The Lichenologist **36**(3&4): 249–260 (2004) © 2004 The British Lichen Society
DOI: 10.1017/S0024282904014112 *Printed in the United Kingdom*

Spatial analysis of lichen species richness in a disturbed ecosystem (Niepołomice Forest, S Poland)

Paweł KAPUSTA, Grażyna SZAREK-ŁUKASZEWSKA and Józef KISZKA

Abstract: The spatial pattern of lichen species richness was analyzed in a forest ecosystem impacted for 50 years by industrial emissions from a steelworks. Geostatistical tools were used to characterize the spatial pattern of the number of lichen species and multiple regression analysis was used to identify factors influencing it. Spatial analysis showed high variation of lichen species richness on a local scale, caused by patchiness of natural habitat factors (species composition of trees, their age, shade, etc.). On a large spatial scale, species richness differentiated the western from the eastern part of the forest. The western part, closer to the sources of pollution, had fewer species (average 6–10 per locality) than the eastern part (10–15 per locality). Multiple regression analysis was used to examine the relationships between the species richness of lichens and several environmental variables: input of ions with bulk precipitation (SO_4^{2-}, NO_3^-, Cl^-, Ca^{2+}, Mg^{2+}, Fe^{3+}, Zn^{3+}, Pb^{2+}, Cd^{2+}), distance to forest edge, tree stand age, and number of species per locality. Regression analysis was preceded by factor analysis for the input of ions to obtain uncorrelated variables. Regression explained 53% of the variation of lichen species richness. Highly significant predictor variables were the factor connected with the input of pollutants (Fe^{3+}, Zn^{2+}) emitted by the steelworks (negative effect) and the number of trees per locality (positive effect). Species richness was also affected by the age structure of the tree stand; more species were recorded in old forests.

Key words: geostatistics, industrial pollution, lichens, multiple regression, spatial pattern, species richness.

Introduction

Lichens are sensitive to atmospheric pollutants, both gases (SO_2, NO_x) and dust (Purvis 2000; Garty 2001). Pollutants affect their metabolism directly and/or indirectly through changes in the properties of the substratum (e.g. acidity) on which they occur (Purvis 2000; Häffner *et al.* 2001; van Herk 2001; Wolterbeek *et al.* 2003). In polluted regions, a shift in species composition of the lichen flora involves the disappearance of sensitive species and spread of tolerant ones (Hawksworth & Rose 1970; Poikolainen *et al.* 2000; Purvis 2000). In extreme situations, these regions are characterized by a small number or even an absence of lichens (Ashmore 1998; Purvis 2000). Many publications confirm the usefulness of lichens as indicators of the state of the atmosphere (de Bakker 1986; Hawksworth & McManus 1989; van Dobben & de Bakker 1996; McCune *et al.* 1997; Falla *et al.* 2000; Garty 2001; Giordani *et al.* 2002) and for this reason these organisms have been the subject of investigations in the Niepołomice Forest in previous studies as well as in the present one.

The Niepołomice Forest (S Poland) is an ecosystem impacted for decades by pollution

---

P. Kapusta (corresponding author): Department of Ecosystem Studies, Institute of Environmental Sciences, Jagiellonian University, Gronostajowa 7, 30-387 Kraków, Poland.
G. Szarek-Łukaszewska: W. Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, 31-512 Kraków, Poland.
J. Kiszka: Department of Botany, Institute of Botany, Pedagogical Academy, Podbrzezie 3, 31-054 Kraków, Poland.

the main source of which was a large metallurgical plant (steelworks) built in 1954 in the vicinity of the forest (Grodziński *et al.* 1984; Weiner *et al.* 1997; Weiner 1999). Until the mid-1970s, the quantity of emitted pollutants, mainly SO_2 and dust, increased as steel production rose (Grodziński *et al.* 1984). Two inventories of lichens were made in the Niepołomice Forest during this period: the first in the 1960s and the second in the 1970s (Kiszka 1964, 1977, 1980, 1990). These inventories showed considerable changes in both the species composition of lichens and their distribution in the forest, the latter being correlated with the distance from the sources of emissions (Grodziński *et al.* 1984). Emissions began to decrease rapidly in the late 1980s as a result of lower industrial production and the installation of filtering equipment. A more recent inventory of the lichens (1999–2000) showed improvement in the state of the environment, manifested by, among other signs, the return of several more sensitive species to areas from which they had disappeared (Kiszka & Grodzińska 2004).

This paper is concerned with ecosystem recovery following a reduction in disturbance. Studies related to this topic involving large-scale investigations in natural situations are rare (Likens *et al.* 1996; Alewell *et al.* 1997). Such studies are difficult to carry out due to our inadequacy in controlling all the variables affecting ecosystem processes. The distribution of lichens depends on the level of contamination as well as on the habitat properties at a given site (Oksanen 1988; Humphrey *et al.* 2002). If the anthropogenic and natural factors are correlated, then inference as to which of them has a decisive impact on the biotic variables remains ambiguous. In the case of the Niepołomice Forest this problem is minimized. The industrial emissions have caused a well documented, longitudinal (approximately W–E) gradient of contamination (Grodziński *et al.* 1984; Godzik & Szarek 1993; Weiner *et al.* 1997; Szarek-Łukaszewska *et al.* 2002; Szarek-Łukaszewska 2003), whereas soil moisture/fertility conditions created a latitudinal (approximately N–S) habitat gradient (Gruszczyk 1981; Grodziński *et al.* 1984). The perpendicularity of these variables ensures the independence of both factors and permits the separation of the influence of anthropogenic pressure from habitat effect.

We hypothesize that if the Niepołomice Forest ecosystem was able to respond quickly to the decrease in emissions, then the gradient of species richness produced in the past by the west-to-east transport of pollutants should have been obliterated and the distribution of lichens should only be affected by habitat variability. However, if the ecosystem reacted more slowly to changes in the input of pollutants, the gradient of species richness would be expected to persist. Here we describe the spatial pattern of lichen species richness and identify the main factors responsible for this pattern.

