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Effects of atmospheric chemistry and bark chemistry on epiphytic lichen vegetation in The Netherlands

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Contents

1.1 Abstract

Epiphytic lichen vegetation was recorded on 125 groups of wayside trees distributed over The Netherlands. From these trees bark samples were taken and analysed for SO_4, NO_3 and NH_4 content and pH. Concentrations of atmospheric SO_2, NO_2, NH_3 and NH_4 were obtained from the National Air Quality Monitoring Network. Statistical analysis was performed to determine the relation between (a) bark chemistry and atmospheric chemistry, and (b) bark chemistry, atmospheric chemistry and the abundance of the lichen species. Only a weak relation was found between bark SO_4, NO_3 and NH_4 and atmospheric chemistry, but there was a strong relation between bark pH and atmospheric SO_2 (acidifying) and NH_3 (alkalizing). According to their effect on the species the environmental variables could be divided into two groups: (1) those with a toxic effect causing a decrease in abundance of nearly all species (SO_2 and NO_2), and (2) those with an effect related to bark pH, causing a shift in the ratio between (presence or abundance of) acidophytic species and nitrophytic species (NH_3, SO_2, bark pH and tree species). There is an unexplained decrease in general species richness at greater distance from the coast. A good correspondence was found between the reaction of the species to measured bark pH and Wirth's (1991) scale of pH indicator values.

1.2 Samenvatting

Op 125 groepen vrijstaande wegbomen verspreid over Nederland werden opnamen gemaakt van de epifytische licheenvegetatie. Op dezelfde bomen werden schorsmonsters genomen, en geanalyseerd op SO_4-, NO_3- en NH_4-gehalte en pH. Atmosferische concentraties van SO_2, NO_2, NH_3 en NH_4 werden geschat op grond van gegevens uit het Landelijk Meetnet Luchtkwaliteit. Door middel van regressie-analyse werd de relatie vastgesteld tussen (a) schorschemie en atmosferische chemie, en (b) schorschemie, atmosferische chemie en abundantie van de soorten. Er is slechts een zwakke relatie tussen de gehalten aan SO_4, NO_3 en NH_4 in de schors en de atmosferische chemie, maar een sterke relatie tussen de schors-pH en atmosferisch SO_2 (verzurend) en NH_3 (alkali-

serend). De omgevingsvariabelen kunnen naar hun effect op de soorten in twee groepen ingedeeld worden: (1) die met een toxisch effect dat tot uiting komt in een negatieve relatie met de abundantie van bijna alle soorten (SO_2 en NO_2), en (2) die met een effect dat tot stand komt via de pH van de schors, dat tot uiting komt in de verhouding tussen de (presentie of abundantie van) de acidofytische en nitrofytische soorten (NH_3, SO_2, schors-pH en boomsoort). Er is een onverklaarde afname in algemene soortenrijkdom op grotere afstand van de kust. Er werd een goede overeenstemming gevonden tussen de reactie van de epifytische lichenen op de schors-pH en de pH-indicatorwaarde volgens Wirth (1991).

2 Introduction

Lichens are generally considered to be good indicators for air quality. Information on the pollutants involved and their working mechanisms is scarce, however. Most authors implicitly (e.g., Barkman 1958) or explicitly (e.g., De Wit 1976) state SO_2 as the main cause for the decline of lichens in polluted areas, but others claim an additional sensitivity to NO_2 (Van Dobben 1991), O_3 (Sigal & Nash 1983), NH_3 (De Bakker & Van Dobben 1988), fluoride (Nash 1971), heavy metals (Folkeson & Andersson-Bringmark 1988) or even air pollutants in general (Nylander 1866, Herzig et al. 1990).

The high concentrations of NH_3 occurring in The Netherlands (Asman & Van Jaarsveld 1990) give the opportunity to study the reaction of epiphytic lichens to this compound. De Bakker & Van Dobben (1988) found the responses to SO_2 and NH_3 to be more or less opposite. The 'pH-hypothesis', proposed by e.g. Johnson & Søchting (1973), Van Dobben (1983) and Gilbert (1986) explains the effect of air pollutants as the result of changes in the pH of tree bark, and provides a good explanation for the joint effects of SO_2 and NH_3 because the former acidifies and the latter alkalizes the bark. The antagonism between SO_2 and NH_3 was also shown by Van Dobben (1991) in a detailed study of the changes in the epiphytic vegetation in The Netherlands over a short period, which therefore supports the pH-hypothesis in an indirect way.

The present study was designed to find direct support for the pH-hypothesis. Detailed statistical analysis was used to describe the relation between bark chemistry and atmospheric chemistry, and the effects of both on epiphytic lichen vegetation. It was expected that, if the pH-hypothesis holds true, the bark pH is a sufficient predictor of epiphytic vegetation, and that atmospheric chemistry would not be needed as an additional predictor.

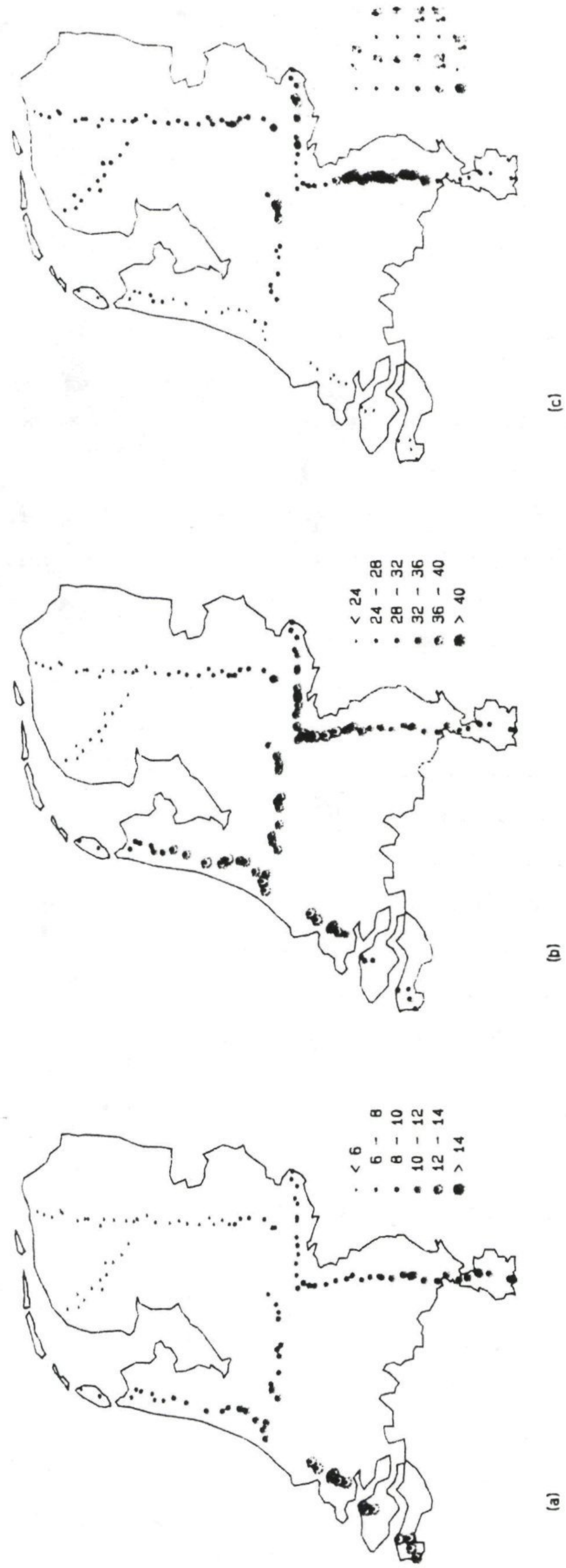
3 Material and methods

Sample points were selected on 125 representative groups of trees along a number of transects through The Netherlands (Figure 1). The mean distance between adjacent sample points was 5 km. A sample point consisted of 11 trees or less if not enough were available. The trees were selected to comply with strict criteria of uniformity. Only wayside trees were used, and very thick or very slender trees, slanting trees, trees that were shaded, and trees that were at the end of rows or bordering drives to farms etc. were excluded. Selected trees were preferably *Quercus robur* L. in areas with sandy soil, and *Populus x canadensis* Moench in areas with clayey soil, but if these species were not available *Salix alba* L. or *Ulmus x hollandica* Miller were used. Before the sampling a pilot study was carried out to determine the effect of sample height, exposition and season on bark chemistry. The effects of all these factors appeared to be relatively small except on one tree at the end of a row.

Most of the epiphyte data and bark samples were collected between August and October 1990. Bark samples were taken at c. 1.5 m above ground level at the side of the trunk that was richest in epiphytes (usually the southwestern side). Bark flakes c. 5 mm thick were cut off with a steel knife, preferably from spots that were free of epiphytes. If there were no such spots, the epiphytes were first carefully scraped off. Samples were collected from three adjacent trees in the middle of the rows that constituted the sample points. The samples were air-dried and stored in the dark until analysis. The abundance of the lichen species at the sample points was estimated in a six-point scale (see De Bakker 1989).

The samples were ground to a grain size of < 1 mm, and 10 ml aqua dist. was added to 0.5 g sample and vigorously shaken by hand. The samples were left over for 30 min, shaken again and centrifuged for 5 min at 4000 rpm. The clear fraction that was then formed was used for further analysis. pH was determined with a Philips PW 9422 pH meter and a Borion electrode, and NO_3, NH_4 and SO_4 were determined with a Skalar SA-40 autoanalyser. Arithmetic mean values for the three samples from each sample point were used in the data analysis.

