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Surface dust impacts on gas exchange in Mojave Desert shrubs

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Summary

1. Windblown dust, an environmental problem in many disturbed arid lands, has the potential to affect the physiological performance of desert shrubs. Physiological parameters of gas exchange for three species (*Larrea tridentata*, *Hymenoclea salsola* and *Atriplex canescens*) were measured at a Mojave Desert site, at which both undisturbed and heavily dusted individual shrubs occurred.

2. Maximum rates of net photosynthesis (A) of dusted organs were reduced to 21% of those of control plants in resinous leaflets of *Larrea*, to 44% in resinous leaves and photosynthetic stems of *Hymenoclea*, and to 58% in non-resinous C_4 leaves of *Atriplex*, which have vesiculated trichomes. Dusted plants of all three species showed reduced maximum leaf conductance (g_s), transpiration (E) and instantaneous water-use efficiency (A/E). Intrinsic water-use efficiency (A/g_s) was also reduced, except in *Atriplex*, in which it remained unchanged.

3. Temperatures of dusted leaves and photosynthetic stems were 2–3 °C higher than those of control plants, due to greater absorptance of infra-red radiation. Dust also significantly increased photosynthetically active radiation (PAR) reflectance.

4. Heavily dusted shrubs had smaller leaf areas and greater leaf-specific masses, suggesting that the short-term effects of reduced photosynthesis and decreased water-use efficiency may cause lowered primary production in desert plants exposed to dust during seasons when photosynthesis is occurring.

Key-words: *Atriplex canescens*, dust pollution, *Hymenoclea salsola*, *Larrea tridentata*, photosynthesis, water relations.

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Introduction

Bare soils, which characterize most desert ecosystems, are a major source of small particulates that produce characteristic desert dust (Péwé 1981). Medium and large soil grains typically move relatively short distances by modified saltation or short-term suspension, whereas smaller particulates ($< 20\,\mu$m) may enter long-term suspension and be transported greater distances (Goudie 1978; Pye 1987). In dry regions subject to dust storms, such as the Thar Desert and American Great Plains, aerosol particle concentrations may exceed 100 μg m^{-3} (Orgill & Sehmel 1976; Goudie 1978). Natural patterns of dust movement often vary annually and seasonally, as in the Mojave Desert of California, where ambient levels of fine aerosol particulates display a sharp seasonal cycle, with high concentrations frequently reaching 80 μg m^{-3} during the dry summer months but with low concentrations of 10 μg m^{-3} during winter, when plant cover increases and surface soils are less dry (California Air Resources Board 1993). Human factors of disturbance and increased desertification, resulting from changes in land management practices, also have significant impacts on dust formation (Glantz 1977; Péwé 1981; Grainger 1990).

The deposition of fine particulate dust on plant surfaces has been reviewed in detail by Chamberlain (1975). Dust grains < 10 μm in diameter predominate on plant surfaces, and such deposition frequently results in dust clothing shrubs bordering dirt roads or downwind of a barren source area, such as a dry lake. For desert shrubs growing along unpaved roads, heavy dust on leaves often appears to reduce the vigour of impacted shrubs. Dust deposition in the Mojave Desert of Nevada has been shown to cause plant defoliation and shoot death in *Larrea tridentata* (Sesse & Moc. ex DC.) Cov. (Beatley 1965), but the ecophysiological impacts of dust on desert plant growth and development have not been quantified.

Investigation of these effects may have implications for land management practices in the Mojave Desert and other arid and semiarid zones, both in indicating how certain types of land use, such as urban development, road building and military training, may affect the natural environment and in determining how the negative impact of human activities in certain areas may be minimized. Furthermore, the examination of naturally occurring dust effects can be expected to contribute to our understanding of the adaptations that allow plants to survive in the desert environment.

This field study investigated the physiological effects of dust accumulation on the photosynthetic organs of three common Mojave Desert shrubs. Creosote bush *Larrea tridentata* (Zygophyllaceae) is a widespread and ecologically dominant C_3 evergreen shrub with resinous, bifoliate leaves (Barbour 1969; Mabry, Hunziker & DiFeo 1977); its leaves show a high degree of tolerance to the low water availability of its desert habitat (Oechel, Strain & Odening 1972; Odening, Strain & Oechel 1974; Syvertsen, Cunningham & Feather 1975; Syvertsen & Cunningham 1977; Mooney, Björkman & Collatz 1978; Meinzer *et al.* 1986, 1990b; Sharifi *et al.* 1988; Lajtha & Whitford 1989; Rundel & Sharifi 1993). Burrobrush or cheesebush *Hymenoclea salsola* Torrey & A. Gray ex A. Gray (Asteraceae), especially common along runnels and washes, is a C_3 shrub with resinous photosynthetic young stems and narrow, drought-deciduous leaves. Because these leaves are relatively short-lived, photosynthesis by stems contributes substantially to seasonal carbon balance (Comstock & Ehleringer 1988). Fourwing saltbush *Atriplex canescens* (Pursh) Nutt. (Chenopodiaceae) is a C_4 facultatively evergreen shrub with non-resinous leaves that have vesiculated trichomes for sequestering salts from chlorenchyma (Osmond *et al.* 1969; Osmond, Björkman & Anderson 1980). *Atriplex canescens* is a glycophyte, widely distributed in arid and semiarid western North America, and has received limited ecophysiological study (Ruess & Wali 1980; Freeman *et al.* 1993).

