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ROAD DUST CORRELATED WITH DECREASED REPRODUCTION OF THE ENDANGERED UTAH SHRUB *HESPERIDANTHUS SUFFRUTESCENS*

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Abstract.—Roads associated with energy development have fragmented much of the Uinta Basin, the Colorado Plateau in general, and other areas of western North America. Beyond reducing available habitat, spreading exotic species, and creating barriers to dispersal, unpaved roads also increase dust loads on plants and pollinators, which may reduce plant growth and reproduction. We studied the effects of an unpaved road on reproduction of an endangered Utah endemic shrub. We measured the size and reproductive output of 156 plants and the dust deposition in plots at increasing distances from the road. We also hand outcrossed 240 flowers from 80 plants to help determine if any reduced reproduction was due to pre- or postpollination mechanisms. Additionally, we experimentally dusted 3 leaves on 30 plants ($n = 90$) and measured stomatal conductance pre-dust and post-dust. We also dusted 3 flowers on 10 plants ($n = 30$) prior to hand pollination and measured fruit set. Generalized linear mixed models were used to examine the relationship between reproduction and dust deposition. When controlling for plant size and distance from the road, fruit set was negatively correlated with increasing levels of dust deposition ($F_{1,15} = 5.26$, $P = 0.036$). The number of seeds per plant, mean plant seed weight, and the proportion of hand-pollinated flowers that set fruit were also negatively correlated with dust, although not significantly. Dusting significantly reduced stomatal conductance ($F_{1,58} = 87.56$, $P < 0.001$). Eighty percent of hand pollinated flowers (24 of 30) set fruit after dusting. These results demonstrate that road dust reduces *H. suffrutescens* reproduction, although the mechanisms are not clear. Although dust negatively affected physiological processes, hand-pollination results suggest that dust might be disrupting pollination. This study documents the effects of road dust on the reproduction of an endangered shrub in Utah's Uinta Basin and highlights the need for further research into the effects of roads and dust on nearby plants.

Resumen.—Los caminos asociados al desarrollo energético dividieron gran parte de la Cuenca Uinta, de la meseta de Colorado en general, y de otras áreas del oeste de América del Norte. Además de reducir el hábitat disponible, de esparcir especies exóticas y de crear barreras a la dispersión, los caminos no pavimentados también aumentan la cantidad de polvo en las plantas y en los polinizadores, pudiendo reducir su crecimiento y su reproducción. Estudiamos los efectos que puede generar un camino sin pavimentar en la reproducción de un arbusto endémico de Utah, en peligro de extinción. Para ello, medimos el tamaño y el esfuerzo reproductivo de 156 plantas y la deposición de polvo en parcelas a distancias cada vez mayores con respecto al camino. También cruzamos 240 flores de 80 plantas para ayudar a determinar si alguna reducción en la reproducción se debe a mecanismos de pre o de post-polinización. Además, limpiamos, a modo de experimento, 3 flores de 30 plantas ($n = 90$) y medimos la conductancia estomatal previa y posterior a tal limpieza. También limpiamos 3 flores de 10 plantas ($n = 30$), previo a la polinización manual, y medimos la producción de los frutos. Se utilizaron modelos lineales mixtos generalizados para examinar la relación entre la reproducción y la deposición de polvo. Al controlar el tamaño de las plantas y su distancia del camino, la producción de los frutos se correlacionó negativamente con los crecientes niveles de polvo ($F_{1,15} = 5.26$, $P = 0.036$). El número de semillas por planta, el peso promedio de las semillas de la planta, y la proporción de flores polinizadas a mano que producen el fruto también se correlacionaron negativamente con el polvo, aunque no de modo significativo. La limpieza del polvo redujo, significativamente, la conductancia estomatal ($F_{1,58} = 87.56$, $P < 0.001$). En el ochenta por ciento (24/30) de las flores polinizadas a mano se dieron sus frutos luego de ser limpiadas. Estos resultados demuestran que el polvo en los caminos reduce la reproducción de *H. suffrutescens*, aunque los mecanismos no estén claros. A pesar de que el polvo afectó negativamente los procesos fisiológicos, los resultados de la polinización manual sugieren que el polvo podría estar interrumpiendo la polinización. Este estudio documenta los impactos que genera el polvo del camino en la reproducción de un arbusto en peligro de extinción en la Cuenca Uinta de Utah y destaca la necesidad de continuar investigando sobre los efectos que, tanto los caminos como el polvo, generan en las plantas del área.

