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DUST DEPOSITION EFFECTS ON GROWTH AND PHYSIOLOGY OF THE ENDANGERED *ASTRAGALUS JAEGERIANUS* (FABACEAE)

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ABSTRACT

Human expansion into the Mojave Desert is a significant threat to rare desert plants. While immediate habitat loss is often the greatest concern, rare plants situated near areas where soil surfaces experience frequent disturbance may be indirectly impacted when fine particulate dust accumulates on leaf surfaces. Remaining populations of the federally listed *Astragalus jaegerianus* (Lane Mountain milkvetch) occur on land open to expanding military activities and on adjacent public land with increasing recreational use. This study was initiated to determine whether dust accumulation could decrease the vigor and fitness of *A. jaegerianus* through reduced growth. Beginning in early May 2004, plants located on Bureau of Land Management (BLM) land were dusted bimonthly at canopy-level dust concentrations ranging from 0 to 32 g/m^2, and physiology and growth were monitored until late June when plants senesced. The maximum experimental dust level simulates dust concentrations of Mojave Desert perennials neighboring military activities at a nearby army training center. Average shoot growth declined with increasing dust accumulation, but seasonal net photosynthesis increased. Further investigation of plants grown in a greenhouse supported similar trends. This pattern of greater net photosynthesis with increasing dust accumulation may be explained by higher leaf temperatures of dusted individuals. Ambient dust deposition measured in traps near field plants (May 2004–July 2004) ranged from 0.04–0.17 g/m^2/ d, which was well below the lowest level of dust on experimental plants (3.95 g/m^2/d). With this low level of ambient deposition, we expect that *A. jaegerianus* plants in this population were not greatly affected by the dust they receive at the level of recreational use during the study.

Key Words: Anthropogenic disturbance, *Astragalus jaegerianus*, endangered species, eolian dust deposition, plant physiology.

Many factors threaten the survival of Mojave Desert plant species. One of the most prevalent and far-reaching is anthropogenic development, which not only impacts species directly through plant injury and habitat loss but generates many indirect threats as well (Lovich and Bainbridge 1999; Belnap and Warren 2002). Atmospheric dust generated by soil surface disturbance is an indirect threat particularly relevant for the federally endangered perennial *Astragalus jaegerianus* Munz (Lane Mountain milkvetch) because the remaining populations occur on lands subject to increased vehicular traffic.

Individuals of *A. jaegerianus* are found in four geographically distinct populations in a limited area of the western Mojave Desert (U.S. Fish and Wildlife Service 2004). Two of the four populations (Brinkman Wash-Montana Mine and Paradise Wash) are located almost entirely within lands withdrawn for the planned expansion of the Department of the Army's National Training Center (NTC) at Ft. Irwin, California. A third population (Goldstone) is on existing NTC lands and the fourth population (Coolgardie Mesa) is found primarily on Bureau of Land Management (BLM) lands just south of the NTC. The U.S. Fish and Wildlife Service listed *A jaegerianus* as endangered due to its endemism and its sensitivity to military activities and other vehicular traffic (U.S. Fish and Wildlife Service 1992, 1998). A better understanding of the impact from multiple land uses will be helpful in evaluating prospects for long-term conservation and recovery of the species.

Protective fencing may prevent direct damage to plants by military vehicles (U.S. Fish and Wildlife Service 1998) or recreation, but concern remains that habitat quality within these protected areas will be adversely affected by airborne dust raised by vehicles (U.S. Fish and Wildlife Service 2004). Long term exposure to a degraded habitat could counteract the effectiveness of fenced areas as a primary means of protection. Studying the effects of dust deposition on the physiology, growth and reproduction of *A. jaegerianus* is necessary for assessing the feasibility of protecting populations that occur near high activity vehicle routes.

