

The effects of snow-N deposition and snowmelt dynamics on soil-N cycling in marginal terraced grasslands in the French Alps

J. C. Clement · T. M. Robson · R. Guillemin ·
P. Saccone · J. Lochet · S. Aubert · S. Lavorel

Received: 10 September 2010 / Accepted: 22 March 2011
© Springer Science+Business Media B.V. 2011

Abstract Atmospheric nitrogen (N) deposition increasingly impacts remote ecosystems. At high altitudes, snow is a key carrier of water and nutrients from the atmosphere to the soil. Medium-sized subalpine grassland terraces are characteristic of agricultural landscapes in the French Alps and influence spatial and temporal snow pack variables. At the Lautaret Pass, we investigated snow and soil characteristics along mesotopographic gradients across the terraces before and during snowmelt. Total N concentrations in the snowpack did not vary spatially and were dominated by organic N forms either brought by dry deposition trapped by the snow, or due to snow-microbial immobilization and turnover. As expected, snowpack depth, total N deposited with snow and

snowmelt followed the terrace toposequence; more snow-N accumulated towards the bank over longer periods. However, direct effects of snow-N on soil-N cycling seem unlikely since the amount of nitrogen released into the soil from the snowpack was very small relative to soil-N pools and N mineralization rates. Nevertheless, some snow-N reached the soil at thaw where it underwent biotic and abiotic processes. In situ soil-N mineralization rates did not vary along the terrace toposequence but soil-N cycling was indirectly affected by the snowpack. Indeed, N mineralization responded to the snowmelt dynamic via induced temporal changes in soil characteristics (i.e. moisture and T°) which cascaded down to affect N-related microbial activities and soil pH. Soil- NH_4 and DON accumulated towards the bank during snowmelt while soil- NO_3 followed a pulse-release pattern. At the end of the snowmelt season, organic substrate limitation might be accountable for the decrease in N mineralization in general, and in NH_4^+ production in particular. Possibly, during snowmelt, other biotic or abiotic processes (nitrification, denitrification, plant uptake, leaching) were involved in the transformation and transfer of snow and soil-N pools. Finally, subalpine soils at the Lautaret Pass during snowmelt experienced strong biotic and abiotic changes and switched between a source and a sink of N.

J. C. Clement (✉) · P. Saccone · J. Lochet ·
S. Aubert · S. Lavorel
Laboratoire d'Ecologie Alpine CNRS UMR 5553,
Université Joseph Fourier, BP 53, 38041 Grenoble
Cedex 09, France
e-mail: jean-christophe.clement@ujf-grenoble.fr

S. Aubert
Station Alpine J. Fourier CNRS UMS 2925, Université
Joseph Fourier, 38041 Grenoble, France

T. M. Robson
Department of Biosciences, Plant Biology, University
of Helsinki, P.O. Box 65, 00014 Helsinki, Finland

R. Guillemin
Laboratoire UMR INRA-UCBN 950 EVA, Esplanade de
la Paix, Université de Caen, BP 5186, 14032 Caen, France

Keywords Wet and dry N deposition · Nitrate ·
Ammonium · Organic N · Mineralization · Snow
depth gradient

Introduction

Over the last 50 years anthropogenic activities (agriculture, industry, transportation, and urbanization) have doubled nitrogen (N) inputs into terrestrial ecosystems around the world (Matson et al. 2002; Vitousek et al. 1997). Long-term records from alpine glaciers reveal substantial increases in ammonium (NH_4^+) and nitrate (NO_3^-) over the last century (Preunkert et al. 2000; Schwikowski 1997). In northern Europe, monitoring during the last few decades shows current atmospheric N deposition to range between 5 and 60 kg N ha⁻¹ year⁻¹ (Aber et al. 2003; Rogora et al. 2006; Singh and Tripathi 2000). For 2050, it is projected that global food demand and N-fertilizer use will again double, leading to N deposition about three times higher than it is today (Tilman et al. 2001). Consequently, even fairly remote ecosystems such as mountainous watersheds may be susceptible to contamination by atmospheric N deposition in highly mobile dry (dust) and wet (snow, rain, fog) forms (Eugster et al. 1998; Fenn et al. 2003; Mayewski and Legrand 1990; Nanus et al. 2003; Nickus et al. 1997).

At high elevations snow can be a key carrier of nutrients from the atmosphere to the soil (Kuhn et al. 1998). Impurities contained in the falling snow result from nucleation nuclei, gaseous components such as HNO_3 dissolved in the ice (Domine and Rauzy 2004), semi-volatile organic components adsorbed at the surface of ice crystals (Domine et al. 2007), and aerosols captured during precipitation (Franz and Eisenreich 1998). However these vectors are usually exceeded by the dry deposition of aerosols carried on the wind and trapped inside the porous structure of the snowpack (Cunningham and Waddington 1993; Domine et al. 2004; Harder et al. 2000). As a result, snowpacks can retain particulates and solutes from atmospheric deposition that are released as an ionic pulse at snowmelt (Williams and Melack 1991b). Although snowpack nutrient accumulation is sometimes negligible relative to soil nutrient status, as for low arctic birch hummock tundra (Buckeridge and Grogan 2010), it has been rarely investigated in the subalpine snowpack. This seasonal release of melt water and nutrients at thaw together with drastic soil temperature changes may still influence the nutrient budget of underlying soils and adjacent headwater streams in subalpine and alpine zones (Brooks and Williams 1999; Buckeridge and Grogan 2010;

Edwards et al. 2007; Litaor et al. 2005; Rixen et al. 2008; Williams et al. 2009).

Remote subalpine ecosystems are usually characterized by nutrient-poor soils (Körner 2004; Seastedt et al. 2004). Hence any atmospheric N deposition can substantially increase bioavailable N contents, and change the rates of soil-N mineralization, nitrification, and ammonification (Hagedorn et al. 2003; Marshall et al. 2008). It may also enhance N losses through N_2O production from soils and snowpacks (Filippa et al. 2009; Meng et al. 2005). Changes in N cycling rates affect ecosystem processes and have consequences for the functional characteristics of subalpine plant communities, such as alteration of root dynamics, compositional changes, and loss of plant diversity (Bassirrad 2000; Jones et al. 2003; Majdi and Andersson 2005; Pennings et al. 2005; Singh and Tripathi 2000).

In the subalpine surroundings of the Lautaret Pass (1,800–2,000 m.a.s.l., Hautes-Alpes, France), nutrient and energy cycling is under the combined influence of climatic conditions (a prolonged cold winter under snow followed by a snowmelt period and a short plant growing season), agricultural practices (mowing, grazing, organic fertilization), and agriculturally modified topography (terraces). The subalpine climate and the traditional agricultural practices have maintained oligotrophic soils and favoured rich plant diversity (Körner 2004; Robson et al. 2007).

The agricultural landscape of this region comprises mid-sized terraces (500–1,000 m²) creating “stairway” mesotopographic gradients (Girel et al. 2010), that potentially influence the range and patterns of key snowpack and ecosystem variables (Litaor et al. 2001). Differential exposure to the wind and solar radiation causes a thick snow layer to accumulate against the bank which gradually decreases towards the slope (Fig. 1). This gradient of snow thickness is paralleled by a kinetic gradient of snowmelt, allowing snow to be retained longer against the bank. The extent to which these patterns influence nutrient dynamics at a terrace scale, and their sensitivity to gradients of atmospheric N deposition across the snowpack, are key factors for our understanding of the role of snowmelt dynamics in this subalpine ecosystem as in alpine and arctic tundra and boreal forests (Baptist et al. 2010b; Brooks and Williams 1999; Buckeridge and Grogan 2010; Williams and Melack 1991b). Furthermore, the snowmelt season is considered as a “hot moment” when

nutrient availability in soils peaks (Robson et al. 2007), with a pivotal effect on the plant and microbial community composition (Bardgett et al. 2005; Robson et al. 2010). Current hypotheses describe this event through a sequence of important changes in the pedosphere which control the nutrient dynamics between soil, vegetation and soil water (Brooks et al. 1998; Buckeridge et al. 2010; Fisk and Schmidt 1996; Jaeger et al. 1999; Lipson et al. 1999; Zeller et al. 2001). Above the Lautaret Pass, in natural hollows where snowbeds persist later into spring, delayed snowmelt affects local N dynamics and promotes particular alpine plant and microbial communities suited to these conditions (Baptist et al. 2010a, b; Zinger et al. 2009). Likewise on subalpine terraces, a deep snow pack could produce more stable conditions leading to larger wintertime soil microbial biomass, which begins to turnover during snow melt, causing higher soil-N concentrations (Buckeridge and Grogan 2010). Whereas, a reduced or absent snowpack may initiate colder wintertime soils with higher nitrate levels due to physical disruption (Groffman et al. 2001), but also earlier and warmer conditions at snowmelt could lead to more rapid loss through denitrification (Brooks et al. 1996, 1997; Filippa et al. 2009; Williams et al. 1998). Yet, it has also been reported that a scarcity of inorganic N under a reduced snowpack in arctic tundra might limit denitrification (Buckeridge et al. 2010). These various findings demonstrate the capacity of snowmelt dynamics to influence N cycling and provide the context for investigating “snowmelt” effects on N dynamics along the above-mentioned mesotopographic gradient in subalpine terraces.

Focusing on the terrace scale, which has not been investigated before in the literature on snow-related N dynamics, we hypothesized that (1) spatial and temporal gradients of snow depth and snow melt dynamics influenced soil conditions creating gradients of temperature, moisture and mineralization (Fig. 1), and (Fig. 2) snow depth and snow melt affect soil-N cycling both directly (through snow-N deposition) and indirectly (through changes in soil conditions).

To test these hypotheses, N dynamics was studied during the snowmelt period in three subalpine terraces located in the grasslands on the south-facing slope beneath the Lautaret Pass. We focused on the amount and the form of N trapped by and released from the snow as well as on the composition of soil-N

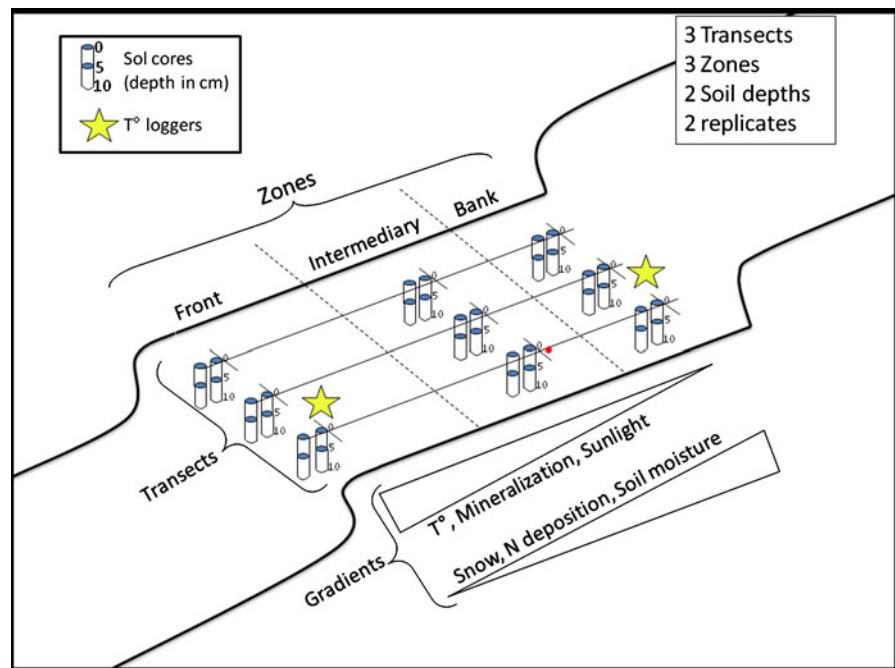
pools and the rates of N processes before, during and after snowmelt.

