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Foliar nutrient uptake from dust sustains plant nutrition

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Main Text

Figures 1 to 5

Abstract

Soils are the mineral inventories from which plants uptake nutrients to build their ionome. The root system is considered the exclusive pathway by which plants tap into the soils for mineral-nutrients uptake. Here we show that plants can absorb nutrients directly from mineral dust deposits on their leaves via foliar absorption. We combine plant physiology with chemical and isotopic analyses to describe and quantify ion transfer from mineral dust lying on leaf surfaces to plant tissues, the foliar pathway. By applying desert dust and volcanic ash to various chickpea varieties we show that within weeks, treated plants had grown significantly and derived essential nutrients such as P, Fe, and Ni primarily via their foliage. We show how the foliar pathway is facilitated by leaf chemical and physiological properties such as low pH and trichome densities. Using Neodymium (Nd) radiogenic isotopes, we quantified that nutrient transfer via the foliar pathway accounts for over 60% of our plants ionome, thus overshadowing root absorption. Further, we grew plants in elevated atmospheric carbon dioxide concentrations and found that foliar uptake from dust can offset the nutrient deficiencies induced due to impairing of root-based nutrient uptake mechanisms (1), and the carbon dilution effect. The foliar nutrient pathway also allows plants to overcome soil fertility degradation our world currently faces (2). Collectively, our results offer a newly discovered pathway in plant nutrition and suggest a pivotal role of foliar nutrient uptake. This discovery opens new avenues for addressing anticipated crop nutritional deficits and the broader issue of 'hidden hunger' malnutrition.

Significance Statement

It is known that plants rely entirely on soils as their mineral nutrient source. Here, we shed light on an untold pathway for plants to uptake nutrients from mineral dust lying on their foliage. Our work combines plant physiology with biological and geochemical analyses, including radiogenic isotopes, to trace the source of nutrients and to quantify significance foliar nutrient uptake. We show that p leaves morphological and chemical properties facilitate the foliar pathway and that this pathway will become even more pronounced at elevated CO_2 conditions. Our results show that mineral dust is used as an alternative nutrient source to plants and describe a possible plant mitigation to deal with declining nutrient status under elevated CO2 world.

Main Text

Introduction

Plants obtain atmospheric carbon (C) through the foliage while most other resources, such as water and nutrients, are taken up from the soil. Hence, it is generally thought that mineral nutrients such as phosphorus (P), potassium (K), iron (Fe), and other macro and micronutrients are acquired predominantly through the plant's roots system (3). Evidence gathered in recent decades demonstrates that the atmosphere is an important source for mineral-nutrients to terrestrial ecosystem via dust deposition (4–9). However, nutrient uptake pathway from dust through the foliage (i.e., direct foliar nutrient uptake) has been overlooked, even though foliar fertilization is used with synthetic soluble fertilizers in agriculture (10, 11). Mineral dust contribution to plant nutrition was never discussed in the context of direct uptake. Dust contribution was documented to outpace the contribution from weathering of host bedrock in montane environments (12), but this may be solely through the soil and root system by long-term pedogenetic processes. Recently, we designed an experiment where desert dust was applied directly on plants foliage and showed that plants uptake notable amounts of P via their leaves (13). In the context of climate change, the foliar pathway may be even more pronounced for plants that will grow under eCO_2 conditions because of two documented phenomena: the 'dilution' effect, where accumulation of C exceeds that of mineral nutrients (1), and more importantly, partial inhibition of key root uptake mechanisms (14), together with soil fertility degradation (2, 15), these changes will drive plants to adapt and look for alternative nutrient uptake pathways. The use of the foliar pathway under eCO_2 may offset the alarming phenomenon where an increasing production of carbohydrates causes stoichiometric imbalances with macro and micronutrients such as P, Fe, calcium (Ca), magnesium (Mg), K, zinc (Zn), copper (Cu), nickel (Ni) and others that are vital for the floral ecological systems (16) and for their dependent human and livestock nutrition (2, 17, 18).

Here, we grew chickpea plants in varying CO_2 conditions, to demonstrate and describe and quantify the foliar nutrient uptake mechanism. The plants were treated with two types of particles on their foliage that represent the most abundant mineral dust particles in the atmosphere: desert dust and erupted volcanic ash (hereafter "dust"), with average annual emissions of 3000 Tgy^{-1} and 300 Tgy^{-1}, respectively (19, 20). We elucidate plant traits that facilitate the foliar nutrient uptake from dust, study its impact on plants ionome, and use Nd radiogenic isotopes to quantify the foliar pathway.

Results & discussion

Foliar mineral-nutrients uptake

In our experiments, we simulated dust outbreaks by manually applying them on chickpea plants (*Cicer arietinum cv Zehavit*, a commercial Israeli cultivar). The dust was applied separately on plant roots or directly on its foliage (**Fig. 1**), while control plants were not treated with dust. After several weeks, a significant impact of the foliar treatment was already noticeable where shoot biomass and P content in the foliage-treated plants had increased, following dust treatment, compared with the control group. Desert dust application resulted in biomass and P content

increases of 35% and 21%, respectively, and volcanic ash application resulted in 28% and 35% increases, respectively (**Fig. 1 D, F**). Interestingly, the root-treated plants did not show any increases in the biomass or P content, suggesting that over short timescales (i.e., several weeks), foliar uptake is the only nutrient uptake pathway from freshly deposited dust **(Fig. 1C, E)**. This result was then replicated when similar experiment was conducted with plants grown on sandy soil (**Fig. S1**).

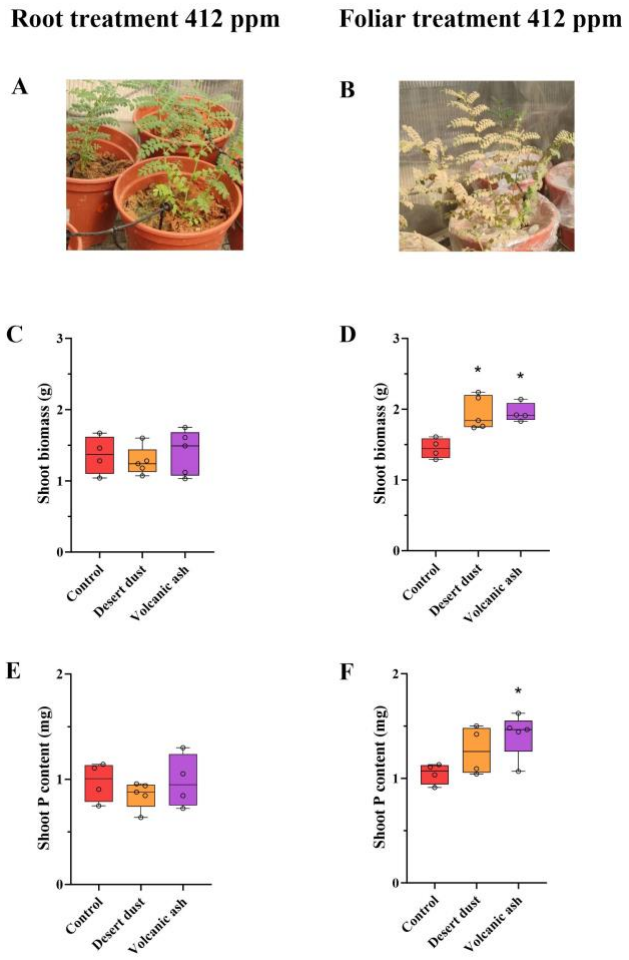

Figure 1. Biomass and P content increases due to dust application treatments at aCO_2 of 412ppm. (A) Image of experiment setting of the root treatment. (B) Image of experiment setting of foliar treatment. **(C)** Shoot biomass of root treated plants. **(D)** Shoot biomass of foliar treated plants. **(E)** Shoot P content of root treated plants. **(F)** Shoot P content of foliar treated plants. The asterisk denotes statistically significant difference from the control. The biomass and P content in the root treated plants do not show increases compared with the control groups. However, the foliar treatment of both desert dust and volcanic ash caused significant increases in the shoot biomass and P content. This implies that plants acquire P from fresh dust deposits on their foliage and not from the root system. Red color represents control plants, orange desert dust treatment and purple volcanic ash treatment.

