

Monitoring of epiphytic lichens in The Netherlands (1977-1990)

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VOORWOORD

Reeds lang is bekend dat epifytische (op bomen groeiende) korstmossen sterk reageren op luchtverontreiniging. Veel soorten ontbreken in dicht bevolkte en geïndustrialiseerde gebieden. Tot op zekere hoogte kan daarom de luchtkwaliteit worden afgeleid uit de plaatselijke epifytenflora en -vegetatie. In het verleden zijn in Nederland landsdekkende studies uitgevoerd naar het voorkomen van korstmossen in relatie tot luchtkwaliteit door Barkman (1958) en de Wit (1976). In 1977 werd door het toenmalige RIN begonnen met de opzet van een systeem voor het permanent monitoren van epifytische korstmossen. Deze monitoring, die deels werd gefinancierd door het RIVM, heeft tot 1990 plaatsgevonden.

Na 1990 werd besloten te komen tot een eind-evaluatie, met accenten op (a) de relaties tussen veranderingen in luchtkwaliteit en epifytenvegetatie in de periode 1973-1990, en (b) de bruikbaarheid van epifyten als biomonitor voor luchtkwaliteit. Het resultaat van deze evaluatie is neergelegd in drie rapporten, waarvan het voorliggende het laatste is. De twee voorgaande rapporten hadden betrekking op resp. (1) de relatie tussen epifytische korstmossen en luchtkwaliteit in acht gebieden van elk ca. 800 km², regelmatig verspreid over Nederland, in de periode 1988-1989 (Van Dobben 1991), en (2) de relatie tussen luchtkwaliteit, chemie van de schors en epifytische korstmossen op ca. 150 punten langs een aantal transecten door Nederland (Van Dobben & Wamelink 1992). Het voorliggende rapport beschrijft de temporele veranderingen in luchtkwaliteit en epifytische korstmosvegetatie, en de relatie tussen deze twee, over de periode 1977-1990.

De drie genoemde rapporten zijn, in enigszins gewijzigde vorm en tezamen met enige additionele informatie, ook te vinden in Van Dobben (1993: Hoofdstuk 3-5). De in het voorliggende rapport opgenomen samenvatting beoogt een integratie te geven van de in de drie rapporten gepresenteerde informatie. Voorts is een evaluatie opgenomen van de beleidsmatige bruikbaarheid van korstmossen als biomonitor voor luchtkwaliteit.

*) De interpretatie van de gegevens in Van Dobben (1991) en in Van Dobben (1993: Hoofdstuk 3) vertoont op een aantal punten wezenlijke verschillen. Dit betreft vooral (a) het effect van NH₄-aërosol, en (b) het werkingsmechanisme van SO₂. Deze verschillen zijn het gevolg van het feit dat bewerkingen (met name op het vlak van de schors-chemie) die uitgevoerd zijn na het verschijnen van Van Dobben (1991) op sommige punten aanpassingen noodzakelijk maakten. Men raadplege voor deze punten dus liever Van Dobben (1993)!

INHOUD

SAMENVATTING	7
ABSTRACT	11
1 INTRODUCTION	13
2 MATERIALS AND METHODS	14
2.1 Data collection	14
2.2 Statistical analysis	16
3 RESULTS	20
3.1 Changes in epiphytic vegetation	20
3.2 Relation between epiphytic vegetation and pollutant concentration: effect of averaging period	22
3.3 Relation between epiphytic vegetation and explanatory variables	23
3.4 Relation between environmental change in epiphytic vegetation	24
4 CONCLUSIONS	26
5 DISCUSSION: EPIPHYTIC AS MONITORS FOR AIR QUALITY	26
REFERENCES	31
TABLES	35
FIGURES	45
APPENDIX	59

SAMENVATTING

De korstmosvegetatie op bomen wordt door een groot aantal omgevingsfactoren beïnvloed. Deze invloed geldt zowel voor het aantal soorten, als voor de aanwezigheid van soorten en de hoeveelheid waarin zij voorkomen. Luchtkwaliteit is hierbij een van de vele omgevingsfactoren. Om korstmossen als biomonitor voor luchtkwaliteit te kunnen gebruiken moet de invloed van alle andere factoren geminimaliseerd worden. Hierdoor is het noodzakelijk de monitoring te doen plaatsvinden op bomen met zo gering mogelijke onderlinge verschillen in standplaats. In Nederland zijn hiervoor vrijstaande (=niet in bos gelegen) wegbomen het meest geschikt. Op zulke standplaatsen is luchtkwaliteit de belangrijkste bepalende factor voor de korstmosvegetatie. Andere factoren zoals boomsoort en boomdikte zijn minder belangrijk.

Van de luchtkwaliteitsfactoren is in de huidige nederlandse situatie de SO_2 concentratie verreweg de belangrijkste. De concentraties van NO_2 en NH_3 hebben een aantoonbaar, maar minder belangrijk effect. De effecten van SO_2 en NO_2 bestaan uit een afname van zowel het aantal soorten als de hoeveelheid van elke soort, met uitzondering van één soort (*Lecanora conizaeoides*). Deze soort neemt juist toe bij hogere SO_2 of NO_2 concentraties. Het effect van O_3 was met de gebruikte methoden niet vast te stellen. De oorzaak hiervan is dat de O_3 concentratie zo sterk negatief is gecorreleerd met de NO_2 concentratie dat hun effecten op grond van veldwaarnemingen niet te scheiden zijn.

NH_3 heeft weinig effect op het aantal soorten, maar wel op de soortensamenstelling van de vegetatie. Bij hoge NH_3 concentratie neemt een bepaalde groep soorten (de 'nitrofyten') sterk toe, terwijl een andere groep (de 'acidofyten') afneemt (in de Appendix is voor elke soort aangegeven of deze tot een van die twee groepen behoort). De effecten van SO_2 en NO_2 komen grotendeels tot stand door hun toxiciteit. Verzuring van de schors is een tweede, minder belangrijk werkingsmechanisme. Het effect van NH_3 komt tot stand door alkalisering van de schors. Nitrificatie van ammonium, een proces dat in het terrestrisch milieu ook verantwoordelijk is voor verzuring, treedt op boomschors waarschijnlijk niet op. De verhoogde beschikbaarheid van stikstof bij hoge NH_3 concentratie heeft -in tegenstelling tot de situatie bij terrestrische vegetatie- geen effect op epifytische korstmossen. De term 'nitrofyten' is dus feitelijk onjuist.

Gedurende de periode 1973-1990 hebben veel soorten epifytische korstmossen zich uitgebreid. De meeste soorten zijn algemener geworden, en de gemiddelde hoeveelheid van elke soort per boom en het aantal soorten per boom zijn toegenomen. Deze toename was het sterkst voor de nitrofyten. De belangrijkste veranderingen in luchtkwaliteit in deze periode waren een toename van de NH_3 concentratie (tot ca. 1980), en een afname van de SO_2 concentratie. Een gedetailleerde statistische analyse toonde aan dat de veranderingen in de epifytenvegetatie over de periode 1977-1990 geheel

verklaard kunnen worden uit de afgenomen SO_2 concentratie. De schijnbare tegenspraak dat de relatief sterke toename van de nitrofytische soorten wordt veroorzaakt door de afname van de SO_2 concentratie en niet door de toename van de NH_3 concentratie kan op drie manieren verklaard worden: (1) de afname in SO_2 concentratie veroorzaakte een algemene stijging van de pH van de schors, hetgeen gunstig was voor de nitrofyten; (2) de nitrofyten zijn in vergelijking tot andere soorten betrekkelijk gevoelig voor SO_2 ; en (3) de nitrofyten zijn in staat zich snel te verspreiden wanneer de milieu-omstandigheden gunstiger worden. Overigens is de huidige epifytenflora en -vegetatie in Nederland nog altijd zeer arm vergeleken met de toestand rond de eeuwwisseling (Van Dobben 1993).

Evaluatie van korstmossen als biomonitor voor luchtkwaliteit

De sterke relatie tussen epifytische korstmosvegetatie en luchtkwaliteit geeft in principe de mogelijkheid korstmossen te gebruiken als biomonitor voor luchtkwaliteit. Regelmatige waarnemingen aan korstmossen worden dan gebruikt om luchtkwaliteit, of veranderingen daarin, te schatten. Zo'n biologisch meetnet is in de Nederlandse situatie alleen zinvol als het een duidelijke meerwaarde vertegenwoordigt boven het reeds aanwezige fysisch-chemisch meetnet. Het zou dus factoren moeten meten waarvoor implementatie in het bestaande meetnet onmogelijk of tenminste zeer kostbaarder is. Het 'geïntegreerd biologisch effect' (zie onder) kan een voorbeeld zijn van zo'n factor: fysisch-chemische meting hiervan is per definitie niet mogelijk. Enkele van de mogelijk te monitoren factoren zullen hieronder behandeld worden.

1. *Algemene luchtkwaliteit.* Monitoring van algemene luchtkwaliteit door middel van epifytische korstmossen wordt aanbevolen door o.a. Nylander (1866) en Herzig et al. (1989). Het vinden van een maat voor algemene luchtkwaliteit op grond van fysisch-chemische metingen kan bemoeilijkt worden door het feit dat niet bij voorbaat duidelijk is welke componenten een schadelijk effect hebben en dus gemeten moeten worden. Het is in principe mogelijk dat onbekende componenten, waarvoor geen fysisch-chemische metingen beschikbaar zijn, wel een effect op korstmossen hebben. Overigens kwamen uit onze gegevens geen aanwijzingen naar voren dat dit in Nederland inderdaad het geval is (Van Dobben 1991, 1993). In feite wordt bij biomonitoring met korstmossen een weging van luchtkwaliteitsfactoren gemaakt, waarbij SO_2 zeer zwaar, en zware metalen in het geheel niet meegewogen worden (Van Dobben & Wolterbeek in prep.). Ook O_3 heeft op korstmossen geen, of slechts een gering effect (Ruoss et al. 1991). Het is twijfelachtig of een dergelijke weging van componenten overeenkomt met de voorstelling die men heeft bij 'algemene luchtkwaliteit'.
2. *Geïntegreerd biologisch effect.* Uitgangspunt bij dit type monitoring is dat de epifytische korstmosvegetatie een gemakkelijk te beschrijven 'model'systeem is, waarvan de reactie op luchtkwaliteit een zekere voorspellende waarde heeft voor de reactie van andere systemen, b.v. terrestrische vegetatie. Voor het effect van SO_2 is dit waarschijnlijk

inderdaad het geval. De gevoeligheid voor SO_2 van sommige terrestrische hogere planten ligt in dezelfde orde van grootte als die van epifytische korstmossen (Van Dam et al. 1986). Een belangrijk deel van het effect van luchtverontreiniging op terrestrische vegetatie komt echter tot stand door de eutrofiërende (bemestende) werking van N-verbindingen. Deze effecten zijn in de huidige Nederlandse situatie waarschijnlijk zelfs belangrijker dan die van verzuring of toxiciteit van SO_2 (Bink et al. 1994). Bij epifytische korstmossen kon een eutrofiërende werking van N-verbindingen echter niet aangetoond worden (Van Dobben & Wamelink 1992). Daarom komt slechts een deel van het effect van luchtkwaliteit op terrestrische vegetatie ook in de epifytische korstmossen tot uiting, zodat van een geïntegreerd biologisch effect geen sprake kan zijn.

3. *Verzuring, vermesting.* Verzuring komt in terrestrische systemen voor een deel tot stand door nitrificatie van ammonium (Anonymus 1991). Dit proces treedt op boomschors waarschijnlijk niet op; ammonium heeft hier juist een pH-verhogend effect (Van Dobben & Wamelink 1992). Een vermestings-effect treedt bij epifytische korstmossen ook niet op (zie 2. hierboven). Epifytische korstmossen zijn dus zeker niet geschikt als monitor voor verzuring en vermesting van terrestrische (en waarschijnlijk ook aquatische) levensgemeenschappen.
4. *SO_2 concentratie.* Epifytische korstmossen blijken sterk te reageren op de SO_2 concentratie. Schatting van de SO_2 concentratie door monitoring van epifytische korstmossen is daarom goed uitvoerbaar. Echter, fysisch-chemische meting levert een veel grotere nauwkeurigheid, en een veel betere resolutie in de tijd (Hoofdstuk 3 van dit rapport).
5. *NH_3 concentratie.* Monitoring van NH_3 concentratie met epifytische korstmossen is in principe mogelijk. Echter, door het sterke effect van SO_2 , en de betrekkelijk grote verschillen in SO_2 concentratie die binnen Nederland optreden is schatting van de NH_3 concentratie alleen mogelijk na correctie voor het effect van SO_2 . Zo'n correctie is in principe uitvoerbaar, maar leidt in de Nederlandse situatie tot een onacceptabel grote onnauwkeurigheid in de geschatte NH_3 concentratie (Hoofdstuk 5 van dit rapport). De oorzaak hiervan is vooral gelegen in het feit dat de verschillen in epifytische korstmosvegetatie binnen Nederland in veel sterkere mate door de SO_2 concentratie dan door de NH_3 concentratie worden bepaald.

Geconcludeerd kan worden dat epifytische korstmossen alleen op zinvolle wijze als monitor gebruikt kunnen worden voor de SO_2 concentratie of het biologisch effect van SO_2 . Voor het laatste zou een voordeel van epifytische korstmossen kunnen zijn dat een reactie op SO_2 gemakkelijker aantoonbaar is dan bij terrestrische vegetatie, waar vermesting, verdroging en biotoopverlies vaak ook een belangrijke rol spelen. Het sterk overheersende effect van SO_2 , en de grote verschillen tussen epifytische en terrestrische vegetatie met betrekking tot processen als nitrificatie en eutrofiëring maken epifyten minder geschikt als modelsysteem voor biologische effecten van luchtkwaliteit in het algemeen.

Conclusies van Van Herk (1990, 1991, 1993) dat aan een biologisch meetnet met korstmossen grote waarde moet worden toegekend, vooral met betrekking tot ammoniak, moeten, gezien het bovenstaande, als voorbarig worden beschouwd. Deze conclusies zijn deels ingegeven door het feit dat bij beschouwing van een klein gebied de ruimtelijke variatie in NH_3 concentratie veel groter is van die in SO_2 concentratie. Hierdoor zijn de verschillen in epifytische korstmosvegetatie binnen zo'n gebied sterker aan de NH_3 concentratie dan aan de SO_2 concentratie gerelateerd. Bij monitoring op landelijke schaal wordt het effect van SO_2 echter dominant, hetgeen een schatting van de NH_3 concentratie zeer bemoeilijkt. Voorts zijn de aanbevelingen van Van Herk slechts gebaseerd op de constatering dat er sterke correlaties bestaan tussen de epifytische korstmosvegetatie en omgevingsfactoren (waaronder SO_2 en NH_3), zonder dat echter ingegaan wordt op de vraag in hoeverre korstmossen ook werkelijk een voorspellende waarde bezitten met betrekking tot deze omgevingsfactoren. Uit de beschouwingen in Hoofdstuk 3 van dit rapport blijkt dat deze voorspellende waarde, behalve voor SO_2 , op landelijke schaal in het algemeen gering is.

