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## The carbon and nitrogen biogeochemistry of a montane Norway spruce (*Picea abies* (L.) Karst.) forest: a synthesis of long-term research

Robert Jandl<sup>a\*</sup>, Stefan Smidt<sup>a</sup>, Andreas Schindlbacher<sup>a</sup>, Michael Englisch<sup>a</sup>, Sophie Zechmeister-Boltenstern<sup>b</sup>, Christian Mikovits<sup>b</sup>, Philipp Schöftner<sup>c</sup>, Friederike Strelb<sup>c</sup> and Gabriele Fuchs<sup>d</sup>

<sup>a</sup>Forest Research and Training Center for Forests, Natural Hazards and Landscape (BFW), Forest Ecology and Soils, Vienna, Austria;

<sup>b</sup>University of Natural Resources and Life Sciences Vienna, Department of Forest and Soil Sciences, Vienna, Austria; <sup>c</sup>AIT Austrian Institute of Technology GmbH, Vienna, Austria; <sup>d</sup>Ministry of Agriculture, Forestry, Environment, and Water Management, Department VII Water, Subdepartment Water Balance, Vienna, Austria

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**Background:** Long-term ecological studies provide reference data for evaluating the response of ecosystems to external factors over time.

**Aims:** At the Mühleggerköpfl forest research site, Austria air pollution, bioindication, hydrology, and biogeochemistry have been studied over 20 years. This paper reports the biogeochemical budget for nitrogen and carbon.

**Methods:** The site is a Norway spruce (*Picea abies*) stand on limestone that intercepts air pollutants from long-range transport. As the over-mature trees have a low ability to assimilate surplus nitrogen (N) the forest is vulnerable to N saturation and the forest overall may release N into the groundwater.

**Results:** Nitrate concentrations in the soil solution of the upper mineral soil indicate a high nitrification rate. Nevertheless, the nitrogen content in spruce needles barely exceeds the threshold of deficiency.

**Conclusions:** Potential N-leaching from the soil is reduced by the slowly increasing N demand of the regenerating European beech (*Fagus sylvatica*) forest that is establishing under the spruce stand. The release of NO<sub>x</sub> is low, yet significant for the greenhouse gas balance. With respect to CO<sub>2</sub> emissions, the forest currently is neutral, but as warming stimulates the decomposition of soil organic matter it can turn the forest into a carbon (C) source. In addition, disturbances, such as bark beetle (*Ips typographus*) attacks that cause tree mortality strongly affect ecosystem dynamics and the biogeochemistry of C and N.

**Keywords:** biogeochemistry; carbon; forest ecosystems; long-term ecological research; nitrogen

### Background

In this paper we summarise temporal trends over ca. 20 years of external ecosystem drivers, such as climate, and atmospheric pollution, including nitrogen (N) deposition, and relate them to forest stand nutrition, forest productivity, leaching of nitrate, and emissions of greenhouse gases from the soil.

The productivity of temperate forests is commonly N limited. The N saturation hypothesis was first coined by Nihlgard (1985) and later elaborated by Aber et al. (1989), and it suggested that high N inputs may even have detrimental effects on forests. Later research has shown that low to moderate N doses mostly had a fertilisation effect, and that the predicted effect of soil acidification on the process of nitrification only occurred at excessive rates of N deposition (Tamm 1991; Binkley and Högberg 1997; Högberg et al. 2006). Due to the linkage of N deposition and soil acidification, early research focused on sites with high N input rates on siliceous bedrock. It was shown that forests were able to retain N efficiently and that N leaching into the groundwater occurred at high rates of N deposition only (Emmett et al. 1998; Adams et al. 2006). In the meantime, sites on calcareous bedrock with N deposition rates only slightly exceeding the N demand of the forest have received less

attention because soil acidification there was not considered a threat. However, as forest ecosystems on calcareous bedrock are common in the peripheral parts of the Alps and theory suggested that forests would not be able to absorb excess N in the long-term, the need for an experiment on dolomitic limestone was established.

The original focus of N saturation hypothesis was soil acidification. Later the scope was expanded, and the response of the entire ecosystem was taken into consideration (Baron et al. 2000), as anthropogenic N emissions cascading through ecosystems increase the growth rate of trees but excessive N input can pollute water bodies with nitrate and lead to the formation of N oxides that are strong greenhouse gases (Sutton 2011). However, the focus remained on sites at low elevation, on siliceous bedrock.

In the debate on climate change, mitigation by forests C dynamics has received much attention (Lindner et al. 2010; Schulze et al. 2010). For example, for the national greenhouse inventory reports that it is relevant to understand whether or not low-productivity forests with sufficient N supply are sinks or sources of C. For the establishment of site-specific C budgets, experimental sites that have been used for N studies are also excellent for C studies, because the dynamics and C and N are interlinked (Cole 1992).

\*Corresponding author. Email: robert.jandl@bfw.gv.at

At the Mühleggerköpfl, Tyrol, Austria, experimental site investigations started ca. 20 years ago in order to assess air pollution and its impacts on the forest ecosystem. Later investigations were extended to N saturation and the estimation of critical loads and levels of N deposition (Smidt and Obersteiner 2007), and finally, to aspects of biodiversity and the biogeochemistry of C. Our data set contains estimates of pools of C and N in the different ecosystem compartments, and aqueous and gaseous fluxes between them. From the wealth of available data we evaluate the ecosystem status with respect to the accrual and release of C and N.

