

Fugitive road dust alters annual plant physiology but perennial grass growth appears resistant

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Abstract Dust is a feature of the natural environment that can be exacerbated by anthropogenic activities. A range of physiological impacts have been attributed to dust deposition on plant leaves, including altered gas exchange and reduced photosynthetic activity—traits associated with yield and overall productivity. Substantially-increased traffic along rural unpaved roads following the development of shale petroleum deposits in the Bakken region of North Dakota, USA, prompted us to investigate the effect of heavy dust exposure on economically-important annual crops and perennial forage grasses. In a greenhouse study, we exposed six species of annual plants (barley *Hordeum vulgare*, durum wheat *Triticum durum*, maize *Zea mays*, sorghum *Sorghum bicolor*, lentil *Lens culinaris*, pinto bean *Phaseolus vulgaris*, sunflower *Helianthus annuus*) and eight species of perennial grasses (creeping bentgrass *Agrostis stolonifera*, crested wheatgrass *Agropyron cristatum*, intermediate wheatgrass *Thinopyrum intermedium*, tall fescue *Schedonorus arundinaceus*, Bermuda grass *Cynodon dactylon*, blue grama *Bouteloua gracilis*, buffalograss *Bouteloua dactyloides*, switchgrass *Panicum virgatum*) to 40 g of scoria road dust every other day for 10 and 14 days, respectively, resulting in cumulative dust exposure of 200 g/m² for annual plants and 280 g/m² for perennial grasses. Chlorophyll concentration tended to increase in all annual plants within 1-2 hours of dust exposure, which remained high (along with photosynthetic yield) over the duration of the study. Stomatal con-

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ductance tended to decrease over the two-week study period, which was expected, while leaf temperature also decreased for most species, which was contrary to previous research. Conversely, we found little evidence that high levels of dust reduces the ability of perennial grasses to recover from repeated defoliation, regardless of photosynthetic pathway or functional group. While perennial grass growth appears unaffected by the heavy dust emissions produced by traffic associated with energy extraction, the effect on annual plants is difficult to determine because dust might actually have a positive, light-scattering effect that improves plant performance.

Keywords Ecology of dust · Energy sprawl · Foliar dust deposition · Plant community ecology · Plant-soil chemistry interactions · Physiological traits

1 Introduction

Plants typically interact with mineral substrate via their roots, but foliar dust deposition brings mineral particulates into contact with aboveground tissues. Dust refers to particulate matter available for transport by wind and can remain suspended in the air; environmental dust particles are primarily 30 microns or greater (Fairweather et al, 1965). While natural aeolian processes can produce dust, *fugitive dust* is anthropogenically-generated dust that escapes from point sources such as industrial operations, and non-point sources such as unpaved roads (Ulrichs et al, 2008). Increases in particulate deposition have several environmental impacts, ranging from faster snow melt driven by reduced albedo, to altered soil chemistry and plant physiology (Farmer, 1993; Organiscak and Reed, 2004; Painter et al, 2010).

Foliar dust deposition can cause a suite of negative physiological responses. Dust can affect plants both chemically and physically once it settles (Farmer, 1993; Ulrichs et al, 2008). Chemical impacts include altered soil chemistry and nutrient availability, such as when calcium carbonate accumulates along unpaved roads surfaced with crushed limestone (Organiscak and Reed, 2004). Physical impacts include fine particles lodging in open stomata, which can interfere with gas exchange (Sharifi et al, 1997). Foliar dust loads increase leaf and canopy temperature, which prompts stomatal closure (Eller, 1977; Zia-Khan et al, 2014). Meanwhile, dust particles can physically block sunlight from entering chloroplasts, which can reduce chlorophyll content and photosynthetic activity (Thompson et al, 1984; Fischer et al, 1998; Chaurasia, 2013; Bao et al, 2015; Sarma et al, 2017). The cumulative effect of physiological responses to foliar dust accumulation is poor plant performance,

typically reported as lower biomass production and reduced yield (Fischer et al, 1998; Zia-Khan et al, 2014; Sarma et al, 2017).

While negative plant impacts generally require exposure to very high dust levels, substantial increases in traffic along unpaved roads push fugitive dust emissions into ranges of concern. Although unpaved roads are typically associated with rural areas with low population density (and thus low traffic impacts), the sprawl of unconventional oil and gas extraction has substantially increased traffic in many rural areas. For example, hydraulic fracturing in the Bakken oil patch of North Dakota, USA, has increased truck traffic so greatly as to raise concern about dust impacts on crops and native rangeland (McGranahan et al, 2017). These concerns are likely warranted, as high-traffic routes can experience nearly 3 g/m² of dust deposition per day within 180 m of unpaved roads (Spiess et al, 2020), but impacts of foliar dust accumulation on these plants are unknown. More generally, concerns about increased dust emissions following energy development have been raised (e.g., Field et al, 2010), but specific research on these effects has been limited. Given that the land footprint of energy production in central North America between 2000 and 2012 summed to more than half of the grazing land area managed by the US Bureau of Land Management and nearly 13% of the 2013 wheat export (Allred et al, 2015), research on second-order ecological impacts of such extensive energy sprawl is critical.

We conducted a greenhouse study in which we repeatedly exposed 15 economically-important plant species to extremely high levels of dust. Among annual crops, we measured several physiological traits related to vapor exchange, photosynthetic activity, and biomass production, generally expecting that dust exposure would reduce each. We also measured leaf temperature, with the expectation of dust-driven increases. Among perennial grasses, we measured biomass recovery following defoliation (to simultaneously relativize responses across different growth forms and simulate herbivory), and generally expected lower recovery under dust exposure. Furthermore, we expected negative effects to be stronger among species with the C₃ photosynthetic pathway, which is generally less able to tolerate heat and water loss (e.g., Killi et al, 2017).

