EFFECTS OF AIR POLLUTANTS ON PLANTS

Edited by

T. A. MANSFIELD

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PREFACE

Studies of the effects of air pollutants on plants have often been criticised because they have over-emphasised the visual symptoms of damage, and have largely consisted of observations made in the field or under unsophisticated experimental conditions. While there is some justification for this criticism, there have also been experimental studies of a more rigorous nature that have led to important advances in our knowledge of the way air pollutants attack metabolic processes, or affect the plant's functioning at the physiological level. It was the purpose of the SEB Seminar held in the University of Liverpool on 10 April 1975 to bring together leading exponents of the experimental approach, and the papers presented covered most of the air pollutants considered to be most damaging to plant life. This volume, based on the seminar, will therefore serve as an introduction to the subject for undergraduates, research students and others, and hopefully will stimulate more scientists to become interested in this important area.

We can foresee that as the subject develops, it will be increasingly necessary for biologists to consider the reactions and interactions between atmospheric pollutants. For this reason the editor invited a physical chemist to prepare an Appendix to this volume to serve as an introduction to a subject that most biologists (and even some chemists) find difficult. Two of the contributors have also prepared an Appendix of tables listing known metabolic and biochemical effects of some of the major air pollutants, and these are intended as guides to the existing literature for those who wish to pursue the responses to particular pollutants in more detail.

The assistance of Dr P. J. W. Saunders in the planning of the meeting was invaluable, and thanks are also due to Dr T. W. Ashenden, Dr R. M. Harrison, Dr T. M. Roberts and Dr A. R. Wellburn for time spent in reading through the typescripts. The Society for Experimental Biology would like to acknowledge, with gratitude, financial assistance from the following sources towards the cost of running the Seminar: Technicon Ltd, Varian Associates Ltd, C. F. Casella & Co. Ltd, T.E.M. Sales Ltd, the British Council, Gelman Hawksley Ltd, the Central Electricity Generating Board, and the Agricultural Research Council.

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T. A. Mansfield
Editor for the Society for Experimental Biology

CONTENTS

A.J.RUTTER

Introduction

Shortly before the Seminar one of the contributors asked me whether its object was to review results or identify problems. This field, the investigation of the biological effects of pollution, is one in which there is considerable activity and the Seminar could hardly have been held were it not that many people have results from good experimental work to present. Nevertheless we have a long way to go, for we just do not know, quantitatively, what are the effects – whether great or small – of atmospheric pollution on our wildlife, agriculture and forestry. Before we can answer this question there are many scientific problems to be solved and experimental difficulties to be overcome, and this Seminar was particularly timely in bringing together a large number of scientists to share discussion and information on problems so far encountered.

I should like to begin the volume by outlining some of the problems which I see in the field of atmospheric pollution and its effects on plants. Some of them will be taken up in more detail in later chapters and some fall outside the scope of the book but are nevertheless very relevant to our work. The contributions will no doubt bring to light other problems than those I enumerate.

First of all, pollution is an ecological problem and as such demands an equal understanding of both environment and organisms. Our first need is to measure the environment, and there is still a shortage of satisfactory apparatus for continuously monitoring the low absolute concentrations in which most atmospheric pollutants occur. Where continuous monitoring has been used it has frequently revealed large fluctuations and the occurrence of high concentrations persisting for hours or days, say ten times or more greater than a longer-term mean. This country has an extensive sampling system for sulphur dioxide and smoke but its data are commonly expressed as weekly or monthly means, and much exploratory experimentation has matched treatment concentrations to these mean levels. We are now reaching a stage where more work is needed on the effects of short incidents of high concentration.