In dry regions like the American Southwest, eolian dust is a natural occurrence. Dust storms

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in the western part of the Mojave Desert are generated primarily by cyclonic activity during winter and spring (Brazel and Nickling 1987). Dry lakebeds (playas) occur within the region where *A. jaegerianus* is found, providing a natural source of fine particulate dust. Human activity on arid soils such as military transports, training maneuvers, off-highway vehicles (OHV), mining activities, and intensive grazing greatly increases fugitive dust by denuding the land of vegetation and exposing areas from which dust can be raised (Adams et al. 1982; Grantz et al. 1998; Padgett et al. 2007). Human-induced changes in playa hydrology may also increase nutrient fluxes and influence plant communities that are downwind of the disturbed area (Blank et al. 1999).

Fugitive dust associated with human disturbances may impact the health of desert plants and is of particular concern for rare species with limited ranges. Sharifi et al. (1997) demonstrated that visibly dusty Mojave Desert perennials proximate to military activities at the NTC exhibit a 21–58% reduction in photosynthesis and a decrease in total shoot length. If leaf surface dust similarly reduces photosynthesis in *A. jaegerianus*, decreased growth and reproduction over time could negatively impact population viability of this rare species.

The goal of this study was to determine whether surface dust accumulation could decrease the vigor of *A. jaegerianus* individuals. We hypothesized that photosynthesis would decrease with accumulation of dust on the leaves, with a resultant decrease in growth. In addition, we examined the site characteristics that influence the amount of airborne dust intercepted by the plant canopy.

Methods

Field Studies

In April 2004, we selected *A. jaegerianus* plants from the previously surveyed Coolgardie Mesa population, located on land administered by California BLM (Barstow Field Office). The plants were then sorted into four size classes based on the dimensions of their canopies. We randomly chose five plants from each size class and randomly assigned leaf-level target dust treatments: 0, 8, 16, 24 and 32 g/m^2, yielding four replicate plants per concentration (total n = 20). The maximum dust treatment was similar to heavily dusted *Atriplex canescens* (Pursh) Nutt. (Chenopodiaceae) growing near trails created by military personnel vehicles at the NTC (Sharifi et al. 1997). The dust concentrations were chosen to reflect potential future conditions for the two *A. jaegerianus* populations (Brinkman Wash-Montana Mine and Paradise Wash) which are located in the planned expansion area of the NTC. Currently, the Coolgardie Mesa population experiences soil surface disturbances created by a nearby OHV recreation site. Off-highway vehicle use is evident throughout the population (personal observation) and may increase in intensity.

The quantity of dust needed to achieve target dust treatments was based on the ellipsoid area of each *A. jaegerianus* canopy. Experimental dust was generated by passing soil collected from nearby roadbeds through a series of soil sieves. This procedure produced dust particles small enough to fall through the L-shaped trichomes and onto the surface of the leaf, which was verified by microscopic examination. We distributed a pre-measured quantity of dust onto *A. jaegerianus* individuals through a 45 μm sieve to ensure uniformity of application on May 07, May 25, June 08, June 22, July 06, and July 20.

We chose three shoots of approximately equal size on each plant for monitoring growth. Shoot length and leaf number were recorded bimonthly prior to and throughout the dusting period (April 28–July 20, 2004). Shoot growth was calculated as the difference in maximum shoot length and initial shoot length, averaged over the three shoots for each plant.

From May 7 to June 22, photosynthesis and water potential were measured on shoots separate than those for growth. Prior to each dust application, one new fully-expanded leaf on each plant was randomly selected. Following the accumulating bimonthly dust applications, we measured leaf-level net photosynthesis (P_{net}) for each plant with an open compensating photosynthesis system (Li-6400, Li-Cor, Inc., Lincoln, NE) and mid-day water potentials (ψ) using a Scholander-type pressure chamber (PMS Instrument Co., Corvallis, OR). To ensure that dust accumulation did not impair the infrared gas analyzer measurements, we cleaned the sample cell using ethanol when sample automatic gain control (AGC) values reached 3000 mV. In an effort to allow plant responses to acclimate, photosynthesis and water potential was not measured until the morning after an evening dusting. Photosynthesis was measured between 0900 and 1200 hr and mid-day water potential (ψ) was measured immediately between 1200 and 1300 hr on the same leaves. Leaf net photosynthesis was expressed on a leaf-area basis by recording an image of each leaf with light-sensitive diazo paper and measuring the area using a leaf-area meter (Li-3000A, Li-Cor Inc.).

