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The Effect of Dust on Photosynthesis and its Significance for Roadside Plants

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ABSTRACT

Dust scraped from a car exhaust and ground to a particle size range of 1–10 μm was applied at measured rates to leaves of Viburnum tinus. *Its effects on photosynthesis and leaf diffusion resistance were measured over a range of light intensities. Photosynthesis was reduced and this appeared to be due to shading when the upper surfaces of leaves were dusted, and to impeded diffusion when lower surfaces were dusted. These effects were observed with 5 to 10 g dust per* m^2 *leaf surface. The maximum dust load found on the leaves of shrubs on the central reserves of motorways was about 2 g* m^{-2}. *Unless this deposit included much material too fine to be observed by light microscopy (i.e.* < ca *0·5 μm) its effects on photosynthesis, mediated either by shading or by interference with diffusion, are likely to be small.*

INTRODUCTION

In trial plantings of shrubs on central reserves of English motorways circumstantial evidence was obtained that their growth was inversely related to traffic density and that it may be difficult to establish shrubs on central reserves when traffic exceeds about 50 000 vehicles per day (Colwill *et al.*, 1982). Direct evidence of an effect of traffic was obtained by Flückiger *et al.* (1978*a*), who placed potted shrubs on the central reserve,

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the verge and at 200 m distance, by a motorway near Basle during the growing season; in six species leaf area was reduced by about 50 % on the central reserve compared with the group at 200 m.

Numerous factors may contribute to this effect of traffic. Vehicles emit gases harmful to plants, especially nitrogen oxides and ethylene, and also oil droplets and solid particles, including those containing lead. Further particles are derived from the abrasion of tyres, brake linings and clutch plates, and the road surface. Air movement over central reserves is highly turbulent and the effect on plants of turbulent wind, and of spray from wet road surfaces, may be exacerbated by the presence of suspended material. Leaves of plants on central reserves of roads with high traffic density are covered with black deposits. The possible effect of many of these factors is discussed in papers presented at a symposium (Colwill *et al.*, 1979).

The present experiments explored the effects of black dust on photosynthesis and gas exchange. There have been numerous reports that dusts, of varying origin, interfere with stomatal function (Ricks & Williams, 1974; Flückiger *et al.*, 1978*b*, 1979), increase leaf temperature (Eller, 1977; Flückiger *et al.*, 1978*b*) and transpiration (Beasley, 1942; Eveling, 1969), reduce photosynthesis (Darley, 1966) and increase the uptake of gaseous pollutants (Ricks & Williams, 1974).

MATERIALS AND METHODS

Source and application of dust

Black material was scraped out of two old exhaust silencers, mixed and ground until most particles were 1 to 10 μm diameter. This stock, which will, for the purpose of this paper, be called exhaust dust, was used in all experiments. In the first experiment, lamp-black with particles $\leq 1\ \mu$m, and a rather crystalline dark grey charcoal dust, of similar texture to the exhaust dust, were also used. Weighed quantities of dust were applied to leaves of measured area with a fine brush and, except in the first experiment, control leaves were also brushed, without dusting.

Plant material

Potted specimens, 30 to 50 cm high, of *Viburnum tinus*, an evergreen shrub with hypostomatous leaves, were obtained from a commercial nursery. The experiments were performed in November and December 1978 and between February and April 1979. During this time the plants were kept in a heated glasshouse with supplementary illumination and they produced new leaves. In some experiments old leaves (i.e. those unfolded during summer 1978) were used, and in others the young leaves produced in glasshouse conditions were used. However, young leaves were not used until they were fully expanded. Measurements of gas exchange were made on individual leaves while still attached to the plants. To obtain the desired replication, leaves on more than one plant were usually used and the treatments to be compared were spread across the same batch of plants. There was considerable variation between leaves but little of this could be accounted for by variation between plants.

Measurement of gaseous exchange

Leaves were sealed into cuvettes, each of which was fitted with gas input and output lines, thermocouples for measuring leaf and air temperature, a photocell and a stirring fan. Gas flow rates into the cuvettes were measured with variable area rotary flow-meters and kept within the range 0·5 to 1·2 litres min^{-1}.