Common name	Scientific name	Functional group	C ₃ /C ₄
Annual crops			
Barley	<i>Hordeum vulgare</i> (Poaceae)	Cool-season grass	C ₃
Maize	<i>Zea mays</i> (Poaceae)	Warm-season grass	C ₄
Sorghum	<i>Sorghum bicolor</i> (Poaceae)	Warm-season grass	C ₄
Wheat (Durum)	<i>Triticum durum</i> (Poaceae)	Cool-season grass	C ₃
Lentil	<i>Lens culinaris</i> (Fabaceae)	Legume	C ₃
Pinto bean	<i>Phaseolus vulgaris</i> (Fabaceae)	Legume	C ₃
Sunflower	<i>Helianthus annuus</i> (Asteraceae)	Forb	C ₃
Perennial grasses			
Creeping bentgrass	<i>Agrostis stolonifera</i> (Poeae)	Exotic cool-season	C ₃
Crested wheatgrass	<i>Agropyron cristatum</i> (Triticeae)	Exotic cool-season	C ₃
Intermediate wheatgrass	<i>Thinopyrum intermedium</i> (Triticeae)	Exotic cool-season	C ₃
Tall fescue	<i>Schedonorus arundinaceus</i> (Poeae)	Exotic cool-season	C ₃
Bermuda grass	<i>Cynodon dactylon</i> (Cynodonteae)	Exotic warm-season	C ₄
Blue grama	<i>Bouteloua gracilis</i> (Cynodonteae)	Native warm-season	C ₄
Buffalograss	<i>Bouteloua dactyloides</i> (Cynodonteae)	Native warm-season	C ₄
Switchgrass	<i>Panicum virgatum</i> (Paniceae)	Native warm-season	C ₄

Table 1: Species included in the two greenhouse trials, identified by functional group and primary photosynthetic pathway. Scientific name includes family for Annual crops, and tribe for Perennial grasses (family Poaceae).

2 Methods

2.1 Species

Our study focused on plants of economic importance throughout North America, and several of particular importance in the Northern Great Plains, a temperate region with high crop diversity and substantial areas of native rangeland. We divided the study into two groups of plants: annual crops used in row-crop agriculture, and perennial grasses used widely in pastures and frequently occurring in rangeland ecosystems. Within each study group, we selected a variety of functional groups (Table 1). All plants were grown in a climate-controlled greenhouse at North Dakota State University, Fargo, North Dakota, USA. Daytime temperatures were consistently recorded at 25°C and as the study was conducted in the summer, plant received approximately 15 hours of sunlight daily.

Annual crops were established in 10 cm pots with one plant per pot; all had reached the 5-leaf stage before study initiation. We used 32 pots of each species, 16 in each of the dusted and undusted treatments. Annual crops were distributed evenly among two benches in the greenhouse,

and although there was no apparent difference in growth conditions between them, benches were treated as blocks in statistical models. Perennial grasses were established in 20 cm pots several months prior to study initiation. For each species, there were a total of 66 pots split evenly between the dusted and undusted treatments. All plants were raised and treated in the same greenhouse room, and annual crops and perennial grasses were kept on separate benches. Pots were filled with typical sphagnum moss–vermiculite greenhouse growth media and placed in shallow pans, which allowed watering via subirrigation so as to not disturb foliar dust.

2.2 Dust acquisition & application

Dust was collected from a scoria-surfaced road in western North Dakota's Bakken oil patch that had not received chemical dust suppressants for at least two years. A sturdy broom was used to sweep scoria particles into a wide, flat shovel. This raw material was sifted through a 200-mesh sieve prior to application.

At the beginning of the study, 50 cm × 50 cm square spaces were delineated on greenhouse benches and alternately assigned to either dust or no-dust treatments (Fig. 1). Pots from each treatment group were randomly assigned to six-pot clusters within each square. Clusters contained six randomly-selected pots of any species. This arrangement facilitated the application of dust to six-pot clusters by enclosing them in a clear vinyl tent with a 56 cm × 56 cm footprint (24040 Pop-up Greenhouse; NuVue, Buffalo, NY, USA). Dust was applied through a small flap in the top of the tent via a hand-pumped plant duster (Chapin Rose and Plant Duster 16 oz. 5000; CHAPIN, Batavia, NY, USA).

Dust treatments were designed to expose plants to very high dust levels similar to those measured along the most heavily-trafficked roads in the Bakken oil patch, where daily deposition rates averaged 2.83 g/m²/day (Spiess et al, 2020). In the greenhouse, each dust application event consisted of quickly pumping 40 g of dust into the tent and allowing 20 min to settle. Annual crops received a dust application every other day for a 10-day period for a total dust exposure of 200 g/m². Dust was applied to the perennial grasses every other day for a 14-day period for a total dust exposure of 280 g/m².

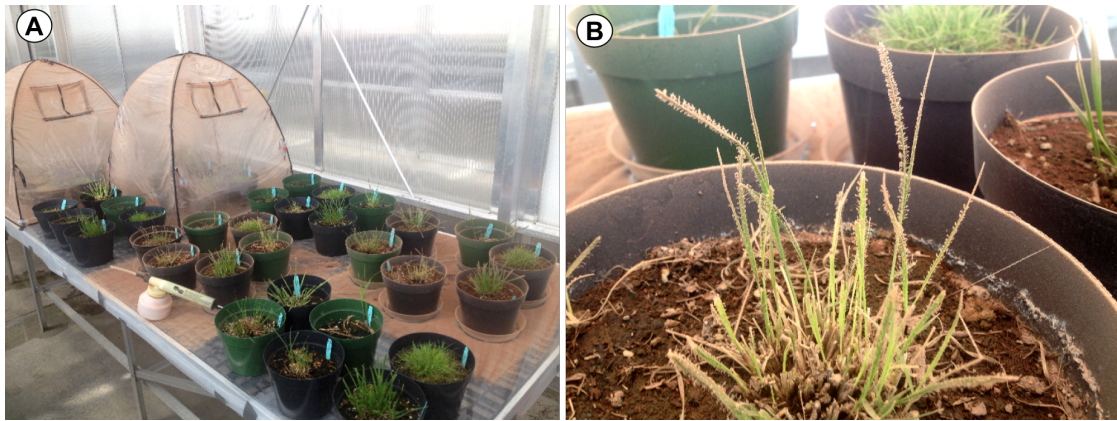


Fig. 1: Applying dust to specific plants in the greenhouse. **(A)** Perennial grasses were randomly assigned to six-pot groups in staggered dust or no-dust treatments. Dust was applied via a hand-powered pump at the top of small vinyl greenhouse tents, and allowed 20 min to fully settle before a tent was lifted. The same protocol was used for annual crops. **(B)** Close-up of scoria road dust on leaf hairs of blue grama *Bouteloua gracilis*.

117 2.3 Data collection

118 We measured five responses from the annual crops, which consisted of the following physiologi-
 119 cal measurements that are effective in determining plant responses to environmental stressors in
 120 controlled environments (McGranahan and Yurkonis, 2018):

- 121 1. *Stomatal conductance*—a measure of vapor flux through the leaf through stomata. Greater flux
 122 can indicate susceptibility to moisture loss, and is one of the first responses to plant stress (Flexas
 123 and Medrano, 2002). We used a clamp-style leaf porometer with a fixed diffusion path chamber
 124 (SC-1; METER formerly Decagon, Pullman, WA, USA).
- 125 2. *Leaf temperature*—was recorded by the SC-1 leaf porometer for calculating stomatal conduc-
 126 tance (Meter Group, 2020). We report leaf temperature here as it has been frequently been
 127 shown to increase following foliar dust deposition and is associated with stomatal closure (Eller,
 128 1977; Zia-Khan et al, 2014).
- 129 3. *Chlorophyll content*—a measure of the plant's ability to assimilate carbon, grow, and produce
 130 fruit based on the density of photosynthetic pigments. We used a chlorophyll content meter to

measured chlorophyll content as the fluorescence emission ratio of light intensity at 735 μm /700 μm wavelengths (CCM-300; Opti-Sciences, Inc, Hudson, NH, USA).