Natural gas and oil development in arid regions has led to increased fragmentation by roads with negative effects for native plants. The direct negative effects of roads on plants include reduction of potential habitat area, spread of exotic species, creation of barriers to dispersal (Trombulak and Frissell 2000, Jones et al. 2014), and disruption of pollinator

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populations or behaviors via habitat fragmentation (Steffan-Dewenter and Tscharntke 1999, Andrieu et al. 2009).

Habitat fragmentation caused by roads can also alter complex plant-pollinator interactions, reducing successful pollination and decreasing reproduction while increasing pollen limitation (Aizen and Feinsinger 1994, Suárez-Esteban et al. 2014). In addition, roads also introduce disturbances related to fugitive dust that have not been addressed in pollination biology and that affect plant populations, pollinator populations, and the pollination process in general. Fugitive dust may reduce plant reproduction through deposition of dust loads on plants, affecting pollination indirectly by increasing physiological stress or directly by interfering with successful pollination and fertilization. Similar to the direct effects of habitat fragmentation, dust on plants may also interfere with complex pollinator-flower interactions, potentially reducing reproductive effort.

The effects of particulate matter (mainly limestone dust from cement plants and vehicle exhaust emissions) on plant photosynthesis and water-use efficiency are fairly well known (Farmer 1993, Grantz et al. 2003). Dust loads on leaves can lower stomatal conductance and transpiration rates, increase leaf temperature, and reduce photosynthetically active radiation (PAR), all by shading leaf surfaces, resulting in reduced photosynthetic rates (Sharifi et al. 1997, Grantz et al. 2003, González et al. 2014). Dust also can obstruct stomata and prevent closure, thereby increasing water loss and reducing photosynthetic rates (Hirano et al. 1995). These physiological effects can reduce plant growth and survival and reduce resources available for reproduction. Dust also can cause physical damage to plant tissues through sandblasting in high winds (Eveling 1986, Grantz et al. 2003). Similarly, Eveling (1986) found that the deposition of dust on flower petals and leaves results in the breakdown of epidermal cells. In addition, Harper (1979) suggested that dust from unpaved roads might cover flower stigmas, potentially inhibiting successful pollination. Increased dust deposition may, therefore, significantly reduce successful reproduction of plants directly by physically preventing pollination or indirectly by reducing resources allocated to reproduction through altered physiological processes.

Effects of dust from unpaved roads on reproduction are poorly understood. In his review of the effects of dust on vegetation, Farmer (1993) concluded that many of the dust-effect studies focused on limestone dust from cement factories and its effects on nearby agricultural fields (e.g., Thompson et al. 1984, Sharifi et al. 1997, Myers-Smith et al. 2006) and suggested that future studies focus on additional types of dust (e.g., road dust) and their effects on plants in natural systems.

Documenting and increasing our understanding of the effects of dust from unpaved roads on plant pollination and ultimately successful reproduction are especially important in arid regions of the western United States where unpaved roads created for mineral extraction (i.e., oil and natural gas) and recreation are proliferating, thereby increasing habitat fragmentation and dust deposition on nearby plants and where numerous potentially vulnerable rare species are found. One such species is the federally endangered shrub *Hesperidanthus suffrutescens* (Rollins) Al-Shehbaz (shrubby reed-mustard; Brassicaceae), which is endemic to Utah's Uinta Basin, an area experiencing rapid energy development. *Hesperidanthus suffrutescens* and its habitat are underlain by oil and natural gas deposits and are threatened by mineral extraction, exploration, and development (USFWS 1994, 2010). All federal lands with known populations of *H. suffrutescens* are managed by the Bureau of Land Management (BLM) and currently have or are leased for oil and gas development (USFWS 2010). As such, many *H. suffrutescens* populations are in close proximity to heavily used roads and oil pads, and road dust was cited as a component of threats to *Hesperidanthus suffrutescens* from oil and gas development (USFWS 2010). This inclusion of dust as a threat was based on generalizations that for every vehicle traveling 1 mile of unpaved roadway once a day, every day for a year, approximately 2.5 tons of dust are deposited along the road corridor (Sanders personal communication 2008 *in* USFWS 2010). This study was designed to determine the effects of fugitive dust from an unpaved road on the reproduction of *H. suffrutescens* and to begin to tease apart mechanisms driving any detected effects.