### Site properties at Mühleggerköpfl

The 20 ha experimental site at Mühleggerköpfl forms a small catchment in the valley of Achenbach at 920 m a.s.l. in a north–north-east-facing exposure in the Northern Limestone Alps (47° 34' 50" N; 11° 38' 21" E; Figure 1). The climate is cool and mesic with maximum precipitation in summer and a snow-free period from April/May to November/December. The mean annual air temperature and precipitation from on-site measurements are 6.8 °C and 1580 mm, respectively (Figure 2). The annual variability of the precipitation is small, and relative air humidity is high.

The vegetation is ca. 120-year-old montane forest, rich in Norway spruce (*Picea abies*). It is interspersed with silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica*). The stand structure has begun to disintegrate due to the mortality of individual trees, a development stage called ‘terminal phase’ or ‘reinitiation stage’ (Mayer 1984; Oliver and Larsen 1990). In recent years the stand has repeatedly been attacked by bark beetle (*Ips typographus* L.). Several infected spruce trees were removed and in the gaps beech and maple (*Acer pseudoplatanus* L.) have regenerated spontaneously. The lush regeneration of deciduous trees in the understorey of spruce forests of low productivity has been observed in the entire region of Tyrol (D. Stöhr, Tyrolean Forest Administration, pers. comm.).

The soils are a mosaic of shallow Chromic Cambisols and Rendzic Leptosols on dolomite. In close proximity to the site the soil depth has been reported to vary from 15–80 cm (Englisch 2001). The soils have a high carbonate content and a near neutral pH. The rock content below the A-horizon is high. The soil temperatures are rather even in the entire profile. The early build-up of a continuous snow

cover ensures that the soil is well insulated and remains unfrozen in most years. Although the soils are rather cool and moist, soil biological activity is high (Härtel et al. 2002; Kitzler et al. 2006; Diaz-Pines Lopez de los Mozos et al. 2010). Root density is highest in the O- and A-horizons, and few roots are found as deep as 60 cm. A detailed description of the site is given by Herman et al. (2002). The retention capacity for pollutants in such coarse-grained and shallow soils is low. Soil water tensions, soil temperatures and continuous soil water contents registered continuously by data-loggers in 4–6 different profile depths are an important data source for the groundwater-recharge programme of the Austrian Hydrographic Survey. Exceptional years like the hot and dry summer of 2003, as reported by Ciais et al. (2005), are not evident from the annual air temperature and precipitation, but from a decrease in the soil water content and air humidity (Table 1, Figure 2).

Approximately 30% of the precipitation is returned to the atmosphere by evapotranspiration and 70% passes through the shallow soil and ultimately charges groundwater and streams (Schöftner 2010). Due to its high porosity the soil can drain even intense rain events. The surface flow of water contributes less than 2% of the water budget (Feichtinger et al. 2002). The length of the growing season, i.e. the number of days with a mean air temperature > 4 °C, is ca. 240. During the last 10 years there has been a trend of lengthening of the growing season driven by a series of unusually mild winters (Figure 2). The site receives air pollutants from long-range transport, by the predominant westerly winds; local point-source emission from rural settlements is low (Kaiser et al. 2007).

Routinely measured parameters over the years have included climate (air temperature, precipitation, and air humidity), soil temperature, soil water content, soil solution chemistry, nutrient content of Norway spruce needles, air quality, deposition of N, and surface runoff (Figures 2–4; Tables 1 and 2). Precipitation was collected in bulk collectors above and below the forest canopy. Soil solution chemistry data have been bi-weekly obtained with ceramic suction cup lysimeters and analysed for N, base cations and dissolved organic matter (DOC) (Schöftner 2010). The chemical composition of precipitation in Table 2 shows a slightly acidic rainfall that is partially neutralised and enriched with N and base cations upon its passage through the forest canopy. The soil water is in equilibrium with the dolomite and consequently its pH is above 8. The nitrate



Figure 1. View to the Mühleggerköpfl experimental site (left) and an aerial infrared image of the site (Scene from Flight Achenkirch 1998, Strip 13/ Picture 1536. BEV, Zl. 37835/2000; right).

