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Foliar nutrient uptake from dust sustains plant nutrition

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Abstract

Mineral nutrient uptake from soil through the roots is considered the exclusive nutrition pathway for vascular terrestrial plants. Recently, desert dust was discovered as an alternative nutrient source to plants, through direct uptake from dust deposited on their foliage. Here we studied the uptake of nutrients from freshly deposited desert and volcanic dusts by chickpea plants under ambient and future elevated levels of atmospheric CO_2, through the roots and directly through the foliage. We found that within weeks, chickpea plants acquired phosphorus (P) from dust only through foliar uptake under ambient conditions, and P, Iron (Fe) and Nickel (Ni) under elevated CO2 conditions, significantly increasing their growth. Using additional chickpea variety with contrasting leaf properties we have shown that the foliar nutrient uptake pathway from dust is facilitated by leaf surface chemical and physiological traits such as low pH and trichome densities. We analyzed Nd radiogenic isotopes extracted from plant tissues after dust application to assess the contribution of mineral nutrients that were acquired through the foliage. Our results suggest that foliar mineral nutrient uptake from dust is an important pathway, that may play an even bigger role in an elevated CO_2 world.

Keywords: plant nutrition; Nd isotopes; hidden hunger; foliage; elevated CO_2

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Introduction

Vascular plants obtain carbon (C) from the atmosphere and most of their mineral nutrients 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 (Marschner et al., 1997). Evidence gathered in recent decades demonstrates that the atmosphere is an important source for mineral-nutrients to terrestrial ecosystems via dust deposition (Chadwick et al., 1999; Goll et al., 2023; Gross et al., 2015; Van Langenhove et al., 2020; Okin et al., 2004; Palchan et al., 2018). The concentration of P (and other nutrients) in mineral atmospheric particles such dust and volcanic ash are enriched relative to most soils and are important plant nutrient source, especially when soil fertility is low or in dusty regions (Arvin et al., 2017; Bauters et al., 2021; Ciriminna et al., 2022; Eger et al., 2013; Gross et al., 2016b). In a montane environment in California, dust P contribution to plants was documented to outpace the contribution from weathering of host bedrock (Arvin et al., 2017). In a recent study we discovered that certain crop plants can gain P directly from the atmospheric dust, via particles that accumulate on their leaves (Gross et al., 2021a; Lokshin et al., 2024b). Over short time scales, foliar uptake was found as the only P uptake pathway from biomass fire ash particles (while the roots played a negligible role (Lokshin et al., 2024a, b). These recent findings highlights the need to better understand the role of the contribution of nutrient uptake from dust through the foliage (i.e., direct foliar nutrient uptake), a process that has been traditionally overlooked and has never been quantified before, even though foliar fertilization has been a well-known agricultural practice for many decades (Fageria et al., 2009; Ishfaq et al., 2022; Bukovac & Wittwer, 1957; Wittwer & Teubner, 1959). In the context of climate change, the foliar pathway may be even more pronounced for plants that will grow under elevated CO_2 (eCO_2) conditions because of two documented phenomena: the 'dilution' effect, where accumulation of C exceeds that of mineral nutrients (Loladze, 2014), and partial inhibition of key root uptake mechanisms (Gojon et al., 2023), together with soil fertility degradation (Lal, 2009; St.Clair and Lynch, 2010). These changes will drive plants to adapt and search for other nutrient uptake pathways. The use of the foliar pathway under eCO_2 may offset the alarming phenomenon where an increasing production of carbohydrates causes dilutes the concentration ofmacro 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 (Clarkson and Hanson, 1980) and for their dependent human and livestock nutrition (Lal, 2009; Loladze, 2002; Lowe, 2021).In this experiment, we cultivated C3 chickpea plants (specifically the 'Zehavit' variety, a widely grown modern cultivar) under both current atmospheric CO_2 concentrations and elevated CO_2 conditions in a controlled glasshouse environment. The primary objective was to demonstrate, describe and quantify nutrient uptake via the leaves. We introduced two distinct types of mineral dust to the plants, applying them either to the surface near the root zone or directly onto the leaves. The two dust types were representative of major atmospheric particulate matter sources, namely desert-derived dust and volcanic ash (referred to as "dust" hereafter), with average annual global emissions estimated at 3,000 Tgy^{-1} and 300 Tgy^{-1}, respectively (Kok et al., 2021; Langmann, 2013a).