Site description

The Niepołomice Forest (49°59′–50°07′N, 20°13′–20°28′E) is situated in southern Poland, the most populated and industrialized region of the country (Fig. 1). The forest complex can be divided into northern and southern parts, with different habitat conditions. The northern part is confined to the flood plain of the Vistula River and is characterized by high groundwater. The southern complex, located on higher terrain, is drier. There are deciduous forests (oak-hornbeam *Tilio-Carpinetum*) in the northern part and coniferous forests (pine and mixed oak-pine *Pino-Quercetum*) in the southern part. The dominant tree species are oak (*Quercus robur* L.) in the northern part and pine (*Pinus sylvestris* L.) in the southern part. The age of stands in the area is highly varied. Economic activity (harvesting of wood and planting of trees) has produced a mosaic of old and young stands (Fig. 2). The average age of pine is about 66 years, and that of oak about 82 years. Close to the Niepołomice Forest (*c.* 10–30 km to the west) is a steelworks and an urban agglomeration (Fig. 1A). The largest industrial

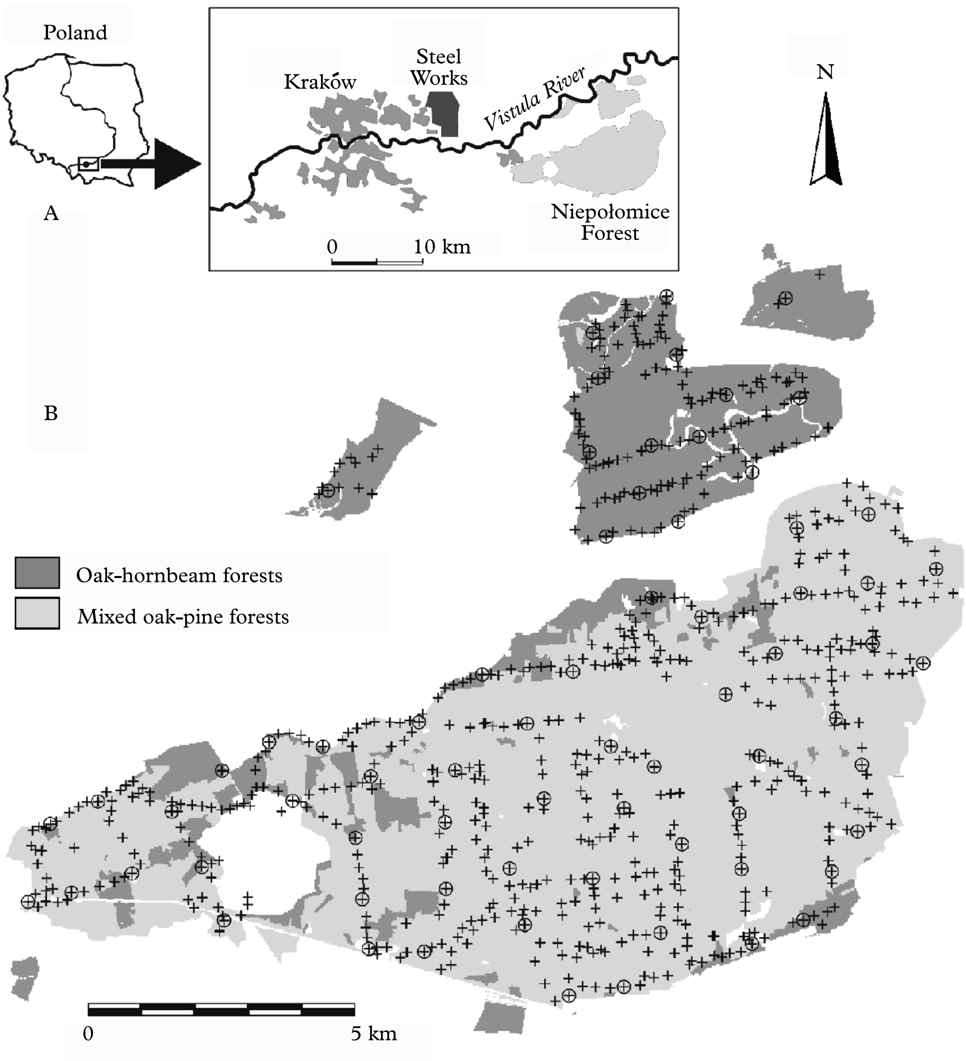


FIG. 1. The Niepołomice Forest. A, location of the study area in the vicinity of the Kraków urban agglomeration and metallurgical plants; B, study plots (+) in oak-hornbeam and mixed pine forests. Symbols in circles denote study plots used in multiple regression analysis.

region in Poland, the Upper Silesian Industrial Region, is *c.* 70–100 km west of the forest. The location of the pollution sources together with the prevailing westerly winds in the area have created a west-to-east gradient of contamination of the Niepołomice Forest (Grodziński *et al.* 1984; Godzik & Szarek 1993; Weiner *et al.* 1997; Szarek-Łukaszewska *et al.* 2002; Szarek-Łukaszewska 2003). The input of chemical elements into the Niepołomice Forest between 1999–2000 is shown in Table 1.

Material and Methods

Lichen data used in this paper were collected for a floristic study between 1999–2000. The aim of the inventory was to characterize completely the lichen flora of the Niepołomice Forest in conditions of decreased impact of industrial emissions (Kiszka & Grodzińska