ABSTRACT

Epiphytic lichen vegetation was recorded yearly at c. 150 permanent stations in The Netherlands from 1977 until 1990. A station consisted of a row of c. 10 wayside trees. During the observation period the atmospheric SO_2 concentration strongly decreased, while the NO_2 concentration remained approximately constant and the NH_3 concentration probably also remained constant. However, for the latter component only few reliable measurements were available.

Between 1977 and 1990 the mean number of species per station increased from c. 11 to c. 18. This increase was almost completely due to the increase in the number of nitrophytic species. The mean abundance significantly increased for many species (including all common nitrophytic species), and significantly decreased for only three species (the acidophytes *Lecanora conizaeoides*, *Hypogymnia physodes* and *Pseudevernia furfuracea*). The mean observed change in epiphytic vegetation was consistent with (a) the observed relation between the spatial pattern of species abundances and SO_2 concentration at a given point of time, and (b) the temporal change in SO_2 concentration. SO_2 alone was sufficient to explain the change, and the contributions of NH_3 , NO_2 and tree diameter to the change have been negligible. The change in the epiphytic vegetation was an almost linear trend, and the influence of peak concentrations was very small. The correspondence between change in species abundances and change in SO_2 concentration was weaker if smaller regions were considered. This is probably due to a non-linear effect of SO_2 .

There are three possible explanations for the apparent contradiction that SO_2 and not NH_3 is the most important cause for the increase of the nitrophytic species: (a) a decreasing trend in SO_2 causes an upward trend in bark pH, (b) on average nitrophytic species are more sensitive to gaseous SO_2 than other species, and (c) in an ameliorating environment, nitrophytic species are probably more efficient colonizers than other species.

1 INTRODUCTION

Epiphytic lichens are generally considered good indicators for air quality. Changes in air quality should therefore be reflected in changes in the composition of epiphytic lichen vegetation. To trace such changes a monitoring network was operated in The Netherlands during the period 1977-1990. The network comprised c. 150 monitoring stations, each consisting of c. 10 trees on which cover estimates of epiphytic lichens were yearly made. During the observation period the SO₂ concentration strongly decreased (from a country-wide mean of c. 30 to c. 15 µg.m⁻³), while the NO₂ concentration remained approximately constant. Measurements of NH₃ concentration over this period are virtually lacking. Estimates on the basis of cattle density indicate an increase over the period 1870-1980 and a more or less constant concentration thereafter.

The aims of the present study were (a) to quantify the changes in the composition of the epiphytic lichen vegetation (i.e., the changes in the abundances of all species) at the monitoring stations, and (b) to relate these changes to the observed changes in air quality. It is improbable that the response of the epiphytes to a change in air quality takes place immediately. Especially in our case of decreasing concentration, recolonization of former 'epiphyte deserts' may take some time. A five-year period is often stated in literature (e.g. Showman 1981). Furthermore, the air quality in one season (e.g. the growing season) may be more important than in another season. Usually winter concentrations are considered most important (e.g. Hawksworth & Rose 1970). The period with the most relevant pollutant concentrations, and the size of a possible lag before the epiphytes react to a change in air quality were estimated by determining which definition of averaging periods for SO₂ and NO₂ concentrations yielded the best regression fit to the epiphyte data.

Evidence for the hypothesis of air quality as a general cause for changes in the epiphyte vegetation can be obtained from a comparison of their relation across space with their relation over time, as follows. We first determined the statistical relationship between air quality and epiphytic vegetation across space, using mean values per site. This spatial relationship was then used to infer the country-wide mean change in pollutant concentrations over time on the basis of the mean change in epiphytic vegetation. Finally we compared the inferred change in pollutant concentrations with the change in measured concentrations. A good correspondence adds proof to the causal hypothesis.

A complication was formed by the scarcity of NH₃ measurements. Although the country-wide mean concentration was probably constant over most of the observation period, the spatial pattern of NH₃ may have been subject to change. We therefore also attempted to derive regional estimates for the change in NH₃ concentration. As a check on the outcome of the regionalization procedure, regional changes in SO₂ concentration were also estimated, because these could be compared with measured values.

2 MATERIALS AND METHODS

2.1 Data collection

Stations. Figure 1 shows the location of the epiphyte monitoring stations. Each station consisted of a row of 11 trees of the same species (a lower number was used in a few places where not enough trees were available). The stations were located in transects of adjacent 5*5 km² squares of the local 'Amersfoort' grid. There was one station in each of these squares; the mean distance between the stations was therefore 5 km. The stations were assigned to eight regions corresponding to the eight regions used by Van Dobben (1991) (see Figure 1).

In order to minimize the influence of environmental variables other than air quality, the stations were selected to comply with strict standardization criteria. All stations were free-standing wayside trees. Slanting trees, very thick or very slender trees, trees close to farmyards, or trees at the end of a row were not used. It was attempted to confine the stations to *Quercus robur* in areas with sandy soil, and *Populus canadensis* in areas with clayey or peaty soil. However, in squares where suitable locations with these tree species could not be found, *Salix alba* or *Ulmus hollandica* were used instead. The same stations were also used to measure the growth of *Parmelia sulcata*, a common foliose lichen. Therefore this species had to be present on the middle tree of each station in the first year of sampling. For the present study this criterion had the advantage of providing a certain amount of standardization in the epiphytic vegetation. The results of the growth measurements will be reported elsewhere.

Each station was visited yearly from 1977 to 1990, except in 1984 and 1985. Therefore a maximum of 12 observations was available for each station. However, for many stations the actual number of observations was lower, for the following reasons: (a) the selection of the stations took three years and many of them were therefore first sampled after 1977, and (b) in each year c. 5% of the trees constituting the stations were cut. If this happened a replacement station was selected within the same grid square, which in the analysis was considered as a new station. The total number of stations (198) therefore exceeded the number of grid squares (149). In total, 1391 observations (station/year combinations) were available (see Table 1 for details). The diameter of the thickest tree was measured yearly. Occasional missing values were replaced by calculated values on the basis of a 2% yearly increase (which was the mean over the complete dataset).

Species abundance. The observed species, together with the abbreviations used to refer to them, their frequency over the complete dataset, and their ecological classification (as nitrophytes or acidophytes) are listed in the Appendix. The abundances of the species were estimated in a semi-quantitative scale. Until 1983 a modified 'Tansley' scale was used, and from 1986

onward the scale described by De Bakker (1988) (Table 2). Estimates in both scales were transformed to a new five-point scale prior to data analysis. Because no sharp definitions existed for most of the 'Tansley' units their conversion was somewhat arbitrary. However, the two lowest units had the same definitions in both scales, and the highest unit (indicating a species present in large quantities) was also assumed to correspond between the scales. Therefore these units were transformed on a one-to-one basis. To find the best transformation for the other units the frequency distribution of the estimates in both scales was considered. The applied transformation (Table 2) minimizes the difference in frequency distribution before and after 1983 (Figure 2). The remaining difference in the frequency of scale unit 5 may be partly artificial and partly caused by a true increase in very abundant species.

In some of the earlier years only species lists were made instead of quantitative observations (Table 1). In that case the abundances of the species were set equal to their abundances at the same station in the next year for which abundance data were available. If no such data existed (either because a species was not found again at the same station, or because a station was replaced) the abundance of the species was set equal to its mean over all years and all stations.

Ecological groups. The species were divided into ecological groups according to their pH preference, viz. nitrophytic (preference for bark pH c. 5-7), acidophytic (preference for bark pH <4), or indifferent (see Appendix). A first classification was made on the basis of Van Dobben & Wamelink (1992: Table 9). Species with $r < 0.0$ were classified as acidophytes, species with $0.0 < r < 0.3$ as indifferent and species with $r \geq 0.3$ as nitrophytic (r is the regression coefficient of species abundance on bark pH). Species not included in this table were classified according to Wirth (1991) ($R < 3$: acidophytic, $3 < R < 7$: indifferent, and $R \geq 7$: nitrophytic. R is the 'Reaktionszahl': the higher this number, the higher the pH optimum of a species). Species occurring in neither of these tables were classified according to Brand et al. (1988).

Air quality. Atmospheric concentrations of SO_2 and NO_2 were obtained from the Dutch Air Quality Monitoring Network (Anonymus 1978 - 1990) as daily mean concentrations at air quality monitoring stations. Before 1985 c. 180 stations were operated for SO_2 and c. 60 for NO_2 , after this date there were c. 60 stations for SO_2 and c. 30 for NO_2 . The measured concentrations at the monitoring stations were recalculated to 6 or 12 month arithmetic mean values. The concentrations at the epiphyte stations were interpolated (Van Egmond et al. 1978) from the mean concentrations at surrounding air quality stations (excluding the stations located in built-up areas). Air quality stations with no data within a single calendar year were excluded for the period containing that year. A check was performed to verify that in all years at least one air quality station was active in each of the eight regions defined in Figure 1. Figures 3 and 4 show the spatial patterns of SO_2 and NO_2 concentration in 1979/80 and 1989/90, respectively (SO_2 April-September, NO_2 July-June).

No measurements of atmospheric NH_3 concentrations were available. Instead, concentrations were estimated from cattle density statistics for 1988 and emission factors per cattle, using the atmospheric transport and deposition model TREND (Asman & Van Jaarsveld 1990). This model had a spatial resolution of 5 km (Figure 5).

There was a considerable variation in monthly mean values of SO_2 and NO_2 (Figures 6 and 7). The temporal behaviour of SO_2 can be approximated by the following linear function:

$\text{SO}_2 = 27.9 - 0.103 \cdot \text{month number}$ ($n=167$; 13.2% variance accounted for) with:

$\text{SO}_2 =$ monthly mean concentration over all rural air quality monitoring stations, in $\mu\text{g}\cdot\text{m}^{-3}$

month number 1 = January, 1977

Addition of a quadratic term did not significantly improve the fit of this model, and the change in SO_2 concentration was therefore treated as a linear trend. The mean NO_2 concentrations at the rural air quality stations did not show any temporal trend (Figure 7); the overall mean concentration at these stations over the period 1978 - 1990 was $27.6 \mu\text{g}\cdot\text{m}^{-3}$. However, due to differences in geographical position between the air quality and epiphyte monitoring stations, the (interpolated) mean NO_2 concentration at the epiphyte stations showed a slight (but statistically significant) tendency to increase over the years (Figure 7).

The temporal trend in NH_3 concentration (Figure 8) was estimated on the basis of data in Asman et al. (1987), Asman & Van Jaarsveld (1990) and Heij et al. (1991). Concentrations before 1980 were established from data compiled by Asman et al. (1987). Between 1980 and 1988 the emission of NH_3 in The Netherlands remained virtually constant (Heij et al. 1991). Therefore no change in NH_3 concentration was expected between 1980 and 1988. However, the mean concentration derived for 1988 by the TREND model (Asman & Van Jaarsveld 1990) was a factor 1.58 higher than the mean concentration derived for 1980 from data in Asman et al. (1987). This difference was mainly caused by the use of different emission factors (Heij et al. 1991). Therefore the values before 1988 were multiplied by a correction factor 1.58 in order to obtain a more realistic representation of the change in NH_3 concentration. The emission survey in 1990 (Asman 1992) yielded an emission that was 21% higher than the value for 1988. Here again the difference was largely due to a difference in emission factors. Therefore the NH_3 concentration was assumed constant over the period 1980-1990. Probably the spatial and temporal patterns of relative NH_3 concentrations can be trusted as fairly reliable estimates. There is however a large uncertainty in the absolute concentrations, which is mainly due to the uncertainty in the emission factors (Heij et al. 1991).

2.2 Statistical analysis

Statistical analysis was carried out with the programs GENSTAT 5.2.2 (Payne et al. 1987) (used for univariate regression and calculation of confidence intervals for canonical coefficients) and CANOCO 3.10 (Ter Braak 1988) (used for PCA = principal component analysis and RDA = redundancy analysis). The application of these techniques to the present data is discussed at length by Van Dobben (1991) and Van Dobben (1993). In the analyses all measured values were used untransformed (including the abundance values) except tree diameter which was transformed to its natural logarithm.

The sign and significance of the change in the abundance of the most common species was determined by linear regression. The overall change in the epiphytic vegetation was described as the change in the total number of species and the numbers of species in the ecological groups, and as the change in the sample scores derived by PCA. The 'fidelity' of the species to the stations was determined as the number of occurrences in 1990 in stations where that species also occurred in 1980, as a percentage of number of occurrences in 1980 or 1990, whichever was smaller.

Effect of averaging period. The season with the most relevant pollutant concentrations was determined by fitting pollutant concentrations averaged over different periods to the epiphyte data. It took c. 3 months to visit all stations and consequently there was a large spread in the observation dates (c. June - November; Figure 9), although the interval between subsequent observations at a given station was kept as close as possible to one year. For practical reasons pollutant concentrations averaged over the same part of the year were used for all stations. The following periods were tested:

- (1) 1/1 year (July-June)
- (2) 1/2 year (January-June)
- (3) winter (October-March)
- (4) summer (April-September)

RDA was used to fit combinations of SO₂ and NO₂ concentrations averaged over these periods to the epiphyte data, using NH₃ concentration, distance to the coast, tree species, number of trees and tree diameter as covariables. The years from which these periods were taken were determined such that each averaging period for air quality preceded the corresponding period of epiphyte observations by the shortest possible time. However, note that period (4) actually preceded the collection of the epiphyte data by c. one year. Also note that the use of pollutant concentrations collected after the epiphyte observations could not always be avoided.

A comparable procedure was used to estimate the size of a possible lag in the reaction of the epiphytes to air quality changes. Concentrations of SO₂ and NO₂ were averaged for each year over the period that yielded the best fit in the above procedure. These concentrations were fitted to epiphyte data collected 0-4 years later. As air quality data were lacking before 1977, epiphyte data from before 1981 were omitted from this analysis. For NO₂ data were lacking before June 1977, and data from the corresponding period in 1978 were used instead.

Importance of explanatory variables. The following environmental variables were used to explain the variance in the species' abundance values: pollutant concentrations (SO_2 , NO_2 , O_3 , NH_3), tree species, number of trees, tree diameter and distance to the coast. Their relative importance was determined by forward selection in RDA. For the variables that change over time the actual values in each year were used for this analysis. To compare the importance of the temporal change in the environmental variables with the importance of their spatial pattern, the variables with a significant effect in the previous analysis and a known change over time (SO_2 , NO_2 , and tree diameter) were split in a spatial component (for each station the mean over all years) and a temporal component (deviation of the actual values from this mean). Forward selection in RDA was performed with these variables, and the year number as an extra explanatory variable. The linearity of the temporal change in the abundance values was tested by including a set of dummy variables for the years (i.e. one variable for each year with value 1 in that year, else 0).

