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Evidence for the effects of atmospheric pollution on bryophytes from national and local recording

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INTRODUCTION

The effects of atmospheric pollution on the lichen flora of the British Isles are well known. They have not only generated a large body of scientific literature, but are familiar to the general public. By contrast, less attention has been paid to the effects of atmospheric pollution on bryophytes. A study of the relevant bibliographies suggests that in the 1980s papers on the effects of pollution on lichens outnumbered those on bryophytes by about four to one. Although these bibliographies are not strictly comparable, and probably exaggerate the preponderance of work on lichens¹, this figure is an indication of the relative attention paid to the two groups. Furthermore, the effects of atmospheric pollution on bryophytes are scarcely appreciated outside scientific circles.

The reason for the marked disparity between the work of bryologists and lichenologists probably lies in the larger number of lichen species available for use in pollution studies. Bryophytes can be shown to demonstrate the same range in apparent susceptibility to atmospheric pollution as can lichens. They are, perhaps, rather more conspicuous and slightly easier to identify; they would therefore be more suitable as monitors of pollution, other things being equal. However, the much larger suite of lichens which can be used in pollution studies is an advantage which greatly outweighs any difference there might be in ease of identification. The numerical

difference in epiphytes, an ecological group which tends to be particularly susceptible to atmospheric pollution, is illustrated in Table 1. This difference probably reflects the greater tolerance of lichens to xeric conditions.

In this paper, we attempt to review the evidence for the effect of atmospheric pollution on bryophytes in Great Britain which can be obtained from national distribution studies (Preston), and to compare it with evidence from intensive recording at the local scale in a highly polluted area, London and Essex (Adams).

THE POLLUTANTS

The deleterious effects of air pollution on cryptogams was first noticed in the mid-19th century. It is not surprising that the earliest observations were made in 'grim, flat, smoky Manchester' (Grindon 1859a²), the town which was such a potent symbol of industrial growth to the early Victorians (eg Disraeli 1844; cf Briggs 1968). Writing in *The Manchester Flora*, Grindon (1859b) commented that 'the majority of those [lichens] enumerated are not obtainable nearer than on the high hills beyond Disley, Ramsbottom, Stalybridge, and Rochdale, and even there the quantity has been much lessened of late years, through the cutting down of old woods, and the influx of factory smoke, which appears to be singularly prejudicial to these lovers of pure atmosphere'.

Table 1. A comparison of the number of epiphytic mosses, liverworts, total bryophytes and lichens in two regions and on one host genus

All species recorded on living bark are included, whether or not they occur in other habitats. The number of epiphytes is also expressed as a percentage of the corresponding species total for the two regions. The numbers are derived from Bowen (1968, 1980), Hill (1988), Jones (1952b, 1953), Pentecost (1987) and Rose (1974).

The areas from which bryophytes and lichens are compared in north Wales are not absolutely identical, as data for bryophytes have been extracted for vice-counties 48, 49 and 52 whereas for lichens the area covered is modern Gwynedd, which covers vice-county 49, 52, much of vice-county 48 and a small area of vice-county 50.

	Mosses		Liverworts		All bryophytes		Lichens	
	Total	Epiphytes	Total	Epiphytes	Total	Epiphytes	Total	Epiphytes
Berkshire and Oxfordshire	305	60 (20%)	86	12 (14%)	391	72 (18%)	366	189 (52%)
North Wales	497	57 (11%)	208	32 (15%)	705	89 (13%)	851	317 (37%)
On oak (<i>Quercus</i> spp.)		48		17		65		303

Although evidence of the effects of pollution gradually accumulated, the lack of recording gauges for sulphur dioxide (SO₂) delayed critical study of the causal agents until 1958 (James 1973). Thus, Jones (1952a,b) was still discussing the effects of pollution in terms of 'smoke'. Since 1958, fieldwork, transplants and experimental studies on cryptogams have demonstrated that SO₂ is the most important of the atmospheric pollutants. Rydzak's (1959) alternative hypothesis, that the disappearance of cryptogams from the vicinity of towns was caused by adverse micro-climatic conditions, particularly lower humidity, was not supported by Skye (1958) or LeBlanc (1961), who both found a correlation between SO₂ levels and epiphyte abundance in areas of high humidity. Rydzak's hypothesis has subsequently been rejected by both bryologists and lichenologists (LeBlanc & Rao 1973a; Coppins 1973).

In both Europe and North America, the major source of SO₂ is the combustion of the fossil fuels, coal and oil, for domestic heating, electricity generating, and industrial uses such as oil refining (Saunders & Wood 1973). Natural gas, by contrast, contains little sulphur. Industrial processes, such as the manufacture of bricks and the sintering of iron ore, can be significant point sources of SO₂ (Warren Spring Laboratory 1972; Rao & LeBlanc 1967; Department of the Environment 1980), although their overall contribution is much less than that of fossil fuels. The

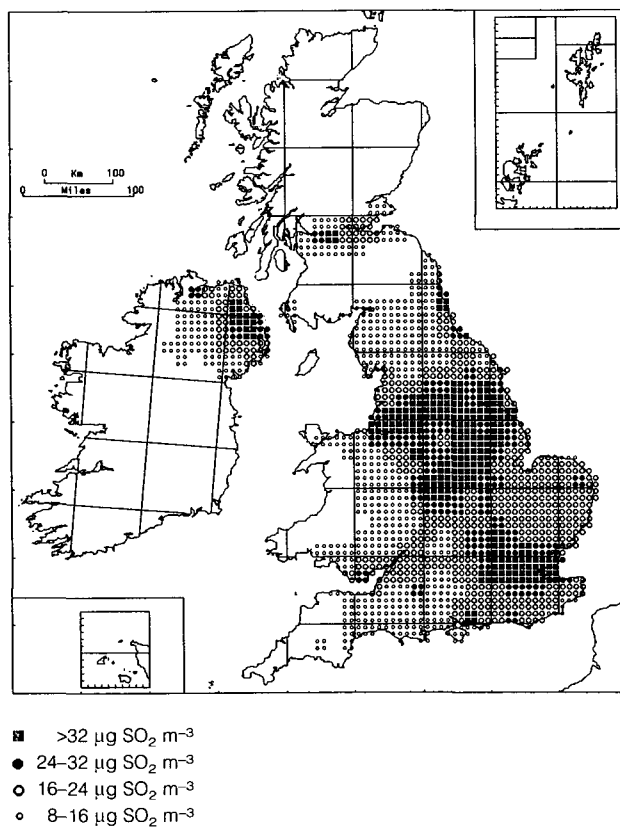


Figure 1. The estimated mean annual concentration of sulphur dioxide in the atmosphere in 1987, expressed as the mass of SO₂ m⁻³, in the United Kingdom. Emissions of sulphur dioxide have fallen sharply during the 30 years of the BBS mapping scheme. Map based on information from Warren Spring Laboratory.

amount of SO₂ emitted by natural phenomena, such as volcanic activity or forest fires, is negligible.

The estimated annual mean concentration of SO₂ in the atmosphere in 1987 is shown in Figure 1. The important feature of the map is the distribution of highly and less highly polluted areas; absolute values for a single year are less significant as they have decreased markedly in recent years (Munday 1990).