We studied leaf traits that facilitate the foliar nutrient uptake from dust, its impact on plants' ionome (i.e., plant elemental status), and used Nd radiogenic isotopes, present within the dust particles and characterized by distinct isotopic values, to quantify the contribution of the foliar pathway. In addition, we used a non-responsive genotype, 'CR934', of the wild progenitor C. reticulatum, to study the impact of dust deposition on plant nutrition and

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compare leaf properties under dust foliar fertilization between the modern chickpea cultivar and its wild counterpart.

Materials and Methods

Experimental design

To study the impact of dust deposition on plant nutrition, two chickpea genotypes (*Cicer*) from the Hebrew University of Jerusalem chickpea collection were selected based on preliminary experiments, showing contrasting response to foliar dust application (Gross et al., 2021b). The non-responsive genotype: 'CR934', of the wild progenitor *C. reticulatum* accession, sampled near Savur, Turkey. And the responsive genotype 'Zehavit' that is a modern, high yield line, and considered popular among the Israeli growers. To test the biogeochemical response of the foliar nutrient uptake we used the 'Zehavit' genotype. Experiments were conducted at Gilat Research Center in southern Israel (31°21' N, 34°42' E) in two separate glasshouse rooms. In one room we set the CO_2 concentration to the ambient 412 ppm (aCO_2) and in the other room to elevated 850 ppm (eCO_2), simulating current and future earth CO_2 concentrations based on high emissions scenario (business as usual, SSP 8.5, IPCC, 2021). 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 pot size was 3 litter, with sufficient room for root growth during the experimental period. The description of the growing conditions and fertigation nutrient supplement is provided in Lokshin et al. (2024a).

At 14 days after germination, when plants were early in the vegetative phase (two or three developed leaves), we changed the nutrient solution of 60 out of the 72 pots to P deficient fertigation (P concentration of 0.1 mg L^{-1}) to create P starvation (-P treatment). Preliminary tests showed that our -P deficient media allows chickpea plants to continue their growth cycle and increase their responsiveness for dust application and eCO_2 condition (Gross et al., 2021, Lokshin et al., 2024). The remaining 12 pots continued to receive the full P sufficient 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 days after germination. At this stage we applied desert dust and volcanic ash on the -P plants.

Of a total number of plants (72) 48 were treated with dust and 24 served as untreated control group. Twenty-four plants were applied with dust on their foliage by manually sprinkling dust through a 63μm sieve in proximity to the foliage and 24 plants received root treatment by applying dust through a 63 μm sieve on the surface of the pot, followed by gentle mixing of the surface to sink the dust particles deeper to enhance the physical contact between the roots and the particles, thereby increasing the chances of having a more significant impact. Among the control plants, 12 plants received the +P fertigation and 12 additional plants received -P fertigation. Each treatment group was divided into two CO_2 levels, 36 plants in each CO_2 growing room. The plants were harvested 10 days after the last dust application (55 days after germination). To ensure that nutrients from dust particles were not washed by the irrigation during the experiment, we monitored the total P (i.e., P that dissolves in strong acid) in the water that drained from the pots (Longo et al., 2014; Gross et al., 2015) throughout the experiment.

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We performed a parallel experiment under aCO_2 where we grew six additional plants, in larger 5 L pots, filled with soil, to test whether our findings also apply to natural soil conditions (Fig. S1).