Actual leaf-level dust concentration was measured both before and after bimonthly dusting. Prior to dust application, a randomly selected leaf adjacent to the physiological leaf was rinsed with 20 ml of de-ionized water to determine the pre-application concentration of dust. Immediately following dust application, another randomly selected adjacent leaf was rinsed as described above to measure the post-application concentration. The resulting residue was dried to a constant mass in a convection oven at 50°C and weighed. All leaves used for dust concentration measurements were marked to avoid using them for future dust-concentration measurements. Dust concentration was expressed on a leaf-area basis by recording an image of each leaf with light-sensitive diazo paper and measuring the area using a leaf-area meter (Li-3000A, Li-Cor Inc.).

To determine the levels of ambient dust deposition, or accumulation rates, for plants in the Coolgardie population, we constructed dust traps based on a design by Reheis and Kihl (1995). Traps were made of bundt cake pans with hardware cloth placed approximately five centimeters below the top rim. Clear marbles were placed on top of the hardware cloth, one layer thick. The rough surface simulated by the marbles caused dust particles to fall out of the flow of air into the traps. The marbles also prevented subsequent passing winds from picking up and lifting away the trapped dust. Traps were installed 10–60 m and 50–170 m from one- and two-track roads, respectively. Fifteen traps were placed within the Coolgardie population, with four traps placed among the study plants and 11 associated with additional milk-vetch plants. The traps were positioned on fence posts at shrub height, approximately one meter above the soil surface. Traps were rinsed monthly using de-ionized water, and the residue dried and weighed. Dust concentration was expressed based on the inside area of the bundt cake pan.

Greenhouse Studies

We established *A. jaegerianus* individuals in the greenhouse in April 2004 using seeds collected from the Goldstone population in 2003. The seeds were scarified with sandpaper (Sharifi and Prigge personal communication) and sown in pots modified from PVC pipe measuring 30 cm in length (10 cm diam.) with wire mesh on the bottom to allow for drainage. Shoots were supported with trellises fashioned from plastic chicken wire and later transplanted to five-gallon pots to discourage constriction of the root system, which might influence photosynthetic responses.

To clarify results obtained from the field experiment, we dusted plants in the greenhouse from December 16, 2004 to January 27, 2005. Five replicate plants were randomly assigned either a dusted treatment or non-dusted control (n = 10). Two shoots of equivalent size on each plant were chosen to monitor growth. Dust was created and applied weekly using the field protocol. The target dust concentration level for the dusted treatment was the same as the target maximum level applied in the field (32 g/m^2). The quantity of dust applied was based on the area of the study plant canopy as in the field experiment. The treated plants were visibly dusty compared to the untreated control plants and retained dust on the shoots and leaves between applications. At the end of each month, we washed three leaves of each target plant with 20 ml of de-ionized water to determine average cumulative dust concentration. Shoot length and leaf number were recorded weekly for the growth shoots. Leaf-level net photosynthesis was also measured weekly on one "new" leaf and one "old" leaf from each plant. New leaves were characterized as the most recent, fully formed leaf on a shoot. Old leaves were initially selected by tagging the fifth leaf from the growing tip on a randomly chosen shoot. Once this initial leaf showed signs of senescence, such as yellowing or desiccation, we switched to the next younger leaf on the same shoot.

