.24 (0.10)	2.25 (0.44)	9.4	0.89 (0.08)	0.60	47 (18)	4.92 (0.70)	0.54 (0.08)	0.56 (0.06)
10–15 cm	0.15 (0.02)	2.26 (0.45)	15.6	0.79 (0.08)	0.56	38 (9)	4.78 (1.95)	0.47 (0.06)	0.49 (0.06)
15–20 cm	0.13 (0.05)	1.39 (0.63)	10.5	0.84 (0.12)	0.49	47 (23)		0.45 (0.05)	0.45 (0.03)
20–30 cm	0.10 (0.04)	1.89 (0.67)	18.9	0.89 (0.07)				0.41 (0.01)	
30–45 cm	0.08 (0.00)	1.29 (0.19)	16.1	0.86 (0.01)				0.40 (0.02)	
45–60 cm	0.09 (0.02)	1.28 (0.11)	15.1	0.65 (0.03)				0.40 (0.02)	
60–75 cm	0.08 (0.01)	1.02 (0.18)	13.5	0.91 (0.13)				0.38 (0.01)	
75–90 cm	0.06 (0.01)	0.81 (0.04)	13.4	0.96 (0.08)				0.37 (0.01)	

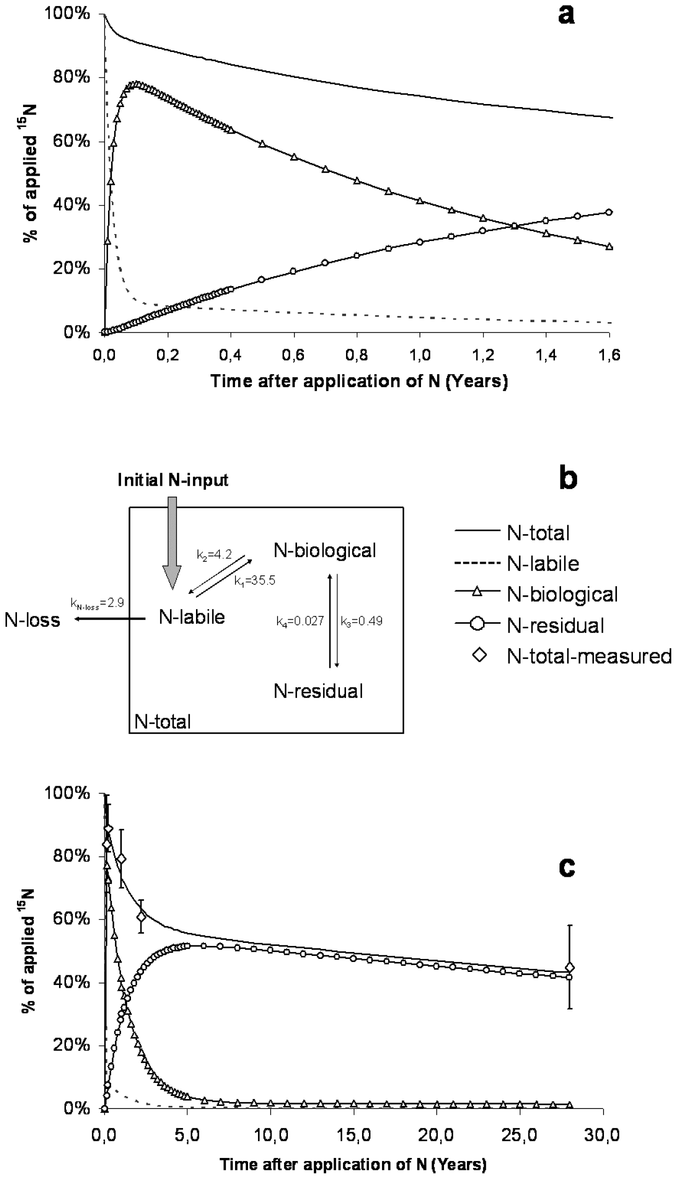

Figure 2. Compartment model to estimate the distribution of initially applied ^{15}N (a) Modelled relative amount of nitrogen in different compartments within the first 1.6 years after ^{15}N application. (b) Schematic presentation of the compartment model, *k* are the experimentally fitted rate constants. (c) Modelled and measured mean values of the four plots plus standard deviations for the first 28 years after application of ^{15}N.

