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THE INFLUENCE OF VARIOUS ECOLOGICAL FACTORS ON THE DISTRIBUTION OF CORTICOLOUS LICHENS, IN HORSLEY HOPE RAVINE, NEAR CONSETT, CO. DURHAM

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Dissertation submitted for the Degree of M.Sc. Ecology,

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ABSTRACT

Rose, Hawksworth and Coppins[77] recorded a rich corticolous lichen flora from Horsley Hope Ravine, despite its position just S.W. of Consett - a major source of SO2-pollution. This study attempts to explain the apparently anomalous presence of a luxuriant lichen vegetation in the ravine.

Three possible explanations were considered:

1. Prevailing winds transport SO2 N.E., so that the entire area S.W. of Consett, including the ravine, is relatively unpolluted.
2. The ravine is protected from SO2-pollution by its physiographical shape and/or woodland cover.
3. The variations of certain abiotic factors within the ravine account for its diverse lichen flora.

Records of corticolous lichen frequency in the area indicate that: (a) the lichen vegetation is impoverished S.W. of Consett, and (b) the E. sides of trees (exposed to SO2-laden winds) support a poorer lichen flora than the W. sides. It is thus concluded that the distribution of lichens S.W. of Consett is affected by SO2-impaction, so that explanation 1. may be discounted.

Measurements of SO2, and other abiotic factors, showed that SO2-concentrations, light intensities and substrate moisture-content varied significantly within Horsley Hope Ravine. Transects down the sides of the ravine revealed two distinct patterns of lichen distribution: (i) the variation in frequencies of species downslope, (ii) the consistent preference of species for the upper or lower sides of trees. Pattern (i) was correlated with downslope changes in SO_2-levels and light; pattern (ii) was explained by variations of SO_2, light, and substrate moisture-content.

Species similarly distributed according to these two patterns were grouped into four lichen units. A model was developed which showed that the luxuriant lichen flora, and distribution of these four units, in Horsley Hope Ravine may be explained by (in order of importance): reduced levels of SO_2, variations in light intensity, and substrate moisture-content.

The decline in SO_2-levels in the ravine was ascribed to topographical shelter from SO_2-bearing winds.

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PREFACE

Throughout this study, all measured values are in the metric system. Sulphur dioxide is abbreviated to SO2, and is measured in micrograms of SO2 per cubic metre of air ($\mu g/m^3$). In figures and tables, the source of the information is given; where no source is given, then the figure or table has been compiled from information collected during the study.

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I. INTRODUCTION ..... THE PROBLEM

In 1969, Rose, Hawksworth and Coppins[77] visited Horsley Hope Ravine (NZ 0649) - a steep-sided, well-wooded, valley system lying 4 kms. W.S.W. of the Consett Steelworks, County Durham. They found 66 species of lichens in the ravine (TABLE I), and were surprised that a site so close to a major source of air pollution (average annual sulphur dioxide concentration[92] in the vicinity of the steel plant is 84μg/m^3) should be characterised by such a rich epiphytic flora. All lichens are considered to be adversely affected by sulphur dioxide (SO_2), but the species-list for this ravine includes some lichens known for their particular sensitivity to this phytotoxic gas. Rose, Hawksworth and Coppins explained this apparently anomalous situation by suggesting that either the prevailing S.W. winds tended to carry the major part of the waste emissions from the steelworks N.E., so that the area S.W. of Consett was relatively pollution-free; or that the lichens in Horsley Hope Ravine were sheltered from SO_2-laden air by the local topography.

Another possible reason for the luxuriant lichen flora recorded in Horsley Hope Ravine by Rose, Hawksworth and Coppins is that the variation in some other ecological parameter(s) is the cause of the observed abundance of lichen species. A dark, densely-wooded ravine, with slopes generally greater than 20°, and a stream occupying the valley floor, constitutes an entirely different type of

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habitat from the surrounding, exposed, undulating, and predominantly agricultural countryside. Such significant changes in ecological conditions might well supply an explanation for a disjunct lichen distribution.

The aim of this study is to examine the corticolous lichen distribution in the area S.W. of Consett, in order to ascertain which of these three theories appears to account for the rich lichen assemblage noted in Horsley Hope Ravine:

(i) That prevailing winds tend to transport most of the SO_2 emitted by Consett Steelworks N.E. of the town, so that Horsley Hope Ravine and the area S.W. of Consett enjoy relatively unpolluted air.

(ii) That the ravine is not characterised by high concentrations of SO_2 owing to its physiographical shape which affords protection from air pollution to the vegetation growing within the ravine.

(iii) That relief from SO_2 pollution is not a significant factor in explaining the lichen flora of Horsley Hope Ravine, but the change in some other ecological variable(s) associated with the conditions of a ravine environment is conducive to the development of a luxuriant epiphytic vegetation.

The published literature on lichen ecology includes some references to the occurrence of diverse lichen communities in ravine situations. The case of Horsley Hope Ravine is thus by no means unique. However, although suggestions have been made as to the underlying cause of this general pattern of lichen distribution, there appears to have been no study devoted solely to examining this problem. It is hoped that by looking in detail at one example - Horsley Hope Ravine - some of the questions concerning this aspect of lichen ecology may be answered.

II. LITERATURE REVIEW : THE PRESENT STATE OF KNOWLEDGE OF LICHEN ECOLOGY

1. Factors governing lichen distribution.

The occurrence of a lichen species; and its frequency of occurrence, abundance, vitality, and associate lichen flora depends on a number of environmental controls. The individual effect of each ecological parameter on lichen distribution is difficult to identify, and due to a lack of adequate research in the field only broad generalisations as to the mode of action and degree of influence of each factor may be put forward. However, to facilitate discussion the lichen environment may be differentiated into:
a) substrate b) microclimate.

(A) Substrate character

Many lichens are substrate-specific[36]. On a broad scale, distinctions may thus be drawn between corticolous, saxicolous, and terricolous species; and as this study is concerned only with species found on living trees, all future comments refer to corticolous lichens. But again, a number of epiphytes tend to be restricted to certain trees only - for example, *Stenocybe septata* only occurs on holly, *Lecidea scalaris* is always found on rough-barked trees, and *Graphis scripta* is a typical member of the flora of smooth-barked trees. On the other hand, there are species with a more ubiquitous distribution, such as *Lecanora conizaeoides*, *Lepraria incana*, and *Hypogymnia physodes* which have all been recorded on a number of tree species. This complex distribution pattern is clearly related to some feature(s) of bark chemistry or structure, and possible controls are: bark pH; bark relief (that is, degree of bark roughness); moisture content of the bark; and concentrations of various nutrients on the bark surface. It is generally believed that the first two factors are the most important, with bark moisture perhaps slightly influential as well (Barkman[5], Almborn[1]).

Bark pH varies a great deal between different trees (from less than 3.5 to over 6.5) and is seen as the principle cause of host-specificity in lichens. Different tree species with bark of the same range of acidity bear similar corticolous lichens; and many epiphytes are confined to bark of a certain pH. Moreover, it is noticeable that those lichens which display no obvious substrate-specificity are either acid-tolerant or have a fruticose growth-form, so that they are not in close contact with the bark - for example, Evernia prunastri. However, bark nutriant concentration correlates fairly well with bark pH[5] and it is therefore difficult to be certain whether it is actually the level of nutrients or the acidity of the substrate which is responsible for the typical lichen floras of certain tree species.

A rough bark is more favourable to lichens for two reasons: firstly, because fruticose and foliose lichens (which are attached by a holdfast and rhizomes respectively) can establish themselves on the irregular surface; and secondly, because the fissures and ridges of rough bark constitute two separate microclimatic niches, and species diversity is consequently increased. On the basis of pH and bark relief, Barkman[5] drew up the following classification of trees bearing similar lichen vegetation because of their similar bark-types:

(i) Conifers and birch - pH 3-4.5 - very poor lichen flora (acidophytic species only).

(ii) Beech and sycamore; also young oak, ash, alder etc. - pH 4.5-5.5 - smooth bark - poor flora (smooth-barked species only).

(iii) Oak and alder - pH 4.5-5.5 - rough bark - good flora.

(iv) Elm, ash and lime - pH 5.5-7.5 - rough bark - rich flora (nitrophilous species).

Thus, different tree species are characterised by their own typical lichen floras.

As mentioned above, the moisture-content of tree bark is another variable to be considered. Each species of tree is characterised by bark of a certain moisture content - and this value is governed by: the shape of the crown (centripetal trees having a wetter bark than those with centrifugal crowns), and the water-retention capacity of the bark (small differences of water-retention capacity having been observed in the bark of various trees). Such differences are attributed to the porosity and texture of bark. Trees with soft bark, like ash and elm, have a higher water-retention capacity than hard barked individuals. But bark moisture-content does not vary sufficiently to explain - by itself - the substrate-specifity shown by some lichens.

However, to turn from the comparison between different tree species and to take any individual tree (regardless of species), variations in bark moisture are seen as very important in explaining the vertical zonation of corticolous lichens. It is a well-documented fact[5,34,35,47,96] that lichen distribution on trees changes significantly with height above ground. For example Hale[34,35] discovered that <u>Parmelia subaurifera</u> and <u>Usnea comosa</u> were confined to the crowns of trees; while <u>Parmelia saxatilis</u> and <u>P. caperata</u> were more characteristic of tree bases - irrespective of tree species. Thus, each lichen species has a 'preference' for a certain position on the tree, with respect to height above ground, and this results in the vertical zonation of lichens. There are two possible explanations for this: change in age of substrate (lichen succession); and variation of bark moisture. Other factors of the tree substrate such as pH, and nutrient concentration evince little, if any, correlation with height above the ground[5].

The oldest part of the tree is the base, and the bark gets gradually younger towards the top of the tree. As bark ages, so also its morphology changes (it becomes more structured)[96] and it is possible that the older rougher bark of tree bases supports a different lichen assemblage from the younger smoother bark further from the ground. Yarranton[96] believes that lichen succession, with young bark bearing pioneer species (mainly crustose species) and climax lichen communities (predominantly fruticose species) developed near the ground, is the cause of the observed vertical zonation. However, there are very often abrubt patterns of lichen distribution in the bottom 3m. of old trees[5]; and bark relief shows no corresponding changes - which is not surprising as there is not likely to be much difference in bark age within 3m. on an old tree. Therefore bark age and lichen succession seems an unlikely cause of vertical zonation - at least for the basal regions of trees.

Kalgutar and Bird[47], and Hale[34] found that the water-retention capacity of bark was greater nearer the tree base. Also the lower parts of the tree are likely to receive more water, due to trunk-drainage from above. Thus, there is a vertical gradient of bark moisture-content, which is particularly steep near the tree base due to the splaying-out of the bole at this juncture (thereby decreasing the velocity of tree surface run-off and allowing more time for absorbtion by the bark[5]). This change in moisture-content of the substrate with height is a more likely cause of vertical zonation of epiphytes than age of the bark. Additional evidence for the importance of substrata moisture content in the control of lichen ecology is provided by the following facts. Firstly, inclined trees have entirely different species on their upper (moisture-collection) and lower (sheltered from rain) surfaces[5]. Hygrophilous species, such as <u>Thelotrema lepadinum</u>, cover the former, while xerophytic lichens, for example <u>Lecanactis abietina</u>, are found on the dry undersides. Factors other than moisture which could conceivably lead to such a striking floral difference may be discounted according to the evidence presented by Barkman.[5] The behaviour of bryophytes - which are very dependant on substrate moisture-supply for their occurrance - is interesting in this respect. On a vertical tree, mosses are often confined to the wetter tree base; but if a tree is leaning, bryophyte distribution is extended up the trunk, and the greater the angle of inclination the further up the tree these plants spread.[5] Secondly, rain-tracks on the bark surface - in which bark run-off is concentrated - tend to receive more water and consequently carry a more hygrophilous flora (including bryophytes) than adjacent areas on the trunk.[5,32] Thirdly, aspect affects the amount of moisture held in the bark on different sides of a tree. In Britain, the S.W. sides of trees tend to be wetter, due to the prevailing winds, than the rest of the tree surface, and - according to Barkman[5] - are thus characterised by a richer lichen assemblage.

Therefore, the corticolous lichen substrate is complex and affects lichen ecology according to: the tree species (pH and bark relief); vertical position on the tree (bark moisture-content and perhaps age of bark); horizontal position on the tree (that is, aspect and amount of moisture received); 'special areas' on the trunk which have a higher moisture-content - such as rain-tracks and tree bases.

(B) Microclimate

Substrate ecology provides only one set of variables controlling lichen distribution; important factors of the local atmospheric environment are:-

(i) Temperature. Lichens are resistant to a wide range of temperatures, such that this parameter is of more significance on a phytogeographical scale. However, temperature has an indirect effect on transpiration, and this may well be of consequence to lichens. As lichens possess no cuticle they have no control on their rate of transpiration, and are thus susceptible to dehydration under adverse conditions (termed "poikilohydric")[87]. Yarranton[96] found that all species of lichens he examined in Ontario were most frequent on the north sides of trees - but this need not be related to the lower temperatures typical of this position, and could simply be a function of the moisture-aspect relations mentioned earlier (although there may be some modification of the most favourable aspect for lichens according to evaporation rates).

(ii) Relative humidity. The influence of substrate moisture on lichen distribution has already been emphasised. However, lichens have very high osmotic pressures and are capable of absorbing considerable quantities of the water they need from the atmosphere. Thus air humidity is a salient feature of lichen distribution patterns. Some epiphytes depend almost entirely on the air for their water supply[5] (for instance, Lecanora conizaeoides, and fruticose lichens, which have little contact with their substrate) and being poikilohydric they are very sensitive to any changes of air humidity[87]. Others depend on the bark for most of their moisture - especially Lobaria species. The great majority, however, use water from either source, as and when it becomes available. The importance of atmospheric moisture to corticolous lichens is reflected in the distribution of these species with respect to relative humidity. Niches of high relative humidity such as dense woodlands and stream-edges are characterised by a high species diversity; but in regions of low relative humidity (RH) impoverished and xerophytic floras are typical[5]. Again, on a smaller scale, aspect is important - for the N. sides of trees with their lower temperatures, will tend to have a higher RH and thus a richer lichen community[5]. Furthermore, any microhabitat on the tree which is sheltered will have a higher RH - thus providing a favourable microclimate for lichens. The fissures of rough bark fit this description, for they are shaded and moist and Barkman[5] found that oak trees in a dark damp situation had Lepraria candelaris in the fissures, with Chaenotheca ferruginea on the bark ridges. Also, treebases are very often sheltered by field-layer vegetation which produces a localised increase in RH at the foot of many trees. This fact (as well as the increase in substrate moisture in this position) may well explain why certain lichens favour tree bases - including Lecidea scalaris and Parmeliopsis ambigua.

Whether their moisture supply is liquid (from the tree) or gaseous (from the air) lichens are undoubtedly dependant on water; and Smith[87] believes that rates of lichen respiration and photosynthesis are governed entirely by the water-content of the thallus. Some evidence to show that lichen distribution is affected by moisture availability has already been given, but overall proof of the significance of water-supply is shown by the correlation between precipitation (which determines both substrate moisture-content and RH) and species occurrence. Barkman[5] found a clear relationship between these two factors in the Netherlands - exemplified by Usnea species, which only occur in regions with more than 700 mm. of rain per annum; and in Great Britain where the wetter western part of the country has a richer flora (including many oceanic hygrophilous species) than the dry eastern districts[11].

(iii) Light. Light is necessary for photosynthesis, and thus lichens prefer well-lit habitats[86]. However, some species are more dependant on light than others, and Almborn terms these lichens "photophilous". Those lichens occurring in Horsley Hope Ravine which are photophilous (according to Almborn[1]) are indicated in TABLE I. It is noticeable that they are mostly foliose and fruticose; and it seems to be a general rule that foliose and fruticose life-forms need more light than crustose lichens. Thus, on an oak tree in the middle of an open field, most of the photophilous lichens mentioned in the list should be found; whilst in a patch of dense dark woodland, an oak is more likely to bear a "photophobous", crustose lichen community. Yarranton[96] found that the distribution of lichens on spruce was statistically dependent on tree density (that is, on amount of light): with photophilous species such as Usnea comosa and Cetraria pinastri having their maximum frequency in low-density stands of spruce. Light is also an important factor in the differentiation of tree microhabitat. S.-facing sides of trees receive most light, but Barkman[5] considers this far from favourable to lichens as more sunlight implies higher temperatures and lower RH. The question of aspect and lichen distribution is thus confused: S.W. sides of trees receive most moisture, while on the S. sides evaporation is at a maximum. Barkman[5] found the N.W. facing sections of trees to be the most favourable for lichens (in terms of species diversity and % cover) and put this down to the combination of increased moisture-supply and lower temperatures found on this side. However, despite the considerable differences observed in lichen floras according to aspect, there is a dearth of background information on this topic. But it is unlikely that variations in light intensity or duration are responsible for the distribution of lichens with respect to aspect.

The crevices of rough bark are not only more moist, they are also darker. While the former may account for the appearance of Lepraria candelaria in this niche, shade is probably responsible for the occurrence of Lecanactis abietina - a xerophytic photophobous species-restricted to bark fissures in fairly well-lit areas; although common over the whole tree surface in dark dry situations[5]. This is clearly another example of lichen distribution in a certain niche being possibly related to the variation of more than one ecological parameter. It is difficult to do more than stress the significance of both light and moisture in this case.

(iv) The effect of man on lichen distribution. Many human activities have a deleterious impact on lichens; such as tree felling (removal of substrate), land-drainage (lowering of RH) and thinning (which affects photophobous species).

However, the greatest influence exerted by man on lichen has been through air pollution, and more will be said on this subject later.

To summarise, therefore, the following factors control the distribution of lichens:-

(a) Substrate: - pH and bark nutrients (varies according to tree species).
- Bark relief (dependent on tree species and bark age).
- Bark moisture (related to tree species, inclination, aspect, and height above ground).

(b) Microclimate: - Temperature (aspect is important).
- Air humidity (aspect and sheltered niches on the tree affect RH values).
- Light (subject to modification by tree-density and bark relief).
- Atmospheric purity.

Obviously in any study of lichen distribution all these controlling parameters need to be born in mind. But some ecological factors are of greater significance than others. Barkman[5] drew up a hierarchy of these variables, in what he considered to be their order of importance to epiphyte occurrence:-

a) pH, nutrient content and moisture content of the substrate
b) RH of air, and precipitation
c) light, and bark relief
d) air pollutants, resin and tannin
e) temperature
f) mechanical influences of animals, wind etc.

Hale[36] reckoned that the distribution of lichens is governed by both substrate (explaining 60% of the observed variation of species) and microclimate (accounting for 40% of the controls on distribution).

However, such attempts to postulate which of all these variables are of greater import to lichens can only be extremely generalised. For different species, certain controls are of more relevance than others[5]. Thus, for example, Usnea species are very sensitive to the degree of air pollution and RH, but show no correlation with substrate moisture; Lecidea scalaris is found on trees of all pH values but only on rough-barked trees - and so bark relief is more important than substrate pH to this species; and the distribution of Cetraria glauca depends more on pH and light than on precipitation or bark relief. Furthermore, any of the factors mentioned above may become limiting under local conditions. For instance, in calcareous regions all trees have bark of a high pH, and this rules out the significance of acidity in coricolous lichen distribution; in dense woods, gaps in the canopy, which let through light, may affect the epiphytic vegetation more than all other variables; and in towns, air pollution is often a limiting factor to species occurrence and abundance - regardless of other ecological controls. Thus the underlying causes of lichen distribution constitute a complex problem - involving the necessity for the careful study of all variables potentially capable of regulating the occurrence of corticolous epiphytes.

TABLE I : The Lichens of Horsley Hope Ravine, with notes on their general ecology.

P = photophilous

H = hygrophilous, preferring damp, shaded niches

S = sensitive to over 65 g/m SO2

Sources:- species list of I969 - 77

general ecology - I, 55, I9, 93, 5

observed on oak - own work

sensitive to SO2 - 42

Species List of 1969	Preferred Substrate	General Ecology	Observed on Oak in the Ravine	Recorded during Survey
Baeomyces rufus	Terricolous			
Peltigera canina	"			
P. praetextata	"	H		
Lecanora polytropa	Saxicolous			
Lecidea macrocarpa	"			
Chaenotheca brummeola	moist peat & rotting wood			
Lecidea uliginosa	"			
Arthopyrenia fallax	trees with smooth bark			
A. punctiformis	"	S		
Graphis scripta	"	S		
Opergrapha atra	"	H		
O. varia	"			
O. vulgata	"	S		
Pertusaria leioplaca	"	S		
Porina chlorotica	"	S		
Cladonia chlorophaea	tree base with humus			
C. fimbriata	"			
C. macilenta	"			
C rangiformis	"			
C. squamosa	"			

Species List of 1969	Preferred Substrate	General Ecology	Observed on Oak in the Ravine	Recorded during Survey
Stenocybe septata	confined to holly			
Gyalecta truncigena	mainly on elm	S		
Alectoria fuscescens	trees with rough bark	SP	X	X
Arthonia didyma	"	H	X	X } X
A. spadicea	"	HS	X	X
Calicium abietinum	"	S	X	
C. viride	"	S	X	X
Catillaria griffithi	"		X	X
C. sphaeroides	"	H		
Cetraria chlorophylla	"	PS	X	X
C. glauca	"	PS	X	X
Chaenotheca ferruginea	"		X	X
Cladonia coniocraea	"		X	
Dimerella diluta	"	S		
Evernia prunastri	"	PS	X	X
Gyalecta flotowii	"	S	X	X
Hypogymnia physodes	"	P	X	X
H. tubulosa	"	P	X	X
Lecanactis abietina	"		X	X
Lecanora chlorona	"		X	X
L. chlarotera	"	S	X	X
L. conizaeoides	"		X	X
L. expallens	"		X	X
Lecidea cinnabarina	"		X	

Species list of I969	Preferred Substrate	General Ecology	Observed on Oak in the Ravine	Recorded during survey
L. limitata	trees with rough bark			
L. scalaris	"		X	X
Lepraria candelaris	"	HS	X	X
L. incana	"	H	X	X
Ochrolechia androgyna	"		x	x
O. turneri	"		X	X
Opegrapha vermicellifera	"	H	X	X
Parmelia glabratula	"	S	X	X
P. saxatilis	"	P	X	X
P. subaurifera	"	PS	X	X
P. sulcata	"	P	X	X
Parmeliopsis ambigua	"		X	X
Pertusaria albescens	"	PS	X	X
P. amara	"	PS	X	X
P. coccodes	"	PS	X	
P. flavida	"	PS	X	
P. hemisphaerica	"	PS	X	X
P. pertusa	"	PS	X	X
Phlyctis argena	"	H	X	X
Pseudevernia furfuracea	"	S	X	
Thelotrema lepadinum	"	HS	X	X
Usnea subfloridana	"	PS	X	X
		Cladonia polydactyla		
		Lecidea quernea		X
		Pertusaria hymenea (S)		X
		Toninia caradocensis		X
Species Totals: 66			45	37

2. Lichens and air pollution

The fact that lichen abundance, frequency, luxuriance of growth and species numbers all show a marked decline in areas of severe air pollution is now fairly well-documented. Indeed, measurements of these parameters - plus the mapping of lichens known to be particularly sensitive to atmospheric impurities - are often used to indicate the extent and severity of air pollution. However, before discussing the nature and evidence of the effects of air pollution on lichen distribution, it will be helpful to clear up one or two points:-

(A) Identification of the phytotoxicant

The term "air pollution" covers a multitude of solids, gases and vapours emitted into the atmosphere by man; and it is important to identify which of these components is responsible for the impoverishment of lichen vegetation. Gilbert[27], Saunders[82] and Wood, and James[45] suggest the following as likely phytotoxicants:-

(i) SO_2
(ii) smoke
(iii) fluorine
(iv) heavy metals
(v) grit and dust
(vi) radio-active materials
(vii) various gases including nitrogen dioxide (NO_2), ammonia (NH_3), carbon monoxide (CO) and ozone (O_3).