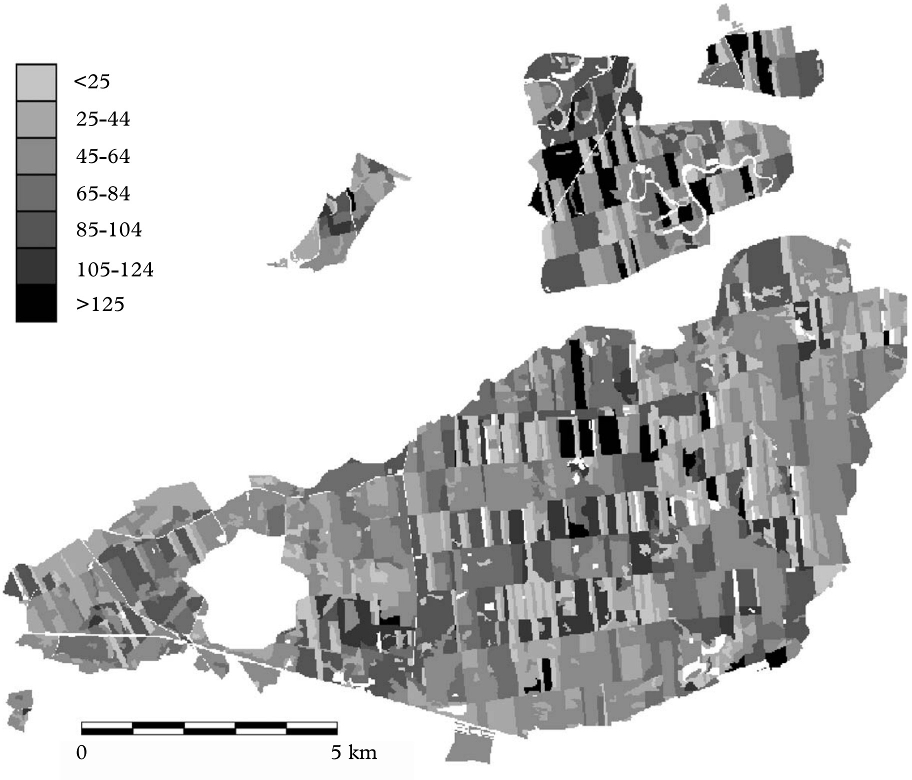


FIG. 2. Generalized map of tree stand age in the Niepołomice Forest.

TABLE 1. *Input of chemical elements with bulk precipitation* to the Niepołomice Forest*

Element	Mean	Min.	Max.
SO_4^{2-} (mg l^{-1})	1·11	0·99	1·27
NO_3^{-} (mg l^{-1})	0·51	0·47	0·56
Cl^{-} (mg l^{-1})	0·86	0·71	1·10
Mg^{2+} (mg l^{-1})	0·09	0·06	0·13
Ca^{2+} (mg l^{-1})	0·68	0·51	0·98
Fe^{3+} (μg l^{-1})	62·4	43·4	113·1
Zn^{2+} (μg l^{-1})	28·6	22·4	63·1
Cd^{2+} (μg l^{-1})	0·84	0·45	8·73
Pb^{2+} (μg l^{-1})	4·97	3·56	5·99

*Annual weighted mean and minimum and maximum for forest complex (1999–2000).

2004). The study covered 662 localities (Fig. 1B) and focused on epiphytic lichens. The inventory was carried out along routes established on the basis of topographical information to cover the entire area of Niepołomice Forest and different types of habitat. Sample plots within routes were spaced 200–250 m apart. However, the distance between sample plots was larger if coppices or cleared areas were present (without epiphytes), or smaller if spatial habitat heterogeneity was higher than average. In other words, in some cases spacing relied on a subjective decision and was tailored to the situation encountered in the field.

The study plots were circles 20 m in diameter. For each stand a list of the lichens found on tree trunks to a height of 2 m was compiled, and the host tree species noted. For deciduous trees lichens occurring on any branches below 2 m were also recorded. Lichen species were identified in the field or were sampled for identification in the laboratory. Lichen nomenclature follows Hafellner & Türk (2001).

The data collected were entered into a geographical information system (GIS) database. The GIS database was developed on the basis of geodetic information for the Niepołomice Forest obtained from the Forest Management and Surveying Office in Kraków, supplemented with 1:5000 principal maps. The GIS database was maintained, processed and analyzed using ArcView 3.2a (ESRI Inc., Redlands, Cal., USA) and Idrisi 32, rel. 2 (Clark Labs, Clark University, Worcester, Mass., USA). The vector layer representing the distribution of plots was introduced to the GIS through digitization of points marked on a map in the field. Each point was provided with geographical coordinates and biocenotic characteristics: the total number of epiphytic lichen species occurring in the study plot, and the number of lichen species found on the most common Niepołomice Forest tree species, pine and oak. We also noted the number of tree species per sample plot as an approximate measure of habitat heterogeneity. In the absence of quantitative data on cover, the total number of species (species richness) within the plot was the only indicator of lichen species diversity.

In the analyses we also used parameters describing the structure of the tree stand, its age (Fig. 2) and tree species dominating in the forest division. Data were obtained from maps of the Forest Management and Surveying Office produced in 1991. The variables were extracted at the coordinates of 662 lichen stands.

Data on atmospheric bulk precipitation was also introduced to the GIS. In 1999–2000, the content of ions (SO_4^{2-}, NO_3^-, Cl^-, Ca^{2+}, Mg^{2+}, Fe^{3+}, Zn^{2+}, Pb^{2+}, Cd^{2+}) was determined in bulk precipitation at 30 sample plots located in open areas and evenly distributed in the Niepołomice Forest, using methods described in detail by Szarek-Łukaszewska (2003). Table 1 shows the annual mean concentrations of ions in bulk precipitation in the Niepołomice Forest.

The spatial structure of lichen richness was examined using semi-variogram analysis. The lag spacing was established to approximately equal the distance between neighbouring stands within the route (0·25 km). The estimation and modelling of the semi-variogram needs to be precise only at short lag distances, because only the points close to the estimation point carry significant weights for interpolation (Webster & Oliver 2001). We counted semi-variance up to 4·5 km (maximum lag), which represented about 30% of the distance of the most separate locations. It was adequate to yield smooth semi-variograms with all details of the spatial structure preserved. Spherical variogram models were fitted to the data using a semi-automatic procedure. After the spans of the possible values of nugget, range and sill were provided, a final least-squares estimation of parameters was made (Goovaerts 1999). The Q ratio was calculated to describe the spatial structure of the data (Görres *et al.* 1998) according to the formula $Q=C/(C+Co)$, where C is the variance of sill and Co is the variance of nugget. The value of Q ranges from 0 to 1. At $Q=0$, no spatial structure is detected at a given spatial scale of sampling; with Q approaching or equal to 1, the majority of spatial variation is accounted for by the variogram model.

We focus here on identification of global spatial patterns rather than on local spatial variability. Therefore ordinary block kriging was used to map variables (Webster & Oliver 2001); this is appropriate when the sampled data are meant to represent a large area (Johnston 1998). Semi-variograms and kriging interpolations were computed with Surfer 7.0 (Golden Software Inc., Golden, Col., USA).

The *t*-test for independent samples was used to compare the average number of lichen species in two different types of habitat (mixed oak–pine and oak-hornbeam forests; see Fig. 1B).

