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Assessing airborne pollution effects on bryophytes − lessons learned through long-term integrated monitoring in Austria

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Bryophytes show ambiguous response to airborne pollutants during 14 years of monitoring in a forest ecosystem.

Abstract

The study uses measured and calculated data on airborne pollutants, particularly nitrogen (ranges between 28 to 43 kg N*ha^{-1}*yr^{-1}) and sulphur (10 to 18 kg SO_4-S*ha^{-1}*yr^{-1}), in order to assess their long-term (1992 to 2005) effects on bryophytes at the UN-ECE Integrated Monitoring site 'Zöbelboden' in Austria. Bryophytes were used as reaction indicators on 20 epiphytic plots using the IM monitoring method and on 14 terrestrial plots using standardised photography. The plots were recorded in the years 1992, 1993, 1998, and 2004/2005. Most species remained stable in terms of their overall population size during the observed period, even though there were rapid turnover rates of a large percentage of species on all investigated plots. Only a few bryophytes (*Hypnum cupressiforme*, *Leucodon sciuroides*) responded unambiguously to N and S deposition. Nitrogen deposition had a weak but significant effect on the distribution of bryophyte communities. However, the time shifts in bryophyte communities did not depend on total deposition of N and S.

Keywords: Integrated monitoring; Biomonitoring; Forest ecosystem; Eutrophication; Acidification

1. Introduction

1.1. Integrated monitoring and air pollution

One of the major tasks of scientists is to investigate environmental changes and their impacts on ecosystems and biodiversity in order to provide policy makers with appropriate information to regulate environmental pollution (see Erisman et al., 2002). A tool that helps to fulfil this task is the multidisciplinary Integrated Monitoring Programme (ICP IM) which is part of the effect-oriented activities under the 1979 Convention on Long-range Transboundary Air Pollution (LRTAP) in the region of the United Nations Economic Commission for Europe (UNECE). The overall aim of integrated monitoring is to determine and predict the state and change of terrestrial and freshwater ecosystems from a long-term perspective with respect to the impact of air pollutants, especially nitrogen (N) and sulphur (S) (Environmental Administration, 2005). The ICP IM sites are small water catchments located in natural or semi-natural areas in 19 European countries. In Austria there is only one site which is called "Zöbelboden" and situated in the National Park 'Northern Limestone Alps'. It was established in 1991 and is also a GTOS (Global Terrestrial Observing System) site (Umweltbundesamt, 2006).

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1.2. Monitoring by bryophytes

Given their morphological and physiological characteristics, bryophytes have proved to be excellent bioindicators for a wide range of contaminants. Lacking a root system and a persistent cuticle, water, nutrients and toxic substances are mainly absorbed via the entire plant surface from air and precipitation, and to a minor extent from the substratum via capillary effects (e.g. Brown, 1984; Brown and Bates, 1990). Bryophytes show a strong resistance to various toxic compounds (e.g. heavy metals, PAHs) which accumulate in mosses and can therefore be used for monitoring these substances (Holoubek et al., 2000; Gerdol et al., 2002; Ötvös et al., 2003; Zechmeister et al., 2003a; Solga et al., 2005). However, bryophytes are sensitive to other chemicals such as S or N compounds (Türk and Wirth, 1975; Rao, 1982). This sensitivity is the reason for their use as reaction indicators (Markert et al., 2003). Single pollutants mostly produce reaction patterns that are different from those produced by mixtures of the same pollutants, which is what usually occurs in the atmospheric environment. Bryophytes respond to air pollution mainly by changes in their distribution and abundance (LeBlanc and DeSloover, 1970), changes in biomass (Bengtson et al., 1982) and health (Nash and Nash, 1974; Greven, 1992), and changes in the structure of communities (Turetsky, 2003). Bryophytes display various modes of reproduction and long-distance dispersal (Longton, 1997), which is a main feature for the quick re-colonisation of habitats once the air quality has improved (for further reading see Löbel et al., 2006).

For monitoring the overall air pollution by epiphytic bryophytes, several methods have been developed (LeBlanc and DeSloover, 1970; ICP IM-Manual, 2004; VDI, 2006) and applied in a wide range of in situ studies (for a review see Zechmeister et al., 2003a). Terrestrial mosses were mainly the target of experimental studies, in which the influence of atmospheric deposition on species and populations was investigated. These experiments were mainly performed within the framework of the global change research in arctic and tundra ecosystems and focused on N and phosphorous deposition (Robinson et al., 1998; Gordon et al., 2001; Jones et al., 2002). Most experimental studies were restricted to a period of two to four years and the outcomes were very controversial, depending on the observed species and ecosystems (Jònsdòttir et al., 1995; Mitchell et al., 2004; Solga et al., 2005). Long-term experiments or biomonitoring programmes using terrestrial bryophytes as reactive indicators for more than ten years have up to now been almost non-existent (Strengbom et al., 2001). The observation of bryophyte population patterns and changes of them is common in population biology but has hardly ever been used for long-term monitoring studies of the impact of environmental pollution. However, we believe that population dynamics have to be taken into account when using bryophytes as biomonitors. The combined observation of environmental data obtained by measurement devices and biomonitoring data (e.g. by bryophytes) over a longer period is highly desirable though hardly ever available. To our knowledge, this study is the first to use this comprehensive approach.

