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Direct Effects of Sulphur Dioxide on Trees [and Discussion]

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Direct effects of sulphur dioxide on trees

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Tree foliage has to withstand many environmental – especially climatic – stresses, but does not show symptoms of stress readily. Nevertheless it may react invisibly. This paper presents evidence that trees are particularly prone to SO_2 effects before or without the appearance of visible symptoms of injury. Of the various factors that affect tree sensitivity to SO_2 only six are mentioned: increased wind velocity in the huge crowns, longevity of foliage, sulphur uptake, supply of nutrients and water, genetic variability and pollution régime.

Biological indications such as direct effects of SO_2 on trees may be expressed either quantitatively or qualitatively. The economic point of view often considers only the quantitative aspect: the immediate effect on growth or wood production. This depends on CO_2 uptake, which in turn is influenced by SO_2. Growth – for example ring width or root weight – is affected in consequence. There may also be effects on buds and generative organs, increased susceptibility to abiotic (snow, frost, etc.) or biotic factors (insects, fungi, etc.), and metabolic changes. The last include increased need for detoxification, changes in enzyme activity or in amounts of organic compounds and increased membrane permeability; all are expressions of an increased risk.

1. INTRODUCTION

This survey covers only a few papers dealing with results from fumigation experiments in which factors other than SO_2 were excluded. In spite of the general belief that all green plants react in the same way, it is important to distinguish between trees and herbaceous species. Organic production is but one of many functions that trees, particularly forest trees, have to fulfil. Past experience has shown that certain trees are among the most sensitive plant species to SO_2. Tree foliage – especially in conifers – has to cope with many environmental (especially climatic) stresses and therefore does not easily show any stress symptoms. Nevertheless it may react invisibly. Trees appear particularly prone to SO_2 effects before or even without the development of visible symptoms of injury. The customary reliance on visible symptoms of injury, and the general opinion that where there are no such symptoms there is neither injury nor risk, cannot be sustained.

2. FACTORS INFLUENCING SENSITIVITY

The SO_2 sensitivity of trees is influenced by several factors, of which the six described below appear to be of particular importance.

2.1. *Crown volume and wind velocity*

Trees have a huge crown. In order to get their CO_2 they filter a much larger air volume per unit ground area than low-growing herbs. In addition, tree crowns reach into higher air layers where there is a greater wind velocity than near the ground. For example a four-week fumigation of grass with SO_2 at *ca.* 290 μg m^{-3} did not depress growth at a wind velocity of 0.16 m s^{-1}, whereas an effect was registered at 0.42 m s^{-1} (Ashenden *et al.* 1978). The latter wind velocity is commonly encountered in tree crowns (Geiger 1965).

2.2. *Longevity*

As a rule trees, in contrast to short-lived herbs, survive for decades. They may therefor be exposed to numerous episodes of air pollution. Many conifers remain green during winter when SO_2 concentrations are often increased. Although this period is considered to be th 'dormant season', conifers may be metabolically active and may be injured. It has bee observed that the low temperature and poor light quality of this period may increase the plant' sensitivity to additional stress (Jones & Mansfield 1982).

2.3. *Sulphur uptake*

In comparison with agricultural crops, trees generally have a low demand for sulphur o other nutrients, and therefore the supply usually meets the demand, particularly since tree root exploit a big soil volume. Fumigation experiments demonstrate that SO_2 uptake from the ai diminishes with the duration of exposure, at least at the concentration used, and this may impl that the filtering action for gases decreases simultaneously (figure 1). Such SO_2 uptake ma also occur during winter. At this time, however, the need for it is very small and the metabolis of detoxification is stressed.