4. *Photosynthetic yield*—another measure of carbon assimilation efficiency, with a positive correlation with crop yield (Fischer et al, 1998). We report quantum yield of photosystem II ($\frac{F_V}{F_M}$; Kalaji et al (2017)) as measured with an Opti-Sciences OS1p (Opti-Sciences, Inc, Hudson, NH, USA).

5. *Specific leaf area*—is calculated as the dry mass of a leaf divided by its leaf area and is a measure of plant tissue available for photosynthesis and gas exchange. We used the first three most-developed leaves at the top of each plant. Leaf area was measured with a bench-mounted leaf area meter (LI-3000C & LI-3050C; LI-COR, Inc, Lincoln, NE, USA), and dry mass determined by placing each leaf in paper envelopes and dried at 60°C for 48 hrs and weighed. Because this is a destructive response, data are limited to only one sampling event per pot.

For each dust application event, non-destructive physiological measurements were made before and after dusting to determine short-term responses to foliar dust deposition. Approximately two hours passed between samples. Care was taken to disturb as little foliar dust as possible. Each subsequent sampling event measured the plants' responses to an increasing level of dust exposure—the most-recent dusting + all dust remaining from previous dustings. As a destructive measurement, specific leaf area was only determined at the end of the study.

The singular response recorded from perennial grasses was aboveground biomass recovery following clipping. After an initial clipping to determine pre-treatment biomass, each pot was clipped twice more, each following 7 dusting events. All plant matter within 1 cm of soil surface was clipped, placed in paper envelopes, and dried at 60°C for 48 h before weighing. We expressed biomass recovery proportionally, as a percentage of the initial pre-treatment clipping.

2.4 Data analysis

After ensuring all response variables followed a normal distribution, we fit linear mixed-effect models with the `lmer` function from the *lme4* package in the R statistical environment (Bates et al, 2015; R Core Team, 2019). We employed a statistical framework developed for the analysis of plant trait and growth recovery data from controlled environmental conditions that emphasizes regression coefficients and associated confidence intervals as measures of effect size (Rinella and James, 2010; McGranahan and Poling, 2018; McGranahan and Yurkonis, 2018). When interpreting these results,

the magnitude of the estimate represents the effect size. If the confidence interval does not include zero, the effect is statistically significantly different than zero, which we report as a *meaningful effect*. Model development followed [Cheng et al \(2010\)](#)'s principles of "good enough" longitudinal mixed models that control for known primary sources of variation in the experimental design. In our models, known sources of random variation included blocks, rounds, and repeated measures of individual pots. Models were fit for each measurement, which served as dependent response variables. Normality of residual error of all models was also confirmed. Data and script for analysis are in the Supplemental Information.

For annual crops, we conducted two sets of analyses comparing short-term and long-term responses. To test the immediate effect of foliar dust deposition on annual crop physiological responses, we subtracted pre-dusting values from post-dusting values for each pot (mean of three leaves/plant) and used this difference as the dependent variable in linear mixed-effect regression models. For species-level analysis, models were fit for each response with species as fixed effect and the intercept term removed to test whether the dust response for each species differed from zero; block, dust application event, and pot were fit as random effects. For an overall analysis of short-term dust impacts on physiology, we fit response as a fixed effect and removed the intercept term, and fit block, round, species, and pot as random effects. To facilitate comparison of effect sizes on a common scale, regression coefficients were centered and scaled by dividing centered columns by their standard deviation using `scale`. 95% confidence intervals were extracted for each fixed effect with `lme4::fixef` and `confint`.

To test the long-term effect of dust accumulation throughout the study, we compared dusted and undusted plants across all sampling periods. Fixed effects consisted of two categorical predictor variables: dust treatment and plant species. The independent variables included dust exposure (dusted or undusted) and the interaction between species and dust exposure; removing the intercept term allowed these interaction terms to test species-specific dust effects along with the overall (average) dust effect. For repeated non-destructive treatments, random effects included block, sampling event, and pot; for the single specific leaf area data, the random effect included only block. Models for each response were compared against a null model via analysis of deviance. Scaled regression coefficients and 95% confidence intervals were extracted for the overall dust effect and each species' interaction with dust exposure as above.

We employed a similar modelling and parameter estimation approach for perennial grass biomass recovery, except we compared several alternative models using an information-theoretic model selection approach. In addition to the dust exposure + species x dust interaction and null models described above, we also compared a model in which the species term was replaced with a term for photosynthetic pathway (C_3 vs. C_4) to test for common responses by functional group. These three models were ranked according to their AIC_c values using the `aiccTab` function in the R package *AICcmodavg* (Mazerolle, 2016).

3 Results

Statistical results of regression modelling are presented here as effect sizes estimated from regression coefficients and 95% confidence intervals. Mean and standard error for each response by sampling event and species are presented in Supplemental Information.

3.1 Annual crops

3.1.1 Short-term responses

Short-term responses to foliar dust application were most apparent in chlorophyll concentration, which tended to increase after dusting for all species (Fig. 2). Stomatal conductance readings were slightly higher for barley and wheat, declined in pinto bean and sunflower, and were highly variable for maize, sorghum, and lentil. Overall photosynthetic yield responses were slightly positive, driven by substantial increases in pinto beans and sunflowers. Other species however were quite variable: Lentils demonstrated a non-zero decrease while C_3 grasses tended to increase and C_4 grasses tended to decrease. Leaf temperature was variable among species such that there was no overall significant difference from zero, but there were non-zero reductions in leaf temperature for wheat and sorghum.