Relation between environmental change and vegetation change. If a change in the vegetation is caused by changes in environmental variables, then the vegetation change should be consistent with the spatial relation between vegetation and environment. More precisely, if an area A_1 has air quality Q_1 at time t_1 which changes to Q_2 at t_2 , while another area A_2 has air quality Q_2 at t_1 , then the vegetation in A_1 at t_2 should be equal to the vegetation in A_2 at t_1 , provided the period between t_1 and t_2 has been long enough to allow for mortality of 'old' or invasion of 'new' species. Under this hypothesis the temporal change in air quality can be derived from (a) the relation between the spatial pattern of epiphytic vegetation and pollutant concentrations, and (b) the temporal change of the epiphytic vegetation. For this, the lichen abundances in space and time were modelled as a linear function of pollutant concentrations and tree diameter. These variables were in turn modelled as the sum of a spatial and a temporal component. For the spatial component the temporal averages were taken (as above). The temporal component was assumed to be linear, i.e. the yearly change of each variable was constant over time. This yearly change is denoted as Δ or subscripted Δ (Δ_{SO_2} is the yearly change in SO_2 concentration, etc). In this model, the yearly change is the only parameter that remains to be estimated. As shown by Ter Braak & Wiertz (1994), this change can be inferred from the change in the abundance of all species by using RDA.

The method used in the present study is described in detail by Van Dobben & Ter Braak (1993: p. 100 ff), and entails (1) applying RDA with the species' abundances as the dependent variables, and year number, and the spatial components of SO_2 , NO_2 , NH_3 and tree diameter as the explanatory variables, followed by (2) modelling the canonical (regression) coefficients for year number as a function of the yearly change (Δ) of SO_2 , NO_2 , NH_3 and tree diameter, and the canonical coefficients of these variables (cf. Ter Braak & Wiertz 1994: p. 372). In principle, this yields a set of four equations (one for each canonical axis), from which the four Δ 's can be solved. The RDA was carried out with the environmental variables that are constant in time (tree species, number of trees and distance to the coast) as covariables. NH_3 was

included as an explanatory variable despite its probably constant concentration over the observation period, because earlier studies (e.g. Van Dobben 1987) attributed the change in epiphytic vegetation largely to an assumed change in NH_3 concentration.

The estimation of the temporal change in environmental variables by RDA was only partly successful because the eigenvalue of the second axis was much lower than that of the first axis ($\lambda_1=0.17$, $\lambda_2=0.03$, $\lambda_3=0.01$). There thus seemed to be only one axis that was really important. This means that the species either react to just one of the environmental variables, or in a similar way to all of them. As all variables had a significant contribution in our data, the latter situation apparently applies. In either case, the regression coefficients for the second and higher axes have little meaning. Using only the coefficients for the first axis (cf. Ter Braak & Wiertz 1994:(A.7)) yields one equation with four unknowns (viz., the temporal components of SO_2 , NO_2 , NH_3 and tree diameter). Two methods of solution are presented here: (1) prediction of each unknown using a zero value for the other ones; or (2) prediction of each unknown using the measured values for the other ones.

The 'measured' Δ values for SO_2 , NO_2 and diameter were obtained by regressing the interpolated (SO_2 and NO_2) or observed (diameter) values at the monitoring stations on year number (excluding station/year combinations with no epiphyte data). For Δ_{NH_3} a 'measured' value of 0 was used. Confidence intervals for the inferred change in environmental variables were obtained by a bootstrap procedure (see Van Dobben & Ter Braak 1993). The vegetation change was judged consistent with the change in air quality if the measured change in the pollutant concentration was inside the 95% confidence interval for the change inferred from the vegetation.

It was further attempted to produce regional estimates for the change in NH_3 and SO_2 concentration. This was accomplished by including terms for the region.year interactions in the RDA model instead of the term for year. The estimation procedure for the regional Δ values was further analogous to the procedure described above, using method (2) and replacing the regression coefficient for the single year term by the regression coefficients for the region.year interactions. Further methodological aspects are discussed by Van Dobben & Ter Braak (1993). The 'measured' regional Δ values for SO_2 , NO_2 and diameter were derived by fitting separate regressions of the environmental variables on year number for each region; for NH_3 a zero value was assumed in all regions.

3 RESULTS

3.1 Changes in epiphytic vegetation

Species numbers. Figure 10 shows the temporal trend in the overall number of species and the numbers of acidophytic and nitrophytic species per station, as mean values of the eight regions defined in Figure 1. The increase in the overall number of species (from a country-wide mean of 10.7 in 1980 to 17.6 in 1990) is largely due to the increase in the number of nitrophytic species. The number of acidophytic species has remained fairly constant or even decreased slightly. The increase in the number of nitrophytic species was found in all eight regions, although in the two southern regions (Braakman and Wijnandsrade) it was somewhat smaller than in the other regions.

Frequency and abundance of the individual species. Table 3 is based on two measures for the temporal change of the most common species. These measures relate to a comparison between 1980 and 1990 for the 87 stations that were present in both these years (Table 3A), and the regression of the species' abundances on time (year number), using data from all years and all stations (Table 3B). For many species the frequency had more than doubled between 1980 and 1990. Only few species had decreased in frequency, of the common species only *Lecanora conizaeoides* and *Hypogymnia physodes* (the decrease in *Parmelia sulcata* is an artifact due to the selection criterium that this species should initially be present at all stations).

Since the abundance scale was approximately logarithmic (Table 2) the difference in mean abundance between 1980 and 1990 reflects the percentual change in abundance. This change is not given in absolute value, but its significance is found in Table 3A (its sign is always equal to the sign of the regression coefficient in Table 3B). The fidelity is a measure for the probability that in 1990 a species is still present at a station where it was found in 1980. Most species had a high fidelity to the stations.

The regression coefficients of abundance on year number (Table 3B) reflect the change in abundance through time, on the basis of data from all years. The significance of these regression coefficients is also given, but should be interpreted with care. The high fidelity of most species shows that a species found in a given station has a high probability to be still there in the next year. Therefore data collected in subsequent years are not independent, and the regression coefficients will be considered significant too soon, especially for the rarer species. Nevertheless there was a rather close correspondence between the significance of the regression coefficients and the significance of the (1990-1980) difference in abundance. Of the common species all nitrophytes had significantly increased. Two acidophytes (*Parmelia saxatilis* and *Cladonia* spp.) had also significantly increased. One acidophyte (*Lecanora conizaeoides*) had significantly decreased according to both the (1990-1980) difference and the regression coefficient, while for two others

(*Hypogymnia physodes* and *Pseudevernia furfuracea*) only the regression coefficients indicated a significant decrease. For the other acidophytes the change was not significant.

The percentages variance explained by time and covariables can be used to compare the magnitudes of the temporal change and the spatial difference (Table 3B). For c. 10 nitrophytic species the variance explained by time was in the same order of magnitude as the variance explained by geography (including tree species, number and diameter). These species have apparently strongly increased at all sites. For the other species the variance explained by time was small compared to the variance explained by geography. Such species may also have increased, but have retained their preference for certain sites (i.e. tree species or regions).

Principal component analysis. Figure 11 shows the first two axes of a PCA on all data. The Figure displays 39% of the total variance. The third axis accounts for 7% variance and is therefore unimportant compared to the plotted axes. Figure 11A gives the species scores and the regression coefficients of a multiple regression of the sample scores on the (standardized) explanatory variables (air quality, distance to the coast, and tree species, number and diameter; the effect of tree species is indicated by the centroids for the sample scores per tree species). The results of this analysis were very similar to the results of the RDA analyses of epiphyte data collected in a single year, e.g. Van Dobben (1991), Van Dobben & Wamelink (1992) or Van Herk (1993).

The first axis separates *Lecanora conizaeoides* from all other species, while the second axis separates the acidophytic species from the nitrophytic species (Figure 11A). Like in the RDA analyses in Van Dobben (1991: Figure 4) and Van Dobben & Wamelink (1992: Figure 3), the first axis is strongly correlated with SO₂ and NO₂, and the second axis with NH₃ and tree species (particularly the contrast between the commonest tree species, *Quercus* with acid bark and *Populus* with neutral bark). This confirms the views of Van Dobben & Wamelink (1992) and Van Herk (1993) that the epiphytic vegetation of wayside trees is primarily determined by two factors, viz. the presence of toxic atmospheric compounds, which determines the overall species richness; and the pH of the bark, which in turn depends upon tree species and NH₃ concentration, and which determines the dominance of acidophytic or nitrophytic species. Note, however, that this interpretation is different from the interpretation in Van Dobben (1991), where the effect of SO₂ was primarily attributed to bark acidification rather than to its toxicity.

The trajectories through time of the mean sample scores per region are given in Figure 11B. Before 1983 their behaviour was somewhat erratic, but after this date there was a steady decrease in the scores on the first axis, and a tendency towards a decrease on the second axis. This indicates a decreasing influence of toxic compounds with a concomitant increase in species richness, and an increasing bark pH with a concomitant increase in dominance of the nitrophytic species.

3.2 Relation between epiphytic vegetation and pollutant concentrations: effect of averaging period

Season. Table 4 shows the correlation between SO₂ and NO₂ concentrations averaged over the periods given in 2.2, and the fit to the epiphyte data of all combinations of SO₂ and NO₂ concentration averaged over these periods. The differences in fit were rather small, particularly for NO₂, obviously because the concentrations averaged over different periods were strongly correlated (Table 4A). The best fit (15.2% variance accounted for) was found for the combination of SO₂ summer mean value and NO₂ yearly mean value (Table 4B). These averaging periods were used to visualize the temporal patterns of SO₂ and NO₂ in Figures 6 and 7. The strong peaks found in the 12-month mean SO₂ concentration are only weakly reflected in the summer mean concentrations (Figure 6). The 12-month mean NO₂ concentration had less pronounced peaks (Figure 7). Apparently peak concentrations do not strongly affect the lichen vegetation.

The reaction of the individual species to changes in SO₂ concentrations was also established. Species abundances were regressed on the January-June mean concentration (which had a pronounced 'peaky' pattern), using the April-September mean concentration of the preceding year, and the mean concentrations of NO₂ and NH₃, distance to the coast, and tree species, number and diameter as covariables. Since the two measures for SO₂ were strongly correlated the percentage variance accounted for was low for most species. Table 5 gives the species for which the effect of the January-June mean SO₂ concentration was significant at $p \leq 0.05$. Nearly all species with negative regression coefficients for the January-June mean SO₂ concentration were nitrophytic species. This suggests that these species did not only increase concomitantly with the general decrease in SO₂ concentration, but also expanded faster than other species in periods with a relatively low SO₂ concentration. Apparently the nitrophytes react more rapidly to changes in SO₂ concentration than other species. For the species with positive regression coefficients (except *Pseudevernia furfuracea* which decreased) the opposite was probably true. These species have also expanded, but their expansion lagged behind in periods with a low SO₂ concentration.

Year. Table 6A gives the correlation matrix of the SO₂ and NO₂ concentrations in different years, determined over the periods that yielded the best fit in the previous section. Table 6B shows the fit of combinations of these concentrations. The concentrations in different years were strongly correlated, which demonstrates that the spatial patterns remained fairly constant through time (see also Figures 3 and 4). The fit to the epiphyte data of air quality data from different years was approximately equal, although there was a tendency towards a smaller fit for SO₂ as the length of the period between the air quality and epiphyte observations increased (Table 6B). The best fit (15.8% explained variance) was found for the combination of SO₂ and NO₂ from the same year as the epiphyte data. These concentrations were used in further analyses.

3.3 Relation between epiphytic vegetation and explanatory variables

Comparison of explanatory variables. Table 7A gives the fit of single explanatory variables, using actual values for each year; Table 7B gives the result of forward selections with these variables. Like in the earlier studies (Van Dobben 1991, Van Dobben & Wamelink 1992) SO₂ and NO₂ concentration were the most important explanatory variables. The fit due to these variables far exceeded the fit due to NH₃ concentration and tree species. The fit due to geographical coordinates and distance to the coast was smaller than the fit due to air quality, and became very small after fitting SO₂ and NO₂. The fit due to time was small compared with the fit due to the variables related with spatial pattern, and became very small after fitting the pollutant concentrations that change over time (SO₂ and NO₂). The fit due to O₃ became very small after fitting NO₂ with which it was strongly correlated (compare Van Dobben 1991, Van Dobben & Wamelink 1992). Possible effects of geographical coordinates and O₃ were further left out of consideration and SO₂ and NO₂ were assumed as true causal factors for the correlations (as in Van Dobben 1991 and Van Dobben & Wamelink 1992). However, note that distance to the coast was retained as an explanatory variable to account for possible biogeographical effects.

The effect of SO₂ was tested for non-linearity. A quadratic term for SO₂ fitted after tree species, number, diameter and air quality terms yielded 1.4% extra fit. The contribution of SO₂ to the sample scores on the first axis reached a maximum at c. 21 µg.m⁻³ (as can be calculated from the regression coefficients). The maximum observed value for SO₂ was c. 30 µg.m⁻³. Apparently the effect of SO₂ had a tendency to level off at high concentrations.

Comparison of temporal and spatial variation. Table 8 gives the results of a RDA with the variables that change over time split in a spatial component (temporal mean at each station) and a temporal component (deviation of actual value from the temporal mean). Table 8A gives the correlation matrix of the year number and the temporal components of SO₂ and NO₂ concentration and tree diameter, and Table 8B the fit of the 'spatial' and 'temporal' variables. The fit due to the spatial variables (c. 27%) far exceeded the fit due to the temporal variables (c. 6%). Of the latter variables year number was the best single explanatory variable (5.3% variance accounted for). The variance explained by a full set of dummy variables for the years was only slightly higher (6.3%). The fit of the temporal components of SO₂ concentration and tree diameter was lower, and the fit of the temporal component of NO₂ concentration was very low. The variables with the highest correlation with year number (i.e. those for which the trend was closest to linearity; Table 8A) yielded the best fit. Thus, the linear term for year number appeared to be a good descriptor of the temporal effect. The change in the epiphytic vegetation was apparently close to linear, and the deviations from linearity in the temporal range were only slight.

The temporal change was further tested for non-linearity by adding a quadratic term for year number after fitting the spatial variables and year number. The extra fit due to this quadratic term was very small (0.3%

explained variance, Table 8B). The regression coefficients showed that the sample scores on the first axis decreased more than linearly with time, with a maximum in 1977. This means that the rate of temporal change had a tendency to increase over time (cf. Figure 11B).

To assess the importance of regional deviations from the general change in epiphytic vegetation, the year number variable was regionalized by calculating its interaction terms with dummy variables for the eight regions defined in Figure 1. The fit of these interaction terms was tested after fitting the dummy variables for the regions as covariables (in order to eliminate the effect of time-independent information contained in the year.region interactions). Table 8B shows that the cumulative fit of these interaction terms was only slightly higher than the fit of the single year variable (6.9% vs. 5.3%). The temporal change has apparently been similar in all regions, although the change tends to be larger in the northern regions (Table 8B). These findings are consistent with the temporal trends that became apparent from the PCA (Figure 11B).