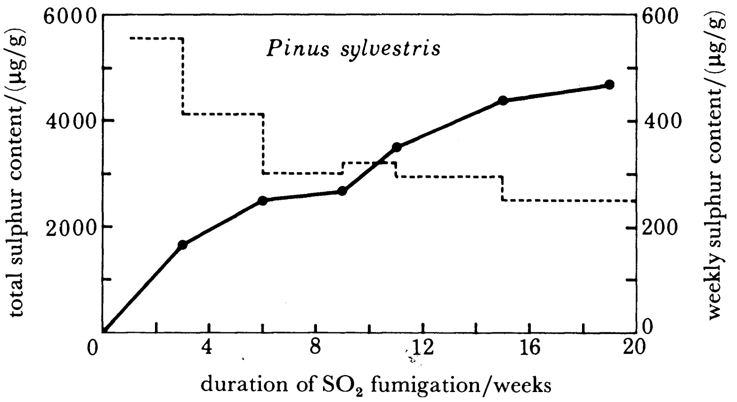

FIGURE 1. Sulphur content and uptake (increase over control) in initially six-month-old pine needles during a prolonged, continuous fumigation with SO_2 at *ca.* 585 μg m^{-3}. Total sulphur content (solid line) and weekly sulphur uptake (broken line), expressed in parts per million of dry matter.

2.4. *Supply of nutrients and water*

Each species is considered to be most resistant to stress when the ecological conditions are optimal. A good supply of water and nutrients may therefore increase resistance. In many areas, however, forestry is now largely confined to infertile, dry or sloping sites because of the clearance of the most favourable land for agriculture.

2.5. *Genetic variability*

It is well known that not all species have the same sensitivity and that certain species may even disappear in polluted areas. Apart from this interspecific variation we also have to recognize an intraspecific variation such as is shown in figure 2. The CO_2 uptake of three spruce (*Picea abies*) clones was observed during a continuous eight-week fumigation with SO_2 at *ca.* 130 μg m^{-3}. Although the depression of CO_2 uptake was distinct in the first clone, it was never significant. In the second clone it reached significance after 8 weeks and in the third clone after only 2 weeks. Visible injury, however, appeared only in the third clone after 8 weeks.

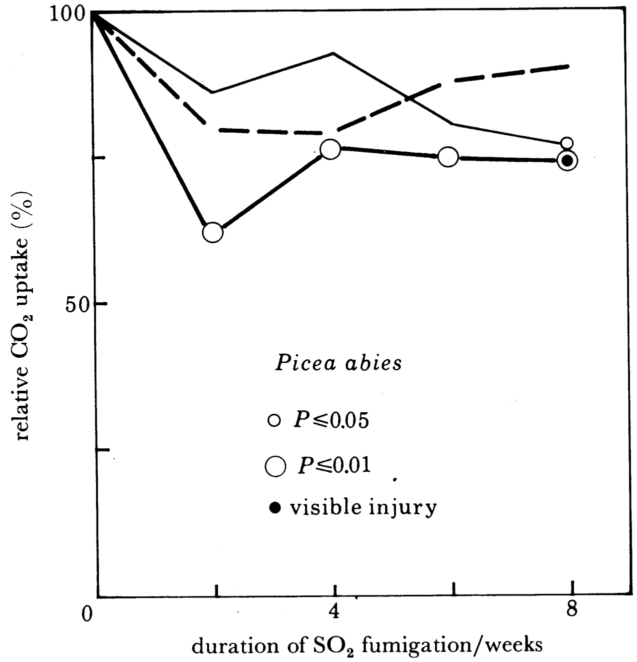

FIGURE 2. The variation in CO_2 uptake in spruce shoots owing to their genetic constitution. The data depict the behaviour of three clones (with five replicates each) during a continuous fumigation with SO_2 at *ca.* 130 μg m^{-3}: data expressed as percentage of uptake by controls. Statistical significance checked by the u-test of Wilcoxon, Mann and Whitney.

2.6. *Pollution régime*

Sensitivity to the pollution régime, for example concentration and duration of impact, varies so greatly that Garsed & Rutter (1982) stated for conifer populations that 'the order obtained at 8000 μg m^{-3} was virtually the reverse of that at 200 μg m^{-3}'. When different fumigation régimes (constant fumigation; intermittent fumigation with short but frequent peaks (s.f.) or long, occasional peaks (l.o.)) were applied to pine (*Pinus sylvestris*) seedlings, Garsed *et al.* (1982) obtained the results shown in table 1 after 650 days. This table indicates that long occasional peaks may be more dangerous to plant life than frequent but short peaks.

