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Loss of *Lecanora conizaeoides* and other fluctuations of epiphytes on oak in S.E. England over 21 years with declining SO₂ concentrations

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Abstract

Epiphytic lichens and algae were studied on the bark of mature, free-standing *Quercus robur* L. at five stations along a transect extending S.S.W. for nearly 70 km into rural Sussex from central London. Percentage cover data for the epiphytes was recorded annually over the period 1979–1999 at chest height (1500 mm) and on the trunk base (450 mm). Data from the nearest pollution monitoring stations in the UK network show that SO₂ concentrations have declined at all transect stations, but particularly dramatically at the three inner sites (Kensington Gardens, Putney Heath, Epsom Common). The crustose lichen *Lecanora conizaeoides*, initially almost ubiquitous on oak bark at Epsom Common and once frequent at all but the innermost site, had declined and is now extinct at the four outer stations. However, it had recently appeared on oak bases in Kensington Gardens, the only station to retain appreciable SO₂ levels. *Lepraria incana* agg. had increased progressively at all sites with the decline of SO₂. ‘Green alga’, probably *Desmococcus viridis*, had also increased with declining importance of SO₂, although there was evidence that it was the most SO₂-tolerant of the three epiphytes. Its abundance at the urban stations is possibly connected with their high NO_x concentrations. *Hypogymnia physodes* was the most common macrolichen but only occurred in significant quantities at the two outer sites (Hesworth Common, Holmwood Common). It too had shown a significant decline with falling SO₂ levels. No significant re-colonization of formally polluted sites by SO₂-sensitive macrolichens had been noted during 21 years of study, probably because of the high acidity of oak bark and elevated NO_x in inner London. The loss of *L. conizaeoides* supports the hypothesis that this species requires elevated SO₂ inputs (or some closely related chemical factor) for healthy growth, but competitive interactions with the other epiphytes and attacks by the parasitic fungus *Athelia arachnoidea* may also be important. The results suggest that *Lecanora conizaeoides* cover on *Quercus* bark is a relatively sensitive bioindicator of SO₂ levels in town air. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: SO₂; NO_x; *Lecanora conizaeoides*; Lichens; Algae; Epiphyte; Bioindication; *Quercus robur*

1. Introduction

The high sensitivities of many epiphytic lichens to atmospheric pollution by sulphur dioxide (SO₂) and their uses as bioindicators of the pollutant have been documented in a large literature (see reviews of Ferry

et al., 1973; Gilbert, 1973; Hawksworth and Rose, 1976; Nash and Wirth, 1988; Richardson, 1988, 1992; Ahmadjian, 1993; Bates, in press). Most studies have focused upon the negative effects of SO₂ on lichens, particularly with reference to worsening conditions in urban areas and around rurally situated pollutant sources. Nevertheless, it has long been known that certain species are much less sensitive to SO₂ than others. This differential sensitivity of species forms the basis of the zone scale method of lichen bioindication (Gilbert, 1970; Hawksworth and Rose, 1970, 1976; Richardson, 1992).

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Since the 1970s, pollution of the air by SO₂ has declined in many areas of western Europe through the combined effects of pollution legislation and abatement, and socio-economic changes. In London, concentrations of SO₂ have ameliorated progressively over the past 25 years (e.g. Laxen and Thompson, 1987) so that at the present time there is only a small increase in concentration on moving inwards to the city centre from the surrounding countryside (Ashmore et al., 1988; Batty, 1997). A phase of lichen recolonization has been reported accompanying this decrease in town SO₂ concentrations (Henderson-Sellers and Seaward, 1979; Rose and Hawksworth, 1981; Hawksworth and McManus, 1989; Kandler, 1987; Seaward and Letrouit-Galinou, 1991; Boreham, 1992). This has been aided, at least in the Netherlands, by the de-acidifying effect of increasing ammonia deposition on tree bark (De Bakker, 1989). Recolonization has also been observed in North America upon closure or reduction of SO₂ emissions from large, rurally situated power plants and smelters (Showman, 1981, 1997; Gunn et al., 1995). Such recolonization has, however, been extremely limited on mature specimens of pedunculate oak (*Quercus robur* L.) one of the most common native trees in S.E. England (Bates et al., 1990). In 1990 the epiphytic lichen and bryophyte flora on mature oaks at stations along an air quality gradient extending into London still reflected the impoverishment caused by high SO₂ concentrations occurring 25 years earlier. For the more pollution sensitive foliose and fruticose lichens this situation has continued to the present day (unpublished results) although considerable lichen establishment on young oaks may be observed. One reason for this appears to be the low pH of the bark of mature oaks, a result of long exposure to acid deposition (Bates et al., 1990). However, experimental work has also indicated that elevated concentrations of nitrogen oxides (NO_x) now prevent the reestablishment of the foliose lichen *Parmelia saxatilis* in and around London (Batty, 1997).

Certain epiphytes have a high tolerance to SO₂, probably through the possession of a range of constitutive and induced mechanisms (Silberstein et al., 1996). In S.E. England, according to the zone scale of Hawksworth and Rose (1970, 1976), the most tolerant taxa on acid tree bark are, in order of decreasing tolerance: [green] algae (probably *Desmococcus viridis*) and the lichens *Lecanora conizaeoides*, *Lepraria incana*, *Hypogymnia physodes*, *Parmelia saxatilis* and *P. sulcata*. Based on evidence from an open air fumigation experiment, Bates et al. (1996) concluded that *Lecanora conizaeoides* was directly dependant on the presence of SO₂ in the atmosphere or on some closely associated chemical factor rather than on reduced competition from SO₂-sensitive foliose species. This hypothesis is supported by field data suggesting that this ubiquitous species of SO₂-polluted environments has started to decline in areas with decreasing SO₂ concen-

trations (Boreham, 1992, 1993; Wirth, 1993). Besides a 'requirement' for SO₂, other hypotheses put forward to account for the decline of *L. conizaeoides* under ameliorating conditions include increased parasitism by the lichenicolous fungus *Athelia arachnoidea*, increased competition by associated crustose lichen and algal epiphytes, and effects of increasing nitrogen deposition.