3.1.2 Long-term responses

When dusted plants were compared to undusted plants over the duration of the study, mixed-effect regression models for each response fit with species and dust terms explained variation better than

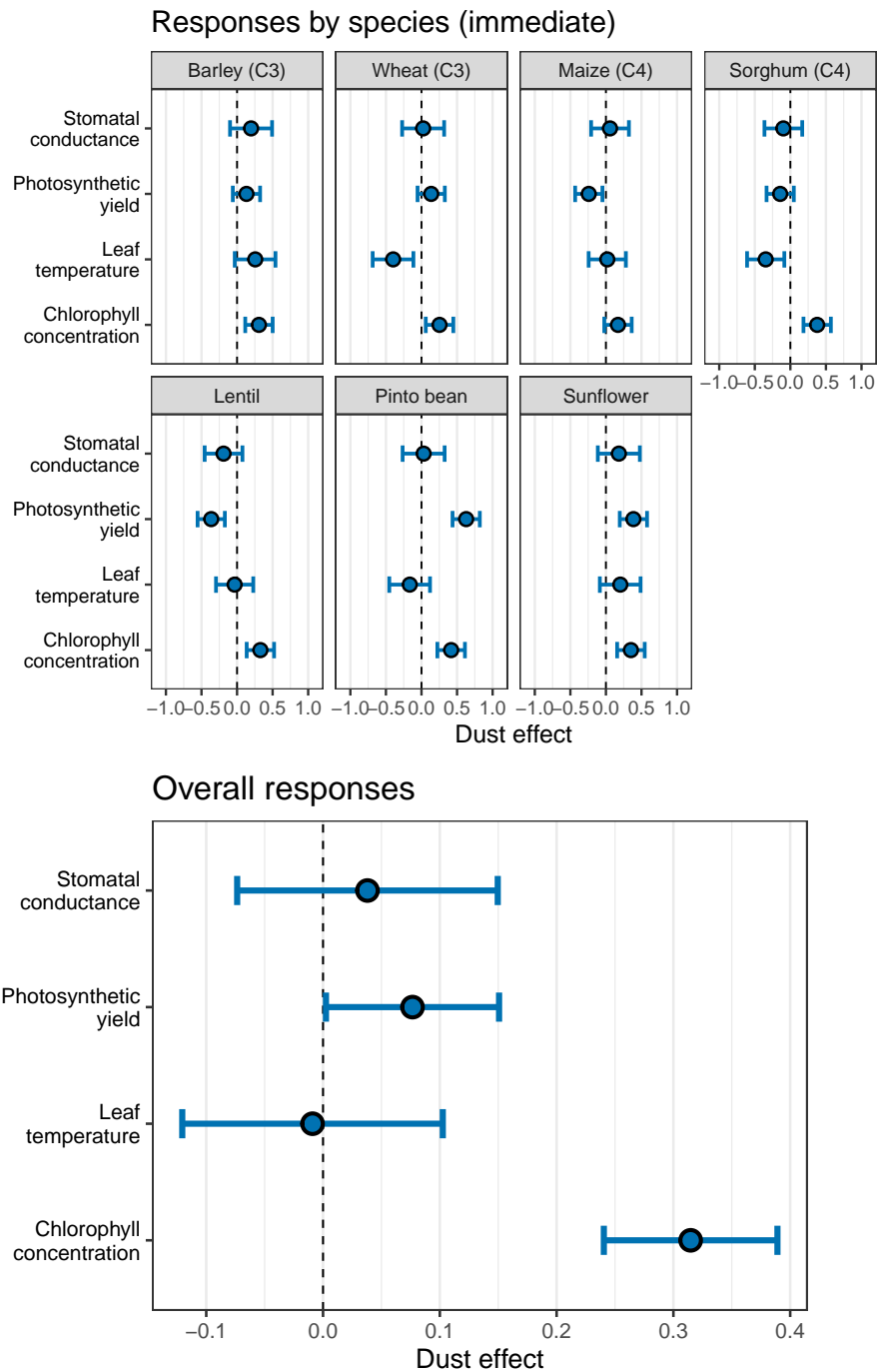


Fig. 2: Short-term effects of dust exposure on annual crop physiology and leaf temperature by species (Top) and by response averaged across all species (Bottom). Approximately two hours passed between pre-dusting and post-dusting readings. When 95% confidence intervals do not overlap zero, dust exposure had an effect equal to the magnitude and sign of the plotted point; when 95% confidence intervals do overlap zero, dust exposure had no effect on the measured response.

null models (Table 2). Highly-ranked models with *species* \times *dust* interaction terms for chlorophyll concentration, leaf temperature, and photosynthetic yield indicate that responses were quite variable among species.

At the species level, photosynthetic yield tended to show meaningful (non-zero) increases among grasses (maize, wheat, and sorghum), but only sorghum showed a meaningful increase in chlorophyll content, as well (Fig. 3). Leaf temperature was highly variable across species—maize, sorghum, and lentil showed strong declines in leaf temperature of dusted plants vs. undusted over the duration of the study; wheat, pinto bean, and sunflower showed no meaningful difference in leaf temperature, and barley tended to increase. For all other measures, 95% confidence intervals overlapped zero, indicating no meaningful response to dust exposure.

Averaged across all species over the duration of the study, chlorophyll content and photosynthetic yield were greater and stomatal conductance lower among dusted plants (Fig. 3).

3.2 Perennial grasses

The mixed-effect regression model testing for species-specific responses to dust exposure was much more explanatory of variation in biomass recovery than responses grouped by photosynthetic pathway (Table 3). There was no consistent effect of dust exposure among perennial grass recovery following repeated defoliation (Fig. 4). The average dust effect was negative, but not different than zero. Tall fescue was the only species to show a non-zero response, in which pots exposed to dust actually grew back more biomass after clipping than those not exposed to dust.