SO₂ accumulates on surfaces as the dry gas, dissolves in water as the highly toxic sulphite and bisulphite ions, or becomes oxidised to SO₃, dissolving in fog and rain drops as sulphuric acid. Winner, Atkinson and Nash (1988) estimated that on a dry weight basis the leaves of mosses absorb SO₂ at least 100 times more effectively than those of vascular plants. In addition to its direct effects, SO₂ modifies the habitat of epiphytes by acidifying bark and reducing its buffering capacity (Coker 1967).

There are numerous other atmospheric pollutants, which are less well documented than SO₂ and are not considered in detail here. However, it is worth pointing out that the concentrations of many (including nitrogen oxides, ozone and chlorofluorocarbons) have continued to increase in recent years, whereas concentrations of SO₂ have fallen in many areas. Any effects which these other pollutants have on bryophytes may become increasingly apparent.

The effect of heavy metal pollution on bryophytes lies outside the scope of this paper. There has been a number of studies on bryophytes in the vicinity of point sources of pollution. The extensive use of bryophytes for monitoring levels of metal pollutants is reviewed by Burton (1986).

THE NATURE OF EVIDENCE FROM FIELD STUDIES

In seeking field evidence about the possible effects of atmospheric pollution on bryophyte distribution, we are attempting to answer four questions.

1. Is the current distribution of a species correlated, either positively or negatively, with that of a pollutant?
2. Does any correlation in space extend to a correlation in time? There has been temporal as well as spatial variation in the concentration of SO₂. If SO₂ is an important factor determining the distribution of a species, we would expect changes in its distribution in response to these variations in concentration. There might, however, be a lag period before the response. The rate at which a species can colonise newly available habitats will depend on the availability of source populations and the mobility of the species. The effects of high concentrations of a pollutant might remain even after those concentrations have fallen. For example, if high levels of SO₂ have resulted in bark acidification, old acidified bark may persist for a period after the deposition levels have dropped.

3. Do correlations observed in Britain also apply in other countries? There is detailed evidence of the past and present distribution of bryophytes in other countries, particularly in north-west Europe. This evidence has been summarised in map form for liverworts in Belgium (Schumacker 1985) and mosses in the Netherlands (Touw & Rubers 1989). There are also studies of bryophytes around point sources of SO₂ pollution in the USA and Canada (reviewed by Winner 1988).
4. Is there another explanation for the past and present distribution of species? Many land use changes have taken place in the areas of greatest SO₂ concentration. Obvious examples include the destruction of semi-natural vegetation by urban development, changes resulting both from agricultural intensification (eg land drainage, destruction of hedgerows, use of artificial fertilizers), and from the increasing predominance of arable agriculture at the expense of pasture. Many species have declined as a result of these changes, one of the more striking examples being *Splachnum ampullaceum*, a moss which grows on mammal dung in fens, moorlands and bogs, and is now extinct in many south-eastern counties.

Answers to these four questions are only likely to be obtainable for taxa which are (or were) common or widespread, occurring in areas with differing concentrations of pollutants. The susceptibility of rare species which have always been confined to a few localities is unlikely to be detected by these methods, although one might suspect it if the trends in the distribution of a rarer species are consistent with those shown by related, commoner species for which more data are available.

Field recording can establish correlations between species distributions and levels of pollutants, and these correlations suggest hypotheses which can be tested by experimental methods. It is always important to bear in mind the fact that our hypotheses based on observed correlations can only be proved by rigorous experimental testing. However, it is also important that those involved in the acquisition and analysis of records should not underestimate the importance of the generation of hypotheses in the scientific process, or allow it to be underestimated by others.

EVIDENCE FROM THE QUATERNARY SUB-FOSSIL RECORD

The most devastating effect of atmospheric pollution on the semi-natural vegetation of the British Isles has been revealed primarily by evidence from the sub-fossil record (Press, Ferguson & Lee 1983). Examination of the peat deposits below the southern Pennine blanket bogs shows that *Sphagnum* species were formerly a much larger component of the blanket bog vegetation than they are today. The two species

which have in the past been major peat formers, *S. imbricatum* and *S. magellanicum*, are now completely absent from the area, and the bogs are currently dominated by cotton-grass (*Eriophorum vaginatum*). The appearance of soot deposits in the peat profile at the time of the Industrial Revolution is followed by the almost complete disappearance of *Sphagnum* remains. Suggestions that the reduction in *Sphagnum* cover was caused by atmospheric pollution are strongly supported by experimental studies, which demonstrate that artificial acid rain reduces the growth and photosynthesis of *Sphagnum*, and proves lethal to the more sensitive species, at concentrations which do not affect vascular plants. The most resistant of the species tested experimentally, the flush-dwelling *S. recurvum*, is the most widespread species in the southern Pennines today (Ferguson, Lee & Bell 1978; Ferguson & Lee 1980). Sulphur dioxide concentrations are much lower in the southern Pennines today than they were in the 19th century. Nevertheless, *Sphagnum* continues to be scarce even in areas where suitable habitats are apparently available for colonisation, and attempts to transplant *Sphagnum* to these sites only succeeded in establishing the most pollution-tolerant of the species investigated, *S. recurvum* (Ferguson & Lee 1983). It seems likely that deposition of atmospheric nitrogen, which has increased four-fold in the Manchester area since the 1860s, now inhibits recolonisation by *Sphagnum* species (Ferguson *et al.* 1984; Lee 1986; Press, Woodin & Lee 1986).

The sub-fossil record of *Sphagnum* is outstandingly rich; no other bryophyte genus is anything like as well represented (Dickson 1973). Nevertheless, sub-fossils of some other moss genera provide valuable distributional evidence for the period before botanical recording and before widespread atmospheric pollution (see, for example, the discussion of *Antitrichia curtipendula* below). Liverworts are, by contrast, very poorly represented in the sub-fossil record.

EVIDENCE FROM STUDIES OF NATIONAL DISTRIBUTION

The British Bryological Society's mapping scheme was launched in 1960, under the supervision of Dr A J E Smith. The scheme has concentrated on field survey, designed to establish the distribution of British bryophytes at the 10 km square scale, but significant historical records have also been extracted from literature sources and herbarium specimens. Over 750 000 records collected by the scheme were added to the computer database at the Biological Records Centre (BRC) between 1985 and 1989, and these have now been summarised as distribution maps. The first volume of a three-volume *Atlas of bryophytes of Britain and Ireland*, covering liverworts, has been published (Hill, Preston & Smith 1991); the moss volumes should be published by 1993. The draft maps prepared for the *Atlas* have

been used in this preliminary study. Once work on the *Atlas* is completed, a more detailed analysis of the dataset will be possible.

Decreasing species

Species which have been most adversely affected by atmospheric pollution at the national scale (judged by the four criteria outlined above) are listed in Table 2. There is evidence that all these species formerly grew in areas which are now characterised by high, or moderately high, mean annual concentrations of SO₂, but are now absent from them or are much rarer in those areas than they were. The 20 taxa listed comprise approximately 2% of the British bryophyte flora.