TABLE 1. THE EFFECT OF DIFFERENT SO_2 FUMIGATIONS ON DRY MASS GAIN IN *PINUS SYLVESTRIS* SEEDLINGS (FROM GARSED *ET AL.* 1982)

treatment	mean concentration/μg m^{-3}	interval/d	mass gain/g
clean air	0	—	118.5
constant	100	—	101.9
s.f.-peaks	100	1	101.3
l.o.-peaks	100	22	92.0

3. BIOLOGICAL INDICATIONS OF AIR POLLUTION

Many plants are being used as bio-indicators of air pollution. Lichens are very often used because their reaction, death of thallus tissue, is easily visible. There are three features of lichens that are sometimes considered to be disadvantages:

(i) special structure (no stomata, less sensitive during drought);
(ii) need of special taxonomic knowledge;
(iii) no direct economic value.

In the range of invisible or latent injury, accumulation of a deposited substance in plant tissue is sometimes used as a measure of air pollution. This accumulation, however, serves only as an indicator of presence, without proving toxicity. The indication of a toxic effect is, however, important as a warning that a biologically unfavourable or even dangerous situation exists. It is of special value in forestry because most trees are particularly prone to latent (invisible) injury. Physiological, biochemical or ecological plant reactions, whether reversible or irreversible, as well as increased susceptibility, depression of vitality, gene erosion, etc. are considered to be bio-indications of latent injury. A standardization, however, is needed because these indications may be modified by many factors. In addition, if we want proofs and not just indications, we need to know the causal relation between a disease and the particular plant reaction. Moreover, when considering SO_2 effects on trees we have to realize that there are qualitative as well as quantitative effects – just as in other plants – although the economic point of view often considers only the latter: immediate yield or harvest.

TABLE 2. CO_2 UPTAKE OF SPRUCE (*PICEA ABIES*) SHOOTS (MILLIGRAMS PER HOUR) AT DIFFERENT SO_2 CONCENTRATIONS

(Average of 5 replicates each ± standard error.)

duration of fumigation	control	130 μg m^{-3}	260 μg m^{-3}
2 weeks	107 ± 9.6	86 ± 5.0	71 ± 6.6
4 weeks	107 ± 26.1	82 ± 21.4	71 ± 11.7
6 weeks	150 ± 18.6	129 ± 22.4	113 ± 11.1
8 weeks	192 ± 35.6	156 ± 19.4	109 ± 15.1
10 weeks	245 ± 31.6	176 ± 28.1	127 ± 19.7

3.1. *Quantitative effects*

The CO_2 uptake of the plant and its conversion to organic matter with the help of pigments and sunlight is the basis of all production, no matter whether foliage, roots or stems are involved. The similarity of the SO_2 and the CO_2 molecules favours the well known competition between the two, and recently Landolt (1982) has shown that the CO_2 uptake of fumigated beech leaves drops with increasing S content that arises from SO_2 uptake during fumigation.

The depression of CO_2 uptake has long been known to be one of the earliest signs of metabolic changes caused by SO_2 pollution. The effect of a continuous SO_2 fumigation on spruce is shown in table 2. The values given are the average of 5 replicates ± standard error, and state mg h^{-1} CO_2 for the whole shoot. Although CO_2 uptake in the shoots exposed to 260 $\mu g\ m^{-3}$ SO_2 dropped to as little as half that of the controls, there were no visible signs of injury.

Chlorophyll is instrumental in photosynthesis of green plants, and chlorosis – a visible sign of SO_2 injury – is related to chlorophyll destruction. Therefore the content of this pigment has often been measured in foliage. The regeneration of spruce in pure air after exposure to injurious SO_2 doses directed attention to pigments in phloem; analyses revealed a significant increase of chlorophyll in phloem tissue with previous fumigation while needle contents dropped as expected.