Plant strategies for foliar mineral-nutrient uptake

Most of the P in the dust is incorporated in the mineral lattice of minerals such as apatite (21), which is largely insoluble under the natural rhizosphere pH range (22). Hence, P in dust has low bioavailability for root uptake. On the leaf surface however, chemical, morphological, and microbial modifications may promote nutrient solubility and bioavailability and thus enable uptake through the leaf surface (13, 23). Examining two contrasting chickpea varieties: wild variety CR934, and common domesticated variety "Zehavit", we found a few properties that facilitate foliar P acquisition from dust **(Fig. 2**). These include structural, morphological, and chemical modifications that are comparable to those reported in the rhizosphere (22). The foliar-uptake-efficient variety "Zehavit" has significantly more acidic leaf surface (pH ~ 1, **Fig. 2b**), and thus promotes both dissolution and mobility of P from the pH sensitive mineral apatite (24), as well as other mineral-nutrients in the dust (13, 23, 25). Additionally, a unique set of metabolites secreted from the leaf surface augments the foliar uptake pathway. These include increased concentrations of oxalate and malate, which are known to release insoluble P in soils through anion exchange reactions (26, 27), and increased levels of sugars such as glucose and sucrose that may promote the activity of nutrient solubilizing microbes on the phyllosphere (28) **(Fig. 2f, fig. S1).** We further found that increased leaf trichome density on both leaf axial and adaxial sides are associated with increased nutrient acquisition **(Fig. 2c, d,e).** These trichomes facilitate the release of metabolites and promote adhesion of dust captured on leaf surfaces (**fig. S2**) (13). We postulate that other plant species share comparable leaf traits that enhance dust capture and solubility such as wheat and various tree species that showed strong responses to foliar dust fertilization (13, 29). Overall, our results suggest that the combination of leaf surface acidification, secretion of organic acids and additional exudations combined with an increased trichome density enhances foliar dust capture and nutrient uptake in chickpeas.

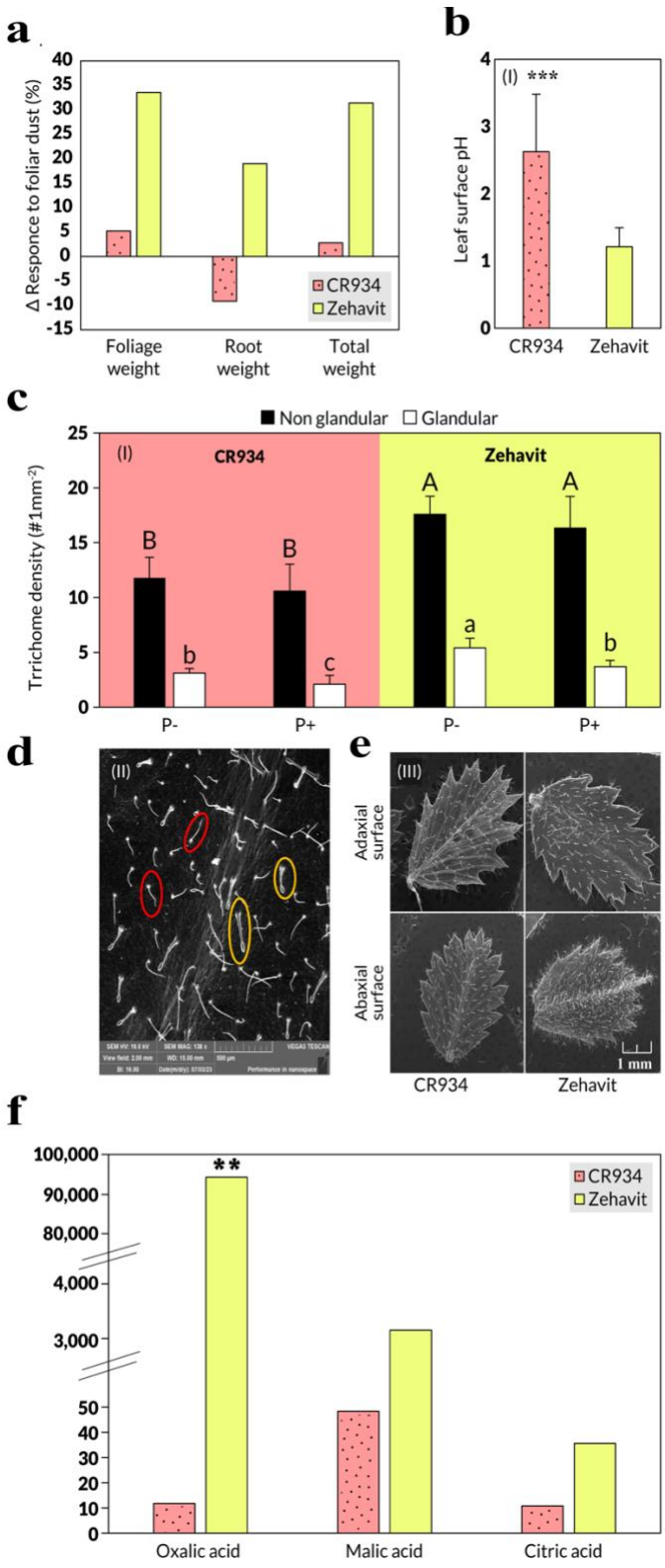

Figure 2. Comparison of two chickpea varieties - CR934 (dotted, pink) and Zehavit (yellow) and their leaf properties under dust foliar fertilization. **(A)** Biomass and P uptake response to foliar dust P. Each column indicates the difference Δ (%) between the foliar dusted plants and the control untreated plants (n=6). **(B)** (I) Leaf surface pH. Each value indicates an average of five measurements on a plant throughout the growth season in control treatment (n=90), and two measurements in foliar dust treatment (n=10). One asterisk indicates significant differences between treatments using a T-test, and a one-way ANOVA (P≤0.05). Three asterisks indicate significant differences between treatments using a T-test, and a one-way ANOVA (P≤0.001). **(C)** Leaf Glandular (black column) and non-glandular (please add a dash to the Non glandular in the figure and change it to Non-glandular) (white column) trichrome density in CR934 and Zehavit control plants (-P and +P). Different letters indicate significant differences between varieties and treatments using Tukey-HSD test (P≤0.05) (n=12). Capital letters refer to non-glandular trichomes and small letters refer to glandular trichomes. **(D)**. SEM scans of non-glandular (red circles) and glandular (yellow circles) trichomes of typical Zehavit leaf. **(E)**. SEM scans of leaves of CR934 (left) and Zehavit (right) varieties. The Zehavit clearly shows higher density of trichomes in the abaxial surface, rendering it as more fit to extract nutrients from dust particles. **(F)**. Exudates of organic acids. Each column indicates the average of leaf washing from four plants, in -P control treatment (n=4). Two asterisks indicate significant differences between treatments using a T-test, and a one-way ANOVA (P≤0.01). Values are concentrations compared with an internal standard.

Quantifying the contribution of foliar nutrient uptake from dust

Traditionally, radiogenic Nd isotopes serve as excellent tracers for sources of magmatic rocks (30), sediment archives (8, 9), and water bodies (31). Since Nd is found in high concentration in nutrient bearing minerals (8, 12, 32), Nd isotopes were recently used to trace nutrient sources in plant tissues, where it was shown that the contribution of dust outpaces the weathering of the local bedrock over geological time scales (12, 32). Here, we utilized the ratio of $^{143}Nd/^{144}Nd$ in the εNd notation to trace the source of Nd in our experiments and quantify the flux of dust-borne nutrients such as P or Fe **(Fig. 3)**. We used a two-component mixing model, where the average εNd value of the control plants, -0.3, which arise from the Nd "inheritance" (i.e., the Nd composition of the seed) is regarded as one end member, and dust εNd values are regarded as the second end member, with values of -11 (desert dust) and 5 (volcanic ash). We found that desert dust treated plants were characterized with εNd values of -8.8 to -5, significantly different than the inheritance value of the control group. Similarly, the volcanic ash treated plants were characterized with εNd values of 3.4 to 4, significantly different than the inheritance value of -0.3. Thus, it is evident that the εNd of the foliage-treated plants comprise a mixture of the inheritance and the type of dust applied. Based on the mixing model, the chickpea plant acquired over 60% of its Nd from desert dust deposited on the foliage. Volcanic ash deposited on the foliage contributed over 70% of its Nd (**Fig. 3**). These results imply that Nd isotopes can be used in future studies to quantify the immediate contribution of freshly deposited dust on the plant's nutrition in field and lab experimental settings.