Materials and methods

Study site

The research site is located on the south-easterly aspect of the upper Romanche Valley in the central French Alps (45.04°N 6.34°E, 1,820–1,880 m a.s.l.) between the village of Villar d’Arène and the Lautaret Pass. The climate is subalpine with strong continental influences. Mean temperatures range between -7.4°C (February) and 19.5°C (July) and mean annual precipitation is 956 mm. The original subalpine forest had been converted to agricultural use prior to the construction of terraces, from the fourteenth century onwards (Quétier et al. 2007). This process involved ploughing, which brought underlying limestone to the surface. The landscape is dominated by these ancient terraces which were previously arable fields (50 years ago) but are now grazed or mown annually for hay at the end of summer. The most-used terraced fields are also fertilised with manure during May, (app. $8 \text{ kg N ha}^{-1} \text{ year}^{-1}$). The reversion to grassland has resulted in plant communities of high conservation value, and it is thought that the particular mowing and grazing regimes practiced today maintain the diversity and structure of the plant community (Quétier et al. 2007). These fields are characterized by low water availability due to high stoniness (Gross et al. 2008; Robson et al. 2007). The dominant vegetation on mown terraces consists in a mixture of *Bromus erectus*, *Sesleria caerulea* and *Onobrychis montana*. When manuring occurs on terraced grasslands tall fast-growing vegetation develops with *Dactylis glomerata*, *Trisetum flavescens*, *Heracleum sphondylium*, *Gentiana lutea* and *Agrostis capillaris*. The terraces have 30–50 cm deep brown soils with a sandy-loam texture (30% clay, 50% silt, 20% sand, $9 < \text{C/N} < 17$, $38 < \text{field capacity (\%)} < 45$, $0.65 < \text{bulk density (g cm}^{-3}\text{)} < 1.24$) at neutral to basic pH values ($6.8 < \text{pH} < 8.2$) due to calcareous stones (>2-cm) well distributed along the profile (Robson et al. 2007). Parent material consists in a mixture of colluviums dominated by calshists with eolian material.

Fig. 1 Diagram of the experimental set-up showing the expected gradients



Snow and soil sampling was performed along nine toposequences distributed on three terraces with similar gentle slope (Fig. 1). Prior to sampling, each toposequence was divided into three stations corresponding to the front of the terrace (front), in middle of the gradient (intermediate) and at the base of the terrace bank (bank). All 27 stations were equipped with 2.50-m long sticks to allow for snow depth measurements.

Snow and soil survey

Snow depth was measured at each station on seven dates spanning between February 2nd and April 19th 2006. Clean acid-washed PVC pipes were used to take three snow cores (d. 12.5-cm, 50-cm long, 6-l) along the vertical snow profile at each station three times during snowmelt (March 29th, April 8th and 17th) and when snow was present ($n = 61$). The PVC pipe length was reduced when snow depth was less than 50-cm. Snow samples of each core were placed in pre-cleaned (acid washed and rinsed with ultra pure water) 250-ml polyethylene flasks, transported in a cool box, and stored at -20°C until nitrogen analysis ($n = 70$). Snow density was measured along each snow profile using 100 ml (or 35-ml when snow

depth was low) stainless steel cylinders and a precision scale ($\pm 0.01\text{-g}$) allowing for calculation of snow accumulated per surface area.

At each station, two soil cores were sampled at two depths (0–5 and 5–10-cm), using a 3.5-cm diameter corer, four times during snowmelt: April 11th (T0), April 19th (T1), May 05th (T2) and May 22nd (T3). The first soil core was divided in two sub-samples. One sub-sample was placed in 100-ml KCl 2 M immediately in the field in order to stop nitrogen transformation (Jones and Willett 2006), and transported to the laboratory where soil extraction was completed (see “Nitrogen analysis” section). Soil extracts were stored at -20°C until chemical analysis. The second fresh soil sub-sample allowed determination of loss on ignition of soil organic matter (SOM) at 550°C , gravimetric soil water content at 105°C , and soil pH in water (Robertson et al. 1999). Net mineralization, nitrification and ammonification rates were measured on the second soil core using the buried bag technique. Net N mineralization (NM), net N nitrification (NN) and net N ammonification (NA) were sequentially evaluated for the 0–5 and 5–10-cm soil layers. Net nitrogen mineralization was calculated from measured changes in the mineral-N content of largely undisturbed soil isolated inside polyethylene bags allowing air to pass through

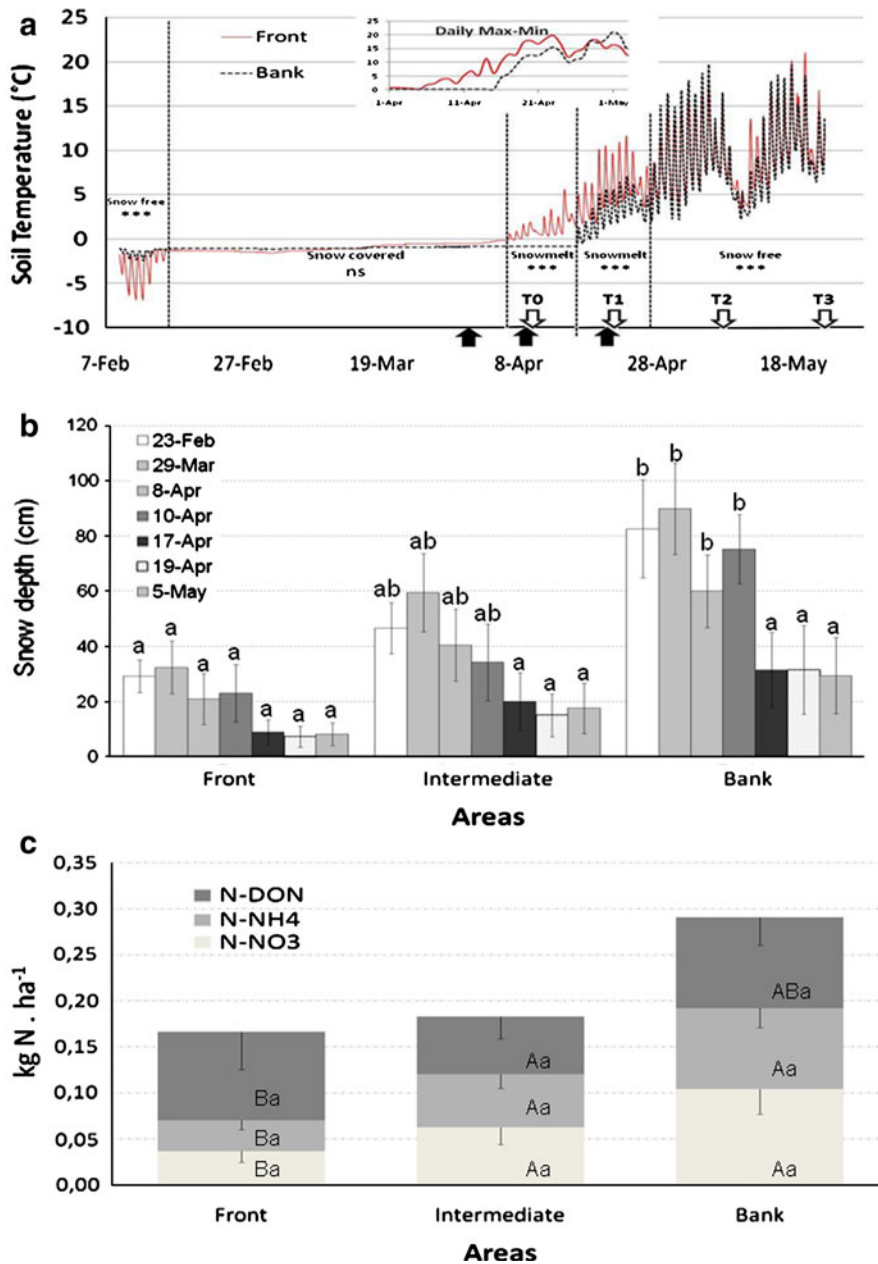


Fig. 2 **a** Time sequence of hourly mean soil temperatures at the front and the bank stations averaged from the triplicated subalpine terraces. *White arrows* represent soil samplings: April 11th (T0), April 19th (T1), May 05th (T2), and May 22nd (T3). *Black arrows* represent snow samplings (March 29th, April 8th and 17th). *Dashed lines* delimit time periods used for Wilcoxon non-parametric t tests: *** $p < 0.001$; NS not significant). The insert graph shows averaged daily differences between maximum and minimum temperatures for each station during the snow melt period. **b** Time sequence of snow depths (mean \pm SE, $n = 9$) measured on seven occasions between February and April for each station. Differences in snow depth

between stations on each date were tested with the Mann–Whitney rank sum test. *Different letters* indicate significant differences at $p < 0.05$. **c** Quantities (mean \pm SE, $n = 27$), of dissolved organic N (DON), N-NH₄⁺, and N-NO₃⁻ measured in the snow pack for each station. Snow chemistry, densities and depths were used to calculate quantities per surface area. For each N species, differences between stations (mean \pm SE, $n = 9$) in N amounts (*upper case letters*) and in N concentrations (*lower case letters*) were tested with the Mann–Whitney rank sum test. *Different letters* indicate significant differences at $p < 0.05$

but preventing leaching (Pastor et al. 1987). Following field incubation, nitrogen content of the bags (T1, T2, T3) was compared to the soil nitrogen content at the beginning of the incubation period (T0, T1, T2, respectively). Net nitrification was estimated from measured changes in $\text{NO}_3\text{-N}$ content in the same incubated soil samples, and, likewise, net ammonification was estimated from measured changes in N-NH_4^+ .

Soil temperature (top 10-cm) was monitored hourly in the front (9 probes) and the bank (9 probes) stations using Hobo U12 loggers (Onset Corp., Bourne, MA).