Table 2. Species which have apparently been most adversely affected by atmospheric pollution at the national scale

Epiphytes (ie plants growing on the bark of trees and shrubs)

* *Cryphaea heteromalla*

† *Frullania dilatata*
(also grows on rocks and boulders in the west)

* *Neckera pumila*

* *Orthotrichum lyellii*

* *O. obtusifolium*

* *O. schimperi*

* *O. speciosum*

* *O. stramineum*

* *O. striatum*

* *O. tenellum*

* *Tortula laevipila*

* *Ulota crispa* var. *crispa*

* *U. crispa* var. *norvegica*

Epiliths (ie plants growing on rocks and boulders)

Grimmia affinis

G. decipiens

G. laevigata

G. orbicularis

G. ovalis

Species which can grow as epiphytes or epiliths

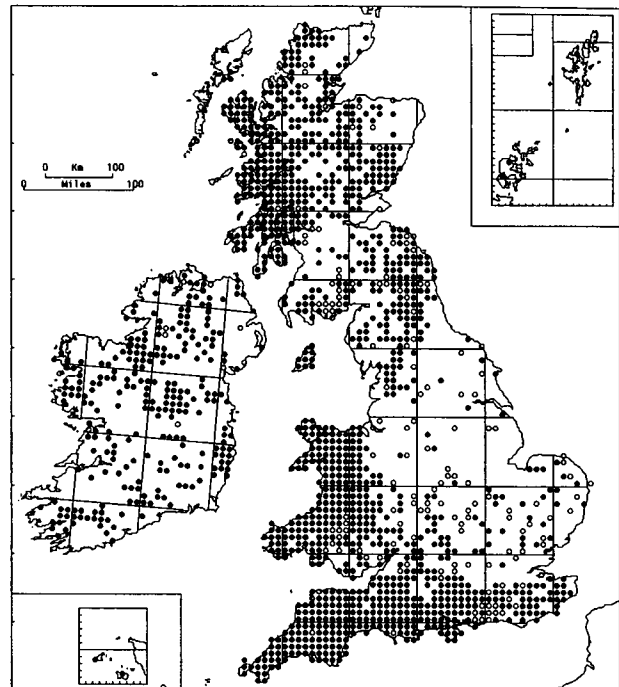
* *Antitrichia curtispindula*

* *Leucodon sciuroides*

† Has declined in Belgium (Schumacker 1985)

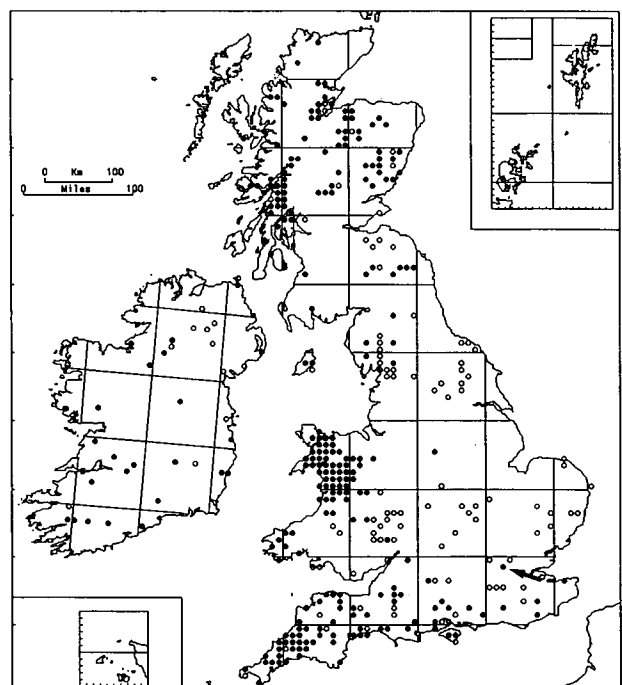
* Has declined in the Netherlands (Touw & Rubers 1989). Evidence from Dutch sources is not available for the *Grimmia* species; *G. laevigata* is the only species recorded in the Netherlands and it is restricted to two recently discovered localities

Most of the species listed characteristically grow as epiphytes, only occasionally occurring on other substrates. These are the 'obligate epiphytes' in the sense that Smith (1982) uses the term, but would more accurately be described as predominantly epiphytic. The sensitivity of some epiphytic bryophytes to pollution is well known (cf Rose & Wallace 1974). Epiphytes which have decreased in areas of high SO₂ concentrations (ie areas shown on Figure 1 with over 24 µg SO₂ m⁻³ in 1987) include *Ulota crispa* (Figure 2); species which have decreased even in areas of moderately high SO₂ concentrations (ie 8–24 µg SO₂ m⁻³ in 1987) include *Orthotrichum striatum* (Figure 3). Both species have shown a similar decline in the Netherlands, and *Ulota crispa* has



● Post-1950
○ Pre-1950

Figure 2. Distribution of *Ulota crispa* in Britain and Ireland. Records of both var. *crispa* and var. *norvegica* are included on the map. Many of the scattered post-1950 records in eastern England represent populations discovered in the last ten years



● Post-1950
○ Pre-1950

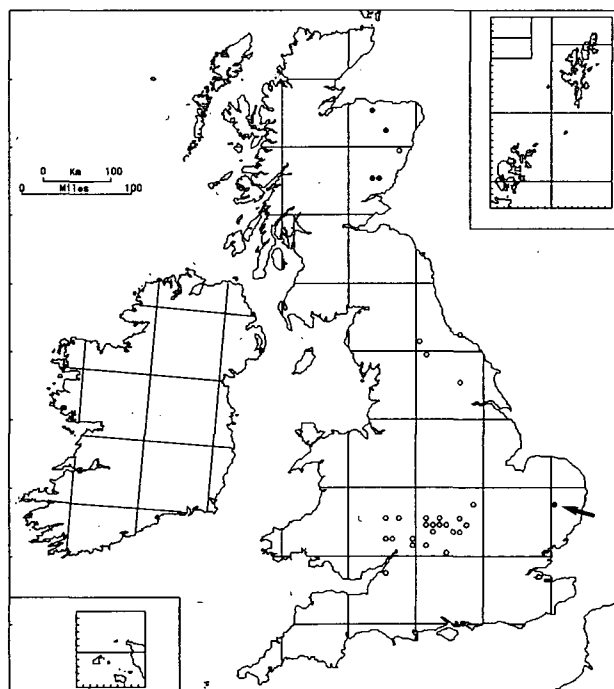
Figure 3. Distribution of *Orthotrichum striatum* in Britain and Ireland. The recently discovered Hampstead population is indicated by an arrow

also been identified as a particularly sensitive species in Canada (Rao & LeBlanc 1967).

Orthotrichum striatum, *Ulota crispa* and most of the other epiphytes listed in Table 2 still survive in areas of low SO₂ concentrations in the north and west. However, there is a very small group of species with a more continental distribution which have never been recorded in the west. These plants of the central and eastern counties have been particularly severely affected, as they have been virtually eliminated from areas of moderately high pollution in England and survive only in eastern Scotland.

Orthotrichum obtusifolium (Figure 4) is the best example; it was extinct in England from 1921 until 1989, when a single tuft was discovered on a roadside elder (*Sambucus nigra*) in Norfolk. *O. obtusifolium* is a frequent epiphyte in Canada, where studies have shown that it decreases greatly in frequency and fertility towards the polluted centre of Montreal (LeBlanc & Rao 1974; LeBlanc & De Sloover 1970) and is damaged by both SO₂ and fluoride pollution when transplanted from unpolluted to polluted sites (LeBlanc, Comeau & Rao 1971; LeBlanc & Rao 1973b). The rarer *Orthotrichum speciosum*, extinct in Sussex and Yorkshire, but still present in Scotland, probably belongs in the same category.