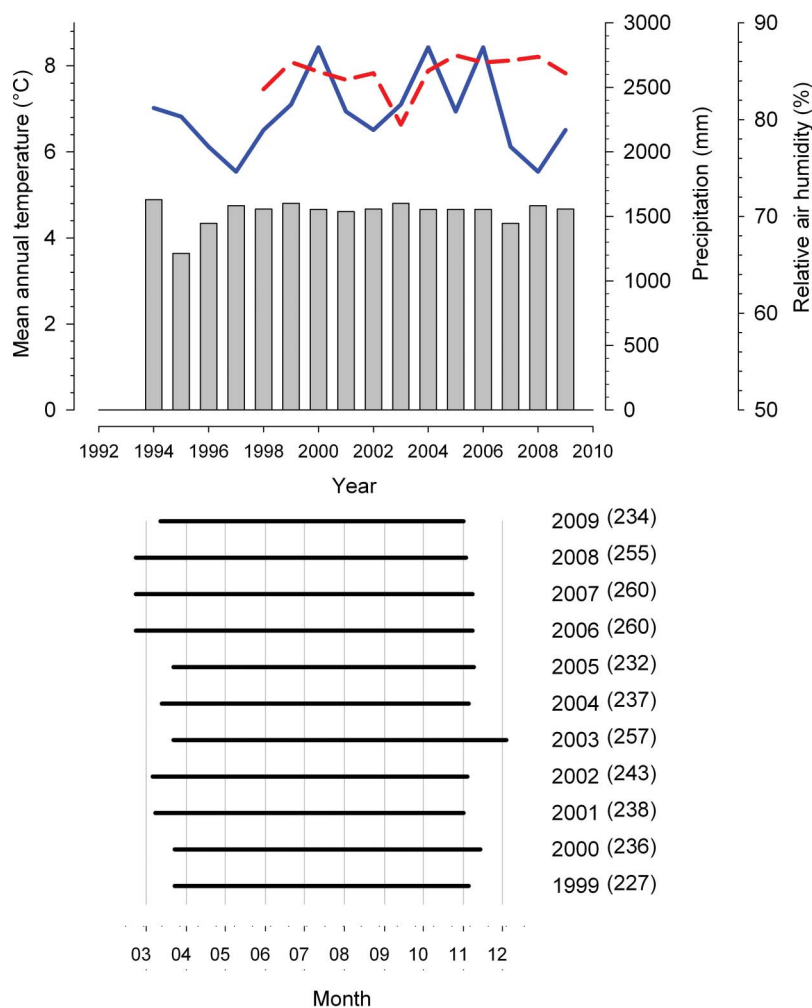


Figure 2. Mean annual temperature (solid line), mean air humidity (dashed line) and annual precipitation (bars) at the Mühleggerköpfl research site, Tyrol, Austria (upper panel) and growing season length (in parentheses after year; lower panel).

( $\text{NO}_3^-$ ) concentration is highest in the upper mineral soil where the nitrification rate is highest. Even at a depth of 50 cm the  $\text{NO}_3^-$  concentration is above 3 mg/L. Due to the low root density in the lower mineral soil it is safe to assume that  $\text{NO}_3^-$  encountered in that depth is leached into the groundwater.

Assessments of the standing tree biomass have been made at irregular intervals by using the standard methods of the Austrian Forest Inventory (Schieler and Hauk 2001). The biomass of the individual compartments was calculated by using locally calibrated biomass functions (Ledermann and Gschwantner 2006; Ledermann and Neumann 2006; Offenthaler and Hochbichler 2006). The emission of the greenhouse gases  $\text{CO}_2$  and  $\text{N}_2\text{O}$  from the soil has been measured within a soil warming experiment and a N-balance assessment (Kitzler et al. 2006 Schindlbacher et al. 2007, 2009; Jandl et al. 2008a,b).

#### Air quality and tree nutrition

Elevated concentrations of ozone and nitric acid damage the cuticula of needles and leaves, and can lead to a reduction

in plant productivity. Seasonally high ozone concentrations that occur in the Alps during high insolation make mountain forests particularly vulnerable (Bytnerowicz et al. 1999; Wieser and Tausz 2006). Air pollution has been investigated within the scope of the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (<http://www.icp-forests.org/>). Ozone and N oxides were recorded with Monitor Labs equipment (ozone: ML 8810,  $\text{NO}_x$  and ML 8840; Teledyne Technologies Inc., USA). Indicators of forest health included the rate of foliage loss of the canopy (data not shown) and the nutrient contents of the needles (Jandl et al. 2004). The ozone concentrations have shown the expected seasonal trends, with highest concentrations in summer. The AOT40 exposition index, i.e. the accumulated exposure over a threshold of 40 ppb  $\text{O}_3$  during the growing season (UN-ECE 1994) has been exceeded in all years. The ozone concentrations showed a significant increase of  $0.84 \pm 0.06 \mu\text{g m}^{-3}$  per year. Ozone has not led to visible symptoms of needle damage, but the measured concentrations may have caused a slight reduction in forest productivity. The concentrations of nitrogen dioxide ( $\text{NO}_2$ ) have been low in summer and

Table 1. Soil temperature averaged over 50 cm profile depths and soil water content of the upper mineral soil at the Mühleggerköpfl experimental site of the Austrian Hydrographic Survey. 'mean' is the annual average; 'std' the standard deviation; 'n.a.' indicates missing values.

Soil depth Year	Soil temperature (°C)		Soil water content (Vol-%)	
	5–50 cm		5–15 cm	
	mean	std	mean	std
1998	7.1	3.8	55	2
1999	6.3	4.1	55	5
2000	7.2	n.a.	54	n.a.
2001	7.4	3.9	50	6
2002	7.4	4.1	53	4
2003	8.1	4.4	42	6
2004	6.9	n.a.	45	4
2005	6.5	4.2	48	5
2006	6.9	n.a.	47	n.a.
2007	6.8	3.9	47	3
2008	6.7	3.8	49	3
2009	6.8	4.6	54	6
2010	6.3	3.9	57	3

had several peaks during winter that were caused by the heating of residential homes. The concentration of nitrogen monoxide has remained always below  $1.3 \mu\text{g NO m}^{-3}$  (Figure 3).