10 cm: 4.7) and a higher average ^{15}N-recovery of 55% than profiles A and C (pH: 6.4; recovery: 34%). Comparing the depth distribution of total N (Figure 1(a)) with that of N applied in 1974/1975 (Figure 1(b)) distinct differences can be observed. Obviously, the applied N stayed in the upper soil horizons, whereas total N exhibits a more even depth distribution.

Aboveground plant parts exhibit 0.71 atom%^{15}N (Table 1), which suggests a still significant contribution of applied ^{15}N to N-uptake of plants. Close to half of total nitrogen is contained in extractable humic substances in mineral soil layers below 5 cm depth (Table 1). The similarity in ^{15}N-enrichment of humic extracts and total soil N suggests applied ^{15}N being contained in humics to a similar proportion.

Mineral N-contents are quite low, NH_4-N and NO_3-N contributing 0.45 and 0.17%, respectively, to total N contents of the 0–5 cm mineral layer. Again the average ^{15}N-abundances (NH_4-N: 0.8 atom%, NO_3-N: 0.7 atom%) are close to that of total N in this layer. These results suggest that the N introduced in 1974/1975 is now quite evenly distributed within the N-soil pools. Soil microbial N amounts to 4.8–6.7% of total N and is strongly related to total N without distinct differences within the soil profile (Table 1). C/N ratios observed are quite low in the litter layer (5.9) and the first 5 cm of the mineral soil (4.6) increasing to quite common values of approximately 9–19 in deeper horizons (Table 1).

Discussion

Adding the present results to those reported earlier (Haunold et al. 1980), the following dynamics of nitrogen introduced into this alpine ecosystem is likely. Nitrogen from $(^{15}NH_4)_2SO_4$ first entered the labile N (mainly mineral N) soil pool within the first 3 cm. Especially in plots B, C, D, which were treated at the end of June, a large portion of ^{15}N was taken up by plants. Combining the measured data from the aboveground biomass with a literature estimate for the root N-pool taking into account that approximately 40% of N is generally stored in below ground plant parts in alpine soils (Körner 1999), plants contained approximately between 22 and 35% of applied ^{15}N during the first vegetation period. About 13% were fixed in clay–mineral interlayers (Haunold et al. 1980). As plant–microbe competition for N might be severe on alpine sites (Jaeger et al. 1999), it could be suggested that another significant portion of ^{15}N was taken up into the microbial N-pool, which was not measured in the 1970s. Parallel to these processes ^{15}N was quickly introduced into the more stable organic-N fraction (humic substances and slowly decaying plant material) being known as the largest N-fraction (Aldag 1976). After only 1 year between 63 and 83% of ^{15}N was found in this fraction, ^{15}N in above ground plant tissues dropped to 4.1% (Haunold et al. 1980).

It can be suggested that the generally slow turnover of plant litter in alpine soils, the quick trapping of N in organic fractions and the recycling of ^{15}N between living and dead plant and microbial biomass are the major factors explaining the slow vertical movement of ^{15}N during the last 27–28 years and the observed flat ^{15}N-depth distribution. This recycling mechanism in alpine soils is also well known for the radioactive elements ^{137}Cs and ^{90}Sr, which are physiological analogues of the plant nutrients K and Ca. The proposed mechanism is basically that plant nutrients released from plant litter immediately are taken up by the highly dense root mat of the vegetation thus minimizing losses both due to leaching and surface run-off (Gastberger et al. 2000).

As we did not observe distinct differences in the N-behaviour on the long term between the N-application in August 1974 and end of June 1975, microbial N-uptake might have partly compensated the lower N-uptake into plants (only 1.65% of the labelled N) in August. In 2002, soil microbial biomass-N contributed about 5% to N_t (Table 1) in 0 – 15 cm depth, which is well supported by literature (Wardle 1992; Ross et al. 1996; Bardgett et al. 2002; Friedel and Scheller 2002). Nevertheless, in midsummer soil microbial N might even rise up to more than 10% of N_t, in these ecosystems depending predominately on N availability (Bardgett et al. 2002). Cold ecosystems are known to store a high proportion of nutrients within the microbial biomass in relation to the vegetation (Jonasson et al. 1999). The slow release from N from the large organic N-pool, paired with the competitive immobilization of N due to soil micro-organisms and vegetation might significantly reduce N losses due to leaching or surface run-off. Recent reports suggest an additional abiotic immobilisation reaction called 'ferrous wheel hypothesis' (Davidson et al. 2003), which in addition might have contributed to the rapid conversion of nitrate into organic N forms.