The epilithic *Grimmia* species listed in Table 2 are species of well-illuminated, dry, acidic or basic rocks, often at low altitude. Their decline has not usually been attributed to atmospheric pollution, but Hill (1988) points out that at least some epiliths are likely to be affected by pollution, and it is difficult to suggest another explanation for the decline. Exper-



- Post-1950
- Pre-1950

Figure 4. Distribution of *Orthotrichum obtusifolium* in Britain and Ireland. The recent Norfolk record is indicated by an arrow

imental studies of the susceptibility of these species to atmospheric pollutants are clearly desirable.

Leucodon sciurioides can grow either epiphytically or epilithically. In some counties of south-east England (eg Cambridgeshire, Surrey), it is no longer present as an epiphyte, but survives on church walls and churchyard monuments, usually, if not exclusively, on calcareous stone. This restriction might be the result of atmospheric pollution alone, but it is also possible that churchyards provide a sanctuary from other potentially adverse changes, such as the eutrophication of substrates by atmospheric drift of agricultural fertilizers.

The remarkable decline of *Antitrichia curtispindula* in England has often been commented on, and has been attributed (by Rose & Wallace 1974) to the particular sensitivity of this species to SO₂, coupled with the felling of ancient trees. *Antitrichia* is an easily recognised species, well represented in the fossil record. It was abundant in the west in the Late Devonian, and spread rapidly to colonise eastern England in the early Flandrian (Dickson 1973). It is found in Bronze Age, Roman and Saxon archaeological sites in Hampshire, Oxfordshire, Suffolk, Huntingdonshire, Lincolnshire, Nottinghamshire and south-east Yorkshire (Dickson 1973, 1981; Stevenson 1986). Its decline in England may have begun before the onset of widespread SO₂ pollution; the decline has been so extensive that it is doubtful whether it can have been caused by atmospheric pollution alone, although this is almost certainly one of the factors responsible.

Increasing species

It is much more difficult to establish that a species is increasing than it is to demonstrate a decrease. This difficulty is especially true for a relatively inconspicuous group such as the bryophytes, where one can rarely be certain that the absence of earlier records indicates the absence of the plant rather than the fact that it was overlooked. However, there is evidence to suggest that three members of the Dicranaceae, which grow epiphytically on acid bark, have increased: *Dicranoweisia cirrata* in the late 19th and early 20th centuries and *Dicranum montanum* and *D. tauricum* (synonym: *D. strictum*) more recently (Rose & Wallace 1974; Smith 1978). *Ptilidium pulcherrimum* is an epiphytic liverwort which may have increased (Wallace 1963), although the evidence is not conclusive; it is interesting to note that Rao and LeBlanc (1967) found that this bryophyte was the most tolerant to SO₂ in the vicinity of a Canadian iron sintering plant.

EVIDENCE FROM LOCAL STUDIES IN LONDON AND ESSEX 1800-1990

The rise and fall of atmospheric pollution in London

With the widespread use of coal for domestic heating in the mid-19th century, and the development of

coal-burning power stations, in response to massive population growth, London became a potent source of atmospheric pollution, dominated by suspensions of smoke and soot particles, and in particular SO_2 . The virtually pristine air of the early 1800s began to deteriorate rapidly soon after that date, and by the 1870s many species of bryophytes and lichens were already becoming scarce in London. The area to the north-east of the metropolis was also affected, as pollutants were dispersed by the predominantly south-westerly winds. As Crombie (1885) noted, 'the paucity of lichen-growth [in Epping Forest] . . . is attributable to the atmosphere being in some states of the weather more or less impregnated with smoke from the increased number of human habitations on the outskirts of the Forest, the acids contained in which are most destructive to lichens. Add to this that the direction of the prevailing winds being from the SW, the smoke and fogs of London and its suburbs extend their deleterious influence at certain seasons of the year to the nearer portions of the Forest, and even considerably beyond. . . .

Despite the toxicity of SO_2 to vegetation and the disastrous effects of sulphuric acid on stonework and human lung tissue, the initial concerns were with the control of smoke emissions. Enormous quantities of particulate matter were being belched into the atmosphere of London by domestic coal-burning fires. The annual-averaged smoke concentration at ground level in London for 1954, for example, was some $250 \mu\text{g m}^{-3}$ (Warren Spring Laboratory 1972), and the smoke plume drifted downwind far out into Essex, coating vegetation and buildings with a layer of sticky black grime. The Clean Air Acts of 1956 and 1968 only legislated against smoke emissions. They were very effective, however, and rapidly cured the smoke problem, the last severe smog in London being recorded over the winter of 1962–63 (Chandler 1976). SO_2 levels in central London during the period 1954–64 were typically around $570 \mu\text{g m}^{-3}$ (0.2 ppm) during the winter months, peaking as high as $5700 \mu\text{g m}^{-3}$ (2.0 ppm); the corresponding figures for sulphuric acid were $10 \mu\text{g m}^{-3}$ and $700 \mu\text{g m}^{-3}$ (Lawther 1965).

Fortuitously, the change-over to less smoky, more efficient, domestic combustion systems coincided with the transition from coal to solid fuels with a lower sulphur content, and a gradual decline in atmospheric SO_2 concentration in London and East Anglia has taken place since the late 1950s. Although, in contrast, industrial/power station output of SO_2 in London continued to rise, the increase was offset by the installation of tall chimneys that disperse the SO_2 and sulphuric acid in the prevailing south-westerly winds, high enough up into the atmosphere for most of it to avoid London and the eastern counties, exporting it instead to Scandinavia as acid precipitation.

The greatest levels of atmospheric SO_2 near ground level do not occur during the coldest months when the output is greatest, but during the autumn when

inversions entrap the SO_2 from domestic sources, and when bryophytes and lichens are in their most active phase of growth. The hot rising plumes from tall power station chimneys 'punch' holes through the inversion layers, allowing long-range dispersal despite the presence of static air at ground level.

The increasing use of sulphur-rich oil for domestic heating since 1950 is thought to have been at least partly responsible for a temporary rise in SO_2 levels in London between 1961 and 1965. Subsequent legislation to reduce the sulphur content of heating oils, and the increasing use of natural gas have promoted a gradual decline in domestic SO_2 output. Since 1965 the rate of fall in the annual-averaged atmospheric SO_2 concentration in London has continued more or less linearly at approximately $60 \mu\text{g m}^{-3}$ per decade (Figure 5). This gradual fall has probably also been assisted by the closing down of several of the older, less efficient, coal-burning power stations in London, and a general decline in heavy manufacturing industry.