When CO_2 uptake is depressed, a reduction of annual ring width could be expected, although some CO_2 is utilized for the formation of other tissues or for the respiration of all tree parts.

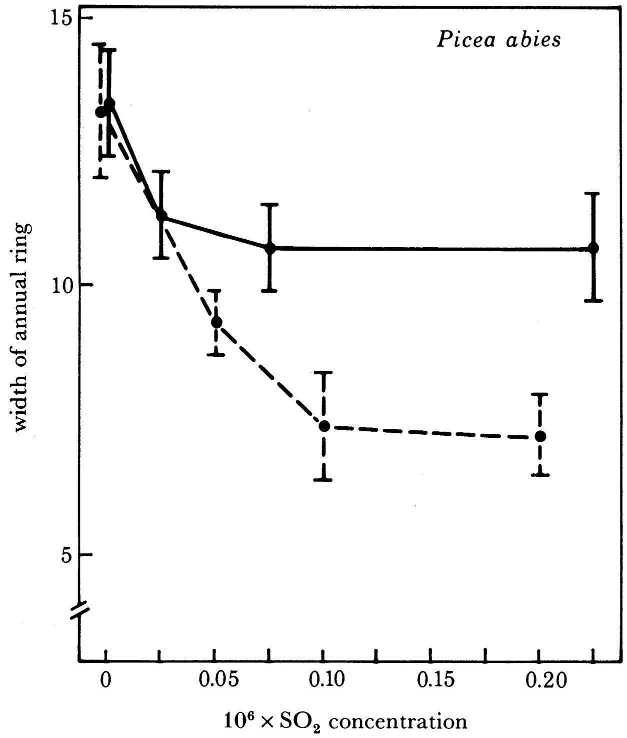

FIGURE 3. The effect of a ten week SO_2 fumigation at different concentrations during summer (broken line) or winter (solid line) on the relative width of the subsequent annual ring in two combined spruce clones. Each value is the average of 18 replicates. Vertical bars denote standard errors.

Figure 3 illustrates for a combined sample from two spruce clones the decrease of ring width after a continuous ten-week fumigation at different SO_2 concentrations, either during summer (broken line) or winter (solid line). It distinctly shows the growth depression because of a summer fumigation; but even the winter fumigation proved to be significantly deleterious in the following growing season. Consequently, wood production was also affected. This means that a forest owner may suffer a severe loss even in the absence of a visible sign of injury.

A reduction in CO_2 uptake may also cause reduced root growth with subsequently impeded uptake of water and nutrients. In addition the tree may no longer be firmly anchored and may become more susceptible to wind-throw by storms. Furthermore, the roots which are no longer well supplied by the shoot may lack symbiotic mycorrhizae and may be more vulnerable to attack by pathogens such as root-rot fungi. Needless to say, all this may lead to decreased growth (production).

3.2. *Qualitative effects*

Beside these quantified effects, SO_2 may also affect plant peculiarities that are considered to be more qualitative than quantitative. Such characteristics may be pertinent to buds or to generative organs. SO_2 may also cause metabolic changes and increased susceptibility to abiotic and biotic factors.

Effects on buds include belated flushing – often observed in fumigations – or even a winter killing (Keller 1978). Where regenerative organs are concerned, we should consider not only flowering but also pollen germination. Tree pollen germination may be severely reduced by a 16 h fumigation with *ca.* 200 μg m^{-3} SO_2 (Keller 1983). Even if fertilization and seed formation are certain, we have to bear in mind that diminishing pollen germination results in an unwanted loss of genes.