It was hypothesized that heavy dust accumulation on leaves would have a significant physiological impact, as a response to changes in both photosynthetically active radiation (PAR) reaching photosynthetic tissues and the overall energy budget of a leaf. This hypothesis was tested during summer drought for the three study species, with dusted and control plants growing along an unpaved road, when the sensitivity of leaf energy budget would be greatest.

Materials and methods

Field studies were conducted at the United States Army Fort Irwin National Training Center/Goldstone Tracking Station in the central Mojave Desert, 50 km north-west of Barstow, California (35°20′N, 116°50′W, elevation 980 m), on a gentle bajada 2 km due east of Goldstone Dry Lake. Vegetation at this site was *Larrea–Ambrosia* desert scrub, which characterizes most lowland habitats of the Mojave Desert (Beatley 1976; Vasek & Barbour 1977). At the site were widely spaced shrubs of *L. tridentata*, *Ambrosia dumosa* (A. Gray) Payne, *H. salsola* and *Atriplex canescens*, with scattered individuals of *Acamptopappus sphaerocephalus* (A. Gray) A. Gray, *Achnatherum hymenoides* (Roemer & Schultes) Barkworth, and *Ephedra nevadensis* S. Watson. Soil was alluvial in origin, sandy loam to fine loam and lacking surface gravel, and A and B soil horizons contained fine particulates eroded from the dry lake. This type of loessial, playa soil is common in the California deserts. The mean annual precipitation at the site was 170 mm. The lower bajada was crossed by a dirt tank trail used for transporting military vehicles during training manoeuvres. A persistent and strong up-slope wind during the period of spring training manoeuvres yielded an extremely heavy dusting on shrubs along the downwind (upper) side of the tank trail and little or no detectable dusting along the upwind (lower) side of the same trail.

Physiological parameters were monitored in July 1994, during a hot period (midday ambient temperature often exceeding 45 °C) of summer drought and when no precipitation had been recorded at the site since the shrubs had been dusted by vehicular traffic. The study was conducted during the summer period, because previous observations indicated that dust was only present on leaves during that season. In winter and spring 1993 and 1994 rainfall prevented dust dispersion. Mature shrubs of *Larrea*, *Hymenoclea* and *Atriplex* occurred on both sides of the tank trail, and for each species five to 10 individuals were selected from the dusted and control areas of the study site. Shrub density was the same for dusted and control plots, which were separated only by the unpaved road and showed no perceptible differences in topography and other site characteristics. The dusted and control sites were essentially homogeneous except with regard to dust exposure.

Net photosynthetic rate (A), stomatal conductance (g_s), transpiration (E), instantaneous (A/E) water-use efficiency (WUE), intrinsic WUE (A/g_s) and internal CO_2 concentration (c_i) were determined under ambient field conditions using a portable photosynthesis system (LI-6200, LI-COR Inc., Lincoln, Nebraska, USA). Small leafy twigs of each individual, having an average photosynthetic surface area of 8–10 cm^2, were sealed into a 250-ml leaf chamber for gas exchange measurements. All gas exchange measurements were made from 9.00 to 12.00 hours, when photosynthetic rates for all species were established to be maximum. After gas exchange measurements were completed, those samples were harvested and the surface area was obtained using a LI-3100 leaf area meter (LI-COR Inc.). Leaf temperatures inside the cuvette were not only measured directly with thermocouples but also calculated from a leaf energy balance (Rochette *et al.* 1990). Whereas the default configuration of the LI-6200 does not make this analysis, a program within the instrument was modified to do this calculation (LI-COR 1987). Measurements were also made to quantify nocturnal transpiration. Midday shoot water potentials were taken on all sampled individuals using a Scholander-type pressure chamber ($n = 10$–15). Reflectance of leaf surfaces from dusted and undusted (control) plants of *Larrea* was measured using a LI-1800 spectroradiometer (LI-COR Inc.) equipped with an integrating sphere to quantify reflectance at 350–1100 nm. Leaf absorptance could not be measured with this apparatus because leaves were too small.

Quantitative phenology, such as changes in shoot growth rates and number of lateral shoots, was followed in control and heavily dusted plants for *Larrea* only. Depending upon canopy size, five to 10 terminal shoots of similar length (8–11 cm), diameter and age were randomly selected in each individual in the four ordinal compass directions for phenological measurements. These shoots were tagged at the ninth or tenth internode from the leader shoot tip using loose-fitting plastic bird bands. Total lateral shoot length and number of lateral shoots were measured.