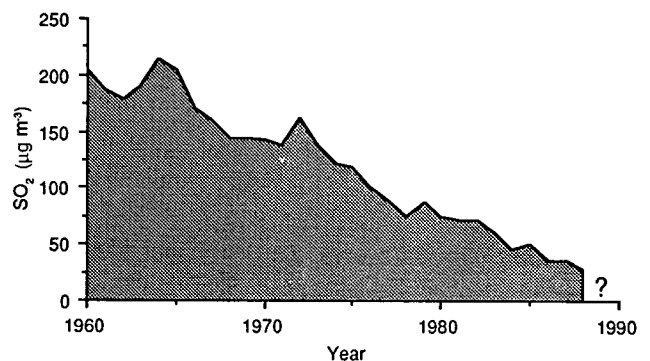


Figure 5. Mean trends in the March–April annual-averaged atmospheric SO_2 concentrations ($\mu\text{g m}^{-3}$) for a selection of sites in London from 1959–60 to 1987–88. The rate of fall in concentration approximates to $60 \mu\text{g m}^{-3}$ per decade

Despite the gradual decline in SO_2 output in London since the late 1950s, levels remained toxic to many lichens and bryophytes in London and south-west Essex until well into the 1970s. Thus, in 1971–72, SO_2 levels reached a mean winter value of $170\text{--}180 \mu\text{g m}^{-3}$ in the south-west corner of vice-county 18 (South Essex), falling to $c120 \mu\text{g m}^{-3}$ in an arc from Chingford to Thurrock; to about $70 \mu\text{g m}^{-3}$ in an arc to the north-east of London passing through Chelmsford; and to around $60 \mu\text{g m}^{-3}$ at the Essex/Suffolk border – only the extreme coastal areas of Norfolk receiving less than $40 \mu\text{g m}^{-3}$. It was not until the mid-1970s that there was any noticeable effect on SO_2 -sensitive lichens, and probably not until the early to mid-1980s on sensitive bryophytes, as a result of the gradual fall in SO_2 levels in London and Essex, and the bryophyte flora was still in obvious decline during the period 1967–74 when a baseline survey was carried out for the *Flora of Essex* (Jermyn 1974).

Even as late as 1984–85, however, winter levels in central London were around $130 \mu\text{g m}^{-3}$ whenever

prevailing easterly winds brought in SO₂ from power stations to the east of London, and short-term episodes peaked in excess of 1000 µg m⁻³ (Harrop, Laxen & Daunton 1985). These seasonal and short-term fluctuations make it extremely difficult to correlate SO₂ levels with damage to bryophytes, as single short-term pulses could well be lethal to some species against a background level which they might otherwise tolerate.

The decline of the bryoflora

The early history of the decline of bryophyte (and lichen) species in the area north-east of London is fragmentary and largely dependent on three collectors: Edward Forster, who collected mainly in the Epping Forest and Walthamstow areas around 1800; Ezekiel G Varenne, mainly in the Kelvedon area from 1860 to 1876; and Frederick Y Brocas in the Saffron Walden area around 1847. Forster's herbarium, in particular, is crucial to our understanding of the lethal effects of air pollution on bryophytes. Around 1800 he collected extensively in the Epping Forest area, finding many species that have not otherwise been recorded in Essex; he effectively set a baseline for future observations.

The decline of epiphytic bryophytes, and particularly lichens (Rose & Hawksworth 1981), has been extensively highlighted nationally. In Essex about 20 bryophyte species have been severely affected, notably members of the Orthotrichaceae. *Neckera pumila*, *Orthotrichum schimperi*, *O. sprucei*, *O. striatum*, *Ulota crispa* var. *crispa* and *Zygodon conoideus* are all extinct in Essex, and *Cryphaea heteromalla*, *Leucodon sciuroides*, *Orthotrichum lyellii*, *Tortula papillosa* and *Ulota crispa* var. *norvegica* are confined to isolated localities in north Essex, though they were formerly widespread. Other species have been severely restricted by pollution in south-west Essex, but are reasonably abundant further out. *Frullania dilatata*, *Radula complanata*, *Porella platyphylla* and *Isothecium myurum* are all now absent in south-west Essex, and *Neckera complanata* only survives as isolated scraps deep in sheltered woodland. These species appear to have become obligate calcicoles, following fairly closely the distribution of chalk and chalky boulder clay deposits in north-west Essex. This pattern may be an artifact, more related to SO₂ levels than substrate acidity, however. Curiously, *Lejeunea cavifolia* persists on a single tree by a deep ditch in Running Water Woods, Upminster, although it now appears to be extinct elsewhere in Essex.

Of the epiphytes that have survived the onslaught of SO₂ in south-west Essex, *Lophocolea heterophylla*, *Brachythecium rutabulum*, *Rhynchostegium confertum*, *Eurhynchium praelongum* and *Isothecium myosuroides* provide the main cover on tree bases and stumps, with *Tetraphis pellucida* and *Orthodontium lineare* taking over in acid areas. *Hypnum mammillatum* is surprisingly abundant in Monks Wood, Epping Forest, seeming to be no more sensitive to

pollution than corticolous *H. cupressiforme* var. *cupressiforme* though more so than *H. cupressiforme* var. *resupinatum*.

Although *Dicranoweisia cirrata* has been compared with *Lecanora conizaeoides* in its ability to colonise the so-called lichen desert, it is far more sensitive to pollution than *Lecanora* in eastern England. *D. cirrata* survived in the urban outskirts of London during the worst of the pollution, though was seldom found fruiting, but in the most heavily polluted areas virtually all the epiphytic species were wiped out. *Hypnum cupressiforme* var. *resupinatum* and *Ceratodon purpureus* were probably the most resistant epiphytic mosses (on tree bases) in heavily polluted areas. *Dicranoweisia* may have been able to establish itself by leaf gemmae, which it produces copiously in eastern England, in areas too polluted for the protonema to establish from spores.

A few species only able to persist intermittently between intense episodes of pollution in eastern England may have been continuously replenished by spores or leaf fragments blown in on the wind, or carried by birds, from the Continent. The sporadic and ephemeral occurrence of *Ptilidium pulcherrimum*, *Dicranum flagellare*, *D. tauricum* and *Ulota crispa* var. *norvegica* in many localities suggests some of them may have arrived in this way.

By looking at the sequence of extinctions against rising levels of SO₂, and the present-day distribution of species in conjunction with known SO₂ levels between 1950 and 1970, it is possible to draw up a table of bryophyte sensitivities equivalent to that of the Hawksworth and Rose (1970) scale for lichens. Table 3 is based on the deduced extinction sequence for Epping Forest and the surrounding counties. This scale must be interpreted with caution, however, as the position of a species on the scale will depend on habitat humidity, and, as in the case of the lichen scale, the acidity of the bark substrate. Thus, species of *Ulota*, *Orthotrichum*, *Zygodon viridissimus*, *Frullania dilatata*, *Tortula laevipila* and *Metzgeria furcata* appear first on neutral barks, such as those of field maple (*Acer campestre*), crack willow (*Salix fragilis*) and elder.

In addition to the familiar pollution-sensitive epiphytic bryophytes, numerous terrestrial and saxicolous species have also been exterminated or rendered infertile by atmospheric pollution in many parts of Britain. Gilbert (1971) noted that in the worst affected areas of Newcastle-upon-Tyne (>170 µg m⁻³ SO₂) only *Ceratodon purpureus* and *Bryum argenteum* appeared able to survive in abundance. Further out, as levels fell to between 130 and 70 µg m⁻³ SO₂, *Tortula muralis* and *Bryum capillare* were added to the list; and *Grimmia pulvinata* and *Orthotrichum diaphanum* appeared on artificial substrates as the level fell to between 50 and 40 µg m⁻³. This describes graphically the situation that prevailed in London and the inner suburbs until the early 1980s.