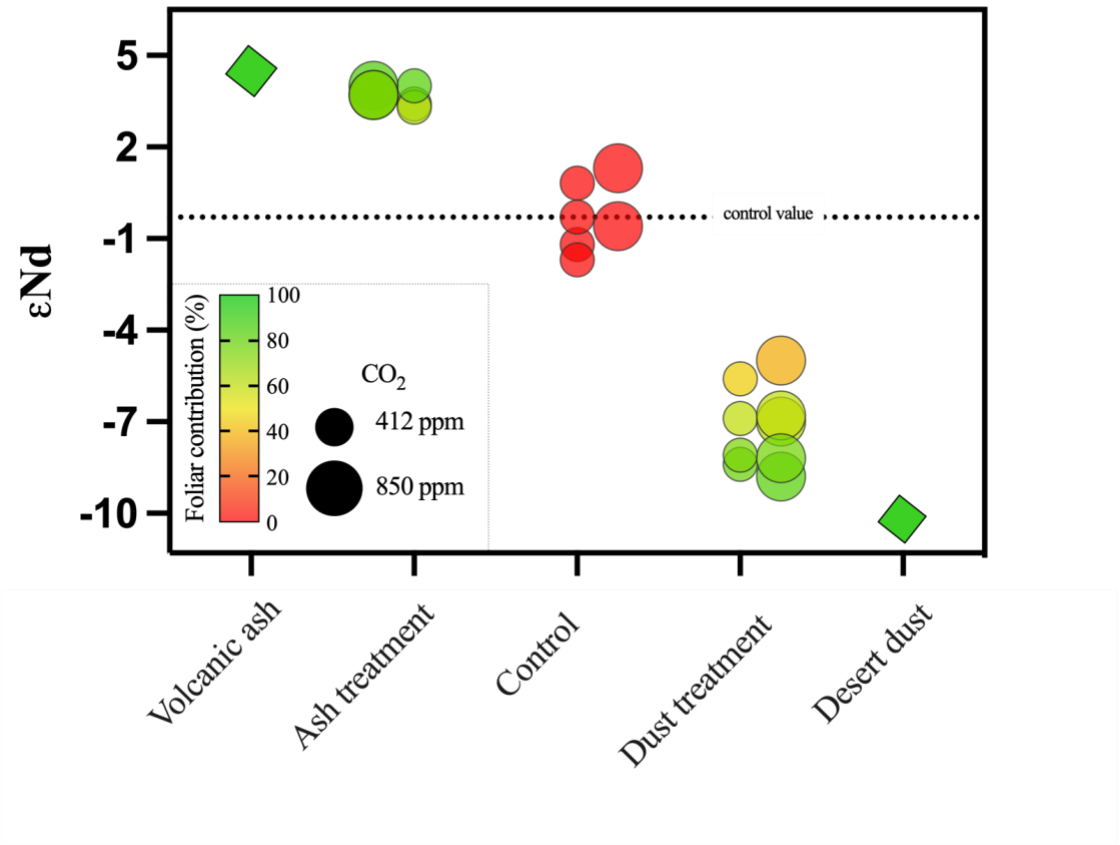

Figure 3. Quantification of dust mineral-nutrient flux from the foliage. Radiogenic isotopic ratios of $^{143}Nd/^{144}Nd$ in the different sample groups (x-axis) expressed in εNd values. Diamonds represent the two applied mineral fractions of volcanic ash and desert dust; circles represent plants treated with the dusts and the control groups. Large circles represent plants growing in the 850 ppm eCO_2 and small circles represent the 412 ppm aCO_2. The color scale reflects the % contribution of Nd originating from the dusts via the foliage, which was calculated using a two-component mixing model. The control plants' Nd signature reflects the inheritance value from the seed, where a value of εNd=-0.3 is set as the control, εNd=-10.3 as the desert dust value, and εNd=4.6 as the volcanic ash value. A foliar contribution of more than 60% is evident in the plants applied with desert dust and more than 70% in the plants applied with volcanic ash. Standard errors on the isotopic values are all smaller than the depicted data points.

Mitigating eCO_2 induced malnutrition

We repeated the foliar nutrient uptake experiment in eCO_2 conditions of 850 ppm CO_2 to mimic high emission scenarios (33) and to examine the foliar pathway under future conditions. Firstly, in accordance with the experiments under aCO_2 only foliar-treated plants had significant increases in the biomass and P content while the root treatment influence was negligible. Root treatments

did not show any increases in biomass or P content (**Fig. 4**). The Nd isotopes study had shown that even under eCO_2, foliar nutrient uptake efficiency remains prominent **(Fig. 3)**.

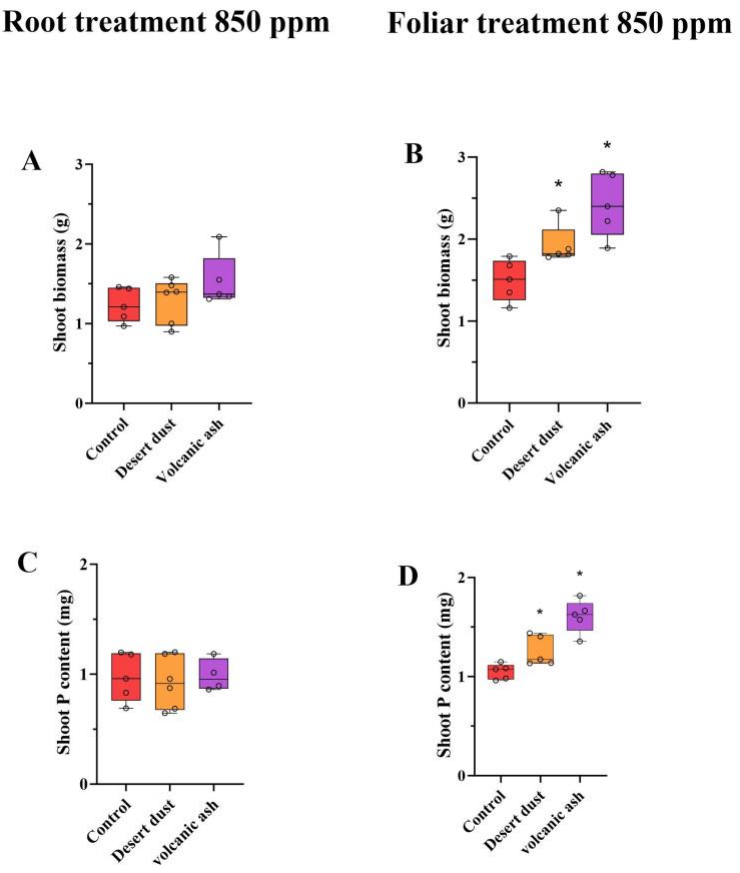

Figure 4. Biomass and P content increases due to dust application treatments at eCO_2 of 850ppm. **(A)** Shoot biomass of root treated plants. **(B)** shoot biomass of foliar treated plants. **(C)** Shoot P content of root treated plants. **(D)** Shoot P content of foliar treated plants. The asterisk denotes statistically significant difference from the control. The biomass and P content in the root treated plants do not show increases compared with the control groups. However, the foliar treatment of both desert dust and volcanic ash caused significant increases in the shoot biomass and P content. This implies that plants acquire P from fresh dust deposits on their foliage and not from the root system. Colors: red – control plants, orange – desert dust treatment, and purple – volcanic ash treatment.

Following this, and in accordance with previous knowledge (18), we found that eCO_2 drastically reduced mineral nutrients concentrations of Mg, K, Ca, Mn, Zn and Fe, with devastating reductions in Cu and Ni, by 72% and 90%, respectively (**Fig. 5**). This reduction in concentrations can't be attributed to the dilution effect (18, 34) as biomass in the aCO_2 and the eCO_2 control groups resemble **(Figs. 1D & 4B**). In the absence of a significant dilution effect the observed nutrient reduction, under eCO_2 conditions, is linked to impairments of mineral nutrient uptake via the root system (14). Surprisingly, the foliar dust-treated plants replenished their Fe and Ni concentrations (both essential micronutrients for plant growth and in human diet) compared with the control group that showed drastic reductions in their ionome. Desert dust treated plants showed increases of Fe and Ni concentrations of 44% and 46%, respectively (**Fig. 5a**). Volcanic ash treated plants showed Fe elevated concentrations of 66% (**Fig. 5b**). The Ni concentrations had more moderate increases from volcanic ash, with 40% higher than in the aCO_2. These results stress how much these dust particles are enriched with P and other essential mineral nutrients relative to most soils (7, 35–37), emphasizing the role of the atmosphere as an important mineral-nutrients source, especially to plants growing on soils with low fertility or in dusty regions (12, 35, 36, 38, 39). We surmise that the foliar pathway significance will grow with rising CO_2 levels in the atmosphere because of the projected downregulation of the root's nutrient uptake pathway (40). However, the Nd isotopes study does not show this excepted trend and more investigation is required in this aspect.