3.4 Relation between environmental change and change in epiphytic vegetation

Both the change in epiphytic vegetation and the changes in air quality and tree diameter were close to linear trends. Therefore the correlations found in the previous section between the species' abundances and the temporal components of the environmental variables could be spurious, i.e. the correlations can be explained by any other variable that changes linearly with time. However, there is good external evidence that some causality is involved (Van Dobben 1991, Van Dobben & Wamelink 1992). In this section a causal model is hypothesized and used to investigate how well changes in air quality can be inferred from changes in lichen vegetation. A close correspondence between the inferred and the actual changes would mean that the change in lichen vegetation is consistent with the change in air quality, which would add evidence for the causal hypothesis.

In Table 9 the inferred changes, estimated by two methods (see 2.2), are compared with the measured changes. With method (1) (which assumed a zero value for the other variables) the inferred Δ_{SO_2} was the only one that was not significantly ($p < 0.05$) different from its measured value. The inferred values for Δ_{NH_3} , Δ_{NO_2} and $\Delta_{\text{In(diameter)}}$ were far outside the range of possible values. With method (2) (which was based on the measured change values for the other variables) the inferred values were quite good; the predicted Δ 's were not significantly different from the measured ones. Apparently the temporal change in epiphytic vegetation is consistent with the observed temporal change in the environmental variables. Note, however, that the contributions of NO_2 and tree diameter to the change were very small and in fact SO_2 alone is sufficient to explain the observed change.

Estimation of regional change in NH_3 concentration. The inferred regional changes in NH_3 concentration are given in Table 10. Both positive and negative values for Δ_{NH_3} were found, suggesting considerable change in the

spatial pattern of NH_3 during the observation period. However, in some of the regions the predicted Δ_{NH_3} values are improbably high. This is e.g. the case in the regions Wieringerwerf and Witteveen, with predicted Δ_{NH_3} values in the order of $+1.5 \mu\text{g}\cdot\text{m}^{-3}\cdot\text{y}^{-1}$. Starting with a zero concentration in 1977, this would mean a concentration of $>20 \mu\text{g}\cdot\text{m}^{-3}$ in 1988, which is far above the value estimated for these regions by Asman & Van Jaarsveld (1990) (Figure 8: c. $5 \mu\text{g}\cdot\text{m}^{-3}$).

Table 11 gives the predicted regional change in SO_2 concentration, together with the measured values. The two regions with unrealistically high predicted Δ_{NH_3} values (Wieringerwerf and Witteveen) also showed large discrepancies between the predicted and measured Δ_{SO_2} values. In both regions the predicted Δ_{SO_2} was far lower (i.e., more negative) than the measured value. Apparently the direction of the change in epiphytic vegetation in these regions is in agreement with the country-wide trend, as shown by the negative value for the predicted Δ_{SO_2} . However, the magnitude of the change seems to be larger than expected on the basis of the overall species-environment relation, and the regional change in environmental factors. It is interesting to note that the areas where the predictions for Δ_{NH_3} and Δ_{SO_2} were least realistic (Wieringerwerf and Witteveen) are the areas with the lowest absolute SO_2 concentrations. Apparently regional predictions of Δ_{NH_3} are not practically feasible and no further attempts have been made to optimize the prediction procedure.

4 CONCLUSIONS

Our data allow the following conclusions with respect to the temporal change of the epiphytic vegetation: (a) the change between 1977 and 1990 has been a near-linear trend, and (b) the magnitude of the overall change is approximately equal to the value expected on the basis of the measured change in SO₂ concentration. The contributions of the change in NO₂ concentration and tree diameter to the change in epiphytic vegetation have been negligible. Furthermore no indications were found for a response to an increased NH₃ concentration. No measurements of this component were available over the observation period, but a constant concentration was also inferred by Heij et al. (1991) on the basis of cattle density statistics.

The above conclusions are in sharp contrast to those of other studies (Van Dobben 1987, De Bakker 1988, 1989a, 1989b, Van Herk 1990, 1991) which attributed the strong increase of the nitrophytic species largely or completely to an assumed increase in NH₃ concentration. The nitrophytic species have strongly increased indeed, but there are three possible mechanisms that can explain this increase as a response to a decreasing SO₂ concentration: (a) SO₂ acidifies bark and therefore a decrease in SO₂ concentration results in an upward trend of bark pH, which tends to favour nitrophytic species (Van Dobben & Wamelink 1992); (b) on average, nitrophytic species are more sensitive to SO₂ than other species, even after correction for the effect of bark pH (Van Dobben & Wamelink 1992: Table 10); and (c) at decreasing SO₂ levels, nitrophytic species colonize new sites more rapidly than other species (see 3.2). The latter may be understandable on the basis of their ecology. In natural circumstances sites with a high bark pH can be found below bark wounds, bird's nests etc., and such sites are ephemeral by their nature. Therefore the ability to rapidly colonize may be a great advantage to species inhabiting those sites.

The winter is usually assumed to be the season in which the SO₂ concentration is most relevant to the epiphytes (Hawksworth & Rose 1970). The rationale behind this is that lichens are physiologically most active during winter, while peak concentrations, which are believed to be most detrimental to lichens, are frequent during this season. In our study, however, no strong effect of peak concentrations was found, and the temporal change in summer mean concentration (which was close to linearity) yielded the strongest correlation with the change in the epiphytes (which was also near-linear). It should however be stressed that this correlation does not imply that SO₂ is more effective in summer than in winter.

Many studies indicate or assume a lag time before an improvement in air quality becomes apparent in the epiphytes (Rose & Hawksworth 1981, Hawksworth & McManus 1989, Seaward 1992). Our study does not allow conclusions on such a lag time. The long-term changes in both epiphytic vegetation and air quality were nearly linear trends, and these may have been

present long before the start of our monitoring. Extensive data on air quality are lacking before 1977, but for SO_2 a time series exists for a number of stations in the region Vlaardingen, which indicates an approximately linear decrease since c. 1965 (DCMR 1984). For NH_3 the estimated historical concentrations indicate a more than linear rise between c. 1860 and 1980 (Figure 8). Our study did not yield indications that the effect of this rise still persisted after 1980.

In general, our data support the hypothesis of consistency between temporal change and spatial pattern set out in the Introduction. It should however be stressed that the present study deals with a situation of a decreasing SO_2 concentration, and the hypothesis is therefore not necessarily true in a situation of increasing concentrations.

Indications were found that the effect of SO_2 levelled off at high concentrations (see 3.3). If such a non-linearity actually exists, and the SO_2 concentration linearly decreases with time, then the rate of change in the epiphytic vegetation is expected to increase with time. The increase in explained variance on including a non-linear term for year number was very small (Table 8), but the regression coefficients for year number (see 3.3), and the PCA results (see Figure 11B) suggested an increasing rate of change after 1983. The possibility of a non-linear temporal effect of SO_2 can therefore not be ruled out, and may be partly masked by the following causes:

- (1) the number of observations before 1981, when the SO_2 concentration was still high, is small compared to the number of observations after this date (Table 1). Non-linear effects occurring before this date will therefore only slightly contribute to the fit of a non-linear explanatory variable.
- (2) if non-linearity (i.e., levelling off of the effect of SO_2 at high concentrations) is important, the highest rate of change in the epiphytes relative to the change in SO_2 would be expected in the regions with the lowest SO_2 concentrations. However, in these regions the smallest change in SO_2 concentration occurred (see Figure 3). A non-linear effect may therefore remain unnoticed if only country-wide mean values are used. This might partly explain why the predicted rate of change in SO_2 was approximately correct for the whole country (Table 9), but showed deviations if smaller regions were considered, especially in those with the lowest absolute concentrations (see 3.5). If this explanation is correct, non-linearity would also be responsible for the high estimates of the change in the NH_3 concentration in these regions (Table 10).

The change in the spatial pattern of SO_2 has probably not been large enough to completely mask the non-linearity: Figure 11B and Tables 8 and 10 suggest that the rate of change in the epiphyte vegetation was smallest in the southern half of the country, where mean SO_2 concentrations were highest. If this interpretation is correct, and if the decrease in SO_2 concentration continues at the present rate, the rate of change in epiphytic vegetation may be expected to increase in the near future, especially in the southern half of the country.

5 DISCUSSION: EPIPHYTES AS MONITORS FOR AIR QUALITY

Epiphytic lichens have been used to make detailed quantitative estimates of air pollutant concentrations, particularly SO_2 (Hawksworth & Rose 1970) and NH_3 (Van Herk 1990, 1991, 1993). Some authors claimed the applicability of epiphytic lichens as monitors for air quality in general, including the presence of gaseous compounds, heavy metals, dust and chloride (Herzig et al. 1989). The present study and those by Van Dobben (1991) and Van Dobben & Wamelink (1992) showed that although there is a strong relation between epiphytic lichen vegetation and air quality, such detailed estimates are not practically feasible. This is due to (a) the impossibility to separate the effects of different pollutants, (b) the interference of environmental factors other than air quality, and (c) the variability that is inherent in field data.

In our data a multiple regression model that included air quality (SO_2 , NO_2 and NH_3 concentrations) and a few other ecologically relevant parameters (tree species etc.) accounted for c. 30% variance in RDA (Van Dobben 1991, Van Dobben & Wamelink 1992, this study). In univariate regression with the number of species as the dependent variable, the percentage variance accounted for was higher, c. 45% for the number of species per sample and c. 65% for the number of species per $5 \times 5 \text{ km}^2$ square (Van Dobben 1991). In all models air quality was more important than tree species, tree diameter or distance to the coast. Of the air pollutants SO_2 was by far the most important explanatory variable, whose effect on both the number of species and the abundances of the individual species was far stronger than the effects of NH_3 or NO_2 . This conclusion is in contrast to De Bakker (1989a) and Van Herk (1990, 1991), who strongly emphasized the importance of NH_3 .

The relatively high percentages of explained variance are partly due to the strict standardization criteria used in the selection of the sample points. In the present data the linear, single-factor explanatory variables accounted for c. 30-40% variance in RDA while in the data used by Van Dobben (1991), where the standardization criteria were applied less strictly, these variables accounted for c. 20% variance. If other sites than those complying with the standardization criteria were included the percentage explained variance would probably strongly decrease.

Van Herk (1990, 1991) made an attempt to estimate the NH_3 concentration on the basis of the epiphytic vegetation. Although his assumption that the effect of SO_2 is negligible does not hold, it might still be possible to produce estimates for NH_3 after correction for the measured SO_2 concentration. However, such a procedure is only practically feasible if the effect of NH_3 is not too small compared with the effect of the other pollutants. In a dataset with a strongly one-dimensional variation (like the present one) the relative importance of two variables can be assessed by comparing their canonical coefficients on the first axis. The ratio between the canonical coefficients for SO_2 and NH_3 on the first axis was 3.36 (see Figure 11). A change in the

measured SO_2 concentration of $1 \mu\text{g}\cdot\text{m}^{-3}$ will therefore result in a change of c. $3 \mu\text{g}\cdot\text{m}^{-3}$ in the estimated NH_3 concentration. With these values the application of a correction procedure is impracticable because of the extremely high sensitivity of the predicted NH_3 concentration to the measured SO_2 concentration.

The strong predominance of the effect of one air pollutant is not the only reason that makes the prediction of individual pollutant concentrations from the epiphytes difficult or impossible. The following phenomena also add to this problem:

1. mutual correlations between pollutant concentrations. This increases the uncertainty in the estimated regression coefficients, and thereby the uncertainty in the predicted concentrations. If the correlation is very strong it is impossible to separate effects in a regression analysis. This was e.g. the case with the pair NO_2 - O_3 ($r=-0.9$). In the present study effects are ascribed to NO_2 because a negative effect of NO_2 on the epiphytes seems more likely than a positive effect of O_3 , and effects of O_3 on epiphytes are unlikely anyhow (McCune 1988, Ruoss et al. 1991). Concentrations of air pollutants may also be confounded with (bio)geographical factors. Van Herk (1991) claimed negative effects of NH_4 aerosol on epiphytes. However, the NH_4 concentration estimated by the TREND model (Asman & Van Jaarsveld 1990) is strongly correlated with distance to the coast. The effect ascribed to NH_4 is therefore more likely a biogeographical effect (in contrast to Van Dobben 1991; see Van Dobben & de Bakker 1993).
2. similarity of effects. SO_2 and NO_2 are both toxic compounds that negatively affect all species except *Lecanora conizaeoides*. It is therefore impossible to ascribe e.g. a high abundance of *Lecanora conizaeoides* to high concentrations of either SO_2 or NO_2 .
3. non-linearity and interaction. The problems arising from non-linearity were discussed above. The studies by Van Dobben (1991) and Van Dobben & Wamelink (1992) did not show strong interactions between air pollutants mutually, or between air pollutants and other environmental factors (including bark factors). However, the results of various studies are conflicting on this point. A strong interaction between pH and SO_2 concentration is often reported from laboratory studies (Puckett et al. 1973, Türk & Wirth 1975). De Wit (1976) found an interaction between SO_2 concentration and distance to the coast. Van Herk (1990, 1991) implicitly assumed a strong interaction between tree species and NH_3 concentration. None of these interaction effects became apparent from our data.

It can be concluded that in The Netherlands the epiphytic vegetation on standardized wayside trees is strongly correlated with air quality, particularly the SO_2 concentration. However, a prediction of air quality parameters other than SO_2 concentration on the basis of the epiphytic vegetation is not practically feasible.

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TABLES

Table 1. Numbers of monitoring stations examined per year and per region. Numbers of stations for which only species lists were available are enclosed in brackets. Explanation of abbreviated region names: Wijn = Wijnandsrade, Vred = Vredepeel, Braa = Braakman, Vlaa = Vlaardingen, Wier = Wieringerwerf, Bilt = Bilthoven, Eibe = Eibergen, Witt = Witteveen. The actual number of stations per region in a given year is always less than the total number of stations over the whole observation period in that region because some stations were replaced by others in the course of time (see text).

year	regions								total
	Wijn	Vred	Braa	Vlaa	Wier	Bilt	Eibe	Witt	
77	-	-	-	-(12)	-	-(13)	-(8)	-	33
78	3	6	5	4	9	2	13	5	47
79	12	7	10	1	8	2	3	19	62
80	15	12 (1)	17	11 (6)	11	15	7	-	95
81	15	12 (1)	16 (1)	17 (1)	18 (1)	15	24	23	144
82	15	13	17	18	19	15	24	24	145
83	15	13	15	16	19	14	24	23	139
86	16	13	18	18	19	14	24	24	146
87	16	13	18	18	19	16	24	24	148
88	16	14	17	18	19	15	23	24	146
89	16	13	18	18	19	16	24	24	148
90	15	12	14	16	18	15	24	24	138
total	19	15	28	31	25	22	28	30	198

Table 2. Scales used for estimating species abundance before 1984 (A) and after 1985 (B). No sharp definitions existed for the Tansley units (used before 1984), except the first two units. All cover estimates were transformed to the five-unit scale in the right-hand columns prior to data analysis.