The nutrient concentrations of needles fluctuated within narrow ranges between 1991 and 2004. The concentrations of N and that of phosphorus (P) remained close to the deficiency threshold, the supply of calcium (Ca) and potassium (K) was sufficient (thresholds of deficiency:  $\text{N} < 1.3\%$ ,  $\text{P} < 0.12\%$ ,  $\text{Ca} < 0.11\%$ ,  $\text{K} < 0.3\%$ ; Hützl 1986). The measured sulphur (S) level in the needles at Mühleggerköpfl has remained always below 0.09%, thereby indicating a low impact of  $\text{SO}_2$  (threshold of damage  $> 0.11\%$  S) (Figure 4).

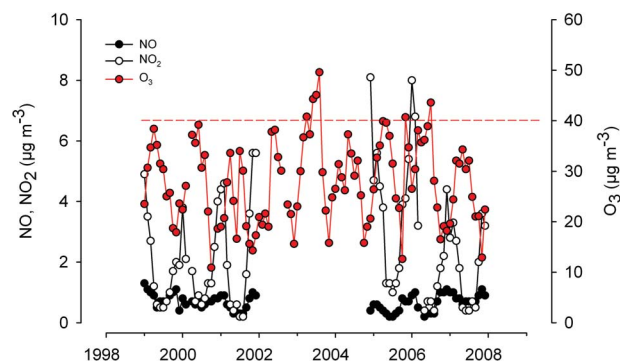


Figure 3. Monthly mean atmospheric concentrations of nitrogen oxides and ozone at the Mühleggerköpfl experimental site. The dashed horizontal line shows the AOT40 exposure index.

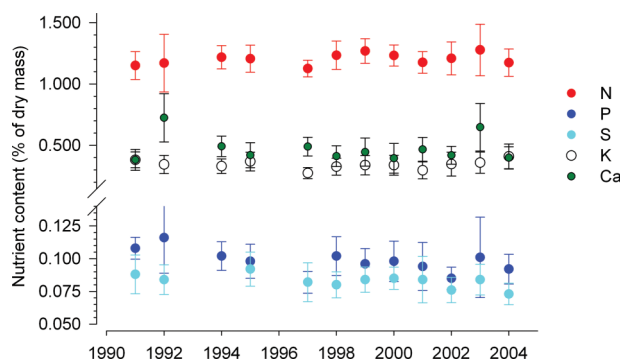


Figure 4. Nutrient concentrations in the needles of Norway spruce ( $n = 10$ ) at the Mühleggerköpfl experimental site (1990–2004).

### Nitrogen saturation

Establishing a N budget for forest ecosystems is challenging because N occurs in the solid phase (in soil organic matter and in the biomass of plants and soil microbes); in the aqueous phase ( $\text{NO}_3^-$  and ammonium ( $\text{NH}_4^+$ ) and dissolved organic N in rain-, runoff- and soil water); and in the gaseous phase ( $\text{N}_2\text{O}$ ,  $\text{NO}_x$  and  $\text{N}_2$ ). By combining field and laboratory measurements and modelling we derived a complete N budget for the site (Herman et al. 2002; Jandl

Table 2. Chemical composition of the rainwater above and below the forest canopy and the soil solution in different depths of the soil profile. Means and standard deviations (std) are calculated from data collected between 1998 and 2008.

	pH		$\text{NO}_3^-$ (mg/L)		$\text{NH}_4^+$ (mg/L)		$\text{K}^+$ (mg/L)		$\text{Mg}^{2+}$ (mg/L)		$\text{Ca}^{2+}$ (mg/L)	
	mean	std	mean	std	mean	std	mean	std	mean	std	mean	std
Bulk deposition above the forest canopy	4.81	0.25	1.35	0.26	0.30	0.11	0.11	0.08	0.22	0.19	1.23	0.98
Bulk deposition below the forest canopy	5.36	0.22	2.03	0.30	0.39	0.11	0.80	0.20	0.55	0.45	2.85	2.92
<b>Soil solution</b>												
5 cm	8.53	0.32	8.07	8.03	0.07	0.06	0.11	0.07	17.41	1.45	30.80	4.78
15 cm	8.21	0.55	4.62	3.09	0.26	0.26	0.09	0.06	16.00	4.80	29.73	10.01
25 cm	8.21	0.61	2.39	2.61	0.11	0.18	0.12	0.09	15.02	5.14	26.28	9.49
50 cm	8.80	0.61	3.03	3.06	0.07	0.07	0.15	0.08	16.05	5.01	27.33	9.67

Table 3. Pools and fluxes of nitrogen at the Mühleggerköpfl site.