In this paper we present a unique dataset showing changes in the cover of several 'pollution tolerant' epiphytes recorded annually at five stations on the gradient of air quality from rural Sussex into London utilized by Bates et al. (1990) and Batty (1997). Our records extend over a 21-year period marked by major changes in SO₂ concentrations and provide important insights into the pollutant relationships of the epiphytes, and hence about their value as pollution bioindicators.

2. Methods and materials

Five stations located along a transect running S.S.W. from Central London into rural Sussex were recorded annually from 1979 until 1999 (Fig. 1). The five main stations, their grid references and periods of use were: (1) Hesworth Common, TQ002194, 1985–99; (2) Holmwood Common, TQ183453, 1980–1999; (3) Epsom Common, TQ182609, 1979–1999; (4) Putney Heath, TQ233740, 1979–1999; (5) Kensington Gardens, TQ265799, 1979–1999. Alternative localities employed as stations 1 and 2 in the early years of the study were: (1) Coolham, TQ113211, 1979 and then Greatham Common, TQ046149, 1980–1984; (2) Newdigate, TQ198406, 1979. The new sites were adopted for reasons of access or to improve standardization between stations. At each location groups of medium-sized (0.5–1.0 m girth at breast height) pedunculate oaks (*Quercus robur* L.) were selected for study which were considered typical of the surrounding area with respect to their epiphytic flora. Important requirements were that the trees should not be in dense woodland, which generally does not favour a rich flora of lichen epiphytes, and that they were not closely adjacent to a major road. Six to ten oaks were sampled on each occasion at each site depending on the number of recorders available. Despite the precautions taken to match sites, some changes in conditions other than concentrations of atmospheric pollutants were inevitably experienced over the long period of the observations. Some of the original sample trees were lost during the storm of 16 October 1987 at Hesworth Common and Epsom Common. The site at Putney Heath was rendered more open by scrub clearance between the 1983 and 1984 visits. Further details of the sites and an analysis of the data for all epiphytes up until 1990 are given by Bates et al. (1990).

All the measurements for a given year were completed in a single day in January or February (1979–1993), or in

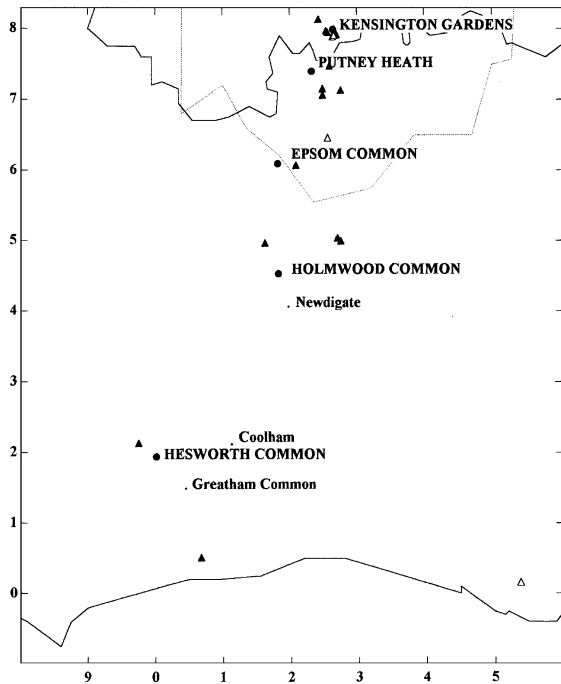


Fig. 1. Map of the area from Central London and the River Thames to the south coast showing the positions of the five main transect stations (large dots and capital letters; earlier alternatives shown with small dots and mixed type). Approximate extent of the built-up area of London shown by dotted outline. Positions of monitoring stations: (▲) older non-automatic network; (△) recent automatic network. Marginal scale indicates 10-km squares of the Ordnance Survey national grid and vertical lines show grid North.

October or November (1994–1999). To simplify the data analysis, the differences in recording dates from year to year have been ignored. Coverage of the lichens was assessed by a method described by Bates (1982). A tape was stretched around the trunk and pinned in position. The intersections of the inch (25.4 mm) graduations with one edge of the tape formed regularly spaced ‘points’ at which ‘hits’ of the underlying epiphytes were recorded. Trees usually show a vertical zonation of their epiphytic flora associated particularly with the steep gradient of decreasing water potential away from the soil and with the lower exposure to pollutants nearer the ground through frictional retardation of air movement. Therefore, measurements were made at two heights on the trunk: the tree base, 450 mm (18 in); chest height, 1500 mm (60 in). In each case the total number of hits for each epiphytic species was expressed as a percentage of the total possible number of hits (i.e. inches) around the trunk circumference. The data presented are the averages of these values for the trees sampled at each station in a particular year.

Lichen nomenclature follows Purvis et al. (1992). *Lepraria incana* agg. may also include *L. lobificans* and one or more *Leproloma* spp. The name ‘green alga’ is used in preference to *Desmococcus viridis*, usually presumed to be the commonest epiphytic green alga in S.E. England, as no critical determinations of algal samples were made.

Air pollution data, consisting of mean winter SO₂ concentrations (non-automatic network), were obtained from Warren Spring Laboratory (1972, and unpublished data cited by Bates et al., 1990). More recent information, including mean annual concentrations (automatic stations), from the UK national monitoring network was obtained from the web site of AEA Technology plc (<http://www.aeat.co.uk/netcen/airqual/>). Positions of the monitoring stations employed are indicated in Fig. 1.