The aim of our study was to evaluate the response of epiphytic and terrestrial bryophytes to atmospheric pollution at the ICP IM site ‘‘Zöbelboden’’ in the Northern Alps in Austria within the last 14 years. For this evaluation, we used data on airborne pollution (SO_4, NO_3, NH_4, N-total) measured by technical equipment together with long-term biomonitoring data on bryophytes. Specifically we tested: 1) if single bryophyte species showed directional trends in their abundance; if 2) species composition changed; and 3) if these changes could be attributed to N and S deposition, particularly to different deposition amounts present in the area.

2. Methods

2.1. Site description

The size of the Austrian ICP IM site is 90 ha. It is situated in the northern part of the National Park ‘‘Northern Limestone Alps’’ (N 47°50′30″, E 14°26′30″, see Fig. 1). It is a karst area dominated by dolomite and its altitudes range from 550 m to 956 m.a.s.l. From a geomorphologic viewpoint, it is divided into a very steep slope (30–70°) from 550–850 m.a.s.l. and an almost flat plateau (850–956 m.a.s.l.) on top of the mountain. The long-term average for precipitation is 1650 mm/year, and for temperature +6.7 °C (taken at 900 m.a.s.l.). Besides two years with extraordinarily hot summers (1997, 2003), there was no increase in the annual average temperature in the observed period. There were also hardly any changes in the amount of precipitation between 1992 and 2004. The humid climate generally favours the luxurious growth of bryophytes. The area is mainly covered by mixed montaineous forest. The trees most commonly found are beech (*Fagus sylvativa*), maple (*Acer pseudoplatanus*) and spruce (*Picea abies*). Spruce predominates on the plateau following plantation after a clear cut around 1910. Today forest management is restricted to single tree harvesting if there is bark beetle infestation. On the slope shallow calcareous soils (Rendsic to Lithic Leptosols) predominate, whereas the plateau is characterised by relict brown soils (mostly Cambisol, but also Stagnic Gleysol). Windthrow is frequent in the area.

2.2. Measurement of deposition

Direct measurement of airborne deposition is carried out according to methodological standards of the ICP IM programme (http://www.environment.fi). For the present study we used data on wet deposition from a clearance area (900 m.a.s.l.), throughfall deposition (= below canopy) in two intensively surveyed forest stands, and on modelled total deposition (including dry, fog and cloud deposition). Wet and throughfall deposition was measured using bulk precipitation samplers. The two intensively surveyed forest stands are located on the plateau (intensive plot I, 895 m.a.s.l.) and on the slope (intensive plot II, 880 m.a.s.l.; Fig. 1). They represent two contrasting forest stands which are typical of the study area: the mixed beech-maple-spruce forests characteristic of the slope and the spruce-dominated forests characteristic of the plateau.

The total deposition of S and N was estimated for the time period 1999–2002 by using measured wet only deposition of the clearance area, modelled occult deposition (CDM-Cloud Deposition Model after Lovett, 1984) and dry deposition (DDM-Dry Deposition Model after Baldocchi et al., 1987 and Meyers et al., 1991) with an active cloud water sampling technique (string collector NESA1). In total, 173 cloud-water events were collected during the observation period. Analyses were performed for SO_4^{2-}, NO_3^-, NH_4^+, basic cations as well as for Cl^-. Gaseous compounds were analysed by continuous monitoring (NO, NO_2 and SO_2) or estimated by using data from other Austrian studies (HNO_3, NH_3, particulate N and S compounds). Wet only samples were collected on a daily basis and analysed for the same ionic components as the cloud water samples (see Kalina and Zambo, 2003 for more details). The estimation of total deposition was performed for 21 forest stands with forest inventory data from 1992. Kalina and Zambo (2003) used tree species, stem diameter, tree height, and canopy height to estimate the surface area index of different canopy layers, a main input variable for the models. For an

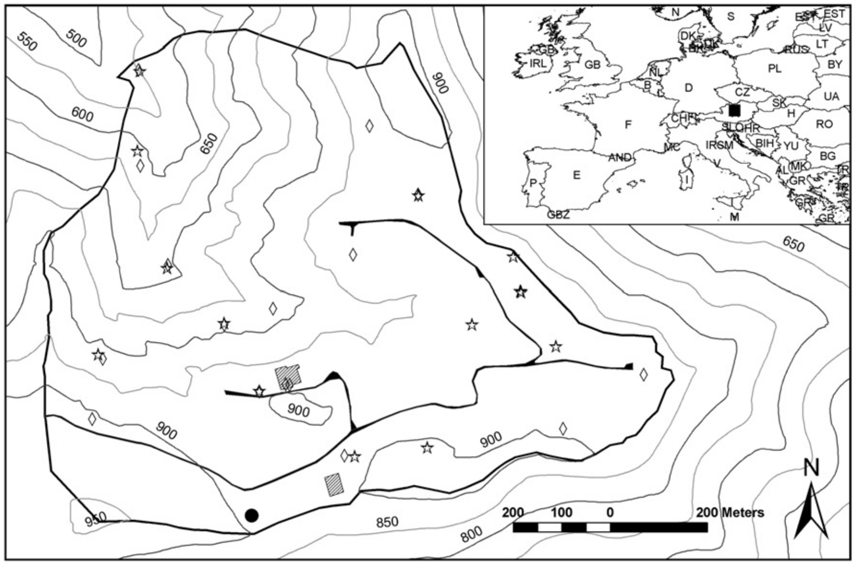

Fig. 1. Map of the study area: boundary of the catchment and forest roads (bold lines); elevation contours (black and grey lines); forest clearing with meteorological measurements and deposition (black dot); intensive-plot I at the plateau in the south and intensive-plot II in the slope (hatched areas); terrestrial (star) and epiphytic plots (diamond).

extrapolation of the results for the 21 forest stands to the entire study area, a forest biotope map from the year 2000 with data on tree species abundance for each polygon was used. The polygons were overlaid with the 21 forest stands and classified into 4 gross forest structural types for which the estimated total deposition had been established. These were henceforth referred to as ‘‘deposition clusters’’, which were subsequently overlaid with the bryophyte plots in order to obtain an estimate of the exposition of each plot to N and S deposition.