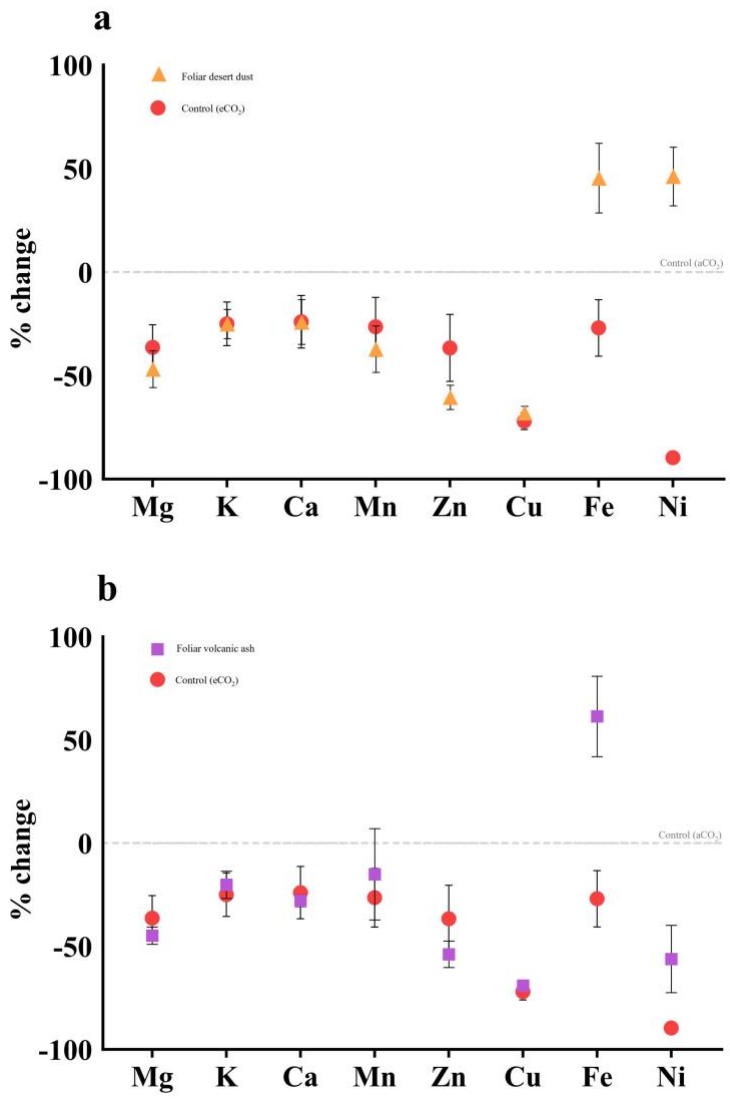

Figure 5. Comparison of the % change in plant ionome of our experiments under various conditions compared with ambient CO2 control plants. Changes in nutrient concentrations of control eCO_2 plants (red circles) show that eCO_2 conditions deteriorate plant root uptake significantly. **(A)** The effect of foliar treatment of desert dust (orange triangles). **(B)** The effect of foliar treatment of volcanic ash (purple squares). Error bars denote SD. Both desert dust and volcanic ash treated plants show that the ability of plants to uptake nutrients from the foliage will replenish, and even increase, concentrations of Fe and Ni in a possible future earth, hence mitigating the plant nutrient reduction caused by elevated CO_2.

Discussion

We showed here that dust nutrient uptake via the foliar pathway in chickpea plants plays a major role in their nutrition. Plant foliage captures and dissolves freshly deposited dust particles, making atmospheric mineral nutrients more accessible through the foliage than via the roots. Thus, our findings highlight that dust serves as an alternative source of nutrients to plants on short timescales of few weeks. Furthermore, that foliar dust acquisition compensates for the reduction in nutrients such as Fe and Ni, induced by downregulation of the roots under eCO_2 conditions (34).

The broader aspect of our findings emphasizes the central role of the foliar pathway to plant nutrition and nutrient cycles in natural ecosystems, but also relates to livestock and human health, nutrition, and wellbeing. The consequence of Fe malnutrition in humans is anemia that can cause morbidity and even mortality if not addressed (41, 42). Iron deficiency anemia (IDA) affects approximately 15% of the world population with higher risk for children under 5 and childbearing women (42–45). As for Ni, although its biological function is not yet fully resolved, it is mainly found in highest concentrations in nucleic acids, particularly RNA (46). Nutrient deficiency will amplify in a future world where eCO_2 will increase the IDA risk factor and Ni deficiency (34, 42). In addition, low plant nutritional values under eCO_2 goes beyond agroecosystems and drives stoichiometric imbalances that impact entire food webs, nutrient cycles, and carbon sinks (47–51). Our findings imply that the foliar nutrient uptake pathway from natural dust will play a central role in eCO2 earth, and that this pathway may be a target for novel fertilization techniques to compensate for the expected decline in the crops' nutritional value. The foliar nutrient uptake pathway (foliar fertilization), therefore, may be one essential mitigation mechanism to cope with expected increasing IDA rates and decreasing Ni availability, as well as other nutritional deficiencies.

Conclusions

Our experiments in ambient and elevated CO2 conditions, where we had sprinkled dust directly onto plant foliage had resulted in biomass and P content increases compared with our control plants. The physiological and bio-geochemical analyses we conducted on these plants rise the following conclusions:

- The physiological study showed plants secrete low molecular organic acids to lower the leaf surface pH and enable ion mobility. These are exuded from trichomes in higher density that also act as dust traps.
- The geochemical analyses we conducted, characterizing plants ionome of different sample groups, showed which elements are transferred by the foliage.
- The Nd radiogenic isotopic composition had allowed us further to quantify the foliar pathway significance. We found that under the experiments conditions the foliar pathway replenishes over 60% of the plant ionome.
- These results illuminate how plants can uptake mineral nutrients in significant quantities via their foliage, and that chickpea plants, that uptake high concentrations of Fe via this pathway, may help to mitigate malnutrition and IDA.

Materials and Methods

1.1 Plant material and growth conditions

Two Chickpea varieties (*Cicer arietinum cv Zehavit*) was chosen as our model plant based on their popularity and positive response to foliar dust application (13). The plants were grown at the Gilat Research Center in southern Israel (31°210N, 34°420E) in two separate glasshouse rooms under 13 hours of natural day light and with a fixed temperature of 25±3°C and relative humidity range of 50-60%. The glasshouse rooms were equipped with a computer-controlled CO_2 supply system (Emproco Ltd., Ashkelon, Israel) that automatically adjusted the CO_2 concentrations. In the first room, CO_2 concentration were set to 412 ppm (aCO_2) and in the second room to 850 ppm (eCO_2), simulating current and future earth CO_2 levels based on high emissions scenario (business as usual, SSP 8.5)(52). Following germination, plants were cultivated in 72 pots containing inert media (perlite 206, particle size of 0.075–1.5 mm; Agrekal, HaBonim, Israel).

The pots were randomly placed inside each room and their locations within rooms were changed once a week. Rooms were twice switched over the course of the experiment to avoid bias due to localized conditions.

Plants were fertigated with: N (50 mg L^{-1}), P (3.5 mg L^{-1}), K (50 mg L^{-1}), Ca (40 mg L^{-1}), and Mg (10 mg L^{-1}). Micronutrients were supplied with EDTA (Ethylene diamine tetra-acetic acid, Koratin, ICL Ltd) for the at concentrations of: Fe (0.8 mg L^{-1}), Mn (0.4 mg L^{-1}), Zn (0.2 mg L^{-1}), B (0.4 mg L^{-1}), Cu (0.3 mg L^{-1}) and Mo (0.2 mg L^{-1}). The plants were drip irrigated three times per day via an automated irrigation system from the germination stage. At 14 days after germination (DAG), when plants were early in the vegetative phase (two or three developed leaves), we changed the nutrient solution of 60 pots to P deficient (P concentration of 0.1 mg L^{-1}) to create P starvation (-P treatment) (13). Preliminary tests showed that our -P deficient media allows chickpea plants to continue their growth cycle without gaining additional biomass under eCO_2, ruling out the CO_2 fertilization effect, which further accounts for the nutrient dilution effect that is common under eCO_2 conditions (1, 34). The remaining 12 pots received the same full nutrient media (+P treatment). Plants fertigated with -P solution started to show P-deficiency symptoms such as chlorosis of mature leaves, slight symptoms of necrotic leaf tips and an overall decrease in biomass accumulation at 35 DAG (13). At this stage we applied desert dust and volcanic ash on the -P plants (see section 1.2).

A total of 72 plants were examined in our experiment with 48 treated plants (see section 1.3) and 24 control plants. The treatment refers to desert dust and volcanic ash applied on the plants. Twenty-four plants were applied with dust on their foliage and 24 plants received root treatment followed by gentle mixing of the surface to sink the dust particles deeper. The control plants were 12 plants of +P solution and 12 plants of -P solution. Each treatment group was divided to the two CO_2 levels, 36 plants in each. The plants were harvested 10 days after the last dust application (55 DAG). To ensure that nutrients from dust particles applied on roots were not washed by the irrigation during the experiment, we monitored the total P (i.e., P that dissolves in strong acid (7, 53, 54)) in the drainage throughout the experiment.