Statistical analysis of the epiphyte data was either by linear regression of cover upon date (year since 1900), or else a polynomial regression was fitted in those cases (*Lecanora conizaeoides* and ‘green alga’ at Putney Heath) where the relationship between these variables was clearly curvilinear. All regressions were fitted utilizing Microsoft Excel and Anovas for the polynomials computed utilizing the reported *R*² values. Where curves were fitted, the order of the polynomial was incremented stepwise to a point beyond which a further increase did not cause a significant reduction in residual error (Cooley and Lohnes, 1971).

3. Results

3.1. Changes in air quality along the transect

Changes in air quality since the end of the era of high SO₂ concentrations for the transect stations are summarized in Table 1 and Fig. 2. Table 1 shows five-year averages for the winter mean SO₂ concentrations obtained from the nearest monitoring sites in the old non-automatic network. All relevant monitoring sites had been discontinued by the end of 1995, but the data clearly show a dramatic improvement in air quality, especially at the urban stations, since the early 1960s. They also confirm a close relationship between distance of the transect stations from the centre of London and SO₂ concentration at all periods. Fig. 2 shows some more recent information (annual mean SO₂ concentrations) from the only three monitoring stations in the present automatic network that are relevant to the transect. The Cromwell Road site possibly experiences greater SO₂ (and especially NO_x) pollution than Kensington Gardens from its high volume of road traffic, but as it is only 800 m distant it is considered reasonably representative. Likewise with Sutton Roadside, but for SO₂ this recent site is probably closely indicative of present conditions at Putney Heath

Table 1
Averages (\bar{x}), within five-year periods, of mean annual winter SO_2 concentrations ($\mu\text{g m}^{-3}$) at monitoring stations from the old UK non-automatic monitoring network taken as representative of conditions at the transect stations, 1961–1995. n , the number of annual means used to compute the figure given in the table

Period	Transect station (above) and nearest monitoring stations (below)							
	Hesworth Common Petworth, ^a Angmering ^b	Holmwood Common Redhill 1 & 2, Dorking	Epsom Common Epsom 1 & 2	Putney Heath Wandsworth 1–6, Wimbledon 3–7	Kensington Gardens Kensington 1, 4, 7–9, 11–13			
1961–1965	\bar{x}	—	147	255	388			
	n	0	2	35	7			
1966–1970	\bar{x}	31 ^a	87	178	290			
	n	4	5	15	14			
1971–1975	\bar{x}	—	40	93	189			
	n	0	1	6	3			
1976–1980	\bar{x}	—	44	80	132			
	n	0	5	19	14			
1981–1985	\bar{x}	6 ^b	40	53	72			
	n	4	1	5	15			
1986–1990	\bar{x}	—	—	30.5	46.1			
	n	0	0	2	9			
1991–1995	\bar{x}	—	—	—	48			
	n	0	0	—	5			

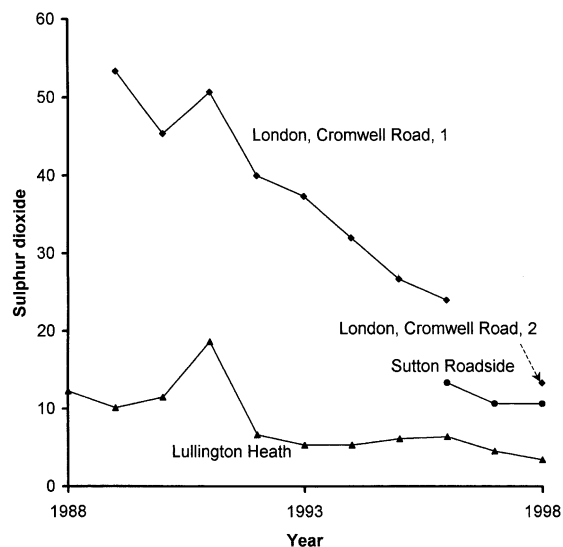


Fig. 2. Annual mean SO_2 concentrations ($\mu\text{g m}^{-3}$) at three automatic monitoring stations in the UK network that are representative of recent conditions in different parts of the transect. The original Cromwell Road site was discontinued after 1996 but measurements were recommenced at a new locality from 1998. Data from AEA Technology plc web site.

and Epsom Common. The coastal Lullington Heath site may very slightly underestimate SO_2 pollution at Hesworth Common but the values in rural Sussex are now extremely low. In summary, Fig. 2 shows that SO_2 pollution has continued to decline in London's urban and rural areas to the point where there is now only about $20 \mu\text{g SO}_2 \text{ m}^{-3}$ (7.7 ppb) separating the least and most polluted environments along our transect.

3.2. Changes in cover of individual epiphytes

3.2.1. *Lecanora conizaeoides*

At the four outer transect stations *L. conizaeoides* was present on pedunculate oak at the start of the observations but had completely vanished by 1998 (Fig. 3, Table 2). At the outermost station *L. conizaeoides* was always relatively scarce and had declined to insignificant coverage by 1991. At Holmwood Common a shallow but highly significant linear decline in its cover was observed over the 21 years. At Epsom Common, a station just beyond the outer suburbs, a spectacular and statistically significant linear decline occurred, from a situation in 1979 where this lichen covered most of the bark surface at the sample heights, to the situation in 1997 where it had completely disappeared. A different pattern was observed at Putney Heath in the inner suburbs. Here *L. conizaeoides* was present initially at relatively low cover, but it increased to reach high cover values in the mid to late 1980s, before declining progressively and finally