Analysis

Maintaining a fixed leaf-level dust concentration on plants in the field was challenging because of the difficulty of dusting whole canopies of disparate branching architecture, as well as varied wind direction and velocity between sampling periods (Fig. 1). Though we were unable to maintain target dust concentrations, we did apply a constant pressure of dust throughout the study period and achieved a dust concentration gradient.

To express this constant pressure, we integrated the fluctuating dust concentration over the study period, using the trapezoidal rule generated in SigmaPlot (version 9.01, Richmond, CA) and

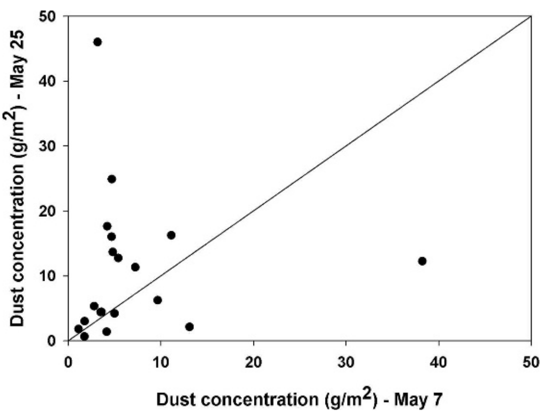

FIG. 1. Leaf dust concentrations measured on May 25 before dust application did not reflect dust concentrations applied 2 wk earlier on May 7 in the field ($F_{1,17}$ = 0.26, P = 0.61, R^2 = 0.02), indicating low retention of leaf dust between applications. Line indicates the expected 1:1 ratio if all applied dust was retained between sampling periods.

divided by the length of the study period to obtain the average daily dust concentration that each individual plant experienced over the duration of growth and physiology measurements (g/m^2). Photosynthesis and mid-day water potential were similarly expressed as an integrated average using SigmaPlot. Physiology data from the fourth sampling period were omitted because plants began senescing by this time; therefore average daily dust concentration for these measurements were adjusted accordingly.

All data were analyzed using SAS statistical software (version 9.1.3, Cary, NC). Patterns in plant physiology and growth associated with dust application in the field were analyzed using simple linear regression. Shoot growth and leaf number data from the field were heteroscedastic, and leaf number data included several zeros. Therefore, shoot growth was log-transformed before analysis, and leaf number was analyzed using Poisson regression with overdispersion included in the model (GLM procedure). Growth responses to dust treatments applied to greenhouse plants were analyzed with a nonparametric Wilcoxon rank sum test. Photosynthetic responses were analyzed using a split-plot ANOVA, with dust treatment as the whole plot and leaf age as the split-plot. A multiple linear regression was used to determine whether dust trap characteristics (elevation and distance from single- and dual-track vehicle routes), mean maximum daily air temperature and rainfall were associated with monthly deposition of dust in traps (Fernandez 2003).