Of these, (iii) and (vi), although known to affect lichens and bring about the depletion of healthy epiphytic vegetation[27], are not emitted in sufficient quantities over a wide enough area to influence the epiphytic flora on a large scale. Lichen impoverishment due to fluorine and radio-activity occurs only in the vicinity of a few sites in Great Britain where such pollutants are emitted in large quantities[45]. Vehicle effluent fumes are likewise known to be toxic to lichens, but are rapidly dispersed in the atmosphere, and even on the busiest roads vehicle emissions only cause appreciable deterioration of the vegetation within 50 m. of the road[91]. Research carried out by Warren Spring Laboratories[91] on the A1, with a traffic flow of 1200 vehicles per hour showed negligable results, and so it seems reasonable to assume that in a quiet rural district, vehicle exhaust fumes are of little significance to lichen survival.

As for grit and dust, they are not known to injure epiphytic vegetation, and moreover solid matter settles mainly in the near vicinity of its source of emission, which would rule out grit and dust as the cause of lichen paucity in Horsley Hope Ravine - 4 kms. away from the steel works.

The effects of various gases such as NH_3 and O_3 on lichen vegetation are known to be of some significance, but there is no evidence to suggest that the wholesale decline in lichen abundance, nationally or around Consett, is in any way related to the occurrence of these gases in the atmosphere.

James[45] stresses the effect of heavy metals on lichen distribution. Lichens take up high concentrations of inorganic cations, and store them in excess of their biological requirements ("luxury uptake"). Such accumulation could be harmful in areas of heavy metal fallout - especially near smelters - and kill the more vulnerable species in the locality. Lounamaa, in 1956, (quoted James[45]), found very high concentrations of iron, zinc, cadmium, lead, copper, and tin in lichens living in an atmosphere rich in these metals. Iron is the only metal likely to be present in the air around Consett, and according to Nieboer et al.[65] lichens have a particular affinity for iron. Nieboer et al.[65] also discovered that lichens selectively absorb iron from the substrate and atmosphere, and that their capacity for iron uptake is greater than their ability to accumulate other cations. This makes iron potentially the most dangerous heavy metal to lichens, and Seaward, 1973, (quoted James[45]) found concentrations as high as 90,000 ppm of iron in Peltigera rufescens around steel smelters in Scunthorpe. It is possible that some species may be able to tolerate high levels of iron, while other corticolous lichens are more sensitive to this metal: this would account for the reduction in species numbers observed near steel works. Seaward, 1973, (James[45]) and Nieboer et al.[65] subscribe to this veiw, and have found gradients of decreasing atmospheric iron content, and increasing lichen species diversity, with increasing distance from steel smelters. Any such correlations between zones of lichen vegetation and iron concentrations are difficult to substantiate in that: species tolerance levels are not known, and a concentration of 90,000 ppm of iron may be quite acceptable to all lichens; and secondly, because materials other than iron (especially smoke and SO2) are emitted from steel works and show a similar gradient of decreasing concentration with distance from source; and thus it is not certain that iron is the toxic agent concerned. However, the possible influence of iron particles in the air on lichen distribution around Consett cannot be ignored.

The majority of research carried out on the subject of air pollution and lichens points to the fact that domestic and/or industrial smoke and SO2 are individually or jointly toxic agents responsible for the wholesale destruction of epiphytic vegetation over a large part of Britain. In many areas heavy metal fallout is neglibible, and it is thought most unlikely that heavy metals could be the cause of observed lichen injury in purely residential and predominantly rural districts. By comparison, smoke and SO2 are reasonably ubiquitous in distribution and are known to be toxic to plant life.

Fuel combustion (both oil and coal) from all industrial and domestic sources releases smoke and SO2 into the air - and the deleterious effects of these pollutants on lichen vegetation is thus best seen in cities, high-density housing estates, areas of heavy industry, and even around isolated fuel-burning plants such as oil-refineries, power-stations, steel works and metal smelters.

Until the last ten to fifteen years most lichenologists were apt to ascribe the paucity of lichens in built-up areas to smoke, and the work of Jones, 1952,[46] and the contents of the Beaver Report (1953[7]) illustrate this. Recently, sound evidence has been provided to show that a component of smoke - SO2 - is in fact the toxic agent, rather than smoke itself. Gilbert[27,28] investigated this subject, and placed twigs and stones covered with lichens next to ten smoke and SO2 recording stations in Northumberland. The ten guages were widely spaced, so that each returned a different average SO2/smoke ratio for the experimental period. The results (see TABLE II) show that the three lichens in question all suffered more damage (bleaching of thallus edges and reduction of lichen size) in areas of abundant SO2 like Newcastle 22; but high smoke concentrations without correspondingly high SO2 concentrations - as at Stanley - left the plants relatively healthy. Additional proof of the lack of correlation between smoke and lichen deterioration was given by Gilbert[27,28] who measured smoke and SO2 pollution levels at the Bedfordshire Brickworks as 26$\mu g/m^3$ and 100$\mu g/m^3$ per annum respectively. The local epiphytic flora showed signs of severe damage, and was notably species-poor. Regression analysis between SO2 levels and species diversity around the works yielded a convincing relationship between these two factors; whereas the low smoke concentrations had no bearing on the floral changes. Similar observations have been made by Morgan-Huws and Haynes[61], and Skye[84]: both studied lichen assemblages around oil-refineries (in rural smokeless areas) which release large amounts of SO2 into the air, but minimal quantities of smoke. Like Gilbert they concluded that the loss of pollution-sensitive species in the vicinity of the plants was due to SO_2 and no other atmospheric impurity. Finally, it is worth mentioning an experiment carried out by Skye[84] who released SO_2 on to an oak tree with a rich lichen flora continuously for two weeks. A month later, many species - including Evernia prunastri and Hypogymnia physodes were blackened and stunted. Adjacent trees were unaffected and still bore healthy specimens. The toxicity of SO_2 to lichens is thus fairly well evidenced, and smoke appears to be only of relevance in that it contains SO_2.

Sulphur Dioxide (SO_2)

As SO_2 is generally recognised as the most lethal air pollutant to vegetation, on a national scale at least[91], it is worth knowing something of its origins and distribution in the atmosphere. SO_2 is a colourless gas given off during (a) the combustion of fuels and (b) the smelting of metals containing sulphurous impurities. The former is by far the major source[63,82]: both oil and coal contain sulphur, and when these fossil fuels are burnt their sulphur content is oxidised to SO_2, and released to the air. On average, coal has a 1.6% sulphur content, and when it is burnt only 10-20% of the sulphur is converted to SO_2 and emitted; but oil contains 3-4% sulphur, and on combustion all of this is released to the atmosphere[91]. A breakdown of the origin of the SO_2 in Britain's air in recent years is shown in TABLE III. It can be seen that total SO_2 output has steadily increased over the last 20 years, and that the relative contributions of the different categories of SO_2 - producers have altered radically in this period. There has been a decline in the direct use of coal and coke,

Site	Average annual SO2 concentration in $\mu g/m^3$	Average annual smoke concentration in $\mu g/m^3$	Hypogymnia physodes	Ramalina Fanineacea	Parmelia saxatilis
Consett	42	194	4	4	4½
Stanley	76	341	3	3	4
Gateshead	100	200	3	3	3
Tynemouth	112	267	3	2	3
Newcastle 22	236	228	1	2	1½
Newcastle 18	294	661	1	1	1

TABLE II : Lichen damage after 11 weeks exposure to varying SO2-smoke ratios. 5 = no damage; 4 = marginal bleaching; 3 = extensive marginal bleaching; 2 = thallus mostly white; 1 = lichen dead. Source: Gilbert.[17]

Source		1953	1956	1959	1962	1965	1968	1970
Coal;	domestic	0.9	0.9	0.9	0.8	0.7	0.6	0.6
	industrial	1.7	1.7	1.4	1.2	1.1	0.8	0.7
	Power-stations	1	1.2	1.3	1.7	2	2.1	2.2
Coke:	domestic	0.1	0.1	0.1	0.1	0.1	0.2	0.2
	industrial	0.4	0.4	0.3	0.3	0.3	0.2	0.1
Fuel oil		0.3	0.4	1	1.5	1.8	2	2.2

TABLE III : SO2 emissions in Britain in million tons. Sources: 91, 64.

and they have been largely replaced by oil. The reduction in domestic coal consumption (due largely to the Clean Air Act of 1956)[54,91] has resulted in less smoke in built-up areas, but SO2 levels have continued to increase because oil-combustion yields relatively more of this toxic gas than the burning of coal. So, the substitution of oil for coal, with the resultant continuous rise in SO2 emission rates, is a subject for concern, in the light of the phytotoxic nature of SO2.

When it is released to the atmosphere, some SO2 is converted to: sulphur trioxide (SO3), sulphuric acid (H2SO4), sulphurous acid (H2SO3) and a variety of sulphates[82]. All of these chemical agents are capable of harming vegetation, animals and man, as well as corroding metals and textiles, if present in large enough concentrations in the air. Therefore the crucial factor which determines the degree of damage done to the lichen flora - not to mention other life-forms - is the atmospheric concentration of SO2.

The mean global background level of SO2 is about $5 \mu g/m^3$, according to the National Society for Clean Air[63]; this amount being supplied by volcanoes, biological decay and other natural sources which are part of the sulphur cycle. Because sulphur is an essential element of living matter, such low concentrations are certainly beneficial - not toxic. But in some parts of the world, levels of SO2 in the air are considerably higher than $5 \mu g/m^3$, as a result of man-made sources of SO2 emitted during industrial and domestic fuel-combustion. Most large cities in Britain[82] record an annual average concentration of over $100 \mu g/m^3$, and the figures for London are $143\mu g/m^3$. Rural areas of England, which do not suffer from the high levels of fuel consumption of large cities, are less polluted, but much of our countryside is characterised by SO2 levels of over $40\mu g/m^3$. This is due to "pollution-drift" of SO2 from neighbouring sources to the surrounding rural areas.[82] Wind direction is clearly an important factor here, and a change in wind-direction can cause a sharp rise in the atmospheric SO2 content of villages as much as 50 kms. away from a pollution source.[82] It is because of the prevailing S.W. winds in Britain that rural areas of E. England have higher average concentrations of SO2 than rural areas in the West. These details of SO2 distribution in Britain are derived from over 1,200 recording-guages, set up in a variety of sites in the country, as part of the National Survey of Air Pollution.[64,72]

Factors Affecting SO2 Concentration

So far, discussion has been confined only to annual average SO2 concentrations. It is important to note that SO2 levels in the air are subject to great spatial and temporal fluctuations, and records for 24-hour periods may be as much as seven times higher than the annual average concentration of a site.[82] The actual amount of SO2 reaching the ground at any place at any time depends on:-[64,81,82,83,95]

(i) Source: point or diffuse. A point-source, such as the Consett Steelworks produces a clear pollution pattern around it, according to the action of other factors; but when SO2 is added to the air from a number of sources, as in a city, then the gas is widely but unevenly distributed as "blanket pollution". In the latter case, whole areas are subject to fairly high pollution-levels, for long periods irrespective of wind-direction, topography etc; but in the former, such influences as wind-direction can decide whether a site is free from SO2 or choked with it, and disjunct pollution-distribution phenomena are common.

(ii) Rate of emission.

(iii) Diffusion of SO2 in the air. Once emitted to the air, SO2 is diluted in the atmosphere, the degree of dilution depending on:- (a) Wind-speed and turbulence. The faster the wind, and the more eddying that there is in the lower atmosphere, the greater the mixing of SO2 and air that results. (b) Velocity and temperature of effluent SO2. With increased temperature and velocity of emitted gases, SO2 is carried higher into the atmosphere, which ensures greater dilution and lower ground-level concentrations of SO2 around the source. (c) Chimney-height. For the same reasons as mentioned above, the greater the height of SO2 emission, the better it is diluted in the air. This explains why domestic sources of SO2 cause high levels of SO2 in cities, for domestic smoke - being emitted at heights of less than 10 m. in the main - stays near the ground and is relatively undiluted. The tall chimneys of SO2-producing works are reasonably successful in minimising ground-level concentrations of this gas near factories, and the Clean Air Act of 1968 gave local authorities the power to determine the chimney-heights for industries emitting SO2.[64] The local authorities decide on a minimum chimney-height for works according to: SO_2 efflux concentration, local meteorology, existing SO_2 levels, and the adjacent population. Although, as was stated previously, there has been an increase, nationally, in the SO_2 emissions since 1953; in fact, average ground-level concentrations of SO_2 have decreased by about a third since this time.[19,91] This apparent paradox may be explained by the shift in energy sources detailed in TABLE III: while the amount of domestic coal-consumption has decreased, the amount of coal and oil burnt in power-stations and oil refineries has obviously increased. Thus low-level diffuse domestic emissions of SO_2, which lead to significant ground-level concentrations, have been replaced by high-level emission point-sources of SO_2 which are better diluted in the air. So, although the actual amount of SO_2 produced in Britain has increased, the quantity reaching the ground has decreased, due in the main to a high-chimney policy which ensures adequate SO_2 diffusion in the atmosphere.

(iv) Characteristics of the site. Because SO_2 emitted from a source is slowly diluted in the air, distance from the source of pollution is an important factor in explaining concentrations at any site: the greater the distance from a source of SO_2, the greater the dilution factor, and a pollution-gradient of decreasing SO_2 concentration with distance from a source of SO_2 has been observed in many studies. Likewise, wind-direction is a basic parameter that must be considered. Skye[84] measured the variation in daily SO_2 levels on the outskirts of Stockholm and discovered that wind-direction had a great influence on the readings.

Garnett[34] and Parry[66] were also aware of the effects of wind-direction on pollutant concentration. Meade and Pasquill[59] found that the distribution of SO2 around Staythorpe Power Station, Notts, was related to wind-direction. This was seen from the variation in the steepness of the pollution-gradient with distance, as wind-direction changed. For example, if a N. wind transported SO2 S. of the power station, then the pollution-gradient to the N. of the works was very steep as SO2 concentrations declined significantly; while to the S. high levels of SO2 were observed over a considerable distance, owing to the effect of the N. wind in transporting SO2 southwards. Average annual pollution gradients reflected the influence of the prevailing S.W. winds (see fig. 1). Robinson[75] believes that pollution drift can affect the atmosphere many hundreds of kms. from the SO2 source.

Minor controls on SO2 concentration in any place may also be exerted by: surface roughness (more roughness produces more turbulence and thus more SO2 mixing[95]), and topography[95] (if SO2 is poured into a narrow valley, the restrictive topography may prevent air-flow, so that the toxin is confined to the valley, and accumulates. On the other hand, when further away from pollution-sources, hills may 'protect' valleys, so that the latter receive less SO2 because of this topographic barrier[55,69,95]).

Many formulae have been produced which attempt to combine some of these factors for the prediction of SO2-concentrations at different places and different times. Sutton, 1953, (from the Beaver Report[7]) suggested that the

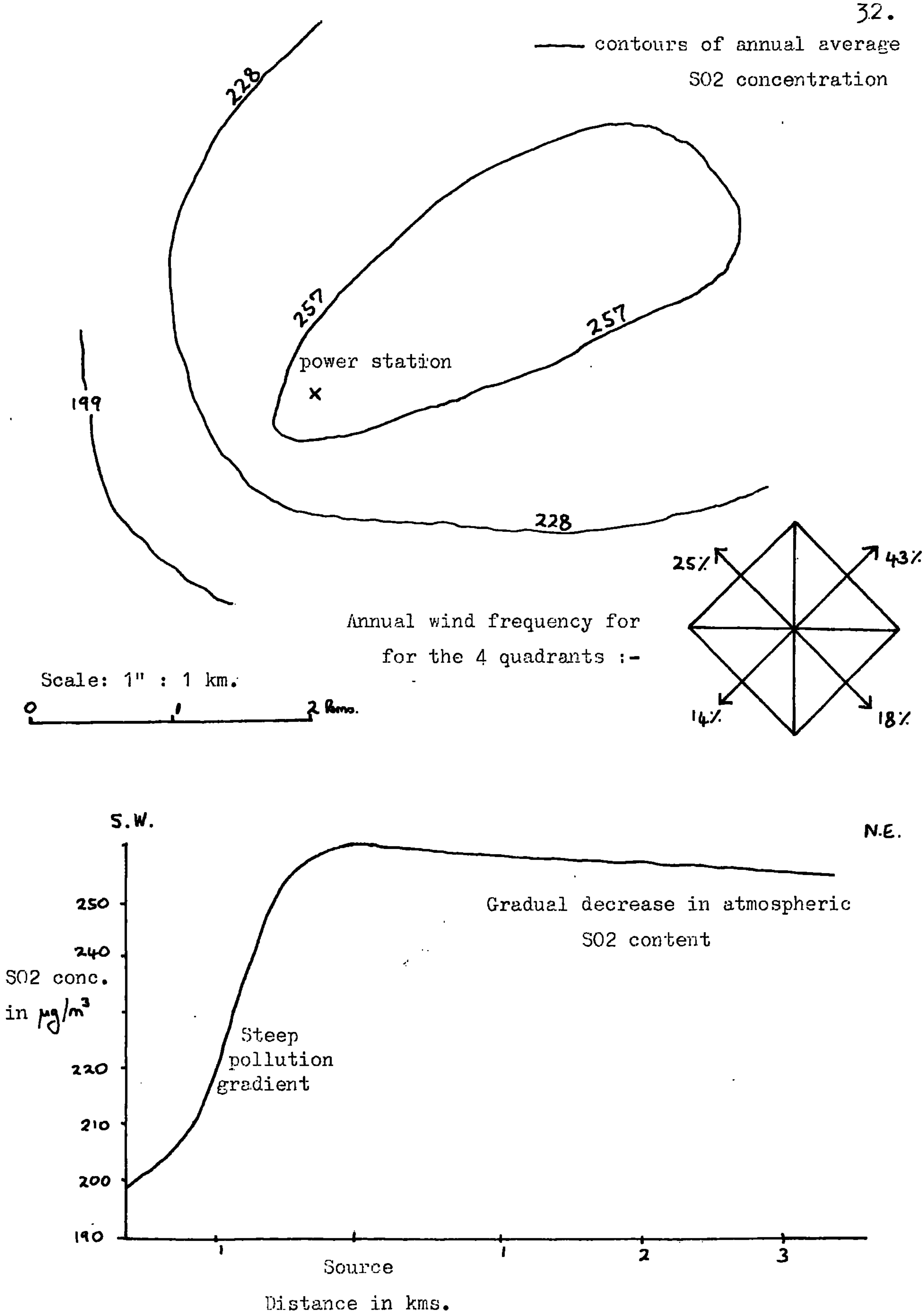


Fig. 1 The distribution of annual average SO2 around Staythorpe power station, Notts.

Source: 59

following empirical equation was applicable:-

$$SO_2 \text{ concentration} = \frac{3.76 \times 10^6 \text{ emission strength}}{\text{wind speed} \times \text{chimney height}}$$

Lucas[57] produced a formula to show expected concentrations according to: rate of emission, wind-speed, and local population-size; and found a good correlation between values calculated from this formula, and those measured in the field in certain localities. Meade and Pasquill[59] were able to relate measured SO_2 levels to those calculated from the formula:

$$p = a + b.\frac{f(\theta)s}{\bar{u}}$$

where p = average SO_2 at that point

a = background pollution (from other sources)

$f(\theta)$ = % frequency of wind from source to p

s = tons of SO_2 emitted / unit time

$\bar{u}$ = mean wind speed

But no matter how elaborate the formula, no theoretical attempt to estimate SO_2-concentration can adequately consider all the controlling variables which affect the distribution of pollutants in time and space. Field-measurement is the only safe method of getting reliable estimates of the amount of SO_2 present in a certain situation.

SO_2, and its derivatives (H_2SO_4, SO_3, H_2SO_3), are removed from the atmosphere quite rapidly, so that the half-life of industrial SO_2 in the atmosphere is only 4 days.[82] According to Sanders and Wood,[82] this removal is accomplished in two ways:-

(i) Wet deposition. Precipitation oxidises gaseous SO_2, and carries it down in solution; and sulphate particles are used as condensation nuclei. Both means result in about 17% of the atmospheric SO_2 in Britain reaching the ground in rain.

(ii) Another 80% falls to the earth's surface by dry deposition (gravitational settling). As gaseous SO_2 is very light it has a low settling velocity, and therefore it is probably deposited on the ground and vegetation by impaction and molecular adhesion to surfaces.[49]

At the earth's surface, the deposited SO_2 is absorbed by the sea, plants and soils. Vegetation absorbs about 40% of all the SO_2 emitted in Britain.[82]

(B) <u>The Effects and Mechanism of SO_2 Toxicity</u>

This section is primarily concerned with the effect of SO_2 on plants but it would be a major omission not to include some comment on human health and the danger of SO_2. Heimann[43] believes that if SO_2 is inhaled, even in minute quantities, it causes a temporary spasm of the bronchioles. At high atmospheric concentrations lung function is thought to be adversely affected, and desquamation of the surface epithelia of the respiratory tract may result. Evidence that SO_2 is harmful to the human respiratory system is provided by the statistics of a number of 'smog incidents'. Bearing in mind that SO_2 diffusion depends on wind-speed and vertical mixing in the air, it is clear that the meteorological conditions of an inversion permit little dilution of any gas poured into the stable air below the inversion layer. The abnormal temperature gradient prevents the rise of toxic gases, and the lack of any wind likewise precludes any lateral diffusion. Because of their inverted temperature profile, inversions are often associated with fog. SO2 and smoke emitted into such a fog are trapped below the inversion layer, to produce a lethal 'smog'. A good example of a smog episode occurred in London between December 5th and 9th, 1952.[43] The air in the London Basin was trapped beneath a low inversion at 130 m. and a fog formed in the cool, damp conditions. Into this stable, foggy atmosphere were released the fumes of London's industry, vehicles, and domestic hearths; and continuous emissions caused the SO2 concentration in the confined air to rise drastically (see TABLE IV). During the 5 days in which these conditions persisted, there were 4,000 more deaths than might be expected in London for the time of year, and most of the increased mortality was from respiratory malfunctioning - bronchitis, asthma, pneumonia and lung cancer.[7,43] On average, the atmospheric SO2 content was six times higher than it normally is in London, and although the levels of other pollutants were higher than usual in this period, medical evidence is of the opinion that SO2 was the toxic agent concerned. Similar smog incidents and related increases in deaths from respiratory difficulties have been reported from the Meuse Valley, 1930 (death-rate ten times above the average); Glasgow, 1909 (five times the usual mortality-rate) and London 1962 (where SO2 levels rose above 4,000 $\mu g/m^3$ for two days![64,91]) But SO2 concentrations do not have to reach astronomical proportions before affecting human health.