In this study we address the following questions: (1) Is there evidence that dust deposition in our study population largely comes from the nearby dirt road? Specifically, does the quantity of dust deposition decrease with distance from the road? (2) Does increasing dust deposition result in decreasing reproductive success expressed as total fruit production, seed set per fruit, or total seed weight? (3) If dust decreases reproductive success, is there evidence that the decrease is due to altered physiology or to disrupted pollination processes?

Examining these questions will help determine whether dust from unpaved roads affects the reproduction of *H. suffrutescens* and, if so, we can begin to tease apart the mechanisms for decreased reproduction.

METHODS

Study Species

Hesperidanthus suffrutescens has several generic synonyms (*Glaucocarpum*, *Shoenocrambe,* and *Thelypodium*) but has been placed in *Hesperidanthus* based on genetic analyses of sister taxa (Al-Shehbaz 2005). A long-lived monoecious perennial shrub with multiple stems from a woody taproot, *H. suffrutescens* has thick, glaucous leaves and numerous yellow flowers on multiple stems (Holmgren et al. 2005). Flowers mature acropetally beginning in mid-April, and the siliques mature and dehisce approximately 4 weeks after corolla loss (Tepedino 2009). It is an obligate outcrossing species that appears to depend on solitary bees for successful pollination (Lewis and Schupp 2014). As such, the plant species is potentially susceptible to indirect impacts (e.g., impacts on pollinator abundance, habitat, and foraging behavior), in addition to direct impacts on the plants themselves.

The species was listed as endangered on 6 October 1987 due in part to declines in population size and abundance that have been observed since the species was described in 1935 (USFWS 2010). The most recent population estimates suggest a total of approximately 2900 individuals from 7 populations (USFWS 1994, 2010). The majority of this study was conducted in the largest of these populations, Big Pack Mountain, Utah. This population is heavily impacted by oil and gas development. The dust and stomatal conductance study was conducted on plants in the Big Pack Mountain, Johnson Draw, and Bad Land Cliffs, Utah, populations. Finally, the dust and outcrossing study was conducted in the Bad Land Cliffs population.

Study Area

The Uinta Basin, located in eastern Utah on the Colorado Plateau (Fig. 1), receives approximately 17.4 cm of annual precipitation and has a mean annual temperature of 8.8 °C (Utah Climate Center 2006–2010). This unique landscape has seen several boom-bust cycles in oil and gas development. The Uinta Basin is also home to many of Utah's endemic and rare plant species (UNPS 2011). *Hesperidanthus suffrutescens* is part of a cold desert shrub community typically dominated by the shrubs *Artemisia nova* (black sagebrush), *Atriplex confertifolia* (shadscale), *Tetradymia spinosa* (spiny horsebrush), and *Ephedra torreyana* (Torrey jointfir); the trees *Cercocarpus montanus* (mountain mahogany), *Pinus edulis* (pinyon), and *Juniperus osteosperma* (Utah juniper); the grasses *Leymus salinus* (Salina wildrye), *Hilaria jamesii* (James' galleta), and *Pseudoroegneria spicata* (bluebunch wheatgrass), along with many native forb species (USFWS 1994). *Hesperidanthus suffrutescens* is found on semibarren rocky outcrops of the Green River Formation (USFWS 1994). Soils in *H. suffrutescens* habitat are shallow (10–20 cm) with fragments of white shale on the surface (Baker et al. 2016). There are small sections of the road in our study area that travel through soils with geology similar to the soils where these plants are found (Green River shale), but much of the road travels in an existing wash where soils are likely deeper and of different parent material (alluvial deposits), and are therefore different in texture, structure, and chemical composition.

Effects of Road Dust on Reproduction

To assess the effects of road dust on reproduction, 16 plots, with 4 in each of 4 distance categories (101–200 m, 201–300 m, 301–400 m, and 401–700 m from the road), were centered on clusters of *H. suffrutescens* and selected indiscriminately. A 0–100 m distance category was planned for the study but was not included because there were no study plants that close to the road. In each plot, up to 10 plants were chosen; if 10 or fewer plants were present, all were used; and if more than 10 were present, the group of 10 plants closest to the plot center was selected. Two of the plots