Compressed air with a CO_2 content between 270 and 350 ppm was obtained from a cylinder. It was saturated with water vapour at 5 °C and then split into six streams. Four of these supplied the cuvettes, one was used as a reference stream and one was used sporadically for calibrating. The air streams from the cuvettes and the reference stream were passed in turn through a dew-point meter to determine specific humidity, and an infra-red gas analyser to measure CO_2 content. The pressures within the dew-point meter and IRGA were monitored with manometers and held approximately constant.

Thus, from all the measurements made, net CO_2 exchange, transpiration rate and leaf diffusion resistance to water vapour could be calculated. Observations were punched on to cards and the calculations were made by computer.

There were four cuvettes, each being placed in an unshaded position and at approximately the same distance from the light source. This was a Xenon arc lamp above a glass bath containing about 30 mm depth of circulating water and giving between 200 and 300 $\mu E\,m^{-2}\,s^{-1}$ photosynthetically active radiation (PAR) at the leaf surface. Shading was provided to each cuvette individually by a series of neutral plastic covers of increasing light attenuation, and in earlier experiments (1 to 5) when different dusting treatments were applied to different leaves, measurements of gas exchange were made at six or seven light intensities on each leaf, from the maximum down to zero. Variation among leaves was high and contributed large random errors to the experiments. In later experiments (6 to 8), errors were reduced by measuring the gas exchange of leaves before and after the application of dust. These experiments were done only at maximum light.

Before use in an experiment plants were placed under the arc lamp for about 1 h. Leaves were then sealed in the cuvettes and a further period of up to 30 min was required for steady-state conditions to be reached. Following each change of light intensity in the earlier experiments, or the application of dust in later experiments, gas exchange was monitored until a new steady state was recorded, usually after 10 to 30 min.

In addition to calculations of leaf diffusion resistance from the cuvette data, measurements were also made in Experiment 5 with a LICOR Li 60 diffusive resistance porometer.

Treatment of light-response curves

In experiments where the response of CO_2 flux to the leaf (P) to changing light intensity (I) was measured, the Marquardt non-linear least squares estimation method (Marquardt, 1963, 1966) was used to fit rectangular hyperbolae of the form:

$$P = \frac{P_{max} I}{I + K} + R$$

The three fitted constants P_{max}, K and R, represent, respectively, the light-saturated value of photosynthesis, the light intensity that gives half P_{max} and the respiration rate as a negative flux.

Variation in P_{max} should reflect changes in diffusion rate due to dusting but since the fitted values of K were approximately the same as the maximum attainable value of I, P_{max} was a considerable extrapolation beyond the data and was too variable to be useful. The slope of the fitted curve at zero light (P_{max}/K) is a measure of the efficiency of utilisation of incident light and was used as an indication of the shading effect of dusts. Finally, P_{250}, an estimate of net photosynthesis at 250 μE m^{-2} s^{-1}, was calculated in order to remove variation attributable to differences between the light intensity incident on different leaves.

Almost all the light response curves for individual leaves were satisfactorily fitted by rectangular hyperbolae. About 5% were discarded either because P_{max} and K were more than an order of magnitude above their expected values, or because the standard error of points about the fitted line was an order of magnitude greater than in the bulk of the data. Although these criteria seem arbitrary, there were marked discontinuities in estimates of P_{max}, K and standard error to justify rejection of data giving extreme values.

The light response of leaf diffusion resistance or conductance might also have been fitted with an appropriate curve but this seemed unnecessary and r_{250}, the leaf diffusion resistance (to water vapour) at $250\,\mu E\,m^{-2}\,s^{-1}$, was estimated by linear interpolation between the values of r at the two values of I on either side of 250.

Dust load of motorway plants

Towards the end of two successive summers leaves were sampled from a range of shrubs and motorway sites. Mature leaves were taken at between 0·5 and 1·0 m height from plants on central reserves. Leaves of the same species were also obtained at the same time from control sites, i.e. more than 0·5 km distant from a road, at Imperial College, Silwood Park, in 1980 and at a site on the North Downs in 1981. Subsamples of measured area (about $100\,cm^2$) were washed in water either with mechanical stirring or by brushing, and the dust was recovered by filtration and weighed. Subsidiary tests showed that there was negligible extra recovery if detergent was added to the water or if the washing was done in chloroform. Leaves from some species and sites, both before and after washing, were fixed in 3:1 ethanol:acetic acid, cleared in lactophenol and examined under a microscope to detect dust retained during washing, and its location.

The transmission of light by leaves from both motorway and control sites was measured before and after washing by the method described below.