Date	Average SO2 concentration in Lambeth in $\mu g/m^3$	Average SO2 concentration in City in $\mu g/m^3$
4th December	4I0	540
5th "	2I50	I770
6th "	2440	2060
7th "	3830	2290
8th "	3830	3490
9th "	I350	3460
I0th "	I050	630

TABLE IV : The London Smog of I952.

Source: 9I

	Urban areas of over I00,000 population	Urban areas of 50 - I00,000 population	Urban areas of less 50,000 population	Rural areas
Pneumonia	47.9	39.2	35.7	3I.5
Bronchitis	6I.8	53.8	48.8	36.9
Other respiratory diseases	I0.2	9.I	8.5	7.8

TABLE V : Death-rates from respiratory diseases in Britain per I,000 population.

Source: 7

The figures presented in TABLE V show that everyday differences in the standard of air we breath can affect our longevity (assuming that population-size is an approximate estimate of long-term SO2 levels). The relationship between SO2 concentrations and human respiratory disease, though still lacking a proven medical link, is conclusive enough to be frightening.

SO2 is known to cause definite and observable injury to vegetation, and this has been studied both in the field and laboratory. Because this gas can cause reduced yield in crops (sufficient to dent the agricultural economy of areas subject to serious air-pollution[49]) most attention has been paid to its effects on vascular plants. For example, Thomas[89] placed pots containing lettuce, cabbage and radish in different parts of Leeds; and found that the lowest yields were returned from the more polluted parts of the city. He discovered a high correlation between yield and atmospheric sulphate content. Bleasdale[8] worked on rye-grass and noticed that plants grown in Manchester air showed a 20-40% reduction in weight, as compared to those specimens cultivated in a greenhouse with washed air. The observable symptoms of SO2 damage to vascular plants include: chlorosis, marginal necrosis of leaves, stunted growth, precocious leaf-fall, blackening of buds, and scorching of foliage.[27,60,62] At high concentrations, SO2 is lethal to higher plants. Thomas[87] cites the case of a copper-smelter at Montana emitting 2,320 tons of SO2 and 220 tons of H2SO4 per day - for 25 kms. downwind from the works all the trees were dead. Rao and LeBlanc[73] found that SO2 from an iron-sintering plant in Ontario was responsible for a landscape devoid of trees for 13 kms. in the direction of the prevailing winds (N.E.). The visible effects of SO2 on lichens are similar to those described for vascular plants: bleaching and discoloration (usually red-brown) of thallus lobes; inrolling of the margins of foliose species; sterility, with few ascocarps produced; reduction in size of individuals (i.e. less luxuriant growth of fruticose species. Gilbert[27] found that Evernia prunastri 50 kms. W. of Newcastle was five times the size of specimens 16 kms. away); lower yield in terms of a decrease in cover-abundance values nearer SO2 sources; chlorosis and necrosis; and at higher concentrations - lichen mortality.[31,38,42,81] Plants from other phyla, such as bryophytes and fungi respond to a high atmospheric SO2 content in a corresponding fashion.[27]

It is a fact that different plant species (of all taxonomic status) are damaged at varying concentrations of atmospheric SO2. It is of fundamental importance in any air pollution/vegetation study to be aware that each species (be it lichen, angiosperm, bryophytes or whatever) can tolerate a certain amount of SO2 before it is killed. This is referred to as the 'sensitivity' of a species and it follows that the more sensitive a plant is to SO2, then the rarer will be its occurrence in polluted air. The tolerance of lichen species to SO2 will be considered in full later, but a few details are included here for comparative purposes. In TABLE VI the results of some studies on the tolerance-levels of vegetation are given. Although the figures do not entirely concur, it is evident that lichens are more

Average annual quantity of SO_2 in $\mu g/m^3/yr$.	Effect	Reference
less than 30	Kills the most sensitive lichens (e.g. Lobaria and Usnea species)	Hawksworth & Rose[41]
56	Reduced growth-rate of conifers	Nash[62]
I70	The most resistant lichen species - Lecanora conizaeoides - cannot exist	Hawksworth & Rose[41]
200	The most sensitive vascular plant - pine - is killed	Nash[62]
280	The least tolerant angio-sperms show signs of injury	Nash[62]
430-570	Damage done to the most sensitive angiosperms (alfalfa, dandelion etc.)	National Society for Clean Air[63]
500	Noticeable effects on humans	"
570	Injury observed in vascular plants	Katz[48]
Over I,000	Most sensitive angiosperms killed	Katz[48]

TABLE VI : Plant sensitivity to SO_2.

Sources: as on table

sensitive to SO_2 than vascular plants. Bryophytes and fungi, while affected by the same range of values as lichens, are not quite as sensitive as these corticolous species are.[27] This begs the question: why are lichens more sensitive to SO_2 than other plants? The answer probably lies in their epiphytic habit which makes them very dependant on the air for their water-supply and nutrients. According to Smith,[87] lichens have efficient mechanisms of absorption (and as mentioned previously high internal osmotic pressures for this purpose) for taking in essential elements from both the air and the substrate over their whole surfaces - but lack any selectivity in the type and amount of materials they absorb. Thus if their environment is saturated with SO_2, lichens will concentrate this substance until it reaches toxic levels.[36,87] There is some proof that this theory is correct in: (a) the concentration-values of sulphur found in lichens near SO_2-sources. Gilbert[27] found that Parmelia saxatilis contained 2,870 ppm of sulphur near Newcastle on Tyne, but such levels of sulphur are unlikely to accumulate in vascular plants owing to their cuticular protection from the atmosphere. Higher plants take in most of their mineral requirements from the soil, which because it acts as a filter, is not necessarily characterised by high concentrations of sulphur in polluted areas.

(b) Gilbert[27] hung specimens of Usnea - both live and dead - in the polluted air of Newcastle on Tyne. After eight weeks, the live individuals had undergone a 70% increase in sulphur content - but dead plants showed a rise of only 11%. Therefore, sulphur uptake in lichens is a metabolic process - not mechanical. (c) It is a well known fact that broadly-speaking, lichen sensitivity depends on lichen growth-form. Fruticose species are more sensitive to SO_2 than foliose, which in turn are more vulnerable than crustose lichens. Fruticose species have a large surface area exposed to the air, and rely on the atmosphere for their supply of moisture and essential elements; whereas crustose species depend more on their substrate to provide these requirements. Again, therefore, this seems to lend weight to the idea that lichen sensitivity to SO_2 is a function of their dependence on the atmosphere for water and nutrients.

It is because lichens are so adversely affected by SO_2 that they have recently come to the fore as accurate and significant biotic indicators of the severity and extent of air-pollution. Few parts of Britain are characterised by SO_2 concentrations outside the range 30-170 $\mu g/m^3$, and within these values the presence or absence of certain lichen species can provide a good estimate of the exact level of SO_2 typical of the locality in question. The distribution of higher plants is rarely affected by SO_2, because the atmosphere is insufficiently toxic to trouble the more resistant vascular species.

A great deal of controversy surrounds the problem of how SO_2 actually damages and kills vegetation. The physiological effects of this toxic gas have been studied in the field and the laboratory, mainly on lichens because of their sensitivity, but no firm conclusions have been reached. The following theories seem tenable:-

(a) SO2 Affects Photosynthesis

A reduction in photosynthesis with increased SO2 has been observed in vascular[8,48,89] plants and in lichens.[16,44,67,68,70,74,88] Rao and LeBlanc[72] explained the toxicity of SO2 to lichens from their laboratory work. They exposed four species to 14,300 $\mu g/m^3$ for 24 hours. The algal component of the lichen showed signs of bleaching after this treatment, the algal cells were plasmolysed, there were brown spots on the chloroplasts, and free Mg^{++} ions were observed. They attributed the bleaching to the action of H2SO4 (formed from SO2 by ionization in the lichen); plasmolysis to the osmotic pressure exerted by SO2; and analysed the brown spots as phaeophytin. Phaeophytin is a breakdown product of chlorophyll, and they hypothesised that the acidifying effect of SO2 was replacing the Mg^{++} component of chlorophyll with H^+ ions, thus degrading chlorophyll to phaeophytin:- chlorophyll + $2H^+$ = phaeophytin + Mg^{++}. Therefore SO2 acts on lichen metabolism by destroying chlorophyll, according to Rao and LeBlanc.[72] This would account for the observed chlorotic and necrotic symptoms seen in damaged plants; and a lower assimilation-rate because of chlorophyll breakdown would certainly explain the reduced yield of SO2 injured vegetation. Katz[48] holds the same theory to be true for vascular plants, and suggested that the quantity of phaeophytin present in SO2-fumigated leaves provides a useful measure of the degree of plant-damage caused by the gas. Moreover, he adds that plant parts without chlorophyll (such as flowers and variagated leaves) are more resistant so SO2.

Hill[44] subjected Lecanora conizaeiodes (a very SO_2-tolerant lichen), Usnea subfloridana (very sensitive) and Hypogymnia physodes (moderately resistant) to a range of sulphite concentrations. All three species exhibited a reduction in photosynthetic carbon-fixation with higher levels of sulphite; but it only took 0.2 mm. to depress photosynthesis in U. subfloridana, whereas L. conizaeoides showed no change in net assimilation with sulphite levels less than 0.8 mm. and H. physodes occupied an intermediate position - being affected by 0.4 mm. Thus, Hill found that species sensitivity in field-situations was closely paralleled by the SO_2/photosynthetic relations of different species in the laboratory.

Gilbert[27] discovered that after five weeks exposure to Newcastle air (300 $\mu g/m^3$) Ramalina farinacea had lost 84% of its chlorophyll, but that Lecanora conizaeoides was unaffected. Coker[16] repeated the experiments of Rao and LeBlanc[72] on bryophytes, and his findings were similar. He was able to correlate SO_2 concentration and amount of chlorophyll damage brought about. Puckett et al.[70] also observed the destruction of chlorophyll by SO_2 but differed in their explanation of the chemistry of this reaction - putting it down to an irreversible oxidation process acting on the chlorophyll and bleaching the chloroplasts of their pigment. Either way, the basic theory is that SO_2 acts on plants by destroying the chlorophyll of the photosynthetic system. Higher plants would be less affected in this case, their cuticles and stomata protecting them from excess SO_2 uptake.

(b) SO2 Affects Respiration

Baddeley et al.[2,3,4] are the chief proponents of this idea (although Katz[48] mentioned that SO2 reduced respiration rates in vascular plants). They exposed lichens to a range of SO2 concentrations (from 3 $\mu g/m^3$ to 300 $\mu g/m^3$) for different periods of time. The results showed wide variation in terms of species response: some species displaying reduced rates of respiration at 10 $\mu g/m^3$ applied for only 15 minutes, while others were breathing normally after receiving a continuous dose of 300 $\mu g/m^3$ for 18 hours. The depressent effect of SO2 on the respiration of different species showed a broad similarity to the observed field-sensitivity of lichens. Thus, as expected, respiration was severely affected by low concentrations of SO2 in sensitive epiphytes like *Parmelia perlata* and *P. caperata* while lichens known to be fairly resistant to SO2, such as *Parmelea saxatilis* maintained normal respiration under higher levels of this pollutant. However, Baddeley et al. found that some species absent from regions with relatively low concentrations of air pollutants and thus very sensitive to SO2 (including *Lobaria* species and *Usnea subfloridana*) did not show as much reduction in respiration-rate under the influence of increasing SO2 as the more resistant *Hypogymnia physodes* and *Evernia prunastri*. That is, the correlation between field-sensitivity of lichens to SO2 and the effect of SO2 on their respiration-rate is not as high as it seems to be for species vulnerability and photosynthetic depression with SO2. In fact, Baddeley et al.[4] state that lichen photosynthesis is between three and five times more vulnerable to SO2 than the respiratory system. Thus although SO2 may upset both physiological processes, and in all species both respiration and photosynthesis are drastically cut with increased concentrations, the anomalous results produced in the work mentioned above suggest that SO2/respiration relations are not the whole answer to the problem of SO2 phytotoxicity, and certainly cannot explain why some lichens are more sensitive than others to this gas. It is possible that the toxic action of SO2 affects some aspect of lichen metabolism common to both respiration and photosynthesis - such as ATP synthesis - which would explain why both processes respond to SO2-fumigation.

(c) SO2 causes the Decomposition of Lichen Acids

Gilbert[31] discovered that when *Parmelia saxatilis* was exposed to SO2, orange granules appeared in the medulla, and the lichen slowly died. The orange granules were analysed as the breakdown products of a lichen acid (salazinic acid), and Gilbert suggested that the mechanism of SO2 toxicity was via the decomposition of lichen acids. Other researchers have observed similar reactions of lichens to SO2: *Xanthoria parietina* died because of the breakdown of the anthraquinone parietin with high SO2 levels[31]; and Pearson[67] found that lichens nearer a pollution-source contained less cystine than specimens further away (with lower SO2 content in the air). While the destruction of lichen acids may explain the inhibitory influence of SO2 on certain species - the idea is not of universal application to epiphytes, and cannot apply to vascular plants, which lack these substances.

(d) SO2 is Toxic to the Lichen Reproductive System or to Young Plant Tissue

Many people who have studied the relation between lichens and SO2 have noted that young colonies of many species are absent from polluted areas.[4,17,53,68] Laundon[53] found that 18th century gravestones bore a richer lichen flora than the 20th. century ones, in grave-yards in London. For example, Caloplaca heppianae occurred on 80% of the 18th century gravestones in London, but on none which post-date 1880. It is thus apparent that while this species is able to tolerate the SO2 in the city, new colonies could not establish themselves in the polluted air of London, after the industrial revolution of the mid-19th century.

There are two ideas as to why no young lichen colonies are found in polluted regions: firstly, that SO2 causes lichen sterility so that reproduction cannot take place; and secondly, that reproduction is unaffected, but the germination of new individuals is prevented by high SO2-concentrations. It is well known that the sexual reproductive organs of lichens are absent where SO2 attains high values;[13,17,29,41] even the most resistant lichen - Lecanora conisaeoides - produces few ascocarps where air-pollution is very severe. A morphological condition known as "sorediate" is characteristic of many species when the SO2-concentration approaches their level of maximum tolerance (thus along a gradient of increasing SO2, lichens become sorediate just before they become extinct). If a species is sorediate, it bears no sexual reproductive organs, but the thallus is covered with "soredia" which are vegetative reproductive organs. However, these too are affected by SO_2, as Margot[58] showed during his studies on the soredia of Hypogymnia physodes subjected to fumigations of this gas. He found that the algal symbiont of the soredia was killed by SO_2, and that the higher the SO_2-concentration applied, and the longer the duration of exposure to the gas, the greater the soredia mortality.

It is clear that lichen reproductive organs (both sexual and vegetative) respond to the SO_2-content of the air, and their sensitivity is higher than that of the vegetative parts of the lichen plant. The soredia of Hypogymnia physodes are damaged at $30 \mu g/m^3$, but this lichen can tolerate concentrations of $60 \mu g/m^3$. Therefore, the inability of lichens to produce spores in impure air may explain their absence from polluted areas.[58] But this theory may be criticised in that, while the epiphytes growing in conditions of considerable atmospheric SO_2-content may be sterile, there is nothing to prevent the immigration of healthy lichen spores from adjacent areas of pure air (lichen spores being capable of long-range dispersal[5]) thus establishing new colonies in polluted regions. The hypothesis of SO_2 preventing the germination of lichen spores is probably a better explanation of the absence of young colonies around SO_2 sources.

Studies on higher plants have shown that young tissues are more sensitive to SO_2 than older vegetation,[48] and Gilbert[27] found that moss protonema were less resistant to SO_2 than gametophytes. Little work has been carried out on germinating lichens, but it is believed that a similar theory is applicable, and Gilbert[27] thought it possible that the rapid cell-division in germinating lichens was the cause of their greater vulnerability.

There is a large body of literature which suggests that any factor causing an increase in the physiological activity of vegetation also leads to an increase in the SO2-sensitivity. Germinating lichens, characterised by high metabolic rates could therefore be killed simply because of this relationship. The evidence for the fact that metabolic rate and SO2-toxicity are connected is:- (a) Vascular plants are more liable to SO2 injury in spring, when physiological activity is greater than at other times of the year. Katz[48] found that in August, alfalfa was not damaged by 220 $\mu g/m^3$; but in March, 140 $\mu g/m^3$ of SO2 injured the plants. Lichens suffer more effects from SO2 in the winter, for two reasons. Firstly, because their metabolism is greater in winter (lower temperatures requiring higher rates of photosynthesis and respiration) than summer (less water means less metabolic activity)[87]; and secondly - atmospheric SO2 concentrations are higher in winter, as more fuel is burnt for heating purposes.[49] Seasonal figures for cities in Britain demonstrate this[91]: Leicester, Wolverhampton, and Sheffield possess average winter levels of SO2 more than double those of summer. (b) Vascular plants are known to be more sensitiive in daylight than at night[48]; a fact which suggests that photosynthesis is the physiological process affected by SO2, as postulated earlier. Thomas[88] is of the opinion that light-intensity controls stomatal operation, and so daylight permits more absorption of gases through the stomata - thereby making plants susceptible to any SO2 in the air. Katz[48] found that the same concentration of SO2 caused four times as much damage to barley at midday as it did when applied at midnight. (c) When vegetation is 'dry' its sssimilation-rate decreases,[20,87] and therefore, if as hypothesized above, photosynthesis and sensitivity to SO2 are correlated, so also should moisture-content and SO2-resistance show parallel trends. For higher plants, Katz found that a low soil moisture-content caused stomatal closure, a reduction of photosynthesis, and less SO2 uptake; and Thomas[88] discovered that with an RH of 100% barley was twice an sensitive to SO2 as it was in air at 40% RH. Coker[16] linked the degree of bryophyte pollution damage with relative humidity, and suggested that more plant-moisture increased metabolic activity which in turn caused a rise in SO2 uptake. Skye,[84] Baddeley et al,[2,3,4] and other researchers have come to the same conclusion with reference to lichens. (d) Smith[87] noted that young lichens have a higher photosynthetic rate than older individuals, and this final piece of evidence seems to put the matter beyond reasonable doubt.

Thus the most likely explanation of the phytotoxicity of SO2 and its compounds is that the photosynthetic mechanism is inactivated (probably as outlined by Rao and LeBlanc[72]) where the SO2 content of the atmosphere is particularly high. Any factor which increases the rate of photosynthesis, (in particular the greater assimilation-rate of young plants, and any increase in environmental moisture-content), causes a corresponding increase in the rate of SO_2-absorbtion, and thus SO_2 sensitivity is correlated with level of metabolic activity. Respiration-rate and lichen acids, whilst affected by SO_2, do not account for the known facts on the mechanism of SO_2 toxicity as well as SO_2/photosynthetic relations do.

(C) The influence of some Environmental Parameters on SO_2 Toxicity to Lichens

In the same way as such factors as type of substrate, position of tree, and aspect affected the microhabitat of lichens with respect to light, moisture, acidity etc; so the degree of SO_2 toxicity to lichens depends upon the influence of certain environmental controls:-

(a) Substrate Acidity

Generally, the more acid the substrate, the greater is the toxic impact of SO_2. Thus, ubiquitous lichen species which can grow on a variety of substrates will be absent from those with a low pH in polluted air, while still being present in habitats of high pH. This may be illustrated by a number of examples: Gilbert[27] found that *Parmelia saxatilis* occurred 15 kms. W. of Newcastle on Tyne on ash trees (high pH); but growth of this species on spruce and birch (low pH) was still not observed 25 kms. W. of Newcastle (a major pollution-source). Also, he recorded that the same lichen could not grow on sandstone walls in the city, but flourished on the calcareous mortar in between the building-stones: an excellent example of substrate pH controlling lichen distribution under conditions of severe SO2 pollution. Further away from Newcastle, <u>Parmelia saxatilis</u> grew on both the acidic sandstone blocks and the mortar. Laundon,[53] working on the saxicolous epiphytes of london, found that calcareous substrates (limestone blocks and mortar) had three times as many species as acidic stonework. Results from a number of sources[4,5,21,27,81,86] imply that in conditions of high concentrations of SO2, corticolous species diversity would mirror the pH of the substrate: with many species on elm and ash; fewer and less sensitive species on oak, alder, beech and sycamore; and only one or two resistant lichens on conifers. Physiologically speaking, Baddeley et al.[1] noticed that the respiration rate of <u>Cladonia impexa</u> with an SO2 atmospheric content of 145 $\mu g/m^3$ was lowest at pH3, and greatest at pH6. Puckett et al.[70] recorded the fact that more chlorophyll was destroyed in lichens exposed to high concentrations of SO2 when the substrate was more acid, and there was a significant difference in rate of photosynthesis between specimens at pH 3.2 and those in a medium of pH 6.6. Thus, it may be accepted that lichen metabolism as well as species distribution responds to pH changes.

Gilbert[27] puts forward two possible explanations for the observation that low pH and SO2 exert a synergistic toxic effect on lichens:- (a) that SO2 acidifies the substrate, so that habitats which are already acid (sandstone walls, and acid bark) possess a very low pH in polluted situations and only the most extreme acidophilous species can survive there, and (b) that the pH of the substrate controls the ionisation of SO2. The first hypothesis is supported by the evidence that tree bark is more acid than normal near SO_2 sources. Gilbert[27] recorded the pH of of ash bark: at 32 kms. from Newcastle it was 4.4, but in the city-centre it had fallen to 3. Skye[84] discovered that in the centre of Stockholm - which is a 'lichen desert' because of the pollution there - all tree species had a bark pH of less than 3. Elm, with a bark pH of 7 in rural areas around the city, averaged only pH 2.7 in the centre of Stockholm. Skye and Hallberg[85] plotted the distribution of lichens around one oil-refinery in Sweden, and found that in 15 years of high SO_2-emissions from the plant, the frequency of acidophytic species had increased. In 1953, acid-loving lichens such as Alectoria fuscescens and Cetraria chlorophylla lived on pine and birch in the vicinity of the works; but by 1968, these trees were bare of lichens, while on oak and ash, which had formerly born 'neutral' associations of species, the acidophiles now dominated. Skye and Hallberg presumed therefore, that during the 15 years in question, the bark of pine and birch had been acidified to such an extent that even acid-tolerant species were exterminated on these trees; while the reduction in pH of oak and ash created suitable habitats for A. fuscescens and C. chlorophylla to migrate to. The lack of any trees of suitable pH for acidophobous lichens to survive on led to a drop in the frequency of species such as Evernia prunastri and Ramalina farinacea in this period.