2.3. Monitoring by bryophytes

2.3.1. Monitoring epiphytic bryophytes

Twenty epiphytic monitoring plots were established for recording the epiphytic bryophytes according to the ICP IM Manual sub-programme EP ‘trunk epiphytes’ (ICP IM Manual, 2004). This method was originally developed for lichens, and adapted to be used for bryophytes in several countries.

2.3.1.1. Tree selection. Initially ten beech trees (*Fagus sylvatica*) were selected, of which eight survived the overall period and two were destroyed by windbreak. Furthermore ten maple trees (*Acer pseudoplatanus*) and two ash trees (*Fraxinus excelsior*) were used for bryophyte recording. Half of the plots were located on the steep slope, and the other half in the flat area on the top. Each species was represented with the same number in both morphological areas. Trees for recording were distributed evenly over the site. The criteria for selection of the plot, and of the individual tree respectively, were as follows: The individual tree should preferably be under mesic ecological conditions, i.e. avoid extremes such as sheltered depressions, wind-exposed heights and forest edges. The tree trunk had to be vertical or near enough, neither crown nor bark were supposed to have severe visible damage, the bryophyte community was not supposed to be deviating too much from surrounding trees of the same species and the recording was restricted to mature trees. Epiphytic plots were established in 1993. Several plots had to be substituted following a loss of recording sites through windfall. Some plots were not established until 1998, and their introduction guaranteed an even distribution across the site, even on the steepest slopes. The location of the epiphytic plots is shown in Fig. 1.

2.3.1.2. Recording bryophytes. The observations were made according to the line cover method. The bryophytes were recorded along a measuring tape fastened around the trunk of the sample tree at a level of around 120 cm above ground. The ring was fixed into place with a permanent nail, so that the recordings were in the same place for each period. Every five cm a recording was taken and the species hitting the tape at these points from the upper edge were recorded. Samples of species unidentifiable in the field were taken for identification in the lab. Empty bark spaces and lichens (as single group) were recorded as well. The frequency of each bryophyte species was recorded and the percentage of coverage was calculated in relation to the stem circumference.

In addition, all trees selected for monitoring were photographed in order to observe visible changes in the surroundings of the trees. Studies were initialised in 1993, and repeated in 1998 and 2004/2005 during the vegetation period. The methodology was the same at all times.

2.3.2. Monitoring terrestrial bryophytes

Fourteen permanent terrestrial plots with a size of 50 × 50 cm were established in the observation period. Terrestrial plots were selected in 1992 on the basis of a evenly distribution over the sites, and the density or composition of bryophytes was not a determining criterion. The location of the terrestrial plots is shown in Fig. 1. Terrestrial plots were marked by four steel posts and were recorded by hand drawing in 1992 and 1993. The contour lines of the bryophytes patches were traced onto plastic shields that were put over the terrestrial plot. Where several species were mixed up very closely, they were included in one recording patch and the percentages of the species were recorded in an extra file. The contours of all bryophyte patches, along with structural elements like vascular plants, lichens, dead wood and bare rocks were digitised from scanned hand drawings using a GIS (Arc-View GIS 3.2 ESRI, 1999). The total coverage (cm^2) of each bryophyte species and additional structures was calculated from these maps. From 1998 onwards, the plots were recorded by taking photographs with high quality photographic cameras (Leica R8, Canon D50), using either high resolution films (Kodachrome 25) or a large pixel storage capacity (9 MB). Photographs were taken by standardising the height and angle of the camera by using a self-made tripod fixed to the four posts of the terrestrial plot. The photographic resolution was appropriate for analysing even single individuals in most cases. However, for reasons of time and the congruency of methods, individuals that were mixed up closely were treated in the same way as in previous years (described above). The production of the maps was followed by ground-truthing on each plot. Individuals or species which could not be identified by the pictures were taken note of and the borderlines of populations adjusted. With these amendments, the maps were finalised.

To assure the congruency of both methods, a simultaneous method comparison of the methods (hand drawing/photographs) was carried out in 1998 by using both methods on the same plots.

After establishing and recording the monitoring plots in 1992, the studies were repeated during the vegetation period in 1993, 1998 and 2004/2005. Besides the change from hand drawing to photographic recording on the terrestrial plots, the methodology was the same at all times.

2.3.3. Nomenclature

The **nomenclature** of bryophytes follows the code list for Integrated Monitoring (Code List M2, 1994), which is closely related to the code lists of Corley et al. (1981) and Grolle (1983).

2.4. Statistics

2.4.1. Deposition of N and S

The difference between N and S deposition of intensive plots I and II was tested using a two-sided paired *t*-test on the annual values.

2.4.2. Univariate (single-species) statistics

According to the data structure (non-normal distribution, differences in variance), we used the Wilcoxon Matched-Pairs Signed Rank Test to test for significant differences, in each species separately, between the independent variables of each year, plot, and host tree species. Overall changes of bryophyte and lichen coverage as well as empty bark were also tested using the Wilcoxon Matched-Pairs Signed Rank Test.