Then there is the whole field of transport and circulation of pollutants in the biosphere. Long-range transport and large-scale circulation phenomena are clearly outside the scope of this book, but it has become clear that plants are strong sinks for many gaseous pollutants, that there are marked concentration gradients in the vicinity of vegetation and that, as with so many other environmental factors, the concept of a plant growing in an independently determined concentration is over-simple. Rather there is often rapid absorption, of which local concentration gradients are a reflection. Analyses of the analogous exchanges of carbon dioxide and water vapour between vegetation and atmosphere have considerably assisted our understanding of the absorption of gaseous pollutants, and it is good that the organisers of the Seminar invited two papers on absorption processes. It need hardly be said that the analysis of the environment and its effects needs carefully planned co-operation between biologists and applied physicists and chemists.

Turning now to the effects on plants, there are I think four basic techniques which have been used to investigate the ecological effects of other classes of environmental factors. These are:

(1) Correlation of plant growth and behaviour with variation of the factor in space or time. This has sometimes been used to good effect in relation to pollution but as a general method is subject to the well-known difficulties of identifying causes from field correlations. To this Society, it is unnecessary to stress the value of experiments.

(2) Artificial alteration of the environment, e.g. addition of inorganic nutrients, water, shading, with suitable controls.

(3) Simulation of natural environments in controlled conditions.

(4) Diagnostic physiological analysis of plants in the field; e.g. leaf analysis as an indication of plant nutrient status, determination of leaf water potential as an index of water stress, analysis of root xylem sap for various products of anaerobic respiration in relation to flooding injury or tolerance.

It is clearly very difficult to change the level of pollutants on limited areas and with adequate controls in the outdoor environment and so most experimenters in this field have relied on controlled-environment chambers and cabinets. They mostly experience doubts as to how effectively they can simulate the outdoor environment or extrapolate from their results to field conditions. Do they over-stress the artificiality of the controlled environment or have workers in other fields been too insensitive to this? The answer is probably that conclusions have the most firm basis when they rest on a combination of experiments both in the field and in controlled environment. In a context where field experimentation, i.e. the alteration of pollutant levels, is very difficult, the specification and design of controlled environment clearly needs careful attention. Open-top chambers, with pollutants blown in at the bottom and out through the top, are attractive in that they appear to control the pollution factor with least alteration of the rest of the environment, and their design and use will be discussed in the chapter by McCune *et al.*

We come now to analysing the effects on plants. It would be very useful if, when shown some apparently unhealthy plants in the field, one could perform physiological tests, reasonably specific to particular pollutants and related in the scale of their responses to the growth responses of the plants. I do not decry the search for such tests – I am to some extent engaged in it myself in relation to sulphur dioxide injury – however there is a danger here of allowing pressing practical considerations to persuade us to put the cart before the horse. In general I am sure it is more important to investigate systematically the physiological mechanisms of responses to pollutants, with which many of the following chapters are concerned, and that the more such work is undertaken the sooner we shall be able to assess the effects of specific pollutants in the field.

A move forward from the investigation of single factors is to be welcomed for there is increasing evidence that mixtures of pollutants interact not only chemically in the atmosphere but also physiologically at the plant level.

Finally, pollution is a recent phenomenon in the environment. Plants have been selected by other environmental factors over very long times and evolution has produced morphologically distinct species with fairly well defined tolerances (although often with ecotypic variation). But in response to pollutants we see the early stages of selection operating and in numbers of species there have been found highly resistant genotypes apparently indistinguishable morphologically from normal populations. The final chapter by Bradshaw will discuss this phenomenon.

I began by saying that we do not know the magnitude of the effects of atmospheric pollution, in this or any other country. To make progress we must enlarge our understanding of the environment, maintain a critical attitude to methods of experimentation, press on with investigations of physiological mechanisms of response, and take full account of the genetic variability of our natural vegetation and economic plants.

M.H.UNSWORTH, P.V.BISCOE & V.BLACK

Analysis of gas exchange between plants and polluted atmospheres

Introduction

Exchanges of gases between plants and the atmosphere are essential features of physiological processes such as photosynthesis, respiration and transpiration; the uptake of gaseous pollutants by plants is another example of gas exchange. In discussing the design and analysis of experiments to study effects of air pollutants on gas exchange, we will use examples of effects of sulphur dioxide, but the *principles* apply to any gaseous pollutant.