Even outside the London suburbs, where the bryophyte flora retained much of its diversity, there

Table 3. Mosses and liverworts found as epiphytes on the trunks, bases, crotches, stumps or roots of trees that showed poor or restricted growth during the maximum phase of SO₂ pollution, or were exterminated, with their approximate equivalent SO₂ thresholds. Based on historical records and field survey from 1967 to 1990 in Epping Forest and outer Essex

NB Some species may fare better on limestone than on trees, or may move up and down the scale depending on whether the bark is acid or neutral. Those species able to survive desiccation must also be expected to move up the table in areas of the country where the average humidity is higher than in the London/Essex area

Mean winter SO ₂ (µg m ⁻³)	Approximate pollution zone*		Last or only date recorded	
			Epping Forest	Outer Essex
'Pure'	9-10	# <i>Antitrichia curtipendula</i>	c 1800	1874
	9	<i>Orthotrichum sprucei</i>	-	1866
<30	9	<i>Orthotrichum schimperi</i>	-	1873
	9	<i>Orthotrichum tenellum</i>	-	1870
	9	<i>Ulota crispa</i> var. <i>crispa</i>	c 1800	1874
	9-8	<i>Orthotrichum striatum</i>	c 1800	1870
c 35	8	<i>Zygodon conoideus</i>	1885	1886
	8	<i>Neckera pumila</i>	1890	1874
	8-7	<i>Tortula papillosa</i>	-	1874
	7	<i>Ulota crispa</i> var. <i>norvegica</i>	-	:
c 40	7	# <i>Anomodon viticulosus</i>	1932	:
	7	# <i>Radula complanata</i>	c 1890	:
	7-6	<i>Leucodon sciuroides</i>	1885	:
	6	<i>Orthotrichum lyellii</i>	1898	:
	6	<i>Cryphaea heteromalla</i>	c 1800	:
c 50	6	<i>Frullania dilatata</i>	1923	:
	6	# <i>Homalia trichomanoides</i>	1973	:
	6	<i>Porella platyphylla</i>	c 1890	:
	6-5	<i>Isothecium myurum</i>	1885	:
	5	<i>Tortula laevipila</i>	c 1980	:
	5	<i>Neckera complanata</i>	:	:
c 60	5	<i>Zygodon viridissimus</i>	:	:
	5	<i>Orthotrichum affine</i>	:	:
	5	<i>Orthotrichum diaphanum</i>	:	:
	5-4	<i>Homalothecium sericeum</i>	:	:
	4	<i>Hypnum mammillatum</i>	:	:
	4	<i>Hypnum cupressiforme</i> var. <i>cupressiforme</i>	:	:
	4	<i>Dicranum scoparium</i>	:	extant
c 70	4	<i>Isothecium myosuroides</i>	:	:
	4	<i>Bryum capillare</i>	:	:
	4-3	<i>Dicranoweisia cirrata</i>	:	:
	3	<i>Hypnum cupressiforme</i> var. <i>resupinatum</i>	:	:
	3	<i>Lophocolea heterophylla</i>	:	:
c 125	3	<i>Lophocolea heterophylla</i>	:	:
c 150	2-3	<i>Ceratodon purpureus</i>	:	:

Species which may be limited by factors other than specific sensitivity to SO₂

* Hawksworth and Rose (1970)

were specific casualties extending well out into East Anglia. Among terrestrial mosses, for example, *Rhytidiadelphus loreus*, last recorded in Epping Forest in 1912, and in Hatfield Forest in 1890, is now extremely rare in eastern England. Its decline was closely fol-

lowed by that of *Rhytidiadelphus triquetrus*. Recorded as 'common' and collected fruiting in Epping Forest in 1800 (Forster), it had become 'very scarce' there by 1885 (J T English) and must have become extinct well before the 1960s when E Saunders noted its

absence, as by 1967 it had also been exterminated over a wide area of Essex. It was last seen in Hatfield Forest at a single site in 1965, for example. Although *R. loreus* appears to be virtually extinct in eastern England today, *R. triquetrus* still occurs in numerous pockets, apparently as an obligate calcicole, in north and east Essex, Suffolk and Norfolk. In contrast *Rhytidiadelphus squarrosus* remained an abundant grassland species (eg in lawns), even in the outer London suburbs, during the maximum phase of pollution. These three species demonstrate just how different the sensitivity to SO₂ can be, even among species in the same genus.

Bartramia pomiformis and *Hylocomium splendens* are further examples of sensitive terrestrial mosses. They were last recorded in Epping Forest in 1931 and 1912, respectively. *Bartramia* is now only found in isolated pockets in north-east Essex, while *H. splendens* is only known in Essex from one site, near Colchester. Even *Tortula ruralis* is not found commonly on the ground until well out into Essex towards Colchester. So far these species have not yet shown any response to the post-1950 SO₂ decline (Table 4).

Table 4. Terrestrial mosses now absent in the south-west of Essex that are believed to have succumbed to SO₂ pollution, in approximately decreasing order of sensitivity

<i>Rhytidiadelphus loreus</i>
<i>Hylocomium splendens</i>
<i>Bartramia pomiformis</i>
<i>Rhytidiadelphus triquetrus</i>
<i>Tortula ruralis</i>
<i>Hypnum cupressiforme</i> var. <i>cupressiforme</i>

In contrast, *Rhytidiadelphus squarrosus*, *Pseudo-scleropodium purum*, *Calliargon cuspidatum*, *Hypnum jutlandicum*, *Brachythecium rutabulum*, *Brachythecium albicans*, *Amblystegium serpens* and *Eurhynchium praelongum* all seem to have maintained their distribution and abundance during the severest period of pollution, but, curiously, *Hypnum cupressiforme* var. *cupressiforme* is largely absent as a terrestrial moss far out into East Anglia.

Ctenidium molluscum, *Philonotis fontana*, the bog mosses *Sphagnum tenellum* and *S. subnitens*, and the liverworts *Scapania irrigua*, *S. nemorea* and *S. undulata* are also suspected to have been affected by acid rain in south-west Essex, but there may have been other factors contributing to the decline of these species.

Bryophyte species characteristic of brick and stone walls, tiled roofs and churchyard tombs have also suffered extensively in London and Essex from atmospheric pollution. *Rhynchostegium confertum*, *Amblystegium serpens*, *Tortula muralis*, *Ceratodon purpureus*, *Barbula convoluta*, *Bryum capillare*, *B. argenteum*, *B. caespiticium* and *Hypnum*

cupressiforme var. *resupinatum* seem to have withstood the worst phase of pollution in the outer London suburbs, but *Barbula revoluta*, *Barbula rigidula*, *Tortula intermedia*, *Orthotrichum anomalum*, *Barbula vinealis*, *Zygodon viridissimus*, *Schistidium apocarpum*, *Homalothecium sericeum*, *Grimmia pulvinata* and *Orthotrichum diaphanum* – roughly in that order of decreasing sensitivity – have been severely affected. All these species became virtually extinct in central London and the inner suburbs during the worst of the pollution. In the outer suburbs, *O. diaphanum* and *H. sericeum* survived as calcicoles on stone, the latter seldom fruiting, but were largely absent as epiphytes. Today *H. sericeum* is only found as tiny scraps on gnarled tree roots in Epping Forest, with the exception of a handful of leaning trees where it occurs in rain tracks on the trunks.