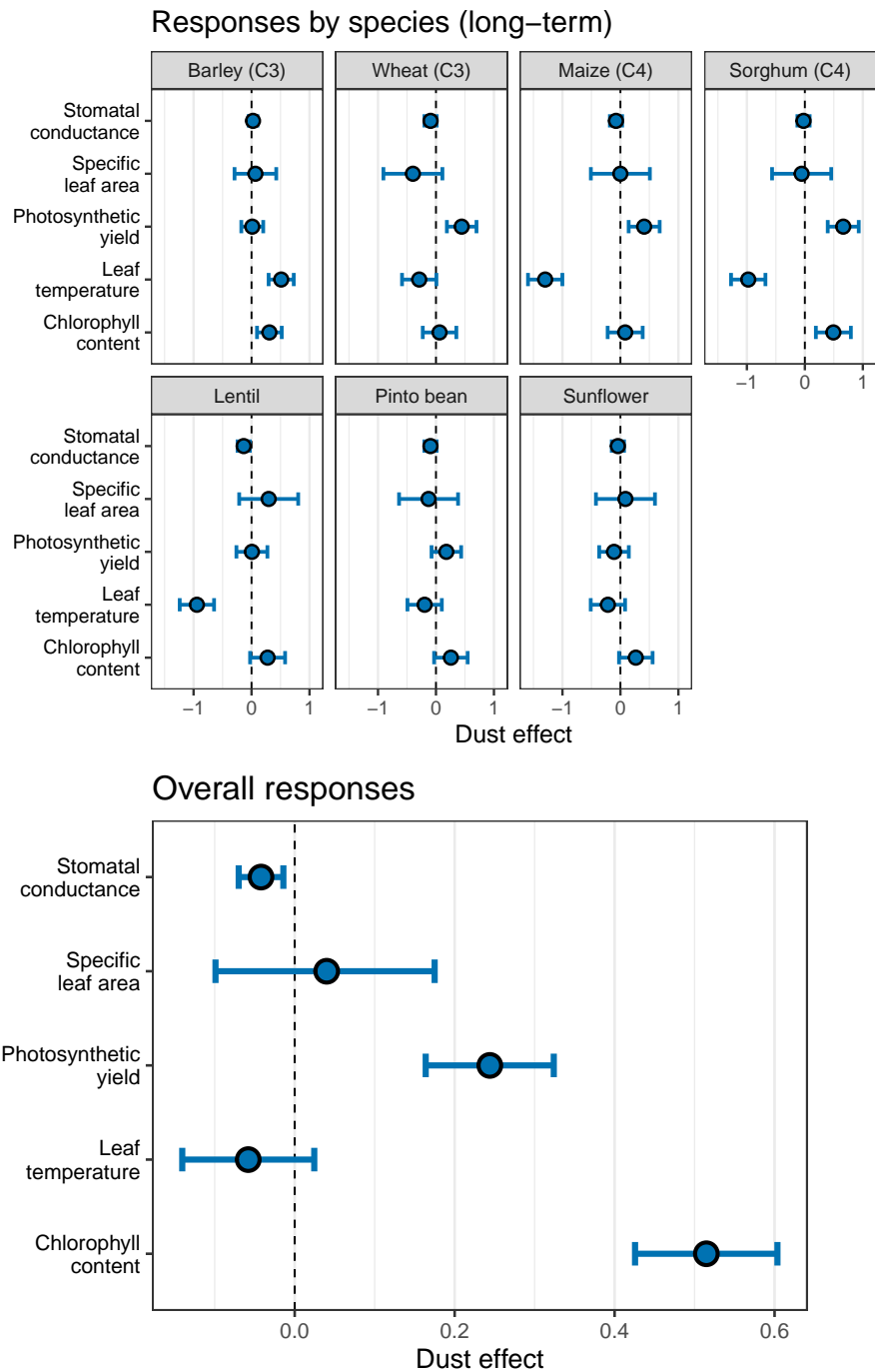


Fig. 3: Effect of dust exposure on annual crop physiology and leaf temperature by species (Top) and by response averaged across all species (Bottom). When 95% confidence intervals do not overlap zero, dust exposure had an effect equal to the magnitude and sign of the plotted point; when 95% confidence intervals do overlap zero, dust exposure had no effect on the measured response.

Response	Model	K	AICc	Δ AICc	AICcWt	Cum.Wt
Chlorophyll concentration	species x dust	16	4023.2	0.0	0.80	0.80
	species + dust	10	4026.0	2.8	0.20	1.00
	species	9	4140.6	117.4	0.00	1.00
	dust	4	4656.6	633.4	0.00	1.00
	null (Intercept only)	3	4683.7	660.5	0.00	1.00
Stomatal conductance	species + dust	10	83.6	0.0	0.80	0.80
	species x dust	16	86.7	3.1	0.17	0.97
	species	9	90.3	6.7	0.03	1.00
	dust	4	1122.6	1039.0	0.00	1.00
	null (Intercept only)	3	1127.9	1044.3	0.00	1.00
Leaf temperature	species x dust	16	2552.7	0.0	1.00	1.00
	species	9	2668.7	116.0	0.00	1.00
	species + dust	10	2668.9	116.2	0.00	1.00
	null (Intercept only)	3	2729.3	176.6	0.00	1.00
	dust	4	2729.8	177.1	0.00	1.00
Photosynthetic yield	species x dust	16	3627.5	0.0	1.00	1.00
	species + dust	10	3669.0	41.5	0.00	1.00
	species	9	3701.6	74.1	0.00	1.00
	dust	4	4749.1	1121.5	0.00	1.00
	null (Intercept only)	3	4769.8	1142.3	0.00	1.00
Specific leaf area	species	9	1798.7	0.0	0.69	0.69
	species + dust	10	1800.4	1.8	0.28	0.97
	species x dust	16	1805.0	6.4	0.03	1.00
	null (Intercept only)	3	1909.2	110.5	0.00	1.00
	dust	4	1911.1	112.4	0.00	1.00

Table 2: Results of AICc-based ranking of linear mixed-effect regression models comparing four physiological responses by species, dust application, an additive multiple-regression model, and a multiple regression model with an interaction term, against a null, intercept-only model.

Model	K	AICc	Δ AICc	ModelLik	AICcWt	LL	Cum.Wt
species x dust	18.0	-197.0	0.0	1.0	1.0	117.9	1.0
C3/C4 x dust	6.0	-85.3	111.7	0.0	0.0	48.8	1.0
null (Intercept only)	3.0	-84.4	112.6	0.0	0.0	45.2	1.0
Dust exposure	4.0	-82.5	114.4	0.0	0.0	45.4	1.0

Table 3: Results of AICc-based ranking of linear mixed-effect regression models comparing perennial grass biomass recovery by species, dust application, photosynthetic pathway (C3/C4), interactions between these variables, and a null, intercept-only model.

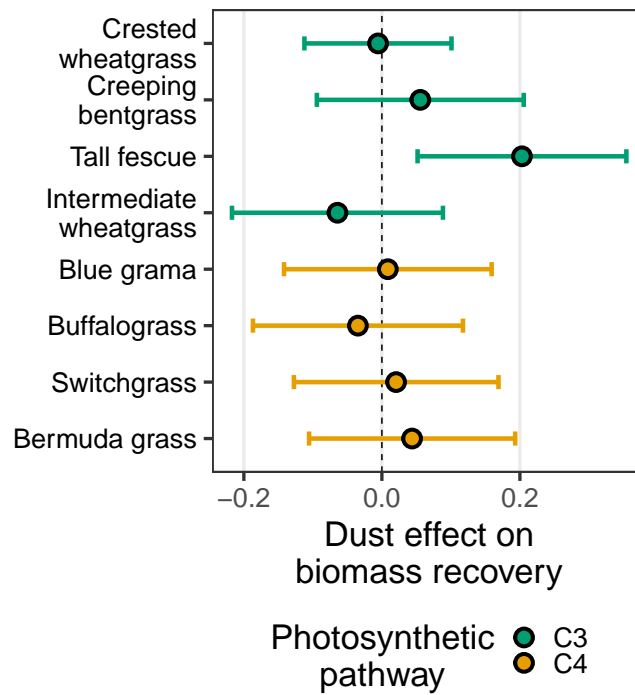


Fig. 4: Effect of dust exposure on perennial grass recovery following two clipping events, by species and photosynthetic pathway. When 95% confidence intervals do not overlap zero, dust exposure had an effect equal to the magnitude and sign of the plotted point; when 95% confidence intervals do overlap zero, dust exposure had no effect on the measured response.