Studies of effects of sulphur dioxide on plants began late in the nineteenth century and the voluminous literature has been reviewed frequently (e.g. Thomas, 1961; Daines, 1968). In general, research has progressed along two lines. First, responses at the cellular level have been studied, showing for example, disruption of chloroplasts in plants exposed to sulphur dioxide (Wellburn, Majernik & Wellburn, 1972), and changes in activities of enzymes (Pahlich, 1975). This type of work is needed to identify sensitive mechanisms, but it cannot be extrapolated to predict how whole plants will respond to a specific period of exposure to sulphur dioxide at a given concentration. The second and more common line of research is concerned with the response to an atmospheric pollutant of leaves, whole plants and crops, e.g. changes in the rate of photosynthesis (Thomas & Hill, 1937; Sij & Swanson, 1974; Watson, 1974), transpiration (Majernik & Mansfield, 1971; Biscoe, Unsworth & Pinckney, 1973) or of dry matter production (Thomas & Hill, 1937; Bell & Clough, 1973; Bleasdale, 1973). The objective of these studies was to provide information of practical use, e.g. in defining minimum concentrations at which a pollutant is likely to reduce yield, but interpretation of experimental results is complicated because plants respond to many other environmental factors.

One example of a problem of interpretation is the continuing controversy over 'invisible injury' by sulphur dioxide, a term coined to describe effects such as reduction in growth and yield when there are no visible lesions on tissue. After a long series of experiments with various species in the USA, Katz (1949) concluded that yields were not reduced without visible damage, and the 'invisible injury' theory fell into disrepute. However, interest in the topic revived following experiments by Bleasdale (1973) and Bell & Clough (1973) who found that yields of ryegrass growing in chambers containing sulphur dioxide at concentrations insufficient to cause visible injury were much less than yields in identical chambers containing filtered air. In contrast, however, Cowling, Jones & Lockyer (1973) found that yields of ryegrass growing in sulphur-deficient soils were greater when the surrounding air contained low concentrations of sulphur dioxide than when clean air was used. When soils with adequate sulphur were used, yields between 'clean' and 'polluted' chambers did not differ significantly. Physiological effects have also been found at sulphur dioxide concentrations below the visible injury threshold. Majernik & Mansfield (1971) and Biscoe *et al.* (1973) showed that stomatal resistance was smaller in air with sulphur dioxide than in sulphur dioxide free air, but Bull & Mansfield (1974) and Watson (1974) showed that rates of photosynthesis decreased when plants were exposed to sulphur dioxide.

Interpretation of these apparently conflicting results is difficult because the plant responses depend not only on the concentration and duration of exposure to a pollutant gas but also on environmental factors such as light, temperature and humidity, and on physiological factors such as species, age, previous history, nutritional and water status. To separate the response of plants to their physical environment from physiological changes induced by pollutants requires careful design of experimental systems, adequate specification of environmental conditions and appropriate quantitative analysis of results. More attention to these basic principles would enable results from different experiments to be compared, and conclusions synthesised. Such work would be more likely to identify the mechanisms of plant responses to air pollutants than many of the descriptive and non-analytical approaches that have been used in the past.

In this paper we discuss the physical principles by which gases are exchanged between plants and the atmosphere. We describe a form of analysis which enables environmental factors governing rates of gas exchange to be separated from physiological factors and we outline experimental techniques useful in such analyses.

Resistance analogues in gas exchange

In describing gas exchange between plants and the atmosphere it is useful to regard the flux of a gas as being driven by a potential difference (difference in gas concentration) and limited by a resistance, so by analogy with Ohm's Law,

$$\text{flux} = \frac{\text{potential difference}}{\text{resistance}}. \tag{1}$$

An appropriate example is the flux, E, of water vapour (i.e. transpiration rate) from a leaf through the stomata. The potential difference driving the flux is the difference between the water vapour concentrations χ_1 in the stomatal cavity and the water vapour concentration χ in the atmosphere. It will be shown later that the limiting resistance, r, is the sum of a component describing properties of the air flow around the leaf and a component related to the dimensions of the stomata. Equation (1) becomes, for this case,

$$E = \frac{\chi_1 - \chi}{r}. \tag{2}$$

Equation (2) shows that E may vary either because the potential difference varies or because of changes in r. If the potential difference is known, then studies of effects of a pollutant on r give information from which transpiration rates in other environments can be predicted.