Mineral dust material

We applied plant foliage and the area near plants' roots, with desert dust and volcanic ash, the two main mineral dust types in the atmosphere (Langmann, 2013b). To achieve enough mass for our experiment, we produced dust analogs from surface desert soil and surface volcanic ash soil, following common procedures described by others (Gross et al., 2021b; Stockdale et al., 2016). The desert dust analog surface soil was collected from the southern Israel Negev desert (30°320N 34°550E) (Gross et al., 2021b). Chemical and mineralogical properties of the resulted dust are comparable to dust collected in the Sahara and other places in the Middle East (Gross et al., 2016a; Palchan et al., 2018). The volcanic ash analog was collected from Mount Etna (Sicily, Italy) two month after the eruption of 21 February 2022. The ash was taken from the upper cable car station "Funivia 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 (Guieu et al., 2010). The chemical and mineralogical properties of the dust analogs are presented in 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 days after germination. Total application mass was 3 g per plant, to simulate the total dust deposition per m^2 for an average growth period in southern Israel (Gross et al., 2021b). Dust treatments were done either directly on the foliage while covering the pot, preventing the dust from touching the roots, or directly on the roots where the pots were subsequently covered with nylon to equalize conditions with the foliage treated plants. Afterwards, the plants were left undisturbed with the settled dust particles on their foliage or surface of the root area.

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 (Gross et al., 2021; Lokshin et al., 2024a). To ensure that the washing procedure removed all the applied dust particles from the leaf surfaces, we scanned surfaces of randomly selected dusted and washed leaves with SEM-EDS which combines scanning electron microscope and energy-dispersive X-ray spectroscopy to detect and analyze materials. After washing, plant tissue was dried, weighed and root and shoot biomass were recorded. Afterwards, the dry shoot material was ground to powder and dry ashed at 550 C° in a furnace for four hours (Tiwari et al., 2022). Approximately 1g of the ashed material was subsequently dissolved using 1 mL 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 (Palchan et al., 2018). The elemental composition of the plants, dusts and nutrient solution were analyzed at the Hebrew University using 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

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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.

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.

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.

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).

Nd isotope chromatography and analysis

Nd isotopes were measured on the dusts and in the above ground plant material at the end of the experiment. Nd was extracted from the samples using TRU followed by LN-spec resins (Palchan et al., 2013). 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 $^{143}Nd/^{144}Nd = 0.512115$ (Tanaka et al., 2000). Rock standards samples of BCR-2 were dissolved and measured along with the plant and dust samples yielding

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$^{143}Nd/^{144}Nd$ value of 0.512628 ± 6 (2σ) that agrees with $^{143}Nd/^{144}Nd$ = 0.512637 ± 13 value of BCR-2 (n=3)(Jweda et al., 2016) . 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 (Wasserburg et al., 1981). A sample isotopic characterization is given in SI Table 4. The percent contribution of Nd within the leaves that comes either from desert dust or volcanic ash (foliar contribution) was 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 $\varepsilon Nd_{\text{sample}}$ refers to plants that were treated either with desert dust or volcanic ash with, $\varepsilon Nd_{\text{control}}$ refers to the untreated control plants and $\varepsilon Nd_{\text{endmember}}$ are the measured end member values of -10.3 for desert dust or 4.5 value for volcanic ash (Table SI-4 & Fig. 4).

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°.

Statistical Analysis

Treatment comparisons for all measured parameters were tested using post-hoc Tukey honest significant difference (HSD) tests ($P < 0.05$). The significant differences are denoted using different letters in the figures. The standard errors of the mean in the vertical bars (in the figures) were calculated using GraphPad Prism version 9.0.0.

Results

Plant biomass and total P under aCO_2 and eCO_2

P starvation did not reduce P concentration in shoots but rather decreased shoot biomass gain. In addition, eCO_2 had no impact on P concentration or shoot biomass gain in the control -P plants, but significantly increased shoot