FIGURE 1



Air pollution data were obtained from the Dutch National Air Quality Monitoring Network. Table 1 gives an overview of the variables that were used in the statistical analysis, together with their extreme and mean values and their sources. Mean concentrations of SO_2, NO_2 and NH_3 at the sample points are given in Figure 1. Multiple regression (carried out with the statistical package GENSTAT 5, Payne et al. 1987) was used to detect the relation between atmospheric chemistry and bark chemistry, and their effects on species numbers, and reduced rank regression (carried out with the program CANOCO 3.1, Ter Braak 1988) was used to detect their effects on the abundance of the individual species. For an easier interpretation (especially of the intercepts and interaction terms) all quantitative variables were centered to zero mean before data analysis. Bark NO_3 content, which had a very skew distribution, was logarithmized. The other explanatory variables were more or less normally distributed.

Table 1. Overview of the variables used for statistical analysis. Min, mean, max are the minimum, arithmetic mean and maximum value occurring in our data. Quadratic terms and interactions are not in this table, and are indicated in the regression models as (variable name)^2 and (variable name 1).(variable name 2), respectively.

name	min	mean	max	source
#spec	4	18	33	total number of species and numbers of nitrophytic and acidophytic species. assignment of species to ecological groups as in Van Dobben (1991) on the basis of literature data: Barkman (1958), Wirth (1980), Brand et al. (1988).
#nitro	0	6	14	
#acido	0	2	10	
aSO2	5	8	15	atmospheric concentrations in $\mu g.m^{-3}$. SO_2, NO_2 and O_3 were estimated from means of hourly measured concentrations (SO_2 April through September 1989, NO_2 and O_3 June 1989 through May 1990) at monitoring stations (Anonymus 1990), followed by interpolation (Van Egmond et al. 1978) of the concentrations at the sample points; NH_3 and NH_4 were estimated from 1988 emission data using the atmospheric transport and deposition model TREND (Asman & Van Jaarsveld 1990).
aNO2	20	31	42	
aO3	41	47	54	
aNH3	1	7	20	
aNH4	2	5	7	
bSO4	6	26	92	measured water extractable fraction of SO_4, NO_3 and NH_4 in bark, in ppm. (bNO3 had a very skew distribution and was logarithmized)
bNO3	0.3	1.8	7.5	
bNH4	4	18	54	
pH	3.8	4.7	5.4	bark pH measured in water extract
qu	0	0.52	1	dummy variabeles for tree species: Quercus, Populus, Salix, Ulmus (1 for samples from this tree, else 0). In backward selection one of the dummy variables is collinear, hence qu is omitted (i.e., used as a reference tree)
po	0	0.35	1	
sa	0	0.04	1	
ul	0	0.08	1	
#trees	1	10	11	number of trees at sample point
coast	1	65	147	distance to the coast (nearest salt water basin, so excluding IJsselmeer but including Oosterschelde), in km
circumf.	74	151	249	circumference of the thickest tree in cm

X, Y geogr coord (A'foord grid)

HEAD 1 if samp was on headed tree, else 0

Table 2. List of species. Abbr = abbreviated name (used in the tables and biplots), freq = frequency on sample points in %, eco: A = acidophytic species, N = nitrophytic species. Nomenclature follows Brand et al. (1988). The table gives the species that occurred in more than 10% of the samples.

abbr	freq	eco	name
bupunc	98.4		Buellia punctata (Hoffm.)Massal.
lexpal	98.4		Lecanora expallens Ach.
psulca	96.0		Parmelia sulcata Taylor
phtene	93.6	N	Physcia tenella (Scop.)DC.
xpolyc	86.4	N	Xanthoria polycarpa (Hoffm.)Rieber
ramfar	75.2		Ramalina farinacea (L.)Ach.
xparie	72.8	N	Xanthoria parietina (L.)Th.Fr.
psubau	70.4		Parmelia subaurifera Nyl.
phadsc	67.2	N	Physcia adscendens (Fr.)H.Olivier
xcande	65.6	N	Xanthoria candelaria (L.)Th.Fr.
evepru	63.2	A	Evernia prunastri (L.)Ach.
lecide	60.0		Lecidella elaeochroma (Ach.)Hazsl.
lchera	54.4		Lecanora chlarotera Nyl.
lepinc	52.0		Lepraria incana (L.)Ach.
lconde	51.2	A	Lecanora conizaeoides Nyl.ex Crombie
psubru	49.6		Parmelia subrudecta Nyl.
hypphy	47.2	A	Hypogymnia physodes (L.)Nyl.
bugris	42.4		Buellia griseovirens (Turner ex Borrer)Almb.
phorbi	42.4	N	Phaeophyscia orbicularis (Necker)Moberg
phcaes	39.2	N	Physcia caesia (Hofm.)Fürnrohr
lecsym	38.4		Lecanora symmicta (Ach.)Ach.
canvit	37.6	N	Candelariella vitellina (Hoffm.)Müll.Arg.
ldispe	37.6	N	Lecanora dispersa (Pers.)Sommerf.
lcarpi	34.4		Lecanora carpinea (L.)Vainio
ramfas	33.6		Ramalina fastigiata (Pers.)Ach.
lchona	26.4	A	Lecanora pulicaris (Pers.)Ach.
canref	25.6	N	Candelariella reflexa (Nyl.)Lettau
pexasp	24.0		Parmelia exasperatula Nyl.
paceta	24.8		Parmelia acetabulum (Necker)Duby
cspeci	15.2		Cladonia spec.
canxan	15.2	N	Candelariella xanthostigma (Ach.)Lettau
phdubi	15.2	N	Physcia dubia (Hoffm.)Lettau
phgris	11.2	N	Physconia grisea (Lam.)Poelt

Less frequent species (in order of decreasing frequency, eco in parentheses):
Parmelia caperata (L.)Ach., Cliostomum griffithii (Sm.)Coppins, Phlyctis argena (Sprengel)Flotow, Physconia enteroxantha (Nyl.)Poelt (N), Diploicia canescens (Dickson)Massal., Parmelia laciniatula (Flagey ex.Oliv.)Zahlbr., Pertusaria albescens (Huds.)Choisy & Werner, Parmelia saxatilis (L.)Ach. (A), Parmelia revoluta Flörke, Pyrrhospora quernea (Dickson)Körber (A), Psilolechia lucida (Ach.)M.Choisy, Rinodina exigua (Ach.)Gray (N), Pseudevernia furfuracea (L.)Zopf (A), Ramalina fraxinea (L.)Ach., Caloplaca citrina (Hoffm.)Th.Fr. (N), Usnea spec. (probably U. subfloridana Stirton), Candelaria concolor (Dickson)Stein (N), Haematomma ochroleucum (Necker)Laundon, Physconia distorta (With.)Laundon (N), Hypocenomyce scalaris (Ach.)Choisy (A), Hypogymnia tubulosa (Schaerer)Haraas (A), Physcia stellaris (L.)Nyl. (N), Hypocenomyce caradocensis (Leight.ex Nyl.)P.James & G.Schneider (A), Pertusaria coccodes (Ach.)Nyl. (A), Lecania cyrtella (Ach.)Th.Fr., Arthonia radiata (Pers.)Ach., Candelariella aurella (Hoffm.)Zahlbr. (N), Caloplaca luteoalba (Turner)Th.Fr. (N), Pertusaria amara (Ach.)Nyl. (A), Opegrapha niveoatra (Borrer)Laundon, Dimerella pineti (Schrader)Vezda, Cetraria chlorophylla (Willd.)Vainio, Bacidia arnoldiana Körber, Hyperphyscia adglutinata (Flörke)Mayrh.& Poelt (N), Parmelia tiliacea (Hoffm.)Ach., Chaenotheca ferruginea (Turner ex Borrer)Migula (A), Placynthiella icmalea (Ach.)Coppins & P.James (A), Parmelia glabratula Nyl., Ochrolecia androgyna (Hoffm.)Arnold (A).

4 Results

Table 1 gives an overview of the explanatory variables, together with their mean and extreme values and the symbols used to refer to them. Table 2 gives a list of the most common species and their frequencies. Table 3 gives the matrix of correlation coefficients of all variables. Very strong correlations (|r|>0.8) were found between NO_2 and O_3, between atmospheric NH_4 and NH_3 and between atmospheric NH_4 and distance to the coast. As the effects of strongly correlated variables cannot be separated by regression, O_3 and atmospheric NH_4 were not used as explanatory variables. Other strong correlations exist between oak and distance to the coast (r=0.7), between oak and NH_3 (r=0.6), between NH_3 and distance to the coast (r=0.7), and between SO_2 and NO_2 (r=0.6). The other correlations between explanatory variables had absolute r-values below 0.5.

Table 3. Correlation coefficients between total number of species, numbers of nitrophytic and acidophytic species, bark and atmospheric chemistry, distance to the the coast, stem circumference, number of trees and tree species (n=125).