But acidification of the substrate by SO_2 cannot explain all the observed features of the SO_2/pH relationship and the way it affects lichen distribution. Thus, although Gilbert[27] measured the pH of ash bark and remarked upon its decline in value towards Newcastle, he also noticed that the drop in species diversity, and lower frequency of sensitive lichens associated with the polluted air of the city were not correlated with the reduction in substrate acidity, That is, the lichen flora showed signs of depletion some distance from Newcastle - whereas the pH of ash had not begun to fall at this point. Griffiths[93] found no reduction of bark pH near the Consett Steelworks. Furthermore, pine with a typical bark acidity as low as 3-3.5 is covered with 4 or 5 acidophilous lichens in unpolluted regions. But these acidophilous species are not at all common on acid bark near SO2-sources.[27] In addition, acidification of the lichen environment with acids containing no sulphur does not affect species distribution.[82] Therefore acidification of the substrate alone does not account for the fact that a lower bark pH and SO2 toxicity are related. While it is true that H_2SO_4 and H_2SO_3 lower bark pH, this fact in itself does not explain why species more sensitive to SO_2 should prefer basic niches in polluted air.

A more subtle theory relates the pH of the substrate to the form of the sulphur compounds formed from SO_2. According to Gilbert,[17] pH affects the ionization products of SO_2, and Baddeley[4] et al. detail this reaction:

pH over 4.5 = SO_2 mostly as SO_4 (sulphates)

pH 3.5-4.5 = SO_2 converted mainly to HSO_3^- (bisulphite ions)

pH less 3.5 = H_2SO_3 (sulphurous acid) predominates (at pH 1 85% of SO_2 becomes H_2SO_3).

The form adopted by SO_2 is dependent upon the rate of its oxidation. At a high pH, a high rate of oxidation is possible, and SO4 results. SO4 is not toxic to plants. However, the lower rates of oxidation in acid habitats cause the conversion of SO2 to H2SO3, and this is very toxic to lichens, (thirty times more toxic than SO4).[88] So in niches with a high pH, such as mortar on walls, nutrient-streaks on trees, and basic tree-bark, SO2 is oxidised to impotent ionic forms, in the substrate moisture. In acid habitats, the SO2 taken into solution from the air, is not oxidised very much, and H2SO3 is formed: when lichens absorb moisture from the substrate they also take in H2SO3 ions and sensitive species are killed by this acid. Gilbert[26] applied 2,000$\mu g/m^3$ of SO4 to bryophytes and they were undamaged; but in the presence of 60$\mu g/m^3$ of H2SO3 sensitive mosses were killed.

This second theory is therefore feasible, but the whole subject is open to debate; although the fact that acid substrates carry the poorest epiphytic floras in polluted areas is well established. One final question is: if substrate pH influences SO2 toxicity, do lichens take in atmospheric SO2 via the substrate solution rather than directly from the air? The answer is that because lichens absorb water and essential nutrients from the air, and the tree-bark - both contribute to the SO2 uptake of these plants.[82] The relative SO2 contribution of each of these sources is not known, and is largely a matter for conjecture.

(b) Substrate Moisture

In the preceeding discussion it was revealed that niches of high pH may carry sensitive species into areas suffering from SO_2 pollution; and a number of people are of the opinion that moisture functions in much the same way, by somehow 'relieving' the toxicity of SO_2 to lichens in damp microhabitats. Lichen distribution in polluted regions shows a preference for the wettest substrates available. Brightman[9] observed that asbestos tiles on a roof in London had a more extensive epiphytic flora than adjacent clay tiles (of the same age, aspect, and angle of inclination). He postulated that the higher water-retention capacity of asbestos make it a more amenable substrate for lichen growth in polluted localities than clay with its poor powers of moisture-absorption and retention.

Tree-bases receive more trunk run-off, have a higher moisture retention capacity, and being sheltered are characterised by lower evaporation-rates than the rest of the corticolous substrate. Tree-bases are therefore moist niches, and this is why, in polluted regions, sensitive species are often restricted to the lower portions of the trunk.[20,33,46,81,82]

Thirdly, dense woods also tend to harbour a richer lichen flora than adjacent 'exposed' trees in built-up areas: a situation put down to the higher RH of woods.[27,46]

Why should moisture alleviate the toxicity of SO_2 to lichens? Sanders[81] asserts that more moisture gives rise to increased metabolism (as Smith[87] found), and so lichens are more able to oxidise SO_2 to harmless SO_4, (although this contradicts the idea that an increase in metabolic rate leads to an increase in SO_2 absorption). According to Griffiths[33] the rise in physiological rate in the saturated lichen thallus leads to more absorption of nutrients from the substrate and atmosphere - but at the same time the power of selectivity of mineral uptake improves in the lichen, so that less SO_2 is absorbed.

The patterns of lichen distribution outlined above are fairly widespread phenomena, and their existence cannot be denied - yet there are alternative theories to account for them. Gilbert[27] also noted that asbestos bore more species than other saxicolous and terricolous substrates in the centre of Newcastle. However, he measured the water-holding capacity of asbestos and found it lower than that of oak and ash; and thus rejected the idea that the luxuriant flora of asbestos was due to variations in substrate moisture content. He went on to record the acidity of asbestos and found it had a pH value of 9 - and bearing in mind that basic substrates can counteract the toxicity of SO_2 to some extent, it does not seem necessary to invoke differences in water-retention capacity of the substrate to explain why lichens are attracted to asbestos.

Gilbert[27] and many others[22,41,42,73] have discovered that along an increasing SO_2 gradient (that is, on approaching a source of SO_2, the atmospheric concentration of it rises), before each species reaches its maximum SO_2 tolerance level and becomes extinct, it tends to be restricted to the base of the tree. Thus in a polluted area, sensitive species may be seen on the lower tree-bole, (and in patches of woodland) but nowhere else. For instance, Griffiths[33] found that Evernia prunastri grew at the base of oaks 1.8 kms. from a source, but did not appear at head-height on trees for a distance of 2.6 kms. from the works. But these researchers believe that the tree-base and wooded sites are favourable habitats - not because of their moisture-content - but because they are sheltered from atmospheric impurities, and so lichens near the bottoms of trees and in woods are exposed to lower levels of SO2 than epiphytic vegetation on other parts of the tree surface, and in open situations respectively. In other words, the tree-base and areas of dense vegetation like woods are sheltered niches which implies that they constitute moist as well as unpolluted environments. As to which of these two beneficial factors encourages lichen growth near the roots of trees and in woods the latter is preferable for the following reasons:-

(i) Lichens can resist long periods of dessication[5,20,84]; for example, Alectoria fuscescens was still alive after 40 weeks of 'laboratory drought'[84]. It is therefore dubious whether the dampness of the habitat influences lichen distribution as much as SO2 concentration.

(ii) It was suggested above, that SO2 is a very light gas, and is readily transported by wind. Thus, a niche which is sheltered from pollution-laden winds will be relatively SO2-free. Habitats such as dense pockets of woodland and tree-bases are characterised by reduced wind-speeds and may therefore be expected to receive lesser quantities of SO2 than surrounding exposed areas. Carruthers[13] measured variations in wind-speed according to height above the ground and found that nearer the earths surface there was a decrease in wind-velocity due to: increased turbulence towards the ground because of the rise in adiabatic lapse-rate just above the surface - turbulence counteracting wind-speed; and surface friction retarding the wind. A general impression of the change in wind-velocity with height[13] is provided by the formula: $v = kh^a$, where v = velocity, k = a constant, h = height above ground, and a is a power which varies according to local conditions. Rough terrain (leading to relatively more frictional drag of wind-speed on the ground) and a rapid change of temperature with height (causing a considerable amount of turbulence) produce a high value of a, and so wind-speed drops markedly with height above ground under these conditions[6]. Using a fairly typical value of 0.17 for a in the formula, Carruthers[13] computed the change of wind-speed with height at a station. Assuming a velocity at 10 m. of 100%: 5 m. = 89%; 3 m. = 81%; 1 m. = 68%. Lawrence[55] discovered a similar vertical gradient of wind-velocity; and moreover his measurements of the change in SO_2 concentration with height above the ground correlated very well with the wind-speed records. At the ground-surface there was less than half the quantity of SO_2 as existed at 60 cms. above the ground, and he postulated that atmospheric SO_2 concentration was proportional to wind-speed and its variation with height. Gilbert[18] tested the SO_2 content of the air above the earth's surface and produced the results shown in TABLE VII. Therefore, it appears that the reduction in wind-speed nearer the ground gives rise to purer air at tree-bases, so that a richer lichen flora can develop there. The braking effect of woods on wind-speeds is well-known[6], and so it is feasible to explain the existence of sensitive lichens in woods by the same theory. The high moisture-content of woodlands and tree-bases may contribute to their ability to support certain epiphytes, but it is more likely that variations in wind-speed are the direct cause of SO2-sensitive lichens flourishing in these niches in polluted localities.

(iii) The suggested physiological mechanisms by which moisture may relieve SO2 toxicity to lichens lack experimental proof of their existence. Furthermore, it was stated previously that more moisture leads to an increase in metabolic activity (especially photosynthesis) and more SO2 absorption. By this theory, therefore, any increase in RH or substrate moisture-levels would cause SO2 to be more harmful to lichens, not beneficial.

It is thus hypothesized that niches sheltered from SO2-laden winds carry richer floras than exposed surfaces - differences in water-availability to lichens between these two sites being unimportant. Shelter and pH are both seen to be very significant for SO2 distribution and concentration, and the resultant patterns of lichen distribution they lead to, bear witness to their influence.

(D) <u>Evidence for the Importance of SO2 as a Controlling-Factor in Lichen Distribution</u>

The regulation of lichen distribution by SO2 has so far been simplistically summarised as: high concentrations of SO2 in the air deplete the lichen vegetation of regions so affected. More detailed evidence in support of this statement is presented below, but it is first necessary to establish exactly what sort of values of atmospheric SO2 concentration are of significance to lichens.

Due to the considerable spatial and temporal fluctuations of SO2 in the air, all manner of intensity/duration ratios of SO2 occur in nature. It is thus pertinent to inquire whether the lichen flora at a site is most affected by the mean annual SO2 levels in that area, or at the other extreme by the highest daily levels recorded locally. Gilbert[27] fumigated Hypogymnia physodes with high concentrations of SO2 (155 $\mu g/m^3$) for differing periods of time. After five weeks of this treatment, specimens were still alive and could regenerate - which suggests that high levels of SO2 of short duration (less than a month) may be tolerated by lichens, and are not of consequence in governing their occurrence. Exposures of longer than five weeks to severe doses killed the plants, and so it is possible that mean monthly readings are the critical values for lichen survival. However, it is unusual to find continuously high concentrations of pollutants in the air for as long as a month - due to the vagaries of the British climate in such matters as wind-direction, wind-speed and adiabatic lapse-rate. Therefore, Gilbert considered[27,30] that mean figures of at least six month periods are the most relevant to lichen distribution. Baddeley and Ferry[23], and Zahn[98] are both of the opinion that vegetation can fully recover from short, severe, sublethal doses of SO2; and that it is the long-term atmospheric SO2 levels of a region which control the corticolous lichen assemblage which can exist there. In practice, the figures used in

Height above ground in m.	SO_2 concentration in $\mu g/m^3$
2.6	173
1.3	175
0.6	164
0.15	130
0	50

TABLE VII : SO_2 concentration at different heights above a site over the same period of time.
Source: Gilbert.[28]

relating lichen distribution to air-pollution are either: mean winter or mean annual SO_2 concentrations. The former are preferred by some[41] on the grounds that there is more SO_2 in the air in winter (see above) and it is thus a critical period for epiphytes; while the latter have the advantage of being more representative of the total impact of SO_2 levels on vegetation. As annual and winter SO_2 levels are not too different for any one place, they both tend to be useful in explaining lichen distribution, and it is of little matter as to which value is utilised. It is more important to note that it is statistics of this order (monthly/annual) which are relevent to lichen occurrence, rather than short-term SO_2 concentrations.

The fact that SO_2 causes impoverishment of lichen vegetation when it is present in sufficiently high concentrations in the air, for long periods of time, has been recognised from the following studies:-

(a) The Sensitivity of Lichen Species to SO_2

A lichen species can tolerate a certain amount of SO_2 and long-term atmospheric levels above this amount are lethal to that species of lichen. Furthermore, because each species differs from other lichens in its degree of sensitivity toSO_2, the presence or absence of a particular species is indicative of the amount of SO_2-pollution in the air. For example, *Lobaria pulmonaria* is believed to be very sensitive to SO_2, and its existence is proof of the fact that the local atmosphere is fairly 'pure'. *Lecanora conizaeoides*, on the other hand, can tolerate high concentrations of SO_2, and so while it cannot compete with other lichen species - and is generally absent - in unpolluted regions, in districts of severe SO_2 emissions it may be the only corticolous lichen recorded.[54] It can thus be seen that if the distribution of these two species in a certain area is plotted, a map may be produced to show the mean SO_2 concentrations characteristic of the area concerned. Extending this idea to include other lichens of known SO_2-sensitivity would permit the finer delimination of the spatial distribution of atmospheric pollution over the area, and a whole series of lichen 'zones' might be mapped. If such a procedure were carried out around a major SO_2 source (such as a city, or a power-station) - because of the pollution-gradient away from the source - the lichen zones should be concentric around it: increasing distance from the emission source (and decreasing SO_2 concentrations) permitting the gradual appearance of more sensitive species.

Studies of this sort have been undertaken by a number of people, who have recorded the absence or presence of certain species in the vicinity of SO_2-sources, and have mapped the resultant zones of species-occurrence. For instance, Brodo[12] examined the distribution of corticolous lichens around New York. He discovered that Parmelia caperata did not appear until 60 kms. away from the city, while a distance of 40 kms. marked the inner limit of P. saxatilis to the city, and the occurrence of Cladonia coniocraea was prohibited within 20 kms. of New York. From his work, Brodo was therefore able to place these three lichens in an order of SO_2-sensitivity (P. caperata being the most sensitive and C. coniocraea the least), and zones mapped on the basis of their distribution (C. coniocraea zone: 20-40 kms; P. saxatilis zone: 40-60 kms; P. caperata zone: 60 kms. +) provided an approximate indication of the SO2 concentration of districts around New York, and showed up the rate of change of the pollution-gradient with distance form the city.

In TABLE VIII are collected the results of eight similar pieces of research. All the contributors to this chart recorded the presence or absence of certain corticolous lichens at various distances around SO2 sources. A number of different tree species were examined in their work; but each research-worker confined his observations to those lichens growing between 1.5 m. and the ground, on tree-trunks, and only studied the epiphytic flora on trees standing in open situations (that is, sheltered trees in woods, valleys or behind walls - protected from atmospheric SO2 to some extent - were not included in the surveys). In all cases, there is assumed to be a relationship between species sensitivity and distance from the SO2 source: the further away from the source that a species is first found (i.e. the more distant the inner limit of that zone) the more sensitive it is assumed to be to SO2. In this way, the differential SO2 sensitivity of certain lichen species is elucidated by virtue of their position of occurrence on the pollution-gradient, and an order of species tolerance was drawn up by each of the eight lichenologists. Some defined lichen zones according to the existence of a number of species, while others just

	B	S	R & L	J	Gi	F	Gr	MH & H
No lichens	I	I	I	I0	2	I	–	–
Lecanora conizaeoides	II	II	III	II	3	2	0	0
Lepraria incana	II	II	–	I3	I0	–	–	–
Lecanora expallens	II	V	–	I3	I0	–	2	–
Hypogymnia physodes	VI	II	II	I5	II	8	I	0
Parmelia sulcata	V	III	II	I5	I3	8	2	I
Lecidea scalaris	VI	II	–	–	–	–	–	–
Parmeliopsis ambigua	–	IV	III	–	I5	–	I	–
Lecanora chlarotera	III	VI	IV	–	I5	–	–	–
Evernia prunastri	VIII	V	–	20	I3	I0	3	I
Calicium viride	–	–	–	–	I6	–	2	–
Parmelia saxatilis	X	–	IV	–	I5	8	I	3
Pertusaria amara	–	V	III	25	I5	–	2	–
P. pertusa	–	–	III	25	I3	–	5	–
Certraria chlorophylla	IX	III	–	–	–	–	–	–
C. glauca	X	IV	–	25	I5	–	3	–
Phlyctis argena	VII	V	–	25	–	–	–	–
Parmelia subaurifera	–	VII	IV	–	–	–	–	–
P. glabratula	–	–	–	–	–	–	5	2
Opegrapha spp.	IX	–	–	25	–	–	–	–
Alectoria fuscescens	XII	VII	III	25	I6	I0	–	–
Usnea subfloridana	–	–	IV	25	I6	I0	5	3

TABLE VIII : Approximate order of sensitivity of certain lichen species to SO_2 (increasing sensitivity toward foot of table). Arabic numbers refer to kms. from SO_2 source that species is first recorded; Roman numerals to position of species in subjectively devised zone (lower values of zones are nearer the SO_2 source) of lichen presence.

Sources: B - Barkman[5] - zones around Dutch cities

S - Skye[84] - concentric zones of lichens around Stockholm

R & L - Rao & LeBlanc[73] - lichen zones in the vicinity of an iron-sintering plant

F - Fenton[22] - transect S.W. of Belfast

Gi - Gilbert[31] - inner limits of spp. N.W. of Newcastle

J - Jones[46] - lichen presence on a transect E. of Birmingham

Gr.- Griffiths[33] - transect W. of Consett

MH & H - Morgan-Huws and Haynes[61] - lichen occurrence S.W. of Fawley oil-refinery recorded the distance from the source at which a particular lichen first appeared: both sets of results have been incorporated into the table in an attempt to draw up an overall picture of the varying sensitivity of some common lichens to SO2.

Because of the discrepancies that exist between the results presented, no truly accurate 'sensitivity league table' may be produced; but it may be fairly safely assumed that the species towards the foot of the table are more sensitive to SO2 than those nearer the top, and would thus usually be found only at some distance from SO2-sources where as a result of dilution-processes, atmospheric concentrations of this gas are less. The inconsistency of the results, in terms of the widely varying positions of the inner limits of certain species, is a reflection on the complex action of the many environmental parameters which control SO2 concentration and distribution. For example, Jones[41] transected east of a SO2 source - a direction liable to high levels of pollution for some distance from Birmingham, as a result of the prevailing winds - and this probably explains why pollution-gradients in the oter surveys, (which were taken along different compass-directions) are steeper. Again, the steep pollution-gradients, represented by narrow lichen zones, in the work of Griffiths[33] and Morgan-Huws and Haynes[61] are almost certainly due to the fact that they are dealing with industrial point-sources of SO2 (rapid dilution of the gas after concentrated emission) which do not produce the 'blanket pollution' of domestic sources (low-level, widespread pollution, not easily dispersed as emission is diffuse) from cities such as Newcastle,[17] Belfast,[22] and Birmingham.[41] But although it is easy to understand why the width of lichen zones may vary considerably according to the local SO2 gradient, the fact that different people have placed the same lichen in very different categories of sensitivity (see for example Parmelia saxatilis) is not so easy to explain. It could be due to: discrepancies in fieldwork methodology (such as type of tree examined), regional differences in species-sensitivity (even a number of ecotypes may exist for each species), or to the influence of other ecological factors, such as RH and light, on lichen distribution being inadequately considered by some. However, although only approximate, the order of species-sensitivity in TABLE VIII may be taken as a reasonably reliable guide to lichen zonation by SO2.

Having established an order of species-sensitivity, it is clearly desirable to relate the survival of each species to a maximum SO2 concentration which it can tolerate - in order to show that the zonation scheme is truly a response to changing atmospheric SO2 content. The precise correlation of each species with a certain lethal value of SO2 is no easy matter, however, for although lichens are excellent indicators of atmospheric SO2 concentrations (having definite extinction-points at certain mean levels of this toxic gas[39,44]), very little work has been carried out for the purpose of establishing the exact SO2 dose which is fatal to each species. Thus, lichen zones, while providing good qualitative proof of the amount of SO2 in the air, lack the quantitative background which should be able to translate their existence into μg SO_2/m^3 of air. The artificial conditions of the laboratory environment preclude the possibility of assessing species-sensitivity to SO2 in any but the field-situation, and the limited amount of relevant fieldwork which has been undertaken so far is summarised below.

Field-measurement of SO2 is carried out at a few places in Britain and North America (see earlier), and by comparing the lichens growing at these sites with the measured local atmospheric SO2 content, some idea of the actual level of SO2 which is toxic to different species may be gained. Gilbert[27] looked for the occurrence of Parmelia saxatilis in the vicinity of a number of pollution-guages and came to the conclusion that this lichen could not tolerate an annual level of SO2 in excess of $65 \mu g/m^3$. He then mapped the distribution of P. saxatilis in Northumberland and was able to show that the area devoid of this species corresponded to the built-up and industrialised eastern part of the county, where an atmospheric SO2 content of over 65 g/m might be expected (and he termed this area the "Parmelia saxatilis desert"). Hawksworth, Rose and Coppins[42], who used the same method, list a number of species as being unable to tolerate a mean winter value of over $65 \mu g/m^3$, including those listed in TABLE I. Others have calculated the annual levels of SO2 at which various species become vulnerable, for instance: Xanthoria parietina: $140 \mu g/m^3$ (laundon[53]); Parmelia saxatilis: $43 \mu g/m^3$ (Fenton[22]); Usnea subfloridana: $50 \mu g/m^3$ (Hawksworth, Rose and Coppins[42]);

and so on. But the most comprehensive attempt to relate corticolous lichen zones to atmospheric SO2 concentration yet made, is the 10-point scale outlined by Hawksworth and Rose[41]. This qualitative biological scale, designating certain species as indicators of atmospheric SO2 content, is reproduced in TABLE IX (it is noteworthy that the order of species-sensitivity produced by Hawksworth and Rose[41] is very similar to that compiled in TABLE VIII). Hawksworth and Rose have applied their zonation scheme to parts of Britain - especially those where SO2 recording-guages are absent or rare - to give an estimate of the mean winter SO2 distribution in various parts of the country according to the lichen vegetation present. The mapping of these zones then provides a clear picture of the pollution pattern of an area. In Fig. 2 the influence of London's SO2 emissions on the purity of the air in south-east England is immediately obvious from the concentric lichen zonation which surrounds the city.