The low organic carbon contents and very low C/N ratios of the top soil horizons (litter layer and 0–5 cm), which are mainly influenced by plant tissue input suggests a low plant productivity of this ecosystem. According to Körner (1999) (i) C/N ratios become lower with less organic matter contained in soil and (ii) N concentration in plants increase with decreasing effective season length.

The model calculations allow us to follow the short and long-term dynamics of the N applied at the investigated site (Figure 2(a) and (c). The original N-application in mineral form is mainly and quickly transformed – as observed in the experiment – to the N-biological pool and to a smaller extent lost (N-loss) (Figure 2(a). Nitrogen of the N-biological pool is then transformed into N of the residual pool. After 5 years almost 50% of the N applied is stored in the N-residual pool (Figure 2(c).

According to the model, 28 years after application about 42% of the originally applied N is in the N-residual pool, which adds to more than 95% of the total ^{15}N remaining from the application 27–28 years ago, <2% are in the N-biological and <1% in the N-labile pool. A mean residence time of approximately 95 years can be estimated for the applied N in the residual pool. This is longer by at least a factor of three than observed in intensive agricultural systems (Jansson 1963; Riga et al. 1980; Gerzabek et al. 1999).

However, a question remaining open and to be addressed in future is, whether the N dynamics after a single high dose N application is similar to chronic, slightly enhanced atmospheric N deposition. The consequence of continuous N-input in alpine soils above the natural background might be enhanced plant growth (Schäppi and Körner 1997), changes in plant community structures (Theodose et al. 1996) and enhanced turnover of soil organic carbon (Neff et al. 2002). Possible consequences for these extremely sensitive ecosystems and further implications on the important alpine water resources deserve attention.

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References

Aldag R. 1976. Verfügbarkeit des Stickstoffs in Ackerböden. Bestimmungsprobleme aus der Sicht der Umverteilung der Stickstoffverbindungen durch Bebrütung. Landwirtsch. Forsch. 32: 91–99.

Amundson R., Austin A.T., Schuur E.A.G., Yoo K., Matzek V., Kendall C., Uebersax A., Brenner D. and Baisden W.T. 2003. Global patterns of the isotopic composition of soil and plant nitrogen. Global Biogeochem. Cylces 17: 1031.

Bardgett R.D., Streeter T.C., Hartley L.C. and Hartley I.R. 2002. Linkages between soil biota, nitrogen availability and plant nitrogen uptake in a mountain ecosystem in the Scottish Highlands. Appl. Soil Ecol. 19: 121–134.

Brookes P.C., Landman A., Pruden G. and Jenkinson D.S. 1985. Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. Soil Biol. Biochem. 17: 837–842.

Davidson E.A., Chorover J. and Dai D.B. 2003. A mechanisms of abiotic immobilization of nitrate in forest ecosystems: the ferrous wheel hypothesis. Global Change Biol. 9: 228–236.

Franz H. 1980. The overall dynamics of the tested high mountain soils. In: Franz H. (ed) Untersuchungen an alpinen Böden in den Hohen Tauern 1974–1978 – Stoffdynamik und Wasserhaushalt. Veröffentlichungen des Österreichischen MaB-Hochgebirgsprogramms Hohe Tauern Vol. 3. Universitätsverlag Wagner, Innsbruck, pp. 287–295.

Friedel J.K. and Scheller E. 2002. Composition of hydrolysable amino acids in soil organic matter and soil microbial biomass. Soil Biol. Biochem. 34: 315–325.

Gastberger M., Steinhäusler F., Gerzabek M.H., Lettner H. and Hubmer A. 2000. Soil-to-plant transfer of fallout caesium and strontium in Austrian lowland and alpine pastures. J. Environ. Radioactiv. 49: 217–233.

Gerzabek M.H., Danneberg O.H. and Kandeler E. 1996. Humification. In: Schinner F. Öhlinger R. Kandeler E. and Margesin M. (eds) Methods in Soil Biology. Springer, Berlin, pp. 116–119.

Gerzabek M.H., Kirchmann H., Haberhauer G. and Pichlmayer F. 1999. The response of soil nitrogen and ^{15}N natural abundances to different amendments in a long-term experiment at Ultuna, Sweden. Agronomie 19: 457–466.

Hackl E., Zechmeister-Boltenstern S. and Kandeler E. 2000. Nitrogen dynamics in different types of pasture in the Austrian Alps. Biol. Fertil. Soils 32: 321–327.