Multiple regression analysis was used to examine possible relationships between the richness of lichen species recorded in a sample plot (dependent variable) and environmental factors (independent variables). Environmental variables included the input of ions with bulk precipitation, the distance of the sample plot from the forest edge, the number of tree species, and the tree stand age. Bulk precipitation may be an indicator of atmospheric pollution. In the regression analysis we used uncorrelated data describing the input of ions, obtained using factor analysis with the principal components method (PCA) for factor extraction (Hair *et al.* 1992). The PCA was performed on the original data (30 sample plots); then the factors with eigenvalues >1 were varimax-rotated. Factor scores were obtained and interpolated for the whole forest area by kriging. After interpolation, the predicted values of factors at the coordinates of the 662 lichen stands were extracted. The next variable (distance of sample plot from the nearest forest edge) may be important in explaining species richness because lichens occurring in the forest interior are potentially less subject to damage by human activity (industrial pollution, agriculture, vehicular traffic) compared to lichens at the forest edge. This is due to limited pollution permeating through the tree barrier (Spangenberg & Kölling 2004). Values for each sample plot (expressed in metres) were automatically computed using the DISTANCE module (Idrisi 32). The number of tree species found in a sample plot was used in multiple regression analysis as an environmental variable constituting a measure of the diversity of available substrata for lichens. The last variable was the age of tree stands in the forest division. It may indirectly convey information about important habitat properties for lichens such as the structure of the bark. In order to interpret correctly the results of multiple regression, it is strongly recommended that no significant relationships occur between predictors (Hair *et al.* 1992). Simple correlation tests revealed that the environmental variables used in the analysis were uncorrelated.

Multiple regression analysis requires the measurements to be statistically independent. This condition is not fulfilled if the data are significantly autocorrelated. To satisfy the condition one may select for analysis points distant enough from each other to ensure the spatial independence of the data. To assess this distance we used semi-variogram analysis.

Variables deviating from a normal distribution (Shapiro-Wilk test) were transformed to normality using STATISTICA, Ver. 5 (StatSoft Inc., Tulsa, Ok., USA).

Results

A total of 120 lichen species was recorded on all species of trees in the Niepołomice Forest; a detailed description of the lichen flora is given by Kiszka & Grodzińska

(2004). The total number of epiphytes found in a stand varied between 1 and 36 with an average value 9·6 ± 4·0. The geostatistical characteristics of lichen richness are shown by the semi-variogram plots in Fig. 3. All the semi-variograms are characterized by poor spatial structure. The highest Q value was only 0·3, estimated for the number of lichen species growing on pines, meaning that semi-variance was in each case dominated by the nugget effect, and only a small part of the variation between particular sample plots was the effect of spatial autocorrelation. The strong nugget effect caused considerable smoothing of kriged surfaces and the obliteration of local variability. A large-scale spatial pattern obtained for the total number of epiphytic lichen species occurring in a sample plot showed a gradual west-to-east increase in lichen species richness as the distance from the sources of contamination (steelworks and Kraków agglomeration) increased; predicted values span from 6 to about 15 species per sample plot (Fig. 3A). On a smaller scale, species richness seems to be related to forest characteristics; higher values of the variable are recorded in the older parts of the forest.

Despite considerable habitat dissimilarity between the northern and southern parts of the forest (see Site description and Fig. 1B), differences in lichen species richness appeared to have little significance (*t*-test; $P<0{\cdot}02$). More species of lichens per stand (10·2 ± 4·6) occurred in the north where the forest is dominated by oak, than in the south (9·3 ± 3·6) where pine prevails.

Of all the tree species with lichens, only pine and oak occurred frequently throughout the forest. This allowed us to interpolate the number of species on pines (Fig. 3B) and oaks (Fig. 3C). These variables did not show any distinct spatial trend, except that higher values were noted mostly in the eastern part of the Niepołomice Forest.

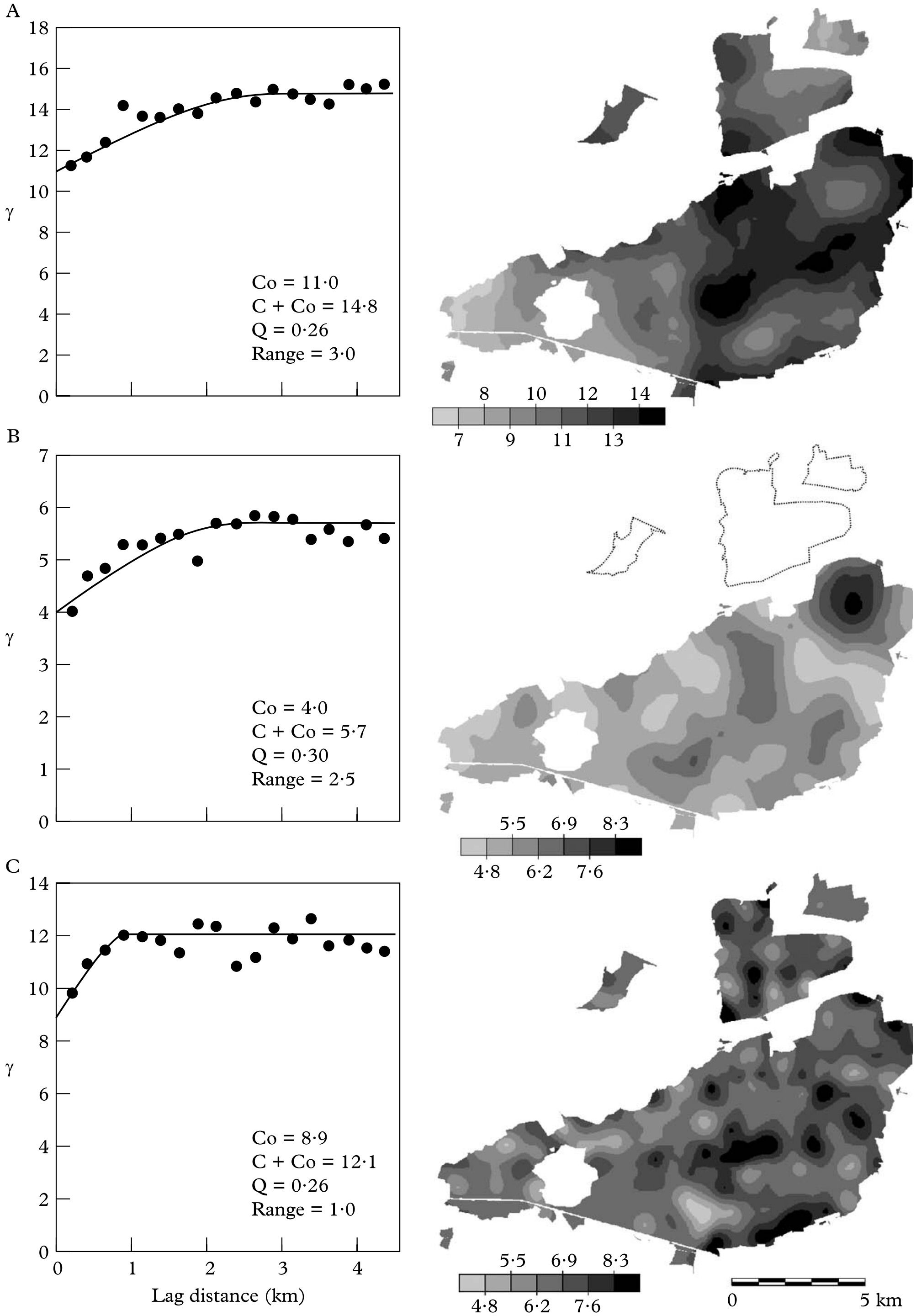
TABLE 2. *Factor loadings (varimax-rotated) of chemical composition of bulk precipitation for 30 sample plots. Data from Szarek-Łukaszewska (2003)*