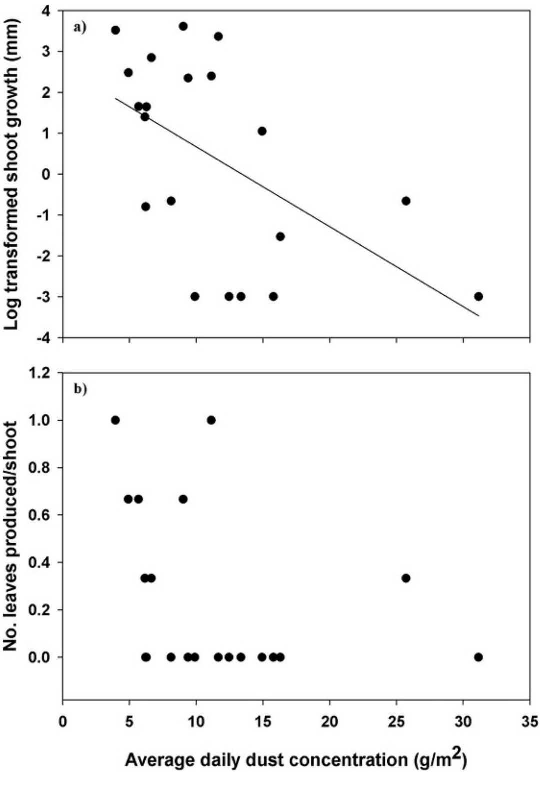

FIG. 2. Seasonal shoot growth (a) (i.e., change in shoot length) declined with increasing leaf dust concentration (Log[shoot growth] = 2.62 − 0.20*[dust concentration]). Leaf production (b) declined slightly as leaf dust concentration increased.

RESULTS

Field Studies

Phenological measurements indicated a steady increase in shoot length across all plants until most plants reached peak growth in mid June. As dust concentration increased, shoot growth decreased (for log-transformed data, $P = 0.01$, $F_{1,18} = 7.67$, $R^2 = 0.37$) and there was a trend towards lower leaf production ($P = 0.06$, $\chi^2_{1,18} = 3.43$; Fig. 2). Net photosynthesis increased as the concentration of dust on leaves increased ($P = 0.02$, $F_{1,18} = 6.47$, $R^2 = 0.26$), but no difference in water stress across the dust concentration gradient was detected ($P = 0.95$, $F_{1,17} = 0.00$, $R^2 = 0.00$; Fig. 3).We found a positive correlation between dust level and leaf temperature (Pearson correlation coefficient $r = 0.49$, $P = 0.03$) and between leaf temperature and leaf-level photosynthesis rate (Pearson correlation coefficient $r = 0.63$, $P < 0.01$; Fig. 4).

Ambient dust deposition rates in the traps for May 2004–July 2004 ranged from 0.04–0.17 g/m^2/day. The study area is intersected by one unimproved single-track route and several dual-track vehicular routes. Rainfall, mean maximum daily temperature and distance to the single-track route were significant factors explaining daily dust concentration (overall model, $P < 0.01$, $F_{2,\ 116} = 39.96$, $R^2 = 0.41$). High dust concentrations were associated with low monthly rainfall, high mean maximum daily temperature (Fig. 5), and proximity to the single track road. Wind direction and speed likely varied throughout the area as well but were not recorded during this study.

Greenhouse Studies

Cumulative leaf-level dust concentration on treated plants at the end of the experiment ranged from 20–40 g/m^2. Neither shoot growth ($P = 0.30$, $z = 0.52$) nor leaf production ($P = 0.46$, $z = 0.11$) differed between dusted plants and control plants (Fig. 6). Dusted plants appear to have higher seasonal photosynthesis than controls but this difference was not statistically significant ($P = 0.33$, $F_{1,8} = 1.06$; Fig. 7). As we expected, new leaves had significantly higher rates of photosynthesis than old leaves ($P = 0.04$, $F_{1,8} = 5.76$; Fig. 7). While greenhouse results were largely

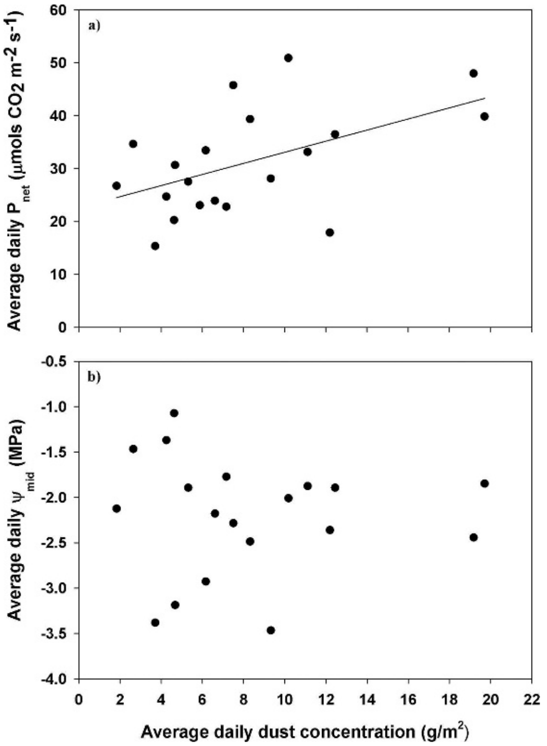

FIG. 3. Average leaf-level net photosynthesis (a) increased with increasing leaf dust concentration. Average midday water potential (b) did not change significantly with increasing leaf dust concentration.