Haunold E., Gludovatz A. and Richter E. 1980. Stickstoffdynamik in einem alpinen Pseudogley unter Curvuletum. In: Franz H (ed) Untersuchungen an alpinen Böden in den Hohen Tauern 1974–1978 - Stoffdynamik und Wasserhaushalt. Veröffentlichungen des Österreichischen MaB-Hochgebirgsprogramms Hohe Tauern Vol. 3. Universitätsverlag Wagner, Innsbruck, pp. 131–153.

Jaeger III C.H., Russell K., Monson K., Fisk M.C. and Schmidt S.K. 1999. Seasonal partitioning of nitrogen by plants and soil microorganisms in an alpine ecosystem. Ecology 80: 1883–1891.

Jansson S.L. 1963. Balance sheet and residual effects of fertilizer nitrogen in a 6 year study with ^{15}N. Soil Sci. 95: 31–37.

Jonasson S., Michelsen A. and Schmidt I.K. 1999. Coupling of nutrient cycling and carbon dynamics in the Arctic, integration of soil microbial and plant processes. Appl. Soil Ecol. 11: 135–146.

Karrer G. 1980. Die Vegetation im Einzugsgebiet des Grantenbaches südwestlich des Hochtores (Hohe Tauern). In: Franz H. (ed) Untersuchungen an alpinen Böden in den Hohen Tauern 1974–1978 – Stoffdynamik und Wasserhaushalt. Veröffentlichungen des Österreichischen MaB-Hochgebirgsprogramms Hohe Tauern Vol. 3. Universitätsverlag Wagner, Innsbruck, pp. 35–67.

Körner C.H. 1999. Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems. Springer-Verlag, Berlin, Heidelberg.

Lipson D.A., Schmidt S.K. and Monson R.K. 1999. Links between microbial population dynamics and nitrogen availability in an alpine ecosystem. Ecology 80: 1623–1631.

Maple 8.00 2002. Waterloo Maple Inc., Ontario, Canada.

Nadelhoffer K.J., Emmett B.A., Gundersen P., Kjonaas O.J., Koopmans C., Schleppi P., Tietma A. and Wright R.F. 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. Nature 398: 145–148.

Neff J.C., Townsend A.R., Gleixner G., Lehman S.J., Turnbull J. and Bowman W.D. 2002. Variable effects of nitrogen additions on the stability and turnover of soil carbon. Nature 419: 915–917.

Riga A., Fischer V. and van Praag H.J. 1980. Fate of fertilizer nitrogen applied to winter wheat as $Na^{15}NO_3$ and $(^{15}NH_4)_2SO_4$ studied in micro plots through a four course rotation: 1. Influence of fertilizer splitting on soil and fertilizer nitrogen. Soil Sci. 130: 88–99.

Ross D.J., Tate K.R. and Feltham C.W. 1996. Microbial biomass, and C and N mineralization, in litter and mineral soil of adjacent montane ecosystems in a southern beech (Nothofagus) forest and a tussock grassland. Soil Biol. Biochem. 28: 1613–1620.

Schäppi B. and Körner C.H. 1997. *In situ* effects of elevated CO_2 on the carbon and nitrogen status of alpine plants. Funct. Ecol. 11: 290–299.

Smidt S. and Mutsch F. 1993. Messungen der nassen Freilanddeposition an alpinen Höhenprofilen. Proceedings of the International Symposium 'Stoffeinträge aus der Atmosphäre und Waldbodenbelastung in der Ländern der ARGE ALP und ALPEN ADRIA'. GSF-report (Neuherberg – München) 39/93: 21–29.

Theodose T.A., Jaeger III C.H., Bowman W.D. and Schardt J.C. 1996. Uptake and allocation of ^{15}N in alpine plants: implications for the importance of competitive ability in predicting community structure in a stressful environment. Oikos 75: 59–66.

Vance E.D., Brookes P.C. and Jenkinson D.S. 1987. An extraction method for measuring soil microbial biomass C. Soil Biol. Biochem. 19: 703–707.

Wardle D.A. 1992. A comparative assessment of factors which influence microbial biomass carbon and nitrogen levels in soil. Biol. Rev. 67: 321–358.

Weiss E. 1980. Weitere Beiträge zur Klimatologie des Untersuchungsgebietes im oberen Bereich der Südrampe der Glocknerstrasse. In: Franz H. (ed) Untersuchungen an alpinen Böden in den Hohen Tauern 1974–1978 – Stoffdynamik und Wasserhaushalt. Veröffentlichungen des Österreichischen MaB-Hochgebirgsprogramms Hohe Tauern Vol. 3. Universitätsverlag Wagner, Innsbruck, pp. 7–28.