Finally, there have been a few studies in which both lichen zones and mean SO2 levels have been mapped and correlated in polluted localities. Such direct links between SO2 gradients and lichen occurrence are of obvious significance for the construction of league tables of species tolerance. Morgan-Huws and Haynes[61] looked at the frequency of epiphytic lichens, and measured the annual average SO2 levels, around Fawley oil-refinery (a large source of SO2) in Hampshire. They were able to show that as atmospheric SO2 concentrations decreased away from the refinery, sensitive species began to appear: successive

Zone	Lichen Vegetation	Approx. Mean Winter SO2 level in g/m .
0	Nil	
I	Pleurococcus viridis*	over I70
2	P. viridis; Lecanora conizaeoides*	I50
3	L. conizaeoides; Lepraria incana*	I25
4	L. incana; Lecidea scalaris; Lecanora expallens; Chaenotheca ferruginea; Hypogymnia physodes*; Parmelia saxatilis*; P. sulcata*	70
5	H. physodes; P. saxatilis; P. glabratula; P. subrudecta; Parmeliopsis ambigua; Lecanora chlarotera; Calicium viride; Lepraria candelaris; Pertusaria amara; Evernia prunastri; Cetraria glauca	60
6	Pertusaria spp.; Opegrapha spp.; Alectoria fuscescens; Parmelia caperata*; P. tiliacea; P. exasperatula	50
7	P. Caperata; Pertusaria hemisphaerica; Usnea subfloridana	40
8	Usnea ceratina; U. rubiginea; Parmelia perlata; P. reticulata; Gyalecta flotowii	35
9	Lobaria spp.; Usnea spp.; Dimerella lutea	under 30
IO	Lobaria spp.; Usnea spp.; Stricta limbrata; Teloschistes flavicans	'pure'

TABLE IX : Qualitative scale for the estimation of SO2 pollution using corticolous lichens. * confined to base of tree
N.B. Pleurococcus viridis is an alga.
Source: 4I

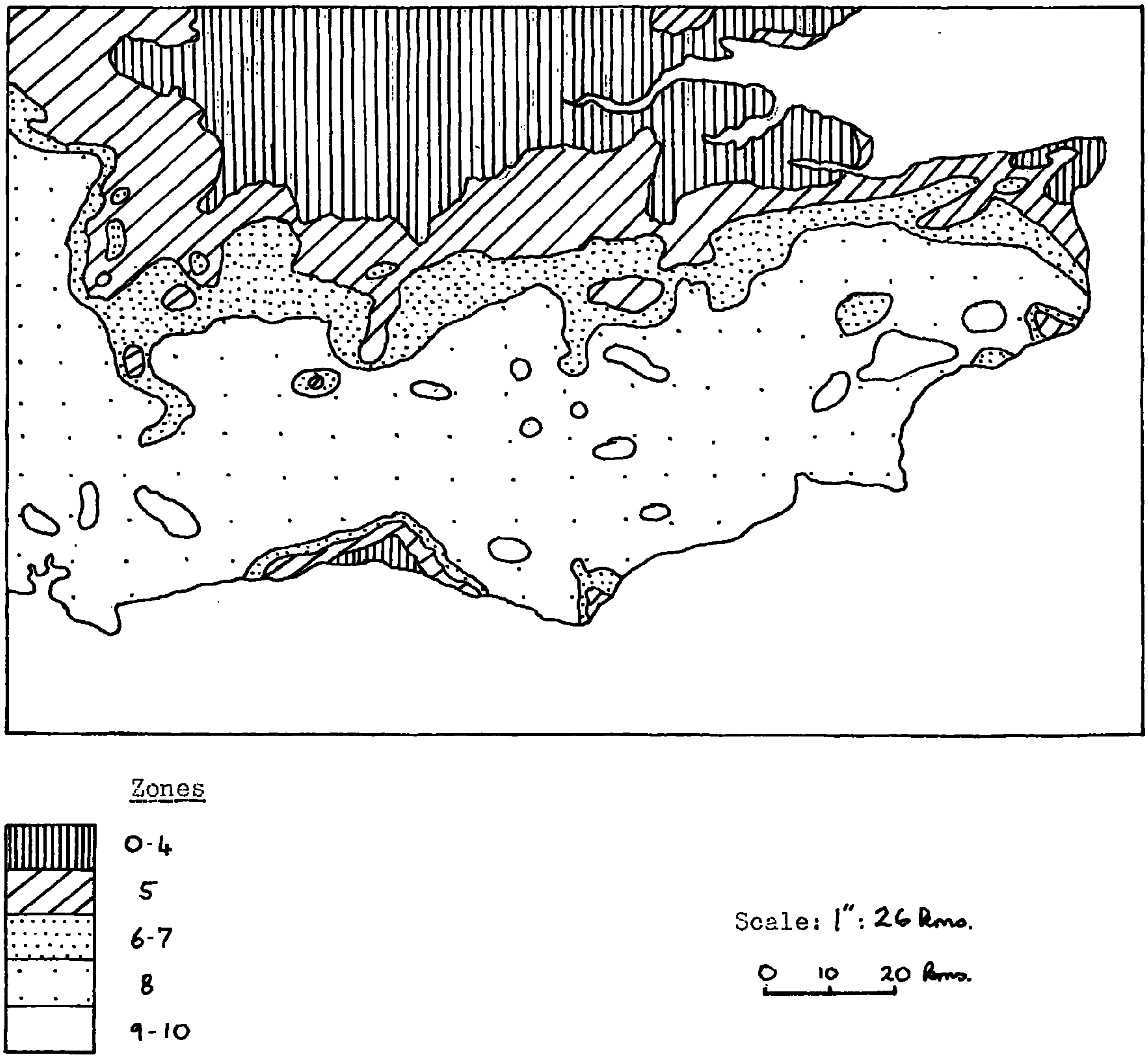
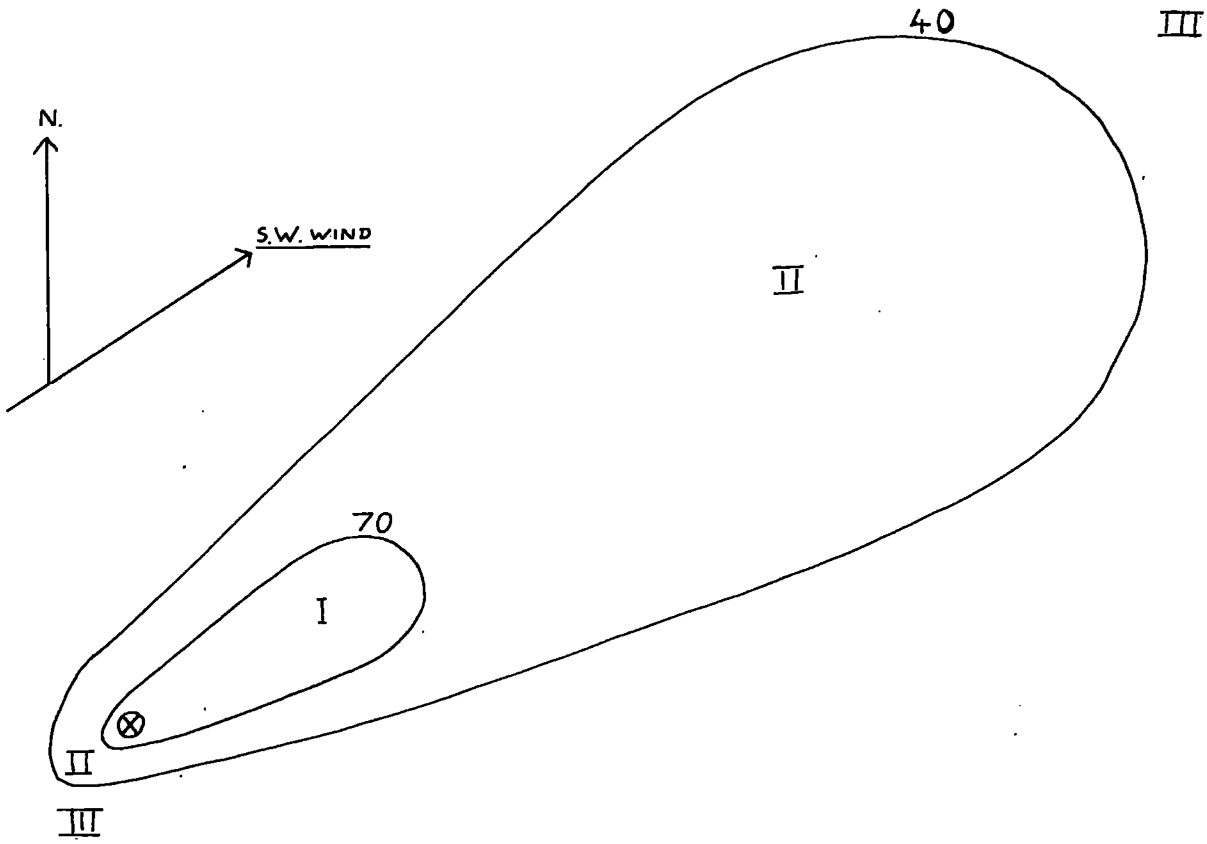


Fig. 2 Pollution zone-map of S.E. England using the Hawksworth and Rose 10-point scale.

Source: 41.

lichen zones (see TABLE VIII) displaying a spatial correspondence to certain levels of SO_2 (Fig. 3). Moreover, as discussed previously, wind-direction has an important effect on SO_2-distribution; and in terms of annual average SO_2 figures it is the prevailing winds which are the most significant. This is apparent in Fig. 3 where the mean yearly SO_2 contours are displaced N.E. by the prevailing winds. The dependence of the lichen flora on SO_2 pollution is shown by the fact that the vegetation zones are similarly orientated in response to the shallow SO_2 gradient to the N.E. For example, Usnea subfloridana occurs 2 kms. S.W. of the refinery, but is not found for a distance of 30 kms. to the N.E. of the plant - its distribution is fairly clearly related to the 40 $\mu g/m^3$ contour. Skye[84] also found that the 7 lichen zones he recognised in Stockholm were related to the spatial distribution of SO_2 in the city: the lichen desert (zone 1) extending further to the east (with the prevailing winds) than to the west of the city-centre. Rao and LeBlanc[73] studied the SO_2 content of the air, as well as the SO_4 concentration of the soils and vegetation around an iron-sintering plant in Ontario, and discovered a decreasing gradient in all these parameters away from the SO_2 source. Moreover, all the gradients were steeper to the S.W. - again because of the prevailing winds carrying SO_2 primarily away from this direction. Their 5 concentric lichen zones correlated well with this SO_2 distribution, no epiphytes being able to live in a zone stretching only 0.5 kms. S.W. but covering 16 kms. in a N.E. direction (Fig. 4).



⊗ = SO2 source

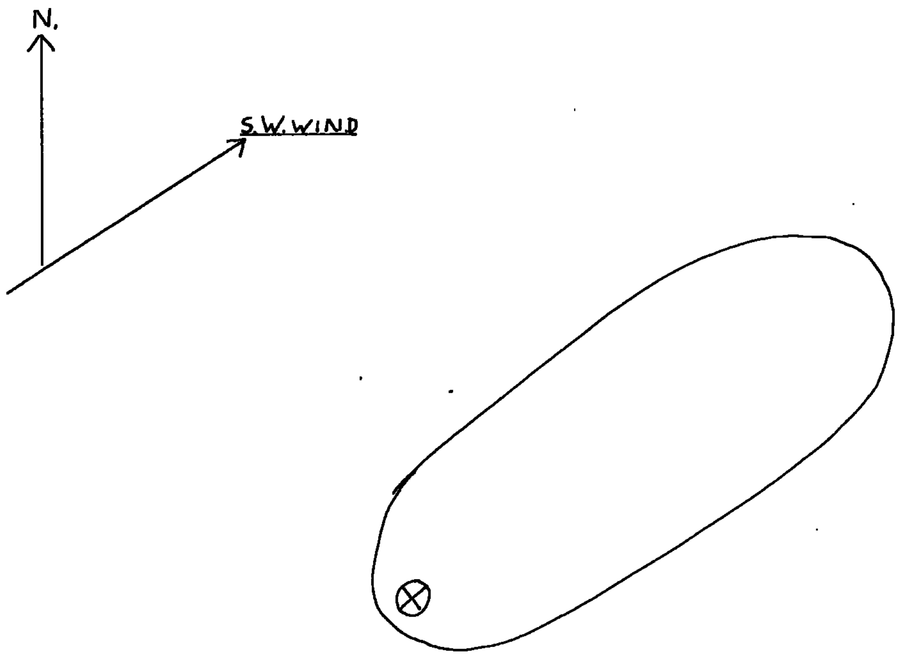
/ = Contours of mean SO2 in $\mu g/m^3$

I, II, III = Zones

Scale = I" : 5 kms.

Fig. 3 : SO2 and lichen zones around Fawley oil-refinery.

Source - 6I



⊗ = S02 source

/ = limits of lichen desert

Scale = I" ÷ 5 kms.

<u>Fig. 4</u> : Lichen desert around an iron-sintering plant, Wawa, Ontario.

Source: 73

Therefore, because certain species of lichens have different mean levels of SO2 which they can tolerate, an order of species-sensitivity to SO2 may be devised. If the distribution of these 'indicator species' is mapped, the pattern of SO2 concentration in a region is clarified in terms of pollution-zones, according to the lichen species present. This is one means whereby the effect of SO2 on lichen distribution may be recognised.

(b) The Sensitivity of Lichen Growth-Forms to SO2

It has been pointed out before, that in the main, a fruticose morphology is more sensitive than a foliose shape, and that foliose lichens are in turn more adversely affected by SO2 than crustose growth-forms. There are exceptions to this theory - for example, the foliose Hypogymnia physodes is far more toxitolerant than sensitive crustose species such as Pertusaria pertusa and Gyalecta flotowii[41] - but as a general rule, the predominant lichen growth-form in a region can give some idea of the local SO2 concentrations expected there. Gilbert[27] noted that in the centre of Newcastle only crustose species could survive (Lecanora conizaeoides, L. expallens and Lepraria incana), and it is evident from TABLES VIII and IX that the most resistant lichens are crustose, while fruticose individuals like Alectoria fuscescens and Usnea spp. are particularly vulnerable to SO2 pollution. Fenton[21] discovered that with increasing distance from Belfast (and lower SO2 concentrations further away from the urban and industrial sources of pollution) there was also an increase in the ratio of foliose/crustose lichen cover % on tree bark (TABLE X);

Distance from Belfast in kms.	% Cover of Crustose Lichens	% Cover of Foliose Lichens
0	0	0
I	I	0
7	I2	3
II	27	I8
I7	28	43
25	26	5I

TABLE X : The change in crustose/foliose % cover ratio along a transect S.W. of Belfast.

Source: 2I

and Jones[41] came up with similar results. So, the recording of lichen morphology may give a crude guide to the changes of mean SO2 concentration in the atmosphere.

A question only briefly considered in the preceding discussion might now be tackled: why are some lichen species and growth-forms more sensitive to SO2 than others? Gilbert[26,27,28] cleared up one aspect of this problem when he found that resistant and sensitive species absorb the same amounts of SO2 from the air (all lichens taking up this gas in proportion to its strength in the local environment); and he therefore stated that SO2 tolerance is not conferred upon certain species because they accumulate less SO2 from the air than sensitive lichens. The question may thus be narrowed down to: how can one species tolerate high levels of SO2 better than another, after both have absorbed considerable quantities of the toxin?

The old explanation for fruticose species being more vulnerable to SO2 is based on the fact that lichens absorb water and minerals over their entire surface-area. Thus, as fruticose growth-forms present a greater exposed surface area to the atmosphere than other lichens they should absorb more materials and hence SO2 from the air. This idea may be rejected: firstly on the basis of Gilbert's assertion that all species accumulate similar amounts of SO2 in a polluted atmosphere; and secondly because it is known[29,67] that lichens absorb SO2 from both the air and the substrate, so that although crustose species take in few elements from the air, they utilize the mineral supply (and associated SO2) of the tree bark far more than fruticose lichens do. Again therefore, SO_2-resistance is a function - not of SO_2 absorption-rates - but of some immunity mechanism which operates more efficiently in some species than others.

A feasible hypothesis on which the differential tolerance of lichens to SO_2 may be founded is suggested below. Thomas[59] discovered that some mosses could survive under conditions of SO_2 pollution by slowly oxidising it to SO_4 (which is not as toxic to vegetation as SO_2); and it is possible that lichen resistance could depend on a similar process of slow SO_2 detoxification. Such a theory would explain some important facts. The relationship between rate of physiological activity and SO_2 toxicity detailed previously would not depend on rate of SO_2-uptake (as suggested earlier) but upon energy and/or time available for the process of oxidation to SO_4. In other words, the maintenance of a high metabolic rate would allow a plant little time and/or energy for the oxidation of SO_2 to SO_4; and so while its SO_2 absorption-rate would remain unchanged, less of the SO_2 could be converted to impotent sulphur compounds in this plant.[27,28] Thus, at times of the day and year when physiological activity is greatest, plants are more sensitive to SO_2 because they cannot detoxify it, although SO_2 absorption-rates appear to stay constant. If two lichen species consistently differ in their overall levels of metabolic activity, then the more active of the two may be expected to be more sensitive to SO_2 by virtue of its lack of time or energy available for oxidation of this gas.[38] Fenton[21] noted that crustose lichens are characterised by slow growth-rates, and that their levels of physiological activity are low; while fruticose and foliose forms, which have relatively rapid growth-rates and are often photophilous (needing light to maintain a high level of photosynthesis) are metabolically more active. Thus, as far as it goes, the theory that differential sensitivity is based on the rate of physiological activity in each species, and its inverse relationship to the ability of lichens to detoxify SO_2 by oxidation to SO_4, fits the known facts on the relative sensitivity of the different lichen life-forms: sensitive fruticose species having higher rates of metabolism than the resistant crustose flora. But the next step is to look at the metabolic rates of each species listed in the 'sensitivity league' (TABLES VIII and IX), to see if level of physiological activity and ability to tolerate SO_2 may be correlated for each lichen species rather than just for morphological form. Also it needs to be clearly shown that lichens can detoxify SO_2 by oxidising it to SO_4, and that this process is retarded by any increase in metabolic rate. Until this work is done, the hypothesis - although it explains the differential sensitivity of lichens quite adequately - must remain an idea only.

There are no other general theories attempting to account for the fact that lichen species differ in their degree of sensitivity to SO_2; and so differences in the rate of detoxification of SO_2 to SO_4 (and its dependence on metabolic activity) may be taken as the most acceptable idea at present. However, it has been suggested[10,27] that

Lecanora conizaeoides - the most SO_2-resistant lichen - is in fact not just toxitolerant, but has a sulphur requirement and therefore actually prefers polluted environments. Kochler[52] and Katz[48] have recorded the fact that small quantities of SO_2 do not adversely affect higher plants but tend to stimulate photosynthesis and growth-rate; and Brightman[11] has found Lecanora conizaeoides flourishing near sulphur springs in Iceland. Furthermore, the distribution of this species suggests it may be toxiphilous, for it is only found in urban areas, and is often absent from unpolluted sites.[10,27,53] The counter-argument is that Lecanora conizaeoides is simply very resistant to SO_2 (by having a very low average metabolic rate according to the theory put forward above) and can flourish in polluted regions where there is little competition with other species. In air with a low SO_2-content, its toxitolerance would confer no competitive advantage on this species and it would be overgrown by other lichens. The question of whether Lecanora conizaeoides is toxiphilous or toxitolerant is related to the uncertainty surrounding the existence of all animals and plants in extreme environments: is the extreme (in this case heavily polluted) environment an optimal niche for the species concerned, or are they 'forced' into these inhospitable sections of their fundamental niches by competition with other species? Current opinion seems to favour the latter concept, and so Lecanora conizaeoides is assumed to have no sulphur requirement, but merely to be less sensitive to SO_2 than other lichen species.

(c) The Effects of SO2 on Species Diversity

Another parameter of lichen distribution which changes as a result of SO2 in the atmosphere is species diversity. As the SO2 concentration of the air increases, so the number of epiphytes which can live in such an environment falls, and consequently the mean species total per tree drops. This is only logical, in that SO2-resistant lichens can grow in pure air - while sensitive individuals cannot survie in an impure atmosphere - and thus there are more species potentially able to occupy a corticolous substrate in unpolluted than polluted conditions. High concentrations of SO2 permit the existence of few epiphytic plants (for example, according to Hawksworth and Rose[44], only 4 lichens can tolerated winter SO2 levels of over 70μg/m^3) - in the way that any extreme environment allows only the most resistant life-forms to survive. The results of the research using numbers of species/tree as an index of the severity and extent of air-pollution are included in TABLE XI. It is obvious that such figures could be used to devise diagrams showing the spatial extent of SO2 pollution, in the same way as zone-maps of the distribution of certain sensitive indicator species were drawn up. However, no attempt has yet been made to quantify the relationship between species numbers and long-term SO2 concentrations in the air.

(d) The Effects of SO2 on the Detailed Distribution and Morphology of Lichens

As acknowledged above, along a gradient of increasing SO2 concentration, lichens are exterminated - the most

Distance	Gilbert[29]	Rao & LeBlanc[72]	Griffiths[33]	Morgan-Huws & Haynes[61]
SO_2 Source	0	0		2
		3	15	
		13		
10 kms	1		25	
				30
20 kms	25			
		16		
30 kms				
↓ Decreasing SO_2 Concentration		22		

TABLE XI : The decline in species numbers with increasing SO_2 concentration (proximity to SO_2 source).

For transect details, see TABLE VIII.

Sources: as above.

sensitive species being the first to be killed. However, no species suddenly disappears at a certain point along the gradient; rather is there a gradual decline in its frequency, luxuriance of growth, fertility and abundance which may extend for a considerable distance before the air finally becomes too toxic for it to survive and it is completely eliminated from the flora. Therefore, recording the variations in (i) size, (ii) sexual capability, (iii) % cover and (iv) frequency of lichen species, and mapping these results, may also provide a guide to the distribution of SO2-pollution over the survey area.

(i) Reduction in lichen size as an indicator of the amount of SO2 in the air - although a sensitive measure of SO2-concentration - suffers from the disadvantage that only in fruticose growth-forms may stunting as a result of sulphur-saturated air really be observed and measured. As fruticose species are absent[41] from air containing more than 60 $\mu g/m^3$ SO2 (TABLE IX), any index of variation in lichen size will only be significant in air purer than this. Because of this drawback, the change in luxuriance of a species under different levels of atmospheric SO2 is rarely employed as the sole criterion of the distribution of air-pollution, but is usually considered incidentally to more detailed research. For example, Griffiths[33] found that Evernia prunastri grew to a length of 5 cms. at a site 6.4 kms. from a steelworks, but at 2.6 kms. from the SO2 source specimens of this lichen were as small as 1.5 cms. However, he did not attampt to expand this approach into a fuller examination of the change in length of the species over the whole study area.

(ii) The reduction in fertility of any one species at higher SO2-concentrations - which it would be theoretically possible to map as a guide to the distribution of SO2-pollution - has not been used as an index of atmospheric sulphur content in any of the publications listed below, because of the overwhelming problems of quantification of lichen fertility. Thus, like species size, the change in the reproductive status of lichens as environmental SO2-concentration increases is often remarked upon,[12,27,84] but never followed up in any detail.

(iii) Thirdly, there is the possibility of utilising figures on the changes of species abundance as a guide to the purity of the air. There are cases in which total % cover of all corticolous lichen species on tree trunks has been used in this way: for example, Fenton[21] observed a total lichen cover of 77% on tree-trunks 17 kms. S.W. of Belfast, this value falling to only 1% in the city-centre. But in using this statistic of total lichen abundance, the change in % cover of individual species of different SO2-sensitivity is obscured. This point may be illustrated from the work of Jones[46] who discovered that although total lichen density decreased towards Birmingham, the abundance of foliose species fell more rapidly than this overall value, while the % cover of crustose lichens actually rose at first (due to the initial extinction of foliose growth-forms, causing reduced competition for the resistant crustose lichens and consequently their successful propagation) before showing a similar drop nearer Birmingham (Fig. 5).