	#spec	nitro	acido	bSO4	bNO3	bNH4	pH	aSO2	aNO2	aO3	aNH3	aNH4	coast	circ.	#trees
# nitro	0.71														
# acido	0.26	-0.27													
bark SO4	-0.10	0.01	-0.12												
bark NO3	0.07	0.13	-0.09	-0.08											
bark NH4	0.06	0.01	0.08	0.00	0.14										
bark pH	0.39	0.48	-0.22	-0.12	0.23	0.26									
atm SO2	-0.64	-0.36	-0.22	0.15	-0.19	0.06	-0.38								
atm NO2	-0.59	-0.13	-0.36	0.09	0.17	0.09	-0.14	0.60							
atm O3	0.46	0.12	0.17	-0.06	-0.28	-0.15	0.06	-0.31	-0.87						
atm NH3	0.01	0.20	-0.18	-0.04	0.20	0.35	0.48	-0.14	0.17	-0.28					
atm NH4	-0.16	0.03	-0.07	-0.06	0.23	0.41	0.41	-0.04	0.26	-0.38	0.85				
dist coast	-0.13	0.01	-0.02	-0.06	0.30	0.35	0.35	-0.12	0.17	-0.34	0.69	0.93			
circumf.	0.09	0.08	0.08	0.08	0.10	0.02	-0.05	0.01	0.08	-0.08	-0.25	-0.25	-0.29		
# trees	-0.04	0.02	0.11	-0.01	-0.20	-0.01	-0.06	0.21	0.15	-0.09	0.04	0.06	0.03	-0.16	
qu	-0.04	-0.20	0.27	-0.05	0.09	0.32	0.23	-0.23	-0.09	-0.18	0.62	0.70	0.71	-0.32	-0.05
po	-0.11	0.07	-0.16	-0.05	-0.17	-0.25	-0.23	0.33	0.18	0.03	-0.47	-0.47	-0.50	0.20	0.21
sa	-0.19	-0.20	-0.14	0.22	0.08	-0.04	-0.24	0.06	0.13	-0.07	-0.13	-0.16	-0.15	0.18	-0.21
ul	0.40	0.38	-0.12	0.01	0.08	-0.13	0.16	-0.20	-0.25	0.33	-0.21	-0.35	-0.31	0.10	-0.12

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Table 4. Regression coefficients for the regression of bark SO4, NO3, NH4 and pH on atmospheric chemistry, distance to the coast, tree circumference and tree species (minimal model, see text). See Table 1 for an explanation of the variables. Qu was used as a reference tree, and all quantitative variables were centered to mean zero (bNO3 after taking its logarithm). The intercept is therefore the expected value on oak at mean value of all explanatory variables. Quadratic terms were tested for all quantitative valiables, and the interactions coast.aSO2 and aSO2.aNH3. R^2_{adj} = percentage variance accounted for. Significance: *** = $p \leq 0.001$; ** = $0.001 < p \leq 0.01$; * = $0.01 < p \leq 0.05$; ns = not significant (n=125).

term	regression coefficients			
	bark SO4	bark NO3	bark NH4	bark pH
intercept	-0.640 ns	0.883 ***	2.15 **	-0.123 **
aSO2		-0.049 ***	0.706 **	-0.0520 ***
aNO2		0.019 ***		
aNH3			1.12 ***	0.0377 ***
aNH3^2			-0.098 ***	
coast		0.0014 *		0.00195 *
coast.aSO2				-0.000621 **
po				0.206 **
sa	16.05 *			
ul				0.493 ***
R^2_{adj}	4	18	21	43

4.1 Relation between atmospheric chemistry and bark chemistry

Table 4 summarizes the relation between bark chemistry and atmospheric chemistry. The multiple regression models given in the table were derived by backward selection, starting with a model containing terms for atmospheric concentrations, distance to the coast, tree species and circumference, quadratic terms for all quantitative variables, and the interactions aSO2.aNH3 and aSO2.coast. From this model the least significant terms were subsequently dropped (starting with the interactions and quadratic terms, then the main effects) until only terms remained that contributed significantly at $p \leq 0.05$. $p < 0.001$

Bark SO_4 content is not significantly related to any of the measured atmospheric variables, although the relation with SO_2 is close to significance ($p \simeq 0.1$). Only tree species has a significant effect, the SO_4 content of *Salix* bark being c. 50% higher compared to the other tree species. The other bark chemical factors are significantly related to atmospheric chemistry. NO_3 content is significantly positively related to atmospheric NO_2, negatively to atmospheric SO_2, and positively to distance to the coast. As SO_2 and NO_2 are rather strongly correlated their single effects cannot simply be derived from the regression model. Moreover, the regression coefficients suggest a stronger effect of distance to the coast than of SO_2 and NO_2. Bark NH_4 content is significantly positively related to atmospheric SO_2 and NH_3, although the effect of NH_3 levels off at high concentrations (expected maximum effect at c. 13 $\mu g.m^{-3}$).

Bark pH significantly increases with increasing atmospheric NH_3 concentration and at greater distances from the coast, and decreases with increasing SO_2 concentration. These is also a significant difference between the tree species: the pH of *Populus* bark is c. 0.3 and the pH of *Ulmus* bark is c. 0.6 units higher than the pH of *Quercus* bark. Furthermore, there is a significant interaction between distance to the coast and SO_2 concentration. The regression coefficients show that the effect of SO_2 on bark pH decreases near the coast, but remains negative. On the other hand, the effect of distance to the coast becomes negative (i.e., the expected pH decreases at greater distance from the coast) at high SO_2 concentrations (above c. 11 $\mu g.m^{-3}$). NO_2 does not have a significant effect on bark pH.

There is no easy interpretation for the effect of distance to the coast. On the one hand, sea-spray, which has a relatively high pH might cause an increase in bark pH (or a neutralization of acidifying components) near the coast. This might explain the interaction between SO_2 and distance to the coast. On the other hand, distance to the coast is rather strongly correlated with atmospheric NH_3 concentration, and therefore its modelled effect might in fact be a non-linear effect of atmospheric NH_3. This might explain its positive main effect on bark pH, and possibly also its positive effect on bark NO_3. In the latter case nitrification of NH_4 to NO_3 would take place, despite the generally low bark pH. However, De Boer (1989) showed that in soil nitrification can still take place at pH values below 4. If nitrification takes place, the bark NO_3 content is expected to be positively related with NH_4 content and pH or their interaction.

There is indeed a significant positive correlation between pH and bark NO_3 content (r=0.25, p≈0.01), but the correlation between bark NO_3 and bark NH_4 is not significant, and neither is the interaction pH.bNH4. Bark NO_3 has a very skew distribution (even after taking the logarithm) and results with respect to this component should be viewed with caution. Definitive conclusions on the occurrence of nitrification on bark are therefore not possible and may require more specific measurements.

4.2 Relation between atmospheric chemistry, bark chemistry and numbers of species

The explanatory variables were divided into four groups related to sample size (number and circumference of trees at a sample point), tree species, bark chemistry and atmospheric chemistry (Table 5). The effects on the total number of species and the numbers of nitrophytes and acidophytes were calculated for the variables from each single group, and for all variables together. In both cases minimal models were derived using the backward selection procedure described in 4.1. Table 5 shows that atmospheric chemistry is generally the most important explanatory variable. Bark chemistry alone is a reasonable predictor for the total number of species and the number of nitrophytic species (15 and 23% variance accounted for, respectively), but if also tree species and atmospheric chemistry are taken into account the extra fit due to bark chemistry is low (5 and 3%, respectively). Also the extra fit due to tree species is generally low, except in the case of nitrophytes (24% variance accounted for).

Table 5. Selection of variables affecting total number of species and numbers of nitrophytic and acidophytic species. The variables have been grouped according to sample size, tree species, bark chemistry and atmospheric chemistry. Qu was used as a reference tree, and all quantitative variables were centered to mean zero (bNO3 after taking its logarithm). The intercept is therefore the expected value on oak at mean value of all explanatory variables. Quadratic terms were tested for all quantitative variables, but the interactions were not. Fitted models are minimal models containing only terms that contribute significantly. The first two columns relate to models with terms from only one group, the last two columns relate to a model with terms from all groups ('final model'). In the latter case the intercept given for the first group relates to the final model and the percentage variance is the loss of explained variance on dropping the terms from one group. Significance: *** = $p \leq 0.001$; ** = $0.001 < p \leq 0.01$; * = $0.01 < p \leq 0.05$; ns = not significant (n=125).
(see next page)

group term	ONE GROUP regr. coef.	ONE GROUP var. expl.	ALL GROUPS regr. coef.	ALL GROUPS var. expl.
	TOTAL NUMBER OF SPECIES			
tree sp.		18		9
intercept	-0.528 ns		-1.59 **	
Populus			2.98 ***	
Salix	-5.46 *			
Ulmus	9.34 ***		6.78 ***	
bark chem.		15		5
intercept	0.00 ns			
pH	7.12 ***		2.60 *	
bNH4			0.145 *	
atm. chem.		49		34
intercept	0.000 ns			
aSO2	-1.064 ***		-0.931 ***	
aNO2	-0.255 **		-0.279 ***	
coast	-0.019 *			
final model				59
	NUMBER OF NITROPHYTIC SPECIES			
tree sp.		16		24
intercept	-0.237 ns		-1.667 ***	
Poplulus			3.44 ***	
Salix	-2.89 *			
Ulmus	4.41 ***		5.72 ***	
bark chem.		23		3
intercept	0.00 ns			
pH	4.37 ***		2.04 **	
atm. chem.		21		12
intercept	-1.291 *			
aSO2	-0.463 ***		-0.306 ***	
aNH3	0.276 ***		0.271 ***	
coast	-0.0238 **			
coast^2	0.00056 **			
final model				49
	NUMBER OF ACIDOPHYTIC SPECIES			
sample size		0		6
intercept			1.291 ***.	
# trees			0.164 **	
circumf.			1.37 **	
tree sp.		6		6
intercept	0.389 *			
Poplulus	-0.712 *		-1.28 ***	
Salix	-1.421 *		-1.81 **	
Ulmus	-1.021 *		-1.57 **	
bark chem.		4		3
intercept	0.000 ns			
pH	-0.928 *		-1.06 **	
atm. chem.		28		26
intercept	0.878 ***			
aNO2	-0.061 ***		-0.070 ***	
aNH3	-0.133 ***		-0.117 ***	
coast	0.012 ***		0.0043 ns	
coast^2	-0.00038 ***		-0.00028 ***	
final model				46