Resistance analogues have been widely used in recent years in analysing exchanges of carbon dioxide and water vapour between the atmosphere and leaves in enclosures (Gaastra, 1959; Chartier, 1970) or crops in the field (Monteith, 1963; Sceicz, van Bavel & Takami, 1973; Biscoe, Cohen & Wallace, 1975). Spedding (1969) and Biscoe *et al.* (1973) interpreted results of laboratory experiments with plants in polluted air in terms of resistance analogues and similar analyses were applied to field data by Garland, Clough & Fowler (1973) and Fowler & Unsworth (1974). Waggoner (1971) and Bennett, Hill & Gates (1973) use resistance analogues to model uptake of air pollutants by plants, but in general the potential of resistance analogues has not yet been recognised by the majority of plant physiologists concerned with air pollution effects.

The form of analysis allows distinction to be made between resistances which are functions of the aerodynamic properties of the experimental system and resistances which describe physiological or surface properties of plants. For water vapour, carbon dioxide and pollutant gases, several sections of the resistance pathway between the atmosphere and the plant are common, so that measurements of the transfer of one gas can be used to determine additional resistances limiting the transfer of other gases. Sestak, Catsky & Jarvis (1971) comprehensively reviewed the component resistances and described experimental procedures for determining resistances of single leaves and of crop canopies. Only a few common techniques applicable to enclosures will be described here.