4 Discussion

The ecology of dust has received little attention, due likely to the study of aeolian processes falling mostly in the geosciences. But desertification, land use intensification, and development of unconventional and alternative energy sources are expected to increase fugitive dust emissions in ecosystems worldwide, with largely unknown ecological consequences (Field et al, 2010). However, most work at the intersection of vegetation and dust focuses on dust generation, rather than the impacts of deposition (e.g., Belnap et al, 2014; Flagg et al, 2014; Nandintsetseg and Shinoda, 2015).

Our data indicate that exposure to extremely high levels of road dust affects physiological parameters related to growth and productivity in annual crops, especially as foliar dust load accumulates. Chlorophyll concentration tended to increase in all annual plants within 1-2 hours of dust exposure, which remained high (along with photosynthetic yield) over the duration of the study, whereas stomatal conductance tended to decrease over the two-week study period. Conversely, we found little evidence that high levels of dust reduces the ability of perennial grasses to recover from repeated defoliation, regardless of photosynthetic pathway or functional group.

Two novel components of this study include the analysis of responses to both immediate exposure to dust deposition and dust accumulation over the duration of the study, and the extremely high levels of dust to which plants were exposed. For example, Bao et al (2015) exposed plants up to a maximum of 16.64 g/m² of dust, and Thompson et al (1984) tested plants at dust concentrations of 5–10 g/m², having only measured foliar dust loads of 2 g/m² in the environment. Matsuki et al (2016) reported plants along roadways were exposed to 20–70 g/m² per month, or 0.67–2.3 g/m² per day, which is still below the average daily deposition rate within the road effect zone along heavily-trafficked, unpaved roads in the Bakken oil patch (2.8 g/m²). To simulate the cumulative effect of such heavy dust deposition, by the end of our dusting study, plants had been exposed to 200–280 g/m².

While we did expect to see dust accumulation leading to lower stomatal conductance, we did not expect the trend towards lower leaf temperatures and higher values of responses related to photosynthetic activity among dusted annual crops. Previously-reported effects of foliar dust deposition include reduced chlorophyll concentration, increased temperature of leaves and the canopy, and reduced efficiency of plant processes (Eller, 1977; Ulrichs et al, 2008; Zia-Khan et al, 2014; Sarma et al, 2017). But in this greenhouse study, undusted plants exhibited some degree of stress that we cannot account for, as evidenced by consistent $\frac{F_V}{F_M}$ values < 0.80 (e.g., Rizza et al, 2001, Fig. S1),

and foliar dust generally increased $\frac{F_V}{F_M}$, perhaps by reducing light saturation via shading. Foliar dust can increase the reflectance of light in the visible spectrum (Wu and Wang, 2016), which could have a cooling effect on leaves. Dust can also create a diffusive, light-scattering effect that reduced photoinhibition at high levels of sun exposure, which has been shown to increase gas exchange and improve photosynthesis in economic plants (Jifon and Syvertsen, 2003; Kromdijk et al, 2016). Whether reflectance or light-scattering occurs in a high-sunlight field situation, or if either effect of foliar dust deposition could actually translate to improved plant performance, is unknown.

Thus, an obvious caveat is the fact that this study was conducted in a greenhouse, which would be assumed to create ideal growth conditions, although low $\frac{F_V}{F_M}$ values do indicate possible light stress. On one hand, plants subject to additional environmental stressors (e.g., heat, drought, insects) in the field might be more susceptible to foliar dust load as a compounding factor (e.g., Zheng et al, 2020). On the other hand, such environmental stressors simply have a greater magnitude of impact on plant condition than foliar dust (Matsuki et al, 2016). Furthermore, we did not track plants to maturity and reproduction—barriers to pollination in such a study would preclude meaningful yield data—but the physiological responses we measured have been correlated with biomass production and crop yield (e.g., Fischer et al, 1998; Zia-Khan et al, 2014). And although we only measured the recovery of perennial grasses to defoliation, our results are relevant indicators of potential in-situ dust response because perennial grasses like those in this study rarely rely on seeds for reproduction. For example, fewer than 1% of prairie grass ramets are seedlings (Benson and Hartnett, 2006).

While we have no certain explanation for why tall fescue recovered more biomass after clipping when exposed to dust, we attribute it at least in part to a potentially novel benefit derived from the symbiotic relationship with a fungal endophyte. The benefits conferred by epichloae endophytes to host grasses have been widely documented, and include increased tolerance of heat and drought stress (Gibert et al (2012); He et al (2013)). Epichloae infection has been shown to increase biomass production under drought stress in the related Arizona fescue *Festuca arizonica* (Morse et al, 2002); further work should test the role of endophyte infection as a modulator of host plant response to foliar dust deposition.

Chemical impacts, via both contact with plant tissues and altered soil chemistry, must also be considered. Dust certainly re-distributes nutrients and leads to increased concentrations where dust settles and accumulates (Brahney et al, 2014; Lawrence et al, 2010). The scoria used to surface unpaved roads in the Bakken has a lava-like nature, having been “formed by the baking of the clay

or shale immediately above the lignite seam (Roe, 1950, p.435)” and is likely relatively inert. Other studies of particulate impacts on plants have included urban pollution (Bao et al, 2015) and limestone (Brown, 2009; Organiscak and Reed, 2004), which can alter vegetation composition through calcium deposition and soil pH changes. Armbrust (1986) specifically noted that physical damage or toxicity was not necessary to reduce photosynthetic activity in crops affected by wind-blown dust, but advised that wind and rain would keep foliar accumulation below critical levels. Increased traffic due to expanded energy development might change that.

We suggest three scales of ecological impacts of dust deposition and accumulation: At the finest scale, the physiology of individual plants is clearly affected by dust at very short (hourly) and short (weekly) time frames, sometimes counter-intuitively. These effects likely scale up to variability in plant productivity and competitiveness to effect changes in community composition that are likely modulated by dust-driven changes in soil chemistry. More broadly, there is increasing evidence that dust affects plant-animal interactions, which might mean dust deposition can affect not only community composition but ecosystem service delivery (Zheng et al, 2020). For example, dust has been shown to interfere with pollen-stigma interactions and fruit set in several species of plants, although the overall effect on individual fitness is not clear (Waser et al, 2017; Zhang et al, 2019). Conversely, mineral dust on foliage can physically inhibit herbivory to such an extent that mineral-based products are being developed for commercial herbivorous pest control (Faraone et al, 2020).