The amount and distribution of dust on photosynthetic organs were determined from samples adjacent to each shoot used for gas exchange but after physiological experiments were concluded, so that shoot water potentials were not affected for gas exchange measurements. For one set of samples, shoot dust was removed by repeated agitation and soaking in a beaker of distilled water for 24 h, precipitating dust for 7 days, filtering, oven-drying the precipitate, and then weighing dust on a Mettler balance. For these, leaf area was measured. Another set of samples was gently air-dried between papers in a plant press, to avoid exposure to dust-removing solvents, and viewed with an ETEC Autoscan Scanning Electron Microscope at 10 kV after sputter coating with 20 nm of gold-palladium. For *Larrea*, 12 adaxial and abaxial surfaces of companion leaflets were compared from dusted and control plants, and for *Hymenoclea* downwind and upwind stem and leaf surfaces were compared. The presence of ruptured bladder cells on leaves of *Atriplex* produced charging and thus interfered with photographic documentation of surface dust. Percentage cover was crudely estimated from electron photomicrographs (600 ×, 1500 × and 10 000 ×) by recording the presence of dust particles within randomly sampled quadrats of millimetre-rule graph paper.

Data were analysed statistically by Student's *t*-test. Unless indicated otherwise, data are presented as mean ± standard error (numbers in parentheses are standard errors of the relevant means; not significant indicates $P > 0{\cdot}05$).

Results

On both sides of the tank trail, leaflets of *Larrea* were orientated with abaxial surface facing the prevailing up-slope wind (Fig. 1a, b). Abaxial and adaxial leaflet surfaces of control plants were bright green and resinous; unicellular trichomes were embedded in resin, numerous unobstructed stomata were evident, and dust particles were virtually absent on adaxial surfaces (away from the wind) (Fig. 2a), either attached to the resin or embedded within it, although abaxial surfaces occasionally had 20% of a field of view with light dust. In sharp contrast, heavily dusted leaves were dull grey on the abaxial surfaces, corresponding to a complete, loose coating of dust on the leaf, hiding trichomes (Fig. 2b), although some green showed on the adaxial surfaces. Many unobstructed stomata could still be observed through the dust cover, and dust particles were also embedded in resin (Fig. 2c); some were irregular in shape, and most were 1–4 μm in diameter (Fig. 2d). Given that materials were dried in a press, there was no reliable way to determine percentage *in vivo* dust plugging of stomata, but dedusted leaves, in which water removed surface particles, had similar stomatal densities to dusted specimens. Washing of heavily dusted leaves produced 16 g dust m^{-2} leaf, or half that amount on each surface, excluding the amount embedded in resin.

On control plants of *Hymenoclea*, resinous green leaves and stems had few or no dust particles on any surface, although some were found on downwind surfaces where they were lodged along cell margins. On heavily dusted specimens, downwind surfaces were distinctly grey due to accumulated dust, especially along cell margins (Fig. 3a), which also adhered to the resin; upwind surfaces were less affected (Fig. 3b). Control plants had very little dust on leaves, whereas on dusted leaves particles covered > 50% of the leaf perimeter but were relatively sparse along the trichome-hidden midvein of the adaxial leaf surface. When viewed with SEM, many stomata of *Hymenoclea* were hidden, occluded by resin, but this was considered to be an artefact because copious resin is excreted from glandular trichomes during drying of these stems and leaves.

In *Atriplex*, a plant that normally has greyish leaves due to the presence of vesiculated trichomes, dusted plants were more grey and released surface dust when shaken. Dust particles were attached to the exposed surface of each bladder cell and occurred among the interior layers of trichomes. Leaf washing of heavily dusted shoots produced 40 g dust m^{-2} leaf area.

Dusted individuals of all three species had consistently smaller mean leaf area but greater leaf specific mass (Table 1).

Whereas midday plant water potentials in control plants of *Larrea* were 0·9 MPa and *Hymenoclea* were 0·7 MPa higher than dusted plants ($P < 0{\cdot}05$), in *Atriplex* water potential in control plants was 0·8 MPa lower than in dusted individuals ($P < 0{\cdot}05$) (Fig. 4).

Fig. 1. (a) *Larrea tridentata* plants growing on opposite sides of a dusty tank trail. Control plant (no dust), growing down-slope and upwind of dust. (b) Heavily dusted plant, growing downwind, immediately adjacent to dust source.

Maximum rates of net photosynthesis were found to be sharply reduced in dusted shoots of all three species. This reduction was smallest in *Atriplex*, with dusted plants having photosynthetic rates equivalent to 58% of those of control plants ($P < 0{\cdot}05$), while this figure was 44% ($P < 0{\cdot}01$) in *Hymenoclea*, and 21% ($P < 0{\cdot}01$) in *Larrea* (Fig. 5a). Maximum leaf conductance was similarly lowered sharply, but proportionally less than photosynthesis (Fig. 5b).