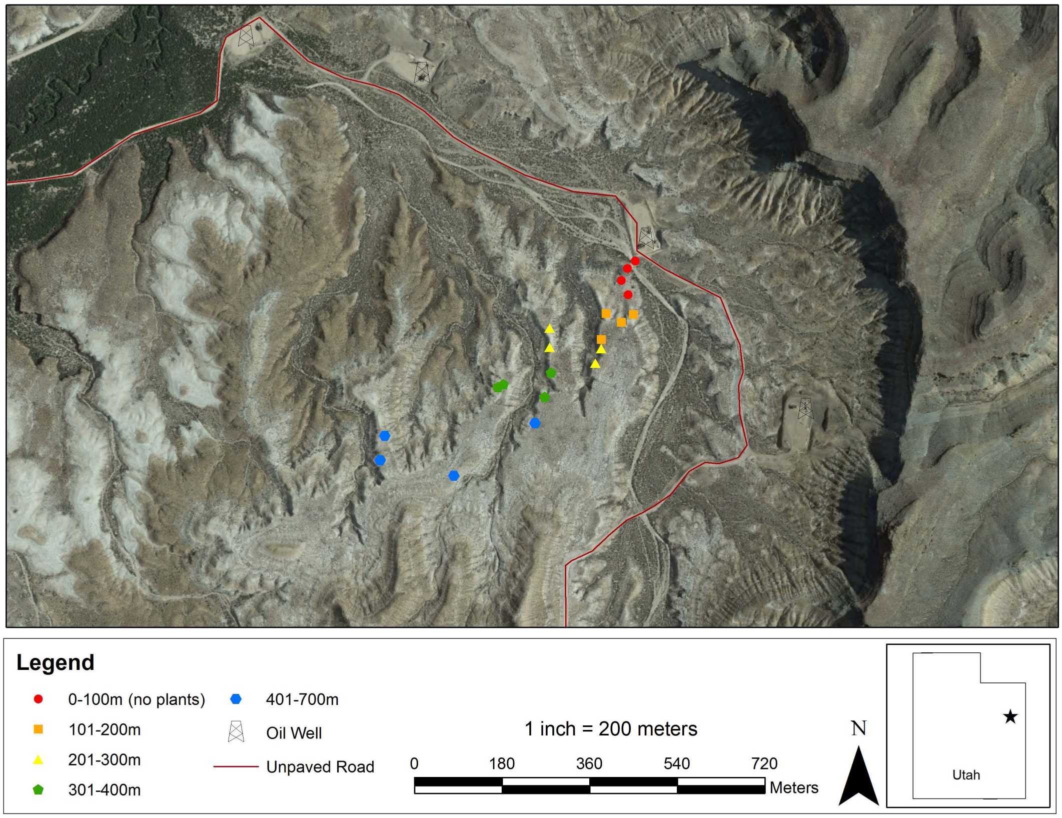

Fig. 1. Map of study area in the Uintah Basin, Utah, and experimental design.

in the 300-m stratum only contained 8 plants each. Thus, this study is based on 16 plots and 156 plants (Fig. 1). Two measures of plant size (number of stems and plant volume) were collected per plant. To estimate volume, we measured circumference on the widest part of the shrub and height of the tallest stem, both in cm; we then calculated volume for a prolate spheroid as $V = 4/3\pi ab^2$ where a is the radius and b is the height (Hatley and MacMahon 1980). Reproductive output was measured as the number of fruits per plant, the estimated total number of seeds per plant (mean seeds per fruit × number of fruits), and the estimated total seed weight per plant (mean seed weight × estimated total plant seeds). The mean number of seeds and mean seed weight (mg) were recorded for 5 indiscriminately selected fruits from each plant. We then assessed the relationship between measures of reproductive output and dust deposition while controlling for plant size and distance from roads (see analyses section below).

In case dust was found to negatively affect reproduction, we applied supplemental outcross pollen to 3 flowers each on 5 plants in each plot to help distinguish between prepollination (e.g., reduced visitation) and postpollination mechanisms (e.g., altered physiology). In this part of the study, a total of 240 flowers from 80 plants were hand pollinated (3 flowers/plant × 5 plants/plot × 4 plots/distance stratum × 4 strata). We then assessed the relationship between these fruit and seed set results with dust deposition while controlling for plant size and distance from roads (see analyses section below) and compared this result to results of the open pollination.