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biomass gains in +P treated plants (Table 1). Thus, the treatment effects are reflected by changes in total plant P (concentration multiplied by shoot biomass). The impact of desert and volcanic dust application on plants' foliage was reflected by the increase of their total P content through shoot biomass gain rather than through changes in shoot P concentration. Under aCO_2 conditions, desert dust application resulted in shoot biomass and total P content increases of 35% and 21%, respectively, and volcanic ash application resulted in 28% and 35% increases, respectively (Fig. 1 d,f). The root-treated plants did not show any increases in the shoot biomass or total P content (Fig. 1 c,e). These trends are also seen in the eCO_2 conditions of 850 ppm atmospheric CO_2 experiment. Desert dust application resulted in shoot biomass and total P content increases of 29% and 20%, respectively, and volcanic ash application resulted in 62% and 51% shoot biomass increases, respectively (Fig. 2 d, f). Similarly, the root-treated plants did not show any increases in the shoot biomass or total P content (Fig. 2 c, e). Unlike the shoots, no significant changes of the biomass of the roots were detected across all treatments, thus changes in the root shoot ratio reflect variations in shoot biomass rather that root biomass (Table 1).

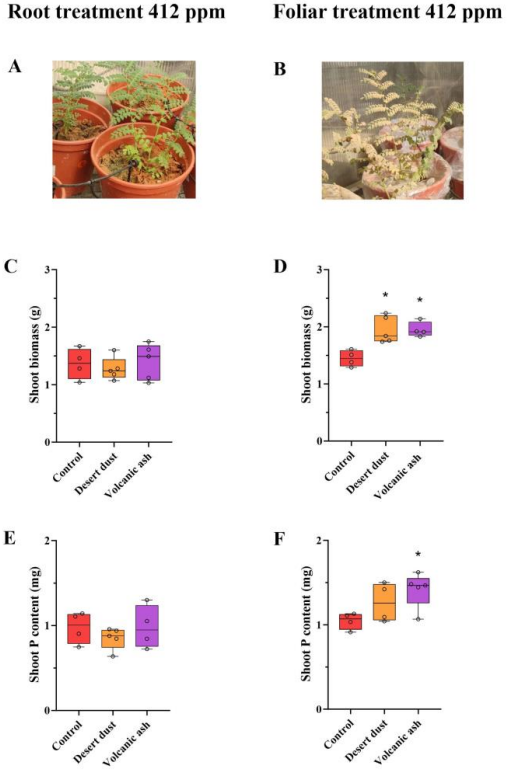

Fig. 1 Biomass and total P content increases due to dust application treatments at aCO_2 of 412ppm. (a) Image of experiment setting of the root treatment. (b) Image of experiment setting of foliar treatment. (c) Shoot biomass of root treated plants. (d) Shoot biomass of foliar treated plants. (e) Shoot total P content of root treated plants. (f) Shoot total P content of foliar treated plants. The asterisk denotes statistically significant difference from the control. The biomass and total P content in the root

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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 total 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.

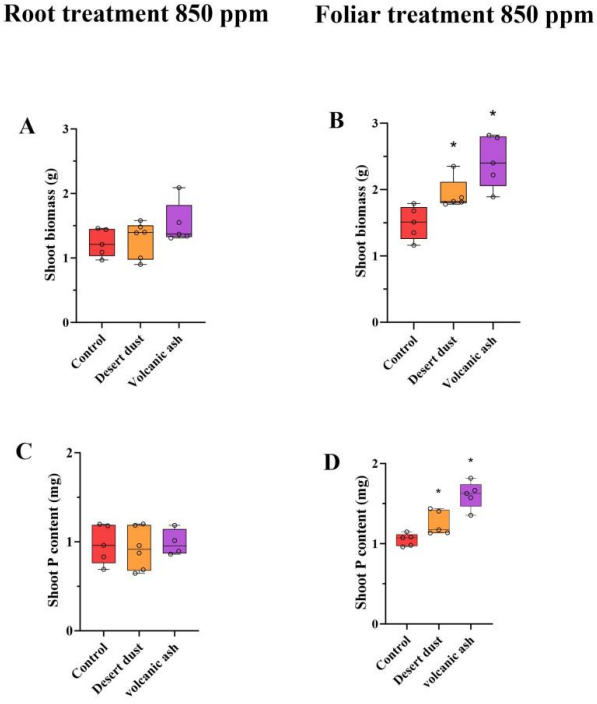

Fig. 2 Biomass and total P content increases due to dust application treatments at eCO_2 of 850ppm. (a) Shoot biomass of root treated plants. (b) shoot biomass of foliar treated plants. (c) Shoot total P content of root treated plants. (d) Shoot P content of foliar treated plants. The asterisk denotes statistically significant difference from the control. The biomass and total 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 total 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.