The net effect of changes in gas exchange parameters on water relations was a reduction in transpiration ranging from 79% of that of control plants in *Hymenoclea* to 47% in *Larrea* ($P < 0{\cdot}05$) (Fig. 6a). Intrinsic WUE was lowered significantly ($P < 0{\cdot}05$) in *Larrea* and *Hymenoclea* but remained unchanged in *Atriplex* (Fig. 6b). All species showed a significant ($P < 0{\cdot}05$) decline in WUE measured as the ratio of A/E (Fig. 6c). The ratio of internal to ambient CO_2 in C_4 leaf tissues of *Atriplex* remained unchanged at about 0·27 (Fig. 6d), reflecting the algebraic relation-

Table 1. Morphological and physiological parameters of control (no dust) and heavily dusted samples from the three species in the study: leaf area per leaf (*LA*), specific leaf mass (*SLM*), maximum rate of CO_2 assimilation (A_{max}) and maximum stomatal water vapour conductance (g_{max}). Values are means obtained from five to 10 shrubs of each species and treatment group. N = 100 leaves per species and treatment group for *LA* and *SLM*; n = 20–40 measurements per species and treatment group for A_{max} and g_{max}. Numbers in parentheses are standard errors of the relevant means. Data were obtained in July 1994

Species	Treatment	*LA* (mm²)	*SLM* (mg cm⁻²)	A_{max} (μmol m^{-2} s^{-1})	g_{max} (mol m^{-2} s^{-1})
Larrea tridentata leaves	Control	21 (7)	19·50 (0·89)	13·2	0·20
	Dusted	17* (6)	24·62 (1·61)	2·3**	0·04**
Hymenoclea salsola stems + leaves	Control	7 (3)	70·02 (28·01)	10·5	0·17
	Dusted	3* (1)	127·90 (50·0)	5·8**	0·10*
Atriplex cancescens leaves	Control	—	28·58 (5·29)	19·9	0·14
	Dusted	—	38·84 (5·84)	12·9*	0·05*

*P < 0·05; **P < 0·01, for difference between treatments.