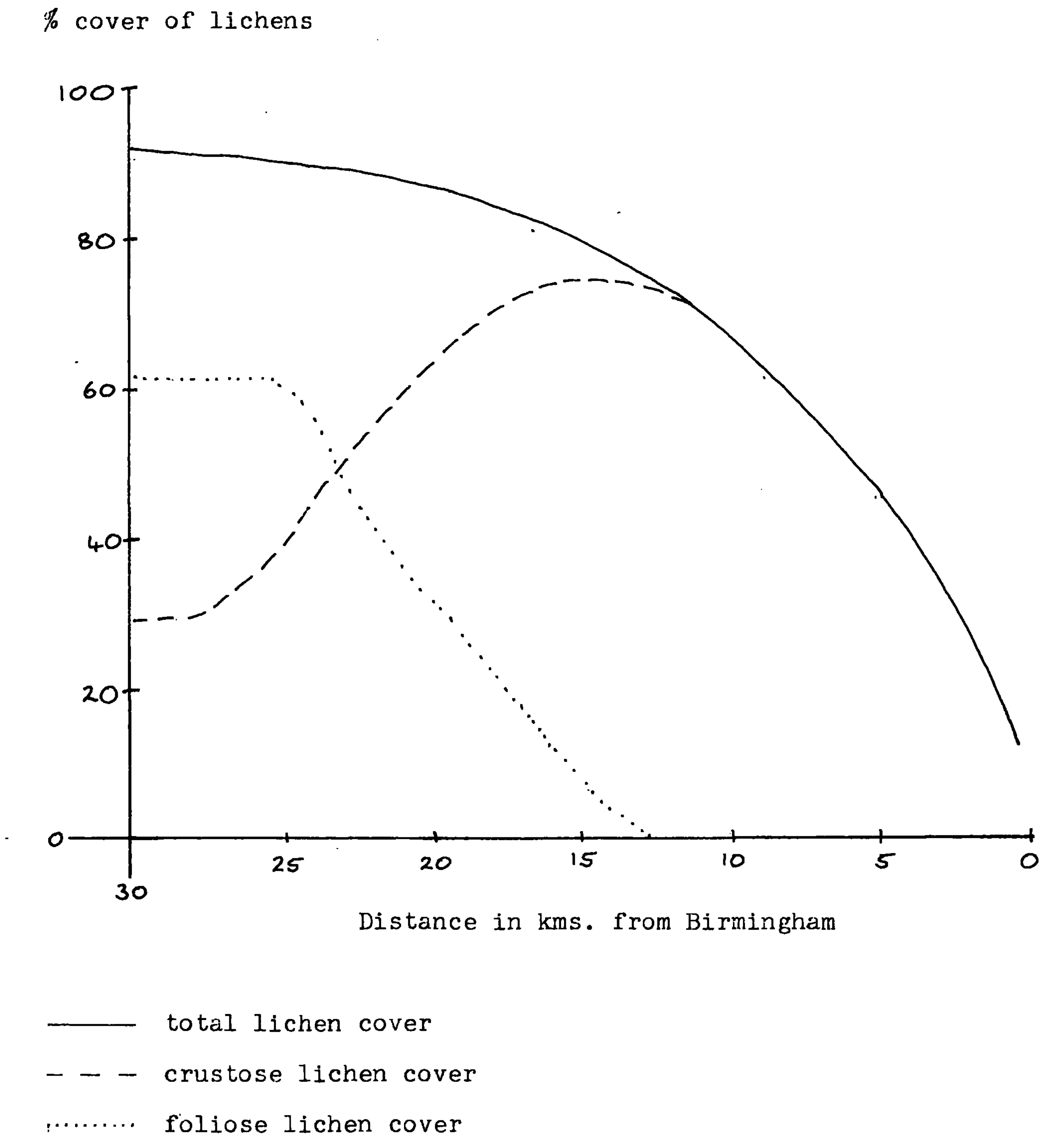


Fig. 5 : The decrease in lichen abundance towards the centre of Birmingham.

Source - 46

It is therefore more profitable to observe the changes in % cover of a certain life-form, or better still of a certain species, when attempting to correlate lichen abundence and SO2-pollution.

Laundon[53] recorded the % cover of Lecanora conizaeoides in London and was able to show its response to the pollution-gradient: this species being absent in the city-centre, covering 10-20% of the tree-surface 10 kms. away and increasing to an abundance value of about 80-90% 15 kms. from the centre. This distribution pattern is related to: concentrations of over 150 $\mu g/m^3$ in central London thereby creating a lichen desert; while 10 kms. from the city-centre, dilution of SO2 in the atmosphere permits Lecanora conizaeoides to survive on tree-bases and in other sheltered spots (10-20% cover) only. At about 15 kms. from London almost the whole trunk is covered with this lichen due to the further decline in SO2-levels with distance from the city-centre. The dominance of Lecanora conizaeoides in the corticolous flora at this station is a function of the amount of SO2 in the air, which is still too high to permit the existence of other lichens, and in the absence of competition this SO2-tolerant species flourishes. As the atmosphere becomes steadily purer beyond the 15 km. mark, so other epiphytes begin to appear and compete for space on trees, and Laundon found that Lecanora conizaeoides declines in abundance from this point away from the city-centre. This is a good example of the use of % cover results for mapping the spatial extent of air-pollution.

LeBlanc and DeSloover[56] devised an index to show the impact of SO_2 on lichens, based on species diversity and the % cover of each species. They termed this statistic the "index of atmospheric purity" (IAP) and calculated the IAP of a certain location from the following formula:-

$$IAP = \frac{\Sigma \frac{1}{n} (Q \times f)}{10}$$

where f = the cover value (on a 1-5 scale) of each species at that site, and Q is a figure purporting to show the SO_2-sensitivity of each species (and represents the mean number of species associated with the lichen in question at all the stations that this particular lichen occurs in). For example, if a study of all the trees in an area reveals that on those trees carrying Hypogymnia physodes the average number of lichens found is 8, the Q for this species is 8. Thus if a tree has a lichen flora comprising H. physodes (cover value 4); Parmelia subaurifera (1); and P. caperata (3); and the Q of these three species is 8, 20, and 23 respectively - then Q x f for H. physodes is 32; for P. subaurifera 20; and for P. caperata 69.

$$\text{The IAP of that tree} = \frac{32 + 20 + 69}{10} = 12.1$$

LeBlanc and DeSloover calculated and mapped the IAP values on a number of old trees (using the lichens present on the bole between 2 m. and the ground) around the heavily-industrialised city of Montreal, to produce a contour-map of increasing IAP further away from the city.

(iv) Statistics on the varying frequency of lichen species with changes of atmospheric SO_2-content constitute in effect a more detailed version of species presence and absence data - as described under (i). That is, recording the presence or absence of lichen species on a number of trees, and collating the results to produce figures of % frequency of lichen species, provides a more accurate and sophisticated record of the distribution of lichen species than is obtained by simply noting the limits of occurrence of lichen species with respect to distance from a source of SO2.

Measuring the % frequency of one species only as a guide to SO2 pollution is of dubious value - for many other factors, such as light, RH etc. influence the frequency of a species. However, recording the % frequency of a number of species, although undoubtedly more valid, is laborious, and has only been carried out in a few detailed studies, the results of which are similar to those obtained from the zonation studies.

(e) Sulphate Content of Lichens

Just as the distribution of sensitive indicator lichens or different growth-forms, and the spatial variations in species numbers and lichen abundance have been employed to portray the extent and severity of SO2 pollution; so also the sulphate content of the lichen thallus is a useful guide to the SO2 content of the air. It was explained earlier that lichens readily absorb SO2, and they convert a lot of this gas to SO4 and store it in the thallus (which, incidentally, is further proof of the theory that lichen resistance is based on the oxidation of SO2 to SO4). Obviously, the more SO2 there is in the air, the more lichens will take up and oxidise; and so the amount of SO4 contained in the lichen thallus accurately mirrors the mean SO_2 concentration of the local air. In other words, as lichens absorb minerals indiscriminately from their environment, it may be assumed that they accumulate SO_2 in amounts consistent with its occurrence in the atmosphere. Griffiths[33] measured the SO_4 content of Hypogymnia physodes thalli and found that specimens nearer Consett Steelworks contained more sulphate (TABLE XII). Gilbert[26] correlated the SO_4 concentration in Parmelia saxatilis and the SO_2 level of the air: 6 kms. from Newcastle, with an air-content of 57 $\mu g/m^3$ SO_2, individuals of this species contained 2870 p.p.m. SO_4; while 14 kms. away, where the air was purer (40 $\mu g/m^3$) an average concentration of only 695 p.p.m. SO_4 was found in lichen thalli. Here then is another means whereby the condition of the corticolous lichen flora may be used to qualitatively assess the levels of air-pollution in a region.

(f) Transplant Experiments

Transplant experiments involve removing healthy lichen specimens from their native habitats and placing them in polluted air to see if they survive. As long as other ecological factors are kept constant (for example, the lichen must be transplanted on to the same species of tree, and be put at the same position on the trunk as it formerly occupied), then if the lichen dies, its mortality may be put down to the toxic effects of SO_2-concentration in its new environment. For example, Hawksworth[38] discovered that Lobaria pulmonaria was common in Dovedale, Derbyshire in the nineteenth century, but does not live there now. According to the Hawksworth and Rose[41] scale, the lichen flora

Distance in kms. from source of SO_2	SO_4 content of thallus in p.p.m.
1.8	610
3.8	446
4	325
4.6	274
5.6	21.2
6.4	10.2

TABLE XII : Sulphate content of *Hypogymnia physodes* near Consett Steelworks.

Source: 33.

of Dovedale belongs to zone 5, so that Lobraria pulmonaria (representative of zone 9) would not be expected to occur there. However, to ensure that the disappearance of this species from the locality was definitely a result of air-pollution, Hawksworth transplanted Lobaria pulmonaria plants from trees in Cumberland and placed them on elms in Dovedale to see if they could tolerate the local atmosphere. The specimens were put in identical positions on the trees in Dovedale, and other conditions - such as light and RH - were the same in Dovedale as in the Cumberland site. But far from flourishing as they did in Cumberland, the transplanted individuals displayed orange discolourations after 6 months, had bleached margins within 9 months, and after 18 months all the thalli were bleached and dead. The cause of the death of Lobaria pulmonaria in Dovedale was the SO2 concentration of the air which decomposed the lichen acids (orange discolouration) and bleached the chlorophyll of the algae. Others who have carried out transplant experiments record similar results, the only differences being in the time taken for the plants to die in their new environments. This varies according to the SO2 level of the air: for example, Lobaria pulmonaria only survived 4 weeks in Leicester[38]! Brodo[11] transplanted Parmelia caperata on to trees at varying distances from New York. The amount of damage done to the specimens decreased away from the city, thereby giving some indication of the slope of the SO2 gradient around New York. In this way, transplant experiments can yield information on the purity of the air in a region.

(g) The Effects of Historical Increases in SO2 on Lichen Vegetation

The preceeding six lines of evidence for the effects of SO2 on lichen distribution have all been concerned with the spatial relationships of mean SO2 concentrations as they exist at one instant of time. However, a great deal of attention has also been paid to the changes of atmospheric SO2 content which have occurred in the same area over a period of time, and the effects that these changes have had on the local epiphytic vegetation.

The Industrial Revolution, and the enormous rise in rates of coal-combustion associated with the urbanisation and industrialisation of this era, was undoubtedly responsible for a large-scale increase in levels of SO2-pollution in Europe and N. America.[53] It is therefore not surprising that the earliest records of lichen decline date from the late nineteenth century, and Grimdon (1859) in S. Lancashire, Nylander (1866) in Paris (noted Hawksworth[39]) and many others, were aware that lichens were sensitive to air pollution and that their distribution was severely inhibited by the presence of atmospheric impurities. More detailed accounts of the history of lichen decline in regions suffering from the impact of sulphurous emissions since the Industrial Revolution are provided by Gilbert[27], and by Hawksworth, Rose and Coppins.[42] Gilbert[27] studied the floral history of Northumberland and Durham, and discovered that the Tyne valley was characterised by a rich and varied lichen vegetation in the early nineteenth century. Woods near the city centre of Newcastle contained Usnea florida (zone 9 of the Hawksworth and Rose scale) and Evernia prunastri (zone 5). In 1884 when these same woods were revisited, no foliose and fruticose lichens were found at all, and Johnson (quoted Gilbert[28]) ascribed this deterioration to "the smoke from the Tyne and Northumberland coalfield". Johnson studied the lichen vegetation in many areas around Newcastle, and Gilbert is of the opinion that about 75% of the species he recorded are now extinct in the Tyneside district. Thus Newcastle has lost its diverse epiphytic flora through the death of many sensitive species since the mid-nineteenth century.

Hawksworth, Rose, and Coppins[42] detail the case of Epping Forest, Essex. In the late eighteenth century, this piece of woodland contained 118 corticolous lichens, including the sensitive Lobaria pulmonaria. In 1885, 48 of these species had vanished and by 1919 Epping Forest bore only 49 tree-loving lichens. Although Usnea subfloridana Parmelia glabratula and other sensitive species still survived there, Lecanora conizaeoides had become the dominant epiphyte. Finally, a survey carried out in 1970 revealed that there were just 28 species left in Epping Forest - all fairly pollution-resistant. Such a decline is clearly attributable to the rising SO2 emissions of the era, and the influence of London's waste-products is still apparent today, in the observation that the least tolerant of the surviving species are congregated in the N.E. part of the Forest (furthest away from London!).

Other woods all over Britain, close to urban and industrial SO2 sources show evidence of a similar decline in lichen vegetation since the mid-nineteenth century. For example, there are no foliose lichens within 8 kms. of Burton-on-Trent, Staffs., but in 1863 Usnea subfloridana and Parmelia caperata grew there[42]; the ancient oaks of of Sherwood Forest, once covered with Lobaria pulmonaria now bear only 8 crustose lichen as a result of Nottingham's pollution[77]; Parmelia caperata has been 'pushed out' of London, and no longer grows within 35 kms. of the city, although it did in the nineteenth century[76]; Lobaria pulmonaria was once common over much of S.E. England, but although there are still mature, well-illuminated tree trunks for this species to thrive on all over the region, it is now confined to 3 small, sheltered sites in the central Weald[45,76]; in Derbyshire, Hawksworth[37] found an impoverished lichen flora developed in the N.E. of the county because of SO2 from Sheffield, while the epiphytic vegetation of the remainder of the region was unchanged (for instance, Alectoria fuscescens was common all over the county in the mid-eighteenth century, but now it is only to be found in the S.W. portion); and Barkman[6] notes that at least 38 lichen species have become extinct in the Netherlands since 1930 - the majority of them known to be pollution-sensitive.

It is thus apparent that the increase in atmospheric SO2 concentration since the Industrial Revolution has had serious consequences for the lichen floras of industrial and urban areas. But on the other hand, in rural unpolluted areas, there has been no recorded deterioration (on a regional scale at least) in the epiphytic vegetation since the nineteenth century. For example, Rose, Hawksworth and

Coppins[77] found in the Lake District in 1969, all those species which had been recorded there in 1833; and the species-list included some extremely sensitive lichens, such as Lobaria and Usnea spp. The policy of conserving the Lake District for its beauty and amenity value has obviously been effective in maintaining the purity of the air in this region. Parts of Dorset, Wiltshire and Devon still have luxuriant floras with over 150 corticolous lichens recorded in some sites[42] - as rich a flora as Epping Forest used to have before sulphurous impurities in the air radically altered its floral composition. Therefore, if historical records are available, the past and present occurrences of corticolous lichens (both in terms of total species numbers, and changes in distribution of sensitive indicator species) in a site provide evidence for the temporal variations of atmospheric SO_2-concentration which have taken place there.

Finally, there have been two studies in which a distinct and sudden increase in industrial point-source SO_2-emission has been monitored, and the effects of this on the adjacent lichen flora observed. Gilbert[31] noted the change in abundance of Parmelia saxatilis when a new power-station was opened at Blyth in Northumberland in 1964. In the next 6 years the mean atmospheric SO_2 concentration in the district rose by 50%, while the % cover of Parmelia saxatilis colonies within 5 kms. of the SO_2-producing power-station fell from 45% to 5% in this period.

Skye and Hallberg[85] compared the distribution of corticolous lichens around an oil-shale works in 1953 and 1968. The output of the plant began to increase in 1953, and as a result of this, SO2 emissions doubled in the following years. Not surprisingly, Skye and Hallberg discovered that the size of the "foliose lichen desert" around the works increased considerably in 15 years; and the inner limits of sensitive species such as Evernia prunastri and Ramalina farinacea to the oil-shale factory were extended outwards quite significantly. Resistant lichens, for example, Lecanora conizaeoides and Hypogymnia physodes became more common around the SO2 source in this period; and it was apparent that the rise in production of toxic gases from the plant between 1953 and 1968 had drastically altered the composition of the local vegetation.

From these seven lines of research, the conclusion that SO2 concentration in the air is an important control on lichen distribution seems inescapable. However, an alternative theory to account for the impoverished epiphytic vegetation of many areas today has been put forward by Rydzak,[78,79] Young,[97] and Brightman[9], and is discussed below.

(E) The "Drought Hypothesis"

Rydzak[79] examined the lichen flora of Lublin, in Poland, in 1950, and again in 1968. Over these 18 years he noticed a decline in the number of species, luxuriance of growth, and abundance of certain lichens in the area, and although coal-combustion figures for Lublin trebled in this period, Rydzak refuted the idea that an increase in SO2 was the cause of this phenomenon. Instead he blamed the 'town climate', and its greater severity as a result of population growth between 1950 and 1968, for the damage done to the epiphytic vegetation. The town climate is known

to be generally drier than that of the adjacent countryside for the following reasons: cement, concrete and brickwork convert most precipitation to surface runoff, and thus there is little infiltration and subsequent soil evaporation in towns; urban areas have few trees, so that transpiration to the atmosphere is negligible in built-up areas; reflection of sunlight from buildings, and domestic and commercial fuel combustion, cause higher air temperatures to prevail in towns, which in turn lead to more evaporation and a lower RH. Rydzak measured RH in a number of Polish towns and found a gradient of decreasing RH towards the centres of these towns - with differences between the outskirts and the built-up parts reaching as much as 12% in places. Moreover, he was able to correlate RH isohyets with zones of lichen growth (according to numbers of species and % cover). He therefore concluded that the urban microclimate was unfavourable to lichens, and that the low RH of towns was the main cause of their depleted lichen floras - not the SO_2 concentration of urban air. By the same hypothesis, Rydzak explained that those niches in which lichens flourished (dense patches of woodland, tree-bases, and other sheltered positions) in urban areas owed their suitability as epiphytic substrates to their locally high RH. He backed up his idea that RH deficiency - and not SO_2 - is the cause of lichen impoverishment with the following general details:
(a) small towns which release little or no SO_2 to the atmosphere still possess lichen deserts in their centres, (b) despite prevailing S.W. winds, the flora of N.E. Lublin was as good as that of the S.W., (c) in some cities which

produce considerable amounts of SO_2, sensitive lichens may still be found; and he quoted the case of a town in Czechoslovakia with a dirtier atmosphere than New York but which still exhibited a rich epiphytic cover on its trees.

Young[7] stressed the reliance of lichens on the moisture-availability of their environment, and like Rydzak believed that their absence near cities was related to RH and substrate moisture rather than pollution. She discovered that the bark of trees in rural woods had a higher water-retention capacity than that of similar tree species in towns.

Coppins[17], Gilbert[27], Skye[54], Laundon[56] and Rao and LeBlanc[72] reject the drought hypothesis, and their reasons are summarised as follows:

(i) Rydzak's assertion that cities with a high atmospheric SO_2-content may still contain sensitive lichens is opposed by the evidence accumulated from many studies (as described earlier). Moreover, of the 44 species he found in Lublin, all but 3 were toxitolerant, and these 3 were confined to the suburbs.

(ii) His claim that 'little towns' with 'pure air' were characterised by the presence of lichen deserts is dubious, for the reason that he did not actually measure the SO_2 levels in the air of any of these towns. An urban area with only a small population, and no heavy industry may still produce enough SO_2 to affect its lichen flora. For instance[41], the town of Newry in Co. Down has a population of only 12,000, but mean winter SO_2 readings of 159 $\mu g/m^3$.

(iii) Rydzak overlooks an important fact in his work on

Lublin: the increase in SO_2 between 1950 and 1968, which may well have had some effect on the corticolous lichen flora[17].

(iv) Sheltered sites not only possess a higher RH - but also lower average SO_2 figures than surrounding localities. The respective importance of these two influences has been argued previously.

(v) Those parts of cities with generally higher RH readings (lakes, marshes, woods etc.) should carry a richer lichen vegetation than adjacent areas according to the drought hypothesis. However, Laundon[54], and Rao and LeBlanc[72] have both investigated moist niches in large urban areas bearing epiphytic vegetation as impoverished as elsewhere in their study areas.

(vi) If city climate were the cause of lichen death in towns, then the epiphytic vegetation might be expected to recover dramatically just outside urban areas. But as previous discussion has shown, sensitive species may be extinct many miles downwind of a city: a fact better understood in terms of pollution-drift rather than by variations in mean RH.

(vii) The fact that sources of SO_2 isolated from cities and the city climate (such as Fawley oil-refinery[61], and the Swedish oil-shale works[84]) produce identical symptoms of lichen damage on nearby trees as cities do is difficult to explain if the drought hypothesis is accepted. No gradients of RH change may be invoked to account for the vegetation distribution around rural industries, while SO_2 concentrations and lichen zones correlate neatly.

(viii) Finally, according to Geiger[25] average differences in RH between cities and rural areas amount to only 5%. It is extremely doubtful whether such small differences in RH could account for the distinct patterns of lichen occurrence observed around cities.

Therefore, although RH certainly affects lichen distribution; for the above reasons, the drought hypothesis as a complete explanation for the depleted lichen floras of cities is considered to be untenable by most lichenologists.

3. Lichens and Ravine Situations

In the light of the general ecological relationships outlined above, it is now profitable to consider what is known of lichen assemblages in ravines. This subject has not previously been approached as a major topic for study in its own right, and the account here has been compiled from a number of short statements included in articles devoted primarily to other scientific problems.

There is general agreement (in the literature) that the lichen flora of ravines is 'richer' than that of other topographical situations in the same area. Steep-sided valleys are therefore seen to constitute favourable habitats for epiphytes: and species numbers, the occurrence of sensitive species, luxuriance of growth, and lichen abundance are parameters which may be expected to testify to this fact. Rose, Hawksworth and Coppins[77] found that ravines on the North Yorkshire Moors contained more species than the surrounding plateaux; Gilbert[27] noted that in

Jesmond Dene, a small steep-sided cutting in the centre of Newcastle, a number of pollution-sensitive lichens flourished; Rose[76] observed Parmelia caperata growing in a sheltered valley 24 kms. S. of London, whereas the trees for 12 kms. around the site were devoid of this species; and in his study of the lichen vegetation of Derbyshire, Hawksworth[37] found that some species (notably SO2-intolerant lichens) were restricted to the Dales.