Nitrogen pools	(kg ha <sup>-1</sup> )	Nitrogen fluxes	(kg ha <sup>-1</sup> yr <sup>-1</sup> )
Stem biomass	400	Deposition above the canopy throughfall	1220
Needles and leaves	160	Above-ground and below-ground litter	55
Roots (litter layer and mineral soil 50 cm)	130	Net mineralisation	27
Litter layer and mineral soil (50 cm)	15,000	Nitrate leaching	7
Soil microbial biomass (litter layer and mineral soil 50 cm)	180	N <sub>2</sub> O emission	0.9

et al. 2002; Table 3). The results have indicated that by far the largest N pool was formed by the soil organic matter where N is bound in labile and recalcitrant forms. The most active pools were N in needles, fine roots and the soil microbial biomass. The N input by precipitation has exceeded the output by leaching and the emission of nitrogen oxides. The site is currently accumulating annually ca. 5 kg N ha<sup>-1</sup>.

The site has had a long history of exploitative land use, and current forest productivity is limited by N (Glatzel 1999; Führer 2000). The N export by timber extraction has partially been balanced by N deposition (7–12 kg ha<sup>-1</sup> year<sup>-1</sup>). Whether or not this external input can be fully utilised by mature forest stands is controversial. The potential of the old forest to take up additional N may be limited because of low stem and root densities. Only a small response to N fertilisation has been shown in other old forests, and N saturation in old growth forests may already be reached at low levels of N deposition (Aber et al. 1989, 2002; Schulze 2000). Leaching of N into the groundwater as observed at Mühleggerköpfl is facilitated by the shallow and coarse-textured soil. Recent bark beetle attacks at the site increased the disposition of the stand towards N leaching because tree mortality has reduced stand density and consequently led to a lower N demand of the forest (Huber 2005). The increased pressure from bark beetles in the montane zone is perceived as a consequence of climate change that has already led to severe problems for forestry in other regions (Kurz et al. 2008; Seidl et al. 2011). An additional driver of elevated rates of NO<sub>3</sub><sup>-</sup> leaching is N mineralisation. The high microbial activity together with the high rate of rainfall and the coarse soil texture are pre-disposing the site to high rates of NO<sub>3</sub><sup>-</sup> leaching (Gundersen et al. 1998). The opening of the canopy leads to higher soil temperature, and the decaying roots and needles of dead trees provide fresh substrate for soil microbial processes.

Measurement of the isotopic signature of nitrate in the rain water, the soil water and the surface water was undertaken to differentiate whether the nitrate in the soil solution was derived directly from deposition or from nitrification. Due to the complexity of the nitrogen cycle the interpretation of <sup>15</sup>N in nitrate is difficult. Therefore we extended the investigation to the analysis of <sup>18</sup>O in the nitrate ion (Figure 5). The wide variability of  $\delta$ -<sup>15</sup>N in the throughfall fraction of precipitation indicated that the nitrate originated from different sources. The differences

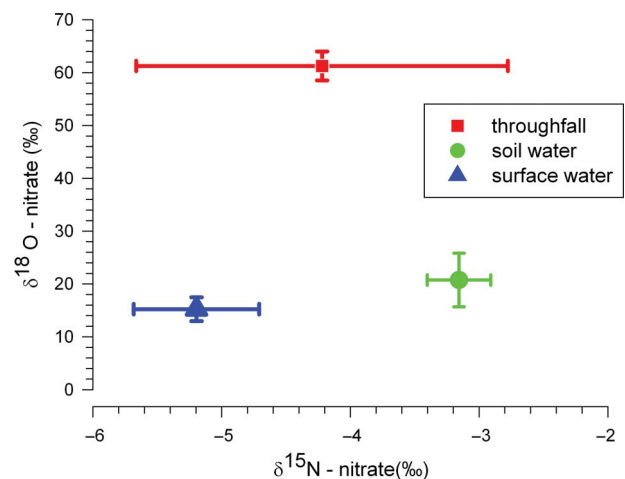


Figure 5. Isotope signatures of nitrogen and oxygen in nitrate from three sources: rainwater (throughfall), soil solution, and surface water. The  $\delta$ -values represent the relative difference in isotope values of the respective sample to the PDB standard.

between soil solution and surface water indicated that during the leaching process <sup>15</sup>N is enriched due to sorption in the soil matrix and denitrification. A comparison of  $\delta$ -<sup>15</sup>N in the surface water and the throughfall, the clear difference in  $\delta$ -<sup>18</sup>O between the rain water and the soil and surface water samples, and the absence of a significant correlation between the  $\delta$ -<sup>15</sup>N-nitrate values of any precipitation sample with the surface water suggested that the main source of nitrate in soil water originated from microbiological activity such as nitrification and less from nitrate input (Haberhauer et al. 2002).