A.

'modified Tansley'	transformed value
1 thallus	1
1 tree	2
rare	3
occasional	3
frequent	4
abundant	4
dominant	5

B.

'Bakker'	explanation	transformed value
1	1 thallus	1
2	any quantity, on 1 tree	2
3	< 1 dm ² per tree on < 5 trees	3
4	> 1 dm ² per tree on < 5 trees	4
5	< 1 dm ² per tree on > 5 trees	4
6	> 1 dm ² per tree on > 5 trees	5

Table 3. Change of species frequency and abundance.

A: comparison of the 87 stations that existed in 1979/1980 and were still operated in 1990 (1979/1980 = 1980 with missing data taken from 1979), using paired t-test. frequency = percentage of stations with species, sign. = significance of difference in mean (1990-1980) abundance (* = $p < 0.05$, ns = $p > 0.05$, n=87), fidel. = fidelity to station (number of occurrences in 1990 in stations where that species also occurred in 1979/1980, as a percentage of number of occurrences in 1979/1980 or 1990, whichever is smaller).

B: comparison of all stations and all years, using linear regression. cf = regression coefficient (multiplied by 100) of year number, in a multiple regression of species abundance on year number, first and second order geographical coordinates, and tree species, number and diameter (temporal mean of each station). sign. = significance of cf (t-test, * = $p < 0.05$, n=1391, see text). % var. expl. = percentage variance explained: covar. = by covariables, time = by year number after fitting covariables. Only species are given with more than 24 occurrences in the complete dataset (=mean of more than 2 occurrences per year), in the order of decreasing regression coefficient. See Appendix for an explanation of the abbreviated species names.

species	A.			B.		
	comparison 79/80 - 90			regression of abundance on year number		
	frequency	sign.	fidel.	cf	sign.	% var. expl.
	79/80	90				covar. time
phzdsc	1.1	60.9 *	0.0	16.8 *	7.8	30.8
xparie	9.2	67.8 *	87.5	11.8 *	24.2	15.1
phtene	67.8	93.1 *	98.3	9.6 *	20.2	8.8
lecide	16.1	57.5 *	100.0	9.3 *	26.9	8.3
xpolyc	58.6	86.2 *	100.0	9.1 *	19.5	8.1
xcande	20.7	64.4 *	94.4	9.0 *	23.4	7.6
lexpal	83.9	100.0 *	100.0	8.2 *	25.9	11.9
ramfar	46.0	75.9 *	95.0	7.3 *	38.6	4.9
lepinc	31.0	52.9 *	96.3	7.1 *	48.5	3.6
phorbi	2.3	33.3 *	50.0	7.0 *	12.3	10.6
psubru	19.5	51.7 *	88.2	6.2 *	18.2	5.3
bupunc	92.0	98.9 *	100.0	6.1 *	6.4	9.0
psubau	32.2	65.5 *	89.3	6.1 *	30.9	3.6
phcaes	5.7	28.7 *	60.0	5.9 *	12.3	6.6
ldispe	8.0	32.2 *	71.4	5.7 *	10.2	5.3
canvit	5.7	28.7 *	80.0	5.3 *	22.4	4.9
bugris	17.2	39.1 *	100.0	5.2 *	56.3	2.8
psulca	97.7	94.3 *	100.0	4.4 *	20.9	5.4
canref	2.3	21.8 *	100.0	4.0 *	10.1	6.6
evepru	57.5	63.2 ns	78.0	3.4 *	20.2	1.1
lecsym	10.3	37.9 *	66.7	3.2 *	17.1	1.8
lcarpi	17.2	32.2 *	86.7	3.2 *	32.5	1.3
lchera	42.5	51.7 *	86.5	3.0 *	45.8	0.7
ramfas	18.4	42.5 *	100.0	2.9 *	56.8	1.1
canxan	0.0	11.5 *	-	2.6 *	7.4	4.6
phdubi	1.1	12.6 *	0.0	2.5 *	4.9	4.0
catgri	3.4	9.2 *	100.0	2.0 *	15.2	2.0
lchona	11.5	20.7 ns	80.0	1.7 *	33.2	0.6
cspeci	3.4	13.8 *	66.7	1.6 *	13.2	1.1
phentx	0.0	3.4 ns	-	1.4 *	21.1	2.1
phgris	3.4	8.0 ns	66.7	1.3 *	29.6	0.7
rinexi	0.0	2.3 ns	-	1.1 *	5.4	1.7
pcaper	1.1	9.2 *	0.0	1.1 *	3.3	2.3
pexasp	19.5	25.3 ns	70.6	0.9 ns	23.4	0.2
peralb	0.0	2.3 ns	-	0.8 *	24.9	0.5
psaxat	1.1	5.7 *	100.0	0.7 *	12.1	0.5
placin	2.3	6.9 *	100.0	0.6 *	13.4	0.3
bucane	4.6	8.0 ns	100.0	0.5 ns	46.9	0.1
paceta	17.2	28.7 ns	93.3	0.5 ns	37.3	0.1
phlarg	3.4	6.9 ns	66.7	0.4 ns	22.6	0.1
prevol	0.0	4.6 *	-	0.4 ns	8.0	0.2
haecoc	2.3	4.6 ns	50.0	0.3 ns	6.9	0.1
perama	0.0	1.1 ns	-	0.1 ns	5.3	0.0
uspeci	4.6	2.3 ns	50.0	-0.1 ns	4.8	0.0
hytub	3.4	2.3 ns	0.0	-0.3 ns	4.8	0.2
psefur	5.7	4.6 ns	75.0	-0.6 *	13.9	0.3
hypphy	55.2	48.3 ns	73.8	-3.1 *	16.6	1.0
lconde	78.2	50.6 *	95.5	-6.5 *	34.0	2.7

Table 4. Correlation (A) and fit to the epiphyte data (B) of SO_2 and NO_2 concentrations averaged over different periods. The fit was determined by RDA after fitting NH_3 concentration, distance to the coast, tree species, number and diameter as covariables ($n=1391$). See 2.2 for an explanation of the period numbers.

A. Correlation matrix of SO_2 and NO_2 concentrations from different periods.

		SO ₂				NO ₂		
period →		1	2	3	4	1	2	3
SO ₂	↓							
	2	0.98						
	3	0.98	0.98					
	4	0.83	0.74	0.75				
NO ₂	1	0.42	0.42	0.37	0.43			
	2	0.48	0.50	0.44	0.45	0.90		
	3	0.46	0.47	0.44	0.40	0.95	0.91	
	4	0.32	0.30	0.25	0.44	0.94	0.84	0.85

B. Fit to the epiphyte data of combinations of SO_2 and NO_2 concentrations from different periods, after fitting covariables.

		NO ₂			
period →		1	2	3	4
SO ₂	↓				
	1	13.9	13.0	13.0	14.2
	2	12.7	11.7	11.6	13.0
	3	12.9	12.0	11.7	13.3
	4	15.2	14.5	14.6	14.8

Table 5. Species with a significant (t-test, $p \leq 0.05$, $n=1391$) effect of the January-June mean SO_2 concentration on their abundance, determined by multiple regression, after fitting tree species, number and diameter, NO_2 and NH_3 concentration, distance to the coast and April-September SO_2 concentration. cf = regression coefficient of the January-June mean SO_2 concentration (multiplied by 100); see Appendix for an explanation of the abbreviated species names.

species	cf	% var. explained by:	
		cover	SO2 jan-jul
ramfas	1.5	51.1	0.5
lchera	1.1	46.0	0.2
paceta	1.0	33.4	0.4
pexasp	0.9	17.3	0.3
psulca	0.8	26.0	0.3
psefur	0.5	11.6	0.4
pcaper	-0.4	3.3	0.5
phdubi	-0.6	8.3	0.4
phgris	-0.8	29.3	0.4
canref	-0.8	13.5	0.5
lexpal	-1.0	27.3	0.3
canvit	-1.1	26.8	0.4
xpolyc	-1.7	26.8	0.5
phtene	-1.9	33.9	0.6
lecide	-2.0	35.5	0.7
phcaes	-2.0	20.9	1.4
ldispe	-2.4	11.9	1.7
xcande	-2.6	27.4	1.1
phorbi	-3.1	14.5	3.7
xparie	-3.5	31.5	2.4
phadsc	-4.6	25.2	4.0

Table 6. Correlation (A) and fit to the epiphyte data determined by RDA (B) of SO_2 concentration (April-September mean) and NO_2 concentration (July-June mean) observed 0-4 year before the epiphyte data. Covariables as in Table 4. # years = number of years between air quality observations and epiphyte observations. Only epiphyte data from 1981 onwards were used ($n=1154$).

A. Correlation matrix of SO_2 and NO_2 concentrations from different years.

		SO ₂					NO ₂			
# years →		0	1	2	3	4	0	1	2	3
	↓									
	1	0.94								
	2	0.88	0.89							
SO ₂	3	0.80	0.79	0.87						
	4	0.84	0.82	0.78	0.82					
	0	0.44	0.45	0.56	0.62	0.59				
	1	0.44	0.42	0.47	0.62	0.65	0.92			
NO ₂	2	0.49	0.46	0.47	0.52	0.66	0.86	0.90		
	3	0.40	0.38	0.44	0.49	0.47	0.82	0.80	0.87	
	4	0.30	0.32	0.38	0.46	0.43	0.78	0.75	0.75	0.88

B. Fit to the epiphyte data of combinations of SO_2 and NO_2 concentrations from different years, after fitting covariables.

		NO ₂				
# years →		0	1	2	3	4
	↓					
	0	15.8	15.4	15.1	15.4	15.7
	1	15.8	15.5	15.3	15.6	15.5
SO ₂	2	15.4	15.5	15.6	15.6	15.6
	3	14.4	14.1	14.6	14.6	14.5
	4	14.0	13.4	13.5	14.2	14.1

Table 7 Fit of explanatory variables in RDA. A: fit of single variables, B: forward selection of best fitting variables (left: in the order tree species, number and diameter - air quality - geographical coordinates - time, right: in the order tree species, number and diameter - geographical coordinates - air quality - time). Variables within a group (as above) are selected in order of decreasing fit. Conc. = actual concentration, coord. = geographical coordinate, diameter = $\ln(\text{diameter of the thickest tree})$, dist. coast = distance to the coast (nearest salt water basin), year = year number (1977...1990), # trees = number of trees. (n=1391).

A. Single variables.

variable	fit
SO2 conc.	14.3
Y coord.	12.8
NO2 conc.	10.2
year	5.9
O3 conc.	4.1
Ulmus	4.0
X coord.	3.8
diameter	2.8
dist. coast	2.8
Quercus	2.5
Populus	2.3
NH3 conc.	1.5
# trees	1.1
Salix	0.8

B. Forward selection.

variable	extra	cumul.
fit	fit	
Ulmus	4.0	4.0
Populus	2.3	6.3
Quercus	0.8	7.2
diameter	2.2	9.4
# trees	1.2	10.6

air quality first:			geographical coordinates first:		
variable	fit	extra	variable	fit	extra
SO2 conc.	12.3	22.9	Y coord.	11.0	21.6
NO2 conc.	4.2	27.2	X coord.	1.3	22.9
NH3 conc.	1.9	29.1	dist. coast	1.8	24.7
O3 conc.	0.3	29.3	SO2 conc.	4.0	28.7
dist. coast	0.6	30.0	NO2 conc.	1.7	30.4
X coord.	1.2	31.2	NH3 conc.	1.3	31.7
Y coord.	0.8	31.9	O3 conc.	0.2	31.9
year	1.5	33.4			

Table 8 Correlation (A) and fit to the epiphyte data (B) of spatial and temporal variables. Covar. = tree species, number of trees, NH₃ concentration, distance to the coast; diam. = ln(diameter); year = year number; year² = squared year number; dummies = set of variables (one for each year) with values 0 or 1; spat. = spatial variable (mean value over all years), temp. = temporal variable (deviation of actual value from this mean) (n=1391).

A: Correlation matrix of temporal variables.

	SO2	NO2	diam.
NO2	-0.34		
diam.	-0.67	0.21	
year	-0.84	0.31	0.77

B: Fit of spatial and temporal variables.

	variable fit	extra fit	cumul. fit
forward selection of spatial variables:			
cover.	12.3		12.3
SO2 spat.	12.6		24.9
NO2 spat.	1.3		26.2
diam. spat.	0.9		27.2

fit of temporal variables as single terms and dummies for the years (spatial variables added to the covariables):

year	5.3
diam. temp.	3.4
SO2 temp.	3.7
NO2 temp.	0.4
dummies	6.3

regionalization of temporal variation (see Figure 1 for an explanation of the abbreviated region names; dummies for the regions (explaining 4.2% variance) and spatial variables added to the covariables):

Eibe	1.3	region.year interactions
Witt	1.2	
Wier	1.1	
Vred	0.8	
Bilt	0.7	
Wijn	0.6	
Vlaa	0.6	
Braa	0.3	
all regions	6.9	
year	6.1	

forward selection of temporal variables (spatial variables added to the covariables):

year first:			year last:			year non-linear:		
year	5.3	5.3	SO2 temp.	3.7	3.7	year	5.3	5.3
NO2 temp.	0.2	5.5	diam.temp.	0.7	4.3	year ²	0.3	5.6
diam.temp.	0.2	5.6	NO2 temp.	0.1	4.5			
SO2 temp.	0.1	5.8	year	1.3	5.8			

Table 9 Predicted and measured yearly change (Δ) in SO_2 , NO_2 and NH_3 concentrations and tree diameter. Predicted values were derived from the change in epiphytic vegetation by RDA (see text for details); estimates are given for each single Δ using a zero value for the other ones (method (1)), or the measured value for the other ones (method (2)). The ranges given are 95% confidence intervals. For the predicted values these were derived from 2500 bootstrap samples. As the ranges were nearly symmetrical they are given in the \pm notation. Units: $\mu\text{g}\cdot\text{m}^{-3}\cdot\text{y}^{-1}$.

variable	predicted values		measured value
	method (1)	method (2)	
ΔSO_2	-0.87 ± 0.11	-0.91 ± 0.13	-0.84 ± 0.06
ΔNO_2	-1.75 ± 0.32	0.02 ± 0.25	0.13 ± 0.09
ΔNH_3	2.92 ± 0.91	0.23 ± 0.45	$0.00 \pm ?$
$\Delta\text{diameter}$	0.31 ± 0.13	-0.04 ± 0.05	0.015 ± 0.004

Table 10 Predicted yearly change (Δ_{NH_3}) per region, as obtained on the basis of the regional change in epiphytic vegetation by RDA (see text for details). Measured values were assumed for Δ_{SO_2} , Δ_{NO_2} and Δ_{diameter} (method (2) in Table 9). The ranges given are 95% confidence intervals, derived from 2500 bootstrap samples, and because they were asymmetrical in many cases the lower and upper limits are given separately. Units: $\mu\text{g}\cdot\text{m}^{-3}\cdot\text{y}^{-1}$. See Figure 1 for the location of the regions; regions are given in approximate order of decreasing SO_2 concentration.