Dust Trap Construction and Sample Collection

Dust traps designed to mimic dust deposition onto plants were constructed following a United States Geological Survey (USGS) protocol (Reheis and Kihl 1995). Dust traps consisted of nonstick angel food cake pans

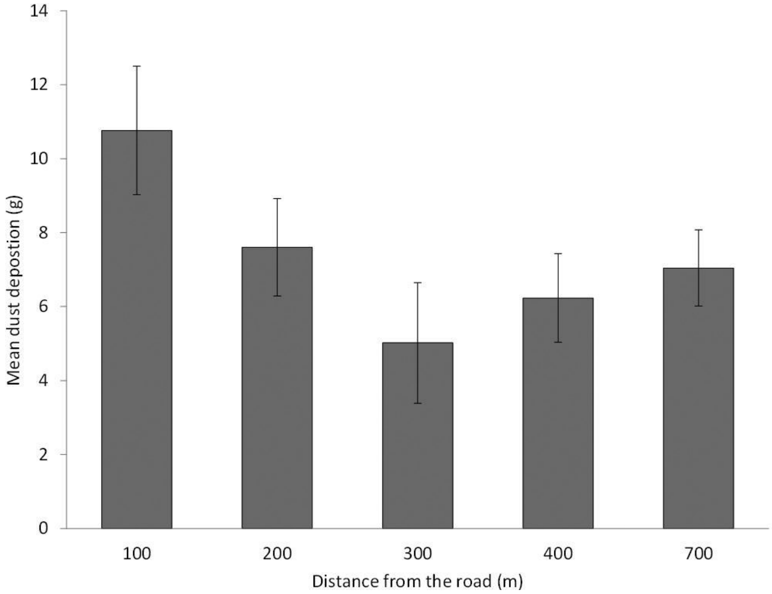

Fig. 2. Dust deposition as a function of distance strata. Values are the mean of the 2 dust traps per plot and 4 plots per distance (n = 8). Error bars represent one standard error.

fitted with 0.25-inch (0.64-cm) mesh galvanized hardware cloth at a depth of 4 cm. Pans were then filled above the mesh with marbles and placed on the ground in the plots on 9 April 2011. Two traps were placed in each plot for a total of 40 traps.

Dust traps were in place through flowering, and dust samples were collected when fruits began to dehisce (1 July 2011) and after all other data were collected from the plots. Dust sample processing followed USGS protocols (Reheis and Kihl 1995). For each dust trap, marbles and hardware cloth were rinsed with distilled water using a 1-L laboratory wash bottle, removed from the dust trap, and placed in a plastic wash pan filled with approximately 2.5 cm of distilled water. The cake pan was rinsed and the water was poured into a clean 1-L laboratory bottle. Marbles were rinsed a final time in the wash pan and placed in a 1-gallon zipper storage bag. Water from the wash pan was then added to the bottle and the samples were returned to the lab for processing.

Each dust sample was gently swirled and decanted through a 0.5-mm sieve into several 500-mL beakers of known empty weight. Decanting removed any plant or insect material present but allowed dust to pass through. Beakers were placed in an oven at 60 °C until the water had evaporated (approximately 4 d). Beakers were allowed to cool in a plastic desiccator and then weighed a final time. Dust weight for each trap was then calculated as the sum of the total weight of the beakers with dust minus the sum of the empty weight of the beakers. Mean dust deposition was calculated from the 8 traps per distance stratum (Fig. 2).

Dust and Stomatal Conductance

For the dusting experiment, 10 plants (>1 km from the road) from one population were used along with 10 plants each from 2 additional populations. On each plant a leaf was indiscriminately selected and marked by placing a paper clip around the petiole. Stomatal conductance was measured using a steady state porometer (SC-1 Leaf Porometer, Decagon Devices, Inc., Pullman, WA) prior to dusting. The leaf was then dusted using sieved road dust and a bulb syringe. Both sides of the leaf were dusted and the excess was gently shaken off. The process was repeated on the remaining 9 plants. Stomatal conductance on the original leaf on the first plant was then measured again and the leaf was gently washed. This process was then repeated on the remaining 9 plants. The amount of time between each measurement of stomatal conductance was approximately 10 to 15 min. The entire process was repeated on 2 additional

TABLE 1. Generalized linear mixed models for the effects of plant size and dust on reproductive measures. Significant *P* values ($\alpha = 0.05$) are in boldface.