Our hypothesis that the investigated forest was in a state of near N saturation due to a combination of decreasing N demand of the forest and increasing inputs from deposition and mineralisation of soil organic matter was partially supported. The ability of the ecosystem to retain N was confirmed by the isotopic signatures of rain water, the soil solution, surface runoff and seepage water. A substantial part of the incoming N is microbially processed in the soil (Haberhauer et al. 2002). We did not find evidence for an increase in N leaching in the last 10 years (Feichtinger et al. 2002, Schöftner 2010). The NO<sub>3</sub><sup>-</sup> concentration in the soil solution has been rather variable (Figure 6; Smidt et al. 2008). A pattern of multi-year stability of NO<sub>3</sub><sup>-</sup> concentrations followed by a period of large variability has also been reported for other experimental

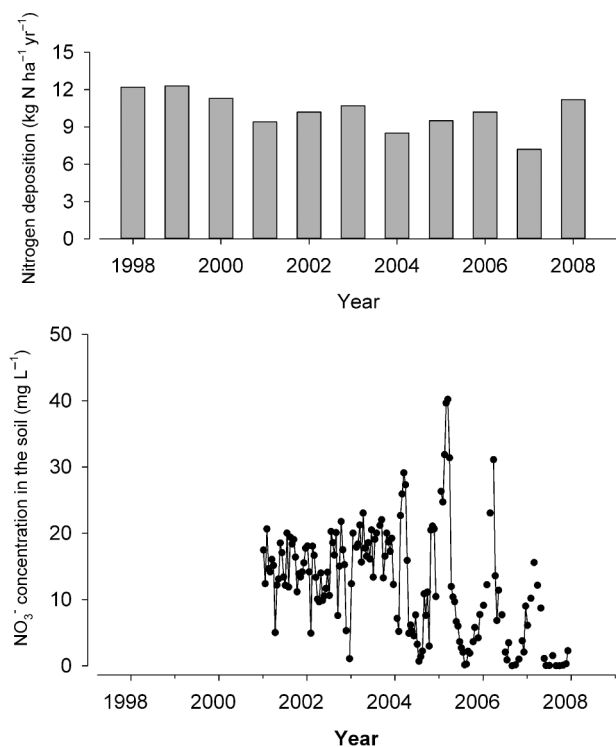


Figure 6. Total nitrogen deposition below the canopy (upper panel) and nitrate concentration in the seepage water collected at 50 cm depth at Mühleggerköpfl (lower panel). Seepage water samples were collected with a forest lysimeter. The EU threshold for drinking water is 50 mg NO<sub>3</sub><sup>-</sup>/L.

watersheds, for example at Hubbard Brook and Fernow, and were interpreted as an early indication of N saturation (Likens and Bormann 1995; Peterjohn et al. 1996; Adams et al. 2006). At Mühleggerköpfl, we found only a weak correlation between the annual N deposition load and the NO<sub>3</sub><sup>-</sup> concentration in the soil solution. The concentrations in the soil solution decreased between 2004 and 2008 compared with the earlier period. We interpret this pattern as consequence of vegetation dynamics. Under the gradually opening canopy of Norway spruce a dense layer of beech has been regenerating. Its nutrient demand appears to take up the available N efficiently and prevents it from leaching.

Overall, it has proven to be difficult to establish a closed biogeochemical cycle of N on the basis of our data. Preliminary evidence from a laboratory experiment suggests that N is partly released as N<sub>2</sub> (Jandl et al. 2008a). Field measurements have shown episodes of high N<sub>2</sub>O and NO<sub>x</sub> emissions after rainfall in summer (Kitzler et al. 2006). However, the release of N<sub>2</sub> has only rarely been measured and quantified, because measuring the formation of small amounts of N<sub>2</sub> against the huge background concentration of N<sub>2</sub> in the atmosphere is difficult (Butterbach-Bahl et al. 2002; Dannenmann et al. 2008; Butterbach-Bahl and Gundersen 2011). Our data suggest that the forest ecosystem is currently absorbing the major part of the incoming N. A part of it is expected to be retained in the soil organic matter, another part supports the regeneration of deciduous trees under the canopy, and only a minor

part is leached into the groundwater body. We have no evidence on the long-term capacity of the ecosystem to accumulate N.

### Montane forest soils as carbon sink, or source

Mountain forests of the temperate zone deserve special attention with regard to C sequestration because their growth rate, i.e. their C fixation, is low, partly due to resource limitations (N, water), partly due to the short duration of the growing season. Carbon is released from the soil by respiration and, to a lesser extent, by the export of dissolved organic C in the aqueous phase. Total soil respiration consists of an autotrophic part, which represents the CO<sub>2</sub> formation from root and rhizosphere respiration, and a heterotrophic part representing the decomposition of soil organic matter or soil C loss by microorganisms. The C fixation is confined to the growing season, whereas heterotrophic soil respiration occurs continuously. At sites where an insulating snow cover forms, soil microbes can decompose soil organic matter even during winter (Hagedorn et al. 2003; Hubbard et al. 2005; Groffman et al. 2006; Trumbore 2006; Schmidt et al. 2009).

An important question is whether or not the soil at Mühleggerköpfl is presently a source or a sink of C. We found that soil respiration released 6 Mg C ha<sup>-1</sup> year<sup>-1</sup> (Schindlbacher et al. 2009). Winter soil respiration, estimated by diffusion measurements of CO<sub>2</sub> through the snow cover (Schindlbacher et al. 2007) contributed about 10% to the annual CO<sub>2</sub> efflux from the soil. The emission has been quite variable between years, dependent on soil temperature and soil water content during the growing season. About 40% of total soil respiration was attributable to autotrophic respiration, and 60% was due to the mineralisation of soil organic matter.