Comparisons of exhaust dust and motorway dust

Particle size distributions were obtained by suspending dusts in water, sampling drops while shaking the suspensions, mounting them on a slide beneath a cover slip and measuring the maximum diameter of 100 randomly chosen particles in each of five drops per suspension, under a microscope. In the case of motorway dust the drops were taken from suspensions washed from leaves, before filtration and weighing.

The transmission of light by known weights of dust brushed on to measured areas of glass or paper was measured and compared with the transmission by glass or paper alone. In these experiments the motorway dust was scraped from the glass fibre filter discs (after they had been dried and weighed) which had been used to recover the dust load of leaves from motorways.

Light transmission studies—Method and treatment of data

A LIKOR sensor, measuring the energy of photosynthetically active radiation, was mounted below a 500 W tungsten filament lamp. Squares of glass or paper, with or without dust on them, were laid on the surface of the sensor and the transmitted PAR was measured. The same technique was used for leaves, before and after washing, except that these were held flat between two pieces of card in which circular apertures coincided in position and just fitted over the circular surface of the sensor.

If the reflection coefficient of the dust is approximately zero, and that of the supporting medium (glass, paper or leaf) is assumed unchanged by the presence of the dust, then the proportion of light transmitted by the dust layer (T_d) is given by:

$$T_d = T_{sd}/T_s$$

where T_{sd} and T_s are the ratio of transmitted to incident light by, respectively, the supporting medium plus dust and the supporting medium alone. In the comparison of unwashed and washed leaves, this assumes that the reflecting and transmitting properties of the leaf itself are unchanged by washing. This assumption was checked by observations on the effect of washing leaves from the control site. In control leaves of *Euonymus europaeus* and *Viburnum lantana* the change in light transmission following washing was less than 10% and a corresponding small correction was made in the calculation of T_d on leaves from the motorway. But when leaves of *Crataegus monogyna* were washed (with brushing) they rapidly became brown and relatively opaque; it was therefore concluded that this method of determining T_d could not be used with this species.

RESULTS

Preliminary experiments

Exhaust dust and charcoal dust were applied to old leaves at the rate of 10 g per m^2 surface, i.e. both upper and lower surfaces received this application. With the fine and loose lamp-black a bulk volume approximately equivalent to the other two dusts was used. In Experiment 1 there were also treatments in which exhaust dust was applied to one surface only. In Experiment 1 there were twelve replicate leaves in the control and six in each of the dusted treatments; there were six replicates throughout in Experiment 2.

Effects on photosynthesis (P_{250}) are shown in Table 1. There were no significant differences among the dusted treatments but in each experiment their mean was significantly less than that of the control ($p < 0{\cdot}01$). The effect of brushing alone was not significant.

In Experiment 1, treatments 1, 2, 5 and 6 (see Table 1) represent all four possible combinations with or without dust on the upper and lower surfaces, and this set was used to analyse the relationships of P_{250}, P_{max}/K and r_{250} and their response to dusting. Table 1 suggests that the effect of exhaust dust applied to both surfaces is not much greater than when it is applied to either the upper or the lower surface only, i.e. the effects on the two surfaces are not additive. However, this interaction was not significant and results presented in Table 2 ignore interactions and simply compare treatments with or without dust on the lower surface (treatments 2 + 6 versus 1 + 5) or with and without dust on the upper surface (2 + 5 versus 1 + 6). Table 2 shows that dust on the lower surface caused a significant increase in leaf diffusion resistance and a significant reduction in photosynthesis. The response of photosynthesis (at 250 $\mu E\, m^{-2}\, s^{-1}$) to dust on the upper surface was similar to that on the lower surface, but was a little less and not quite significant. However, there was a significant reduction of P_{max}/K, indicating a shading effect that reduced photosynthesis, at least at low light intensities. Dust on the upper surface did not affect diffusion resistance.

The significant reduction in photosynthesis caused by dusting both leaf surfaces in Experiment 2 was accompanied by a significant reduction in P_{max}/K and an apparent increase in r_{250}, which was not, however, significant (Table 3).