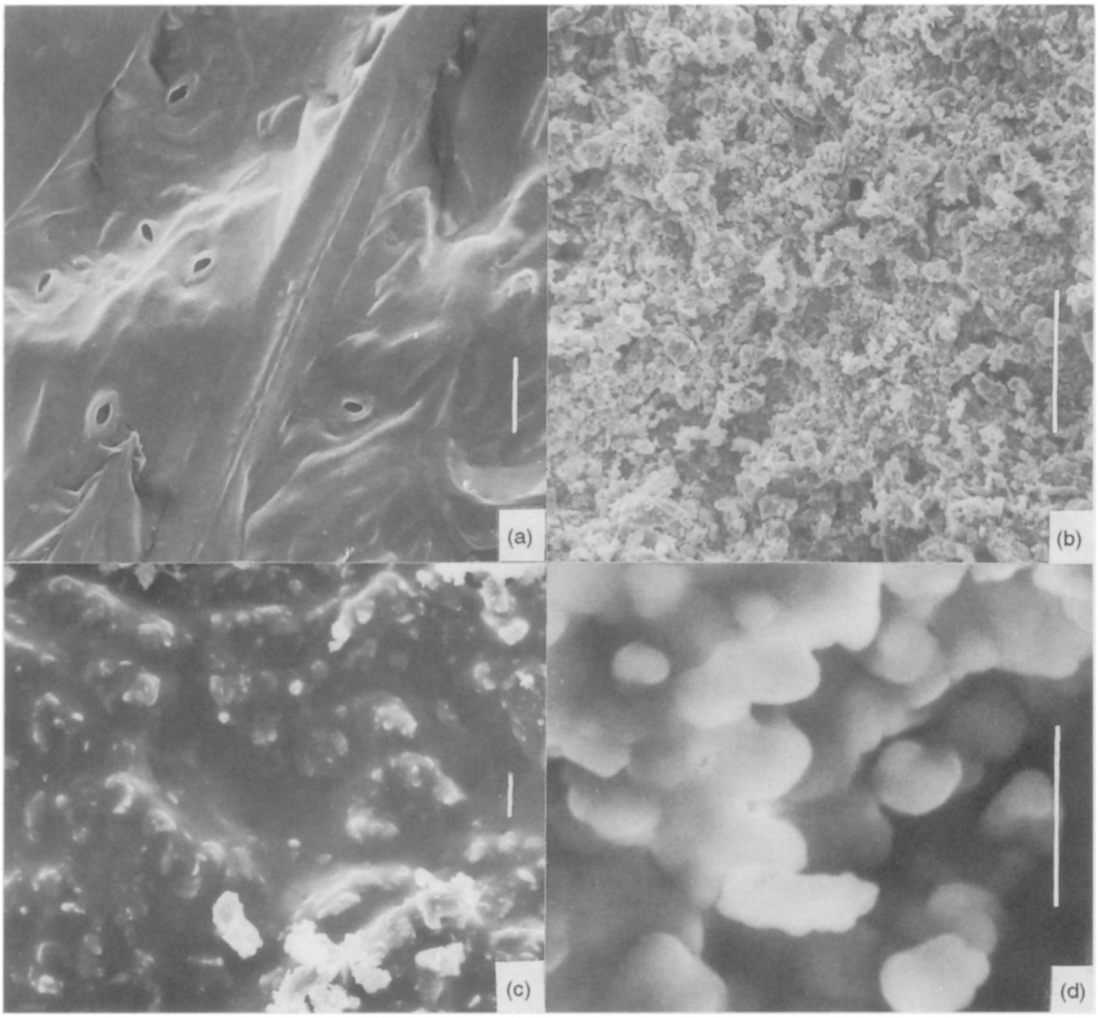

Fig. 2. Scanning electron photomicrographs of leaves of *Larrea tridentata*. (a) Adaxial surface of control leaf, showing prominent stomata and trichomes embedded in resin coating but essentially free of particulates. (b) Abaxial surface of heavily dusted leaf; all epidermal features are hidden, but gaps in dusted surface show locations of some stomata. (c) Adaxial surface of dusted leaf in patch where surface dust is mostly absent but particulates have been embedded in resin. (d) Abaxial surface with some tightly adhered clay particulates. Magnification bars for Fig. 2a–b = 25 μm; 2c, d = 3 μm.

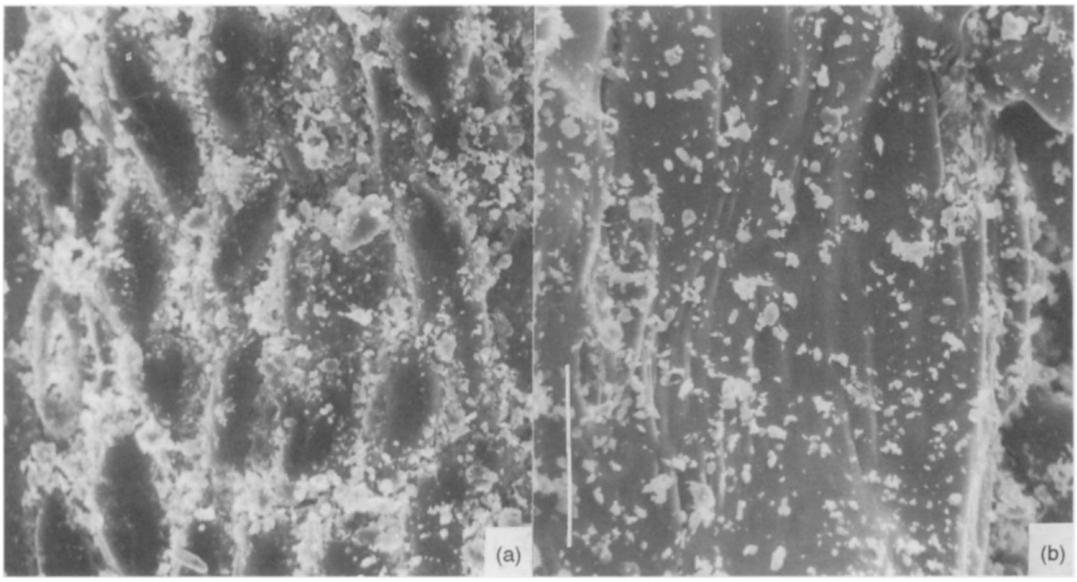

Fig. 3. Scanning electron photomicrographs of stems of dusted *Hymenoclea salsola* plants. (a) Dusted downwind surface on which particulates are mostly lodged in depressions along cell margins. (b) More lightly dusted upwind surface, having particulates widely dispersed. Magnification bar = 25 μm.

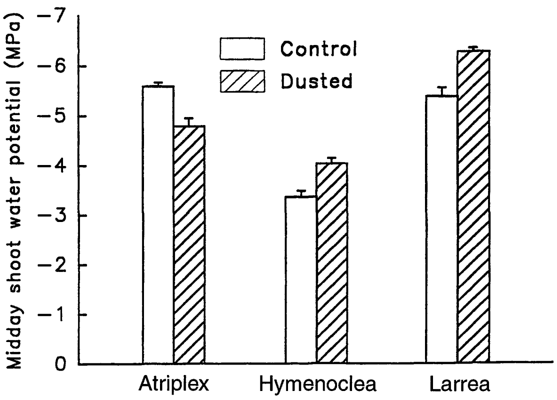

Fig. 4. Midday shoot water potential (MPa) of control (no dust) and heavily dusted shrubs of *Larrea tridentata*, *Hymenoclea salsola* and *Atriplex canescens*. Bar indicates standard error. Data were collected in July 1994.

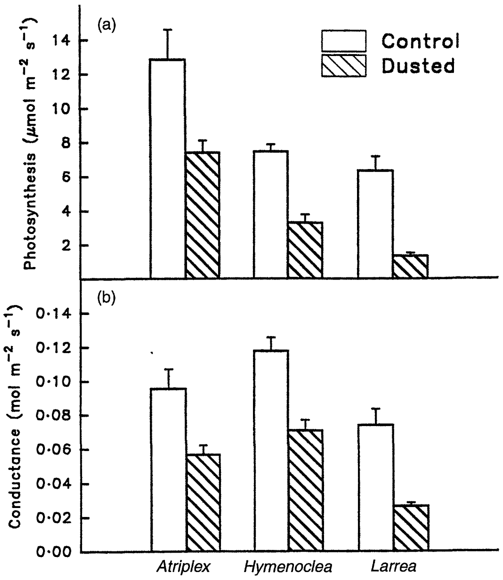

Fig. 5. (a) Mid-morning average rates of photosynthesis for control (no dust) and heavily dusted samples of *Larrea tridentata*, *Hymenoclea salsola* and *Atriplex canescens*. (b) Mid-morning average values of stomatal conductance for water vapour. Bar indicates standard error. Data were collected in July 1994.

ship of this calculation with values of intrinsic WUE. The c_i/c_a ratio of dusted shrubs increased in *Larrea* and *Hymenoclea* to levels of about 0·65, and the most significant ($P < 0{\cdot}05$) change occurred in *Larrea*.