2.4.3. Multivariate (community) statistics

Changes in the species composition of the plots between the years 1992, 1993, 1998, and 2005 were evaluated using non-metric Multidimensional Scaling (nMDS). This scaling technique reduces a multidimensional space, represented by a dissimilarity matrix comprising pairwise distances between plots, to a configuration with an a priori defined number of dimensions (nMDS-space) mostly ranging from two to four for vegetation data. To minimise the loss of information, nMDS iteratively searches for the best position of the plots in the nMDS-space. The quality of this transformation is indicated by ''stress'', which is defined as the square root of the ratio of the sum of squared differences between the input distances and those of the configuration to the sum of configuration distances squared. nMDS, as other iterative algorithms, is susceptible to getting stuck at local minima. To reach the global minimum (i.e. the configuration with the lowest stress) calculations were repeated sixty times with random starting arrangements of the plots. The model with the lowest stress was chosen as the final configuration. To ease the drawback of an indeterminable orientation and scaling of the axes, some post-processing of the results was carried out. The configuration was rotated to maximise the variance of points on the first dimension using a Principle Component Analysis. The configuration was centred to the averaged axes values. Additionally, the axes were rescaled so that one unit represented a halving of community similarity from replicate similarity (Oksanen et al., 2005). For the epiphytic plots, percentage coverage was used, and for the terrestrial plots the area of bryophyte species. The dissimilarity matrix applied in the nMDS arrangement was constructed using Jaccard distances and thus acounted only for species composition. Abundance-based dissimilarity indices like Bray-Curtis did not provide any significant differences. Vegetation data from all years of observation were included in the matrix. A three-dimensional nMDS space was chosen.

In order to test the significance of different amounts of N and S deposition on the bryophyte species composition of the terrestrial and epiphytic plots, Kendall's *tau* correlation coefficient between nMDS-axis scores and the ranked deposition cluster were used.

Values in nMDS-axis scores derived from plots between observations in 1992 or 1993 and 1998, 1998 and 2005, and 1992 and 2005 were subtracted to obtain vectors (each with 3 elements according to axes 1 to 3) of distances from paired plots in the nMDS space. These vectors were tested using Multivariate Analysis of Variance (MANOVA) with the Pillai-Bartlett test statistic. The deposition cluster and, in the case of the epiphytic plots, the host tree species were used as grouping variables. A significant deviation of the intercept from zero would thus indicate a shift through time. The significance of the grouping variables would indicate whether there were differences in vegetation shifts among deposition clusters and host tree species.

Univariate statistics were carried out with SPSS Version 10.0. The statistical package R 2.2.0 was used for nMDS [metaMDS function of the vegan library from Oksanen et al., (2005)] and MANOVA.

3. Results

3.1. Measurement of deposition

Data from the bulk deposition measurements of N-total, NO_3, NH_4 and SO_2 in the clearance area between 1995 and 2004 are given in Fig. 2A. The annual average values for this period were 16.5 ± 2.7 kg N-total*ha^{-1}*yr^{-1}, 7.5 ± 2.6 kg NH_4-N*ha^{-1}*yr^{-1}, 6.9 ± 1.0 kg NO_3-N*ha^{-1}*yr^{-1}, 6.2 ± 1.5 kg SO_4-S*ha^{-1}*yr^{-1}. The deposition of N in 2004 was comparable to that in 1995 but showed a considerable peak around the year 2000 with up to 22 kg N-total. S showed a slightly decreasing trend over all the years (see Fig. 2).

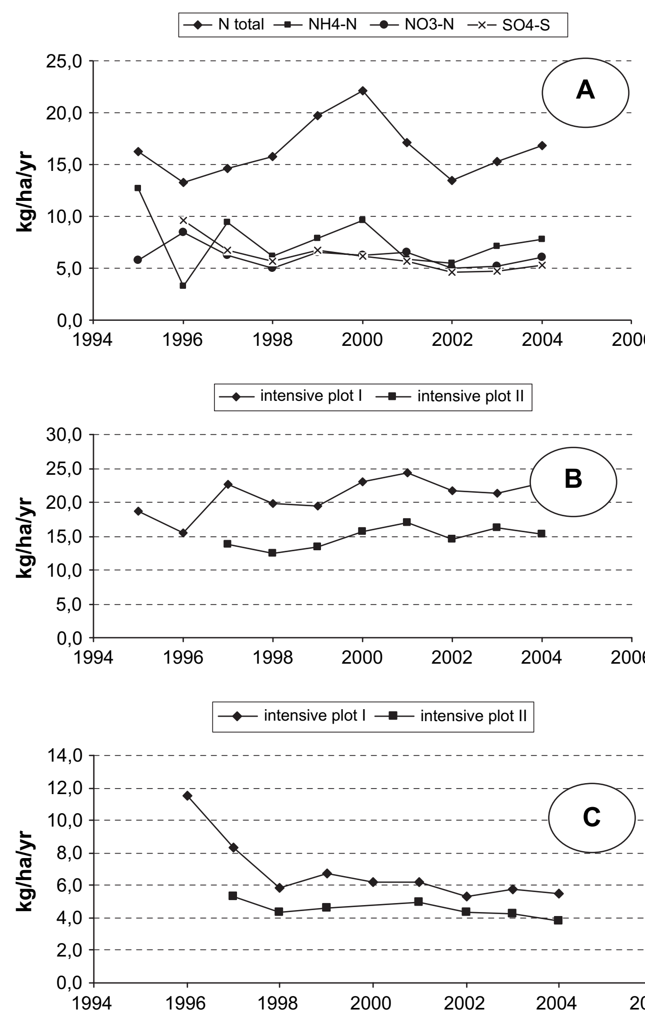

Fig. 2. (A) Bulk deposition of N-total, NH_4-N, NO_3-N, and SO_4-S measured at the clearance area between 1995 and 2004. Throughfall bulk deposition of N-total (B) and SO_4-S (C) of forest stands in intensive plots I and II between 1996 and 2004. Values give annual sums of bulk deposition measurements on a two-weekly basis.