Component	F1	F2
Ca^{2+}	**0·883**	0·069
Cl^{-}	**0·737**	0·386
Cd^{2+}	0·159	**0·544**
Fe^{3+}	0·232	**0·648**
Mg^{2+}	**0·926**	0·165
NO_3^{-}	**0·813**	0·311
Pb^{2+}	− 0·469	**0·780**
SO_4^{2-}	**0·840**	0·052
Zn^{2+}	0·233	0·457
Explained variance %	43·3	20·1

Loadings greater than 0·5 are presented in bold print.

The original values of ion concentrations (SO_4^{2-}, NO_3^{-}, Cl^{-}, Ca^{2+}, Mg^{2+}, Fe^{3+}, Zn^{2+}, Pb^{2+}, Cd^{2+}) in bulk precipitation were used in PCA. This allowed us to reduce the number of variables describing bulk precipitation chemistry to two factors jointly explaining 63·4% of all variation (Table 2). These factors were interpolated for the entire area of the Niepołomice Forest. Their spatial patterns are presented in Fig. 4. Although the individual components of the factors may have different emission sources, they all probably originate from the same general source region. The first factor of bulk precipitation (F1) may reflect the transport of pollution from Upper Silesia and the Kraków industrial region. Air masses originating from these regions are laden with emissions of gases and dust derived from combustion of coal (SO_4^{2-}, NO_3^{-}, Ca^{2+}, Mg^{2+}) and other industrial and urban sources such as motor vehicle exhaust (NO_3^{-}, Cl^{-}). The second factor (F2) may represent emissions from the steelworks (Fe^{3+}, Zn^{2+}), domestic heating, and local traffic (heavy metals).

FIG. 3. Variograms and kriged surfaces for richness of the lichen species. A, total number of species; B, number of lichen species on pine trees (surface is not interpolated for the northern parts of forest, where pine is infrequent); C, number of lichen species on oak trees. Parameters of spatial structure are presented by the variograms. Notice that units of semi-variance [nugget (C_0) and sill ($C+C_0$)] are squared numbers of species. Range is expressed in km.


A
18
16
14
12
10
γ
8
6
4
2
0
Co = 11·0
C + Co = 14·8
Q = 0·26
Range = 3·0
8 10 12 14
7 9 11 13
B
7
6
5
4
γ
3
2
1
0
Co = 4·0
C + Co = 5·7
Q = 0·30
Range = 2·5
5·5 6·9 8·3
4·8 6·2 7·6
C
14
12
10
8
γ
6
4
2
0
Co = 8·9
C + Co = 12·1
Q = 0·26
Range = 1·0
0 1 2 3 4
Lag distance (km)
5·5 6·9 8·3
4·8 6·2 7·6
0
5 km

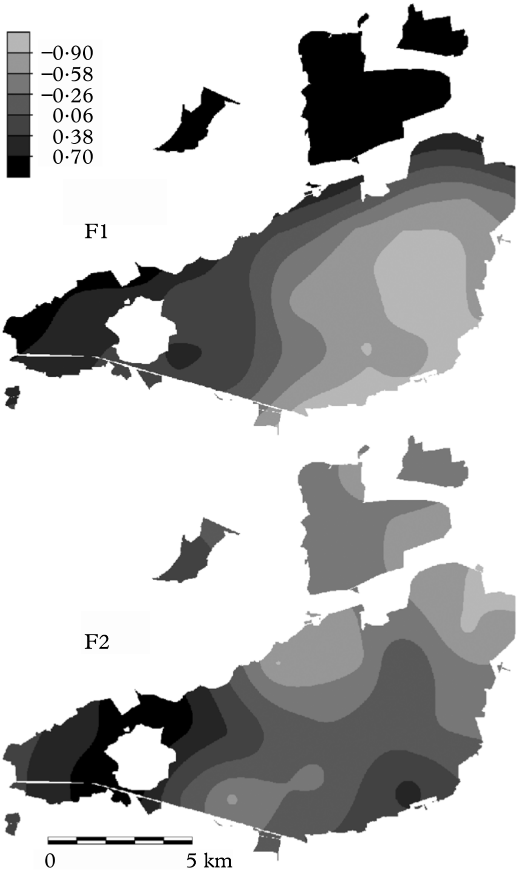


FIG. 4. Spatial patterns of the factors F1 and F2 for chemistry of bulk precipitation. Composition of factors is shown in Table 2.