Table 6. Effect of the interaction terms (tree species).(bark chemistry), (tree species).(atmospheric chemistry), (tree species. circumference) and (bark pH).(atmospheric chemistry). The effect was tested by adding single terms to the final models given in Table 5. No significant interaction effects were found for the number of nitrophytic species. Significance: *** = $p \leq 0.001$; ** = $0.001 < p \leq 0.01$; * = $0.01 < p \leq 0.05$.

interaction term	sign of regr. coef.	extra variance accounted for	significance
		TOTAL NUMBER OF SPECIES	
qu.aSO2	-	2	**
qu.aNO2	-	1	*
qu.pH	+	1	*
		NUMBER OF ACIDOPHYTIC SPECIES	
qu.aNO2	-	2	*
qu.coast	-	3	*
pH.aNO2	+	3	**
pH.aSO2 [1]	+	5	***

[1]) after fitting the non-significant term aSO2.

Of the atmospheric variables both SO_2 and NO_2 have a significant negative effect on the total number of species. The number of nitrophytes is significantly negatively correlated with SO_2, the number of acidophytes with NO_2. NH_3 has no significant effect on the total number of species, but a positive effect on the number of nitrophytes and a negative effect on the number of acidophytes. In all models the atmospheric chemistry accounts for the highest percentage variance compared to the other groups. The prediction of the total number of species by atmospheric chemistry alone is quite good (49% variance accounted for) and can only slightly be improved by also taking tree species and bark chemistry into account (10% extra fit).

Of the bark chemical factors SO_4 and NO_3 content do not have any significant effect on numbers of species, while NH_4 content has a significant positive effect on the total number of species (although only if atmospheric chemistry and tree species are also taken into account). Significant effects of bark pH occur in all models, with a positive effect on the total number of species and the number of nitrophytes, and a negative effect on the number of acidophytes.

The numbers of both nitrophytic and acidophytic species have a non-linear relation with distance to the coast. The number of nitrophytes decreases on going inland and reaches a minimum at 86 km from the coast, while the number of acidophytes increases to reach a maximum at 81 km from the coast. For both groups the strongest effect is found close to the coast (+4 nitrophytic species and -2 acidophytic species). The total number of species linearly decreases with distance to the coast.

The effects of the interaction terms (tree species).(bark chemistry), (tree species).(atmospheric chemistry), (tree species).(circumference) and (bark pH).(atmospheric chemistry) were tested by adding single terms to the final models in Table 5. Significant effects were found for the total number of species and the the number of acidophytes, with a low extra fit (1-5%) (Table 6). The effects of SO_2, NO_2 and pH on the total number of species are stronger on oak, the effect of distance to the coast on the acidophytes is less on oak, and the effects of SO_2 and NO_2 on the acidophytes are less on oak.

4.3 Relation between atmospheric chemistry, bark chemistry and species abundance

Reduced-rank regression (Davies & Tso 1982, Ter Braak & Looman 1991) was used to describe the effects of the environmental variables on the abundance of the individual species. This technique is a form of principal component analysis in which the axes are restricted to linear combinations of environmental variables. It is therefore also a form of multiple regression. A more elaborate description of the technique and its application to epiphyte data is found in Van Dobben (1991). Reduced rank regression models were derived by forward selection, i.e. stepwise inclusion of the terms that result in the largest increase of fit, using the terms for the main effects as in the previous section, and the following interaction terms (groups of variables defined as in the previous section): aSO2.aNH3, qu.(atmospheric chemistry), qu.(bark chemistry), pH.(atmospheric chemistry) and pH.circumference. Significance of the observed effects was tested by random permutation of the residuals (Ter Braak 1992). The results are presented in the form of biplots; for their interpretation, see Jongman et al. (1987: pp. 127-129), Ter Braak & Looman (1991) or Van Dobben (1991).

Table 7a gives the fit of single variables, Tables 7b-7g give the fit of multiple regression models derived by selecting variables in different orders. The order of selection has no strong effect on the final model. The total percentage variance accounted for is c. 45%, of which c. 20% is accounted for by atmospheric chemistry, c. 8% by bark chemistry and c. 8% by tree species. The contribution of the interaction terms is c. 9%, the interactions between oak and atmospheric chemistry being the most important ones.

Figures 2 and 3 are biplots that graphically approximate the relation between the species and the explanatory variables. Figure 2 approximates the correlation coefficients of the single terms that have a significant effect (Table 7a). Figure 3 approximates the regression coefficients of the terms from Table 7b, after the elimination of terms with weakly significant canonical coefficients on the first two axes. Since no formal significance test exists for canonical coefficients an arbitrary criterion of $|t| < 2.5$ was used to reject a term.

Both the limited shift in the arrows for the explanatory variables in Figure 3 compared to Figure 2, and the independence of the final models in Table 7 of the order of selection show that the influence of multicollinearity among the explanatory variables is small. On the basis of their positions in Figures 2 or 3 the species can be divided into four groups with corresponding reactions to the environmental variables: (1) *Lecanora conizaeoides* (positively related to aSO2 and aNO2), (2) the other acidophytic species plus *Buellia griseovirens* and *Lepraria incana* (negatively related to aSO2, aNO2, aNH3 and pH, positively to qu) (3) the nitrophytic species plus *Lecidella elaeochroma* and *Buellia punctata* (negatively related to aSO2 and qu, positively to aNH3 and pH and (4) all other species (negatively related to aSO2 and aNO2, no strong relation with the other variables). The positions of the interaction arrows in Figure 3 show that at high SO_2 concentrations the effect of NH_3 is less, and the difference between oak and the other tree species is smaller.

Table 7. Forward selection of variables in reduced-rank regression. The variables have been divided into three groups, related to atmospheric chemistry (including distance to the coast), bark chemistry, and tree species (including stem circumference). In addition the following interactions were tested: aSO2.aNH3, qu.(atmospheric chemistry), qu.(bark chemistry), pH.(atmospheric chemistry) and pH.circumference. Table 7a gives the fit (percentage variance accounted for) of single variables (excluding interactions), the other tables relate to multiple regression models. Selections have been carried out without (7b) and with (7c-7g) restriction. In the latter case variables from each group were selected until none of the remaining variables in this group could improve the fit significantly. In some cases a variable could improve the fit significantly after the inclusion of terms from the next group; these are given in parentheses. The extra fit is determined by including a term in a model containing the terms listed above this term. Its contribution to the fit of the final model may be lower, or even not significant. Differences in the cumulative fit and the sum of the extra fit and the cumulative fit in the preceding row are due to rounding errors. Significance (determined after 199 permutations): ** = $p \leq 0.01$; * = $0.01 < p \leq 0.05$; ? = $0.05 < p < 0.1$ (only given if terms with $p < 0.05$ could be added after this term); ns = $p > 0.05$ (n=125)

7a	extra fit	sign.
<u>single variables</u>		
aSO2	16	**
aNO2	15	**
pH	8	**
ul	6	**
coast	3	**
qu	3	**
aNH3	3	**
po	3	*
sa	1	ns
bSO4	1	ns
circumf.	1	ns
bNH4	1	ns
bNO3	1	ns

(continued next page)

7b	extra fit	cumul. fit	sign.
no restriction			
aSO2	16	16	**
aNO2	5	21	**
pH	4	25	**
qu	5	30	**
qu.aNO2	3	32	**
ul	2	35	**
coast	2	37	**
qu.coast	2	38	**
qu.aSO2	1	39	**
bNH4	1	41	*
aNH3	1	42	*
aSO2.aNH3	1	43	**
circumf.	1	44	*
pH.aNO2	1	45	*
pH.coast	1	46	?
qu.pH	1	47	**

7c	extra fit	cumul. fit	sign.
atmospheric chemistry			
aSO2	16	16	**
aNO2	5	21	**
coast	3	24	**
aNH3	2	25	**
aSO2.aNH3	2	28	**
tree species			
qu	5	33	**
ul	3	35	**
qu.aNO2	2	37	**
qu.coast	2	39	**
po	1	40	*
bark chemistry			
pH	2	42	**
bNH4	1	43	**
(circumf.	1	44	*)
pH.aSO2	1	45	*