SO_2 may also increase susceptibility to abiotic factors, such as frost, heat, drought or heavy snow. Although often observed in the field, it has only recently been experimentally demonstrated that SO_2 may increase sensitivity to frost. An average shoot kill by late frost was noted in spruce, increasing by 15 % after three winter months at *ca.* 130 μg m^{-3}, although the u-test did not reveal significance (Keller 1981). A sluggish reaction of stomata may increase drought sensitivity owing to increased transpiration (Larcher 1980). Competition within an ecosystem may be changed by snow-bending of SO_2 affected species (Keller & Beda-Puta 1981).
Beda-Puta 1981).

An increased susceptibility to biotic factors, such as attack by insects, fungi, etc. is often difficult to determine, particularly if the injurious agent is more susceptible to SO_2 than is the host.

In addition, there is quite a wide individual variability in host susceptibility, making experimentation even more difficult. Thus, in spring 1983 we observed an increased attack of gall aphids on a particular clone of spruce after exposure to different SO_2 concentations in the summer of 1982. Although the values reflect the tendency to increased attack after increased SO_2 concentrations, the correlation is poor, as shown in figure 4.

Qualitative SO_2 effects may also be reflected by metabolic changes, e.g. by decreased ascorbic acid content (Keller & Schwager 1977), increased SH-group content (Grill *et al.* 1982), enzyme activity (Jäger 1982) or increased membrane permeability. Figure 5 shows how a winter fumigation of spruce caused increased peroxidase activity. Working on *Pinus banksiana* seedlings, Khan & Malhotra (1982) suggested that the stimulated activity observed was mainly a matter of increased isoenzyme production. The enzyme peroxidase is considered to be a detoxifying enzyme, produced in the plant cell to destroy peroxides formed under stress or in ageing. Highly toxic superoxide radicals involved in this process may attack membrane lipids and increase loss of nutrient with increased membrane permeability. The latter is shown in figure 5, measured as electrical conductivity in needle diffusates. Some leaching and transport occurs through the

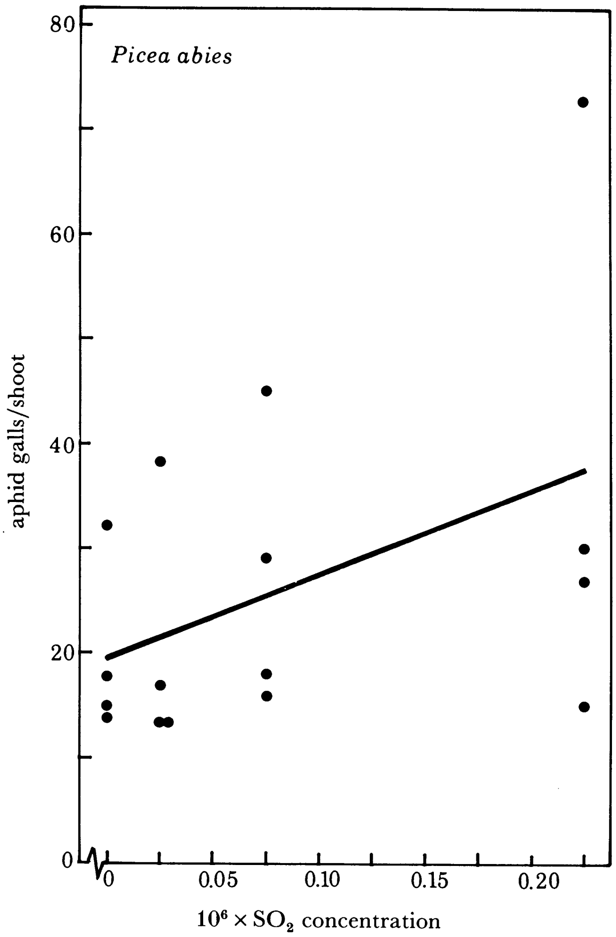

FIGURE 4. The correlation ($r^2 = 0.182$) between a summer fumigation of a spruce clone at different SO_2 concentrations and the subsequent gall formation by aphids.