Throughfall bulk deposition measurements on the two intensive plots showed different results (Fig. 2B,C). The average N-total deposition for intensive plot I was 20.9 ± 2.6 kg $N*ha^{-1}*yr^{-1}$ and for intensive plot II 14.8 ± 2.4 kg $N*ha^{-1}*yr^{-1}$. N-total showed a slight increase from 1995 to 2004. There was a significant difference between the deposition of N-total on intensive plot I and that on intensive plot II ($P < 0.001$; two-sided paired *t*-test). The average SO_4-S deposition was 7.1 ± 2.0 kg $N*ha^{-1}*yr^{-1}$ for intensive plot I and 4.0 ± 1.5 kg $N*ha^{-1}*yr^{-1}$ for intensive plot II. Again, there was a significant difference between the S deposition on intensive plot I and that on intensive plot II ($P = 0.005$; two-sided paired *t*-test). These differences can be explained by the stand structure and tree species composition of the two plots (Kalina and Zambo, 2003). The dominance of evergreen conifer (Norway spruce) on intensive plot I caused higher amounts of dry and occult deposition. The snow regimes in the slope area (less snow due to wind in the upslope areas) and on the plateau (snow accumulation in flat areas) might additionally have influenced deposition.

The estimated total deposition, accounting for occult and dry deposition, ranged between 28 and 43 kg $N*ha^{-1}*yr^{-1}$ and 10 to 18 kg SO_4-$S*ha^{-1}*yr^{-1}$ for the different forest structural types. Occult and dry deposition accounted for 45 to 59% of total N and 40 to 67% of total S deposition. The four predominant structural forest types received deposition amounts within the above ranges: deposition cluster 1 < deposition cluster 2 < deposition cluster 3 < deposition cluster 4. In accordance with the throughfall measurements of intensive plots I and II, high amounts of total deposition were concentrated on the plateau owing to the high proportion of the conifer *Picea abies*, whereas the slope area was characterised by mixed beech-maple-spruce forests receiving fewer air pollutants.

3.2. Monitoring with bryophytes

The comparison of the method using hand drawings with that using photographic recording from 1998 onwards on 10 plots did not reveal any significant differences regarding overall coverage (Wilcoxon signed rank test; $P = 0.946$) or single species.

3.2.1. Species-specific results

In total, at least 55 species were found on all the monitoring plots during one observation year. 33 of these were found on epiphytic and 33 in terrestrial plots. 11 species occurred on both types of plots. With the exception of a few dominants, coverage was low for most of the species and the turnover rate high over the observed period. When looking at all the monitoring plots, only six terrestrial (18.2%) and eight epiphytic species (24.2%) covered more than 5% of the plot area. *Hypnum cupressiforme* was the only species covering more than 5% on both types of the monitoring plots. There was a high turnover rate of populations: only one epiphytic species (*Hypnum cupressiforme*) and three terrestrial species (*Dicranum scoparium*, *Polytrichum formosum*, *Bazzania trilobata*) were found on the same plots in all the observation years. Ten epiphytic and 15 terrestrial species occurred only in one single monitoring year. Changes within the observed species were inhomogeneous between the two periods (1992 to 1998 and 1998 to 2004/2005) and only very few species showed a constant directional trend over all periods.

3.2.1.1. Epiphytic bryophytes. Within the observation period there was an overall increase in bryophyte cover, associated with a significant reduction of empty bark (Wilcoxon Matched Pairs; $P = 0.035$) and a constant but not significant reduction of lichen coverage. Significant increases of coverage were found for *Hypnum cupressiforme* (Wilcoxon Matched Pairs; $P = 0.009$) from 1992 to 2004. *Leucodon sciuroides* did not increase from 1992 to 1998 but increased significantly from 1998 to 2004 (Wilcoxon Matched Pairs; $P = 0.027$). All the other species did not show significant changes. However, decreases were found for *Metzgeria furcata* and *Pylaisia polyantha*. Slight increases were observed for both the *Frullania* species and *Ulota crispa*. For all other species, coverage was stable over all the years of observation.

3.2.1.2. Terrestrial bryophytes. The area covered by bryophyte species differed extremely among plots during one observation, and also between repeated observations of a plot. The differences in the area covered by the species were extremely heterogeneous among the various plots and years. Only one single species (*Dicranodontium denudatum*) showed a significant decrease across all the investigated plots (Wilcoxon Matched Pairs; $P = 0.043$) within the observed periods. Most species increased on one plot and decreased on another. Some species showed decreasing linear trends over the investigation period, e.g. *Leucobryum glaucum* and *Thuidium tamariscinum* but these trends were not significant.

3.2.2. Plot-specific results

3.2.2.1. Epiphytic plots. An nMDS of the epiphytic plots resulted in a stress value of 14.56. The species composition was significantly different (signed rank test; $P = 0.999$, sign < 0.001) on the various host trees, which is also shown by the clustering of epiphytic plots along the nMDS axis in Fig. 3.