Night-time stomatal conductance and transpiration were low in both control and dusted plants of *Larrea* (Table 2). This contrasted with significant differences in daytime stomatal conductance and transpiration (Figs 5b and 6a) between these sets of plants.

Temperatures of dusted photosynthetic organs were 2–3 °C higher than those of control individuals (Fig. 7). This increase in temperature was largely due to altered spectral properties of dusted leaves, which decreased reflectance of infra-red radiation. In *Larrea*, reflectance in near infra-red was decreased by approximately 20% while reflectance of PAR irradiance was increased by about 40% (Fig. 8).

While phenological measurements showed no growth or even a slight decrease in total shoot length in dusted individuals, in control plants there was a steady increase in total shoot length and the total number of lateral shoots (Fig. 9).

Discussion

Physiological influences of dust accumulation on photosynthetic surfaces of these desert shrubs parallel results obtained in previous research of dust impacts on European roadside plants (Eller 1977; Thompson *et al.* 1984). Lowered g_s of dusted surfaces produced changes in leaf energy balance and promoted higher leaf temperatures. In leaves of *Viburnum tinus* L., a dust load of 10 g m^{-2} leaf reduced PAR absorptance by 20% and caused a 17% decrease in photosynthesis (Thompson *et al.* 1984). Increased weight of dust per unit leaf surface was also found to be inversely related to absorptance of PAR, thereby suggesting that increased density of dust would further reduce the rate of photosynthesis under summer conditions of high ambient air temperatures. It could be argued that an increase in the density of dust would be beneficial to a desert plant, if the leaf operates above light saturation, but this would not apply in this study, where the species studied have extremely high light saturation values (Comstock & Ehleringer 1988; M. R. Sharifi, unpublished data).

Our results indicate that dusted plants had lower *WUE*, measured as instantaneous *WUE* (A/E) or intrinsic *WUE* (A/g_s). A/E, A/g_s and c_i/c_a are all components of plant *WUE* that refer to the same physiological set point determined by the interaction of photosynthetic capacity and the stomatal control of gas exchange. Meinzer, Goldstein & Grantz (1990a) suggested that A/g_s should provide more consistent estimates of water use-efficiency than A/E, because the difference between the evaporative demand in the leaf chamber and that which prevailed before sealing the leaf inside is immediately reflected in E, but not in g_s. Several mechanisms may contribute to the decrease of *WUE* in dusted individuals. Flückiger, Oertli & Flückiger (1979) found that complete closure of stomata can be prevented by dust particles. Rawson & Clarke (1988) reported that stomata of dusted wheat leaves took several hours to reach their most closed position, and the current vapour pressure deficit (*VPD*) had a major effect on the amount and pattern of night transpiration. More field and laboratory studies will be required to elucidate how dust affects physiological performance in the desert environment.

Because green leaves are almost totally reflective of near infra-red radiation (Nobel 1991), it was not surprising to observe that accumulated leaf dust increased absorptance of near infra-red solar irradiance and therefore caused higher leaf tempera-