A soil respiration assessment alone does not allow the evaluation of whether or not a forest site represents a sink or a source of CO<sub>2</sub>. To establish a C budget, the soil C model Yasso07 was applied to the site (Liski et al. 2009). The model requires supplying the site climate, the C input (litter) to the soil and its chemical quality. Climate data have been recorded on the site (Figure 2). The annual C input flux was computed from the standing stock of the tree biomass (Table 4), assuming turnover times of 5 years for needles and coarse roots, and turnover of 1 year for fine roots, respectively. Annually, the trees shed 2–4% of the branch biomass. These calculations were based on previous parameterisations of the Yasso07 model and on measured data at the site (Lehtonen 2005; Thürig et al. 2005; Helmissaari et al. 2007; Palosuo 2008; Diaz-Pines Lopez de los Mozos et al. 2010). The above-ground biomass and root litter each contributed ca. 2.5 Mg C ha<sup>-1</sup> year<sup>-1</sup> input. More than 80% of the C input originated from Norway spruce; the remaining 20% was equally contributed by fir and beech. For the chemical quality of the above-ground and below-ground litter we used data from Liski et al. (2009) and Heim and Frey (2004). The simulation output was validated by measured data of the above-ground

Table 4. Carbon stock in the tree biomass at the Mühleggerköpfl site, based on an inventory of the above-ground biomass.

	(Mg C ha <sup>-1</sup> )						Above-ground biomass	Below-ground biomass
	Stem	Needles/leaves	Branches	Coarse roots	Fine roots			
<i>Picea abies</i>	69.5	7.4	12.8	17.9	0.9		89.7	18.8
<i>Abies alba</i>	1.2	0.2	0.2	0.3	0.0		1.6	0.3
<i>Fagus sylvatica</i>	11.5	0.2	2.4	2.8	0.1		14.0	2.9
Total	82.2	7.7	15.4	21.1	1.1		105.3	22.1

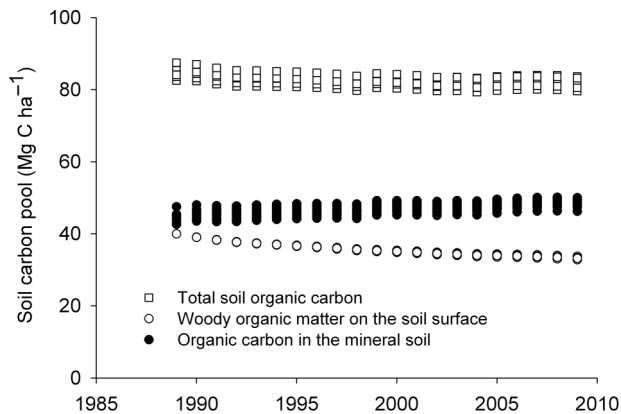


Figure 7. Temporal change in the soil organic carbon pool at Mühleggerköpfl, obtained by a simulation using the Yasso07 model. The range of predicted values at each time presents the model parameter uncertainty.

litterfall, the heterotrophic soil respiration and the soil C stock in the year 2006.

The simulated temporal trend of the soil C pool appeared remarkably stable under current climatic conditions (Figure 7). A decline in soil C was driven by increase in temperature, while the gradual decomposition of woody material supplied by tree mortality in recent bark beetle attack caused slight increases in the soil C pool. The simulated change in the stock of soil organic matter was smaller than that could be detected by field surveys (Stevens 2008). We conclude that the site is presently neutral with respect to C sequestration.

To assess potential future changes, a soil warming experiment that distinguished between heterotrophic and autotrophic respiration, quantified the C gains and losses at Mühleggerköpfl (Schindlbacher et al. 2008, 2009; Diaz-Pines Lopez de los Mozos et al. 2010). Previous soil warming experiments at other sites had shown heterogeneous results. Often the increase in the soil respiration rate was transient (Rustad et al. 2001; Melillo et al. 2002; Strömgren and Linder 2002). An increase in soil temperature by 4 °C, i.e. a hypothetical warming that is currently considered to represent a realistic temperature increase in central European mountain regions in the coming decades (Beniston 2006), at Mühleggerköpfl increased total soil respiration by more than 40%, of which more than 50% was attributable to heterotrophic respiration (Schindlbacher et al. 2009). Soil warming therefore did not only accelerate

the biogeochemical C cycle by stimulating autotrophic respiration rates, but it also reduced the stock of soil organic matter. Seven years after the warming treatments its effect has not worn off. So far no evidence has been found that the amount of easily decomposable soil organic matter could be exhausted. A density fractionation has shown that two-thirds of the soil C was in the light and presumably more labile fraction (Schindlbacher et al. 2010). We expect that the site will be a source of CO<sub>2</sub> in a warmer world. This prediction is based on an extrapolation of the field measurements over 7 years and carries substantial uncertainties.