As stated above, the ecological consequences of the anthropogenic processes that drive dust emissions and the aeolian processes that transport and deposit fugitive dust are poorly understood, but are receiving more attention (Field et al, 2010). As such, the ecological implications of the results demonstrated here are equally unclear, although the unexpected direction of some responses in this greenhouse trial merit extension to longer-term field experiments.

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Supplemental Information Supplemental information is available at the online version of this paper:

324 **S1** Plots of summarised data and R script. Plant data for analysis is attached in the .pdf as an R
325 workspace.

326 *Compliance with Ethical Standards* This paper complies with all relevant ethical standards.

327 References

- 328 Allred BW, Smith WK, Twidwell D, Haggerty JH, Running SW, Naugle DE, Fuhlendorf SD (2015)
329 Ecosystem services lost to oil and gas in North America. *Science* 348(6233):401–402, DOI 10.
330 1126/science.aaa4785
- 331 Armbrust DV (1986) Effect of particulates (dust) on cotton growth, photosynthesis, and respiration.
332 *Agronomy Journal* 78(6):1078–1081
- 333 Bao L, Ma K, Zhang S, Lin L, Qu L (2015) Urban dust load impact on gas-exchange parameters and
334 growth of *Sophora japonica* L. seedlings. *Plant Soil Environment* 61(7):309–315, DOI 10.17221/
335 215/2015-PSE
- 336 Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *Jour-*
337 *nal of Statistical Software* 67(1):1–48, DOI 10.18637/jss.v067.i01
- 338 Belnap J, Walker BJ, Munson SM, Gill RA (2014) Controls on sediment production in two US deserts.
339 *Aeolian Research* 14:15–24
- 340 Benson EJ, Hartnett DC (2006) The Role of Seed and Vegetative Reproduction in Plant Re-
341 cruitment and Demography in Tallgrass Prairie. *Plant Ecology* 187(2):163–178, DOI 10.1007/
342 s11258-005-0975-y
- 343 Brahney J, Ballantyne AP, Kociolek P, Spaulding S, Otu M, Porwoll T, Neff JC (2014) Dust medi-
344 ated transfer of phosphorus to alpine lake ecosystems of the Wind River Range, Wyoming, USA.
345 *Biogeochemistry* 120(1-3):259–278
- 346 Brown WE (2009) Impacts of Road Dust on Forest Soils and Roadside Vegetation. MSc, The Penn-
347 sylvania State University
- 348 Chaurasia S (2013) Effect of cement industry pollution on chlorophyll content of some crops at Ko-
349 dinar, Gujarat, India. *Proceedings of the International Academy of Ecology and Environmental*
350 *Sciences* 3(4):288–295

- Cheng J, Edwards LJ, Maldonado-Molina MM, Komro KA, Muller KE (2010) Real longitudinal data analysis for real people: Building a good enough mixed model. *Statistics in Medicine* 29:504–520, DOI 10.1002/sim.3775
- Eller BM (1977) Road dust induced increase of leaf temperature. *Environmental Pollution* (1970) 13(2):99–107, DOI 10.1016/0013-9327(77)90094-5
- Fairweather JH, Sidlow AF, Faith WL (1965) Particle Size Distribution of Settled Dust. *Journal of the Air Pollution Control Association* 15(8):345–347, DOI 10.1080/00022470.1965.10468389
- Faraone N, Evans R, LeBlanc J, Hillier NK (2020) Soil and foliar application of rock dust as natural control agent for two-spotted spider mites on tomato plants. *Scientific Reports* 10(1):12108, DOI 10.1038/s41598-020-69060-5
- Farmer AM (1993) The effects of dust on vegetation—a review. *Environmental Pollution* 79(1):63–75
- Field JP, Belnap J, Breshears DD, Neff JC, Okin GS, Whicker JJ, Painter TH, Ravi S, Reheis MC, Reynolds RL (2010) The ecology of dust. *Frontiers in Ecology and the Environment* 8(8):423–430, DOI 10.1890/090050
- Fischer RA, Rees D, Sayre KD, Lu ZM, Condon AG, Saavedra AL (1998) Wheat yield progress associated with higher stomatal conductance and photosynthetic rate, and cooler canopies. *Crop Science* 38(6):1467–1475, DOI 10.2135/cropsci1998.0011183X003800060011x
- Flagg CB, Neff JC, Reynolds RL, Belnap J (2014) Spatial and temporal patterns of dust emissions (2004–2012) in semi-arid landscapes, southeastern Utah, USA. *Aeolian Research* 15:31–43, DOI 10.1016/j.aeolia.2013.10.002
- Flexas J, Medrano H (2002) Drought-inhibition of Photosynthesis in C3 Plants: Stomatal and Non-stomatal Limitations Revisited. *Annals of Botany* 89(2):183–189, DOI 10.1093/aob/mcf027
- Gibert A, Volaire F, Barre P, Hazard L (2012) A fungal endophyte reinforces population adaptive differentiation in its host grass species. *New Phytologist* 194(2):561–571, DOI 10.1111/j.1469-8137.2012.04073.x
- He L, Hatier J, Card S, Matthew C (2013) Endophyte-infection reduces leaf dehydration of ryegrass and tall fescue plants under moderate water deficit. *Proceedings of the New Zealand Grassland Association* 75:151–156
- Jifon JL, Syvertsen JP (2003) Moderate shade can increase net gas exchange and reduce photoinhibition in citrus leaves. *Tree Physiology* 23(2):119–127