As indicated by the configuration of the epiphytic plot on the nMDS plot (Fig. 3), the species composition correlates, at least to some extent, with the deposition cluster representing different amounts of total N and S deposition (significant 2nd axis in Table 1).

When looking at all plots, no significant differences in species composition were found between the years of observation. Also, the host tree species and deposition regime did not lead to divergent shifts in the composition of bryophytes within plots (Table 2). Salient changes on single plots were counterbalanced by others showing trends in the opposite direction. Even the species compositional change of single plots showed

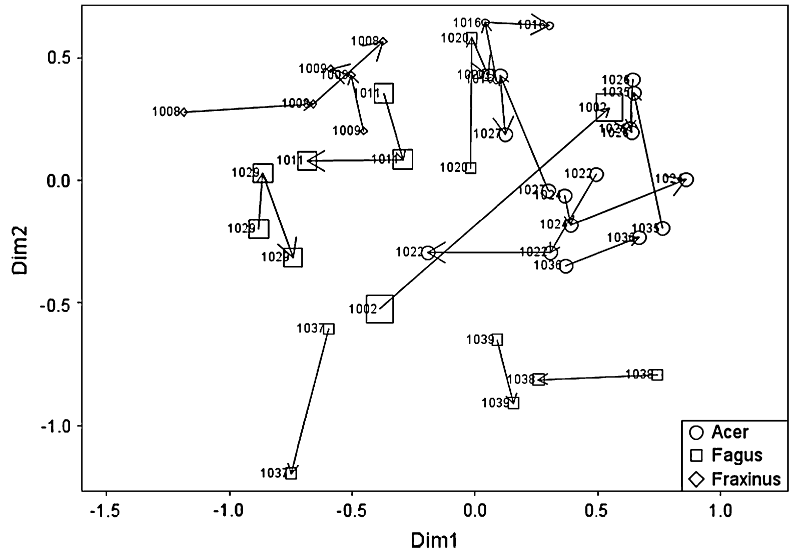

Fig. 3. Non-metric Multidimensional Scaling (nMDS; axes 1 and 2) of the epiphytic monitoring plots. The sizes of the symbols stand for the amount of N and S deposition (deposition cluster 1–4, see Fig. 4) on each epiphytic monitoring plot. The direction and size of the arrows represent the temporal development from the first (1992) to the last (2004) observation. Plot numbers are given for each year of observation.

remarkable differences in the magnitude and direction of the changes between the years of observation (Fig. 3).

3.2.2.2. Terrestrial plots. An nMDS of the epiphytic plots resulted in a stress value of 15.88. On the terrestrial plots, there was a clear pattern of bryophyte species composition depending on the total N and S deposition regimes, as represented by the deposition clusters (Fig. 4 and Table 3). Some species like *Hypnum cupressiforme* or *Thuidium tamariscinum* tended to be found in the clusters with high deposition levels, but were not restricted to them. The first axis of nMDS in Fig. 4 can be interpreted as a gradient of total bryophyte coverage within the plots. The second axis stands for the magnitude of change.

However, similar to the epiphytic plots, no consistent and significant directional trend in the variation of the bryophyte communities could be found over the various years. Neither did a divergent compositional change occur in the different deposition clusters (Table 4). Some plots showed clear trends in a single direction (e.g. a stringent decrease of populations in plot 1012; see Fig. 4), on others there were trends in the opposite direction (e.g. plot 1007). Several plots showed no discernible trends within the periods of investigation, which are illustrated by a zigzag line. In several cases the controversial change of directions clearly follows the decrease and increase of single dominant species (e.g. *Thuidium tamariscinum* in 1023, *Dicranodontium denudatum* in 1006).

Table 1
Kendall's *tau* correlation coefficient between nMDS axis scores of the epiphytic plots and the deposition cluster representing different amounts of total deposition of N and S

nMDS axis	Deposition cluster
1	0.012
2	**−0.328****
3	0.002

Significant correlations are given in bold (* *p*-value <0.05, ** <0.01, *** <0.001).

4. Discussion

The empirical critical loads for deteriorating effects of excess N upon forest habitats are between 10 and 20 kg N*ha^{-1}*yr^{-1} for the observed forest types (Bobbink et al., 2003). With a bulk deposition of 14 to 22 kg N-total*ha^{-1}*yr^{-1} in throughfall at forests stands, the study area is in the upper range of the critical loads for N. Taking occult and dry deposition into account, the forests within the study area are exposed to N deposition above the threshold up to a double exceedance (ranging between 28 and 43 kg

Table 2
Overall changes in bryophyte species composition from 1993 to 1998, 1998 to 2005, and overall from 1993 to 2005, analysed by a MANOVA of the differences of nMDS axis scores from epiphytic plots between observation years

	Pillai	*F*	df	*P*
Time shift 1993–1998	**0.502**	**1.346**	**1, 3**	**0.378**
Deposition cluster	0.800	0.727	3, 9	0.680
Host tree species	1.157	2.286	2, 6	0.119
Time shift 1998–2005	**0.034**	**0.324**	**1, 3**	**0.808**
Deposition cluster	0.025	0.124	2, 6	0.993
Host tree species	0.349	2.041	2, 6	0.075
Overall time shift 1993–2005	**0.422**	**0.731**	**1, 3**	**0.599**
Deposition cluster	0.623	0.603	2, 6	0.722
Host tree species	0.879	1.045	2, 6	0.463

An intercept significantly different from zero would indicate a time shift, whereas an interaction of the observation year and the host tree species or deposition cluster would indicate differences in the time shift between tree species and/or deposition clusters representing different amounts of total deposition of N and S. The relevant time shift is given in bold with the respective interactions in the two rows below. The Pillai-Bartlett test statistic was used.