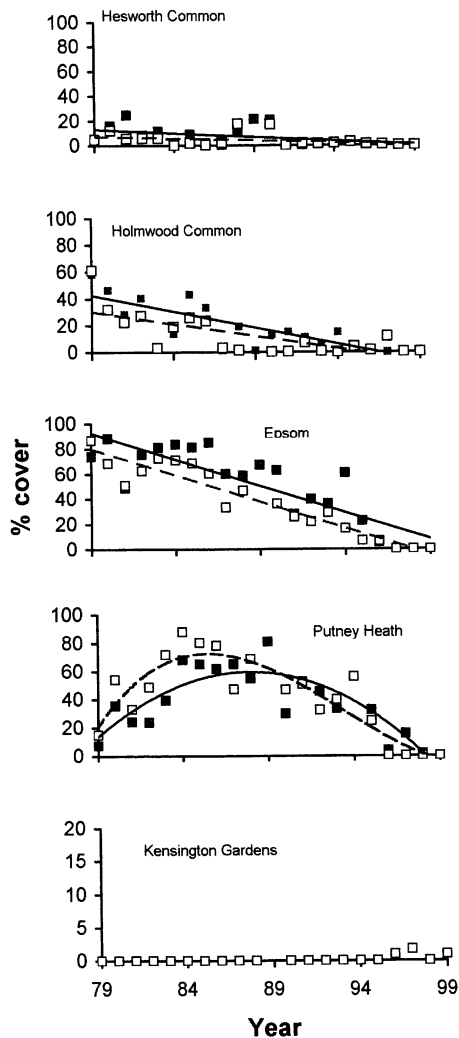


Fig. 3. Annual fluctuations in mean cover of *Lecanora conizaeoides* on oak at the five transect stations, 1979–1999: (■) measurements made at chest-height, (□) measurements made on tree base. Regression lines or polynomial curves are shown where these give a significant fit to the data (see Tables 2 and 3): solid line, chest-height; dashed line, tree base.

vanishing in the late 1990s. This pattern is approximated by quadratic and cubic polynomials, respectively, at chest height and on the tree base (Table 3). At Kensington Gardens, *L. conizaeoides* was not observed on pedunculate oak in the first 17 years, but it had colonized some tree bases by 1996 and was recorded with low mean cover values thereafter.

Cover of *L. conizaeoides* was usually greater in the chest height (1500 mm) samples than on the tree bases (450 mm) at the three outer stations. However, the reverse was observed on many occasions at Putney Heath and at Kensington Gardens.

3.2.2. *Lepraria incana* agg

The powdery (leprose) lichen *Lepraria incana* agg. showed increasing cover with the passage of time at all transect stations (Fig. 4). Significant linear increases were observed at the three outer sites (Table 2), although cover values were noticeably lower at Epsom Common where *L. incana* was absent initially on the sample trees. At Putney Heath this species was very scarce up until the mid-1990s, after which higher cover values were recorded. *L. incana* colonized some oak bases in Kensington Gardens around 1995 and was particularly noticeable, albeit at low cover, in the last two years of our study. Although primarily a species of the tree base, this lichen also occurred commonly in bark crevices at chest height on oak trunks, especially at the outer (rural) stations.

3.2.3. Green alga

At the two outer sites the cover of ‘Green alga’ showed no significant change with time (Table 2) and remained at modest levels throughout the period of observations (Fig. 5). At Epsom Common a significant increase in cover of ‘Green alga’ was observed with time, and was particularly noticeable after 1990. At Putney Heath the changes in cover of the alga are to some extent the reverse of those recorded for *Lecanora conizaeoides*: the cover of ‘green alga’ was initially high (>70%); it declined to 20–30% in the mid-late 1980s; recovery of green algal cover was evident in the 1990s. These changes have been approximated by polynomial curves. As with *Lecanora conizaeoides* these are quadratic at chest height and cubic and steeper for the tree base (Table 3). ‘Green alga’ was absent at Kensington Gardens before 1986, but it has been noted on the tree bases with low mean cover on several recent sampling visits.

3.2.4. *Hypogymnia physodes*

H. physodes was by far the most common of the foliose lichens encountered on the transect. Even so, it was recorded in measurable quantities only at the three outer sites (Fig. 6). There is evidence of a significant decline in the cover of *H. physodes* over the period of study (Table 2). Taking into account the fact that different sites were employed during 1979–1984 for station 1 (Hesworth) and in 1979 for station 2 (Holmwood), there is evidence of a progressive decline of *H. physodes*. Records at Epsom Common were too sparse to permit any conclusions being reached. Although there is also evidence for colonization of pedunculate oaks in London (e.g. Putney Heath) by this lichen (Bates et al., 1990; Batty, 1997), the tiny coverages involved are beyond accurate determination by normal methods.

3.3. Relationship of epiphyte cover to SO_2 concentrations

We have attempted to link the abundance of the various epiphytes directly to SO_2 pollution by plotting the

Table 2

Summary of linear regressions (including Anovas) of percentage cover data for epiphytes upon date (years after 1900). 'Not applicable' indicates a sparse dataset unsuitable for statistical analysis