The wind of change

Although the prevailing south-westerly winds from London cast a pall of death on the bryophyte and lichen communities in eastern England for over 100 years, the decline in SO₂ levels now appears to be taking effect. Spores and other propagules carried in on the wind from south and west Britain, and from the Continent of Europe, are leading to a spectacular recovery and recolonisation of bryophyte (and lichen) species.

The lichens were the first to respond, with recolonisation of the inner suburbs of London by foliose species in the period 1970–80 (Rose & Hawksworth 1981), and further spectacular improvements since then (Hawksworth & McManus 1989). In Essex and Middlesex there has been a dramatic recolonisation by lichens on crack willow, sallow (*Salix* spp.) and oak (*Quercus* spp.). In the period 1987–89 the recolonisation got well under way in outer Essex, but in the autumn of 1989 and spring of 1990 foliose lichens (with *Parmelia sulcata* in the vanguard) began to appear in quantity in Epping Forest and Bedfords Park. Large thalli of *Parmelia perlata* were discovered on sallows (*Salix cinerea*) by Baldwins Pond in 1989 in Epping Forest, and on willow in Pond Wood, Middlesex, and Hatfield Forest, Essex. Even more spectacularly, they were discovered on crack willow just north of Hampstead Ponds, Hampstead Heath in central London, growing together with *Usnea inflata*, formerly regarded as a species of the western and southern coasts.

Bryophytes have been much slower to respond than lichens. Possibly either residual acid in tree bark held them back for several additional years or the airborne density of propagules was a limiting factor. Significant increases in the luxuriance of existing plants have been noted in Essex, possibly encouraged by the mild winters of 1988–89 and 1989–90, in addition to the decrease in rainfall acidity. *Isoetium myosuroides*, formerly confined to tree bases, now clothes the trunks, up to the crowns, of many pollards in Gurnon Bushes, north of Epping, and *Orthotrichum affine*, previously only ever found as tiny sterile

scraps a few millimetres high, has suddenly become an abundant and luxuriant, characteristically fruiting plant, on elder in several areas. In Bedfords Park a colony of *Frullania dilatata* appeared on a young oak in 1989–90, the first time it has been seen in south-west Essex since 1926, and *Orthotrichum pulchellum* has been reported for the first time ever (1990) in north Essex.

Perhaps most spectacularly of all, however, has been the finding (Adams 1990) of several bryophyte species formerly regarded as extinct in London, all growing together on crack willows in the Hampstead Ponds and Highgate Ponds valleys, on either side of Parliament Hill on Hampstead Heath. Some ten tufts of fruiting *Orthotrichum striatum* were found in the spring of 1989 on the horizontal bough of a crack willow by Hampstead Ponds. Subsequently numerous fruiting tufts of *Orthotrichum affine*, three tufts of *Ulota crispa* var. *norvegica* – also in fruit and all on different trees – and two colonies of *Frullania dilatata* were all discovered on the same patch of willows, virtually within sight of the Royal Free Hospital. Over in the next valley was a large tuft of *Ulota phyllantha*, again on willow. These records suggest that these newcomers must have established themselves several years previously, possibly as early as 1985, and clearly indicate that not only has SO₂ pollution been brought firmly under control in London, but that other gaseous pollutants, in particular ozone and the nitrogen oxides (which are still known to be rising in concentration due to vehicle emissions), do not seem to have a toxic effect on either bryophyte growth or re-establishment.

Tortula intermedia is also making a comeback, having reappeared on both old and new tiled roofs in Loughton, Essex, in about 1986–87, rapidly forming large cushions. *Orthotrichum diaphanum* has become much more luxuriant and is appearing in fruit on concrete walls all over the London suburbs, and *Schistidium apocarpum*, together with *Orthotrichum anomalum*, is reappearing on limestone surfaces, as by Highgate Ponds on Hampstead Heath.

Although it would appear that SO₂ is toxic to many species of bryophyte, and in particular, in varying degree, to members of the Orthotrichaceae, it may not be so for all species of bryophytes. In addition to being sensitive to SO₂, some species may be affected by other pollutants. Indeed, some SO₂-resistant species may be succumbing to other pollutants. Two species which appear to exhibit an anomalous response to the decline in SO₂ levels are *Homalia trichomanoides* and *Anomodon viticulosus*. Both these species have continued to decline throughout eastern England, and only occur in isolated pockets on neutral bark substrates in microhabitats with a high humidity. Most surviving colonies are still showing signs of tissue damage, and many of the shoots are dead. Could these two species be sensitive to nitrogen oxides, ozone, or perhaps ammonia, in addition to SO₂?

PHYSIOLOGICAL EFFECTS OF POLLUTANTS

Very little is known about the precise effects of SO₂ and sulphite on epiphytic bryophytes (and still less on terrestrial species). Most experimental work has been centred on the experimental gassing of established gametophytes or reciprocal transplant experiments in the field. Coker (1967) has shown, however, that SO₂ can acidify bark and reduce its buffering capacity. Rotten bark apparently has a higher buffering capacity, which may explain why this is preferentially colonised by epiphytic bryophytes in heavily polluted areas. Re-establishment could, however, be affected by poisoning of the protonemal stages (Gilbert 1968), or the antherozoids, or even the spores, or gametophyte stress could result in suppression of gametangia.

Experimental gassing of epiphytic bryophyte gametophytes with known concentrations of SO₂ has shown that they respond to SO₂ exposure by attempting to oxidise the sulphite to sulphate, the latter being some 30 times less toxic (Thomas 1961). Most sensitive species appear to use respiratory energy for this purpose, exhibiting a burst of oxygen uptake following exposure, but at the higher SO₂ levels are rapidly overcome, beginning to show signs of physiological damage (eg chlorophyll breakdown and a fall in respiration rate) within a few hours of exposure, followed rapidly by cell death (Syratt 1969). A particularly obvious reducing effect of sulphurous acid is the replacement of the Mg⁺⁺ ion in the porphyrin ring of chlorophyll by 2H⁺, causing a bleaching of the characteristic green colour and formation of the grey phaeophytin.

Dicranoweisia cirrata has been shown by gassing experiments to be able to use photosynthetic energy to detoxify SO₂ and accumulate sulphate with relative impunity (Syratt 1969). In darkness, however, it has to rely on respiratory energy and appears to be no more efficient at accumulating sulphate than such sensitive species as *Ulota crispa*. It would appear, therefore, that an ability to sustain a high level of oxidative capacity to detoxify continuously absorbed sulphite may be the critical factor enabling a species to resist SO₂ poisoning, rather than any species-specific variation in sensitivity to accumulated sulphate. Thus, species capable of utilising light energy for this purpose are likely to gain a competitive advantage over those restricted by limited reserves of respiratory substrates. Furthermore, Syratt (1969) has shown that even resistant species suffer some chlorophyll breakdown on exposure to SO₂, and so a high chlorophyll content may be a further prerequisite to resistance, enabling plants to survive exposure to short pulses of very high SO₂ levels. He was able to show an inverse correlation between average chlorophyll content of a species and sensitivity in gassing experiments.