In a parallel experiment in the same growing rooms, we grew nine additional chickpea plants in a pot containing local, low P sandy soil. This was to test whether natural soil

conditions have any impact on dust nutrient utilization from the roots. This small experiment included three pots of -P treatment, three pots of -P treatment + dust on foliage, and three treatments of -P + dust applied on roots (**Fig. S1**). It is evident that the root treated plants did not grow larger than the foliage treated plants, suggesting that over short timescales, the plants acquire nutrients from freshly deposited dust quicker from the foliage than from the roots (**Fig. S1**).

1.2 Chickpea lines experiment

Two chickpea genotypes (*Cicer*) from the Hebrew University of Jerusalem chickpea collection were selected based on preliminary experiments showing contrasting response to eolian dust application to the shoot. The non-responsive genotype: CR205, of the wild progenitor *C. reticulatum* accession, sampled near Savur, Turkey. The responsive genotype 'Zehavit' is a modern, high yield line, and considered popular among the Israeli growers.

From September to November 2022, the experiment was conducted in a sealed climate controlled growing room with natural light at the Gilat Research Center. The temperature was set to 19C° during the day and 16C° at night. The experimental setup included two P levels: 3 mg l^{-1} P (P+) and with low P (P- ~0.2 mg l^{-1}). Plants from P- treatment were divided into two groups; the first group was dusted with rock phosphate during the season, and the other group served as a control and did not receive any additional treatment. The three treatments were: P+, DUST P, and P-. One plant from each variety was planted in a 2.3L pot, containing perlite substrate. Each genotype treatment had six repetitions that adds up to 72 pots.

Two weeks after germination, when the P- plants showed P deficiency symptoms expressed in reduce biomass and yellowing of the mature leaves, we dusted the DUST P plants with 1g of rock phosphate (14.07 ± 0.12 total %P), and the second time was a week afterward. The substrate was covered with paper to ensure that the DUST P would not leach to the root system. One day after dust foliar application, we evaluated the dust holding capacity (SI-2).

1.3 Dust types and its application

The plants were applied with desert dust and volcanic ash, the two main mineralogical dust types in the atmosphere (55). To achieve enough mass for our experiment, we produced dust analogs [11] from surface desert soil and surface volcanic ash soil, following common procedures described by others (13, 56). The desert dust analog surface soil was collected from the southern Israel Negev desert (30°320N 34°550E) (13). Chemical and mineralogical properties of the resulted dust are comparable to dust collected in the Sahara and other places in the Middle East (9, 57). The volcanic ash analog was collected from Mount Etna (Sicily, Italy) two month after the eruption of February 2022. The ash was taken from the upper cable car station "Finuvia dell'Etna" (37°704N, 14°999E). The samples were then processed through a setup of sieves to achieve a particle size smaller than 63μm that are considered windblown (58). The chemical and mineralogical properties of the dust analogs are presented in SI Table 1.

To mimic dust deposition which typically occurs during a few major desert storms or volcanic eruption each year, we applied the dust in two equivalent doses between 35-42 DAG. Total application mass was 3g per plant, to simulate the total dust deposition per m^2 for an average

growth period in southern Israel (13). Dust treatments were done either directly on the foliage while covering the pot, preventing the dust to touch the roots, or directly on the roots where the pots were subsequently covered with nylon to equalize conditions with the foliage treated plants. Dust treatment was done by manually sprinkling the dust through a 63μm sieve in proximity to the foliage.

2. Analyses

2.1 Plant biomass and elemental analysis

After harvesting, the plants were separated for roots and shoots, washed in 0.1M HCl and rinsed three times in distilled water to remove dust particle residue (13). Later, plant tissue was dried, weighed, ground to powder and dry ashed at 550 C° in a furnace for four hours (26). Approximately 1g of the ashed material was subsequently dissolved using 1ml concentrated HNO_3 to achieve a clear solution. To prepare the dust types for elemental analysis, the samples were dissolved on a hotplate by sequential dissolution using concentrated HNO_3, HF, and HCl, resulting in clear solutions (9). The elemental composition of the plants, dusts and nutrient solution were analyzed at the Hebrew University using a ICP-MS (Agilent 8900cx; Agilent Technology). Prior to analysis, the ICP-MS was calibrated with a series of multi-element standard solutions (1 pg/ml - 100 ng/ml Merck ME VI) and standards of major metals (300 ng/ml - 3 mg/ml). Internal standard (50 ng/ml Sc and 5 ng/ml Re and Rh) was added to every standard and sample for drift correction. Standard reference solutions (USGS SRS T-207, T-209) were examined at the beginning and end of the calibration to determine accuracy. The calculated accuracies for the major and trace elements are 3% and 2%, respectively. Biomass and elemental properties of the dust analogs, control plants, and dust root and foliage-treated plants are given in SI Tables 1-3.

2.2 Leaf surface pH

Leaf surface pH was measured by manually attaching a portable pH electrode designed for flat surfaces (HI-1413; HANNA pH instruments) onto the surface of three leaves from each plant. The measurements were performed four times throughout the growing season (19, 24, 35 and 40 DAG) in the morning, two hours after sunrise.

2.3 Trichome density

Trichome density was determined in four young, fully developed leaves from four different plants per variety in the P- treatment only (n=16). Leaves were scanned in a scanning electron microscope (VEGA3; Tescan, Czech Republic). From each leaf, three photos of a $1mm^2$ field were taken, and glandular and regular trichomes were counted.

2.4 Leaf exudates

For analysis of the organic exudates, 2g of fresh leaves were sampled randomly from the P+ and P- treatments before harvesting. The leaves were rinsed in 2 ml of distilled water and methanol (50:50) for 10 s. The extracted surface metabolites were supplied with 50 µl of internal standard (ribitol, 0.2 mg ml^{-1}) and stored at -80°C until analysis. Before analysis, the extracted samples were vacuum dried overnight at 35°C. The dried material was redissolved in 40 µl of 20 mg ml^{-1} methoxamine hydrochloride ($CH_3ONH_2 HCl$) in pyridine (C_5H_5N) and derivatized for 90 min at 37°C, followed by a spike of 70 µl MSTFA (*N*-methyl-*N* (trimethylsilyl) trifluoroacetamide ($CF_3CON(CH_3)Si(CH_3)_3$) at 37°C for 30 min**.** The dissolved metabolites were then introduced to a mass spectrometry gas chromatograph (Agilent 6850 GC/5795C; Agilent Technology) for analysis. The metabolites were detected by a mass spectrometer, where 1 µl of each sample was injected

in split-less mode at 230°C to a helium carrier gas at a flow rate of 0.6 ml min^{-1}. GC processing was carried out using an HP-5MS capillary column (30 m 9 0.250 mm 9 0.25 µm) and the spectrum was scanned for *m/z* 50–550 at 2.4 Hz. The ion chromatograms and mass spectra obtained were evaluated using the MSD CHEMSTATION (E.02.00.493) software, and sugars and amino acids were identified via comparison of retention times and mass spectra with certified GC plant metabolite standards (Sigma Aldrich).

2.5 Nd isotope chromatography and analysis

Nd isotopes were measured on the dust and on the plant material. Nd was separated from the samples using TRU followed by LN-spec resins (59). Measurements of the isotopic ratios were performed using a Thermo Neptune multi-collector ICP-mass spectrometer at the Weizmann Institute of Science. A JNdi Nd standard bracketed the samples, resulting with $^{143}Nd/^{144}Nd$ value of 0.512035 ± 1^{-5} (2σ, n=60). The data was normalized to $^{143}Nd/^{144}Nd$ = 0.512115 (60). Rock standards samples of BCR-2 were dissolved and measured along with the plant and dust samples yielding $^{143}Nd/^{144}Nd$ value of 0.512628 ± 6 (2σ) that agrees with $^{143}Nd/^{144}Nd$ = 0.512637 ± 13 value of BCR-2 (61) . The Nd isotopic ratio is expressed as:

$$\varepsilon Nd = \left(\frac{\left({}^{143}Nd / {}^{144}Nd \right)_{Sample}}{\left({}^{143}Nd / {}^{144}Nd \right)_{CHUR}} - 1 \right) * 10{,}000$$

where the present value of $^{143}Nd/^{144}Nd$ = 0.512638 in CHUR (62). A sample isotopic characterization is given in SI Table 4.

Foliar contribution percentages were calculated using simple mixing equation of two components:

$$\%\ Foliar\ contribution = \frac{\varepsilon Nd_{sample} - \varepsilon Nd_{control}}{\varepsilon Nd_{end\ member} - \varepsilon Nd_{control}} * 100$$

Where εNd end member values of desert dust and volcanic ash are -10.3 and 4.5, respectively (Table SI-4 & Fig. 4). Due to the large variation in the control plant εNd values, we decided to present a conservative calculation, where the values of the control were εNd = -1.7 when computing the mixing with desert dust, and εNd =1.3 when computing mixing with volcanic ash.