Nitrogen analysis

Soil sub-samples were extracted for NO_3^- and NH_4^+ by shaking for 1 h in KCl 2 M at 20°C, and filtered through Whatman #42 paper. Extracts were analyzed for NO_3^- and NH_4^+ using standardized protocols on a Flow Solution IV colorimetric chain (OI-Analytical Corp., TX, USA). Total dissolved nitrogen (TDN) was determined on extracted sub-samples after persulfate digestion (Cabrera and Beare 1993). Dissolved organic nitrogen (DON) was then calculated as the difference between TDN and the sum of inorganic nitrogen forms. Snow samples were melted and immediately analyzed for NO_3^- , NH_4^+ , TDN, and DON using the above mentioned methods. The melted samples were not filtered, to preserve the large spectrum of the N fractions contained in the snow and to avoid contamination from air contact or the filtration process. Therefore only the supernatant part of each sample was used for analysis to limit problems with solid particles. Finally, using snow depth, snow density and snow N concentration results, quantities in kg N ha^{-1} of N deposited were calculated.

Statistical analysis

Differences between soil temperatures at the “front” and “bank” were tested with a Wilcoxon non-parametric *t* test for pair-wise independent samples.

Differences between stations, depths and sampling times for snow N contents and soil-N pools and fluxes were tested using non-parametric analyses of variance (ANOVA). Specifically, to test for inter-depth differences at the three stations for each sampling day, data

from the three terraces were pooled by station ($n = 9$), and a non-parametric ANOVA [Mann–Whitney sum test (thereafter MW)] equivalent to a one-way ANOVA based on sum of ranks was used.

To test interstation and inter-sampling time differences, a Kruskal–Wallis test (thereafter KW) data was used (H is the value of the KW test). Finally, non-parametric Spearman correlation test was used to calculate R values with their p levels and identify relationships between measured variables. For each terrace and each station twelve soil temperature variables were computed by calculating daily (averaged for T0, T1, T2 and T3), weekly (averaged for the last 7 days before sampling time) and monthly (averaged for the last 30 days before sampling time) means, minimums, maximums and absolute differences between maximum and minimum. These data were used to test for correlations with other variables. All statistical tests were done using Statistica 8.0 software (StatSoft France).

Results

Soil temperature

Five temporal phases during the winter and spring were delimited from soil temperature data on the bank and front of the terraces (Fig. 2a). First, soil temperature was close to 0°C on the bank while it fluctuated around negative values on the front, illustrating a classic process of early winter where snow is blown into drifts at the back of the terrace (i.e. the bank) where it accumulates. The second phase stretched from February 15th to April 6th when snow covered the whole terrace and soil temperatures at both the front and the bank were stable and similar. Between the 6th and 15th April, soil temperature started to fluctuate daily at the front as snow was melting, while the bank remained under snow with an average soil temperature of -0.8°C . During the fourth phase, from April 15th to 27th, snow melt occurred on the bank with daily fluctuations of soil temperature. During this time period, the front soil was warmer and experienced larger diurnal temperature changes (insert graph in Fig. 2a). Finally, between April 27th and May 22nd both stations were snow free and, although their soil temperatures followed the same trends, they remained significantly different with globally warmer soils for

the front (mean = +9.6°C) than for the bank (mean = +9.1°C).

Nitrogen pools in snow

Snow depth surveys between February and April confirmed that the snow pack was significantly thicker towards the bank until April 10th (Fig. 2b). During the whole season snow depths ranged from 0 to 77-cm for the front and from 0 to 200-cm for the bank. Snow densities ranged from 0.22 to 0.42-g.cm⁻³ (mean = 0.33-g.cm⁻³ ± 0.13) depending on the snowpack depth and the sampling time. The front was rarely covered by more than 30–40-cm of snow whereas the bank was commonly covered by snow of this depth or more.

Overall, nitrogen in snow samples was split into dissolved organic forms (ca. 41.9%), NO₃⁻ (ca. 30.8%), and NH₄⁺ (ca. 27.3%). Snow N concentrations were not significantly related to position on the terrace and did not show temporal variations: [N-NO₃⁻] ranged from 0.02 to 0.19-mg l⁻¹, [N-NH₄⁺] from 0.02 to 0.09-mg l⁻¹, and [organic-N] from 0.00 to 2.35-mg l⁻¹. Yet, once transformed into deposited quantities, total snow N-NO₃⁻, N-NH₄⁺ and N-DON significantly increased towards the bank (Fig. 2c). Proportions of the organic and inorganic N in the snowpack changed along the toposequences: N-NO₃⁻ and N-NH₄⁺ made up approximately 42% of the total snow N for the front and approximately 66% for the intermediate and the bank stations. In contrast, DON represented around 33% of the total snow N for the intermediate and the bank, and 58% for the front station.

Soil characteristics

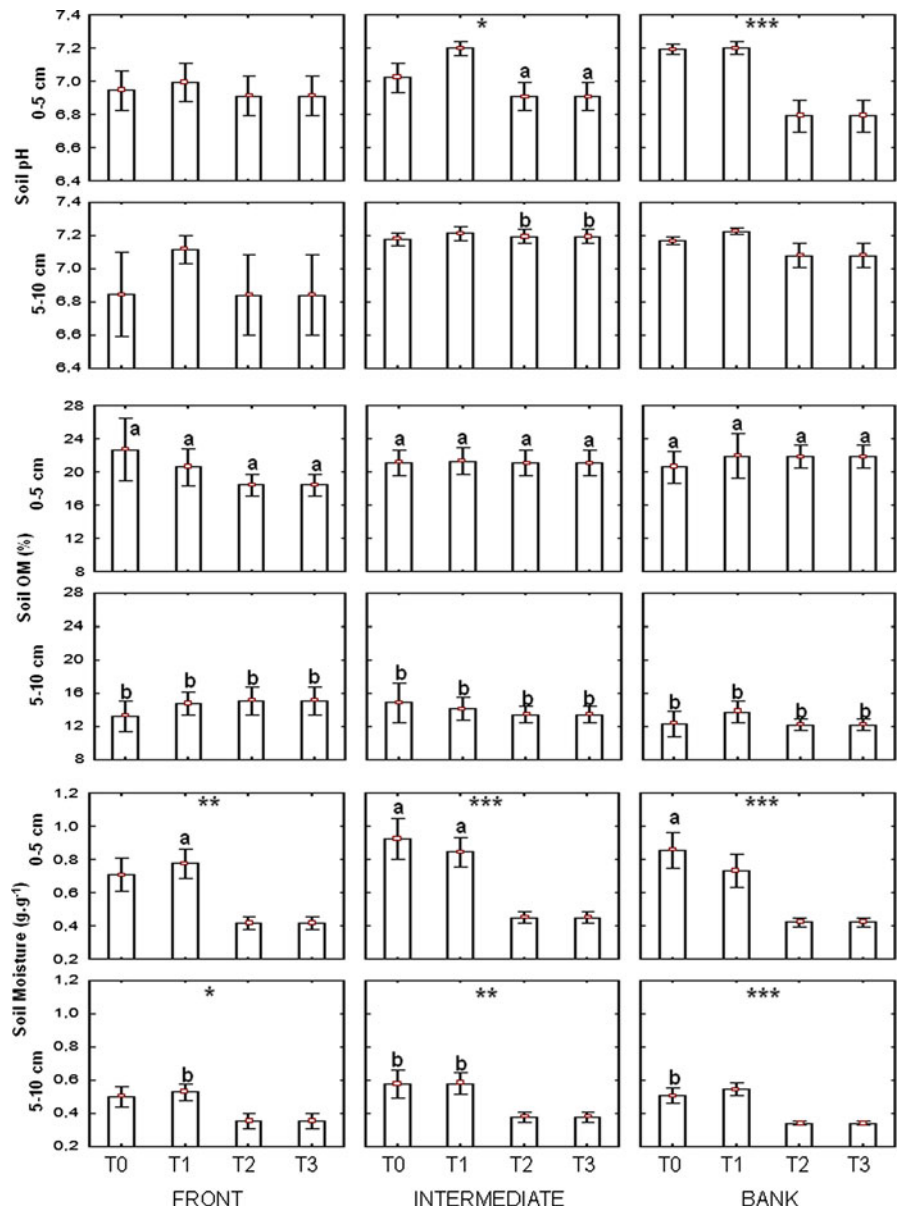
Soil characteristics and microbial processes involved in the nitrogen cycle were compared at each depth and station along the toposequence for the four sampling times (Fig. 3). Soil pH did not significantly differ between depths except at the intermediate station in T2 and T3. For the 0–5-cm soil layer of the intermediate and the bank, pH significantly dropped between T1 and T2 (i.e. after snow melt, Figs. 2a, 3). Soil OM contents were significantly and consistently higher in the upper soil layer than in the lower one, and did not change during the survey. Depth

differences in soil moisture were only significant for T0 and T1, and decreased at both depths between T1 (mean 0.7-g.g⁻¹ ± 0.3, which corresponds to soil saturation measured in a parallel study) and T2 after snow melt (mean 0.4-g.g⁻¹ ± 0.1, which is close to field capacity). Finally, soil pH, OM content and moisture did not show statistically significant trends along the toposequences from the bank to the front for any of the sampling times or depths.

Soil extractable N was dominated by dissolved organic forms which ranged from 46 to 94% of total dissolved N, while N-NH₄⁺ and N-NO₃⁻ ranged respectively from 6 to 54% and from 0 to 28% of total dissolved N (Fig. 4). Other studies have also reported N-NH₄⁺ to be the predominant form of inorganic nitrogen in the soil during the snowmelt period (Mullen et al. 1998), as it can be effectively retained within the uppermost centimetres of the soil in situations when N-NO₃⁻ is leached (Hagedorn et al. 2001) or denitrified (Brooks et al. 1996). Across 0–10-cm soil depth, patterns of soil-N-NH₄⁺ and N-DON contents increased from the front towards the bank (Fig. 4), with significant differences between stations for N-NH₄⁺ (T0), and DON contents (T0 and T2). The front had significantly lower N-NH₄⁺ (T0) and N-DON (T0 and T2) than the bank while soil-N-NO₃⁻ was not clearly distributed along the toposequences. However, within each station, temporal patterns were significant for most soil-N forms. Mean soil N-NH₄⁺ and N-DON doubled between T0 and T2 and then dropped at T3, though temporal DON variations were not significant for the bank station. Finally, soil-N-NO₃⁻ peaked twice in the front and the bank stations at T1 and T3.