Semi-variogram analysis showed the species richness of Niepołomice Forest lichens to be characterized by low spatial autocorrelation. The range of the variogram models generally reaches 3 km, but the effect of spatial autocorrelation is clearly visible only at the first three lags (range = 750 m). To eliminate this effect, we selected a number of sample plots (from the 662 plots) at least 800 m distant from their nearest neighbours for regression analysis. We simply chose every fifth sample plot within the routes. After this the sample plots that still did not meet the criteria of minimum distance to their neighbours were excluded manually. In this manner we obtained 70 spatially independent points (Fig. 1B). Residuals analysis showed the presence of 5 outliers, which were removed. The results of multiple regression for 65 points are given in Table 3. Independent variables explain 53% of the variation of the total species richness of the lichens. The best predictor variables appeared to be factor F2 (beta = − 0·444) and the number of tree species (beta = 0·389). Both variables were statistically significant with $P<0·0001$. Tree age was a considerable predictor as well (beta = 0·311; $P<0·01$). The remaining variables—distance of the sample plot from the forest edge and factor F1—do not significantly explain the independent variable.

Discussion

The distribution of lichen species depends to a large extent on the quality of available substrata. In the case of epiphytic lichens the character of the substratum is determined above all by the pH, chemical composition, moisture and texture of the bark. These properties depend not only on the species of phorophyte but also on the conditions prevailing in a given area. These are shaped by factors including the structure and age of the tree stand and the input of chemical elements with atmospheric precipitation (Oksanen 1988; Bates *et al.* 2001; Humphrey *et al.* 2002).

The Niepołomice Forest is an ecosystem with a mosaic structure. The tree stand consists of small forest divisions differing in species composition and age structure. These patches are mixed and for this reason habitat conditions in sample plots situated not far from each other may differ significantly in their suitability for particular lichen species. The spatial distribution of tree stand age is a good example (Fig. 2). The semi-variogram computed for this variable is characterized by a strong nugget effect (Fig. 5) because fragments of the old forest are often adjacent to the middle-aged ones or to the young tree stands. Thus, great variation of habitat properties exists on a small spatial scale. This mosaic of habitats is probably the main cause of the nugget

TABLE 3. *Multiple regression analysis for lichen richness*†

	B‡	SE of B	Beta‡	SE of Beta
Intercept***	1·526	0·111		
Number of tree species§***	0·359	0·083	0·389	0·090
Tree age*	0·004	0·001	0·311	0·093
Distance from the forest edge§	0·004	0·003	0·157	0·102
F1	0·071	0·052	0·136	0·101
F2***	− 0·381	0·075	− 0·444	0·088

R=0·752; R^2=0·565; Adjusted R^2=0·529; F(5, 59)=15·352; *P*<0·0001.
†Natural logarithm of the number of lichen species.
‡B—regression coefficients; Beta—standardized regression coefficients.
§Log-transformed variable.
Variables are statistically significant at *P*<0·0001 (***) or at *P*<0·01 (*).

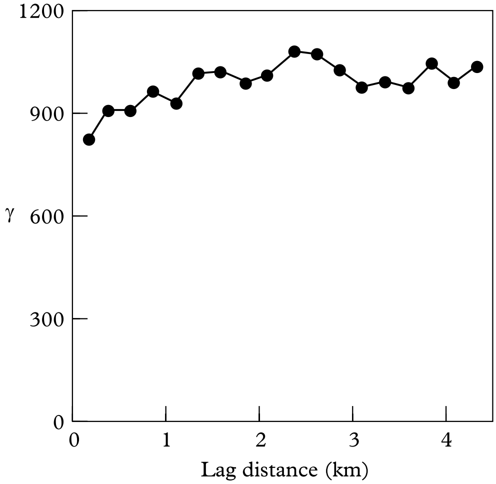


FIG. 5. Semi-variogram computed for tree age. Values were extracted from map (Fig. 2) at the coordinates of the 662 lichen stands.

variance, which accounts for the greater part of spatial variability in the structure of the variograms of lichen species richness.

Although the spatial autocorrelation is low and has a small range, it allows for the use of kriging for interpolation of variables. Kriging is an optimal method in this case, because by masking details of local variability (between sample plots) it makes it easier to analyze the large-scale variability of species richness, and areas with lower species richness (western part), probably affected by pollution, can be identified (Fig. 3).

Analysis of the spatial pattern of the number of lichen species, carried out separately for pine and oak, reveals the role of particular tree species in creating the spatial pattern of total lichen species richness. On average, pine provides the substratum for a smaller number of species than oak, because it has a low pH, low moisture, and a high rate of evaporation. In addition, the bark surface is unstable and flakes off readily (Humphrey *et al.* 2002). These properties, together with other parameters such as insolation of the trunk or social position, are similar throughout the forest complex, because pine, the main economically exploited species, has been improved to produce trees of uniform quality. Therefore the species richness of lichens on pine is characterized by greater spatial autocorrelation (range=2·5 km) than in the case of oak (range=1 km); this difference is observed in the properties of the interpolated surface: smooth for pine (Fig. 3B) and patchier for oak (Fig. 3C).

Selection of substratum type could account for differences in lichen species richness between the northern part of the Niepołomice Forest, with prevailing deciduous stands (mainly oak and hornbeam), and the southern part dominated by pine (Fig. 2A). We expected species richness to be greater in the north because the bark of deciduous trees is an attractive substratum for more lichen species than the bark of pine

(Barkman 1958). Results have shown that this tendency exists but is rather weak. We predict that a more significant difference between the two types of forest will be visible in species composition (not analyzed here).

Semi-variance analysis and spatial pattern mapping are often used as independent statistical tools to describe spatial variability, but their usefulness for testing hypotheses is limited. To examine the significance of factors responsible for the spatial differentiation of species richness, we had to rely on multiple regression analysis. Geostatistics was helpful in identifying independent variables, formulating hypotheses and elaborating a method for sampling the data used in statistical analysis. The effect of autocorrelation in studies of spatial phenomena is repeatedly underestimated. In this work the result of semi-variance analysis forced us to reduce the sample size by an order of magnitude; otherwise the statistical significance of the results would have been compromised.

In multiple regression analysis the independent variables explained 53% of the variation of lichen species richness. This value should be considered high, firstly because species richness is a poor measure of diversity as it does not include species composition and cover in the assessment. Secondly, variables describing the effect of contamination were obtained either by interpolating measurements from a small number of sample plots (factors F1 and F2) or indirectly by making assumptions about pollution dispersion (through distance of sample plot from forest edge). Thirdly, many variables that were not controlled significantly influence species richness (e.g., shade, interactions between species and random effects); these are probably responsible for the unexplained part of variation in species richness.