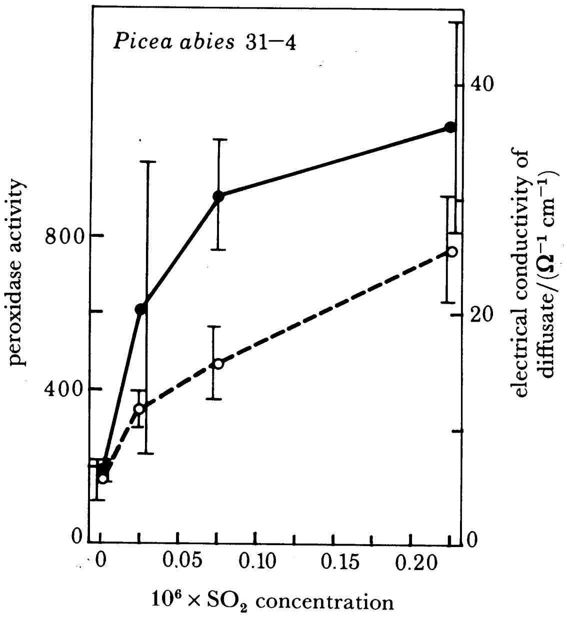

FIGURE 5. The effect of a winter fumigation (October–March) at different SO_2 concentrations on peroxidase activity (broken line) and electrical conductivity (solid line) in a young spruce clone. Each value is the average of 5 replicates. Vertical bars denote standard errors.

vascular tissue of the needles in any case, and influences the electrical conductivity of the diffusate. This effect, however, was found to be very small in comparison with direct leaching through the cuticle and stomata.

Conclusions

Owing to their long life-span, trees may be repeatedly subjected to air pollution episodes which may weaken their vitality. Because many trees, particularly evergreens, have sturdy foliage that resists many climatic stresses, they do not easily manifest visible symptoms of injury; they do, however, react in the latent range. This phenomenon is often neglected until a serious forest die-back gives cause for concern.

Air pollution as a result of household heating is highest in winter, the very time when many physiological processes are minimal; nevertheless an impact even during this 'dormant' season may affect trees. This concerns not only strictly quantitative factors, such as wood production in the following season, but also factors which, in spite of their more qualitative nature, are also quantifiable.

The present paper deals mainly with European forest tree species, in particular spruce, and the air pollutant SO_2. Fumigations lasting several weeks or months were performed to see whether they had effects at concentrations considered to be harmless, i.e. overpowered by detoxification. In forested areas even lower concentrations than those applied are usually (but not always) found, except in agglomerations or in heavily industrialized areas, where the same species may be grown in gardens, parks or city forests.

We must bear in mind, however, that forests comprise many specimens of differing sensitivity (genetical make-up) and that SO_2 is only one of many active air pollutants, just as growth is only one of the many expressions of life in trees.

We should not seek simple dose–response relations in forestry since there are so many ecological and genetical factors modifying dose–response relations.

We must balance economy and ecology in managing our environment. If man calls himself *Homo sapiens* and considers himself to be the Lord of Creation he must act wisely, and recognize that our planet is becoming more and more crowded. A one-sided attitude towards economy will prove to be a short-sighted *après nous le déluge*. Our children or grand-children will have to pay for it in terms of the fight for survival.

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Discussion

A. J. Rutter (*Imperial College, Silwood Park, Ascot, Berks.*). In Britain, areas with annual mean ground level concentration of SO_2 exceeding 100 μg m^{-3} are largely urban, but the zone of 50–100 μg m^{-3} includes a significant proportion of farm and forest land. Dr Garsed and I have found that 100 μg m^{-3} reduces the growth of Scots pine (*Pinus sylvestris*) and Dr Keller has found that there are effects at even lower concentrations on photosynthesis and other processes in Norway spruce (*Picea abies*). Dr Keller says that effects on dry mass growth in *P. sylvestris* are initially 'hidden' in that they are hardly detectable during the first year of treatment but become appreciable during the second year. In comparisons of species we find *P. sylvestris* to be more sensitive than several deciduous species to low concentrations of SO_2, but less sensitive than the economically important Sitka spruce (*Picea sitchensis*) and Lodgepole pine (*Pinus contorta*). I suggest therefore that for trees in Britain a sensitive field for further investigation is the growth and yield of economic forestry in areas with between 50 and 100 μg m^{-3} mean annual SO_2 concentration, e.g. those parts of the Pennines that are comparatively close to large urban and industrial areas.