These records illustrate the accepted fact that ravines tend to be characterised by a fairly luxuriant lichen flora. However, when it comes to seeking the underlying reason for this phenomenon, opinion is more divided. It may be assumed that any parameter(s) of the lichen environment which changes in ravine situations is the possible causal factor of the observed lichen distribution. Referring back to those ecological factors discussed in part (i), Barkman[5] believes that "ravines are characterised by a very calm, damp atmosphere, frequent mists, reduced light intensity, and a cool climate". In other words, a steep-sided wooded valley may be expected to differ from its surroundings in that; (a) light intensity is reduced (b) temperatures are lower (c) RH and bark moisture-availability are greater (d) wind-speed is reduced. Any of these four factors might be directly or indirectly responsible for the rich lichen flora of ravines.

A further possibility, which should not be overlooked, is that well-wooded ravines are likely to have a wide variety of tree species, such that the epiphytic habitat (specifically bark pH and moisture-content) in

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ravines might be more diverse than that of neighbouring areas. This would in turn account for the diversity of the corticolous lichen flora.

Finally, there is a sixth plausible explanation for the luxuriance of ravine lichen vegetation. A ravine is an excellent example of what has been discribed as a "sheltered niche": and so lichens are to some extent protected from air-pollution. Gilbert[28] measured the winter SO_2 content of the air in and around Jesmond Dene, and discovered that while the average figure for the ravine was 70 $\mu g/m^3$, the area immediately around it was characterised by a mean atmospheric concentration of 171 $\mu g/m^3$.

There have been two theories put forward to explain exactly why ravines should contain purer air than exists in their polluted environs. Gilbert[27], Brodo[12], and Barkman[5] are of the opinion that the vegetation canopy acts as a protective umbrella to the corticolous lichens growing beneath it, in that pollutants are filtered out of the atmosphere by the tree foliage, and consequently the air beneath the canopy is purer than that above it. Brodo[12] states: "as polluted air passes through vegetation it is undoubtedly cleaned to some extent"; and Barkman[5] makes the point "the leaves of trees and shrubs filter the air by their intensive gaseous exchange". Gilbert[27] proved that contact with surfaces could remove SO_2 from the atmosphere, by hanging nylon hair-nets containing glass-wool in a suburb of Newcastle. After 8 weeks the glass-wool contained 342 p.p.m. sulphur. He suggested that leaves operated in the same way, absorbing SO_2 from the air and thereby purifying it.

"Canopy filtration" might explain the rich lichen flora of ravines, but Hawksworth[37,40], Lawrence[55], and Rose, Hawksworth and Coppins[77], lend their support to another equally plausible reason for the low levels of SO_2 recorded from ravines. They believe that it is the topography of ravines - not the vegetation they carry - which protects them from SO_2 and other atmospheric toxins. As Barkman[5] noted, wind-speeds are reduced in ravines (as in other sheltered situations) and if, as postulated earlier, localities with lower wind velocities receive lesser quantities of SO_2 - then this might be the explanation for the pure quality of ravine air. Lawrence[55] studied the distribution of SO_2 in an undulating rural area near a pollution-source. He found that the lowest concentrations of this gas occurred in valley bottoms, and SO_2 readings increased in value with distance up the valley-sides. Lawrence was able to correlate the decreasing SO_2 gradient from hills to valley-floors with the gradual reduction in wind velocity downslope. Thus he came to the conclusion that because valleys were protected by the nature of their physiography from high winds, they were also sheltered from air-pollution. Lawrence termed the decrease in SO_2 concentration down valley-sides the "pollution inversion profile", and described the flow of polluted air over the top of ravines as "over-barrier transport" (see Fig. 6). This concept of valleys being unpolluted because they are sheltered from pollution-laden winds is also mentioned by Wexler[95],

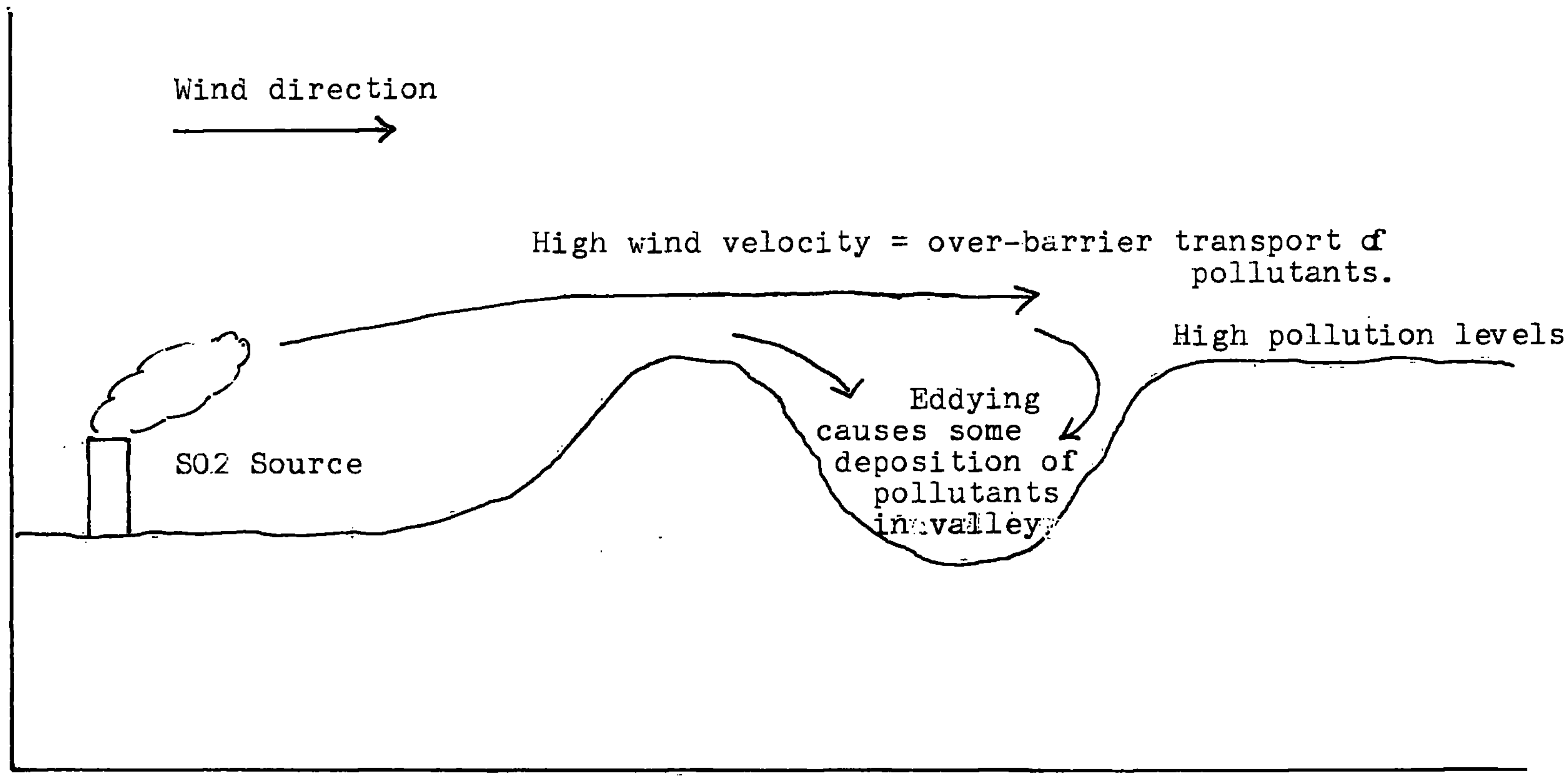

Fig. 6 : Pollution inversion profile

Source - 55

Hawksworth[37,40], and Hawksworth, Rose and Coppins[77].

In terms of feasibility, either of these theories is acceptable; and no comprehensive study to invalidate one, and prove the other correct hasbeen attempted (to the author's knowledge). Proponents of canopy filtration might cite the fact that woodlands on flat ground in polluted areas often bear more SO2-sensitive species than isolated trees in the same locality - suggesting that a thick and extensive layer of leaves is an effective barrier to pollutant fall-out. On the other hand, the direct relationship between altitude and lichen performance noted by Hawksworth and Walpole[39] for % cover of sensitive species in Bradgate Park, Leicestershire: and the inverse relationship of SO2 concentration and elevation recorded in Sheffield by Pemberton et al[69]., constitute two independent lines of inquiry which support the findings of Lawrence[55] and others. This problem is clearly some way from being resolved and there is room for further research into the subject.

The aims of this study as briefly outlined in the introduction, may now - in the light of the preceeding discussion on lichens and ravines - be elaborated as follows:

1. To confirm that the corticolous lichen flora of Horsley Hope Ravine is species-rich (as described by Rose, Hawksworth and Coppins[77]); and more diverse than that observed on trees in the neighbourhood of this ravine.
2. If there is little or no difference between the epiphytic lichen vegetation of Horsley Hope Ravine and the surr-

surrounding countryside, then it may be assumed that all trees to the S.W. of Consett bear a uniformly rich species assemblage, and that the effects of prevailing S.W. winds are such that the SO_2 emitted from Consett Steelworks is not a significant ecological factor in the distribution of lichens S.W. of Consett.

3. If surveys should indicate that there is a distinct improvement in the quality of the epiphytic vegetation in Horsley Hope Ravine, then the following should be investigated as possible causes of this anomalous distribution of corticolous lichens:

(i) The dense leaf barrier of the thickly wooded ravine protects the lichen vegetation beneath the canopy from pollutant fallout. But while the lichens in the ravine are sheltered in this way, those epiphytes on trees in exposed situations around the ravine are vulnerable to the action of atmospheric impurities which occur in the air S.W. of Consett.

(ii) Because SO_2 (believed to be the most phytotoxic air pollutant) is a light gas, its distribution in the air is governed to a marked degree by wind-velocity. Wind-velocity near the ground is controlled by surface configuration, and sheltered sites - such as Horsley Hope Ravine with its steep sides and distinct breaks of slope - are characterised by low wind speeds. Thus the topographical shape of the ravine may be effective in reducing wind-velocity and hence SO_2 concentrations - in contrast to the values expected for these two variables in sites outside the ravine environment.

(iii) The luxuriant flora of the ravine may not be a direct response to variation in pollution concentration, but could reflect the action of other ecological variables: (a) light, (b) temperature, (c) humidity. The significance of these three factors for lichen abundance has been considered earlier, and according to Barkman[5] they undergo marked changes in intensity and duration towards the floors of ravines. It is thus possible that one, or any combination, of these variables is responsible for the disjunct lichen distribution.

(iv) It may be expected that an area of semi-natural woodland as extensive as Horsley Hope Ravine will possess a wider variety of tree species than is to be found in neighbouring hedgerows and copses; and so it must be born in mind that any deterioration in the corticolous lichen flora on trees outside the ravine could be a simple response to the decrease in variety of tree bark habitat available to the epiphytic vegetation.

III. METHODOLOGY

The following methods were used during the study:

1. Lichen Distribution

Information on lichen distribution was collected from within Horsley Hope Ravine and from around the ravine itself in a zone S.W. of Consett, as shown on Fig. 7. Various details of lichen distribution were required, and the methods employed to obtain this data are described below:

(A) Lichen Frequency and Abundance

In the previous section, it was suggested that a number of methods of floristic analysis might be used to plot changes in the distribution of lichens. These are:

(i) Species presence or absence data
(ii) Life-form presence or absence data
(iii) Species diversity
(iv) Variations in size or fertility of lichen species
(v) % cover of species
(vi) % cover of different life-forms
(vii) Index of Atmospheric Purity (I.A.P.)
viii) % frequency of species

For the purposes of this study it was considered that of these methods, recording detailed presence or absence data for a number of lichen species (and collating this information to produce % frequency figures where appropriate) was the most accurate, meaningful and readily measurable means of obtaining data on variations in corticolous lichen distribution. Species presence or absence data produce figures which show both the change in frequency of certain species, and the change in species diversity (i.e. the change in total numbers of species per tree, of those species recorded in the presence or absence analysis).

It was felt that the other methods listed above had limitations which precluded their use in this study. The lichen growth-form is a rather general characteristic which may not be simply correlated with other ecological variables. For example, as a general rule, fruticose lichens are light-demanding and pollution-sensitive - but so are some crustose species; and although many crustose lichens are pollution-tolerant their other requirements, such as bark pH and moisture-content, vary significantly from species to species. Consequently, the analysis of lichen distribution by measuring the variations in life-form distribution, was not considered sufficiently accurate for this project.

Reference has already been made to the essentially prohibitive problems associated with using size and fertility as indicators of 'lichen performance'; and nor would the results of such an exercise be directly relevant to the aims of this study.

Many of the published works on lichen distribution employ the % cover of certain species as a means of recording changes in the lichen flora. Data on % cover are more comprehensive than presence or absence information, for an additional measure of abundance is incorporated in % cover analysis. However, recording % cover is time-consuming (especially if quantitative methods are used) and, according to Barkman[5], produces results which are very similar to those gained from frequency data. For these reasons, it was decided not to measure changes in the % cover of corticolous lichen species in order to show the variation in lichen distribution.

Le Blanc and De Sloover's[56] I.A.P. is considered by Hawksworth[40] to be a somewhat laborious method which, again, produces results little different from those which may be obtained from simple frequency data.

Therefore, presence or absence data concerning the occurrence of certain corticolous lichen species was collected and analysed by various means in order to provide information on lichen distribution in the study area.

(B) Type of Substrate

One of the reasons put forward as a possible explanation for the luxuriant lichen flora of Horsley Hope Ravine was the increase in tree species diversity likely to occur within this well-wooded valley. A greater variety of tree species would afford lichens a wider range of types of substrate to colonise, and this increase in number of available niches might be expected to cause an increase in lichen species diversity.

However, preliminary studies showed that for any one tree species there were distinct changes in the corticolous lichen flora throughout the study area, particularly as concerns differences in epiphytic vegetation between the same tree species within and without the ravine. Thus, although the long species list compiled by Rose, Hawksworth and Coppins[77] was undoubtedly, in part, a product of the variety of trees in Horsley Hope Ravine, the predictable ecological relationship between tree species (i.e. corticolous lichen habitat) diversity and lichen species diversity is not the major cause of the observed variation in lichen distribution in the area (see TABLE I).

In order that the influence of substrate type on lichen distribution might be eliminated from further consideration, it was necessary to sample the lichen flora of a uniform habitat throughout the study area. In this way, the significant variation in corticolous lichen distribution S.W. of Consett might be related, as far as possible, to the ecological factors other than tree species diversity suggested in chapter II part 3.

To take account of this requirement for sampling the lichen vegetation of a single, uniform type of substrate, the following sampling pattern was incorporated in the methodology:-

(i) All the lichen records were taken from one tree species - oak (Quercus robur). Oak has a rough bark with a low to mesotrophic base-status (pH approximately 4.5-5.5) and a fairly low water-retention-capacity[5]. Oak was selected as a suitable tree from which to gather lichen data because it is common in the study area, and because it generally supports a fairly rich epiphytic flora[5].

(ii) The presence or absence of species was recorded between the base of the trunk and 2 m. above the ground on the bole of the tree. As outlined in chapter II, the epiphytic vegetation is generally better developed toward the base of trees, and it is therefore reasonable to expect that all the lichen species growing on a tree will be represented within the bottom 2 m. This appeared to be the case in practice, for occasional observations of the boles of trees above 2 m. did not reveal species which were not found in the section between the base of the trunk and 2 m. above the base.

(iii) Only oaks with a diameter greater than 1 m. at breast-height (1 m. d.b.h.) were sampled. The minimum value of 1 m. d.b.h. was introduced to ensure that only reasonably mature oaks which had lived a sufficient length of time to enable a mature lichen flora to develop were included in the sampling programme.

(iv) Where a significant part of the bole of a tree was obscured by vegetation or a structure which might influence the micro-environment of the trunk, then the tree was not sampled. All the lichen records are taken from free-standing trees.

(v) It was originally intended that only vertical trees should be sampled, as leaning trees are likely to exhibit an irregular pattern of lichen distribution[5] with xerophytic species on the lower sides and hydrophytic species on the upper sides. However, it soon became apparent that this aim was unrealisitc - particularly as the great majority of trees growing on the sides of the ravine lean towards the floor of the ravine. Therefore, trees with an angle of inclination greater than 15^{o} from the vertical (as measured by a clinometer) have been excluded from the sampling programme. For all trees which were sampled - their angle and direction of inclination were noted.

(C) Recording Lichen Species

Clearly, if presence or absence data is collected for a large number of lichen species, then the distribution pattern which emerges from the study should be fairly comprehensive and capable of detailed scientific interpretation. Hawksworth[40] makes this point in discussing lichen mapping studies, and indicates that research involving the mapping of many species is likely to lead to a more accurate understanding of the ecological processes in operation than work which has concentrated on plotting the distribution of one or a few species of lichen only.

For these reasons, it was considered desirable that the frequency of a large number of lichen species should be recorded during the survey. Of the 66 species of lichen noted by Rose, Hawksworth and Coppins[77] for Horsley Hope Ravine, preliminary fieldwork showed that 41 of these occurred on oak trees. In addition, a further 4 species were observed on oaks during the course of the fieldwork - making a total of 45 species seen on oak trees within the study area (see TABLE I).

In fact, the presence or absence of 37 species on oak trees was recorded for the sampling programme. The decision to exclude 8 species found on oaks from the detailed survey of lichen frequency was based on a number of reasons. Where specimens of Cladonia polydactyla and Cadonia coniocraea occurred, they were invariably located at the bases of trees, and it was considered that these species were more properly terricolous lichens which were able to colonise tree bark only where some humus overlay the bark. Moreover, the distribution of these two lichens did not appear to follow any meaningful ecological pattern, and therefore no record was made of the occurrence of Cladonia polydactyla and Cladonia coniocraea.

Five species - Lecidea cinnabarina, Pertusaria coccodes, Pertusaria flavida, Calicium abietinum, and Pseudevernia furfuracea - were all observed on oak trees in the ravine during the preliminary survey, but were found on only one or two trees, if at all, in the course of the detailed fieldwork. Insufficient information concerning the distribution of these lichens thus explains their exclusion from further consideration.

Finally, because of the problems of differentiating between Arthonia didyma and Arthonia spadicea in the field, it was decided that the two species should simply be recorded as one i.e. Arthonia spp. As the two species tend to occupy similar niches, and often occur together in field situations, this means of simplifying the process of data collection appeared to be fully justified.

Therefore, of the 45 species of lichens known to colonise oak trees in the study area, the presence or absence of 37 species (see TABLE I) was recorded during fieldwork.

The position of lichen species on the trunks of trees, with respect to compass direction, was taken into consideration, for it soon became apparent that aspect was an important factor in the distribution of corticolous lichens. A distinctive pattern was observed in which certain species were consistently associated with one side of the trees sampled. Because of the existence of this clear-cut pattern, the matter of aspect could be conveniently treated by dividing the tree circumference into two halves, and recording the occurrence of lichens in one half or the other, or on both sides. Furthermore, for reasons discussed later, it was possible to recognize two major patterns of lichen distribution on tree trunks in relation to aspect: one being a N./S. pattern, and the other E./W. The two patterns never occurred on the same tree, and thus on each tree sampled, the distribution of lichens was referrable to either:

(a) a N./S. pattern in which certain lichen species were concentrated on that half of the tree trunk between 270° and 90° E. of N., with 0° as the mid-point, and certain other species were restricted to a semi-circle described on the trunk etween 90° and 270° E. of N. with 180° as the mid-point; or

(b) an E./W. pattern in which certain lichen species were concentrated on that half of the trunk between 0 and 180° E. of N., with 90° as the mid-point, and certain other species were restricted to a semi-circle described on the trunk between 180° and 360° with 270° as the mid-point.

Therefore, for each tree sampled the broad distribution of lichen species on the tree was assessed and a decision made as to whether the general pattern displayed E./W. or N./S. differentiation. In practice this was most obvious, and only a few trees gave any room for doubt about the pattern of lichen distribution in relation to aspect. Then, the presence of lichens was recorded in terms of their position with respect to aspect. A species might be restricted to one half of the tree (e.g. E. side only) or occur on both sides (e.g. E. and W. sides). Many species were more or less confined to one side of the tree only, for as explained above, the relationship between species distribution and aspect was most marked.

Finally, concerning the recording of lichen species, a note was made if a species was confined to the base of a tree.

(D) Sample Size

The sample population for studying lichen distribution, as defined above, is: the presence or absence and position of 37 species of corticolous lichens, below a height of 2 m. above the ground, on the boles of oak trees - which are greater than 1 m. d.b.h., are not inclined at an angle of more than 15^{o} from the vertical, and are not obscured by any object - within an area S.W. of Consett (the study area).

The study area is delimited on the accompanying map (Fig. 7) and covers 28 sq. kms.