As expected, the number of tree species explained much of the variation of the dependent variable (Table 3). The greater the number of tree species in a sample plot, the greater the diversity of substrata and thus the probability of the occurrence of more lichen species. Species richness was affected by age structure of tree stands as well; more species were noted in old forests. A possible explanation of this phenomenon is that the ageing of trees is accompanied by structural and chemical changes which create more suitable microhabitats for lichens (Barkman 1958).

Among the factors describing the input of pollutants, only factor F2 had a significant role in forming the spatial pattern of lichen species diversity. The components of F2 (mainly Fe^{3+} and Zn^{2+}) are characteristic of emissions originating from the nearby steelworks (Grodziński *et al.* 1984). In the past the steel works emitted large amounts of SO_2 [70 000 tonnes/year, (Szarek-Łukaszewska 2003)]. Research done in the 1970s has shown that in the Niepołomice Forest the bark of oak and pine was more acidified in the west, in proximity to the source of emission, than in the east (Grodziński *et al.* 1984). Simultaneously in the western part, the regress of epiphytes sensitive to contamination and the spread of SO_2 tolerant species, such as *Lecanora conizaeoides* Nyl. *ex* Crombie, were observed (Kiszka 1980, Kiszka & Grodzińska 2004). At the present time, SO_2 pollution of the air seems to be too low (Szarek-Łukaszewska 2003) to affect considerably the distribution of lichens, however, the gradient of species richness persists to date. This leads to the conclusion that the spatial pattern of the number of lichen species identified in this paper is a relic of the former pollution climate and is not the result of present pollution. Long-term exposure to large doses of SO_2, which was the case until the mid-1980s, probably resulted in considerable acidification of the bark of trees, which according to Bates *et al.* (2001) may have persisted for many years. We believe that persisting changes in the chemistry of microhabitats are first and foremost responsible for the low species richness of lichens in the western part of the forest. This effect may be strengthened by additional factors. Vehicular traffic in the western part of the forest is heavier, so the lichens there are subjected to the action of NO_2 and Pb more than the lichens in the eastern part. Another mechanism may consist of species interactions. Domination by species with low sensitivity to air pollution (e.g., *Lecanora conizaeoides*), which spread in the Niepołomice Forest in the period of the highest industrial emissions (Kiszka & Grodzińska 2004), may effectively hamper colonization of trees by other species for some time to come. The species composition of lichen communities in the forest will be analyzed in detail in a separate publication.

The main pollutant responsible for the state of lichens in the ecosystem is SO_2, but NO_2, high deposition of ions, and heavy metals are also important. At the present time, the input of SO_4^{2-}, NO_3^- and other ions which are components of factor F1 are considered to be moderate or low in the Niepołomice Forest (Szarek-Łukaszewska 2003). In all probability, F1 is important for some species but does not affect species richness.

Species richness is a poor indicator of processes occurring in the structure of lichen communities. Determining only the number of species occurring in a sample plot, one may overlook important ecosystem changes consisting of replacement of certain species by others (e.g., the replacement of sensitive lichens by others resistant to air pollution), reduction of the cover of lichens, or deterioration of the state of their thalli. Analysis of the number of species may show only major differences in diversity. The results obtained in this study confirm that the observed differences between the western and eastern parts of the forest are not a chance phenomenon. They are correlated with the existing gradient of contamination in the area investigated, but more probably, they are an effect of lingering changes that occurred in the ecosystem during the period of high emissions of gases and dust. Irrespective of the mechanism of this phenomenon, our study shows that the ecosystem of the Niepołomice Forest is characterized to some extent by inertia that is revealed in the slow and limited restoration of the lichen flora after a disturbing factor has ceased to operate.

We wish to thank reviewers for their valuable comments to the manuscript. We thank M. Jacobs and M. Pabijan for help in editing the manuscript, and our colleagues from the Department of Lichenology IB PSci for helpful criticism. This research was supported by the State Committee for Scientific Research, grant no. 3 P04G 107 25 and grant no. 6 P04F 023 15/p02.

REFERENCES

Alewell, C., Bredemeier, M., Matzner, E. & Blanck, K. (1997) Soil solution response to experimentally reduced acid deposition in a forest ecosystem. *Journal of Environmental Quality* **26:** 658–665.

Ashmore, M. (1998) Impacts on urban vegetation and ecosystems. In *Urban Air Pollution—European Aspects* (J. Fenger, O. Hertel & F. Palmgren, eds): 363–372. Dordrecht: Kluwer Academic.

Barkman, J. J. (1958) *Phytosociology and Ecology of Cryptogamic Epiphytes*. Assen: Van Gorcum.

Bates, J. W., Bell, J. N. B. & Massara, A. C. (2001) Loss of *Lecanora conizaeoides* and other fluctuations of epiphytes on oak in S.E. England over 21 years with declining SO_2 concentrations. *Atmospheric Environment* **35:** 2557–2568.

de Bakker, A. J. (1986) Verandering in de epifytische flora van het Staelduinse bos in de periode 1949–1984. *Gorteria* **13:** 70–74.

Falla, J., Laval-Gilly, P., Henryon, M., Morlot, D. & Ferard, J. F. (2000) Biological air quality monitoring: a review. *Environmental Monitoring and Assessment* **64:** 627–644.

Garty, J. (2001) Biomonitoring atmospheric heavy metals with lichens: theory and application. *Critical Review in Plant Sciences* **20:** 309–371.

Giordani, P., Brunialti, G. & Alleteo, D. (2002) Effects of atmospheric pollution on lichen biodiversity (LB) in a Mediterranean region (Liguria, northwest Italy). *Environmental Pollution* **118:** 53–64.

Godzik, B. & Szarek, G. (1993) Heavy metals in mosses from the Niepołomice Forest, southern Poland—changes in 1975–1992. *Fragmenta Floristica et Geobotanica* **38:** 199–208.

Goovaerts, P. (1999) Geostatistics in soil science: state-of-the-art and perspectives. *Geoderma* **89:** 1–45.

Görres, J. H., Dichiaro, M. J., Lyons, J. B. & Amador, J. A. (1998) Spatial and temporal patterns of soil biological activity in a forest and an old field. *Soil Biology and Biochemistry* **30:** 219–230.