Species/station	Position	Intercept	Slope	R ²	F	n	P
<i>Lecanora conizaeoides</i>							
Hesworth Common	Chest ht	60.2	− 0.6	0.22	5.08	20	a
	Base	25.2	− 0.23	0.06	1.06	20	ns ^b
Holmwood Common	Chest ht	234.2	− 2.43	0.7	41.07	20	c
	Base	174.8	− 1.83	0.53	20.53	20	c
Epsom Common	Chest ht	426.4	− 4.22	0.74	52.85	21	c
	Base	413.1	− 4.21	0.91	173.2	20	c
Putney Heath	Chest ht	See Table 3					
	Base	See Table 3					
Kensington Gardens	Chest ht	Species absent					
	Base	Not applicable					
<i>Lepraria incana</i> agg.							
Hesworth Common	Chest ht	− 154.7	2.14	0.58	26.23	21	c
	Base	− 129.4	1.9	0.42	13.01	20	d
Holmwood Common	Chest ht	− 176.5	2.37	0.59	27.07	21	c
	Base	− 109.4	1.64	0.32	8.53	20	c
Epsom Common	Chest ht	− 107.6	1.32	0.56	24.52	21	c
	Base	− 124.2	1.58	0.55	22.45	20	c
Putney Heath	Chest ht	− 69.1	0.83	0.54	22.63	21	c
	Base	− 81.2	0.98	0.42	12.96	20	d
Kensington Gardens	Chest ht	Species absent					
	Base	Not applicable					
'Green alga'							
Hesworth Common	Chest ht	2.2	0.09	0	0.06	21	ns
	Base	16	− 0.09	0	0.12	20	ns
Holmwood Common	Chest ht	18.7	− 0.08	0	0.12	21	ns
	Base	43.1	− 0.31	0.05	0.95	20	ns
Epsom Common	Chest ht	− 230.2	2.78	0.63	32.59	21	c
	Base	− 147.1	1.91	0.69	40.22	20	c
Putney Heath	Chest ht	See Table 3					
	Base	See Table 3					
Kensington Gardens	Chest ht	Species absent					
	Base	Not applicable					
<i>Hypogymnia physodes</i>							
Hesworth Common	Chest ht	85.4	− 0.77	0.29	7.24	20	a
	Base	86.9	− 0.82	0.31	7.78	19	a
Holmwood Common	Chest ht	58.4	− 0.48	0.22	5.08	20	a
	Base	72.05	− 0.69	0.39	10.8	19	d
Epsom Common	Chest ht	Not applicable					
	Base	Not applicable					
Putney Heath	Chest ht	Not applicable					
	Base	Not applicable					
Kensington Gardens	Chest ht	Species absent					
	Base	Species absent					

^a $P < 0.05$.

^bns, not significant.

^c $P < 0.001$.

^d $P < 0.01$.

cover of each species against mean SO₂ concentration for those stations and years in which monitoring station data were available. Owing to the sparseness of the monitoring network stations and their eventual discon-

tinuation, we were unable to use our floristic data for many years, especially at the three outer transect stations. Similar results were obtained for the two sampling heights and only the chest height data are presented in

Table 3

Summary of polynomial curve fitting (including Anovas) for 'best fit' regressions of cover data upon date (years after 1900) for *Lecanora conizaeoides* and 'Green alga' at Putney Heath

Position	Model	R^2	Overall fit		Improvement ^a	
			F	P	F	P
<i>Lecanora conizaeoides</i>						
Chest height	Quadratic	0.73	24	< 0.001	41.72	< 0.001
Eq.	$y = -0.5697x^2 + 100.21x - 4347.2$					
Tree base	Cubic	0.81	22	< 0.001	5.62	< 0.05
Eq.	$y = 0.041x^3 - 11.474x^2 + 1063.6x - 32593$					
'Green alga'						
Chest height	Quadratic	0.51	9.24	< 0.01	18.4	< 0.001
Eq.	$y = 0.4104x^2 - 73.205x + 3295.5$					
Tree base	Cubic	0.65	10.08	< 0.01	18.87	< 0.001
Eq.	$y = -0.0666x^3 + 18.038x^2 - 1624.2x + 48630$					

^a'Improvement', refers to the improved fit of the 'best fit' model over the next simplest polynomial.

Fig. 7. This shows quite different responses of the three principal epiphytes. *Lecanora conizaeoides* (Fig. 7a) appeared to have an optimum at moderately high levels of SO_2 ($30\text{--}50\ \mu\text{g m}^{-3}$) but occurred over a wide range ($> 0\text{--}75\ \mu\text{g m}^{-3}$). *Lepraria incana* agg. (Fig. 7b) was clearly the least tolerant of the three with its highest cover values concentrated below $10\ \mu\text{g m}^{-3}$ and few records above $20\ \mu\text{g m}^{-3}$. 'Green alga' (Fig. 7c) also showed a wide amplitude with respect to SO_2 concentrations, but was clearly the most tolerant epiphyte with its highest cover at nearly $80\ \mu\text{g m}^{-3}$. Kensington Gardens was distinct from the other transect sites in that cover values for all epiphytes were zero, or nearly so, even when the SO_2 concentration in a particular year fell within the range of tolerance of the species as revealed at the other sites.

4. Discussion

The major environmental change occurring during the 21-year period of this study has been the progressive decline in SO_2 concentrations at all transect stations. NO_x is now a more important pollutant than SO_2 in central London. Measurements of NO_2 at the Cromwell Road monitoring station indicate that the annual mean has remained between 40 and 50 ppb through most of the period 1980–1999. In contrast, concentrations of NO_2 have varied between 7.1 and 11 ppb at the rural Lullington Heath monitoring station (data from AEA Technology web site). Effects of long-term variations in climate (i.e. global warming) are believed not to be significant for these lichens, which are very widely distributed.