In order to further approximate potential future site conditions the soil warming experiment was combined with a drought experiment. Climate scenarios predict prolonged periods of summer droughts. Therefore, rain was excluded for ca. 4 weeks during July and August in two consecutive years. The untreated control released 7.1 t C ha<sup>-1</sup> annually via total soil respiration. Droughting alone reduced soil respiration by 20% as compared with the control. In heated and droughted conditions the two treatments have cancelled the effects on soil respiration (Schindlbacher et al. 2012). The impact of the future C input into the soil from a more productive forest in the future and the possible non-linearity of the relationship between temperature and soil respiration remain to be explored (Bond-Lamberty and Thomson 2010; Smith and Fang 2010). However, we expect that C fixation will respond to future climatic conditions less than the C release. The C accrual in the forest ecosystem is expected to increase due to the elongation of the growing season and the more favourable temperature regime during summer. However, the nutrient supply from the shallow soils forming on calcareous bedrock will impose limits to forest productivity. On the other hand, heterotrophic respiration will fully benefit from higher temperatures and the abundance of readily decomposable substrate from soil organic matter. Superimposed on the balance between C fixation and C release are the ecosystem dynamics with a yet unpredictable disturbance regime (Seidl et al. 2011).

### Synthesis and future research

The Mühleggerköpfl research site has been instrumental in addressing a sequence of topics in the last 20 years. Research on air pollution and deposition has led to research on bioindicators for early stress diagnosis in Norway



spruce (Bolhar-Nordenkampf 1990; Herman et al. 1998, 2005), and later, to an assessment of the biogeochemical cycles of N and C. Based on our results, we have not refuted the hypothesis that the Mühleggerköpfl site is gradually approaching N saturation. So far the ecosystem is capable of retaining the incoming N within the system. Nevertheless, considering a stable or even declining net uptake of N in the stand biomass and a positive balance between N inputs and outputs (Table 3), we assume that the N supply already matches or even exceeds the N demand of the forest. The present mature spruce-dominated forest will not, in the long run, be able to retain the N from deposition. Potential scenarios include: (1) the site develops into a N source and pollutes the ground- and surface water with  $\text{NO}_3^-$ ; or (2) as the mature stand continues to disintegrate the aggrading new forest captures the available N. Our hypothesis of a rapid response by the ecosystem to external N input by an increase in nutrient concentrations in spruce needles, increasing N concentrations in the soil solution and ultimately the pollution of seepage water with  $\text{NO}_3^-$  has not been not corroborated. Unexpected results from a modelling exercise included the release of over  $15 \text{ kg N ha}^{-1} \text{ year}^{-1}$  as  $\text{N}_2$  from the soil and the emerging dominance of seedlings of beech and maple over spruce seedlings. Measuring the release of  $\text{N}_2$  from soils is a field of future research with technical challenges that are yet only partially resolved (Dannenmann et al. 2008; Butterbach-Bahl and Gundersen 2011). The increasing success of deciduous trees in a formerly spruce-dominated ecosystem is attributable to global change in its entire complexity, i.e. climate change, modified forest management practices, and an increase in N availability.

With respect to C dynamics, we have established that the site was quasi C neutral, because the accretion of C in tree biomass was offset by C loss from the soil. In a warmer world, soil organic matter is likely to be mineralised at a higher rate than today, thereby diminishing the potential C sink strengths of forest ecosystems. Abundant labile soil organic matter can fuel heterotrophic respiration for a long time (Knorr et al. 2005; Davidson and Janssens 2006; Schindlbacher et al. 2010). Dynamic processes originating from an increased frequency of disturbances such as storms, or insect attacks, as predicted by climate scenarios, and natural regeneration of deciduous trees will have a strong effect on biogeochemical fluxes.

Although our results on the biogeochemistry of C are based on a single site, we emphasise that mountain forests on calcareous bedrock cover almost a third of the Austrian forest area and that the observed processes are indicative for this forest type on a larger scale. The dynamics of N at the Mühleggerköpfl closely resemble the results of the long-term monitoring site Zöbelboden in Upper Austria in an otherwise similar environmental setting (Jost et al. 2011).

In the future a detailed study of the water cycle at the site is planned. This is particularly complicated because watersheds on dolomitic bedrock are difficult to delineate. Karst phenomena and rapid water flow in large pores of the heterogeneous soil profile turn hydrological measurements into a challenging endeavour.

Continued research will investigate the greenhouse gas budget, with particular attention to the interaction of artificial warming and artificial drought in order to narrow the speculation on the effects of climate change (e.g. if the effect of soil warming on soil respiration will diminish or continue). This topic is of high relevance for policy advice.

A comprehensive topic is the assessment of forest ecosystem dynamics. We expect that disturbances in the current developmental phase of the present forest stand will provide new insights into ecological processes. An unresolved question is the interaction of C and N in the context of greenhouse gas emissions. High loads of N increase the productivity of the forest and can thereby increase the soil C pool (Högberg et al. 2006; Quinn Thomas et al. 2009). In addition, N may retard the decomposition of soil organic matter (Hyvönen et al. 2008; Janssens et al. 2010).

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### Notes on contributors

Robert Jandl conceived and wrote the paper; Stephan Smidt conducted the air pollution experiments; Andreas Schindlbacher took responsibility for the soil warming experiment; Michael Englisch made a detailed soil morphological analysis; Sophie Zechmeister-Boltenstern conducted experiments on soil microbiology and nitrogen oxide emissions from soils; Christian Mikovits worked on the carbon cycle; Philipp Schöftner and Friederike Strebl modelled the N dynamics; and Gabriele Fuchs supplied an interpretation of the soil hydrological data.

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