Grodziński, W., Weiner, J. & Maycock, P. F. (eds) (1984) *Forest Ecosystems in Industrial Regions*. Heidelberg: Springer Verlag.

Gruszczyk, A. (1981) Siedliskowe typy lasu Puszczy Niepołomickiej (Types of forest site of Niepołomice Forest). *Studia Ośrodka Dokumentacji Fizjograficznej PAN* **9:** 205–219.

Hafellner, J. & Türk, R. (2001) Die lichenisierten Pilze Österreichs—eine Checkliste der bisher nachgewiesenen Arten mit Verbreitungsangaben. *Stapfia* **76:** 3–167.

Häffner, E., Lomský, B., Hynek, V., Hällgren, J. E., Batič, F. & Pfanz, H. (2001) Air pollution and lichen physiology. Physiological response of different lichens in a transplant experiment following an SO_2-gradient. *Water, Air and Soil Pollution* **131:** 185–201.

Hair, J. H., Anderson, R. E., Tatham, R. L. & Black, W. C. (1992) *Multivariate Data Analysis with Readings*. New York: Macmillan.

Hawksworth, D. L. & McManus, P. M. (1989) Lichen recolonization in London under conditions of rapid falling of sulphur dioxide level, and concept of zone skipping. *Botanical Journal of the Linnean Society* **100:** 99–109.

Hawksworth, D. L. & Rose, F. (1970) Qualitative scale for estimating sulphur dioxide air pollution in England and Wales using epiphytic lichens. *Nature* **227:** 145–148.

Humphrey, J. W., Davey, S., Peace, A. J., Ferris, R. & Harding K. (2002) Lichens and bryophyte communities of planted and semi-natural forests in Britain: the influence of site type, stand structure and deadwood. *Biological Conservation* **107:** 165–180.

Johnston, C. A. (1998) *Geographic Information Systems in Ecology*. *Methods in Ecology*. Oxford: Blackwell Science.

Kiszka, J. (1964) Porosty Kotliny Sandomierskiej. Część I: porosty Okręgu Puszczy Niepołomickiej (The lichens of the Sandomierz Lowland. Part I: lichens of Niepołomice Forest district.) *Fragmenta Floristica et Geobotanica* **10:** 527–564.

Kiszka, J. (1977) Wpływ emisji miejskich i przemysłowych na flore porostów Krakowa i Puszczy Niepołomickiej. *Prace Monograficzne WSP w Krakowie* **19:** 5–132.

Kiszka, J. (1980) Lichens. In *Acidification of forest environment (Niepołomice Forest) caused by SO_2 emissions from steel mills. Final report on investigations from the period July 1 1976–June 30 1980* (K. Grodzińska, ed.): 86–89. Cracow: IB PASc.

Kiszka, J. (1990) Mapa lichenoindykacyjna województwa krakowskiego (Lichenoindication of the area of the Cracow voivodeship). *Studia Ośrodka Dokumentacji Fizjograficznej PAN* **18:** 201–212.

Kiszka, J. & Grodzińska, K. (2004) Lichen flora and air pollution in the Niepołomice Forest in 1960–2000. *Biologia Bratislava* **59:** 25–37.

Likens, G. E., Driscoll, C. T. & Buso, D. C. (1996) Long-term effects of acid rain: response and recovery of a forest ecosystem. *Science* **272:** 244–245.

McCune, B., Dey, J., Peck, J., Heiman, K. & Will-Wolf, S. (1997) Regional gradient in lichen communities of the Southern United States. *Bryologist* **100:** 99–158.

Oksanen, J. (1988) Impact of habitat, substrate and microsite classes on epiphyte vegetation: interpretation using exploratory and canonical; correspondence analysis. *Annales Botanici Fennici* **25:** 59–71.

Poikolainen, J., Kuusinen, M. & Mikkola, K. (2000) Epiphytic lichens as indicators of air quality. In *Forest condition in a changing environment—the Finnish Case. Forestry Sciences* (E. Mälkönen, ed.) **65:** 162–170. Dordrecht: Kluwer Academic.

Purvis, O. W. (2000) *Lichens*. London: Natural History Museum.

Spangenberg, A. & Kölling, C. (2004) Nitrogen deposition and nitrate leaching at forest edges exposed to high ammonia emissions in southern Bavaria. *Water, Air and Soil Pollution* **152:** 233–255.

Szarek-Łukaszewska, G. (2003) Sulphur input to the Niepołomice Forest (S. Poland): changes during 30 years. *Polish Journal of Environmental Studies* **2:** 239–244.

Szarek-Łukaszewska, G., Grodzińska, K. & Braniewski, S. (2002) Heavy metal concentration in the moss *Pleurozium schreberi* in the Niepołomice Forest, Poland: changes during 20 years. *Environmental Monitoring and Assessment* **79:** 231–237.

van Dobben, H. F. & de Bakker, A. J. (1996) Re-mapping epiphytic lichen biodiversity in the Netherlands: effects of decreasing SO_2 and increasing NH_3. *Acta Botanica Neerlandica* **45:** 55–71.

van Herk, C. M. (2001) Bark pH and susceptibility to toxic air pollutants as independent causes of changes in epiphytic lichen composition in space and time. *Lichenologist* **33:** 419–441.

Webster, R. & Oliver, M. (2001) *Geostatistics for Environmental Scientists. Statistics in Practice*. Chichester: John Wiley & Sons.

Weiner, J. (1999) Long-term research in the Niepołomice Forest. In *Long Term Ecological Research—Examples, Methods, Perspectives for Central Europe. Proceedings of the ILTER Regional Workshop* (O. Bijok & M. Prus, eds): 153–154. Dziekanów Leśny: PASc.

Weiner, J., Fredo-Boniecki, S., Reed, D., Mclean, A. & Strong, M. (1997) Niepołomice Forest—a GIS analysis of ecosystem response to industrial pollution. *Environmental Pollution* **98:** 381–388.

Wolterbeek, H. T., Garty, J., Reis, M. A. & Freitas, M. C. (2003) Biomonitors in use: lichens and metal air pollution. In *Bioindicators and Biomonitors: Principles, Concepts and Applications. Trace Metals and Other Contaminants in the Environment* (B. A. Markert, A. M. Breure & H. G. Zechmeister, eds): 377–419. Amsterdam: Elsevier.

Accepted for publication 26 April 2004