TABLE 1

The Effect of Dust Applied at 10 g per m^2 Surface on Net Photosynthesis at 250 $\mu E\,m^{-2}\,s^{-1}$

Treatment No.	1	1a	2	3	4	5	6	
Type of dust	None (leaves not brushed)	None (leaves brushed)	Exhaust dust	Lamp-black	Charcoal	Exhaust dust	Exhaust dust	
Surface treated	Neither	Both	Both	Both	Both	Upper	Lower	
	Net photosynthesis ($\mu g\,m^{-2}\,s^{-1}$)							*Probability* (p) *dusted versus non-dusted*
Experiment 1	270		196	202	232	221	211	$<0{\cdot}01$
Experiment 2	161	144	117	85				$<0{\cdot}01$

TABLE 2

The Effects of Exhaust Dust, on the Lower or Upper Surfaces of Leaves on Photosynthesis (P_{250}) and Leaf Diffusion Resistance (r_{250}) at 250 $\mu E\,m^{-2}\,s^{-1}$, and on the Efficiency of Utilisation of Incident Light (P_{max}/K) (Experiment 1)

	Dust on lower surface			*Dust on upper surface*		
	P_{250} ($\mu g\,m^{-2}\,s^{-1}$)	r_{250} ($s\,m^{-1}$)	P_{max}/K ($\mu g\,\mu E^{-1}$)	P_{250} ($\mu g\,m^{-2}\,s^{-1}$)	r_{250} ($s\,m^{-1}$)	P_{max}/K ($\mu g\,\mu E^{-1}$)
Without dust	246	762	1·76	241	946	1·93
With dust	204	1 082	1·71	209	898	1·54
Probability (p)	$<0{\cdot}05$	$<0{\cdot}05$	NS	$<0{\cdot}2$	NS	$<0{\cdot}05$

NS, not significant.

TABLE 3
The Effects of Dusting Both Leaf Surfaces on Leaf Diffusion Resistance (r_{250}) at $250\,\mu E\,m^{-2}\,s^{-1}$ and on the Efficiency of Utilisation of Incident Light (P_{max}/K). (Experiment 2)

	Control	*Control (brushed)*	*Exhaust dust*	*Lamp-black*	*Probability (p) Dusted versus non-dusted*
$r_{250}\,(s\,m^{-1})$	1 089	1 119	1 334	1 590	NS
$P_{max}/K\ (\mu g\,\mu E^{-1})$	1·09	1·24	0·87	0·69	<0·01

NS, not significant.

Application of exhaust dust at varying rates to upper leaf surface only

In Experiment 4, exhaust dust was applied to the upper surface of young leaves (six per treatment) at rates varying from 2 to $30\,g\,m^{-2}$, and there was a control treatment. Applications exceeding $10\,g\,m^{-2}$ appeared to reduce P_{max}/K (Table 4), but the errors were high and there were no significant effects on either this or P_{250}.

In order to reduce the errors arising from differences between leaves, further experiments were performed in which photosynthesis was measured before and after applying exhaust dust. In Experiment 6 photosynthesis was measured in six young leaves. A thin plastic film was then placed on the upper surface of each leaf on which a drop of water ensured adhesion. Photosynthesis was remeasured after applying the film, and after successive additions of exhaust dust ranging from 5 to $30\,g\,m^{-2}$. Finally, the film plus dust was stripped off and one further measurement made. As a further check on unforeseen effects of the film, in Experiment 7 photosynthesis was measured on six young leaves before and after the application of $10\,g\,m^{-2}$ exhaust dust directly to their upper surfaces, and after the dust had been washed off again. Results of these experiments are also presented in Table 4. Placing film over the upper surface had a negligible effect on photosynthesis. A significant reduction was caused by $5\,g\,m^{-2}$ dust and the effect increased with each successive addition. When film and dust were removed, photosynthesis was restored to 0·83 of its initial level. The effect of $10\,g\,m^{-2}$ dust was similar in experiments with or without the interposition of plastic film, but when this

TABLE 4
The Effects of Varying Rates of Exhaust Dust, Applied to the Upper Surfaces of Leaves, on Photosynthesis (P) and Efficiency of Utilisation of Incident Light (P_{max}/K)

	Dust application rate ($g\,m^{-2}$)								*Least significant difference* ($p=0{\cdot}05$)	*Standard error*
	0[a]		*2*	*5*	*10*	*20*	*30*	*0*[b]		
Experiment 4										
P_{250} ($\mu g\,m^{-2}\,s^{-1}$)	163		149	188	141	114	167		NS	±21
P_{max}/K ($\mu g\,\mu E^{-1}$)	1·77		1·60	1·86	1·59	1·40	1·33		NS	±0·20
Experiment 6	Without film	With film								
P^c ($\mu g\,m^{-2}\,s^{-1}$)	189	186		143	132	112	93	157	20	±7
Experiment 7										
P^c ($\mu g\,m^{-2}\,s^{-1}$)	206				157			190	16	±5

[a] Control rate at start of experiment.
[b] Control rate at end of experiment.
[c] In Experiments 6 and 7, photosynthesis was measured at mean light intensity 275 $\mu E\,m^{-2}\,s^{-1}$.
NS, not significant.

dust was applied directly to the leaf surface (Experiment 7) and washed off again, photosynthesis was restored to 0·92 of its initial value.