Response	Source	Estimate	df	*F*	*P*
Fruit set	Dust	−0.0417	1, 15	5.26	**0.0366**
	Plant size[a]	1.3587	1, 140	140.25	**<0.0001**
Estimated plant seeds[b]	Dust	−0.0402	1, 15	2.86	0.1112
	Plant size	1.4045	1, 140	91.29	**<0.0001**
Estimated plant seed weight[c]	Dust	−0.0586	1, 15	3.29	0.0900
	Plant size	1.5276	1, 140	84.73	**<0.0001**
Hand-pollinated flowers	Dust	−0.0004	1, 14	0.00	0.9895
setting fruit	Plant size	0.7145	1, 63	17.26	**0.0001**

[a]Plant size was measured as the log(number of stems).
[b]Plant seeds were estimated by the mean number of seeds per sampled fruits multiplied by the total number of fruits per plant.
[c]Net plant seed weight was estimated by multiplying the mean seed weight (mg) of sampled fruits by the estimate of plant seeds.

leaves per plant ($n = 90$ leaves). The protocol was conducted at approximately the same time of day (late afternoon, between 16:00 and 18:00) over 3 separate days, one for each population. Weather conditions were warm and sunny for each population sampled.

Dust on Flowers and Hand Pollination

A total of 10 plants from the Bad Land Cliffs population received flower dusting and hand pollination treatments. On each plant 1 flower was selected, and the pedicel was marked with a permanent marker. Sieved road dust was applied inside the flower (intentionally covering the stigma) using a bulb syringe, and the excess dust was shaken off. The flower was hand pollinated using one or more anthers from another plant approximately 10 m away. This process was repeated 2 more times per plant for a total of 3 flowers and on 9 more plants for a total of 30 treated flowers. Flowers were not bagged after treatment. Successful pollination was recorded as the total proportion of fruit set.

Data Analyses

The effects of increasing dust deposition on reproductive success were examined using a generalized linear mixed-model (GLIMMIX procedure) analysis of variance (ANOVA) in SAS/STAT® 9.2 for Windows (SAS Institute, Inc. 2002) at the $\alpha = 0.05$ level of significance. Plant and plot were random effects, while plant size, distance, and dust were fixed effects. Of the 2 measures of plant size, the number of stems was the best predictor of fruit set and was therefore used in all the models after log (base 10) transformation of the data to meet the assumptions of normality. Each plant was assigned the measure of dust associated with the plot in which it was found. The most parsimonious linear models included the untransformed reproductive measure of interest (number of fruits, total plant seeds, plant seed weight, and hand pollinated fruits) as the response. These models used the predictor variables of dust and plant size and were blocked by plot and distance, with plant as the random effects term, thus controlling for plant size and distance from the road. This allowed us to test for correlations between dust deposition and reproductive measures. All models included a random intercept term and used a negative binomial distribution function. The denominator degrees of freedom for each model were set manually.

Comparisons of stomatal conductance between pre- and postdusting were conducted using a generalized linear mixed-model analysis of covariance (ANCOVA), which was analogous to a paired *t* test, as each paired measurement came from the same leaf. This model does not require independence of samples or normality and allowed for the examination of potential effects from different populations. The most parsimonious model included predusting, postdusting, and population as fixed effects, plant as the random effect, and leaf as the block.

RESULTS

Generally, dust deposition declined as distance from the road increased, although dust deposition began to increase again in the 2 farthest distance strata (Fig. 2).

The number of stems per plant (plant size) was significantly correlated with increased reproduction for all measures (Table 1). When controlling for plant size and distance from the road, the number of fruits matured was

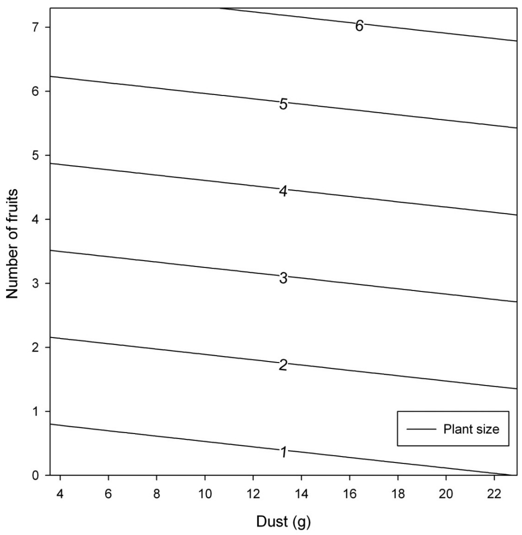

Fig. 3. Modeled relationship between dust deposition and fruit set by plant size category (1–6). Plant size is represented as the log-transformed total number of stems on a plant.

significantly negatively correlated with increasing levels of dust deposition ($F_{1,15}$ = 5.26, P = 0.0366; Fig. 3). Although nonsignificant, total number of seeds per plant and total seed weight per plant showed a similar negative pattern associated with increased dust deposition (Table 1). The effect of dust on the proportion of hand-pollinated flowers that set fruit was not statistically significant (Table 1).