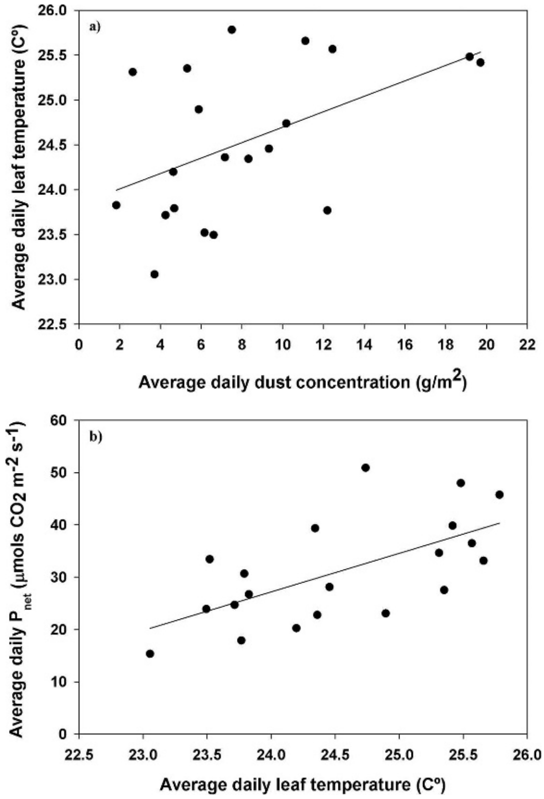

FIG. 4. Relationships between (a) dust concentration and leaf temperature (leaf temperature = 23.84 + 0.09* [dust concentration]) and (b) leaf temperature and leaf-level photosynthetic rate (photosynthesis = −149.78 + 7.37 *[leaf temperature]).

non-significant, the trends are consistent with field results.

DISCUSSION

Studies of dust deposition on desert plants suggest that photosynthesis and growth are negatively impacted by the dust that falls on the surfaces of leaves (Beatley 1965; Sharifi et al. 1997, 1999). Though not all of the dust experimentally applied to *A. jaegerianus* plants was retained on the leaf surfaces in our field study, the net accumulation of dust after repeated applications reduced shoot growth. *Astragalus jaegerianus* individuals are rarely observed growing outside of the canopy of desert shrubs (Prigge et al. 2000), which they use as a trellis for support (Gibson et al. 1998). At the same time, *A. jaegerianus* requires at least two-thirds full sunlight to reach maximum net photosynthetic rates (Gibson et al. 1998). Consequently, we expect that *A. jaegerianus* individuals experiencing prolonged exposure to dust next to heavily used vehicle routes may not grow to the height needed to acquire adequate sunlight and achieve maximum net photosynthetic rates. Flower and fruit production during the study was poor irrespective of dusting treatment and were not analyzed (i.e., only 28% of the shoots measured had flowers or fruits), thus it remains to be seen whether reproductive effort over the life of the plant is compromised by diminished growth.