In none of these experiments (4, 6 and 7) was there any effect of treatment on leaf diffusion resistance.

Application of exhaust dust to lower leaf surface only

In experiments in which dust was applied to the lower surfaces of leaves, the rates are nominal since some dust dropped off when the leaves were restored to their normal positions. In Experiments 3 and 5 exhaust dust was applied either at midday, when the stomata were open, or at night after the lapse of sufficient time for stomatal closure, as indicated by a porometer, to have occurred. These treatments were compared with untreated leaves. In Experiment 3, $10\,g\,m^{-2}$ dust was applied to young leaves. In Experiment 5, $20\,g\,m^{-2}$ was applied to old leaves but test weighing showed that only about half of this was retained. There were six replicates in each treatment, and measurements were made 12 to 24 h after dust applications.

As in previous experiments based on comparisons among leaves, errors were high. Dusting at a nominal $20\,g\,m^{-2}$ (Experiment 5) produced an apparent decrease in photosynthesis but this was not significant (Table 5). Calculations, from cuvette data, of leaf diffusion resistances at 250 and $0\,\mu E\,m^{-2}\,s^{-1}$ did not indicate any significant effects of dusting. However, in Experiment 5 leaf diffusion resistances were also measured with a porometer, at noon under $300–400\,\mu E\,m^{-2}\,s^{-1}$ provided by the Xenon lamp, or in darkness at midnight. In measurements at noon, leaves that had been dusted at noon on the previous day had significantly higher ($p <$ 0·001) diffusion resistances, but the effect of dust applied at midnight was not significant. At midnight (12 h later) stomatal closure appeared to be less in dusted leaves than in the controls; this was true whether the dust had been applied at midnight or at midday, but the failure to close was significantly greater ($p < 0{\cdot}01$) in plants dusted at midday.

In Experiment 8, gas exchange was measured before and after the application of $20\,g\,m^{-2}$ dust on the lower surface of young leaves in sixfold replication. The dust was applied about midday, and again about half of it was shed before measurements began. Leaf diffusion resistance (estimated from the cuvette data) was increased by 16% ($p < 0{\cdot}05$) and photosynthesis was reduced by 15% ($p < 0{\cdot}001$) as a result of this treatment (Table 5).

TABLE 5

The Effects of Exhaust Dust, Applied to the Lower Surfaces of Leaves, on Photosynthesis (P) and Leaf Diffusion Resistance (r)

	Control	*Dusted at*		*Probability*	*Standard*
		midnight	*midday*	(p)	*error*
Experiment 3					
P_{250} ($\mu g\,m^{-2}\,s^{-1}$)	155	185	175	NS	± 15
Experiment 5					
P_{250} ($\mu g\,m^{-2}\,s^{-1}$)	299	275	253	NS	± 30
r ($s\,m^{-1}$), midday at 300–400 $\mu E\,m^{-2}\,s^{-1}$	262	281	390	$< 0{\cdot}001$	± 22
r ($s\,m^{-1}$), midnight in darkness	$6\,370 \pm 1\,355$	$2\,984 \pm 338$	$1\,501 \pm 123$	$< 0{\cdot}01$	
Experiment 8[a]					
P ($\mu g\,m^{-2}\,s^{-1}$)	252		214	$< 0{\cdot}001$	$\pm 0{\cdot}3$
r ($s\,m^{-1}$)	743		865	$< 0{\cdot}05$	± 29

[a] Mean light intensity at experimental leaves, 275 $\mu E\,m^{-2}\,s^{-1}$.
NS, not significant.