region	ΔNH_3 predicted		
	lower	mean	upper
Wijnandsrade	-1.38	-0.92	-0.36
Braakman	-0.16	0.28	0.67
Vlaardingen	0.18	1.10	1.81
Vredepeel	-0.50	0.34	1.05
Bilthoven	0.66	1.73	2.57
Eibergen	0.32	0.99	1.53
Wieringerwerf	1.00	1.83	2.43
Witteveen	0.80	1.52	2.04

Table 11 Predicted and measured yearly change (Δ) in SO_2 concentration per region, as obtained on the basis of the regional change in epiphytic vegetation by RDA (see text for details). Measured values were assumed for Δ_{NO_2} and Δ_{diameter} (method (2) in Table 9); the measured Δ_{NH_3} was assumed to be zero in all regions. The ranges given are 95% confidence intervals. For the predicted values these were derived from 2500 bootstrap samples, and because they were asymmetrical in many cases the lower and upper limits are given separately. Units: $\mu\text{g}\cdot\text{m}^{-3}\cdot\text{y}^{-1}$. See Figure 1 for the location of the regions. regions are given in approximate order of decreasing SO_2 concentration.

region	ΔSO_2 predicted			ΔSO_2 measured
	lower	mean	upper	
Wijnandsrade	-0.81	-0.60	-0.37	-1.18 ± 0.09
Braakman	-1.38	-1.14	-0.76	-0.94 ± 0.08
Vlaardingen	-2.03	-1.54	-0.69	-0.84 ± 0.08
Vredepeel	-1.56	-1.14	-0.45	-0.93 ± 0.10
Bilthoven	-2.64	-2.03	-0.96	-0.94 ± 0.08
Eibergen	-1.77	-1.39	-0.73	-0.96 ± 0.07
Wieringerwerf	-2.14	-1.66	-0.85	-0.50 ± 0.08
Witteveen	-1.80	-1.42	-0.75	-0.46 ± 0.08

FIGURES



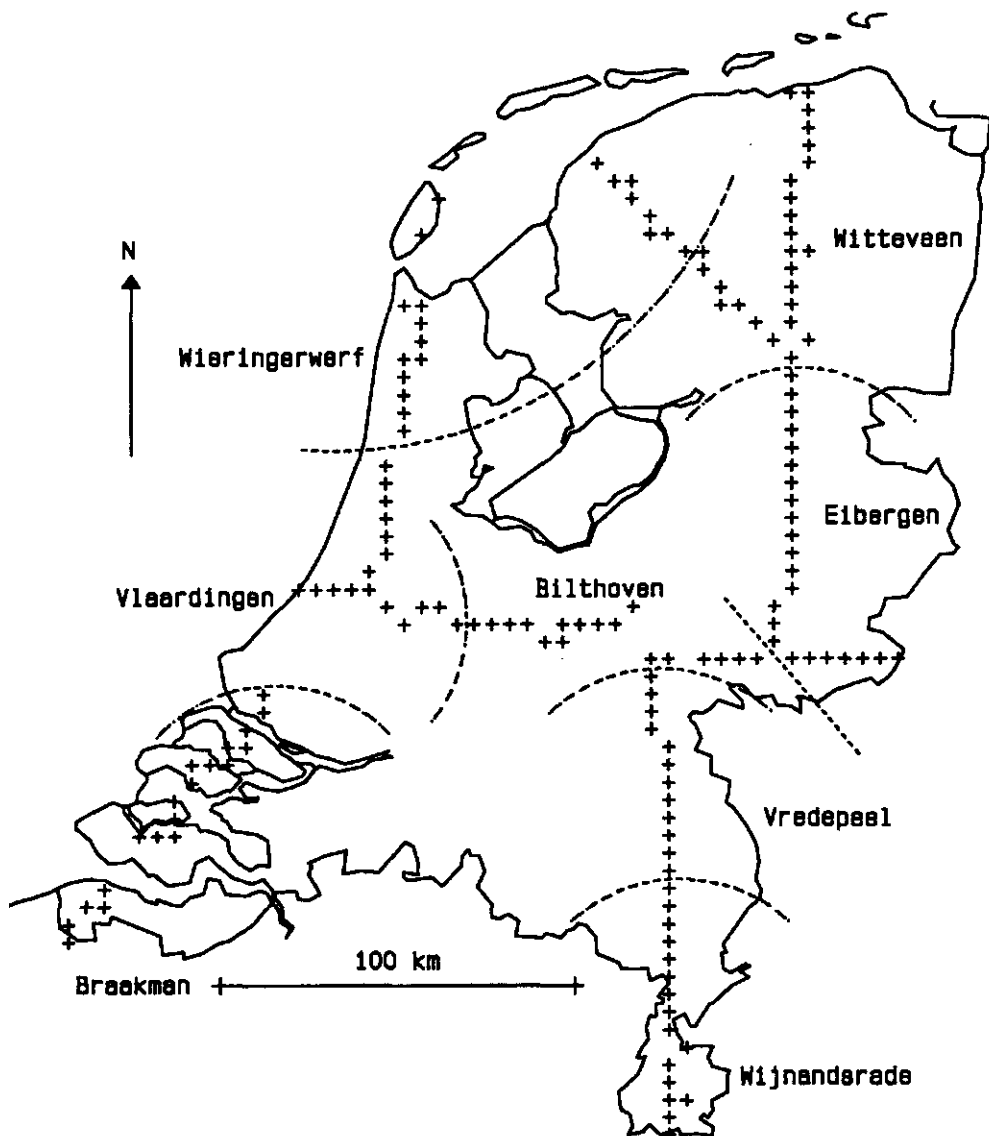


Fig. 1. Approximate location of epiphyte monitoring stations. For the interpretation of spatial patterns the stations have been assigned to eight regions, whose boundaries are indicated as dashed lines. The names of the regions are the names of the 'macro' monitoring stations of the Dutch Air Quality Monitoring Network.

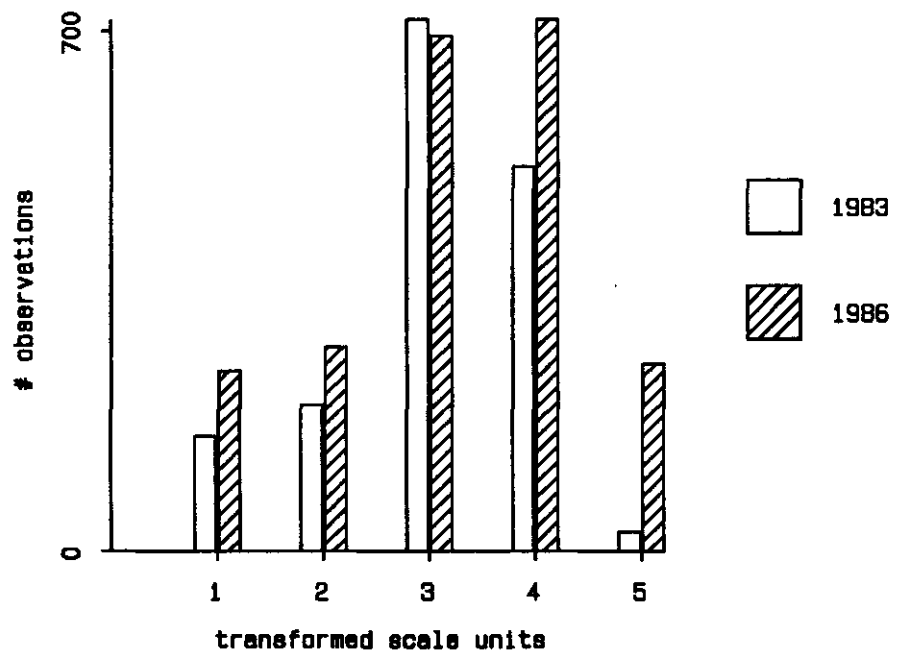


Fig. 2. Histogram of frequency distribution of transformed cover estimates in 1983 and 1986. For an explanation of the scale units see Table 2.

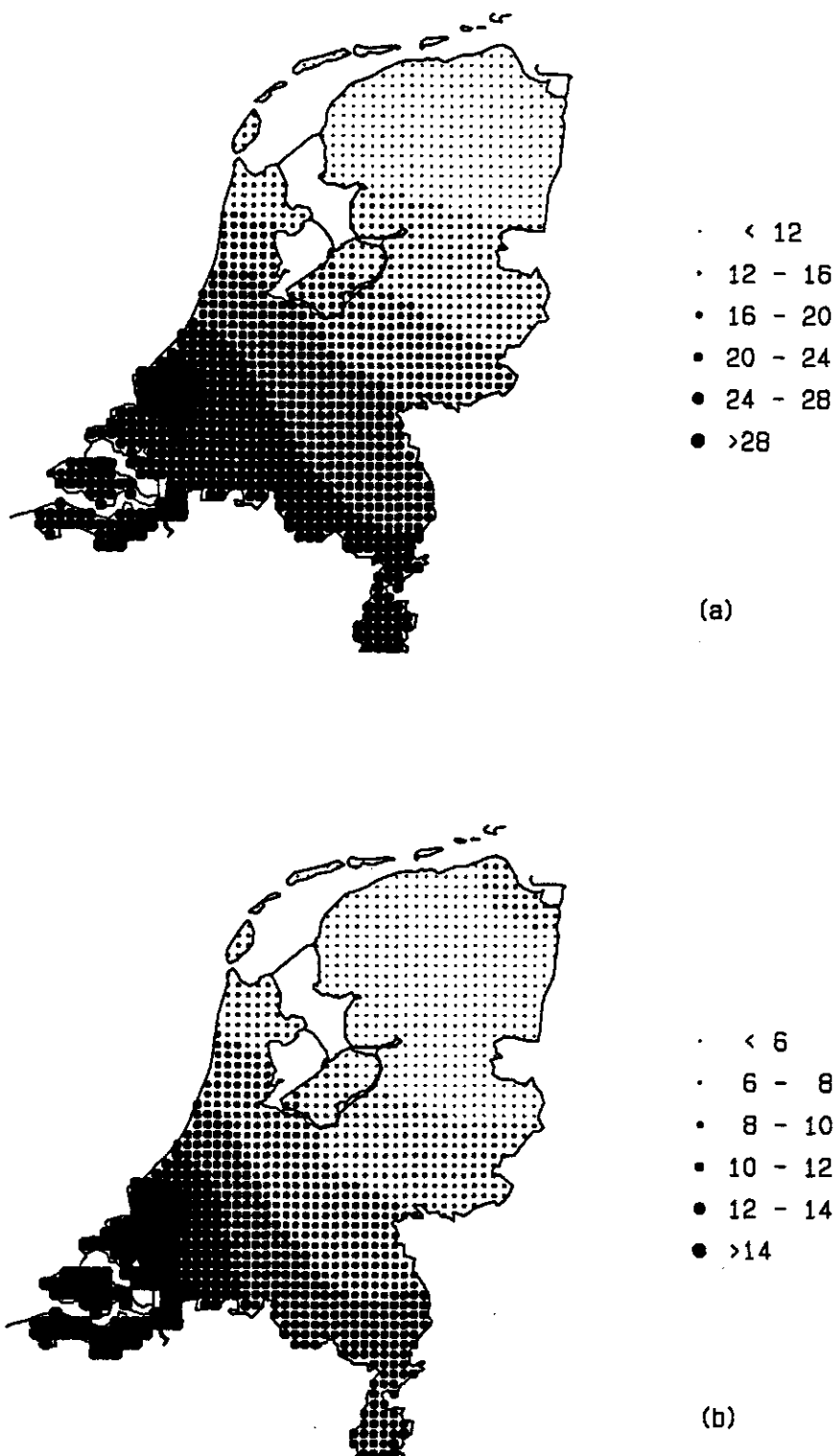


Fig. 3. Spatial pattern of summer (April-September) SO_2 mean concentration (in $\mu\text{g}\cdot\text{m}^{-3}$): (a) in 1979, (b) in 1989.

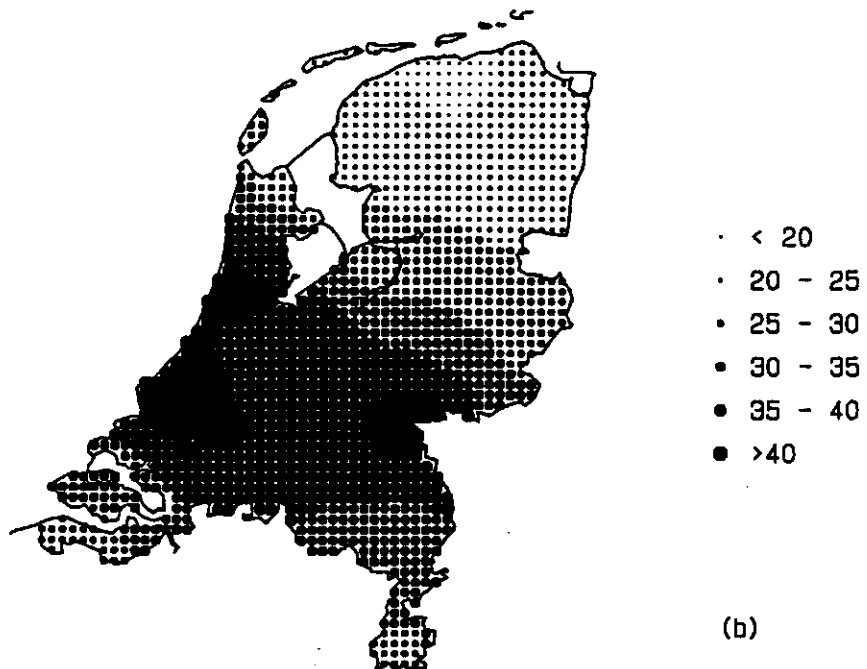
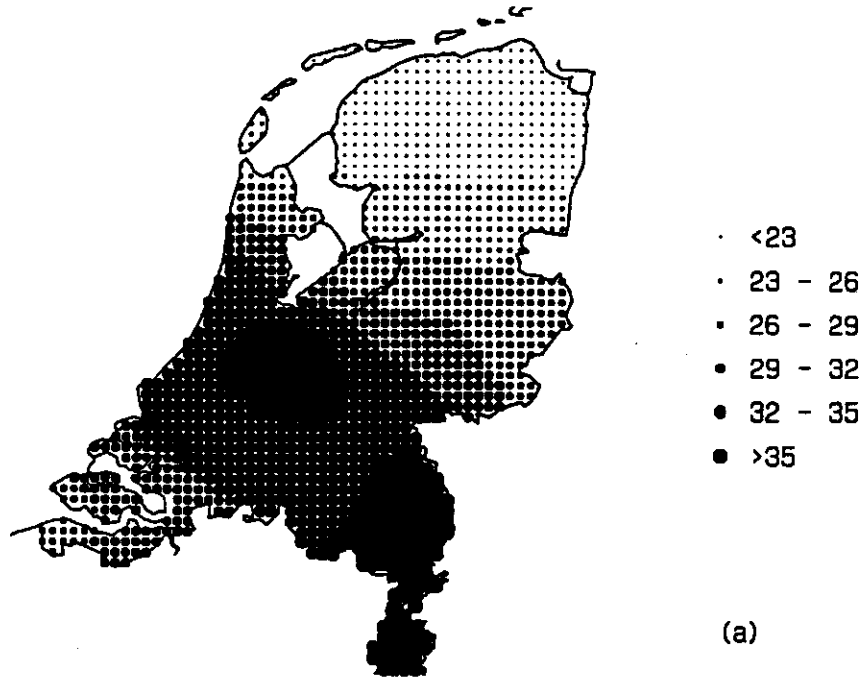


Fig. 4. Spatial pattern of yearly (July-June) NO_2 mean concentration (in $\mu\text{g.m}^{-3}$): (a) in 1979/1980, (b) in 1989/1990.