Although snow and soil-N quantities were two orders of magnitude apart, we examined the relationships between snowpack N and soil-N pools during snowmelt by taking two consecutive spring samples of snow and soil at each station; April 8th and 17th for the snowpack and April 11th and 19th for the soil (Fig. 5). Focusing on the bank and the front stations and on a specific daily basis, significant Spearman correlations were almost absent between soils N pools (kg-ha⁻¹) and the corresponding snow pack N quantities (kg-ha⁻¹). When snow-N pools were averaged by date and tested against soil-N pools measured at each sampling time and station (Table 1), there were significant relationships between mean inorganic snow-N pools (i.e., NO₃ and NH₄) and soil-N

Fig. 3 Mean values ($n = 9$; \pm SE) of soil pH, soil organic matter content and soil moisture at two depths (0- to 5-cm, 5- to 10-cm) and four sampling times: April 11th (T0), April 19th (T1), May 05th (T2), and May 22nd (T3). Different letters above the bars show significant differences ($p < 0.05$) between depths using a Mann–Whitney U test. Asterisks above graph show the significance of inter sampling time differences using a Kruskal–Wallis Test (** $p < 0.001$; * $p < 0.01$; * $p < 0.05$)



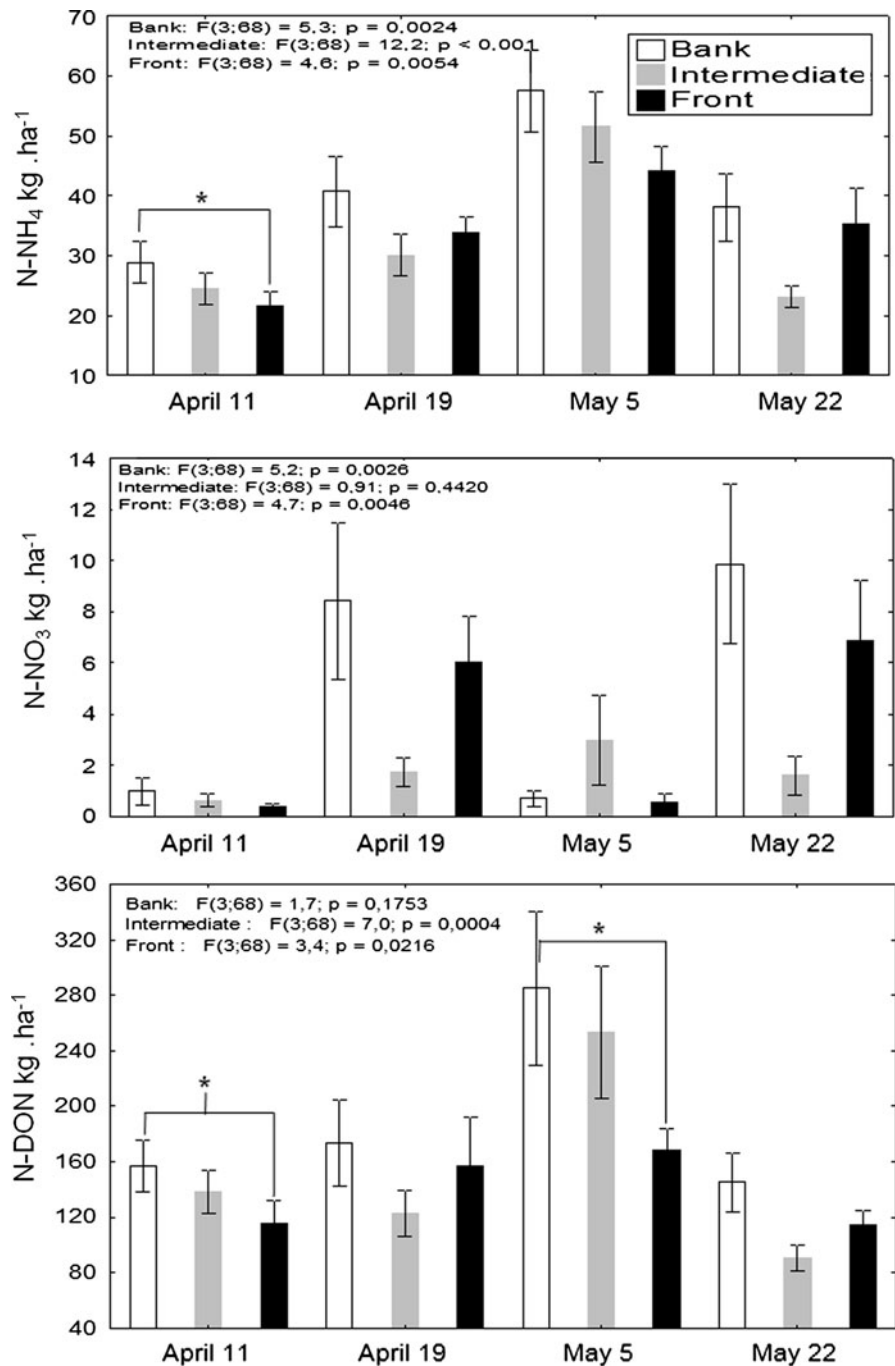
pools up to and including May 22nd, but spatial or temporal patterns remained unclear.

Soil nitrogen mineralization

There was no difference between soil depths in net N transformation rates (i.e. NM, NN, and NA), apart from at the intermediate station on T2 and T3 (KW test, $p < 0.05$). An inter-station difference was found only for the top soil on T3 (KW test, $p < 0.05$). However, the time of sampling during the

experimental period significantly affected the rates of the soil-N processes. Regardless of soil depth and station, N mineralization rates decreased during the survey from T0–T1 to T2–T3. Mean net N mineralization (NM) was initially positive at all stations and became negative between T2 and T3. Mean net N nitrification (NN), i.e. the production of N-NO_3^- , was positive between T0 and T1 in all stations, weakly negative between T1 and T2 and positive again afterwards. Finally mean net N ammonification (NA), i.e. the production of N-NH_4^+ , was positive between

Fig. 4 Soil-N-NH₄⁺, N-NO₃⁻, and dissolved organic-N contents (mean ± SE, *n* = 18) for each station and the four sampling times: April 11th (T0), April 19th (T1), May 05th (T2), and May 22nd (T3). The data from the two depths were pooled by station. Intersampling time differences (significant at *p* < 0.05) for each N forms and station were tested and results (*F* and *p* values) are inserted in each graph. Asterisks above bars give *p* levels of inter-station differences based on a Mann-Whitney test (**p* < 0.05)



T1 and T2 for all stations, and became negative later on, similar to the drop in NM.

Cumulative mineralization, nitrification and ammonification rates were calculated for the whole period of 46 days between T0 and T3 (Table 2). Cumulative net N mineralisation rates were at the lower end of values reported for soils from other

subalpine meadows surveyed between May and October using the resin core method (Zeller et al. 2000). Cumulative NM rates differed between stations only for the top soil layer (KW, *p* < 0.05), and this was mainly due to the intermediate station which had much lower mineralisation rates (negative values at 0–5-cm) than the front or the bank stations. When

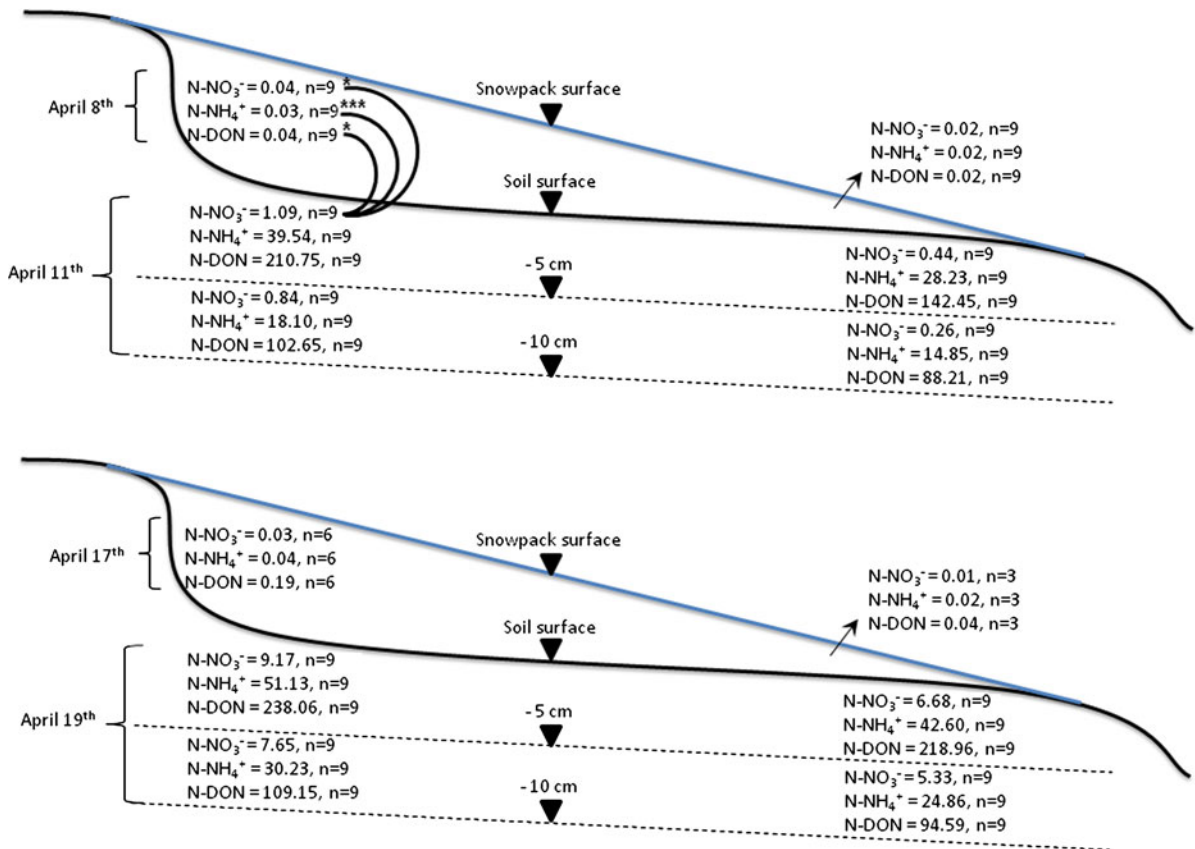


Fig. 5 Mean N stocks ($\text{kg}\cdot\text{ha}^{-1}$, $n = 9$, standard errors are not reported) measured simultaneously in the snowpack and the soil layers along the terrace toposequence (bank and front stations) at two different times during snowmelt. N is variable for snow data depending on the actual presence of snow. When

tested pair-wise, no inter-station differences in cumulative net N mineralisation rates were evident between the front and the bank.

Discussion

Limited atmospheric N deposition occurred with snow

Total N deposited with snow followed the mesotopography of the terraces with twice as much snow-N accumulation towards the bank than at the front (Fig. 2b, c). We observed a shift favouring the relative dominance of dissolved organic-N forms in the snowpack towards the front area. Snow-N inputs were relatively low ($\sim 0.2\text{--}0.3\text{-kg N ha}^{-1}$) when compared with other alpine and subalpine sites worldwide

significant, asterisks give the p level (** $p < 0.001$; * $p < 0.05$) of the non-parametric Spearman correlations (R values not shown) between snow-N pools from April 8th and 17th and soil-N pools from April 11th and 19th respectively

(Aber et al. 2003; Sievering et al. 1996; Williams et al. 2009), though they remained close to values from the Swiss Alps (Hiltbrunner et al. 2005; Nickus et al. 1998). In fact, we measured $0.2\text{--}0.3\text{-kg N ha}^{-1}$ in the snow between February and April which, therefore, represented just a small portion of the total annual N deposition (dry and wet) which is reported to range between approximately 12 and $22\text{ kg N ha}^{-1}\text{ year}^{-1}$ at the regional scale (Hiltbrunner et al. 2005).