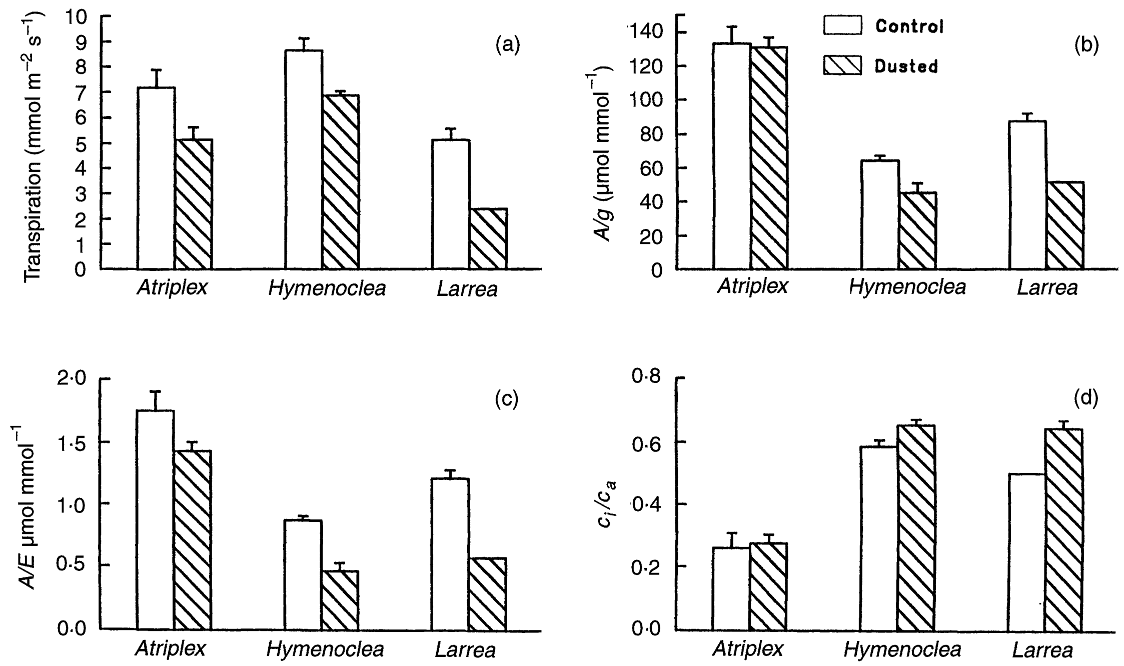

Fig. 6. Effects of dust on gas exchange parameters of control (no dust) vs. heavily dusted shoots of *Larrea tridentata*, *Hymenoclea salsola* and *Atriplex canescens*: (a) transpiration; (b) intrinsic *WUE* (A/g_s); (c) instantaneous *WUE* (A/E); (d) ratio of internal CO_2 concentration to ambient CO_2 concentration (c_i/c_a). Bar indicates standard error. Data were collected in July 1994.

Table 2. Night-time (15 September) and daytime (16 September) rates of stomatal water vapour conductance and transpiration for *Larrea tridentata* at the study site at Goldstone Tracking Station during 1994. Numbers in parentheses are standard errors of the relevant means

	Daytime		Night-time		Day/night ratio	
	g_s mol m^{-2} s^{-1}	E mmol m^{-2} s^{-1}	g_s mol m^{-2} s^{-1}	E mmol m^{-2} s^{-1}	g_s	E
Control	0·076 (0·009)	2·49 (0·28)	0·018 (0·002)	0·40 (0·05)	4·31	6·15
Dusted	0·039 (0·008)	2·08 (0·33)	0·0016 (0·002)	0·33 (0·03)	2·35	6·38

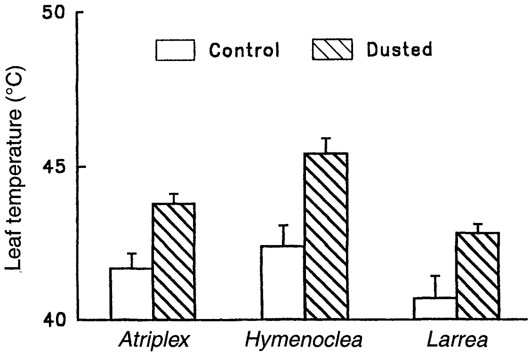

Fig. 7. Measured leaf temperature of control (no dust) and heavily dusted samples of *Larrea tridentata*, *Hymenoclea salsola* and *Atriplex canescens*. Bar indicates standard error. Air temperature was 42·5 °C at the time of data collection in July 1994.

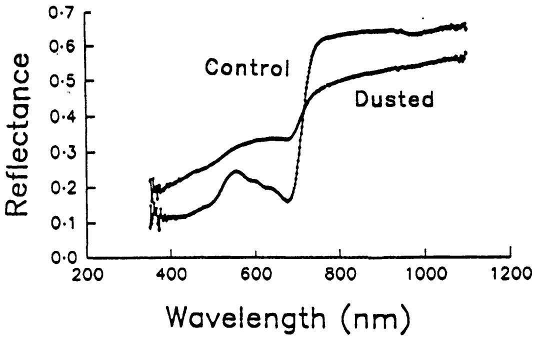

Fig. 8. Measured reflectance of solar irradiance (wavelengths 350–1100 nm) for control (no dust) and heavily dusted leaves of *Larrea tridentata*. Data were collected in July 1994.

tures. Experimental studies in Switzerland showed a doubling of absorptance in the near infra-red (700–1350 nm) for dusty leaves compared with control leaves, sufficient to cause a 2–4 °C increase in leaf temperature (Eller & Brünner 1975; Eller 1977). This matches the 2 °C increase observed in *Larrea* and *Atri-*

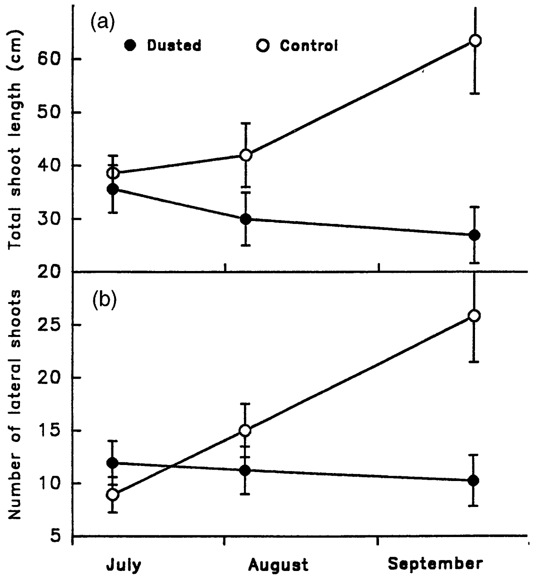

Fig. 9. Phenological data for individuals of *Larrea tridentata* sampled on 7 July, 3 August and 16 September 1994 at the study site at Goldstone Tracking Station. Bar indicates standard error.