2.6 Mineralogical analysis

Mineralogical composition of the dusts was determined with an X ray powder diffraction (XRD) using a Panalytical Empyrean Powder Diffractometer equipped with a position sensitive X'Celerator detector. Cu Kα radiation (k = 1.54178_A) at 40 kV and 30 mA. Scans were done over a 2h period, between 5° and 65° with an approximate step size of 0.033°.

Acknowledgments

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Figures and Tables

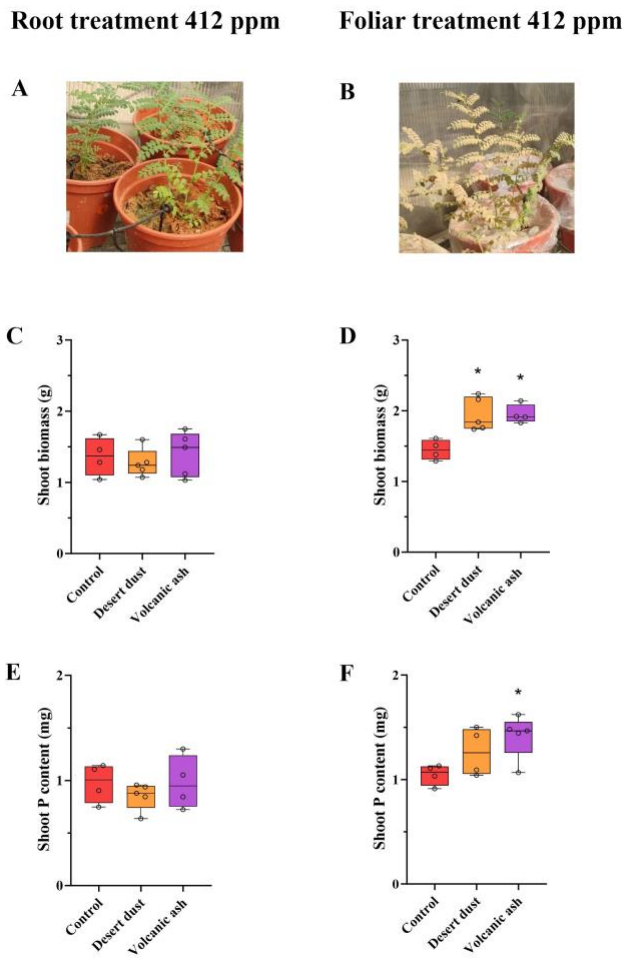

Figure 1. Biomass and P content increases due to dust application treatments at aCO_2 of 412ppm. (A) Image of experiment setting of the root treatment. (B) Image of experiment setting of foliar treatment. **(C)** Shoot biomass of root treated plants. **(D)** Shoot biomass of foliar treated plants. **(E)** Shoot P content of root treated plants. **(F)** Shoot P content of foliar treated plants. The asterisk denotes statistically significant difference from the control. The biomass and P content in the root treated plants do not show increases compared with the control groups. However, the foliar treatment of both desert dust and volcanic ash caused significant increases in the shoot biomass and P content. This implies that plants acquire P from fresh dust deposits on their foliage and not from the root system. Red color represents control plants, orange desert dust treatment and purple volcanic ash treatment.

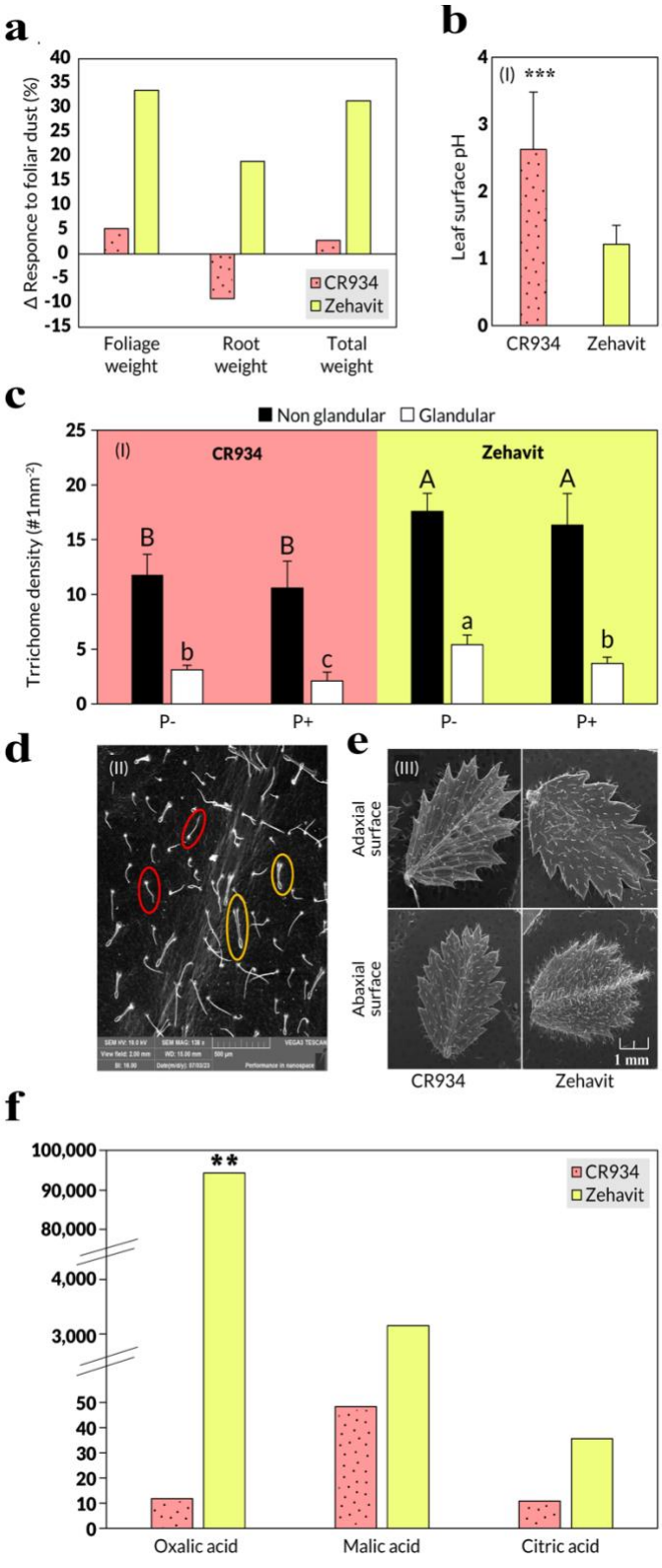
a
Δ Responce to foliar dust (%)
CR934
Zehavit
Foliage weight
Root weight
Total weight
b
(I) ***
Leaf surface pH
CR934
Zehavit
c
Non glandular
Glandular
(I)
CR934
Zehavit
Trrichome density (#1mm-2)
P-
P+
P-
P+
d
(II)
e
(III)
Adaxial surface
Abaxial surface
1 mm
CR934
Zehavit
f
**
CR934
Zehavit
Oxalic acid
Malic acid
Citric acid

Figure 2. Comparison of two chickpea varieties - CR934 (dotted, pink) and Zehavit (yellow) and their leaf properties under dust foliar fertilization. **(A)** Biomass and P uptake response to foliar dust P. Each column indicates the difference Δ (%) between the foliar dusted plants and the control untreated plants (n=6). **(B)** (I) Leaf surface pH. Each value indicates an average of five measurements on a plant throughout the growth season in control treatment (n=90), and two measurements in foliar dust treatment (n=10). One asterisk indicates significant differences between treatments using a T-test, and a one-way ANOVA ($P \leq 0.05$). Three asterisks indicate significant differences between treatments using a T-test, and a one-way ANOVA ($P \leq 0.001$). **(C)** Leaf Glandular (black column) and non-glandular (please add a dash to the Non glandular in the figure and change it to Non-glandular) (white column) trichrome density in CR934 and Zehavit control plants (-P and +P). Different letters indicate significant differences between varieties and treatments using Tukey-HSD test ($P \leq 0.05$) (n=12). Capital letters refer to non-glandular trichomes and small letters refer to glandular trichomes. **(D)**. SEM scans of non-glandular (red circles) and glandular (yellow circles) trichomes of typical Zehavit leaf. **(E)**. SEM scans of leaves of CR934 (left) and Zehavit (right) varieties. The Zehavit clearly shows higher density of trichomes in the abaxial surface, rendering it as more fit to extract nutrients from dust particles. **(F)**. Exudates of organic acids. Each column indicates the average of leaf washing from four plants, in -P control treatment (n=4). Two asterisks indicate significant differences between treatments using a T-test, and a one-way ANOVA ($P \leq 0.01$). Values are concentrations compared with an internal standard.