Turning to concentrations of N within the snowpack, these did not vary among terraces showing that snow quality was homogeneous across the site within a set altitudinal range ($\sim 1,800\text{-m.a.s.l.}$). Snow inorganic N concentrations in the area of the Lautaret Pass during winter 2006 were consistent with other studies (Edwards et al. 2007; Hiltbrunner et al. 2005; Kuhn 2001; Nickus et al. 1998; Williams et al. 2009). They probably originated from local pasture

Table 1 Non-parametric Spearman correlations (*R* values are given with *p* level: *** *p* < 0.001, ** *p* < 0.01, * *p* < 0.05, NS non significant) between mean snow-N pools calculated forthe entire period and soil-N pools measured at different times (April 11th and 19th, and May 5th and 22nd) during snowmelt and at two locations along the toposequences (*n* = 9)

Snow	Soil												
	Bank						Front						
	N-NO ₃		N-NH ₄		N-DON		N-NO ₃		N-NH ₄		N-DON		
	0–5 cm	5–10 cm	0–5 cm	5–10 cm	0–5 cm	5–10 cm	0–5 cm	5–10 cm	0–5 cm	5–10 cm	0–5 cm	5–10 cm	
N-NO ₃ (kg/ha)	11-Apr	0.84**	NS	NS	NS	NS	NS	NS	NS	0.70*	0.75*	NS	0.87**
	19-Apr	NS	0.85**	NS	0.83**	NS	0.68*	NS	NS	NS	NS	NS	NS
	5-May	NS	0.92***	NS	NS	NS	NS	0.91***	NS	NS	NS	NS	NS
	22-May	0.88**	NS	NS	NS	NS	0.75*	NS	NS	NS	NS	NS	NS
N-NH ₄ kg/ha	11-Apr	NS	NS	NS	0.67*	NS	NS	NS	NS	NS	NS	0.78**	0.72*
	19-Apr	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	5-May	NS	0.70*	NS	NS	NS	NS	0.75*	NS	NS	0.77*	NS	0.77*
	22-May	NS	NS	NS	NS	NS	0.85**	NS	NS	NS	NS	NS	NS
N-DON kg/ha	11-Apr	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	19-Apr	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	5-May	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	22-May	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

Table 2 Cumulative net mineralisation (NM), nitrification (NN) and ammonification (NA) rates for each station and by depth individually or averaged (mean and standard errors, *n* = 9) between April 11th and May 22nd 2006 (i.e., 46 days)

	Front		Intermediate		Bank	
	0–5 cm	5–10 cm	0–5 cm	5–10 cm	0–5 cm	5–10 cm
CumNM ($\mu\text{g N g}^{-1}46 \text{ d}^{-1}$)	9.3 ± 3.3 a	11.1 ± 6.7 a	−2.0 ± 1.7 b	1.5 ± 1.6 a	9.9 ± 4.4 a	9.8 ± 3.7 a
CumNN ($\mu\text{g N g}^{-1}46 \text{ d}^{-1}$)	3.9 ± 1.9 a	3.2 ± 1.8 a	0.3 ± 0.4 a	0.7 ± 0.6 a	5.6 ± 1.8 a	4.5 ± 2.5 a
CumNA ($\mu\text{g N g}^{-1}46 \text{ d}^{-1}$)	5.4 ± 3.3 a	7.9 ± 5.8 a	−2.4 ± 1.6 a	0.8 ± 1.3 a	4.3 ± 3.9 a	5.3 ± 1.9 a
CumNM ($\mu\text{g N g}^{-1}46 \text{ d}^{-1}$)		10.2 ± 3.7 a		−0.2 ± 1.2 b		9.8 ± 2.8 a
CumNN ($\mu\text{g N g}^{-1}46 \text{ d}^{-1}$)		3.5 ± 1.3 a		0.5 ± 0.1 b		5.0 ± 1.6 a
CumNA ($\mu\text{g N g}^{-1}46 \text{ d}^{-1}$)		6.7 ± 3.3 a		−0.8 ± 1.1 b		4.8 ± 2.1 a

Inter-station differences were tested using non parametric ANOVA (Mann–Whitney sum test). Different letters indicate significant differences at *p* < 0.05

fertilisation (NH₄⁺) and transportation (NO₃[−]) (Fenn et al. 2003; Williams and Melack 1991a), though dominant weather patterns at our site suggest that deposited N might also originate from atmospheric pollution from Grenoble or the Pôvalley (Schmitt et al. 2005). Relative to inorganic N, snow organic-N concentrations at the Lautaret Pass were much higher than typically found in the literature and represented about 40% of the snow pack N; with the absence of filtration probably contributing to this high proportion. Melted snow samples were not filtered prior analyses to limit contamination. Thus they integrated both wet and

dry N depositions. The latter would include dust and organic matter particles, which can be an important component of N deposition, as reported in Colorado where dry deposition contributed 25–33% of total N deposition (Burns 2004). In subarctic and arctic snowpacks, dry deposition forms include organic-nitrate and other organic-acids (Franz and Eisenreich 1998; Taillandier et al. 2006; Wadham et al. 2006). This concurs with organic N forms dominating the N pool deposited with snow at our site.

We acknowledge that possible abiotic transformations of inorganic N within the snowpack such as

NH_4^+ volatilization, nitrification or photochemical reactions were not investigated here and, therefore, cannot be ruled out to explain the N trends along the toposequence. Yet, at Niwot Ridge, Colorado, Williams et al. (1996) traced isotopically labelled inorganic N in a seasonal snowpack and found no evidence of such transformations. Other changes within the snow pack could also explain the shift favouring the relative dominance of organic-N forms in the snow towards the front of the terraces (Amoroso et al. 2010). It is possible that snow porosity and structure differed between the front of the terraces where snow was more often disturbed by the wind than at the back and had difficulty accumulating. As a result, the proportion of dry deposition of aerosols carried by the wind and trapped inside the front snowpack could be higher because of a more porous and disturbed snow mantle when compared with the bank's snowpack (Cunningham and Waddington 1993; Domine et al. 2004; Harder et al. 2000). Further investigations of the physical properties and dynamics of the subalpine snowpack are necessary before conclusions can be drawn about these internal abiotic processes. Another possible explanation for the high concentration of organic N forms in the snowpack proposes that water percolation and increasing heat due to solar radiation during snow melt stimulates microbial activities in snowpacks (Jones and Pomeroy 1999). In which case, resulting increases in N immobilization and turnover by snow-microbial communities could have been responsible for the concomitant spatial decreases in snow- NO_3^- and NH_4^+ and increase in snow organic-N at the terrace front. A spatial and temporal survey of the snow microbial communities would be needed to confirm this hypothesis.

Snow N inputs versus soil-N pools: does it matter?

Direct effects of N deposited with snow on soil-N cycling must be extremely limited as total N brought by the seasonal snowpack was negligible relative to subalpine soil-N stocks (mean $\sim 200\text{-kg N ha}^{-1} \pm 10$ SE, $n = 216$) and plant available soil-N (mean $\sim 47\text{-kg N ha}^{-1} \pm 5$) measured for the same terraces in a previous study (Robson et al. 2010). When considering their relative contribution to each soil-N pool, snow-N deposition was almost always

negligible. Organic N in the snow pack represented 0.1% of the soil DON pool, while NO_3^- and NH_4^+ in the snow pack represented 3 and 0.2% of soil- NO_3^- and NH_4^+ pools respectively. Although such a small accumulation of N in the snowpack has been found elsewhere (Buckeridge and Grogan 2010), the relatively small snow pack during the winter 2005–2006 leading to a lower than usual snow accumulation on the terraces could partially explain why the contribution of the snowpack-N to soil-N cycling was small.

In our study, the decoupling between snow and soil- NO_3^- pools during snowmelt was mainly due to the pool-size differences but snow-N was still eluted to the top soils. Fine-scale investigation of the spatial and temporal dynamics failed to reveal a clear relationship between that N held in the snowpack and soil-N pools, suggesting that any patterns that did exist were complex and varied along the soil profile or the toposequence (Table 1; Fig. 5). Based on the literature, we suggest that snow-N was either eluted and directly transported by runoff on frozen soils, preferentially in the front area and before snowmelt (Sickman et al. 2003), or incorporated into the soil-N pools, predominantly towards the bank and during snowmelt. The latter suggestion is in line with results from the Soddie site, Colorado, where inorganic N released from the snowpack infiltrated the underlying substrate where it underwent biogeochemical transformation (Williams et al. 2009). This is also likely to occur at our site with subalpine soils assimilating inorganic N released from the seasonal snowpack via microbial mineralization or immobilization, or abiotic adsorption on SOM (Baptist et al. 2008; Lipson et al. 1999; Williams et al. 1996). The newly formed organic N can also be released as DON from subsequent microbial cells lyses as discussed in the next section. Additionally, Piatek et al. (2005) used isotopic approaches to show that snow- NO_3^- was not directly responsible for the soil- NO_3^- flush in surface waters during early spring snowmelt discharge, but that this NO_3^- flush actually originated mainly from the nitrification of NH_4^+ (Spoelstra et al. 2001). Similarly, we found significant mean cumulative nitrification rates in the studied subalpine terraces producing pulse-releases of soil- NO_3^- (and joined protons), which was flushed at thaw and lost as leachate or denitrified in saturated soils. Denitrification (i.e. microbial nitrate reduction into N_2 or N_2O)

is a very likely sink for snow and soil- NO_3^- , because of anaerobic conditions resulting from excess soil water inputs during snow melt (Brooks et al. 1997; Brooks et al. 1996; Filipina et al. 2009; Williams et al. 1998).

Soil parameters respond to snowmelt dynamics

Soil-N cycling was strongly affected by snowmelt via its impact on soil biotic and abiotic parameters. As anticipated, the snowpack distribution and the snowmelt dynamic on the terraces were paralleled by a spatial and temporal evolution of soil parameters (except for SOM). Soil temperature at the front started to fluctuate 10 days earlier than at the bank coinciding with an average snowpack depth below 30-cm; a snow-depth threshold suggested sufficient to decouple soil temperature from air temperature (Cline 1995). This trend was later confirmed for the bank where daily variations of soil temperatures also started once mean snow depth had fallen below 30–40 cm. Finally, as snow was melting, daily variations in soil temperatures increased, together with subsequent changes in soil moisture and pH.

Before snow melt (T0), soil moisture was higher for the top soils and towards the bank where the snowpack was thicker, favouring anaerobic microbial activities such as denitrification. Additionally, snow accumulation at the bank implied that more snow water reached the soil and that daily variations in soil temperatures were buffered for longer than at the front or the intermediate stations. During snow melt, soil moisture initially remained close to saturation between T0 and T1, and then dropped rapidly as terraces became snow-free. However, we did not capture an earlier decrease in soil moisture at the front station as expected from soil temperature monitoring. A plausible explanation is that front soil moisture had already dropped prior to T0 or, more likely, that the amount of accumulated heat due to daily variations of soil temperatures was constrained below a threshold value that limited water evaporation before T2 (Rixen et al. 2008). In fact, soil moisture at all stations dropped by ca. 50% after T1, which was timed after only a few days of diurnal fluctuations in soil temperature. The speed of water loss reflects the importance of evapo-transpiration as a direct consequence of the soil's exposure to solar radiation in the absence of snow. This was confirmed

at both depths by significant negative correlations ($-0.3 < \text{Spearman } R < -0.8$, $p < 0.001$) between the 12 computed soil temperature variables (mean, min, max, max–min; calculated for the soil sampling day or averaged for the 7 and 30 days before sampling) and mean soil moistures measured for each date and station (data not shown).