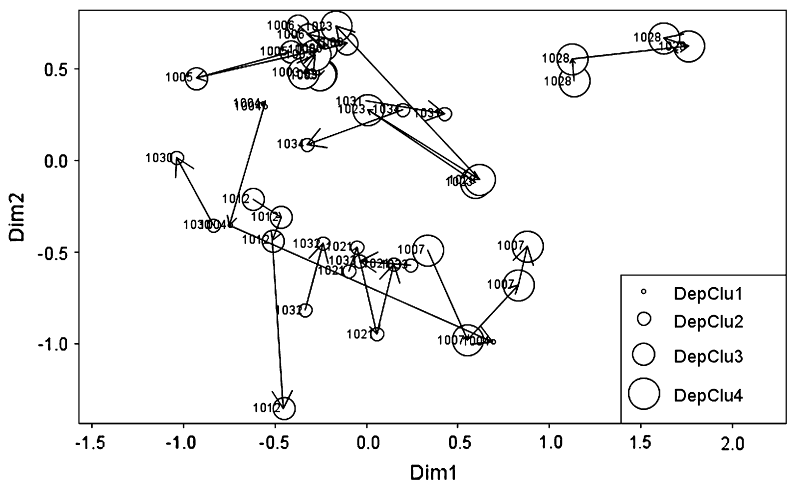

Fig. 4. Non-metric Multidimensional Scaling (nMDS) of terrestrial monitoring plots (axes 1 and 2). The size of the circles represents the amount of N and S deposition (deposition clusters 1–4) on each terrestrial plot. The direction and size of the arrows represent the temporal development from the first (1993) to the last (2005) observation. Plot numbers are given for each year of observation.

N-total$*ha^{-1}*yr^{-1}$). The substantial share of occult and dry deposition is characteristic of mountain forests with frequent fog and cloud events (Lovett, 1984; Wesely and Hicks, 2002). S deposition has decreased, as in many other parts of Europe, so that acidification has become less of a problem (Bouwman et al., 2002) and recovery from already acidified situations might be expected.

The bryophyte species composition clearly differed between host trees species, which does not come as a surprise and is a matter of varying bark properties (Smith, 1982). As we compared only bryophytes species on the same host tree-species, host-specific differences were not assumed to influence shifts in plot-specific species.

Bryophyte species composition on both the epiphytic and the terrestrial plots reflects the total N and S deposition regime, including occult and dry deposition. This is supported by a correlation of the plot position in the nMDS space and the corresponding deposition cluster (Tables 1 and 3). However, the correlation of the deposition cluster with the host tree species may partly be responsible for this pattern. Temporal trends of bryophyte species composition on epiphytic and terrestrial plots did not reveal any significant directional shift throughout all years of observation. However, some comparable patterns of airborne pollution and changes in overall species composition could be found. These patterns are reflected by elongated arrows (relatively big change in species composition) and their direction (pointing towards eutrophication in Fig. 4), which could be attributed to a peak in N deposition in 2000 (Fig. 2).

If the overall observation period is taken into account, time trends are indicated by single species (e.g. *Hypnum cupressiforme*, *Leucodon sciuroides*) rather than by whole communities. But even with single species changes, the populations of only a few bryophytes showed a monotone trend during the 14 years of monitoring. These species (e.g. *Hypnum cupressiforme*) are well-established indicators for eutrophication through N deposition and decreasing acidification due to lower S deposition (Kuhn et al., 1987). But even with the rather high deposition levels of N and the substantial decrease of S deposition, there was a surprisingly weak and ambiguous response of the bryophytes. Some common bryophytes (e.g. *Dicranum, Racomitrium*) are reported to decrease their biomass production at levels as low as 10 kg N$*ha^{-1}*yr^{-1}$ (Jones et al., 2002; Van der Wal and Pearce, 2005). This reaction is due to physiological mechanisms, e.g. inhibition of the enzyme

Table 3
Kendall's *tau* correlation coefficient between nMDS axis scores of the terrestrial plots and the deposition cluster representing different amounts of total deposition of N and S

nMDS axis	Deposition cluster
1	**0.283***
2	**0.256***
3	0.218

Significant correlations are given in bold (*p-values <0.05, ** <0.01, *** <0.001).

Table 4
Overall changes in bryophyte species composition from 1992 to 1998, 1998 to 2005, and overall from 1992 to 2005, analysed by a MANOVA of the differences of nMDS axis scores from terrestrial plots between observation years

	Pillai	*F*	df	*P*
Time shift 1992–1998	**0.847**	**5.519**	**1, 3**	**0.097**
Deposition cluster	1.391	1.441	3, 9	0.255
Time shift 1998–2005	**0.619**	**1.623**	**1, 3**	**0.350**
Deposition cluster	1.196	1.104	3, 9	0.415
Overall time shift 1992–2005	**0.886**	**7.779**	**1, 3**	**0.063**
Deposition cluster	1.465	1.590	3, 9	0.205

An intercept significantly different from zero would indicate a time shift, whereas an interaction of the observation year and the deposition cluster would indicate differences in the time shift between deposition clusters representing different amounts of total deposition of N and S. The relevant time shift is given in bold with the respective interactions in the row below. The Pillai-Bartlett test statistic was used.

nitrate reductase (Pearce and van der Wal, 2002; Koranda et al., in press), or it is a matter of diminished competition ability, when co-occurring species like graminoids make better use of the enhanced N input (Jones et al., 2002; Zechmeister et al., 2003b).