- 381 Kalaji HM, Schansker G, Brestic M, Bussotti F, Calatayud A, Ferroni L, Goltsev V, Guidi L, Ja-
382 joo A, Li P, Losciale P, Mishra VK, Misra AN, Nebauer SG, Pancaldi S, Penella C, Pollas-
383 trini M, Suresh K, Tambussi E, Yanniccari M, Zivcak M, Cetner MD, Samborska IA, Stirbet A,
384 Olsovska K, Kunderlikova K, Shelonzek H, Rusinowski S, Bąba W (2017) Frequently asked ques-
385 tions about chlorophyll fluorescence, the sequel. *Photosynthesis Research* 132(1):13–66, DOI
386 10.1007/s11120-016-0318-y
- 387 Killi D, Bussotti F, Raschi A, Haworth M (2017) Adaptation to high temperature mitigates the impact of
388 water deficit during combined heat and drought stress in C3 sunflower and C4 maize varieties with
389 contrasting drought tolerance. *Physiologia Plantarum* 159(2):130–147, DOI 10.1111/ppl.12490
- 390 Kromdijk J, Głowacka K, Leonelli L, Gabilly ST, Iwai M, Niyogi KK, Long SP (2016) Improving
391 photosynthesis and crop productivity by accelerating recovery from photoprotection. *Science*
392 354(6314):857, DOI 10.1126/science.aai8878
- 393 Lawrence CR, Painter TH, Landry CC, Neff JC (2010) Contemporary geochemical composition and
394 flux of aeolian dust to the San Juan Mountains, Colorado, United States. *Journal of Geophysical*
395 *Research: Biogeosciences* 115(G3), DOI 10.1029/2009JG001077
- 396 Matsuki M, Gardener MR, Smith A, Howard RK, Gove A (2016) Impacts of dust on plant health,
397 survivorship and plant communities in semi-arid environments. *Austral Ecology* 41(4):417–427,
398 DOI 10.1111/aec.12328
- 399 Mazerolle MJ (2016) AICcmodavg: Model Selection and Multimodel Inference Based on (Q)AIC(c)
- 400 McGranahan DA, Poling BN (2018) Trait-based responses of seven annual crops to elevated CO₂
401 and water limitation. *Renewable Agriculture and Food Systems* 33(3):259–266, DOI 10.1017/
402 S1742170517000692
- 403 McGranahan DA, Yurkonis KA (2018) Variability in grass forage quality and quantity in response to
404 elevated CO₂ and water limitation. *Grass and Forage Science* 73(2):517–521, DOI 10.1111/gfs.
405 12338
- 406 McGranahan DA, Fernando FN, Kirkwood ML (2017) Reflections on a boom: Perceptions of energy
407 development impacts in the Bakken oil patch inform environmental science & policy priorities.
408 *Science of The Total Environment* 599-600:1993–2018, DOI 10.1016/j.scitotenv.2017.05.122
- 409 Meter Group (2020) SC-1 Leaf Porometer for Stomatal Conductance Measurements. Pullman, WA
- 410 Morse L, Day T, Faeth S (2002) Effect of Neotyphodium endophyte infection on growth and leaf
411 gas exchange of Arizona fescue under contrasting water availability regimes. *Environmental and*

- Experimental Botany 48(3):257–268, DOI 10.1016/S0098-8472(02)00042-4
- Nandintsetseg B, Shinoda M (2015) Land surface memory effects on dust emission in a Mongolian temperate grassland. *Journal of Geophysical Research: Biogeosciences* 120(3):414–427
- Organiscak JA, Reed W (2004) Characteristics of Fugitive Dust Generated from Unpaved Mine Haulage Roads. *International Journal of Surface Mining, Reclamation, and Environment* 18(4):236–252, DOI 10.1080/1389526042000263333
- Painter TH, Deems JS, Belnap J, Hamlet AF, Landry CC, Udall B (2010) Response of Colorado River runoff to dust radiative forcing in snow. *Proceedings of the National Academy of Sciences* 107(40):17125–17130
- R Core Team (2019) R: A Language and Environment for Statistical Computing (v. 3.5.3). R Foundation for Statistical Computing
- Rinella MJ, James JJ (2010) Invasive plant researchers should calculate effect sizes, not P-values. *Invasive Plant Science and Management* 3(2):106–112, DOI 10.1614/IPSM-09-038.1
- Rizza F, Pagani D, Stanca AM, Cattivelli L (2001) Use of chlorophyll fluorescence to evaluate the cold acclimation and freezing tolerance of winter and spring oats. *Plant Breeding* 120(5):389–396, DOI 10.1046/j.1439-0523.2001.00635.x
- Roe WB (1950) Geologic features of North Dakota lignite. *Economic Geology* 45(5):434–440
- Sarma B, Chanda SK, Bhuyan M (2017) Impact of dust accumulation on three roadside plants and their adaptive responses at National Highway 37, Assam, India. *Tropical Plant Research* 4(1):161–167, DOI 10.22271/tp.r.2017.v4.i1.023
- Sharifi MR, Gibson AC, Rundel PW (1997) Surface Dust Impacts on Gas Exchange in Mojave Desert Shrubs. *Journal of Applied Ecology* 34(4):837, DOI 10.2307/2405275
- Spiess J, McGranahan DA, Whippo C, Poling B, Daigh ALM, Hovick T (2020) Bird and invertebrate communities appear unaffected by fracking traffic along rural roads despite dust emissions. *Ambio* 49(2):605–615, DOI 10.1007/s13280-019-01207-9
- Thompson JR, Mueller PW, Flückiger W, Rutter AJ (1984) The effect of dust on photosynthesis and its significance for roadside plants. *Environmental Pollution Series A, Ecological and Biological* 34(2):171–190
- Ulrichs C, Welke B, Mucha-Pelzer T, Goswami A, Mewis I (2008) Effect of solid particulate matter deposits on vegetation: A review. *Function Plant Sci Biotechnol* 2(1):56–62

- 442 Waser NM, Price MV, Casco G, Diaz M, Morales AL, Solverson J (2017) Effects of Road Dust on the
443 Pollination and Reproduction of Wildflowers. *International Journal of Plant Sciences* pp 000–000,
444 DOI 10.1086/689282
- 445 Wu C, Wang X (2016) Research of foliar dust content estimation by reflectance spectroscopy of
446 *Euonymus japonicus* Thunb. *Environmental Nanotechnology, Monitoring & Management* 5:54–61,
447 DOI 10.1016/j.enmm.2015.09.001
- 448 Zhang L, Beede RH, Banuelos G, Wallis CM, Ferguson L (2019) Dust Interferes with Pollen–Stigma
449 Interaction and Fruit Set in Pistachio *Pistacia vera* cv. Kerman. *HortScience* 54(11):1967–1971,
450 DOI 10.21273/HORTSCI14330-19
- 451 Zheng M, Song J, Ru J, Zhou Z, Zhong M, Jiang L, Hui D, Wan S (2020) Effects of Grazing, Wind
452 Erosion, and Dust Deposition on Plant Community Composition and Structure in a Temperate
453 Steppe. *Ecosystems* DOI 10.1007/s10021-020-00526-3
- 454 Zia-Khan S, Spreer W, Pengnian Y, Zhao X, Othmanli H, He X, Müller J (2014) Effect of Dust De-
455 position on Stomatal Conductance and Leaf Temperature of Cotton in Northwest China. *Water*
456 7(1):116–131, DOI 10.3390/w7010116