Fig. 1 shows a transverse section through a typical leaf and gives the

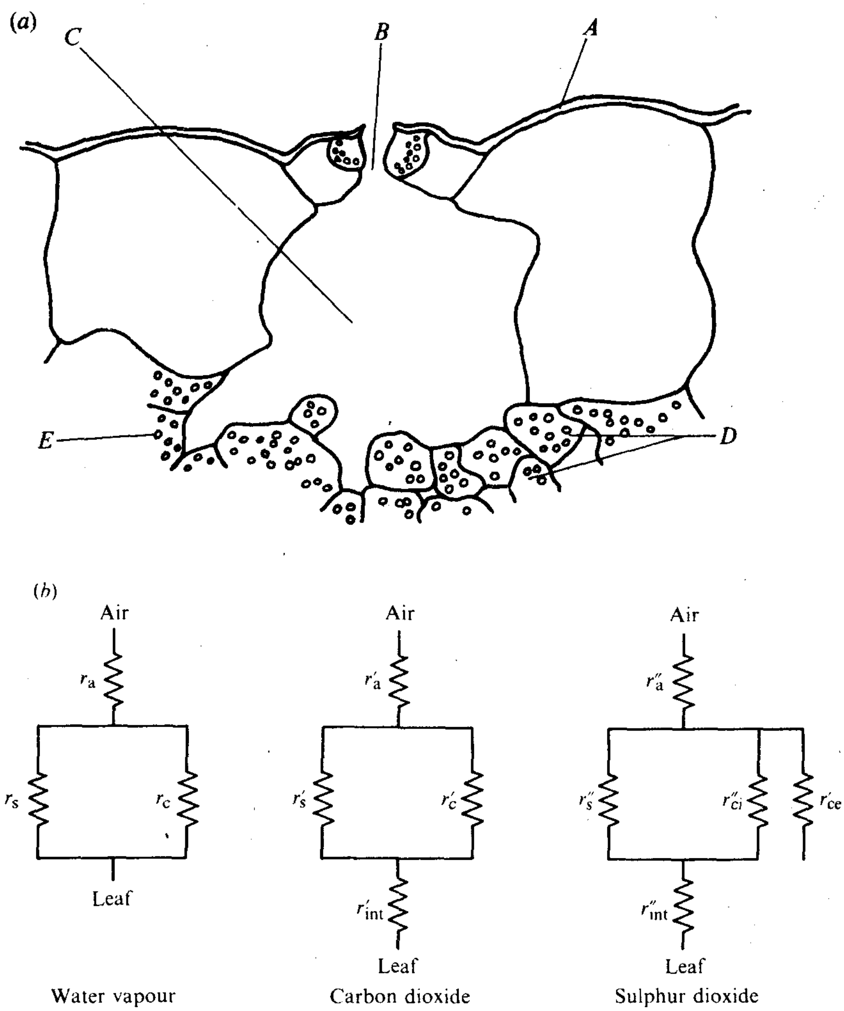

Fig. 1. (*a*) Cross-section through a stoma showing *A*, cuticle; *B*, stomatal throat; *C*, substomatal cavity; *D*, mesophyll cells; *E*, chloroplast.
(*b*) Resistance analogues for transfer of water vapour, carbon dioxide and sulphur dioxide between the atmosphere and a leaf. r_a, aerodynamic resistance; r_s, stomatal resistance; r_c, cuticular resistance; r_{int}, internal resistance. For further explanation see text.

analogue resistance chains describing exchange of water vapour, carbon dioxide and sulphur dioxide between a leaf and the atmosphere.

The total resistance, r, restricting the transfer of an entity is found by combining resistances according to the rules $r = r_1 + r_2 \ldots$ for resistances in series and $1/r = (1/r_1) + (1/r_2) \ldots$ for resistances in parallel (note that if

r_2^* is much greater than r_1, $1/r \simeq 1/r_1$). Knowledge of the physical and physiological factors determining resistances clarifies the importance of alternative pathways.

Aerodynamic resistance

Diffusion of gases takes place by turbulent (eddy) diffusion in the free atmosphere where diffusion rates are identical for all gases. In a thin boundary layer close to the leaf there is a transition from turbulent to molecular diffusion, a much less efficient transfer process, and this has two consequences. First, the main aerodynamic resistance to transfer between the atmosphere and the leaf surface arises in the boundary layer and second, the resistance differs for different gases. In forced convection, when flow in the boundary layer is laminar, the aerodynamic resistance is proportional to $D^{-\frac{2}{3}}$, where D is the molecular diffusion coefficient of the gas in air (Thom, 1968; Monteith, 1973). This means that in Fig. 1(*b*):

$$r_a : r_a' : r_a'' = 1:1.39:1.57, \qquad (3)$$

(based on numerical values of D for CO_2 and water vapour at 20 °C from Monteith (1973) and assuming that $DSO_2 = DCO_2[MCO_2/MSO_2]^{\frac{1}{2}}$ where M is the molecular weight).

For brevity, values of resistances common to several gases will refer to water vapour throughout this paper; the conversion factors in equation (3) should be applied to find corresponding aerodynamic resistances to carbon dioxide and sulphur dioxide transfer.

In enclosures, r_a is determined frequently by measuring the evaporation of water from a model leaf constructed so that there are no additional internal resistances to evaporation. Green blotting paper, or plaster of Paris models soaked in water are commonly used (Sestak *et al.*, 1971). The evaporation rate E (g m^{-2} s^{-1}) is determined either by weighing the model or by measuring the flow rate and water vapour concentration of the air entering and leaving the chamber. In applying equation (2), the potential difference is the difference between the water vapour concentration (absolute humidity) in the chamber χ (g m^{-3}) and the water vapour concentration χ_1 (g m^{-3}) at the surface of the model leaf. χ_1 is found by measuring the leaf temperature and assuming that the air is saturated at the 'leaf' surface. Then

$$E = \frac{\chi_1 - \chi}{r_a}, \qquad (4)$$

from which r_a (s m^{-1}) may be found. Precise measurement of leaf temperature is the main experimental difficulty in this technique.

In field crops, r_a, interpreted as a bulk aerodynamic resistance of the crop