Fluctuations in populations of cryptogams have been monitored in Britain over several decades by a variety of methods (Ferry et al., 1973; Hawksworth et al., 1974;

Rose and Wallace, 1974; Gilbert, 1977; Bates and Farmer, 1992). Notwithstanding, the floristic changes described in the present study are some of the most dramatic population reversals observed among cryptogams in the second-half of the 20th century. At the start of our observations, *L. conizaeoides* had long been established as a ubiquitous covering on oak bark along the transect, except in the then heavily polluted centre of London. By contrast, it is now quite difficult to find healthy patches of this lichen on pedunculate oak in the areas which formerly comprised its strongholds. Nevertheless, we have found that *L. conizaeoides* still persists locally in a thin and scarcely identifiable, sterile condition, usually on birch (*Betula* spp.) and beech (*Fagus sylvatica* L.) trees, and on old fence palings. Further study of these 'refugia' may eventually provide key information about the reasons for extinction elsewhere.

The differing initial abundances and the progressive losses of *L. conizaeoides* at Hesworth, Holmwood and Epsom Commons support the hypothesis that this is an SO_2 -requiring species that has contracted as concentrations of the pollutant in and around the capital have decreased. This is especially supported by the pattern of events at Putney Heath where initially *L. conizaeoides* was uncommon. Its rise and later demise can be equated, firstly with the fall of SO_2 levels to tolerable and then optimal concentrations, and secondly with the reduction of SO_2 to levels that no longer support the lichen. Its belated appearance in the city centre at Kensington Gardens also fits in with this interpretation, although there is less colonization here than might be expected on the basis of SO_2 concentrations alone (see below). Comparison of the cover values for *L. conizaeoides* (Fig. 7) with the data for SO_2 indicates that the optimal conditions for this species on oak are $30\text{--}50\ \mu\text{g m}^{-3}$, somewhat lower than the range $50\text{--}150\ \mu\text{g m}^{-3}$ over which this species is

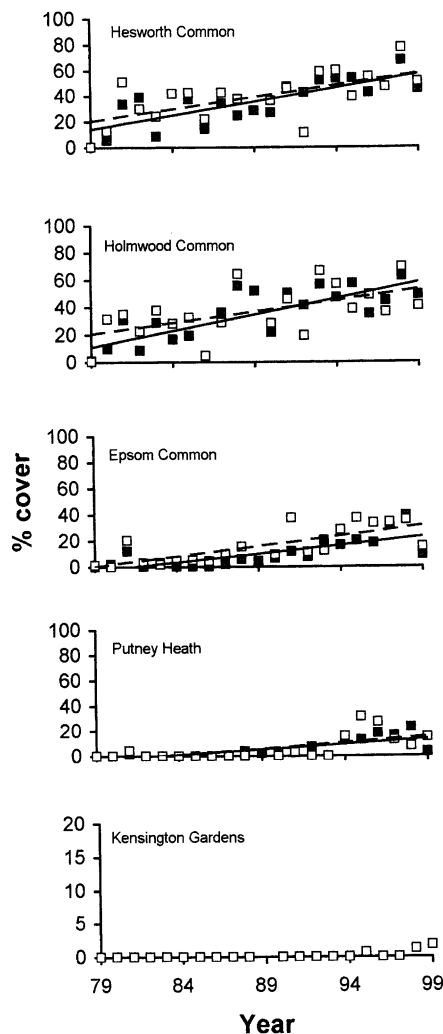


Fig. 4. Annual fluctuations in mean cover of *Lepraria incana* agg. on oak at the five transect stations, 1979–1999: (■) measurements made at chest height, □, measurements made on tree base. Regression lines are shown where these give a significant fit to the data (see Table 2): solid line, chest height; dashed line, tree base.

said to occur on all substrata in the British Isles (Seaward and Hitch, 1982). The optimum identified in the present study is also well below the SO_2 concentrations given by Hawksworth and Rose (1970, 1976) in bands 2 and 3 of their zone scale: Zone 2, *L. conizaeoides* ‘... present but confined to bases’, about $150 \mu\text{g m}^{-3}$; Zone 3, ‘*L. conizaeoides* extends up the trunk ...’, about $125 \mu\text{g m}^{-3}$. In contrast, the present data agree closely with results obtained in the Liphook Forest Fumigation Project (Bates et al., 1996) where *L. conizaeoides* established higher coverages on the barks of three conifer species fumigated at 53 and $32 \mu\text{g m}^{-3}$ (long-term means) than at ambient

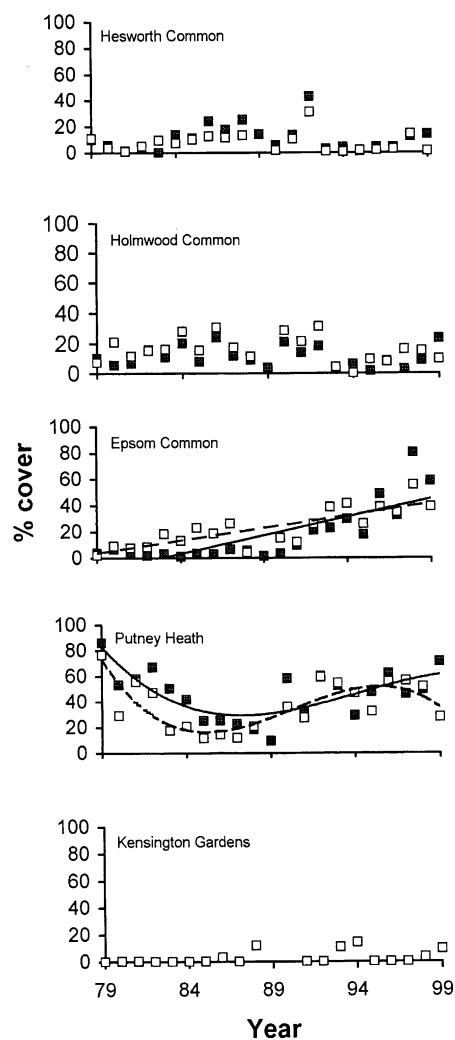


Fig. 5. Annual fluctuations in mean cover of ‘green alga’ on oak at the five transect stations, 1979–1999: (■) measurements made at chest height, (□) measurements made on tree base. Regression lines or polynomial curves are shown where these give a significant fit to the data (see Tables 2 and 3): solid line, chest height; dashed line, tree base.