7d	extra fit	cumul. fit	sign.
atmospheric chemistry			
aSO2	16	16	**
aNO2	5	21	**
coast	3	24	**
aNH3	2	25	**
aSO2.aNH3	2	28	**
bark chemistry			
pH	4	31	**
bNH4	1	33	*
pH.aSO2	1	34	*
tree species			
qu	4	38	**
qu.aNO2	2	40	**
ul	2	42	**
qu.coast	2	43	**
circumf.	1	44	*

7e	extra fit	cumul. fit	sign.
tree species			
ul	6	6	**
qu	3	9	**
circumf.	1	10	*
bark chemistry			
pH	7	17	**
atmospheric chemistry			
aNO2	13	30	**
aSO2	3	33	**
coast	2	35	**
qu.aNO2	2	37	**
qu.coast	2	39	**
(bNH4	1	40	**)
qu.aSO2	1	42	**
aNH3	1	43	**
aSO2.aNH3	1	44	**
pH.aNO2	1	45	*
pH.coast	1	46	?
(qu.pH	1	47	**)

7f	extra fit	cumul. fit	sign.
bark chemistry			
pH	8	8	**
tree species			
ul	5	13	**
qu	3	16	**
circumf.	1	17	*
atmospheric chemistry			
aNO2	13	30	**
aSO2	3	33	**
coast	2	35	**
qu.aNO2	2	37	**
qu.coast	2	39	**
(bNH4	1	40	**)
qu.aSO2	1	42	**
aNH3	1	43	**
aSO2.aNH3	1	44	**
pH.aNO2	1	45	*
pH.coast	1	46	?
(qu.pH	1	47	**)

7g	extra fit	cumul. fit	sign.
tree species			
ul	6	6	**
qu	3	9	**
circumf.	1	10	**
atmospheric chemistry			
aSO2	13	24	**
aNO2	5	29	**
aNH3	4	33	**
aSO2.aNH3	2	35	**
qu.aSO2	2	37	**
coast	2	38	**
qu.coast	1	40	**
(po	1	41	*)
bark chemistry			
pH	2	43	**
bNH4	1	44	**
(qu.aNO2	1	45	*)
pH.aSO2	1	46	*

FIGURE 2

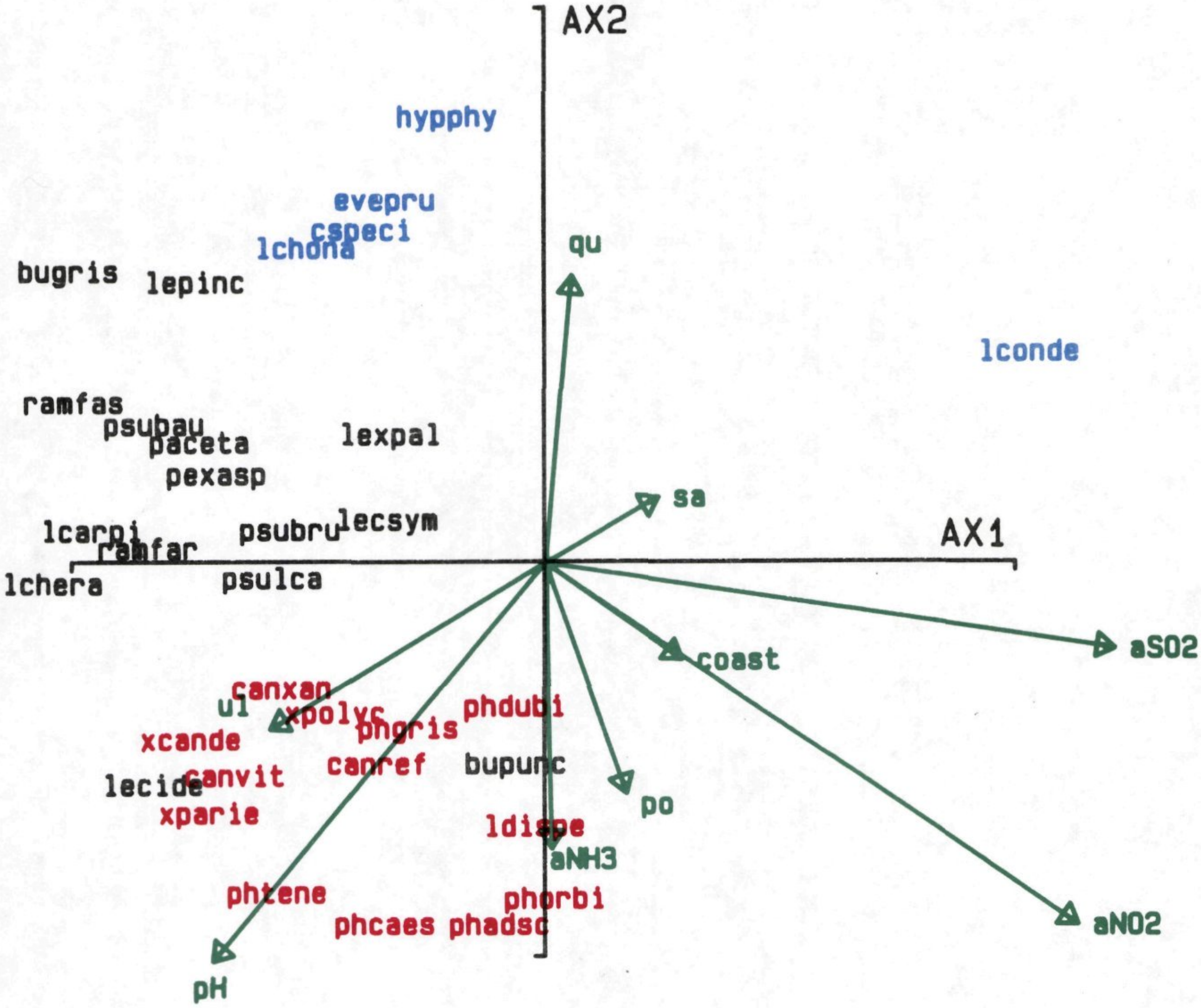

AX2
hypphy
evepru
cspeci
lchona
qu
bugris
lepinc
lconde
ramfas
psubau
paceta
lexpal
pexasp
sa
lecsym
lcarpi
psubru
ramfar
AX1
lchera
psulca
aSO2
coast
canxan
ul
xpolyc
phdubi
phgris
xcande
canref
bupunc
lecide
canvit
xparie
po
ldispe
aNH3
phtene
phorbi
phcaes
phadsc
aNO2
pH