Mean stomatal conductance significantly decreased from 117.0 to 74.9 mmol · m^{-2} per second after dusting the leaves ($F_{1,88}$ = 88.23, P = 0.0003, Fig. 4). Eighty percent (24 of 30) of the flowers dusted prior to hand pollinating set fruit.

DISCUSSION

Dust Deposition Pattern

Dust deposition mostly followed the expected pattern, with most dust deposited near the road and trending downward as distance increased to the 201–300 m stratum. However, dust deposition began to increase again in the 400-m and 700-m distance categories, but not nearly to the levels seen near the road. This may be due to the road curving back around the population at these distances, resulting in the plots in these 2 more distant categories (400 m, 700 m) being closer to this section of the road than from the point where distances were measured. However, there is a small ridge between this section of the road and the plots that may limit the amount of dust that reaches these plants. As this was a field study, there were several variables that we were unable to control for, including this curvature in the road and any wind variability due to topography of the site.

Effects of Dust Deposition on Reproduction

While many of the effects of dust on plant physiology and growth are known (Hirano et al. 1995, Sharifi et al. 1997, Grantz et al. 2003), few studies have investigated the impacts of dust from unpaved roads on reproduction, and many simply assume that reduced growth will result in reduced reproduction. Dust can indeed reduce plant growth. Experimentally dusting endangered *Astragalus jaegerianus* plants reduced overall growth and vigor (Wijayratne et al. 2009), while *Sambucus mexicana* plants were more likely to exhibit decreased water potential and decreased growth with increased dust deposition (Talley et al. 2006). However, our results indicate that increasing dust deposition significantly reduces the reproduction of *H. suffrutescens* independent of plant size; when plant size and distance from the road were controlled statistically, total fruit production showed significant decreases with increasing dust deposition. Though the other measures of reproduction (i.e., number of plant seeds and plant seed weight) were not statistically significant, the overall pattern of decreasing reproduction with increasing dust deposition strongly suggests that dust has a negative impact. Interestingly, Gleason et al. (2007) found that windblown soil had no significant impact on either rare or common plants beyond a distance of 40 m from a road in Hawaii. In our study, no plants grew within 100 m of the road, and we found that dust impacted fruit set regardless of distance. Similar to our study, while studying effects of carbonate dust on 4 endangered plants in California, Padgett et al. (2007) found that dust deposition significantly affected photosynthesis and reduced the growth of 4 substitute plant species near limestone mines. The authors recommended that mining operations (dust production source) be located at least 400 m from the endangered

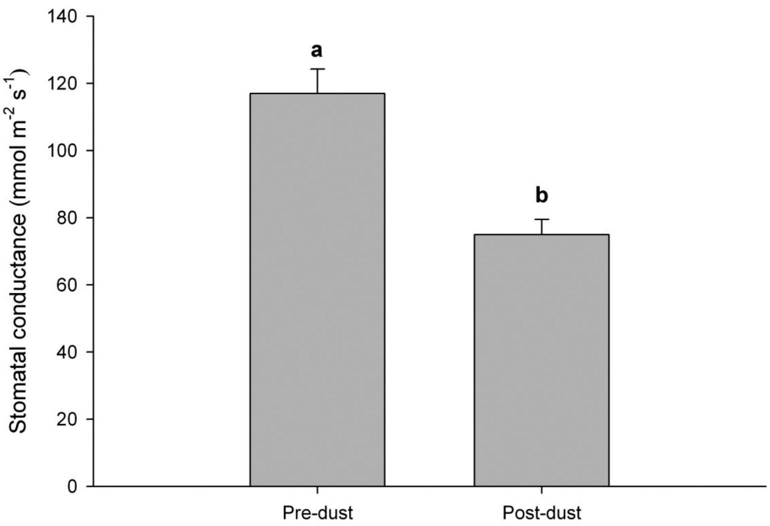

Fig. 4. The effects of dusting leaves on stomatal conductance. Different letters indicate significant differences ($\alpha = 0.05$). Error bars represent one standard error.

plants, and farther if prevailing winds are in the direction of plants. Many of the plants in the Big Pack Mountain population are within 400 m of the road.

Why Does Dust Reduce Reproduction?