SO_2 concentration ($11 \mu\text{g m}^{-3}$). Two possible explanations may be put forward for the lack of agreement between the present and earlier assessments of SO_2 tolerance in this species. First, the various studies may differ in the extents to which the lichen flora had equilibrated with ambient SO_2 concentrations, and there are doubts about the accuracy of the pollution data available to early workers. Second, the average pH of the substrata on which *L. conizaeoides* was growing in each study may have varied. Oak and conifer bark are relatively acid substrata, and acid conditions are known to increase lichen susceptibility to dissolved SO_2 by increasing the

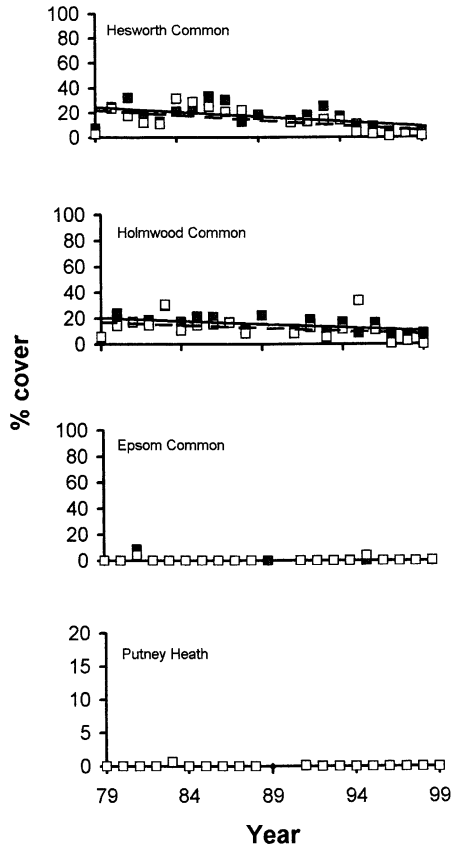


Fig. 6. Annual fluctuations in mean cover of *Hypogymnia physodes* on oak at the four outer transect stations, 1979–1999. The species was never found at Kensington Gardens: (■) measurements made at chest height, (□) measurements made on tree base. Regression lines are shown where these give a significant fit to the data (see Table 2): solid line, chest height; dashed line, tree base.

proportions of phytotoxic HSO_3^- and ‘ H_2SO_3 ’ in solution (Bates et al., 1996; Bates, in press).

Wirth (1993) described some comparable changes to *Lecanora conizaeoides* in Baden-Württemberg on the basis of cover records from permanent quadrats scored initially in 1985–1986 and then again five years later. *L. conizaeoides* had started to decline at several heavily polluted sites where it had previously been dominant. The decline was attributed to declining acidic emissions but no quantitative data on atmospheric pollutants were presented. Our results accord closely with those of Wirth (1993) but we reject the suggestion that lessening of acidity is the sole reason for the demise of *L. conizaeoides* as SO_2 declines. Our data (Bates et al., 1990; Batty, 1997) show clearly that the bark of mature oaks in polluted areas has become strongly acidified by their long exposure to SO_2 and that this acidity is retained for many years. Except in areas experiencing high ammonia depo-

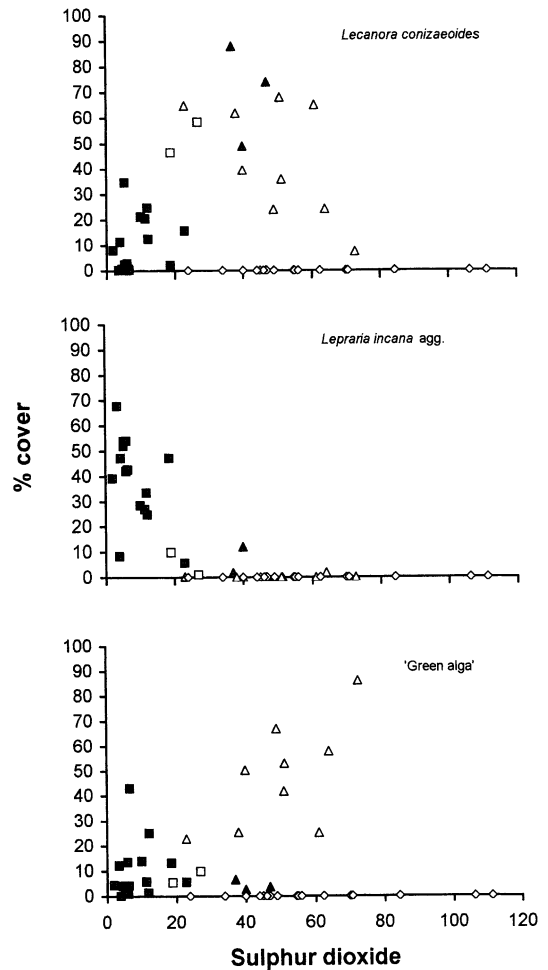


Fig. 7. Annual cover values of the three principal oak epiphytes at the five transect stations, plotted against annual winter mean SO_2 concentrations ($\mu\text{g m}^{-3}$) for those years and sites where pollution data were available from the non-automatic monitoring network. Key to sites: (■) Hesworth; (□) Holmwood; (▲) Epsom; (△) Putney; (◇) Kensington.

sition (De Bakker, 1989; Van Dobben and Ter Braak, 1998), we believe it is far more likely that the decline of *L. conizaeoides* is linked to the decrease in sulphur deposition than to bark neutralization.