FIGURE 3

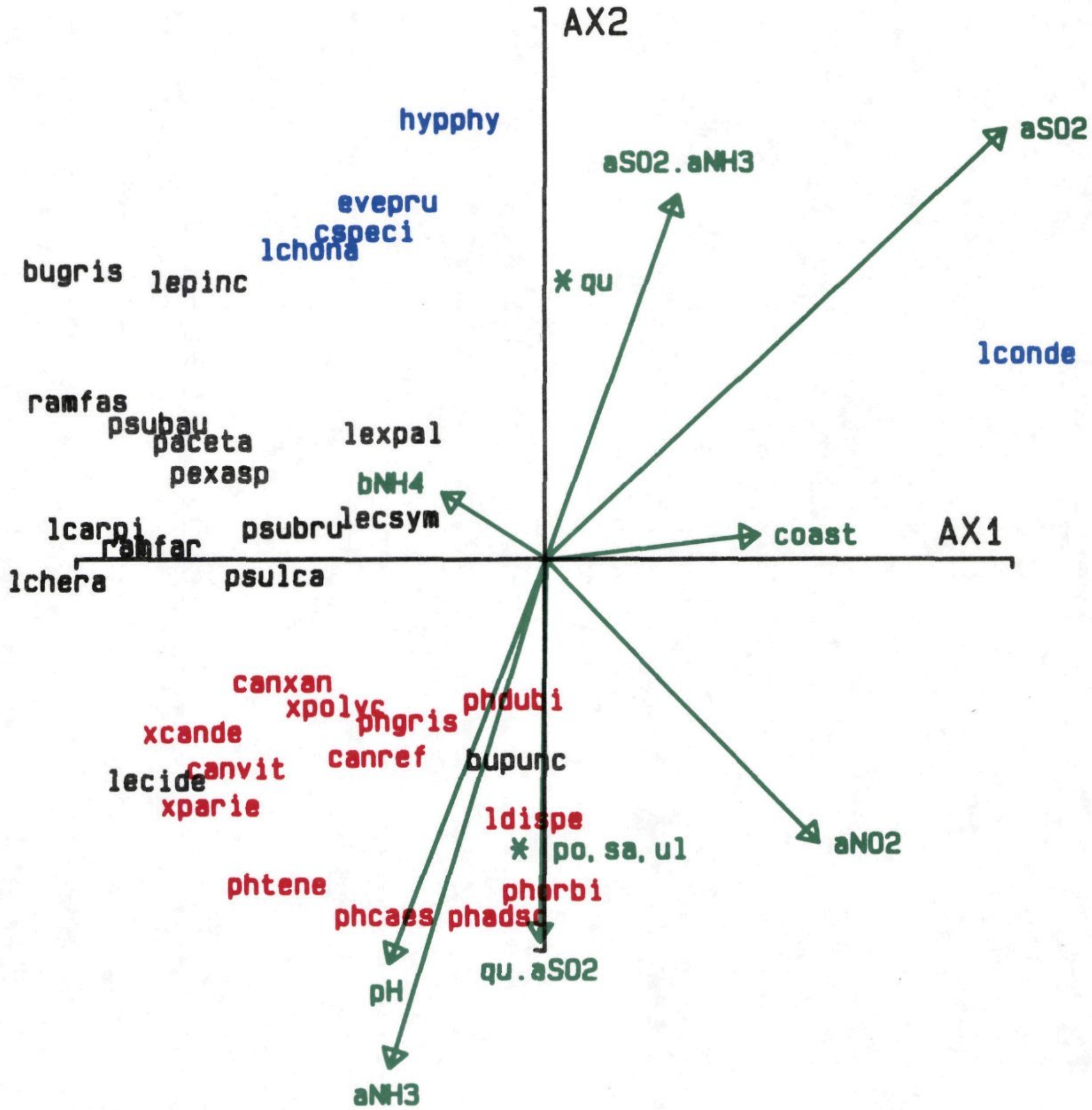
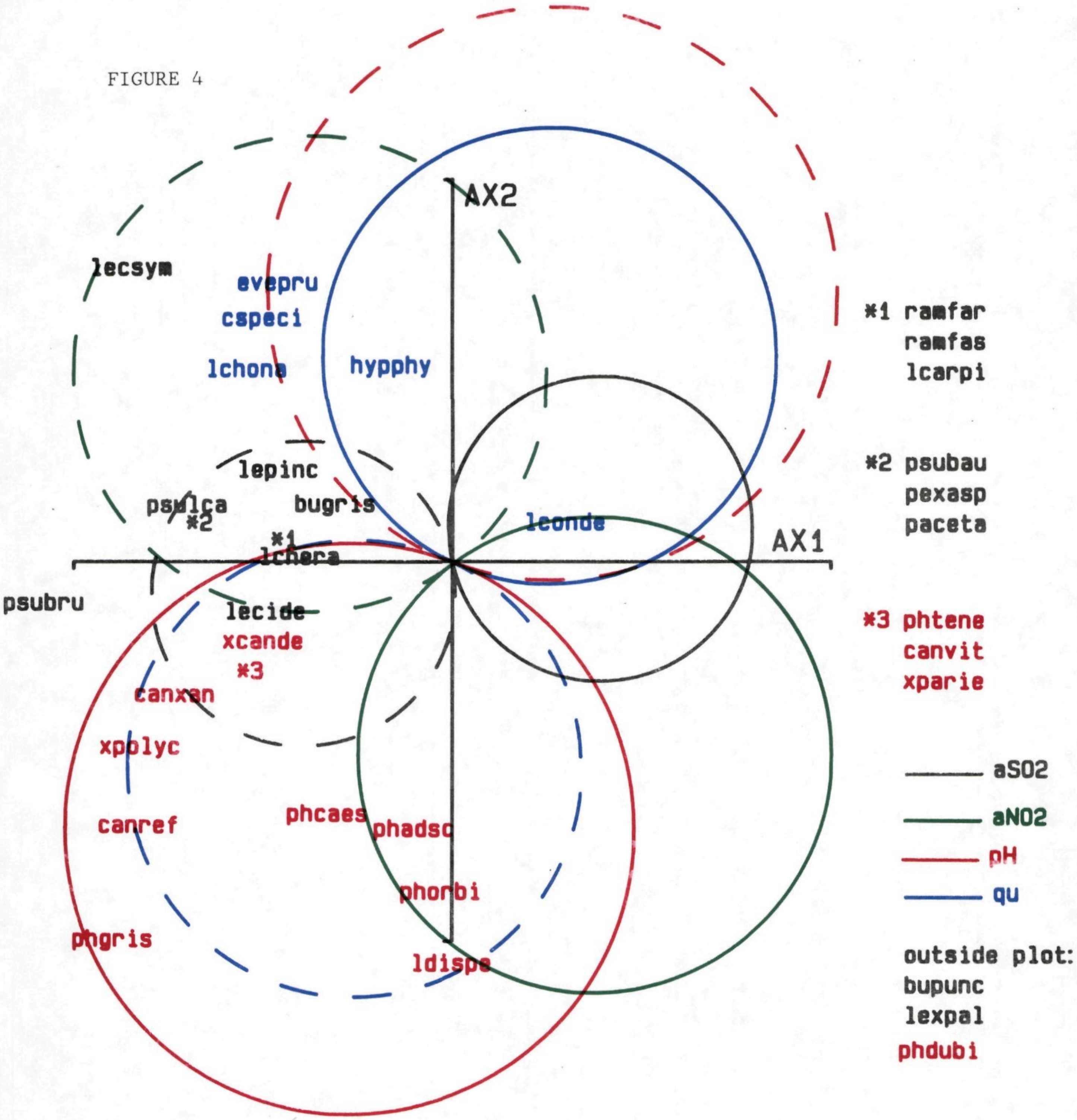

AX2
AX1
hypphy
evepru
cspeci
lchona
bugris
lepinc
lconde
ramfas
psubau
paceta
lexpal
pexasp
bNH4
lcarpi
ramfar
psubru
lecsym
lchera
psulca
aSO2
aSO2.aNH3
* qu
coast
canxan
xpolyc
phgris
phdubi
xcande
canvit
canref
bupunc
lecide
xparie
ldispe
* po, sa, ul
aNO2
phtene
phorbi
phcaes
phadsc
qu.aSO2
pH
aNH3

FIGURE 4


AX2
AX1
lecsym
evepru
cspeci
lchona
hypphy
lepinc
psulca
*2
bugris
lconde
*1
lchera
psubru
lecide
xcande
*3
canxan
xpolyc
canref
phcaes
phadsc
phorbi
phgris
ldispe
*1 ramfar
ramfas
lcarpi
*2 psubau
pexasp
paceta
*3 phtene
canvit
xparie
aSO2
aNO2
pH
qu
outside plot:
bupunc
lexpal
phdubi

A graphical approximation of the t-values belonging to the regression coefficients of the multiple regression of the abundance of the individual species on the four most important variables (aSO2, aNO2, qu and pH) is given in Figure 4. Only *Lecanora conizaeoides* is significantly positively related to aSO2 (inside the black circle for aSO2), and *Lecanora conizaeoides*, *Physcia adscendens* and *Ph. orbicularis* are significantly positively related to aNO2 (inside the green circle for aNO2). All other common species except *Parmelia subrudecta*, *Candelariella xanthostigma*, *C. reflexa*, *Xanthoria polycarpa*, *Physcia caesia*, *Physconia grisea* and *Lecanora dispersa* are significantly negatively related to aSO2, aNO2 or both. All nitrophytic species are significantly negatively related to qu and positively to pH.

Table 8. Effect of bark NH_4 content on the abundance of individual species. One sample with an extreme value for bNH4 was omitted. The table gives the significance (determined after 199 permutations) of the term bNH4 in forward selection: ** = $p \leq 0.01$; * = $0.01 < p \leq 0.05$; ? = $0.05 < p < 0.1$; ns = $p > 0.1$.

species	sign.	terms fitted before bNH4
bugris	ns	
canxan	ns	
lcarpi	ns	
lchera	*	aNO2, pH, coast
lchona	ns	
lecide	ns	
lecsym	ns	
lepinc	?	aSO2, po, circ., sa, aNH3
lexpal	ns	
paceta	**	ul, aNO2
pexasp	ns	
psubau	*	aSO2, aNO2, sa
psubru	*	aSO2
psulca	ns	
ramfar	*	aNO2, qu, aSO2
ramfas	?	aNO2, coast, aSO2, ul
xcande	ns	
xparie	ns	

No significant effects of bark SO_4 and NO_3 content were found, and a small but significant effect of bark NH_4. To further identify this effect, the abundance of 16 species for which Figure 3 suggests an effect of bNH4 was regressed on the variables in Table 7a, using forward selection. Table 8 gives the result, suggesting that species that optimally occur in a species-rich vegetation on neutral bark (**Parmelion acetabulae** Barkman 1958) have a preference for bark with a high NH_4 content.

4.4 Comparison of scales of SO_2 sensitivity and pH indicator value

The reaction of the species to the measured pH was compared with the a priori classification of the species as acidophytic or nitrophytic used in the previous paragraphs, and with Wirth's (1991) scale of pH indicator values. The regression coefficient for bark pH was calculated for each species by regressing its abundance on bark pH, aSO2, aNO2 and distance to the coast. Table 9 gives the results, showing a good correspondence between the different measures for pH preference. The correlation between the regression coefficients and Wirth's R-value is highly significant ($r=0.65$ using the regression coefficients themselves, $r=0.73$ using their rank numbers; $n=37$, $p<0.001$). Also the classification of the species as nitrophytic or acidophytic is a reasonable qualitative measure for their reaction to bark pH.

In a similar way the regression coefficients for SO_2 concentration were calculated by regressing species abundances on aSO2, aNO2, pH and distance to the coast. Table 10 gives the result, together with Hawksworth & Rose's (1970) SO_2 indicator value, and Wirth's (1991) degree of poleotolerance. In this case the correspondence between the regression coefficients and the indicator scales is rather poor ($r=-0.34$ for the correlation between regression coefficients and Hawksworth & Rose's scale, $r=0.29$ with Wirth's scale; $r=-0.31$ and 0.30, respectively, if rank numbers instead of regression coefficients are used; $p>0.1$ in all cases, $n=29$). Different explanations are possible for the lack of correspondence. The regression coefficients are calculated after correction for the effect of pH and therefore part of the effect of SO_2 is not accounted for. Another difference is that the scales relate to presence or absence of species, while the regression coefficients relate to abundance. Further comments on the comparison of indicator value scales are given by Van Dobben (1991).