Dust load of leaves on central reserves

The amount of dust washed from leaves sampled from central reserves in August 1980 tended to increase with mean traffic density (Fig. 1). Dust was observed on both leaf surfaces but its distribution between upper and lower surfaces was not determined. To make these data comparable with the rates applied in experiments, surface area (i.e. twice the projected area) is used as a basis of expression. Maximum dust loads were found by the M4 but the absolute values (1 to 2 g m^{-2}) were low compared with those used experimentally. Summer rainfall in 1980 was greater than average but a more restricted sampling, undertaken in September 1981 before the onset of autumnal rain, gave substantially the same result as in 1980. However, clearing and microscopic examination of leaves of *Viburnum lantana* and *Euonymus europaeus* from the M4 in September 1981 showed that not all dust was removed by washing. In the small sample examined, about 90% of the cells of both the upper and lower

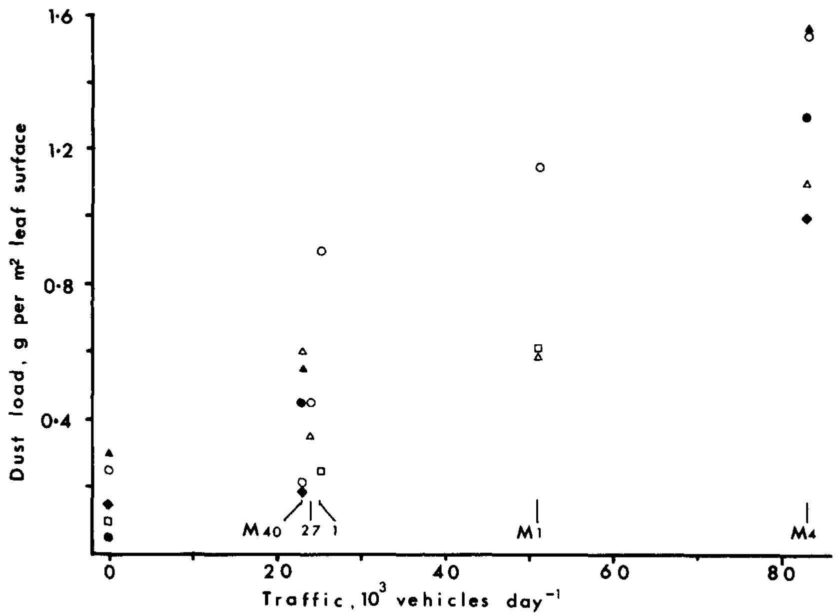

Fig. 1. The dust load of leaves from shrubs on the central reserves of various motorway sites and on sites remote from traffic, in relation to mean traffic density. ○ ●, *Crataegus monogyna*. △ ▲, *Viburnum lantana*. □, *Acer campestre*. ◆, *Euonymus europaeus*. Open symbols, 1980. Closed symbols, 1981.

epidermis retained some fine dust ($\bar{<}5\,\mu m$ diameter) adherent to, or incorporated in, the cuticle, and the mean cover of this material was estimated to be about 5 % in both species. Many stomatal pores contained one or more particles of this fine material.

Particle size distributions of exhaust dust and motorway dust

Examined under the microscope, exhaust dust was seen to consist entirely of black opaque particles. Dust from the relatively smooth leaves of *Euonymus europaeus* beside the M4 was also black and opaque except for a small proportion of brown or pale translucent mineral particles. The dust washed from leaves of *Viburnum lantana*, which are covered with stiff stellate hairs, contained about 20 % of mineral matter.

Table 6 shows the frequency distribution of particles in given diameter classes, for exhaust dust and dust washed from *E. europaeus* leaves, both suspended in water. The exhaust dust was not readily wettable, and if a little detergent was added to the water most of the particles exceeding 10 μm diameter proved to be aggregates and broke down to smaller primary particles. It could be seen that the *Euonymus* dust was also aggregated to some extent, but these aggregates tended to maintain their identity when treated with detergent.

Table 6 shows that the exhaust dust is finer than the motorway dust washed from *Euonymus* leaves. But, as has been mentioned, fine material is retained on the leaves during washing. Assuming this to consist of spherical particles of mean diameter 3 μm and specific gravity 2, then its

TABLE 6
The Frequency Distribution of Particle Sizes in Exhaust Dust, and Dust Washed from Leaves of *Euonymus europaeus* by a Motorway

Particle diameter range (μm)	*Frequency in* *Exhaust dust*	*Motorway dust*
<3·1	71	0
3·2 to 10·0	258	79
10·1 to 31·6	145	171
31·7 to 100·0	24	198
100·1 to 316	2	52
	500	500

observed cover of 5 % of surface area would represent a weight of about 0·2 g per m^2 surface area. This would add only 20 % to the dust load determined by washing but would add a very large number to the smallest particle size classes in Table 6, and would correspondingly reduce the proportional frequencies in the classes of large diameter.