Dusted *A. jaegerianus* individuals in the field had reduced shoot growth compared to undusted plants. Contrary to our original hypothesis, however, average net photosynthesis increased with leaf dust concentration and is counter-intuitive because of the decrease in shoot growth. We considered that dust accumulation could stimulate compensatory leaf production or shift internal plant resources within the photosynthetic mechanism to enhance photosynthesis. Consequently, we expected greater leaf production and/or higher photosynthetic rates in new leaves on dusted plants than those on undusted plants. We measured photosynthesis on both new and old leaves on dusted and control plants in the greenhouse. Similar leaf production and photosynthetic rates between dusted and undusted leaves do not support this explanation. Alternatively, higher dust loads on leaves are known to increase absorption of incident radiation, raising leaf temperature and shifting the temperature-

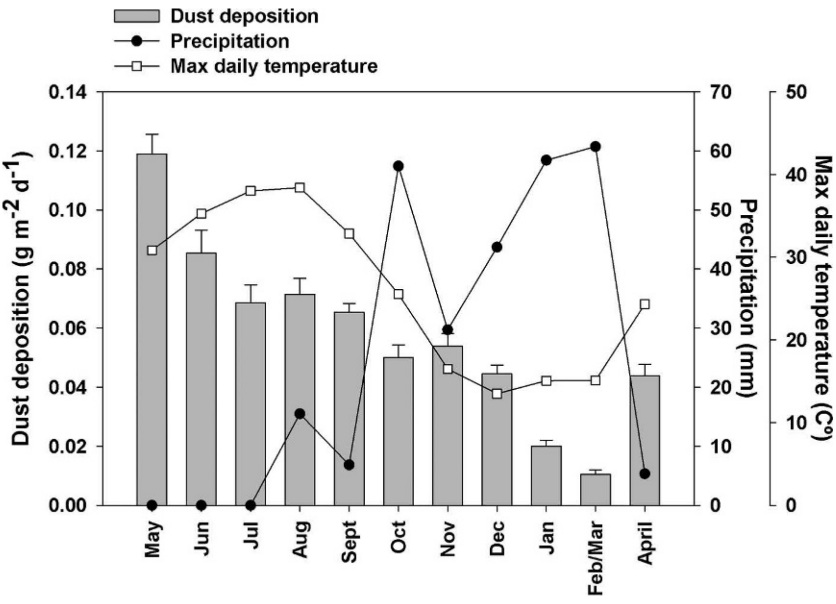

FIG. 5. Mean ambient dust deposition (±standard deviation) collected in 15 traps over the study area was highest during the late spring months when *A. jaegerianus* plants were active. No precipitation fell during May, June and July. Dust concentrations were averaged over February and March because trap contents were not emptied at the end of February.

response curve (Hirano et al. 1995). Leaves of plants in the field that had higher dust concentrations also had higher leaf temperatures. Dust-induced increases in leaf temperatures and subsequent photosynthetic rates during early spring would extend the activity period that milkvetch could maintain positive net photosynthetic rates, but as spring temperatures increased, leaf temperatures of dusted plants likely lowered net photosynthetic rates, thus reducing shoot growth.

Dusted plants in the greenhouse tended to have lower shoot growth and greater net photosynthesis, though the results were not statistically significant. While it is possible that we were unable to detect a significant treatment difference due to the low number of plants available for the experiment, enhanced water status of greenhouse plants may also have offset the negative effects of dust. Sharifi et al. (1999) showed that naturally dusted *Larrea tridentata* (Sessé & Moc. ex DC.) Coville individuals that received irrigation had higher shoot water potentials and more growth than non-irrigated individuals. The greenhouse *A. jaegerianus* plants were watered regularly, which may have been sufficient to counteract any effect of dust accumulation.

Ambient dust deposition for the Coolgardie population during the study period was on the

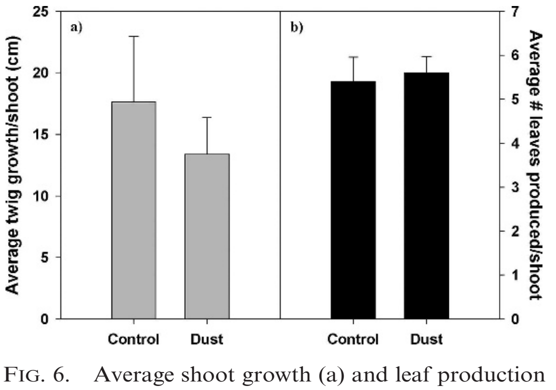

FIG. 6. Average shoot growth (a) and leaf production (b) for greenhouse grown plants (n = 5 for each treatment; ±standard deviation). Neither shoot growth nor leaf production were significantly different between dusted and control plants.