Table 9. Regression of species abundance on measured pH. Atmospheric SO_2 and NO_2 and distance to the coast were used as covariables. Species = species code (see Table 2 and Van Dobben 1991), regr. coef. = standardized regression coefficient, % variance = percentage variance accounted for by pH and covariables (first column) or pH alone (second column), R = acidity indicator value according to Wirth (1991), eco = ecological group (as in Table 2). Species are given in order of increasing regression coefficient, those for which the percentage variance accounted for by pH is less than 1% have been omitted.

species	regr. coef.	% variance		R	eco
		pH+cova	pH		
lconde	-1.13	59.2	17.6	2	A
hypphy	-0.69	30.8	13.3	3	A
evepru	-0.44	14.4	4.0	4	A
cspeci	-0.21	18.7	3.3	-	A
lecsca	-0.14	12.0	8.4	2	A
psefur	-0.14	14.4	4.5	2	A
chaenf	-0.12	8.5	6.6	2	A
psaxat	-0.09	7.3	1.8	3	A
perama	-0.07	8.5	6.6	3	A
hyptub	-0.07	3.6	1.5	3	A
cetchl	-0.03	3.7	1.9	3	
opnive	0.02	2.5	1.2	-	
pglagl	0.02	3.6	1.4	3	
aradia	0.03	6.6	1.9	5	
phadgl	0.04	3.6	1.8	7	N
dimdil	0.04	3.6	1.8	4	
phpulv	0.05	9.1	1.5	7	N
cancon	0.05	2.4	1.7	6	N
bucane	0.10	12.6	2.6	8	
phlarg	0.11	19.7	1.4	4	
phgris	0.11	17.1	1.2	7	N
peralb	0.15	15.6	3.2	6	
phentx	0.17	24.4	2.9	6	N
bupunc	0.19	4.0	3.5	5	
lcarpi	0.22	44.5	1.1	5	
paceta	0.24	23.5	3.2	7	
canref	0.25	10.0	3.2	5	N
canxan	0.34	16.7	7.9	5	N
xcande	0.38	25.8	3.1	6	N
xpolyc	0.43	13.4	4.6	6	N
phcaes	0.45	16.9	6.7	8	N
ldispe	0.49	15.0	7.1	8	N
phorbi	0.49	14.9	7.3	7	N
phtene	0.49	21.9	7.0	6	N
canvit	0.53	20.7	8.0	5	N
lchera	0.69	52.9	7.4	6	
lecide	0.72	33.6	10.0	5	
xparie	0.80	36.5	14.3	7	N
phadsc	0.80	25.1	12.8	7	N

Table 10. Regression of species abundance on SO_2 concentration. Bark pH, *atmospheric* NO_2 *and distance to the coast were used as covariables.* Species = species code (see Table 2 and Van Dobben 1991), regr. coef. = standardized regression coefficient, % variance = percentage variance accounted for by pH and covariables (first column) or SO_2 alone (second column), H&R = degree of sensitivity to SO_2 according to Hawksworth & Rose (1970), Wirth = degree or toxitolerance according to Wirth (1991), eco = ecological group (as in Table 2). Species are given in order of increasing regression coefficient, those for which the percentage variance accounted for by SO_2 is less than 1% have been omitted.

species	regr. coef.	% variance		H&R	Wirth	eco
		SO2+cova	SO2			
lepinc	-0.88	34.5	11.6	3	9	
xcande	-0.67	25.8	9.7	5	5	N
psubau	-0.54	29.2	7.8	*	*	
xparie	-0.53	36.5	6.4	4	7	N
bugris	-0.51	53.0	4.9	*	5	N
lcarpi	-0.49	44.5	5.8	*	5	
ramfar	-0.45	39.1	4.7	5	6	
ramfas	-0.42	59.0	4.2	7	2	
phtene	-0.35	21.9	3.6	5	8	N
lchera	-0.34	52.9	1.9	5	6	
lchona	-0.34	19.9	4.7	*	6	A
phcaes	-0.32	16.9	3.3	*	*	N
lecsym	-0.30	12.6	3.5	*	4	
canvit	-0.28	20.7	2.2	*	*	N
xpolyc	-0.28	13.4	2.0	6	7	N
psubru	-0.23	11.6	2.1	5	6	
pexasp	-0.22	19.9	2.2	6	6	
psulca	-0.20	26.8	1.7	4	8	
cspeci	-0.20	18.7	3.0	*	*	A
catgri	-0.17	14.0	2.3	*	*	
canref	-0.16	10.0	1.3	*	4	N
paceta	-0.16	23.5	1.5	5	6	
lexpal	-0.16	6.0	1.6	2	9	
phgris	-0.13	17.1	1.7	5	7	N
psefur	-0.09	14.4	1.9	6	7	A
psiluc	-0.08	9.2	1.1	*	*	A
rinexi	-0.08	8.4	1.6	*	5	N
bucane	-0.07	12.6	1.3	3	8	
psaxat	-0.07	7.3	1.0	4	7	A
hyptub	-0.06	3.6	1.1	*	6	A
lecsca	-0.06	12.0	1.7	4	8	A
chaenf	-0.05	8.5	1.1	4	8	A
perama	-0.03	8.5	1.1	5	5	A
lconde	0.91	59.2	11.2	2	9	A

5 Discussion

Our results indicate that the factors affecting epiphytic lichen vegetation on 'standardized' wayside trees can be divided into two groups: (1) those with a high score on the first axis in Figures 2-3, to which nearly all species are negatively related and whose most important effect will therefore be a reduction in species richness (aSO2, aNO2 and distance to the coast), and (2) those with a high absolute score on the second axis in Figures 2-3, which determine the presence of either nitrophytic or acidophytic species (qu, pH, aNH3 and the interactions). The easiest interpretation for this distinction is that the former variables are related to toxic effects, while the latter are related to changes in bark pH.

The effects of SO_2 and NO_2 can most simply be explained as direct toxic effects, which at least for SO_2 is supported by a wide range of laboratory experiments (for a review see Nash 1988). The toxic effect of SO_2 is apparently not caused by SO_4 for which no significant effect was found. Probably the SO_3 ion is the directly toxic compound, which is also suggested by Nash (1988). Although the abundance of most species is negatively related to NO_2, a few nitrophytic species are positively related. A higher availability of nitrogen cannot explain this phenomenon. No significant effects of bark NO_3 were found, while bark NH_4 had a significant effect on some species, but these were not nitrophytic species (Table 8).

The effect of distance to the coast is hard to interpret. The general decrease in species richness at greater distance from the coast suggests the presence of a toxic compound whose concentration increases on going inland. This compound might be atmospheric NH_4 aerosol which is strongly correlated with distance to the coast ($r = 0.93$), but the results for atmospheric NH_3 and bark NH_4 make a toxic effect of atmospheric NH_4 unlikely. The effect of distance to the coast on bark NH_4 is not significant (Table 4), and also the effect of bark NH_4 on the species is limited and entails an increase rather than a decrease in species number (Table 8, Figure 3). Effects of a direct uptake of NH_4 from the atmosphere are also unlikely as these would be expected to be similar to those of atmospheric NH_3, and Figure 3 shows that atmospheric NH_3 and distance to the coast have more or less opposite effects. Another explanation for the effect of distance to the coast might be a neutralizing effect of sea-spray. However, the regression coefficients in Table 4 indicate that such an effect is only present at high SO_2 concentrations. A strong modification of the effect of SO_2 on the epiphytes at various distances to the coast, suggested by De Wit (1976) does not become apparent from our data. Finally, there is the possibility of a biogeographical effect determined by climatic or edaphic differences at various distances from the coast. The study of such factors was outside the present scope.

The directions of the arrows for pH, aNH3 and qu in Figure 3 are nearly equal, indicating that these variables are substitutable with respect to their effects on the species. This suggests that the effects of atmospheric NH_3 and tree species come about through changes in bark pH. However, in that case the measured pH should be sufficient to describe their effects, while in practice a model that also includes aNH3 and qu yields a better fit. A possible explanation is that the pH was measured in a small sample of the much larger area where the abundance of the species was determined, and the combination of tree species, atmospheric NH_3 and measured pH is a better estimator for the true pH than the measured pH alone. The positive score of aSO2 on the second axis is in agreement with its acidifying effect (Table 4). Therefore SO_2 is not only toxic, but an additional effect comes about through bark acidification. The effect of SO_2 as a combination of bark acidification and toxicity was also suggested by Van Dobben (1983). There is no explanation for the negative score of aNO2 on the second axis. An effect of NO_2 on bark pH did not become apparent from our data (Table 4). However, the correlation between SO_2 and NO_2 is rather strong (Table 3), and the apparent effect of NO_2 on the second axis might be explained as a non-linearity in the acidifying effect of SO_2.