Light interception by dusts

Figure 2 compares the transmission of light through given densities of exhaust dust with that of dust samples washed from leaves. The data points for exhaust dust over the range 2 to 30 g m^{-2} are based on five replicates and show that the transmission coefficient (T_d, as defined earlier) falls exponentially with dust load. Data points for motorway dust are single observations. Note that in this context the dust load of leaves is expressed per unit projected area rather than unit surface area. All but one of the seven observations on motorway dust have transmission coefficients 0·05 to 0·1 higher than for the corresponding weights of

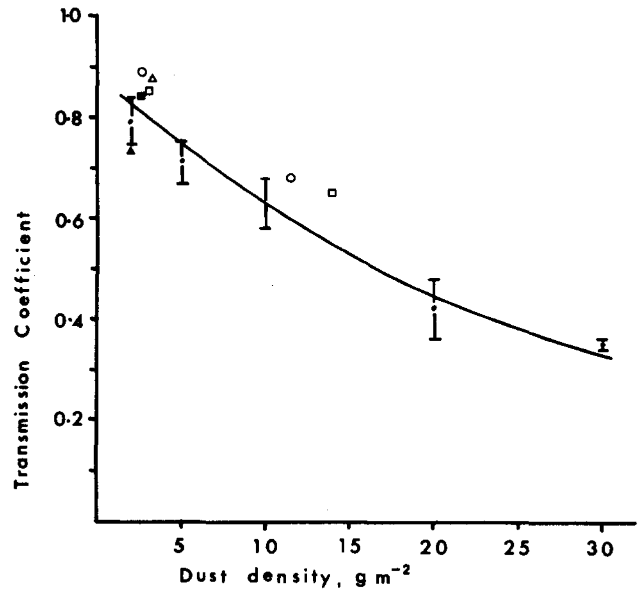

Fig. 2. The transmission coefficient for photosynthetically active radiation of dusts at varying density. Points with vertical bars: 'exhaust' dust on glass, means and standard deviations. The line fitted to these points is $y = 0{\cdot}89\,e^{-0{\cdot}033x}$. Dust from motorway leaves: ○, on glass; □ ■, on paper; △ ▲, on leaves; open symbols, *Viburnum lantana*; closed symbols, *Euonymus europaeus*.

exhaust dust, but this difference should be virtually eliminated when account is taken of fine dust remaining on the leaves after washing, and covering approximately 0·05 of each surface.

It was noticeable that, even after washing, leaves from motorway sites, especially the M4, were darker and less translucent than leaves of the same species from a control site. After correcting for small differences in leaf thickness, washed leaves of *Viburnum lantana* from the M4 transmitted only 0·66 of the light transmitted by washed control leaves; in *Euonymus europaeus* the corresponding fraction was 0·87. In *V. lantana* this opaqueness is too great to be accounted for by the fine material remaining after washing. It may possibly be explained by the observation that a high proportion of the mesophyll cells contained tannin whereas, in the control leaves, tannin was restricted to cells around the base of hairs.

DISCUSSION

The material deposited on plants by motorways has many origins and some components may have chemical and physiological, as well as physical, effects. Oil droplets will almost certainly penetrate leaves and have a range of physiological effects depending on their composition (Baker, 1970). The disintegration of aggregates of exhaust dust under the influence of detergent suggests that the material used in the experiments may have included some oil, but since photosynthesis and transpiration were measured within 24 h of application of the dust, it is likely that the effects observed were due mainly to immediate physical influences. The similarity of the effects produced by exhaust dust, lamp-black and charcoal dust in Experiment 1 supports this conclusion.

Among the possible physical effects of dust are shading, interference with gaseous diffusion, abrasion of leaf surfaces by dust transported in wind and spray, and modification of leaf temperature by black deposits. The experimental technique precluded abrasion except insofar as it could be caused by brushing on the dust. Increases in leaf temperature caused by dust deposits have been observed by Eller (1977) and Flückiger *et al.* (1978*b*) but none were found in these experiments even when the water filter beneath the light source was removed. It is likely that the high air-flow rate and mixing in the cuvettes kept leaf temperature very near air temperature. To summarise, roadside deposits may have a variety of chemical and physical effects on plants but these experiments are mainly relevant to effects on illumination and gaseous diffusion only.