plex and 3 °C increase in photosynthetic stems of *Hymenoclea*. At high ambient summer temperatures of 40–45 °C in the central Mojave Desert, these relatively small absolute changes in leaf temperature may significantly reduce rates of net photosynthesis. *Larrea* has a summer optimum temperature for photosynthesis near 40 °C (Mooney *et al.* 1978). Any decrease in PAR would be expected to yield a lowered rate of net photosynthesis of dusted organs. In addition, leaf temperatures approaching or exceeding 45 °C have the potential to cause significant heat stress and permanent tissue damage.

Another potential physical effect of dust on photosynthetic surfaces could be a change in boundary layer conditions due to increased surface roughness. A thick coating of dust particles on a leaf surface theoretically would produce a small decrease in boundary layer conductance across the leaf/air transition that would lower transpiration rate, thus leading to lower evaporative cooling and consequently increased leaf temperatures and reduced growth (Darley 1966; Eveling 1969; Borka 1980). At the same time, irregular accumulation of dust would produce changes in turbulence for air flow over the plant organ. Probably more important, heavy dust on a leaf could also cover a significant percentage of the stomatal pores, thereby lowering leaf conductance and causing elevated leaf temperatures. The methods employed in the current study were not capable of determining to what extent stomata were blocked by dust.

Where dust particles are very fine, individual grains have been reported to occlude stomata, presumably lowering leaf conductance during daylight and increasing water loss at night or under conditions of water stress (Ricks & Williams 1974; Eller & Brünner 1975). While our results for nocturnal conductance do not support this mechanism in *Larrea*, there are numerous studies (Ricks & Williams 1974; Eller & Brünner 1975; Eveling & Bataille 1984) that have reported that fine dust particles occlude stomata, presumably by lowering leaf conductance to water vapour during the daytime and increasing water loss at night. Incomplete closure of stomata would cause a decrease in *WUE*, make impacted plants more susceptible to drought, and expose interiors of organs to increased oxidant air pollutants, which in turn may have direct and indirect effects on plant performance. The potential for small particulates to wedge open stomatal pores certainly exists for desert plants, but direct observations did not confirm that this occurred, because closure was virtually complete at night, and thus particulates wedged into stomatal pores are unlikely to have any significant effect on plant water loss.

The minimum midday plant water potentials reported here are comparable to values previously reported. Midday summer plant water potentials of −6·5 MPa were found for *Larrea* growing in the Sonoran Desert (Nilsen, Sharifi & Rundel 1984), while values of −5·8 MPa (Bamberg *et al.* 1975) and −6·1 MPa (M. R. Sharifi, A. C. Gibson & P. W. Rundel, unpublished data) have been reported for *Larrea* in the Mojave Desert. While higher water potentials were noted in control plants than in dusted plants of *Larrea* and *Hymenoclea*, the opposite effect was noted in the C_4 plant *Atriplex*. Pre-dawn water potential, an indicator of the equilibrium between soil water potential and plants, was not measured at our site. However, in a companion study of *Larrea* alone at the same site and during the same month and year, no significant differences were found between dusted and control individuals with regard to pre-dawn water potentials (−4·7 and −5·0 MPa, for dusted and control plants, respectively) (M. R. Sharifi, A. C. Gibson & P. W. Rundel, unpublished data).

The phenological development of *Larrea* control plants showed a steady increase in the total shoot length and the total number of lateral shoots. However, dusted individuals showed no growth or even a slight decrease (due to branch senescence) in total shoot length. In most C_3 shrubs in the Mojave Desert, peak growth activity continues until mid-summer, while even C_4 plants such as *Atriplex* reach peak biomass production at midsummer (Ackerman, Romney & Kinnear 1980). However, peak growth and phenological activity may shift by weeks, or even months, towards spring or summer, depending on temperature and precipitation (Ackerman *et al.* 1980). *Hymenoclea* showed a similar phenological pattern to *Larrea*. *Atriplex*, on the other hand, had higher growth rates than the two C_3 plants towards the end of July.

The physiological impacts of dust on Mojave Desert shrubs suggest that significant short-term effects of reduced photosynthesis and decreased *WUE* may well have long-term effects on net primary production and shrub vigour, as quantified here in smaller leaf areas and greater leaf specific weight, when exposed to fine particulates along unpaved roads. Whereas these results are based on studies at a single site, and must therefore be extrapolated with some caution, we believe that our conclusions may apply broadly to the expected impacts of dust on plant productivity in many systems. Future studies investigating dust effects at multiple sites should provide further support for these findings.

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