Several authors (Arvidsson, 1976; Boreham, 1993; Wirth, 1993) have considered losses of *L. conizaeoides* in relation to attacks by the lichenicolous fungus *Athelia arachnoidea*. We regularly noted the characteristically cream-coloured patches where *L. conizaeoides* had been killed by this parasitic basidiomycete, but did not record the information in a systematic fashion as only a small fraction of the total coverage was affected at a particular visit. Nevertheless, Wirth (1993), who similarly did not record the parasite quantitatively, considered that it was undoubtedly important in the dynamics of *L.*

conizaeoides. Boreham (1993) recorded the decline of *L. conizaeoides* on a sample of 170 *Betula pendula* trees in Epping Forest (N.E. of London) from 1987 to 1991. Although *A. archnoidea* became locally abundant on neighbouring *Fagus sylvatica* trees in autumn 1987, it achieved no more than 0.4% cover on *Betula* in the following year and then declined. On balance, it appears that although *A. archnoidea* may infect an increasing number of weakened thalli of *L. conizaeoides* under a falling SO₂ regime, it is unlikely that it is the only or even primary cause of extinction of the lichen.

Our study revealed significant changes in the coverages of oak epiphytes associated with *L. conizaeoides* that were also closely mirrored in the shorter-term investigation of these species on birch by Boreham (1993). In particular, the decline of *L. conizaeoides* was associated with an increase in *Lepraria incana* agg. and 'Green alga' (probably *Desmococcus viridis*). Thus, it is possible that extinction of *L. conizaeoides* might represent competitive interactions rather than simple changes in performance related to changing conditions. In the case of *L. incana* agg., it can be seen (Figs. 3 and 4) that the strongest increases of this lichen (at Hesworth and Holmwood Commons) are not directly linked to the strongest declines of *L. conizaeoides*. The more spectacular decline of *L. conizaeoides* at Epsom Common accompanied a rather weaker increase of *Lepraria incana*; furthermore, the period of low cover of *L. conizaeoides* at Putney Heath in the early 1980s was not marked by the significant presence of *L. incana* agg. Although the possibility of interference between the two lichens cannot be entirely ruled out, particularly under ameliorating conditions, it appears that *L. incana* agg. has benefited directly from the lowering of SO₂ concentrations and performs best where these are lowest (also see Fig. 7b). Boreham (1993) recorded only a slight increase of *L. incana* on birch in Epping Forest and did not infer a competitive effect of this lichen upon the ebbing *L. conizaeoides*. 'Green alga' appears to be more SO₂ tolerant than *L. conizaeoides* (Fig. 7c) and yet it showed strong evidence of increase at the three inner transect stations in the second-half of the study when SO₂ was declining. At Epsom Common 'Green alga' showed an inverse trend to that of *L. conizaeoides* that could indicate interspecific competition; however, there was no evidence of increase of green algae at the two outermost stations where *L. conizaeoides* experienced a significant decline (Table 2, Figs. 3 and 5). A likely explanation is that 'Green alga' has benefited from the high levels of NO_x pollution occurring in central London. Increases in the abundance of algae occurring on conifer needles in Scandinavia have been linked to increasing deposition of nitrogenous pollutants (Bråkenhielm and Quinhong, 1995; Søchting, 1997; Poikolainen et al., 1998). At Epsom Common and Putney Heath dead thalli of *L. conizaeoides* were frequently noted beneath a film of living 'Green alga' suggesting

strongly that overgrowth and shading of the lichen had been the cause of death, but this requires direct verification. It is not impossible that more than one species of alga is involved and that the recently increasing form in London is a different species to that found in lower quantities at the rural stations.

As noted in the earlier report (Bates et al., 1990) and further discussed by Gilbert (1992), there is little evidence of macrolichen recolonization of the oaks in the four inner stations, where the macrolichen flora had been impoverished by pollutants long before this study commenced. This is related partially to the acidity of the bark (in places below pH 3), but probably also to suppression of colonization by the current high levels of NO_x (Batty, 1997). The latter author studied tiny thalli (mainly *Hypogymnia physodes*) recolonizing oaks at Putney Heath and found that these exhibit a rapid population turnover and occur selectively on trees with higher bark pH. It is likely that low pH, including its effects on phytotoxicity of dissolved SO₂, and elevated NO_x concentrations also limit the colonization of the city centre station (Kensington Gardens) by the epiphytes considered in this paper. Our study has provided evidence of a decline in the most pollution tolerant of the foliose lichens, *Hypogymnia physodes*, at the two most rural stations. *H. physodes* is known to be favoured by mild SO₂ pollution and acid conditions. As there is no evidence of increasing bark pH at our transect stations (Batty, 1997), *H. physodes* may be responding to lowered S input, but a detrimental effect of increased N deposition is also a possibility.

In contrast to much earlier work concerning the value of lichens in bioindication of atmospheric pollutants, the present study emphasises the strongly dynamic nature of the relatively inconspicuous epiphytes occurring at the junction between the 'lichen desert' of heavily polluted environments and the much more diverse and macrolichen-dominated communities of relatively unpolluted air. Under these more modestly polluted conditions, which are increasingly likely to characterize modern cities, a small selection of well understood bioindicators may be sufficient to provide a very detailed and dynamic picture of changing pollutant levels. Our results highlight the strong bioindicator value of *Lecanora conizaeoides* in situations where SO₂ pollution remains a significant component of town air, with particular value as a monitor of falling concentrations of this pollutant. This contrasts with the clear demonstration that the use of macrolichen indicator scales is not appropriate in the face of ameliorating SO₂ levels (Bates et al., 1990; Gilbert, 1992; Seaward, 1997).

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