Since the stomata of *Viburnum tinus* are virtually restricted to the lower leaf surface, deposition of dust on the upper surface should not interfere with diffusion into, or out of, the leaf but may affect photosynthesis by shading. A shading effect was indicated in Experiments 1 and 2 where reduction of photosynthesis was accompanied by a reduction of P_{max}/K, a measure of the efficiency of utilisation of incident light. A dust load on the upper surface of as little as $2\,g\,m^{-2}$ was used in Experiment 4 but high errors among leaves made this experiment inconclusive. The lowest dust load shown to reduce photosynthesis (by 23%) was $5\,g\,m^{-2}$ in Experiment 6. A dust load of $10\,g\,m^{-2}$ on the upper surface reduced photosynthesis by 18%, 30% and 24% in Experiments 1, 6 and 7, respectively.

A dust load of $10\,g\,m^{-2}$ on the lower leaf surface reduced photosynthesis by 17% in Experiment 1 and there was an accompanying increase of 42% in leaf diffusion resistance. Further experiments (3 and 5) on the effects of dust on the lower surface on photosynthesis were inconclusive because of high random errors, although dusting increased leaf diffusion resistance (in the light) by 50% in Experiment 5. In Experiment 8, with $<20\,g\,m^{-2}$ on the lower surface, an increase of 16% in diffusion resistance accompanied a decrease of 15% in photosynthesis. In none of these cases did dusting affect P_{max}/K. It is of interest that, although dusting increased leaf diffusion resistance by day, it appeared that at night stomatal closure was less complete in dusted plants than in controls. Ricks & Williams (1974) observed a similar effect and suggested that particles within stomatal pores prevented complete closure; small particles were observed in stomatal pores of motorway plants in the present investigation.

The experiments have then established that dust may affect photosynthesis both by shading and by obstructing diffusion, and that a dust with particle diameters mainly in the range 1 to 10 μm has appreciable effects at densities of 5 to 10 g per m^2 leaf surface area. There are difficulties in assessing the significance of these results for photosynthesis in roadside plants.

Fenelly (1975), quoting Mueller *et al.* (1964), stated that 80% of the particulate mass of vehicle exhaust emissions is contained in particles with aerodynamic diameters of less than 2·0 μm. Dolan *et al.* (1979) measured particle size distributions in diesel exhausts and found that 'measured number mean diameters' ranged from 0·01 to 0·1 μm. These observations suggest that the particulate matter of exhaust emissions is finer than that scraped from silencers and used in the present experiments. However, the deposition velocity to vegetation is an order of magnitude less for particles $< 1\ \mu m$ diameter than for particles of $5\ \mu m$ diameter or more (Chamberlain, 1967; Belot *et al.*, 1976). Consequently, the material deposited on roadside plants is likely to be proportionately richer in the larger particle diameters than the material emitted from exhausts. On the other hand, if particles of less than $0{\cdot}5\ \mu m$ diameter are a significant part of deposits on plants they will not be observed by light microscopy.

Insofar as the exhaust dust used in the experiments and the dust found on roadside shrubs absorbed a similar amount of light for similar densities (weight per unit area) it is likely that they had similar particle size distributions and that the exhaust dust satisfactorily simulated the effects of deposits on leaves by motorways. But the highest dust loads found on shrubs by the M4, with approximately 80 000 vehicles per day, were about $1{\cdot}5$ g per m^2 leaf surface area. The effect on photosynthesis of such low levels of deposit was not established in the experiments but, by extrapolation, it is likely to be small. This would lead to the conclusion that the physical effects of dust deposits on photosynthesis, mediated by reductions of illumination or CO_2-diffusion, play only a small part in the general effects of motor traffic on plants.

It may be that the deposits on leaves contain significant quantities of particles of less than $0{\cdot}5\ \mu m$ diameter, which would not have been discovered by the microscopic examination described. Such fine material could have considerable effects on light absorption in proportion to its contribution to the total dust load and it may therefore be important to explore further the concentration of such material in the air of motorways, the rate at which it is deposited on roadside plants, and the reasons why leaves from these plants are often dark-coloured and transmit light rather poorly, even when they have been washed.

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