Overall, our results provide the first evidence that increased dust deposition on plant surfaces reduces reproduction of *H. suffrutescens*, although the mechanisms are not clear. The results of experimentally dusting plant leaves indicate that dust can significantly impact the physiology of *H. suffrutescens* by decreasing the stomatal conductance of leaves, which could result in reduced fruit production due to reduced resource availability. This result is compatible with results from other studies. Dusted leaves of *Larrea tridentata* had significantly lower stomatal conductance rates than leaves that were not dusted (Sharifi et al. 1997), and carbonate dust significantly decreased the stomatal conductance of several plants in California (Padgett et al. 2007). Additional studies indicate that dust accumulation causes negative physiological impacts on leaves by decreasing photosynthesis (van Heerden et al. 2007), increasing leaf temperatures (Wijayratne et al. 2009), decreasing water potential (Talley et al. 2006), and decreasing chlorophyll content (Prusty et al. 2005). While our results indicate that road dust decreases stomatal conductance, likely by shading the leaf surface, dust could potentially increase water loss (i.e., increase stomatal conductance) by clogging stomata and preventing closure (Hirano et al. 1995). Our measurements provide some support for this hypothesis as stomatal conductance increased on a small number of leaves after dusting, although we did not notice any immediate reduction in turgor. By influencing both the opening and closing of stomata, dust can significantly impact the photosynthetic capacity of plants by decreasing the uptake of CO_2 and increasing water loss. In arid systems such as this, even small changes in water use could have major implications for plant growth, reproduction, and survival, while decreased CO_2 uptake could have significant impacts on growth and ultimately reproduction. Considering our results in light of these additional studies, it is reasonable to expect that reduced total seed production independent of plant size is at least partially explained by reduced resource availability, leading either to reduced initial flower production or reduced ability to mature fruits. However, if dust were altering physiological processes and thus reducing resources available for successful fruit maturation, then we would expect that fruit set of hand-pollinated flowers would also decline with increasing dust deposition. We found no evidence of this, as our hand-pollinated flowers were not affected by dust deposition (Table 1); although there was a slight negative trend, it was impressively nonsignificant ($P = 0.99$).

Alternatively, the reduced reproduction we document could be due to dust disrupting pollinators, their behavior, or the pollination process in some manner. However, if dust were preventing successful pollination through, for example, stigma clogging, then the proportion of hand-pollinated flowers that set fruit would also be expected to decrease with increasing levels of dust deposition. But as noted above, we found no evidence for this in our study. In addition, heavily dusting flowers experimentally apparently did not reduce fruit set, as 80% of dusted flowers set fruit, compared to the approximately 47% fruit set of hand-outcrossed flowers in a breeding system study of the same populations (Lewis and Schupp 2014). We have no data that can address the possibility that dust interferes with pollinator abundance or behavior.

Several caveats must be considered when interpreting mechanisms of reduced reproduction in our study. First, it has long been acknowledged that interpretations of plant-level fruit set based on hand pollination of only a small number of flowers on a plant can be misleading due to reallocation of resources (e.g., Kearns and Inouye 1993). Second, as hand pollinating does not mimic pollinator behavior, perhaps the dust was removed through hand pollination but not through pollination by bees. Secondly, during the short time between dusting and hand pollinating (approximately 5 min) the dust may not have fully adhered to the stigmatic surface. Thirdly, because we did not count the total number of flowers produced, we cannot assess proportional fruit set, which would help address potential mechanisms of reduced fruit production. Lastly, invasive plant (e.g., *Halogeton glomeratus*) management along roads and around oil pads involves sprayed herbicides, which can be transported by wind erosion and deposited up to 250 m away (Larney et al. 1999). Dust-transported herbicides might be contributing to the decreased reproduction observed in this study. However, we have seen no evidence of herbicide damage to plants.

CONCLUSIONS

Our results document that fugitive dust from unpaved roads negatively impacts the physiology and the reproduction of *H. suffrutescens.* These impacts may have major long-term consequences for this endangered plant species and its pollinators. Although we demonstrate that dust has negative consequences, our results cannot clearly identify the exact mechanism or mechanisms involved. Future research should (1) include increased field monitoring efforts in populations close to development, (2) control for dust loads on plants and flowers using various amounts of dust, (3) investigate the direct effects of dust on pollinator behavior and pollination success, (4) investigate the long-term effects of dust on reproductive success, and (5) examine the direct impacts that dust may have on pollinators and their habitat. Overall, our study shows that a greater emphasis should be placed on dust mitigation and suppression measures in populations of *H. suffrutescens* surrounded by anthropogenic development and constant traffic on unpaved roads.

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