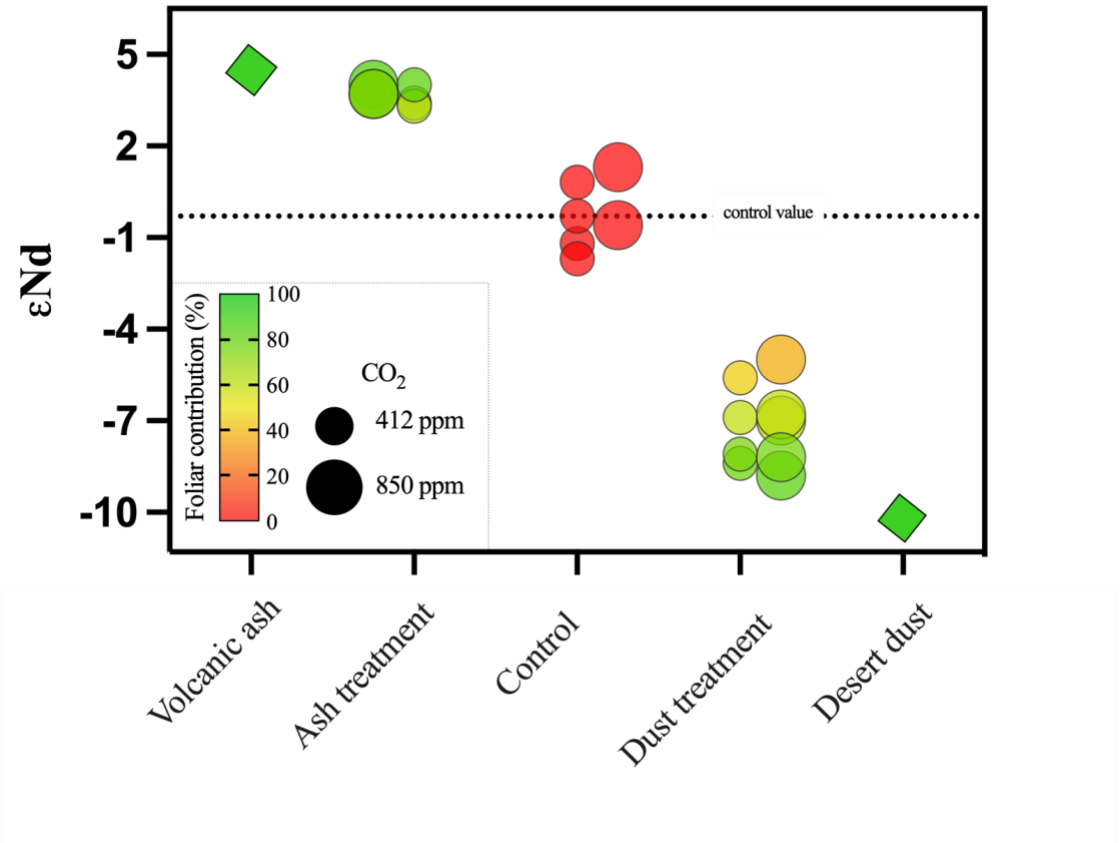

Figure 3. Quantification of dust mineral-nutrient flux from the foliage. Radiogenic isotopic ratios of $^{143}Nd/^{144}Nd$ in the different sample groups (x-axis) expressed in εNd values. Diamonds represent the two applied mineral fractions of volcanic ash and desert dust; circles represent plants treated with the dusts and the control groups. Large circles represent plants growing in the 850 ppm eCO_2 and small circles represent the 412 ppm aCO_2. The color scale reflects the % contribution of Nd originating from the dusts via the foliage, which was calculated using a two-component mixing model. The control plants' Nd signature reflects the inheritance value from the seed, where a value of εNd=-0.3 is set as the control, εNd=-10.3 as the desert dust value, and εNd=4.6 as the volcanic ash value. A foliar contribution of more than 60% is evident in the plants applied with desert dust and more than 70% in the plants applied with volcanic ash. Standard errors on the isotopic values are all smaller than the depicted data points.

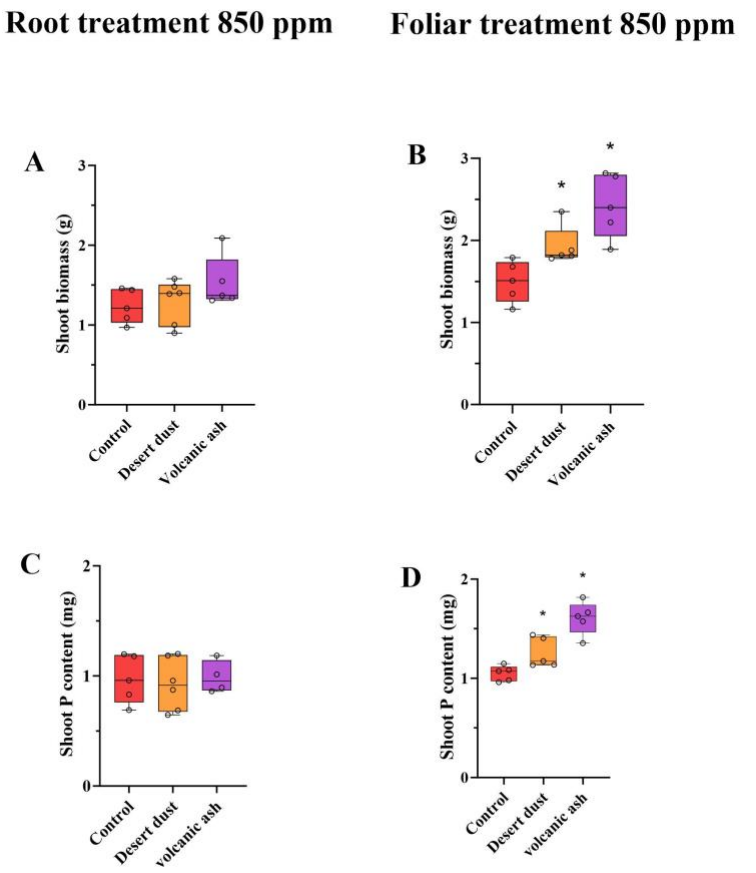

Figure 4. Biomass and P content increases due to dust application treatments at eCO_2 of 850ppm. **(A)** Shoot biomass of root treated plants. **(B)** shoot biomass of foliar treated plants. **(C)** Shoot P content of root treated plants. **(D)** Shoot P content of foliar treated plants. The asterisk denotes statistically significant difference from the control. The biomass and P content in the root treated plants do not show increases compared with the control groups. However, the foliar treatment of both desert dust and volcanic ash caused significant increases in the shoot biomass and P content. This implies that plants acquire P from fresh dust deposits on their foliage and not from the root system. Colors: red – control plants, orange – desert dust treatment, and purple – volcanic ash treatment.

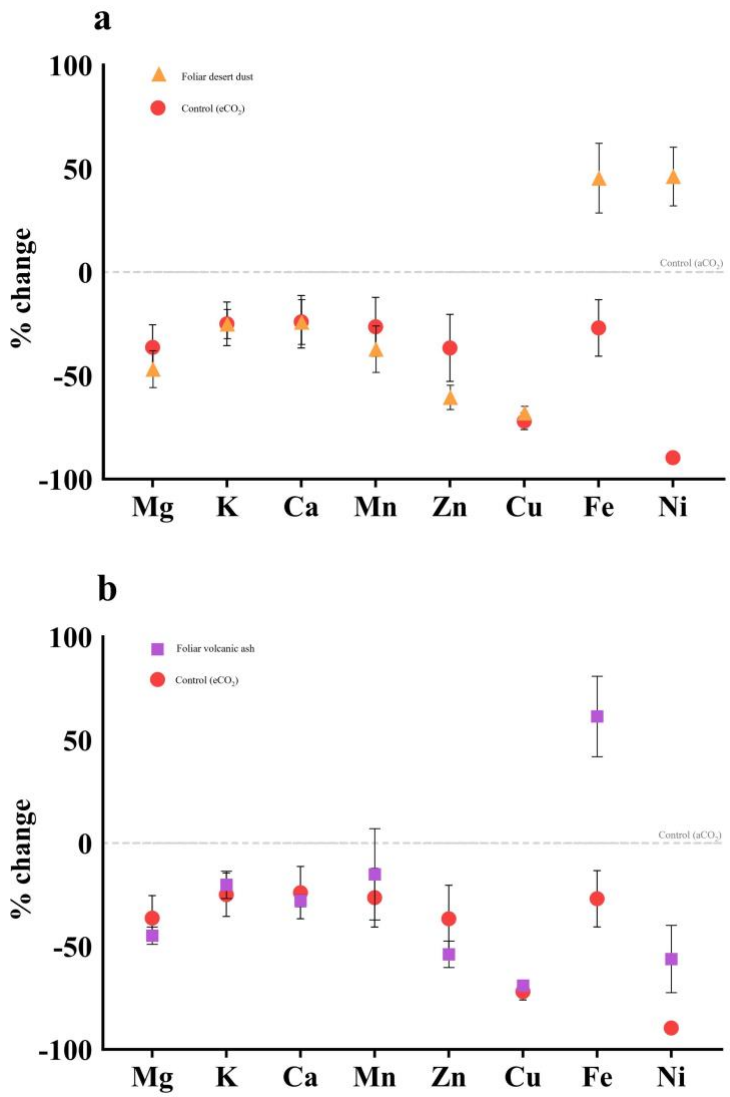

Figure 5. Comparison of the % change in plant ionome of our experiments under various conditions compared with ambient CO2 control plants. Changes in nutrient concentrations of control eCO_2 plants (red circles) show that eCO_2 conditions deteriorate plant root uptake significantly. **(A)** The effect of foliar treatment of desert dust (orange triangles). **(B)** The effect of foliar treatment of volcanic ash (purple squares). Error bars denote SD. Both desert dust and volcanic ash treated plants show that the ability of plants to uptake nutrients from the foliage will replenish, and even increase, concentrations of Fe and Ni in a possible future earth, hence mitigating the plant nutrient reduction caused by elevated CO_2.