Similarly, soil pH was significantly correlated to all soil temperature variables at the intermediate and bank stations ($-0.3 < \text{Spearman } R < -0.5$, $p < 0.02$), and to soil moisture at all stations (Spearman $R = -0.18$, $p < 0.007$). We suggest that snowmelt and subsequent snow water influenced soil temperature and moisture, creating the conditions for a flush of elements, such as organic acids released from the DON-rich snowpack, from soil organic matter mineralization and from microbial turnover. This flush acidified the soil solution at least temporarily, as reported by others (Brooks et al. 1999; Hood et al. 2003; Williams et al. 1994). Furthermore, soil moisture and temperature changes during and after snow melt favoured some soil microbial activities (i.e. nitrification, see next section) which produced protons and decreased soil pH (Fitzhugh et al. 2003). Melt water can become enriched with acidic solutes, and lower the pH of soil and surface waters during the early spring (Helliwell et al. 1998). As such, the amount of snow accumulated on subalpine terraces and the speed at which it melted influenced soil physical, chemical and biological conditions which cascade down to the N cycling and the soil solution pH (Rixen et al. 2008). Yet, different N forms behave distinctly under these early spring conditions.

Soil-N pools and processes during snowmelt

When terraces were snow-covered and during snowmelt (i.e., from T0 to T2), plant uptake was at a minimum and rapid soil- NO_3^- loss occurred (as illustrated by its sharp spatial and temporal fluctuations). This implies nitrate pulse releases from overwinter mineralization and subsequent flushes during snowmelt through leaching or denitrification (Edwards et al. 2007; Hagedorn et al. 2001; Vitousek and Melillo 1979; Williams et al. 1995). In contrast, soil- NH_4^+ and DON tended to accumulate towards the bank and during snowmelt until May 5th. Deeper snowpacks towards the bank for longer periods could have locally extended steadier soil conditions until

snowmelt (T1), delaying the microbial turnover. Yet, N mineralisation rates measured between T0 and T1 did not differ between the bank and the front areas, even though soil diurnal temperature changes occurred 10 days earlier at the front. Therefore, higher soil-NH₄⁺ and DON accumulations towards the bank observed on T0 were likely to result from other processes such as NH₄⁺ production from dissimilative nitrate reduction (Stanford et al. 1975), or DON release from an overall higher microbial biomass turnover.

Nevertheless, N mineralisation was measured at all sites before and during snow melt, implying that snow and soil organic N could be taken up or mineralised by soil microorganisms into NH₄⁺, which was further nitrified into NO₃⁻, or retained by the cation exchange complex made of clay minerals and organic matter (Baptist et al. 2008; Hagedorn et al. 2001). The drop in soil pH supports this suggestion. Additionally, highly dynamic edapho-climatic changes occurred during snowmelt (pH, moisture, temperature) and could be responsible for soil microbial turnover releasing DON into the soil solution. Although not measured here, increasing labile C limitation to microbial growth and activity, together with osmotic and redox stresses, at thaw could also be involved in the death, lyses and release of microbial cells contents (Schimel et al. 2007).

Soil-N processes and snow-N

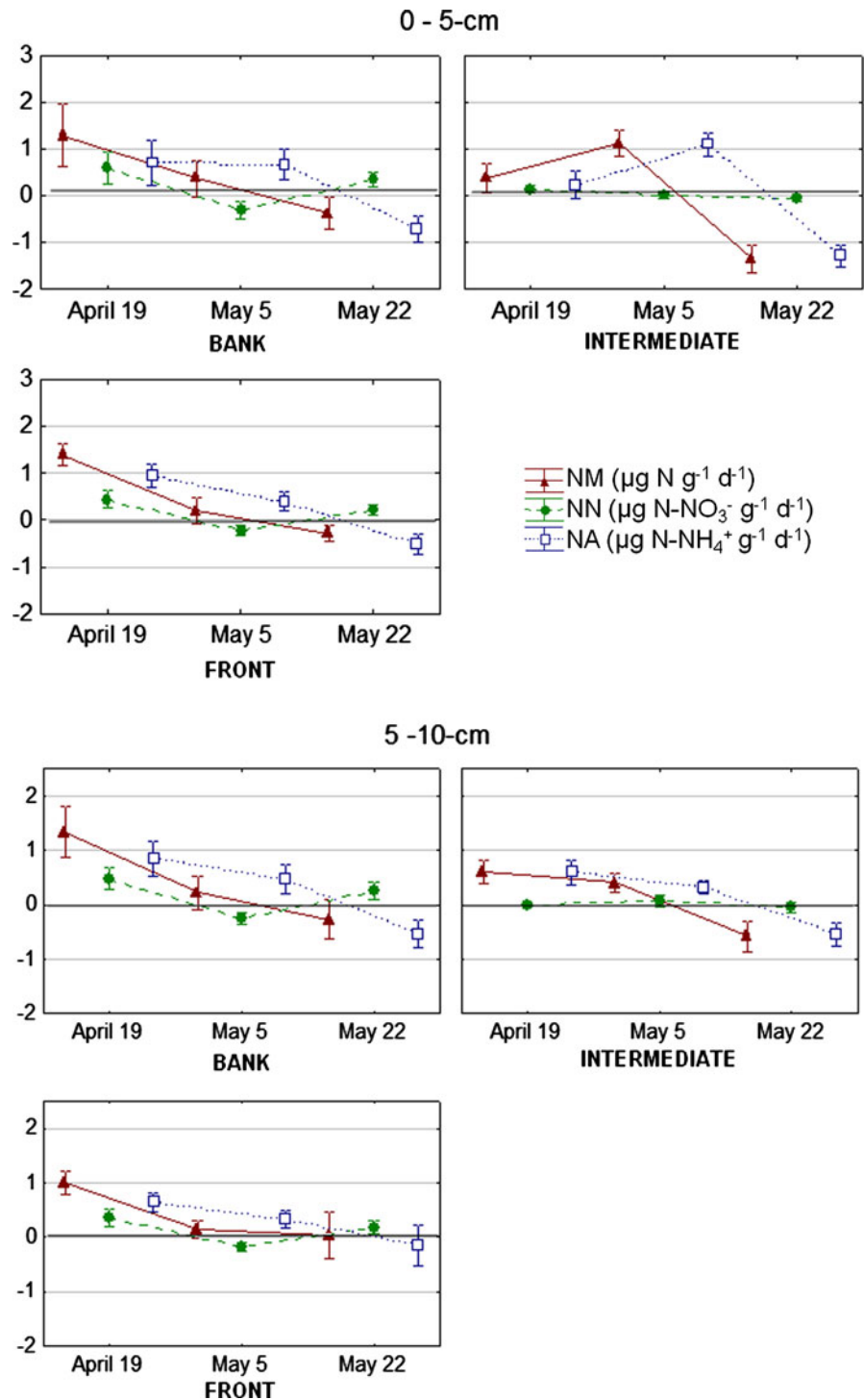
Soil-N processes showed weak spatial patterns but strong temporal variations during our survey. In alpine grasslands, Brooks et al. (1995, 1998) described a positive relationship between snow depth and N processes (e.g. NO₃⁻ production). Here, subalpine soil net N mineralization rates did not display strong spatial trends along the mesotopographic terraced gradients; therefore they were weakly influenced by the local snow depth differences and homogeneous subalpine soil conditions prevailed at this scale for microbial-mediated N processes. This assertion was supported by soil pH, moisture and OM contents which likewise did not vary between stations. Only the intermediate station differed, giving mean negative cumulative mineralization and ammonification rates (i.e. CumNNM and CumNNA, Table 2) as if soil-NH₄⁺ was locally depleted, but this trend was actually related to

negative rates at the end of the survey (i.e. between May 5th and 22nd) when snow melt was almost over (Fig. 6). This decrease in mineralization rates at the end of the snow melt season also occurred for the bank and the front but was particularly acute for the intermediate station and, when integrated over the whole study period, resulted in negative cumulative rates for that station. To conclude, significant trends in N processes along the terrace topography were absent during our study and over the time resolution we used here. However, it does not mean that the mesotopography and its corresponding snowpack distribution would not influence soil-N cycling over a longer time scale: years or decades.

Most importantly, soil-N mineralization rates were extremely sensitive across the entire terrace to snowmelt dynamics and to the direct and indirect effects of snowmelt on soils over time (Rixen et al. 2008). Overall, the soil-N processes that we monitored, and which are linked to microbial activities, decreased after the onset of snowmelt, as found for alpine ecosystems (Baptist et al. 2008; Brooks et al. 1996, 1998). The decrease in net N mineralization during snowmelt was mainly attributable to a decline in ammonification since nitrification remained stable. In other words, over the snow melt period, soil-NH₄⁺ release was reduced while soil-NO₃⁻ production was steady, even though the latter primarily depends on the former. This implies either an increasing shortage in labile-DON for mineralisers or reduced mineralization capacity of the soil microbes during snow melt. Soil-DON contents dropped by approximately 50% between May 5th and May 22nd and indeed corresponded with the reduction in N ammonification rates over the same period. Thus, we suspect organic substrate limitation to be responsible for the decrease in N mineralization in general, and in NH₄⁺ production in particular at the end of the snowmelt season.

Although not directly evaluated, vegetation uptake probably became increasingly dominant and influenced soil-N depletion at the end of May (Bardgett et al. 2005). Early N uptake by plants and algae at the end of snow melt could impact soil-N pools and in situ N mineralization rates. Preferential microbial NH₄ uptake/immobilization might also account for NH₄ depletion as found in a parallel study on the same subalpine terraces (Robson et al. 2010) and in alpine soils (Fisk and Schmidt 1995; Fisk et al. 1998). Finally, NH₄⁺ depletion could also

Fig. 6 Evolution of soil net N mineralization (NM), nitrification (NN) and ammonification (NA) rates (mean \pm SE; $n = 9$) during the experiment for the each station and at two soil depths (0- to 5-cm, 5- to 10-cm). Values given for T1 (April 19th), T2 (May 5th) and T3 (May 22nd) integrate the elapsed time between that sampling day (T_n) and the previous sampling day (T_{n-1}); see the “Materials and methods” section for details



originate from either adsorption onto negatively charged surfaces of clay minerals and organic matter, or volatilization. NH_3 volatilization is only

possible if soils are basic (Bouwman et al. 2005; Smith et al. 1983) as found at the beginning of the snowmelt season, but cold temperatures and high

soil Ca^{2+} contents (data not shown) probably limited this process here.