The fit of different regression models can be used to estimate the quantitative importance of the factors that determine epiphytic vegetation (toxic gases, bark pH, other factors such as tree species). The percentage variance accounted for by atmospheric NH_3 (after fitting tree species, SO_2 and NO_2) decreases from 4% (Table 7g) to 1% after fitting bark pH (Table 7b, 7f). However, the relative decrease in the percentage variance accounted for by SO_2 and NO_2 after fitting bark pH is much less: from 18% (after fitting tree species, Table 7g) to 16% (Table 7f). Therefore the effect of NH_3 can probably be largely attributed to its alkalizing effect, but for SO_2 the toxic effect is far more important than the acidifying effect. The pH hypothesis is only partly supported by these findings. It largely explains the effect of atmospheric NH_3, partly explains the effect of atmospheric SO_2, but it does not explain the effect of atmospheric NO_2.

The difference between the various tree species is partly caused by differences in bark pH. Figure 3 suggests that the difference between oak and the other tree species can largely be explained from a naturally lower pH of oak bark (although in our data oak has a higher mean pH than the other tree species because it mainly occurs in areas with high levels of atmospheric NH_3). However, the percentage variance accounted for by tree species only slightly decreases after fitting bark pH (from 9%, Table 7c, 7e, 7g to 6-8%, Table 7d, 7f), indicating the importance of other bark properties besides pH.

Differences in bark pH and atmospheric chemistry give a reasonable explanation for the difference in total species number found on the various tree species (the percentage variance exclusively accounted for by tree species being only 9% out of a total of 59%, Table 5). The number of acidophytic species does not strongly depend upon tree species, only oak has on the average c. one more acidophytic species than the other tree species (Table 5). For the nitrophytic species the situation is different, and tree species is an important explanatory variable even after fitting bark and atmospheric chemistry (24% explained variance out of a total of 49% exclusively due to tree species). After correction for bark and atmospheric chemistry willow has c. 2 more nitrophytic species than oak, poplar c. 3-4 and elm c. 8 more (Table 5). For this group other bark properties besides those presently measured seem to be important.

The nature of the interaction effects in Tables 6 and 7 is hard to determine except the ones plotted in Figure 3. Both the effect of tree species and atmospheric NH_3 become less at high SO_2 concentrations. The former was also found by Van Dobben (1991). A strong co-deposition of SO_2 and NH_3, as indicated by some studies on stemflow chemistry (Van Dobben et al. 1992a) does not become apparent from our data. The effect of the interaction between SO_2 and NH_3 on bark chemistry is not significant. The small but significant effect of this interaction on species abundances may indicate a stronger effect of SO_2 at high NH_3 concentrations (and thereby also co-deposition). However, a more plausible explanation is a smaller effect of NH_3 at high SO_2 concentration, because the nitrophytic species are rather sensitive to SO_2 (Table 10). The effect of the interaction term pH.aSO2 is not or weakly significant (depending on the order of selection, Table 7b-f), and its canonical coefficients have low t-values on the first two axes. This is rather unexpected as the effect of SO_2 is usually assumed to increase at low pH (Türk & Wirth 1975, Bates et al. 1990). In our data the effect of SO_2 on the number of acidophytic species even decrease at low pH (Table 6).

As no significant effects of bark NO_3 and only a small effect of bark NH_4 were found, nitrogen is probably not an important growth-limiting factor for epiphytic lichens as is usually the case with vascular plants (Van Dobben et al. 1992b). However, the strong effects of bark pH do suggest that ion uptake processes are limiting factors for epiphytes, so other ions than those presently analysed are probably limiting. Van Dobben et al. (1992a) found that in stemflow water of *Pinus sylvestris* all macronutrient ions are present in large quantities except phosphate. Therefore bark PO_4 might be an important factor for epiphytes, which is now subject to further study.

From an ecological point of view it is rather unexpected that different groups of species are being favoured by a high bark pH and a high bark NH_4 content (Tables 8 and 9). In an unpolluted situation these factors would be expected to occur together, e.g. below bird's nests. The effect of bark NH_4 might in fact be an apparent correlation caused by some other bark chemical factor that was not measured. The present results do not confirm the effect of bark NH_4 suggested by Van Dobben (1991), and therefore the interpretation of the effect of atmospheric NH_4 is different. Van Dobben (1991) assumed atmospheric NH_4 to be a causal factor, influencing epiphytes through bark NH_4. As the effect of bark NH_4 was found to be small and different from the apparent effect of atmospheric NH_4, the correlations between species abundance and atmospheric NH_4 are probably apparent correlations, the true cause being another factor that is closely related with distance to the coast.

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Figure captions for RIN Report 92/23

(Figure 1 p. 7, Figures 2-4 p. 20-22)

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Figure 1. Concentrations (in mg.m-3) of SO_2 (a), NO_2 (b) and NH_3 (c) at the sample points. SO_2 and NO_2 were estimated from means of hourly measured concentrations (SO_2 April through September 1989, NO_2 and O_3 June 1989 through May 1990) at monitoring stations (Anonymus 1990), followed by interpolation (Van Egmond et al. 1978) of the concentrations at the sample points; NH_3 was estimated from 1988 emission data using the atmospheric transport and deposition model TREND (Asman & Van Jaarsveld 1990).

Figure 2. Species scores (black: indifferent or not determined, red: nitrophytic, blue: acidophytic) and scores of explanatory (environmental) variables (green), calculated by reduced rank regression. For an explanation of the abbreviations, see Table 1 (environment) and Table 2 (species). Species occurring in less than 10% of the samples have been omitted. Arrows can be drawn from the origin to the center of the species names, and the scalar inner products (product of arrow lenghts and cosine of enclosed angle) of any pair of arrows (species-species, environment-environment or species-environment) is an approximation of the correlation coefficient between that pair of variables. Eigenvalues are 0.21, 0.08 and 0.03, respectively, for the first three axes; the sum of all canonical eigenvalues is 0.36 and the biplot therefore represents 81% of the variance in the fitted values.

Figure 3. Species scores and canonical coefficients of the explanatory variables. The interpretation of this Figure is the same as Figure 2, but here the scalar inner products of the species-environment pairs are approximations of the regression coefficients of the multiple regression of the species' abundance on the terms given in Table 7b. The centroids for the sample scores belonging to a given tree species are indicated as asterisks; their projections on the species arrows are a measure for the fitted abundances on the various tree species (the difference between po, sa and ul was only weakly significant on the first two axes, hence these are represented by a single asterisk). The quantitative variables were centered to zero mean before the calculation of the interaction terms. The main effect of a variable therefore represents its effect at mean value of the other variables. For the interactions the effects on oak can be found by displacing the vector of the interacting variable from the origin to the qu asterisk, the effects at extreme values of interacting quantitative variables can be found by addition of the respective vectors. Eigenvalues are 0.22, 0.08 and 0.04, respectively, for the first three axes; the sum of all canonical eigenvalues is 0.39 and the biplot therefore represents 77% of the variance in the fitted values.

Figure 4. Significance of regression coefficients for the regression of species abundance on atmospheric SO_2, NO_2, oak and bark pH. Only species occurring in more than 10% of the samples are plotted. For explanation of names and colours see Tables 1 and 2 and Figure 2. If the center of a species name is inside a drawn circle the t-value of the corresponding regression coefficient is $> c.\ 2$, if it is inside a dashed circle the t-value is $< c.\ -2$. Eigenvalues are 0.20 and 0.07 for the first and second axis, respectively; sum of canonical eigenvalues is 0.29. For technical details see Van Dobben (1991) and Ter Braak & Looman (1991).

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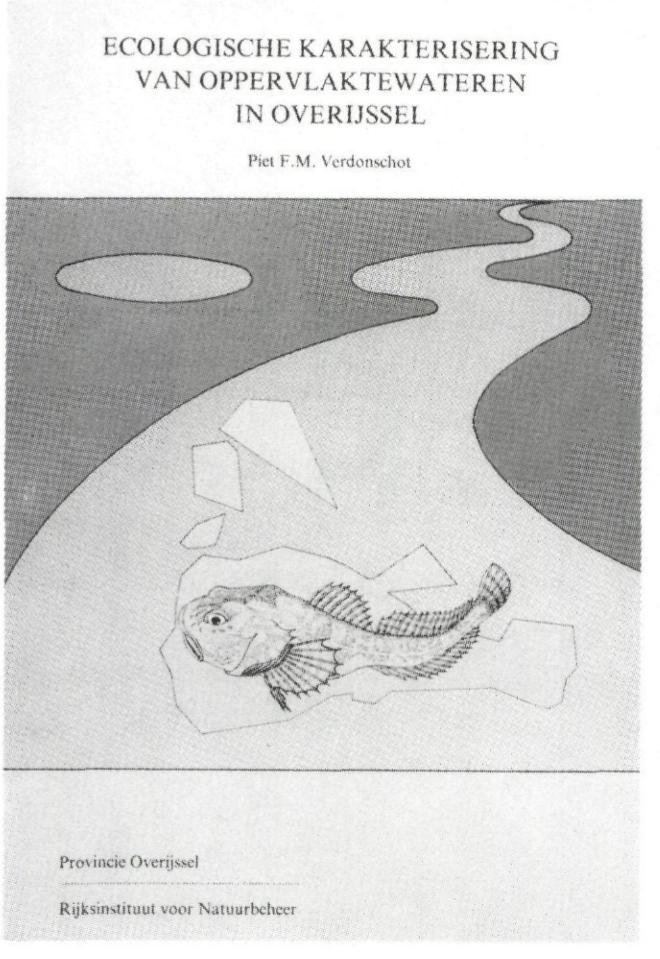

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