Supplementary Text

Soil pot experiments

We performed a parallel experiment under aCO_2 conditions to test whether our findings also apply for natural soil conditions. The conditions and experimental design were identical to the perlite medium experiments. The only difference was that instead of perlite we used local sandy “Hamra” soil that is common in the Israeli costal plains. Chemical analysis of the sandy soil showed that the total P concentration was very low (less than 50 µg per g), and mostly in unavailable Ca-P bounded forms. Six plants were fertigated with low P solution: two were used as the control group, two plants were applied with desert dust on their foliage, and two plants had desert dust applied to their roots. The soil was gently mixed to let the fresh dust settle deeper towards the roots system.

The results of this experiment confirmed the results of the main experiment. The root treated plants showed biomass and P content identical to the control group whereas the foliar treated plants show increases in biomass (**Fig. S1**). This experiment indicates that over a short timescale (few weeks), mineral nutrients from dust are not acquired via the roots system, rather they are only acquisitioned via the foliage.

Dust holding capacity

One of our challenges in conducting dust application experiments, is to quantify the dust interacting with the foliage, as not all the dust that was sprinkled remains on the leaves. Quantifying the dust that interacts with the foliage will allow to distinguish the plant variants that are more capable and fit to acquire mineral nutrients from their foliage. Furthermore, this quantification will enable to determine the optimal dust coverage/weight with minimum decreases in photosynthesis and maximum mineral nutrient acquisition.

The estimate that we used is the dust holding capacity, i.e., a visual evaluation of the dust coverage following application of 1g of dust. The values were given to plants by the same person and range between 0-5, where 0 had no dust visible on the leaves and 5 was fully covered by dust. This method can only be used within one species between different variants. In our chickpea lines experiment where we compared two variants, one wild type (CR934, inefficient) and a common domesticated variety (“Zehavit”, efficient), we noticed differences between the two varieties where the CR934 received a value of 2 and Zehavit received a value of 3 (**Fig. S3**).

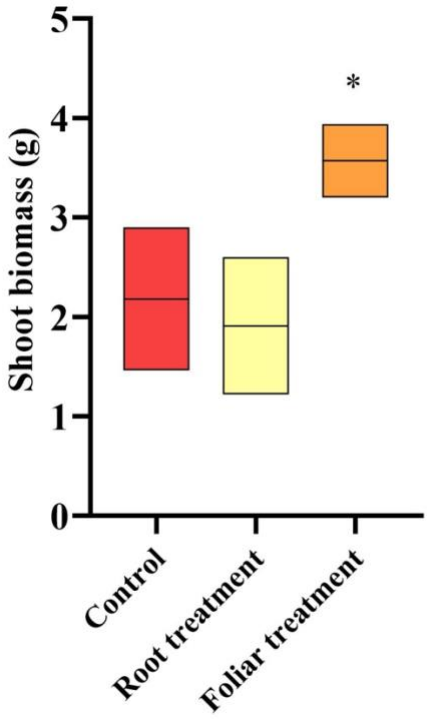

Fig. S1. Shoot biomass of experiment setting on sandy soil. Control plants (red, no dust application), plants that were applied with desert dust on the roots (yellow, root treatment), and on the foliage (orange, foliar treatment) that were grown on local natural soil. The foliar treated plants show an increase in biomass whereas the root treatment does not. This suggests that mineral nutrient uptake via the foliage is the only mechanism that enables plants to uptake nutrients from freshly deposited dust.

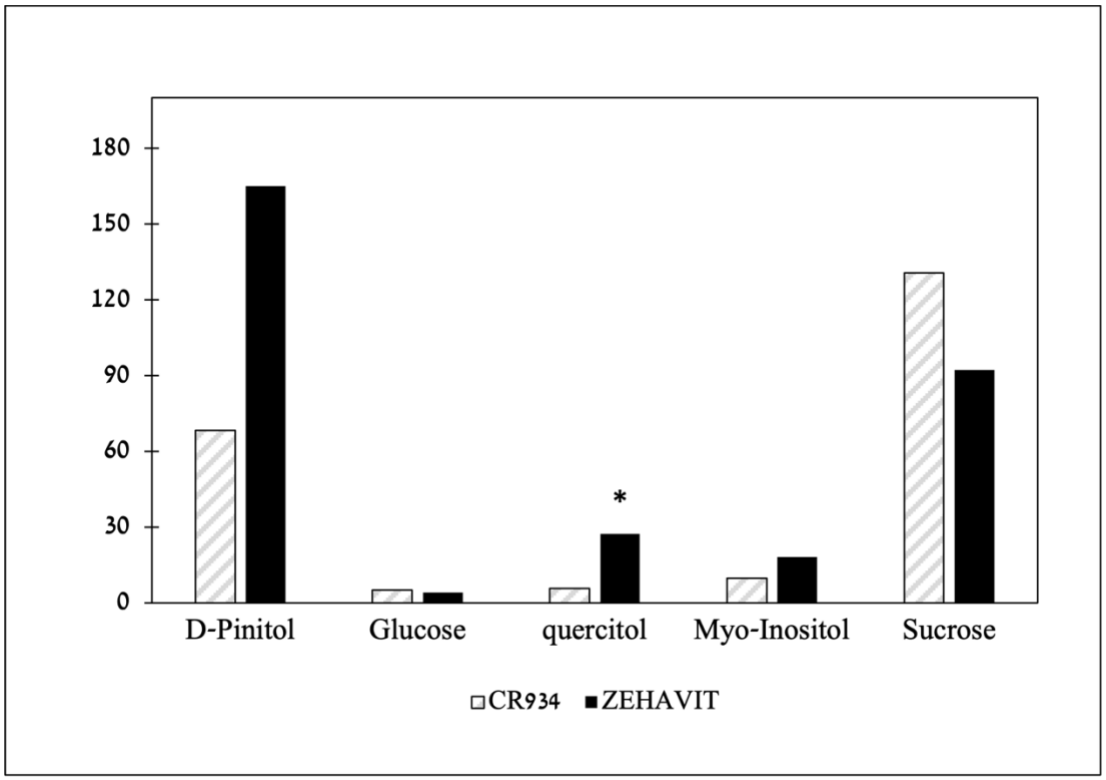

Fig. S2 Phyllosphere sugars profile when compared to an internal lab standard. Values on the y axis are relative to the standard.

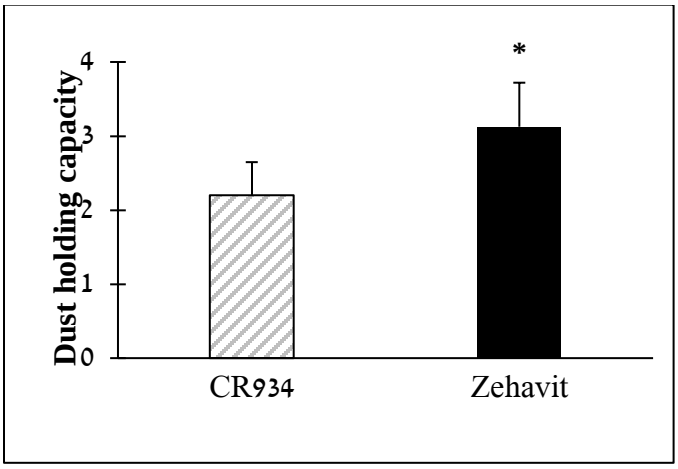

Fig. S3. Dust holding capacity in two chickpea types. The wild CR934 showed less dust following dust application compared with the cultivated Zehavit. This is probably due to higher density of trichomes and their properties (see Fig. 2 in main paper).