Conclusions

We characterized the snow accumulation gradient on subalpine terraces at the Lautaret Pass which followed their mesotopography with snow accumulating towards the bank. This was paralleled by gradients of inorganic and organic N deposition contained in the snow pack, brought by either direct transportation or capture. The total input of N contained in the snow was negligible when compared to the soil-N status whatever the N species considered, and relationships between the snowpack and the soil-N pools were spatially and temporally limited. We suggest that during snow melt snow-N was eluted to the soil where it was either flushed with runoff on frozen soils, or incorporated into the soil water where it could be transformed by biotic or abiotic processes. Soil-N mineralization rates and N pools did not differ significantly along the terrace topography during our survey, except for N-NH_4^+ and DON when snowmelt had started at the front but not yet at the bank. Actually, N mineralisation rates were much more responsive across the terraces to snowmelt dynamics and to the direct and indirect effects of snowmelt on soils over time. At thaw, soils experienced drastic changes in temperature and moisture, which are proximal controls of soil-N cycling. As a result, soil N-NH_4^+ and DON tended to accumulate during snowmelt while NO_3^- had pulse-release behaviour. Meanwhile, N ammonification rates decreased during snowmelt, probably because of an increasing shortage of DON, suggesting that labile organic compounds became limiting. This slowing down of the N cycling after snowmelt might also result from (1) the concurrent drop in soil pH partially resulting from nitrification, and (2) the microbial turnover partially due to limitation in organic resources.

Finally, subalpine soils during snowmelt switched from a source to a sink of N (Heuer et al. 1999). Future investigations, including isotopic tracing, microbial investigations, in situ denitrification monitoring, and the evaluation of runoff and leaching rates will help to clarify the potential influence of subalpine watersheds on water and nutrients cycling and how global changes (snow fall rates, snow melt

dynamics, snow mantle structure...) may alter their functioning.

Acknowledgments We greatly appreciated the comments and suggestions from two anonymous reviewers who helped to improve the quality of this paper. We gratefully acknowledge the logistical and funding supports provided by the “Laboratoire d’Ecologie Alpine” (UMR 5553 CNRS/UJF) and the “Station Alpine Joseph Fourier” (UMS 2925 CNRS/UJF). CNRS directly supported this study, and provided a post-doctoral research grant to TMR. This research was conducted on the long term research site Zone Atelier Alpes, a member of the ILTER-Europe network. ZAA publication No 005.

References

- Aber JD, Goodale CL, Ollinger SV, Smith ML, Magill AH, Martin ME, Hallett RA, Stoddard JL (2003) Is nitrogen deposition altering the nitrogen status of northeastern forests? *Bioscience* 53:375–389
- Amoroso A, Domine F, Esposito G, Morin S, Savarino J, Nardino M, Montagnoli M, Bonneville JM, Clement JC, Ianniello A, Beine HJ (2010) Microorganisms in dry polar snow are involved in the exchanges of reactive nitrogen species with the atmosphere. *Environ Sci Technol* 44:714–719
- Baptist F, Zinger L, Clement JC, Gallet C, Guillemin R, Martins JMF, Sage L, Shahnava B, Choler P, Geremia R (2008) Tannin impacts on microbial diversity and the functioning of alpine soils: a multidisciplinary approach. *Environ Microbiol* 10:799–809
- Baptist F, Flahaut C, Streb P, Choler P (2010a) No increase in alpine snowbed productivity in response to experimental lengthening of the growing season. *Plant Biol* 12:755–764
- Baptist F, Yoccoz NG, Choler P (2010b) Direct and indirect control by snow cover over decomposition in alpine tundra along a snowmelt gradient. *Plant Soil* 328:397–410
- Bardgett RD, Bowman WD, Kaufmann R, Schmidt SK (2005) A temporal approach to linking aboveground and below-ground ecology. *Trends Ecol Evol* 20:634–641
- Bassirirad H (2000) Kinetics of nutrient uptake by roots: responses to global change. *New Phytol* 147:155–169
- Bouwman AF, Van Drecht G, Van der Hoek KW (2005) Global and regional surface nitrogen balances in intensive agricultural production systems for the period 1970–2030. *Pedosphere* 15:137–155
- Brooks PD, Williams MW (1999) Snowpack controls on nitrogen cycling and export in seasonally snow-covered catchments. *Hydrol Process* 13:2177–2190
- Brooks PD, Williams MW, Schmidt SK (1995) Snowpack controls on soil nitrogen dynamics in the Colorado alpine. In: Tonnessen KA, Williams MW, Tranter M (eds) *Biogeochemistry of seasonally snow-covered basins*. International association for hydrological sciences, pp 283–292
- Brooks PD, Williams MW, Schmidt SK (1996) Microbial activity under alpine snowpacks, Niwot Ridge, Colorado. *Biogeochemistry* 32:93–113
- Brooks PD, Schmidt SK, Williams MW (1997) Winter production of CO_2 and N_2O from Alpine tundra:

- environmental controls and relationship to inter-system C and N fluxes. *Oecologia* 110:403–413
- Brooks PD, Williams MW, Schmidt SK (1998) Inorganic nitrogen and microbial biomass dynamics before and during spring snowmelt. *Biogeochemistry* 43:1–15
- Brooks PD, McKnight DM, Bencala KE (1999) The relationship between soil heterotrophic activity, soil dissolved organic carbon (DOC) leachate, and catchment-scale DOC export in headwater catchments. *Water Resour Res* 35:1895–1902
- Buckeridge KM, Grogan P (2010) Deepened snow increases late thaw biogeochemical pulses in mesic low arctic tundra. *Biogeochemistry* 101:105–121
- Buckeridge KM, Cen YP, Layzell DB, Grogan P (2010) Soil biogeochemistry during the early spring in low arctic mesic tundra and the impacts of deepened snow and enhanced nitrogen availability. *Biogeochemistry* 99:127–141
- Burns DA (2004) The effects of atmospheric nitrogen deposition in the Rocky Mountains of Colorado and southern Wyoming, USA: a critical review. *Environ Pollut* 127:257–269
- Cabrera ML, Beare MH (1993) Alkaline persulfate oxidation for determining total nitrogen in microbial biomass extracts. *Soil Sci Soc Am J* 57:1007–1012
- Cline D (1995) Snow surface energy exchanges and snowmelt at a continental alpine site. In: Tonnessen K, Williams MW, Tranter M (eds) *Biogeochemistry of seasonally snow-covered basins*. International Association for Hydrological Sciences, pp 157–166
- Cunningham J, Waddington ED (1993) Air-flow and dry deposition of non-sea salt sulfate in polar firn: paleoclimatic implications. *Atmos Environ Part A Gen Topics* 27:2943–2956
- Domine F, Rauzy C (2004) Influence of the ice growth rate on the incorporation of gaseous HCl. *Atmos Chem Phys* 4:2513–2519
- Domine F, Sparapani R, Ianniello A, Beine HJ (2004) The origin of sea salt in snow on Arctic sea ice and in coastal regions. *Atmos Chem Phys* 4:2259–2271
- Domine F, Cincinelli A, Bonnaud E, Martellini T, Picaud S (2007) Adsorption of phenanthrene on natural snow. *Environ Sci Technol* 41:6033–6038
- Edwards AC, Scalenghe R, Freppaz M (2007) Changes in the seasonal snow cover of alpine regions and its effect on soil processes: a review. *Quat Int* 162:172–181
- Eugster W, Perego S, Wanner H, Leuenberger A, Liechti M, Reinhardt M, Geissbuhler P, Gempeler M, Schenk J (1998) Spatial variation in annual nitrogen deposition in a rural region in Switzerland. *Environ Pollut* 102:327–335
- Fenn ME, Haeuber R, Tonnesen GS, Baron JS, Grossman-Clarke S, Hope D, Jaffe DA, Copeland S, Geiser L, Rueth HM, Sickman JO (2003) Nitrogen emissions, deposition, and monitoring in the western United States. *Bioscience* 53:391–403
- Filippa G, Freppaz M, Williams MW, Helmig D, Liptzin D, Seok B, Hall B, Chowanski K (2009) Winter and summer nitrous oxide and nitrogen oxides fluxes from a seasonally snow-covered subalpine meadow at Niwot Ridge, Colorado. *Biogeochemistry* 95:131–149
- Fisk MC, Schmidt SK (1995) Nitrogen mineralization and microbial biomass nitrogen dynamics in three alpine tundra communities. *Soil Sci Soc Am J* 59:1036–1043
- Fisk MC, Schmidt SK (1996) Microbial responses to nitrogen additions in alpine tundra soil. *Soil Biol Biochem* 28:751–755
- Fisk MC, Schmidt SK, Seastedt TR (1998) Topographic patterns of above- and belowground production and nitrogen cycling in Alpine tundra. *Ecology* 79:2253–2266
- Fitzhugh RD, Driscoll CT, Groffman PM, Tierney GL, Fahey TJ, Hardy JP (2003) Soil freezing and the acid-base chemistry of soil solutions in a northern hardwood forest. *Soil Sci Soc Am J* 67:1897–1908
- Franz TP, Eisenreich SJ (1998) Snow scavenging of polychlorinated biphenyls and polycyclic aromatic hydrocarbons in Minnesota. *Environ Sci Technol* 32:1771–1778
- Girel J, Quéfier F, Bignon A, Aubert S (2010) Histoire de l'agriculture en Oisans: Haute Romanche et pays faran-chin. Villar d'Arène, Hautes-Alpes
- Groffman PM, Driscoll CT, Fahey TJ, Hardy JP, Fitzhugh RD, Tierney GL (2001) Effects of mild winter freezing on soil nitrogen and carbon dynamics in a northern hardwood forest. *Biogeochemistry* 56:191–213
- Gross N, Robson TM, Lavorel S, Albert C, Le Bagousse-Pinguet Y, Guillemin R (2008) Plant response traits mediate the effects of subalpine grasslands on soil moisture. *New Phytol* 180:652–662
- Hagedorn F, Schleppei P, Bucher J, Fluhler H (2001) Retention and leaching of elevated N deposition in a forest ecosystem with Gleysols. *Water Air Soil Pollut* 129:119–142
- Hagedorn F, Spinnler D, Siegwolf R (2003) Increased N deposition retards mineralization of old soil organic matter. *Soil Biol Biochem* 35:1683–1692
- Harder S, Warren SG, Charlson RJ (2000) Sulfate in air and snow at the South Pole: implications for transport and deposition at sites with low snow accumulation. *J Geophys Res Atmos* 105:22825–22832
- Helliwell RC, Soulsby C, Ferrier RC, Jenkins A, Harriman R (1998) Influence of snow on the hydrology and hydrochemistry of the Alt a'Mharcaidh, Cairngorm mountains, Scotland. *Science Total Environ* 217:59–70
- Hiltbrunner E, Schwikowski M, Komer C (2005) Inorganic nitrogen storage in alpine snow pack in the Central Alps (Switzerland). *Atmos Environ* 39:2249–2259
- Hood EW, Williams MW, Caine N (2003) Landscape controls on organic and inorganic nitrogen leaching across an alpine/subalpine ecotone, Green Lakes Valley, Colorado Front Range. *Ecosystems* 6:31–45
- Jaeger CH, Monson RK, Fisk MC, Schmidt SK (1999) Seasonal partitioning of nitrogen by plants and soil microorganisms in an alpine ecosystem. *Ecology* 80:1883–1891
- Jones HG, Pomeroy JW (1999) The ecology of snow-covered systems: summary and relevance to Wolf Creek, Yukon. In: Pomeroy JW, Granger R (eds) *Wolf Creek research basin: hydrology, ecology, environment*. National Water Research Institute, Minister of Environment, Saskatoon, pp 1–14
- Jones DL, Willett VB (2006) Experimental evaluation of methods to quantify dissolved organic nitrogen (DON)