As the sample units are oak trees with the characteristics described above, the maximum number of samples of lichen distribution which could be taken is equal to the number of suitable oak trees within the study area. The actual number of samples recorded must inevitably, however, be related to the time available and the minimum

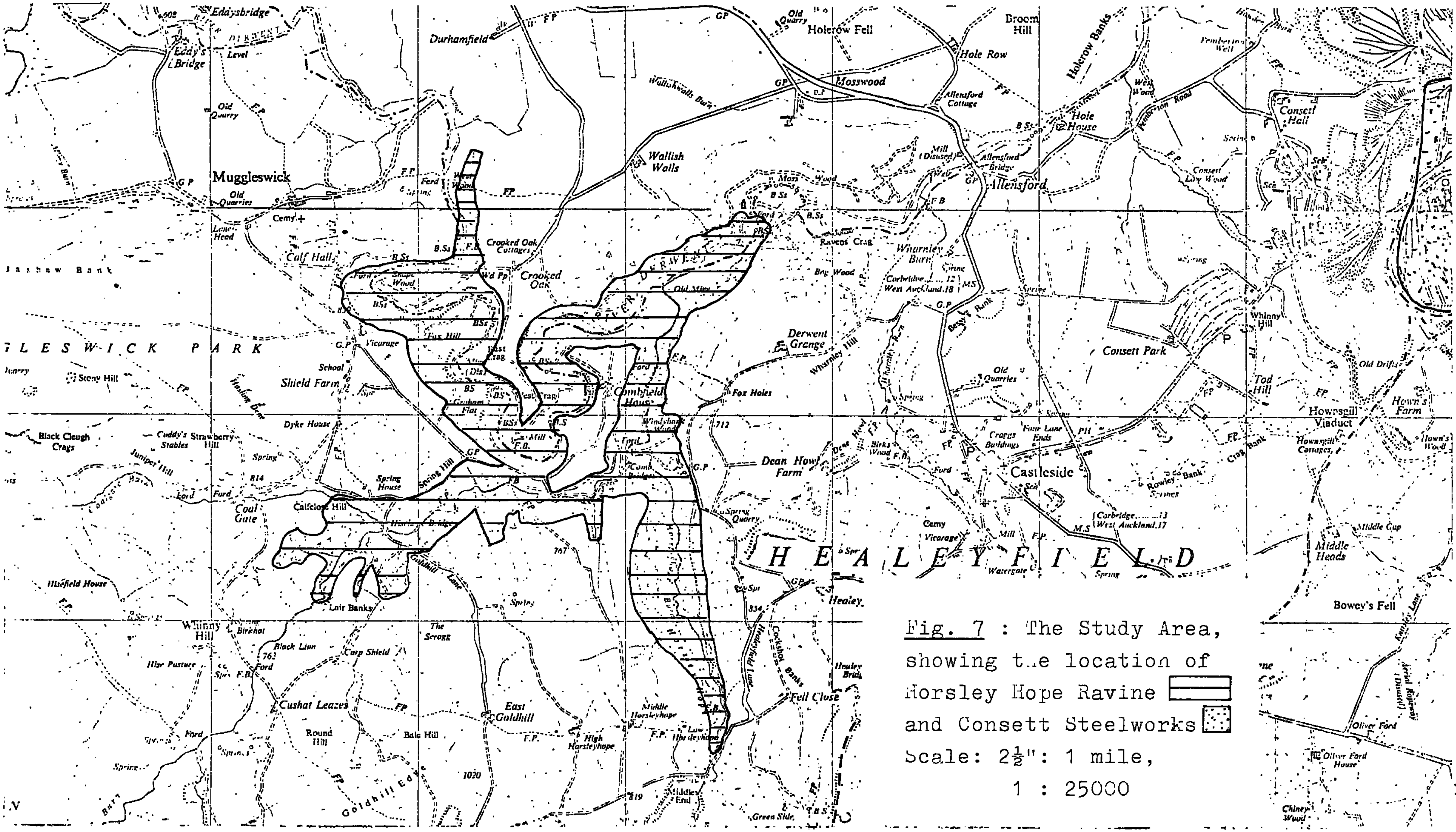

Fig. 7 : The Study Area, showing the location of Horsley Hope Ravine [horizontal hatching] and Consett Steelworks [stippled]

Scale: $2\frac{1}{2}$": 1 mile, 1 : 25000 number of samples required to ensure accuracy of results. In keeping with these requirements, the following methods of sampling the lichen vegetation were introduced:

(i) Within Horsley Hope Ravine, the woodlands vary considerably in tree species composition according to the management regime adopted. Certain parts of the woods have been managed to encourage the development of a fairly uniform stand of mature oak and ash, and these parts contain many oak trees suitable for the purposes of sampling the corticolous lichen flora. Other wooded sectors of Horsley Hope Ravine are planted up with beech or softwoods, or are pioneer birch-sycamore-rowan woods (see Fig. 8).

Within the areas of oak-ash woodland, the lichen flora of oak trees was sampled along 12 transects. The positions of the transects are shown in Fig. 8.

Each transect extended from the fence which marked the outside edge of the woods (the woodland/agricultural land boundary) to the river on the floor of the ravine. In order that detailed changes in the lichen flora of the ravine might be recorded, the distance of trees sampled from the edge of the woods was measured, and this information sorted into 10 m. lengths. For each 10 m. length of valley side, 20 trees were sampled. Thus 20 trees were sampled in the length of valley-side between 0 and 10 m., 20 trees between 10 and 20 m. from the outside edge of the wood etc. This data was used to obtain % frequency values of the corticolous lichen flora of each 10 m. length of valley-side.

The requirement for sampling 20 trees per 10 m.

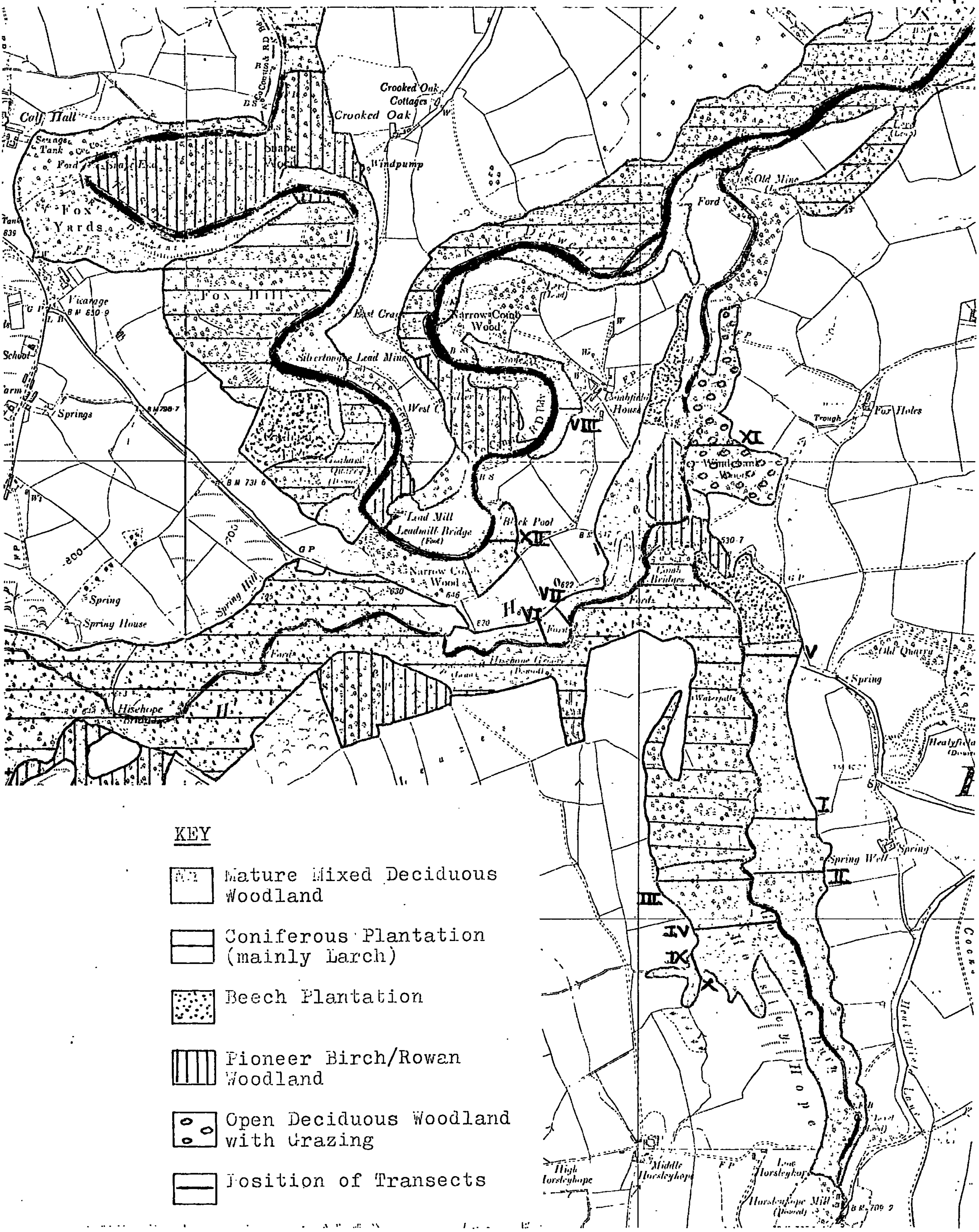

Fig. 8 : The Woodlands of Horsley Hope Ravine and location of Transects I - XII. Scale : 6" - 1 mile
1 - 10560

length of valley-side meant that the width of transects was not fixed. A metre tape was laid down the valley-side parallel to the direction of the slope. Then within each 10 m. length, the 20 (suitable, according to the criteria considered above) oak trees nearest to the tape were selected as sampling units for recording lichen distribution. The width of transects was thus flexible and depended on the occurrence of mature, free-standing, upright oaks in relation to the metre tape, which essentially formed the mid-line of the transects. The transect was rarely more than 30 m. wide at any point, however.

In addition, for each transect, the angle of slope and aspect of the valley-side were noted.

(ii) For sampling the lichen distribution on oak trees outside the ravine and within the study area, the size of the sample simply constituted all oak trees of appropriate size, shape and position observed from a car driven along all the accessible roads within the study area. A total of 324 trees was sampled during this survey, and their situations recorded by means of six figure grid references. A distinction was drawn between trees sampled in open situations and those which were components of small woods in the study area.

The lichen presence or absence data for the whole study area was analysed in a number of ways, in order to demonstrate the distribution of corticolous lichens S.W. of Consett. Changes in species numbers, % frequency, and lichen zones (according to the Hawksworth and Rose pollution scale, which employs presence or absence information) were plotted from the raw presence or absence data collected.

Few records were obtained from the western and southern parts of the study area, which are mainly open moorland without any suitable oak tree cover.

2. Air Pollution

The following methods were used in order to collect information about levels of atmospheric SO2 in the area S.W. of Consett:

A) Average SO2 Concentrations in the Area

Data contained in the National Survey of Smoke and Sulphur Dioxide[92] on levels of SO2 in the air around Consett were abstracted. In this way, information about the average levels of SO2 pollution generally associated with the Consett area was obtained.

B) Measurement of SO2 Concentrations at Horsley Hope Ravine

As more detailed knowledge of SO2 levels within, and in the vicinity of, Horsley Hope Ravine was required, it was necessary to actually take measurements of atmospheric SO2 concentration at the ravine.

The method used for measuring SO2 was a standard "volumetric method" in which a known quantity of air is drawn through a solution of hydrogen peroxide. The hydrogen peroxide retains SO2 in a form suitable for determination by titration with an alkali. This is the method used by the Warren Spring Laboratory[90] and is the means of measuring atmospheric SO2 recommended in the Beaver Report[7].

The equipment used for taking SO_2 samples comprised:

(i) A plastic inlet funnel with a mouth of diameter 4cms.

(ii) Polythene tubing with an intermal diameter of 6.5cms.

(iii) A brass filter clamp, 5 cms. in diameter.

(iv) Whatman No. 1 filter papers, 6 cms. in diameter.

(v) A glass dreschel bottle, capacity 125 mls.

(vi) 50 mls. of hydrogen peroxide solution (1 part hydrogen peroxide, 99 parts distilled water).

(vii) An electric suction pump.

(viii) A petrol-driven, portable generator which provided enough power to run 4 electric pumps (and therefore 4 sets of SO_2-measuring equipment could be operated simultaneously).

The equipment was assembled as shown in Figs. 9 and 10.

For each test conducted, the following procedure was carried out:

(i) The 4 sets of SO_2-measuring equipment were placed on the ground in the required locations i.e. at different points within and around Horsley Hope Ravine.

(ii) The inlet funnels were fixed to the trunks of oak trees by staples, at a height of 1 m. above the ground. Thus the air being sampled was the air circulating around the corticolous lichen flora of tree boles, and the measured SO_2-content of the air was representative of the levels of SO_2 experienced by the lichen vegetation. Two tests were carried out in which the inlet funnels were placed only 15 cms. above the ground, in order to assess the levels of SO_2 occurring around tree bases. In all cases, the

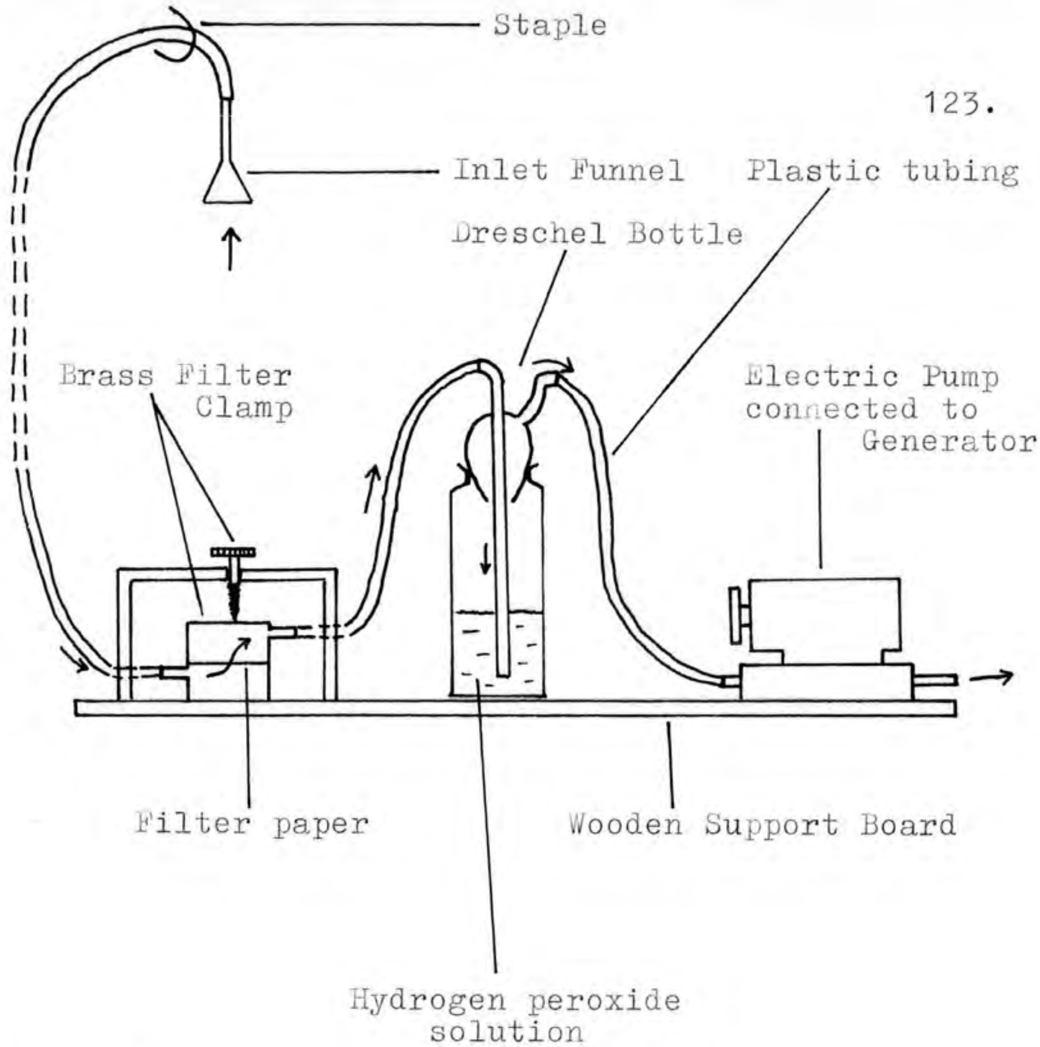

Fig. 9 : SO2-Measuring Equipment.

⟶ Direction of air-flow.

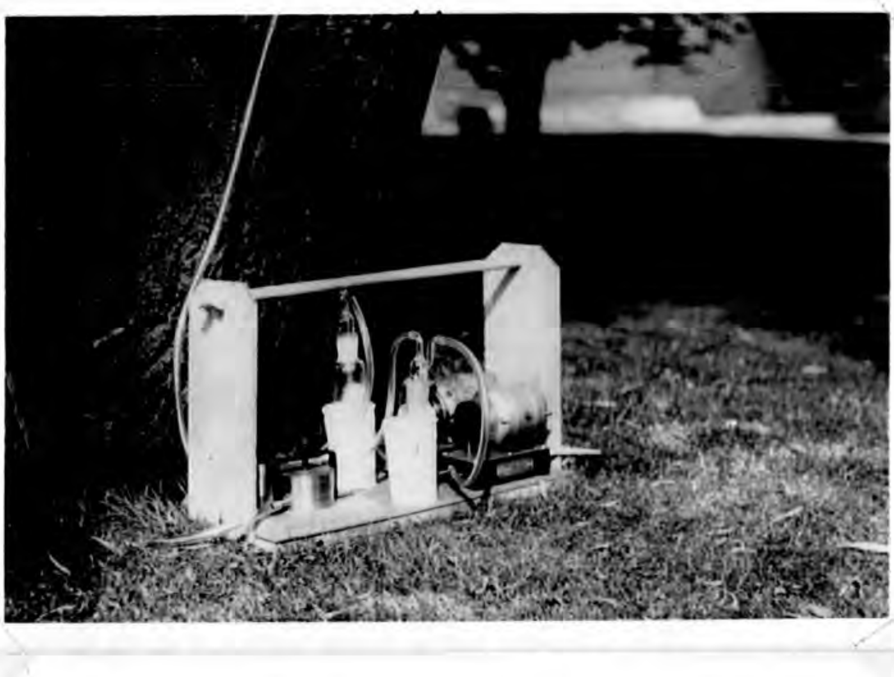

Fig. 10: Photograph of SO2-Measuring Equipment

funnels were allowed to hang down so that the inlet ends pointed towards the ground (see Fig. 9). This prevented leaves, twigs etc. from falling into the funnels and blocking the inflow of air.

(iii) Clean filter papers were inserted in the clamps, in order to trap particulate matter drawn into the equipment. The clamps were securely tightened.

(iv) Fresh hydrogen peroxide solution was added to clean dreschel bottles.

(v) The pumps were wired up to the generator. Preliminary tests showed that the pumps could draw air through the system at a rate of 5 cubic feet per hour.

(vi) The generator was started, and the 4 sets of equipment were allowed to operate continuously for 24 hours, so that 120 cubic feet of air was drawn through the hydrogen peroxide solution in each system. In 8 of the samples, practical problems (e.g. rainfall causing an electrical short) reduced the duration of the experiments, and lesser volumes of air were sucked through the equipment.

(vii) At the end of the 24 hour period, the bottles containing the hydrogen peroxide solution plus SO2 were taken to the laboratory for analysis. In the hydrogen peroxide solution, SO2 is oxidised to sulphuric acid, and it is retained in solution in this form. Thus, by titrating the sulphuric acid with an alkaline solution ($^{N}/_{250}$ sodium hydroxide) it is possible to calculate the volume of alkali required to neutralize the sulphuric acid contained in the sample. This figure is equal to the volume of SO_2 retained by the hydrogen peroxide solution, and measured the increased acidity of the hydrogen peroxide resulting from the addition of SO_2. The concentrations of SO_2 in the sample may be converted to $\mu g/m^3$ by using the following equation:

$$\text{Concentration of } SO_2 \text{ in } \mu g/m^3 = \frac{4520.T}{V}$$

where T = amount of sodium hydroxide in mls., required to neutralize the sulphuric acid solution, and V = the volume of air in cubic feet, passed through the solution.

A total of 36 samples of 24 hour atmospheric SO_2 concentrations was taken. Ideally, more extensive coverage might have been given to this aspect of the project, but the necessity for sampling over a continuous 24 hour period limited the number of tests which could be conducted. A 24 hour period (i.e. 120 cubic feet of air) was considered to be a minimum requirement for ensuring that the results were valid.

This method of volumetric SO_2 measurement is considered to be fairly accurate. As it is simply the acidity of the air which is being measured, it is possible that atmospheric substances other than SO_2 are contributing to the acidity of the hydrogen peroxide solution. If this is the case, then the figures of atmospheric SO_2 content produced from titration of the hydrogen peroxide solution with sodium hydroxide are over-estimates. However, the Beaver Report[7] considers that the contribution of other atmospheric substances to the acidity of the hydrogen peroxide solution is insufficient to cause errors of greater than 10% in the results of volumetric analysis. Clifton et al.[14] found that volumetric SO2 instrumentation was accurate to within 5% of the correct figure. Therefore, the method used in this study to measure atmospheric SO2 is considered to provide a good approximation of the actual concentration of SO2 in the air.

During the 24 hour periods of SO2 sampling, regular observations were taken of wind direction and velocity (as estimated by the Beaufort Scale). As wind direction varied significantly from day to day - so also the measured SO2 concentrations of each set of samples showed considerable variation. A N.E. wind, for example, caused higher levels of SO2 to be recorded than a S.W. wind. For this reason, only the results of each set of 4 contemperaneous SO2 samples could be directly compared. The conditions under which different sets of 24 hour period SO2 samples were taken were too variable to permit collective consideration.

C) Measurement of Atmospheric Particulate Iron

Buildings, cars, and trees in the centre of Consett are visibly tinged a dull red colour, due to the deposition of iron particles (referred to locally as the "red peril") emitted from the steelworks. The possibility that high levels of particulate iron are an important influence on lichen distribution was considered. For this reason, the filter papers used in the SO2-measuring equipment were analysed for particulate iron concentration, in order to test whether high levels of iron are transported as far as Horsley Hope Ravine. Through each filter paper, 120 cubic feet of air had been passed, and the iron content of this volume of air was measured by subjecting each filter paper to Atomic Absorption Spectrometry.

D) Wind Velocity and Direction

It has been generally assumed that the prevailing winds of the Consett area are S.W., in line with the position for the British Isles as a whole. To ensure that this situation does in fact apply, and that local conditions do not alter the pattern of prevailing winds in any way, the velocity and direction of the wind were recorded at a point outside the ravine (NZ065483) at the start of each days fieldwork. Direction was measured by using a compass, and the velocity assessed by the Beaufort Scale. A total of 68 days wind velocity and direction records were taken.

3. Measurements of Light, Relative Humidity and Temperature

Finally, in order to consider fully the possible ecological relationships pertaining to ravine situations, information was collected about the variation in three abiotic parameters (light, RH, and temperature) within and without Horsley Hope Ravine. For all three factors, changes in value at different locations along a transect were measured at approximately the same time. Thus, for example, measurements of light intensity at points 10 m. apart along a transect beginning outside the ravine, and terminating at the river on the valley-floor, were all taken within a period of about 10 minutes. This ensured that any significant differences in the results of each transect were due to spatial rather than temporal variations in light, RH and temperature. A series of transects was completed in order to obtain a representative sample of light conditions inside and outside the ravine.

The relative areal changes of these three abiotic factors in a ravine situation were measured by the following means:

A) Temperature

Temperature was measured in absolute terms with a mercury thermometer. Variations in air temperature were recorded at approximately 10 m. intervals (at a height of 1 m. above the ground) along 3 transects - each beginning outside the ravine and running parallel to the direction of the slope down the valley-side to the river on the valley-floor. The thermometer was shaken well between each reading.

B) Relative Humidity (RH)

A revolving wet-and-dry bulb thermometer was used to guage changes in RH. Again, measurements were taken every 10 m., at a height of 1 m. above the ground, and each transect extended from a point outside the ravine to the valley floor so that the variations in RH inside and outside the ravine might be recorded. Four transects measuring RH were carried out.

C) Light

Light intensity was measured in relative terms by using a Weston Master Mark V light meter. Preliminary tests with the meter established values for dark and bright conditions which were assumed to be end-members in a range of conditions of light intensity.

Then, readings were taken along 7 transects running down the valley-side parallel to the direction of slope, from outside Horsley Hope Ravine to the floor of the valley. Each reading was taken with the base of the light meter resting at 90° on the trunk of a tree at a height of 1 m. from the ground. The photo-sensitive cell was thus placed in a position to receive light incident on the tree trunk - in the same way as epiphytes. As before, trees leaning at an angle of more than 15°, or overgrown by other vegetation, were excluded from the sample. Aspect was recorded as described above. Between readings, the shutter was placed over the photo-sensitive cell.

Because of the requirement for utilising the tree trunk as a sampling point, light readings were not taken at regular 10 m. intervals, but the distances of trees used for sampling purposes from the edge of the wood were noted.

The measurements obtained by this method provided a relative means of assessing the changes in light intensity associated with the epiphytic habitat in a ravine environment.

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