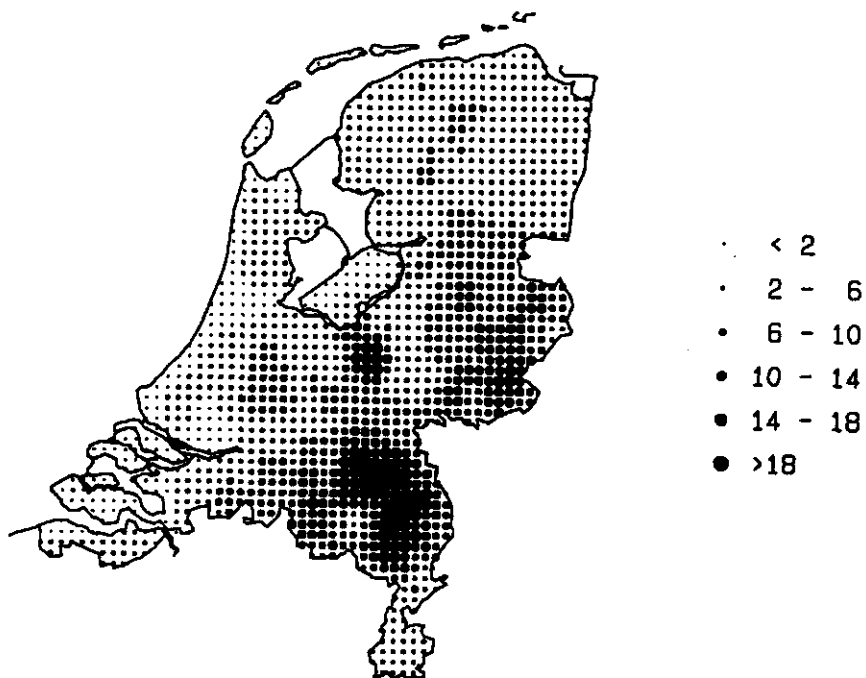


Fig. 5. Spatial pattern of estimated NH_3 concentration (in $\mu\text{g.m}^{-3}$) in 1988 (data from Asman & Van Jaarsveld 1990).

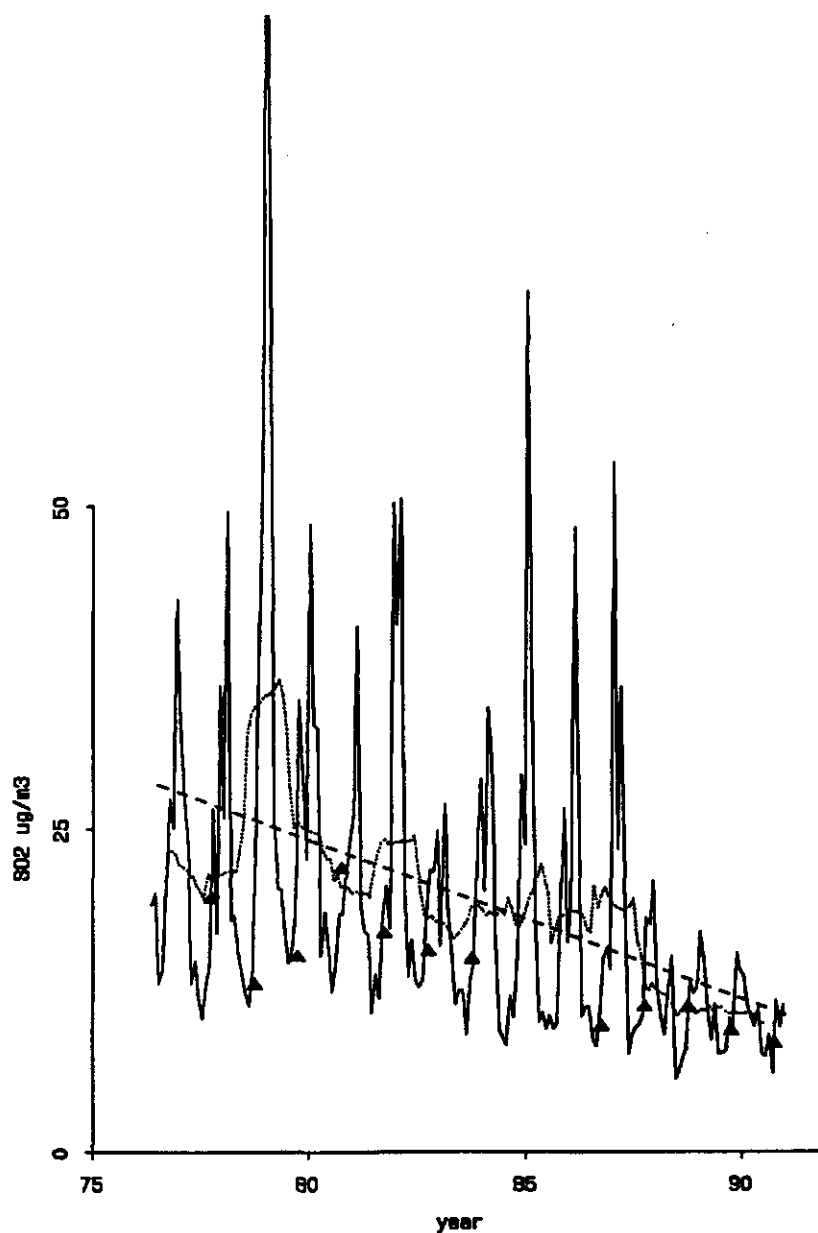


Fig. 6. SO_2 concentration (in $\mu g.m^{-3}$) as a function of time.

drawn line: monthly mean of concentrations at rural air quality monitoring stations

dotted line: 12-monthly running mean of concentrations at rural air quality monitoring stations

dashed line: regression line of monthly mean concentration at rural air quality monitoring stations on time

triangles: mean of interpolated concentrations at epiphyte monitoring stations.

The concentrations at the epiphyte stations are generally lower than the overall mean concentrations, and follow these concentrations with a time lag of ca. 1 year. This difference is caused by the method of averaging, as explained in section 2.2.

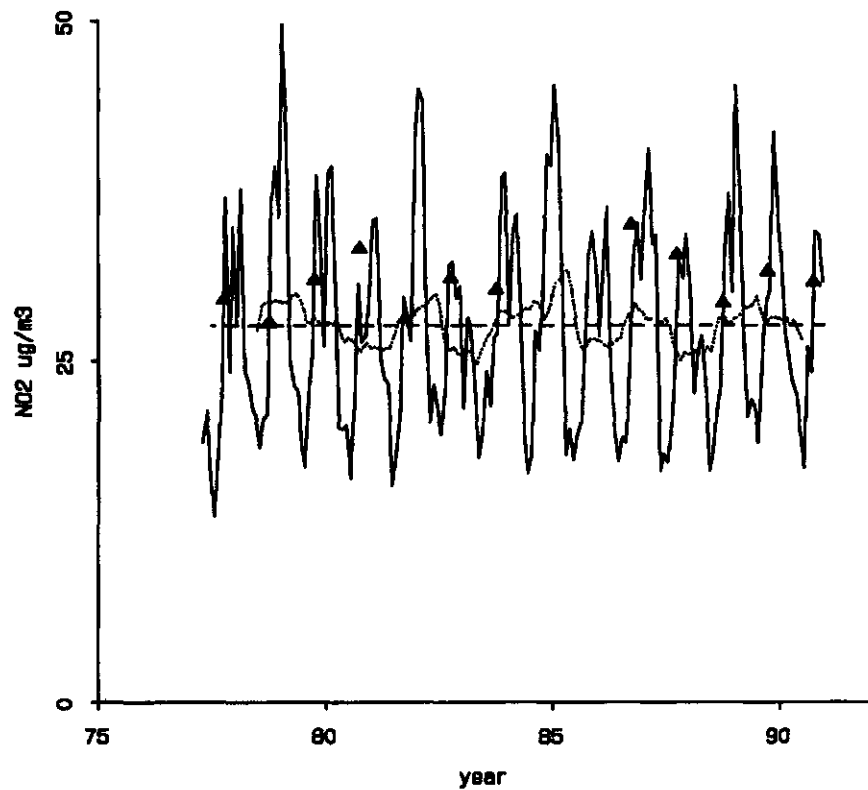


Fig. 7. NO_2 concentration (in $\mu\text{g.m}^{-3}$) as a function of time.

drawn line: monthly mean of concentrations at rural air quality monitoring stations

dotted line: 12-monthly running mean of concentrations at rural air quality monitoring stations

dashed line: overall mean of concentrations at rural air quality monitoring station

triangles: mean of interpolated concentrations at epiphyte monitoring stations.

The concentrations at the epiphyte stations are generally higher than the overall mean concentrations, and tend to increase over time. This difference is caused by a difference the geographical position between the air quality and the epiphyte monitoring stations.

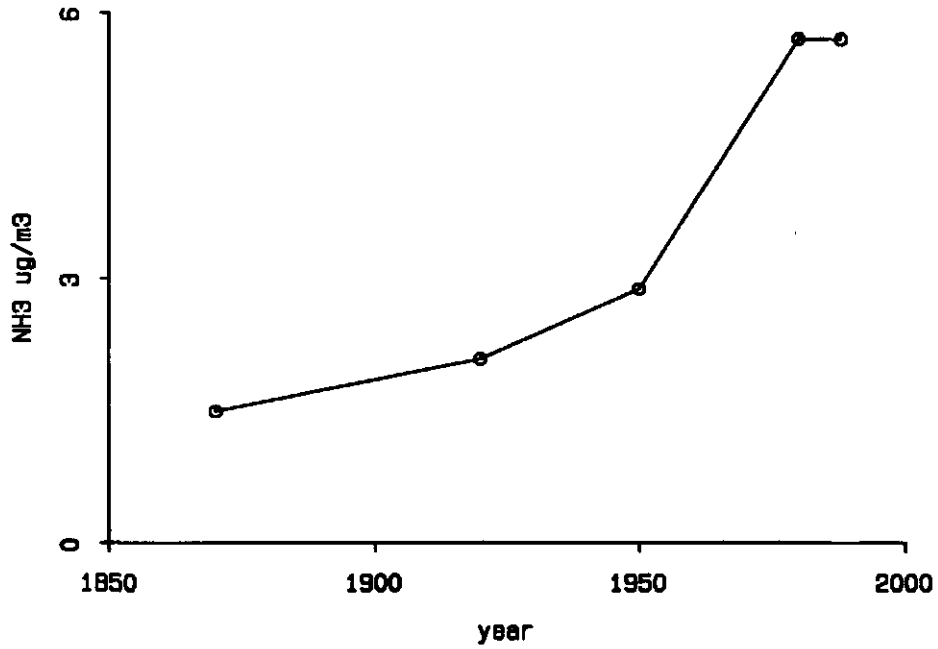


Fig. 8. *NH₃ concentration (in µg.m⁻³) as a function of time. Values for 1870-1980 are taken from Asman et al. (1987) as the mean value of the four EMEP squares that are (partly) located in The Netherlands, multiplied by a correction factor 1.58 (see text); the value for 1988 is the country-wide mean estimated by the TREND model (Asman & Van Jaarsveld 1990).*

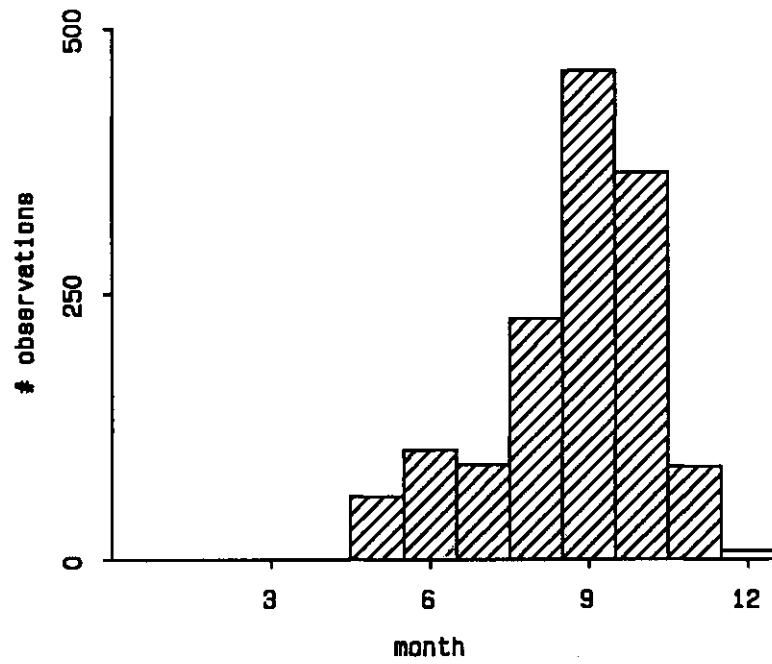


Fig. 9. Histogram of numbers of observations per month (cumulative over all years). Month number 1 = January, etc.