T. Keller. I do agree with Dr Rutter that it is important to investigate the behaviour of different tree species at low SO_2 concentrations. I should like to point out, however, that it is dangerous to rely on the selection of less sensitive species for growth or yield within a relatively short time. Vitality may decline in trees over the years and susceptibility to other harmful agents may increase without immediately showing up in reduced yield.

S. R. Elsden (*University of East Anglia, Norwich, U.K.*). Dr Keller used the size of the annual rings of *Picea abies* as an index of the effect of SO_2 on the growth of the plant but instead of showing the dimensions in absolute units, or the mean values if a number of plants were used for each treatment, presented the data as relative ring width. How were the rings of these small plants measured (and how precise and repeatable was the method)? What were the absolute sizes of the rings in the treated and untreated plants and the variation within each group?

T. Keller. Professor Elsden's question refers to figure 3 where I gave the average of 2 clones with 9 replicates each for each value. The vertical bars denote the standard error in each case.

The small stems were cut and the whole cross section (1.25 ± 0.01 mm thick) was radiographed. The X-ray-picture was enlarged by a factor of 4. Ring width (on two diameters at a right angle equal to 4 measurements for each replicate) was measured on these enlargements to 0.1 of a millimetre. The precision of measurements is estimated to be about the same; 10 relative units of ring width correspond roughly to 2.5 mm.

J. N. B. Bell (*Department of Pure and Applied Biology, Imperial College, Silwood Park, Ascot, Berkshire, U.K.*). Both Dr Keller and Dr Roberts have touched on an issue which I feel is seriously neglected. They mentioned effects of sulphur dioxide on fungal pathogens and aphids. I am sure we all accept that, on a worldwide scale, pests and pathogens cause substantially greater crop losses than do the direct effects of air pollutants. However, there are indications from the limited amount of data available that air pollutants can have both positive and negative effects upon pests and pathogens. Furthermore, in view of the extreme sensitivity of many lichen species to levels of sulphur dioxide considerably lower than the threshold of about 100 $\mu g\ m^{-3}$ for higher plants that has been proposed by some speakers today, there must be a distinct possibility that the performance of pathogenic fungi is affected by SO_2 over a much greater area than that where direct effects of the pollutant on crop growth occur. The marked impact of air pollution on an insect pest was demonstrated by our group this summer when it was shown that the ambient London air produced a substantial increase over a ten day period in the growth rate of the black bean aphid, feeding on *Vicia faba*, compared with aphids on plants growing in charcoal-filtered air.

The indirect effects of air pollutants on crop growth, mediated via impacts on the performance of pests and pathogens, could conceivably be more important economically than direct effects on the crops, themselves.

This is a topic which should be given high priority for future investigations.

A. Hüttermann (*Forstbotanisches Institut der Universität Göttingen, Büsgenweg* 2 *D*-3400 *Göttingen, West Germany*). I would like to support the question brought up by Dr Keller about invisible damage very much. From everything we know about the response of a great variety of biological systems and organisms to environmental signals (cf. the work on biochemistry of differentiation), it is evident that visible changes are preceded by rather pronounced changes in the biochemistry and physiology of the organisms. For an evaluation of the impact of any possible pollutant, or a combination thereof, the assessment of these early changes and responses is much more essential than the monitoring of visible damage only. The latter approach could lead to completely wrong interpretations of the impact of any given pollutant. The work of Dr Keller has already provided us with a variety of good methods which have been proven to be useful and applicable for the detection of invisible SO_2 influence. This spectrum of methods, however, should be broadened by now, making use of the well established methodology of modern plant physiology and biochemistry.