There might be several reasons for the weak long-term changes of bryophytes when facing substantial N and S deposition. Although relatively high, N deposition did only negligibly increase over the years (Fig. 2). Quite a number of experimental studies did not show any significant reactions of bryophytes even to N applications which represented deposition levels (Nordin et al., 1998; Gordon et al., 2001) comparable to the estimated N deposition in the investigated forest ecosystems. However, the question is to which amount of the calculated N and S deposition the bryophytes are exposed in our monitored ecosystem. It has to be assumed that mosses capture less dry and occult deposition then is estimated by using models for whole tree canopies. Also, there is a particular seasonality in the different pathways of deposition, which might lower total exposure to some extent since they do not necessarily overlap with the growth periods of bryophytes. Occult deposition predominately occurs in autumn in the form of extreme events. Wet deposition, on the other hand, is in accordance with the seasonality of precipitation, thus being at its peak in the summer. Whereas the relatively short periods with heavy rainfall can cover up to 25% of the yearly total deposition of the study area, the monthly background deposition was found to be rather low, ranging between 1–2 kg N ha^{-1} and 0.5–1 kg S ha^{-1} (Kalina and Zambo, 2003).

Bryophytes acquire nutrients by atmospheric deposition rather than by uptake from the soils (Bates, 1992). Therefore, it has to be assumed that the pH of the soil should not have major influence on the results. Some of the terrestrial plots were established at soils with a thick layer of duff, and these did not respond different from those strongly influenced by the calcareous soil. The usefulness of bryophytes as an indicator for the deteriorating ecosystem effects of long-term chronic N addition, caused by an increase of soil N pools and nutrient imbalances of plants (Erisman and de Vries, 2000; Bobbink et al., 2003; Magill et al., 2004) has to be questioned. Integrated monitoring, which includes additional biomonitors (like forest undergrowth or tree leaf chemistry), soil and groundwater chemistry, is necessary in order to obtain a conclusive picture of ecosystem changes in response to the observed N and S deposition (Pitcairn et al., 2003; Krupa, 2003).

Bryophytes cannot be treated as a single functional group with regard to the effects of the response to fertilisation (Gordon et al., 2001). Only some bryophytes might be limited by N and P and show better growth with increasing N inputs (Aerts et al., 1992; Jònsdòttir et al., 1995). *Hypnum cupressiforme* and *Leucodon sciuroides* seem to belong to this group, or are at least species which can cope with enhanced N deposition by increasing their biomass.

Many bryophytes are reported to be sensitive to S deposition. Many investigations in urban areas have shown major changes of bryophyte diversity, which were mostly attributed to SO_2 or related substances (LeBlanc and DeSloover, 1970; Türk and Wirth, 1975; Zechmeister et al., 2003a). The strongest decline of formerly very high S deposition levels occurred in the years between 1986 and 1990 (Umweltbundesamt, 2004), incidentally before investigations at the Integrated Monitoring site Zöbelboden started. Also, decreasing S deposition has been measured during the observation period and is typical of many other parts of Europe. *Dicranodontium denudatum* is a rather acidophytic species, and its significant decline could be attributed to this S deposition trend. A strong recovery of species susceptible to S deposition, as reported from other regions, is not evident from our data (Franzen, 2001; Zechmeister and Hohenwallner, 2006), although the (not significant) increases of *Ulota crispa* and *Frullania*-species could be seen as a first indicator for this process.

A stunning result was the high turnover of many bryophyte populations within the observed period. With their small size and comparably low assimilation rates (Turetsky, 2003), a lot of bryophyte species have a rapid life cycle, resulting from a wide range of dispersal abilities and the production of a large number of diaspores. Colonisation, extinction and re-colonisation as essential features of a vivid meta-population had been described a few times in bryophytes population studies before (During and Van Tooren, 1988; Söderström and Herben, 1997; Snäll et al., 2005; Löbel et al., 2006), but had never been taken into account for air pollution monitoring studies. The separation of potential signals of anthropogenic disturbance by airborne pollution from the background "noise" of natural variation is a prerequisite for a biomonitor to be applicable and should thus be studied in more detail.

5. Conclusion

During the 14 year period of observation most bryophyte species remained stable in their overall abundance in the area, although there were rapid species turnover rates in the investigated plots. The observed changes can only to some extent be attributed to effects of airborne pollution. A few bryophytes (*Hypnum cupressiforme*, *Leucodon sciuroides*) responded to N deposition levels in the observed period by an increment in their population coverage. Accordingly, the changes in only a few other species point to a recovery from acidification. Considerable year-to-year variation of the species composition was found which is due to population dynamics. The bryophyte communities as a whole did however not show directional changes attributable to the observed amounts of N deposition and the decrease of S deposition. Thus, the substantial exceedance of critical loads for eutrophication effects did not lead to acute injuries. If at all, such injuries tended to be chronic injuries of individuals within the bryophyte populations and recovery processes from former acidification seem to be slow. This resulted in a spatial distribution of bryophyte communities which were at least to some extent related to different deposition regimes. These results underpin the importance of long-term investigations and permit a critical view of the results obtained by short-term experiments. Moreover, chronic ecosystem effects, like those from excess N deposition, can only be interpreted conclusively within the framework of an integrated approach using different biological indicators, soil and groundwater monitoring.

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