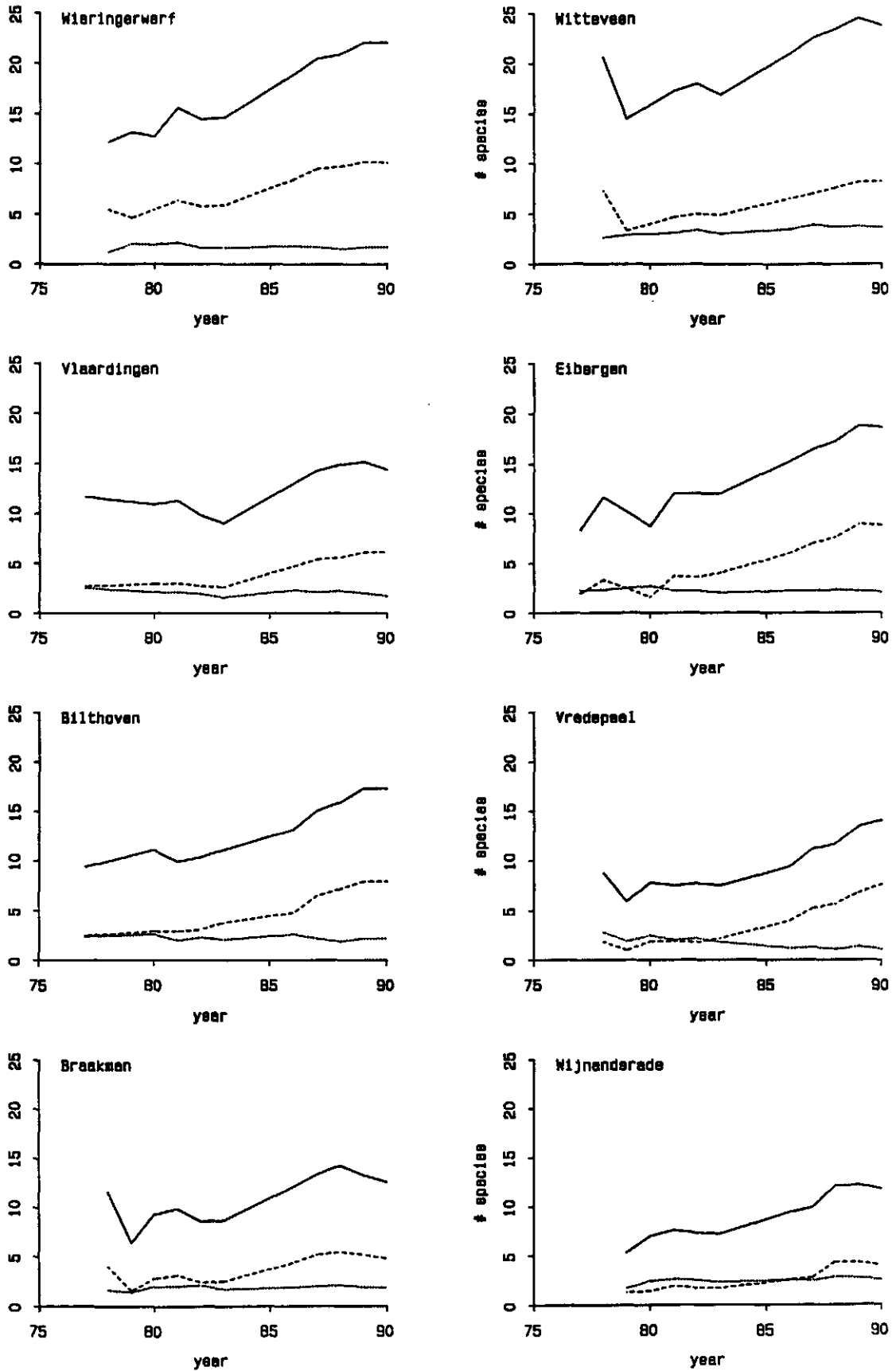


Fig. 10. Number of species per station, averaged per region, as a function of time. Solid line = all species, dashed line = nitrophytes, dotted line = acidophytes. Region/year combinations with less than five observations have been omitted. See Figure 1 for the location of the regions.

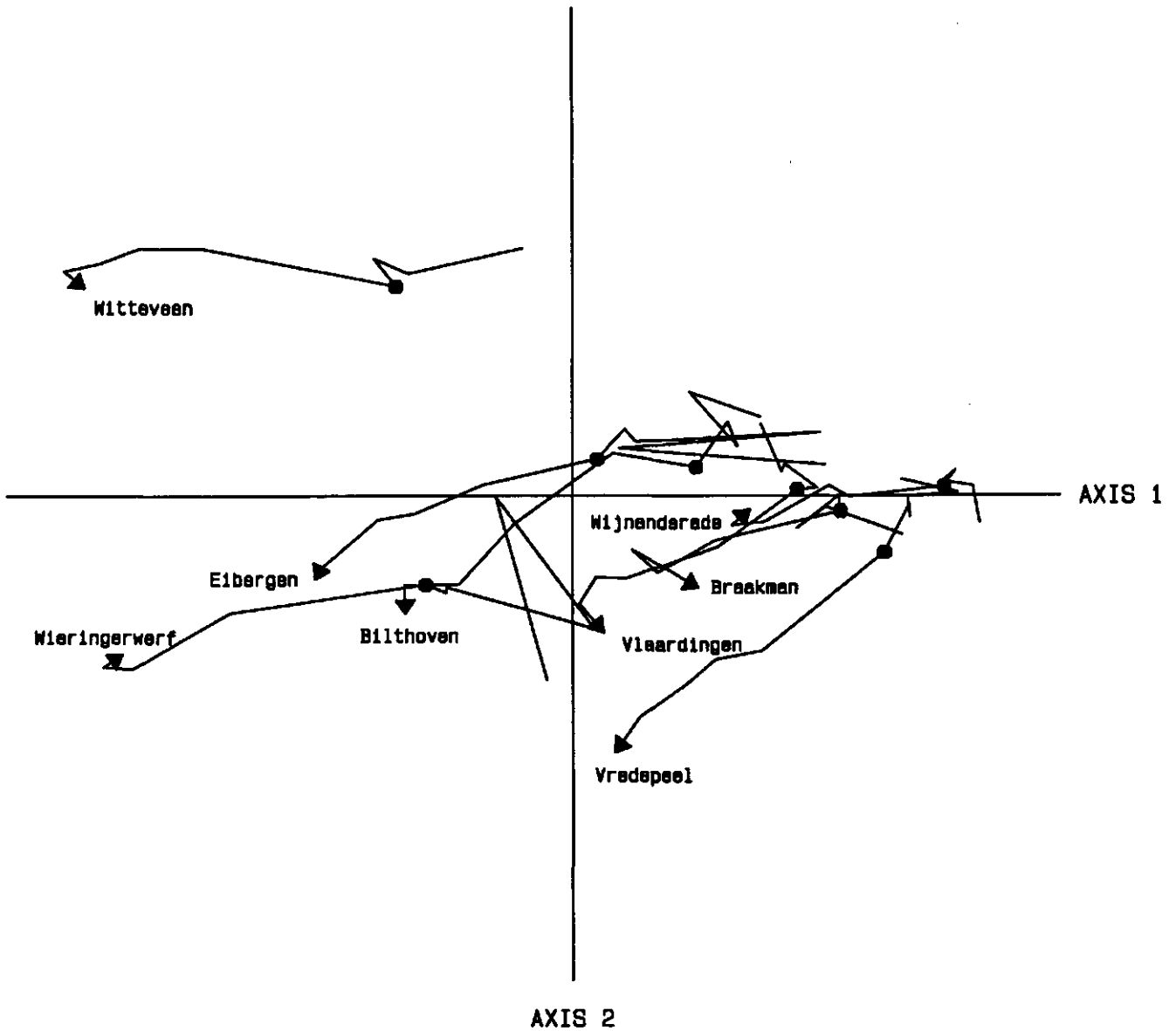


Fig. 11b. B: trajectories of sample scores through time (mean values for each region/year combination, combinations with less than five observations have been omitted). Base of arrow = first year with ≥ 5 stations (see Table 1), circle = 1983, head of arrow (triangle) = 1990. The species scores, sample scores and regression coefficients are plotted on different scales (sample scores = $2.3 \times$ species scores, regression coefficients and centroids for tree species = $4 \times$ species scores).

Appendix: list of species. abbr = abbreviated name (used in Figures and Tables), freq = frequency over all year/station combinations, eco = ecology: N = nitrophyte, A = acidophyte.

abbr	freq	eco	full name
aexili	0.1		<i>Arthonia exilis</i> (Flörke) Anzi
anacil	0.8	N	<i>Anaptychia ciliaria</i> (L.) Körber
aradia	0.6		<i>Arthonia radiata</i> (Pers.) Ach.
bacarn	0.1		<i>Bacidia arnoldiana</i> Körber
bacrub	0.4		<i>Bacidia rubella</i> (Hoffm.) Massal.
biapin	0.4		<i>Strangospora pinicola</i> (Massal.) Körber
bucane	6.6		<i>Diploicia canescens</i> (Dickson) Massal.
bugris	27.2		<i>Buellia griseovirens</i> (Turner ex Borrer) Almb.
bupunc	96.0		<i>Buellia punctata</i> (Hoffm.) Massal.
calivi	0.7		<i>Calicium viride</i> Pers.
caloci	0.9	N	<i>Caloplaca citrina</i> (Hoffm.) Th. Fr.
calolu	0.4	N	<i>Caloplaca luteoalba</i> (Turner) Th. Fr.
canaur	0.3	N	<i>Candelariella aurella</i> (Hoffm.) Zahlbr.
cancon	1.4		<i>Candelaria concolor</i> (Dickson) Stein
canref	9.5	N	<i>Candelariella reflexa</i> (Nyl.) Lettau
canvit	21.1	N	<i>Candelariella vitellina</i> (Hoffm.) Müll. Arg.
canxan	5.2	N	<i>Candelariella xanthostigma</i> (Ach.) Lettau
catgri	6.0		<i>Cliostomum griffithii</i> (Sm.) Coppins
cetchl	0.9	A	<i>Cetraria chlorophylla</i> (Willd.) Vainio
chaenf	1.5	A	<i>Chaenotheca ferruginea</i> (Turner ex Borrer) Migula
cspeci	8.1	A	<i>Cladonia spec.</i>
dimdil	0.6		<i>Dimerella pineti</i> (Schrader) Vezda
evepru	66.4	A	<i>Evernia prunastri</i> (L.) Ach.
haecoc	4.3		<i>Haematomma ochroleucum</i> (Necker) Laundon
hypphy	54.2	A	<i>Hypogymnia physodes</i> (L.) Nyl.
hyptub	1.8	A	<i>Hypogymnia tubulosa</i> (Schaerer) Havaas
laitem	0.6	A	<i>Lecanora aitema</i> (Ach.) Hepp
lcarpi	27.9	N	<i>Lecanora carpinea</i> (L.) Vainio
lchera	45.5	N	<i>Lecanora chlorotera</i> Nyl.
lchona	15.5	A	<i>Lecanora pulicaris</i> (Pers.) Ach.
lconde	61.5	A	<i>Lecanora conizaeoides</i> Nyl. ex Crombie
ldispe	21.1	N	<i>Lecanora dispersa</i> (Pers.) Sommerf.
lecacy	0.4	N	<i>Lecania cyrtella</i> (Ach.) Th. Fr.
lecide	37.0	N	<i>Lecidella elaeochroma</i> (Ach.) Hazsl.
lecsca	1.2	A	<i>Hypocenomyce scalaris</i> (Ach.) Choisy
lecsym	28.3		<i>Lecanora symmicta</i> (Ach.) Ach.
lepinc	43.2		<i>Lepraria incana</i> (L.) Ach.
lexpal	94.5		<i>Lecanora expallens</i> Ach.
llaevi	0.1		<i>Lecanora sienae</i> B. de Lesd.
micade	0.1	A	<i>Micarea denigrata</i> (Fr.) Hedl.
norpul	0.1		<i>Normandina pulchella</i> (Borrer) Nyl.
ochand	0.1	A	<i>Ochrolecia androgyna</i> (Hoffm.) Arnold
opatra	0.1		<i>Opegrapha atra</i> Pers.
opnive	0.1		<i>Opegrapha niveoatra</i> (Borrer) Laundon
opvari	0.7		<i>Opegrapha varia</i> Pers.
paceta	20.5		<i>Parmelia acetabulum</i> (Necker) Duby
pcaper	4.5		<i>Parmelia caperata</i> (L.) Ach.
pelega	0.1		<i>Parmelia elegantula</i> (Zahlbr.) Szat.
peralb	4.2		<i>Pertusaria albescens</i> (Huds.) Choisy & Werner
perama	2.1	A	<i>Pertusaria amara</i> (Ach.) Nyl.
percoc	0.9		<i>Pertusaria coccodes</i> (Ach.) Nyl.
pexasp	16.7		<i>Parmelia exasperatula</i> Nyl.
pglagl	0.7		<i>Parmelia glabrata</i> Nyl.
phadgl	0.3		<i>Hyperphyscia adglutinata</i> (Flörke) Mayrh. & Poelt
phadsc	33.1	N	<i>Physcia adscendens</i> (Fr.) H. Olivier
phaipo	0.2	N	<i>Physcia aipolia</i> (Ehrh. ex Humb.) Fűrnrrohr
phcaes	23.1	N	<i>Physcia caesia</i> (Hoffm.) Fűrnrrohr
phdubi	7.3	N	<i>Physcia dubia</i> (Hoffm.) Lettau
phentx	2.7		<i>Physconia enteroxantha</i> (Nyl.) Poelt
phgris	8.6		<i>Physconia grisea</i> (Lam.) Poelt
phlarg	7.0		<i>Phlyctis argena</i> (Sprengel) Flotow
phorbi	16.1	N	<i>Phaeophyscia orbicularis</i> (Necker) Moberg
phpulv	1.1		<i>Physconia distorta</i> (With.) Laundon
phstel	1.1	N	<i>Physcia stellaris</i> (L.) Nyl.
phtene	84.0	N	<i>Physcia tenella</i> (Scop.) DC.
placic	0.2	A	<i>Placynthiella icmalea</i> (Ach.) Coppins & P. James

placin	3.9		<i>Parmelia laciniatula</i> (Flagey ex. Oliv.) Zahlbr.
prevol	3.2		<i>Parmelia revoluta</i> Flörke
proque	1.6	A	<i>Pyrrhospora quernea</i> (Dickson) Körber
psaxat	3.2	A	<i>Parmelia saxatilis</i> (L.) Ach.
psefur	5.4	A	<i>Pseudevernia furfuracea</i> (L.) Zopf
psiluc	1.2		<i>Psilolechia lucida</i> (Ach.) M. Choisy
psubau	51.6		<i>Parmelia subaurifera</i> Nyl.
psubru	38.7		<i>Parmelia subrudecta</i> Nyl.
psulca	97.1		<i>Parmelia sulcata</i> Taylor
ptilia	1.4		<i>Parmelia tiliacea</i> (Hoffm.) Ach.
ramfar	62.3		<i>Ramalina farinacea</i> (L.) Ach.
ramfas	25.7		<i>Ramalina fastigiata</i> (Pers.) Ach.
ramfra	1.7		<i>Ramalina fraxinea</i> (L.) Ach.
rinexi	2.7	N	<i>Rinodina exigua</i> (Ach.) Gray
toncar	0.2	A	<i>Hypocenomyce caradocensis</i> (Leight. ex Nyl.) P. James & G. Schneider
tragra	0.4	A	<i>Trapeliopsis granulosa</i> (Hoffm.) H.T. Lumbsch
uspeci	2.2		<i>Usnea spec.</i> (probably <i>U. subfloridana</i> Stirton)
xaureo	0.6	N	<i>Xanthoria calcicola</i> Oxner
xcande	46.6	N	<i>Xanthoria candelaria</i> (L.) Th. Fr.
xparie	41.8	N	<i>Xanthoria parietina</i> (L.) Th. Fr.
xpolyc	76.4	N	<i>Xanthoria polycarpa</i> (Hoffm.) Rieber

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