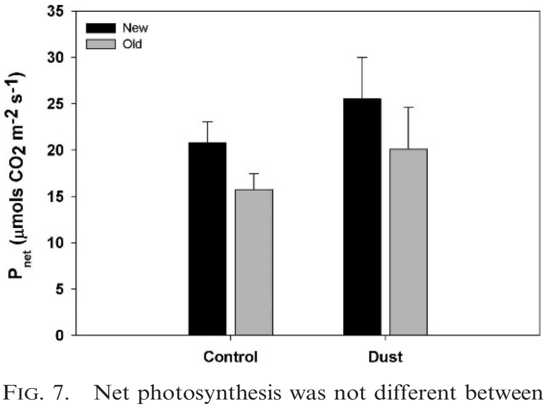

FIG. 7. Net photosynthesis was not different between dusted and control plants in the greenhouse. However, new leaves did exhibit significantly higher rates of net photosynthesis than old leaves.

upper end of yearly dust accumulation rates reported for the Mojave (Reheis 2006) over a 16-year period. The dust traps used in this study create local turbulence causing any dust remaining on the top of the trap to be carried away, and thus may be underestimate the true rate of accumulation on vegetation (Reheis and Kihl 1995). Integrating trap dust fluxes over May and June, which roughly corresponds to the field dusting experiment, enabled us to compare the result to control (non-dusted) study plants. The cumulative daily dust concentration in the traps ranged from 1.14–2.82 g/m^2, while cumulative dust concentration on control plants was 4.15–9.10 g/m^2. With this low level of ambient cumulative deposition, we expect that *A. jaegerianus* plants in this population were not greatly affected by the dust they received from unimproved vehicle routes by the end of the study. In addition, all of our study plants recovered from experimental dusting after heavy winter rains and put out new growth for the 2005 season. Future protection of this population will depend on minimizing the proliferation of single-track routes, especially during periods of low rainfall when dust evolution is greatest.

Experimental dust accumulation on study plants simulated potential scenarios for the Brinkman Wash-Montana Mine and Paradise Wash populations, located in the expansion area of the NTC, where fugitive dust is expected to increase due to military training. Proposed conservation areas (U.S. Fish and Wildlife 2005) will be more beneficial if there is an adequate buffer zone between the dust source and the plants. Buffer zones have been an effective means of preventing other airborne contaminants such as pesticides that drift onto non-target plants or areas (de Snoo 1999; Robinson et al. 2000; Burn 2003) and may help prevent excess dust from drifting onto *A. jaegerianus* populations.

Even though direct loss of habitat is the greatest threat for *A. jaegerianus*, dust generated by recreation and expanded military training near *A. jaegerianus* habitat is a concern for the continued persistence of plants, whether protected in conservation areas or in areas fenced to prevent direct losses of individuals. Low ambient dust levels for the Coolgardie population did not pose a hazard during this study; however, monitoring of dust generation should continue because increased recreational use of the area is a concern.

Dust impacts within the NTC expansion area can potentially be reduced by providing sufficient distance, or a buffer, between the source of dust and *A. jaegerianus* populations. Designation of buffer zones should also take into consideration the dust concentration threshold at which *A. jaegerianus* reproduction is reduced to below the rate required to maintain minimum viable populations. Monitoring of dust deposition, as well as measurements of *A. jaegerianus* physiology, growth and reproduction should continue after the expansion occurs to assess efficacy of the buffer zones in maintaining *A. jaegerianus* populations.

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