- and dissolved organic carbon (DOC) in soil. *Soil Biol Biochem* 38:991–999
- Jones RH, Mitchell RJ, Stevens GN, Pecot SD (2003) Controls of fine root dynamics across a gradient of gap sizes in a pine woodland. *Oecologia* 134:132–143
- Körner C (2004) Mountain biodiversity, its causes and function. *Ambio* 13:11–17
- Körner C (2004) *Alpine plant life*. Springer, Berlin
- Kuhn M (2001) The nutrient cycle through snow and ice, a review. *Aquat Sci* 63:150–167
- Kuhn M, Haslhofer J, Nickus U, Schellander H (1998) Seasonal development of ion concentration in a high alpine snow pack. *Atmos Environ* 32:4041–4051
- Lipson DA, Schmidt SK, Monson RK (1999) Links between microbial population dynamics and nitrogen availability in an alpine ecosystem. *Ecology* 80:1623–1631
- Litaor MI, Seastedt TR, Walker DA (2001) Spatial analysis of selected soil attributes across an alpine topographic/snow gradient. *Lands Ecol* 17:71–85
- Litaor ML, Seastedt TR, Walker MD, Carbone M, Townsend A (2005) The biogeochemistry of phosphorus across an alpine topographic/snow gradient. *Geoderma* 124:49–61
- Majdi H, Andersson P (2005) Fine root production and turnover in a Norway spruce stand in northern Sweden: effects of nitrogen and water manipulation. *Ecosystems* 8:191–199
- Marshall JD, Blair JM, Peters DPC, Okin G, Rango A, Williams M (2008) Predicting and understanding ecosystem responses to climate change at continental scales. *Front Ecol Environ* 6:273–280
- Matson P, Lohse KA, Hall SJ (2002) The globalization of nitrogen deposition: consequences for terrestrial ecosystems. *Ambio* 31:113–119
- Mayewski PA, Legrand MR (1990) Recent increase in nitrate concentration of Antarctic snow. *Nature* 346:258–260
- Meng L, Ding WX, Cai ZC (2005) Long-term application of organic manure and nitrogen fertilizer on N₂O emissions, soil quality and crop production in a sandy loam soil. *Soil Biol Biochem* 37:2037–2045
- Mullen RB, Schmidt SK, Jaeger CH (1998) Nitrogen uptake during snowmelt by the snow buttercup, *Ranunculus adoneus*. *Arct Alp Res* 30:121–125
- Nanus L, Campbell DH, Ingersoll GP, Clow DW, Mast MA (2003) Atmospheric deposition maps for the rocky mountains. *Atmos Environ* 37:4881–4892
- Nickus U, Kuhn M, Baltensperger U, Delmas R, Gaggeler H, Kasper A, KrompKolb H, Maupetit F, Novo A, Pichlmayer F, Preunkert S, Puxbaum H, Rossi G, Schoner W, Schwikowski M, Seibert P, Staudenger M, Trockner V, Wagenbach D, Winiwarter W (1997) SNO₃-P: ion deposition and concentration in high alpine snow packs. *Tellus Ser B Chem Phys Meteor* 49:56–71
- Nickus U, Kuhn M, Novo A, Rossi GC (1998) Major element chemistry in alpine snow along a north-south transect in the Eastern Alps. *Atmos Environ* 32:4053–4060
- Pastor J, Stillwell MA, Tilman D (1987) Nitrogen mineralization and nitrification in four Minnesota old fields. *Oecologia* 71:481–485
- Pennington SC, Clark CM, Cleland EE, Collins SL, Gough L, Gross KL, Milchunas DG, Suding KN (2005) Do individual plant species show predictable responses to nitrogen addition across multiple experiments? *Oikos* 110:547–555
- Piatek KB, Mitchell MJ, Silva SR, Kendall C (2005) Sources of nitrate in snowmelt discharge: evidence from water chemistry and stable isotopes of nitrate. *Water Air Soil Pollut* 165:13–35
- Preunkert S, Wagenbach D, Legrand M, Vincent C (2000) Col du Dome (Mt Blanc Massif, French Alps) suitability for ice-core studies in relation with past atmospheric chemistry over Europe. *Tellus Ser B Chem Phys Meteor* 52:993–1012
- Quétiér F, Prebay Y, Thébaud A, Rivoal F, Lavorel S (2006) Assessing the effects of ecological trade-offs on the provision of ecosystem services using plant functional traits and stakeholder descriptions of ecosystems (in preparation)
- Rixen C, Freppaz M, Stoeckli V, Huovinen C, Huovinen K, Wipf S (2008) Altered snow density and chemistry change soil nitrogen mineralization and plant growth. *Arct Antarct Alp Res* 40:568–575
- Robertson GP, Coleman DC, Bledsoe CS, Sollins P (1999) *Standard soil methods for long-term ecological research*. Oxford University Press, New York
- Robson TM, Lavorel S, Clement JC, Le Roux X (2007) Neglect of mowing and manuring leads to slower nitrogen cycling in subalpine grasslands. *Soil Biol Biochem* 39:930–941
- Robson TM, Baptist F, Clement JC, Lavorel S (2010) Land use in subalpine grasslands affects nitrogen cycling via changes in plant community and soil microbial uptake dynamics. *J Ecol* 98:62–73
- Rogora M, Mosello R, Arisci S, Brizzio M, Barbieri A, Balestrini R, Waldner P, Schmitt M, Stahl M, Thimonier A, Kalina M, Puxbaum H, Nickus U, Ulrich E, Probst A (2006) An overview of atmospheric deposition chemistry over the Alps: present status and long-term trends. *Hydrobiologia* 562:17–40
- Schimel J, Balser TC, Wallenstein M (2007) Microbial stress-response physiology and its implications for ecosystem function. *Ecology* 88:1386–1394
- Schmitt M, Thoni L, Waldner P, Thimonier A (2005) Total deposition of nitrogen on Swiss long-term forest ecosystem research (LWF) plots: comparison of the throughfall and the inferential method. *Atmos Environ* 39:1079–1091
- Schwikowski M (1997) Analytical chemistry in high-Alpine environmental research. *Chimia* 51:786–789
- Seastedt TR, Bowman WD, Caine TN, McKnight D, Townsend A, Williams MW (2004) The landscape continuum: a model for high-elevation ecosystems. *Bioscience* 54:111–121
- Sickman JO, Leydecker A, Chang CCY, Kendall C, Melack JM, Lucero DM, Schimel J (2003) Mechanisms underlying export of N from high-elevation catchments during seasonal transitions. *Biogeochemistry* 64:1–24
- Sievering H, Rusch D, Marquez L (1996) Nitric acid, particulate nitrate and ammonium in the continental free troposphere: nitrogen deposition to an alpine tundra ecosystem. *Atmos Environ* 30:2527–2537
- Singh KP, Tripathi SK (2000) Impact of environmental nutrient loading on the structure and functioning of terrestrial ecosystems. *Curr Sci* 79:316–323
- Smith CJ, Wright MF, Parick WHJ (1983) The effect of soil redox potential and pH on the reduction and production of nitrous oxide. *J Environ Qual* 12:186–188

- Spoelstra J, Schiff SL, Elgood RJ, Semkin RG, Jeffries DS (2001) Tracing the sources of exported nitrate in the turkey lakes watershed using N-15/N-14 and O-18/O-16 isotopic ratios. *Ecosystems* 4:536–544
- Stanford G, Dzienia S, Van der Pol RA (1975) Denitrification rates in relation to total and extractable soil carbon. *Soil Sci Soc Am J* 39:284–289
- Taillandier AS, Domine F, Simpson WR, Sturm M, Douglas TA, Severin K (2006) Evolution of the snow area index of the subarctic snowpack in central Alaska over a whole season. Consequences for the air to snow transfer of pollutants. *Environ Sci Technol* 40:7521–7527
- Tilman D, Fargione J, Wolff B, D'Antonio C, Dobson A, Howarth R, Schindler D, Schlesinger WH, Simberloff D, Swackhamer D (2001) Forecasting agriculturally driven global environmental change. *Science* 292:281–284
- Vitousek PM, Melillo JM (1979) Nitrate losses from disturbed forests: patterns and mechanisms. *For Sci* 25:605–619
- Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG (1997) Human alteration of the global nitrogen cycle: sources and consequences. *Ecol Appl* 7:737–750
- Wadham JL, Hallam KR, Hawkins J, O'Connor A (2006) Enhancement of snowpack inorganic nitrogen by aerosol debris. *Tellus Ser B Chem Phys Meteor* 58:229–241
- Williams MW, Melack JM (1991a) Precipitation chemistry in and ionic loading to an Alpine Basin, Sierra-Nevada. *Water Resour Res* 27:1563–1574
- Williams MW, Melack JM (1991b) Solute chemistry of snowmelt and runoff in an Alpine Basin, Sierra-Nevada. *Water Resour Res* 27:1575–1588
- Williams MW, Losleben M, Caine N, Greenland D (1994) Changes in climate and hydrochemical responses in a high-elevation catchment in the Rocky Mountains, USA. *Symposium on Regional Assessment of Freshwater Ecosystems and Climate Change in North America*, Leesburg, VA, pp 939–946
- Williams MW, Bales RC, Brown AD, Melack JM (1995) Fluxes and transformations of nitrogen in a high-elevation catchment, Sierra-Nevada. *Biogeochemistry* 28:1–31
- Williams MW, Brooks PD, Mosier A, Tonnesen KA (1996) Mineral nitrogen transformations in and under seasonal snow in a high-elevation catchment in the Rocky Mountains, United States. *Water Resour Res* 32:3161–3171
- Williams MW, Brooks PD, Seastedt T (1998) Nitrogen and carbon soil dynamics in response to climate change in a high-elevation ecosystem in the Rocky Mountains, USA. *Arctic Alpine Res* 30:26–30
- Williams MW, Seibold C, Chowanski K (2009) Storage and release of solutes from a subalpine seasonal snowpack: soil and stream water response, Niwot Ridge, Colorado. *Biogeochemistry* 95:77–94
- Zeller V, Bahn M, Aichner M, Tappeiner U (2000) Impact of land-use change on nitrogen mineralization in subalpine grasslands in the Southern Alps. *Biol Fertil Soils* 31:441–448
- Zeller V, Bardgett RD, Tappeiner U (2001) Site and management effects on soil microbial properties of subalpine meadows: a study of land abandonment along a north-south gradient in the European Alps. *Soil Biol Biochem* 33:639–649
- Zinger L, Shahnavaz B, Baptist F, Geremia RA, Choler P (2009) Microbial diversity in alpine tundra soils correlates with snow cover dynamics. *Isme J* 3:850–859