Several workers have noted that the resistance of species to SO₂ has a marked dependence on

humidity (Coker 1967). This dependence has been shown to be due in part to the ability of bryophytes to shut down their metabolism in the dehydrated state. Unlike higher plants, many bryophytes also have cell walls that crumple around the shrinking protoplasts thus preventing plasmolysis, and in many species the protoplasts can sustain very high osmotic pressures by shutting down their metabolism until rehydrated. This may be the reason why *Lophocolea heterophylla* and *Hypnum cupressiforme* var. *resupinatum* were so successful at surviving in the bryophyte/lichen desert in the east London area during the worst phases of pollution, and why *Hypnum mammillatum* survives in Epping Forest despite its high sensitivity to SO₂ in the hydrated state (Syratt 1969).

Bryophytes differ considerably in their internal osmotic potentials (OP). Members of the Orthotricaceae, *Cryphaea*, and *Antitrichia* typically have high internal OPs (about 25 atmospheres), making them tolerant of areas of low humidity. On wetting they rehydrate rapidly, however, and are more likely to take in surface-accumulated and dissolved pollutants. More SO₂-tolerant species such as *Mnium hornum* and *Isoetecium myosuroides* have lower internal OPs and rehydrate much more slowly (Coker 1967).

DISCUSSION

Relationship between national and local recording

The observations on the effect of atmospheric pollution outlined above illustrate the value of national recording and of detailed local studies, and demonstrate their inter-dependence. The national recording scheme has identified species which appear to have shown very marked responses to atmospheric pollution over large areas. This national picture is, however, inevitably imprecise, as it aggregates records from areas with differing histories of recording and different degrees of recent coverage. It is therefore valuable to be able to test correlations derived from national recording against a dataset derived from London and Essex, one of the few areas with a long history of bryophyte recording.

The lists of epiphytes which are apparently susceptible to atmospheric pollution in Great Britain (Table 2) and Essex (Table 3) were derived separately, by Preston and Adams respectively. (It is impossible to claim, however, that the lists are truly independent as we must share many basic beliefs and assumptions.) There is a good correspondence between the national and local lists: eleven of the 18 species regarded as most susceptible to pollution on the basis of evidence from Essex appear in the national list of adversely affected species, and three of the remainder are suspected of being limited by factors other than SO₂ pollution. Discrepancies between the lists could arise if the evidence of national distribution currently available is insufficient to indicate susceptibility to atmospheric pollution, or if the

decline in Essex was actually caused by other factors.

The effect of atmospheric pollution on the fruiting performance or vegetative vigour of a species is most likely to be identified by intensive local studies. The work of Jones (1952b, 1953) in Berkshire and Oxfordshire, another area with a long history of bryophyte recording, led him to conclude that 19th century specimens of epiphytes such as *Neckera pumila* and *Orthotrichum lyellii* were much more luxuriant than material which he could have gathered in the area. The increase in luxuriance of some mosses which followed the recent decrease in SO₂ pollution in the London area has been discussed above.

Studies in an area which has been as heavily polluted as London also identify species which have declined locally in areas of extremely high SO₂ concentrations, but which are scarcely affected at the national scale. *Grimmia pulvinata*, *Homalothecium sericeum* and *Orthotrichum diaphanum*, although almost eliminated from central London and the inner suburbs during the period of maximum SO₂ pollution, are nevertheless virtually ubiquitous elsewhere in southern England.

Future recording in a period of falling SO₂ levels

The remarkable return of epiphytic species to the London area described above has been paralleled elsewhere in southern England. In Cambridgeshire, for example, *Ulota crispa* was recorded in 1984 for the first time since 1881; subsequently *Cryphaea heteromalla*, *Leucodon sciuroides* and *Orthotrichum lyellii* have all been discovered in new sites in the county (Whitehouse 1985; Preston & Whitehouse 1989).

It will be fascinating to observe the sequence in which bryophytes return to the formerly polluted areas. SO₂ levels have fallen so rapidly in London that species are unlikely to recolonise in an order which reflects their sensitivity to pollution. No species are likely to be limited by SO₂ concentrations alone. The sequence of recolonisation is likely to be determined by the proximity of source populations and the mobility of the species. Epiphytes are amongst the more mobile bryophytes. Smith (1982) noted that there is a high proportion of monoecious taxa amongst obligate, as opposed to facultative, epiphytes. He interpreted this finding as an adaptation to promote homozygosity amongst species with specific habitat requirements, but it might also be validly interpreted as an adaptation to maximise the likelihood of sporophyte production, and hence the possibility of colonising a habitat which is regularly created by growing trees. In addition, many epiphytes reproduce asexually by gemmae.

Species may colonise areas from which they have never been recorded in the past. There are, indeed, already signs that this is beginning to happen. Since 1984 *Orthotrichum pulchellum* has been found in five

English vice-counties from which it had not previously been recorded (North Essex, Hertfordshire, West Suffolk, Cambridgeshire and Huntingdonshire). *Ulota phyllantha*, a distinctive epiphyte which is most abundant in coastal areas, has been found in eight new English vice-counties since 1983 (and rediscovered in a further three in which it was believed to be extinct). These records may arise from the recolonisation of areas in which the species previously grew, but was not recorded because of the paucity of 18th and 19th century bryologists. However, habitats which are available to epiphytes now will not be exact replicas of those present before the most severe SO₂ pollution. Eutrophic bark in areas with low SO₂ levels must, for example, be a much commoner habitat now than it was in 1800. It is conceivable that this niche is being exploited by *Ulota phyllantha*, a species known to be tolerant of high ionic concentrations in sea water (Bates & Brown 1974).

Although SO₂ levels have fallen in Britain, it should be remembered that SO₂ levels which were once regarded as innocuous to higher plants nevertheless cause considerable reductions to crop yield under field conditions (Bell 1980). Furthermore, SO₂ pollution is still a major problem on the Continent of Europe and in North America. An accurate bryophyte scale comparable to that for lichens (Hawksworth & Rose 1970) would be a valuable additional tool for the bioassay of pollution levels. The continuing rise in the atmospheric levels of nitrogen oxides, ozone, ammonia and an increasing number of organic compounds also emphasises the importance of a detailed baseline knowledge of bryophyte distribution which can be used if one of these pollutants reaches critical levels.

NOTES

1. The bibliographies we have compared are *Literature on air pollution and lichens* XII-XXX (Henderson 1980-89) and the references listed under the heading 'Pollution' in *Recent bryological literature 53-72* (Clarke 1980-89). Henderson's bibliography includes any reference of relevance to the study of air pollution and lichens, whereas Clarke only lists papers under the heading 'Pollution' if they deal predominantly or exclusively with this topic. Additional bryological references which are relevant to pollution studies will appear under other headings.
2. Grindon's *Manchester walks and wild-flowers* is undated. According to the preface, it was based on articles published in the *Manchester Weekly Times* from May to July 1858. Simpson (1960) and Desmond (1977) give the date of publication as 1858. Internal evidence strongly suggests that 1859 was the true date of publication. On p109, Grindon contrasts the early spring vegetation at Mobberley and Heywood 'this present season (1859)'. The title page refers to Grindon as

'author of *The Manchester flora*', which was published in 1859. In the preface to *The Manchester flora*, dated 28 March 1859, Grindon writes of 'its little companion, *Manchester walks and wild-flowers*, published simultaneously'.

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