Elemental analysis of the plants

The concentrations of selected micro and macro nutrients that build plants ionome, together with plants shoot biomass, are given in Table 1.

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Table 1 Total elemental analysis of the plants (*Cicer arietinum cv 'Zehavit'*) fertilizers and dusts (ICP-MS analysis). The concentration of the different micro and macro elements are shown in ppm and plant biomass in g.

Plant material (ppm)	Shoot biomass (g)	Root biomass (g)	Root/Shoot ratio	Mg	P	K	Ca	Mn	Fe	Ni	Cu	Zn
Control -P 412 #1	1.03	0.91	0.89	2749	715	21928	7257	52	75	1.3	2.9	22.9
Control -P 412 #2	1.29	0.95	0.74	2828	860	21147	7266	45	112	2.3	10.8	23.5
Discarded plant												
Control -P 412 #4	1.51	1.36	0.90	2814	686	23832	7462	33	97	2.4	3.7	21.9
Control -P 412 #5	1.38	1.22	0.88	2863	663	21883	7684	38	94	1.0	2.7	23.7
Control -P 412 #6	1.61	1.39	0.87	2513	704	19705	6531	19	69	1.3	3.3	23.4
Control -P 850 #1	1.35	1.02	0.75	2585	727	23099	6323	22	71	1.0	1.9	23.4
Control -P 850 #2	1.16	1.02	0.88	3848	827	27768	7922	61	79	0.2	2.8	38.9
Control -p 850 #3	1.79	1.39	0.78	2785	607	20121	7118	50	67	1.2	2.5	24.9
Discarded because plant did not grow/withered												
Control -P 850 #5	1.51	1.25	0.82	2847	759	27272	7572	21	88	2.2	4.7	26.4
Control -P 850 #6	1.68	1.44	0.86	3180	640	24460	8732	31	93	1.6	2.9	29.1
desert dust foliar-trated 412 ppm #1	2.24	1.65	0.74	2490	1458	23743	7040	47	125	0.9	2.6	21.9
desert dust foliar-trated 412 ppm #2	1.74	1.44	0.83	2450	628	19416	6715	29	102	0.6	2.0	19.2
desert dust foliar-trated 412 ppm #3	1.76	1.57	0.90	2326	855	17424	6576	27	97	1.0	2.3	20.5
desert dust foliar-trated 412 ppm #4	2.16	1.87	0.87	2224	658	17576	6060	28	101	1.1	3.3	23.2
desert dust foliar-trated 412 ppm #5	1.84	1.33	0.72	2611	566	21928	6817	40	116	1.1	3.0	20.3
Discarded because plant did not grow/withered												
desert dust foliar-treated 850 ppm #1	1.82	1.18	0.65	2274	626	21092	6599	26	151	2.2	2.8	22.1
desert dust foliar-treated 850 ppm #2	1.78	1.58	0.89	2083	808	20320	5877	34	125	1.9	3.7	17.1
Discarded because plant did not grow/withered												
desert dust foliar-treated 850 ppm #4	2.35	1.52	0.65	2182	482	20380	7336	43	135	2.2	3.4	18.6
desert dust foliar-treated 850 ppm #5	1.81	1.57	0.87	2995	648	24419	8366	39	169	2.4	3.5	25.0
desert dust foliar-treated 850 ppm #6	1.88	1.92	1.02	2848	749	24303	8087	39	144	3.4	3.2	21.1
volcanic ash foliar-treated 412 ppm #1	1.91	1.44	0.75	2499	755	20825	6058	34	137	0.6	3.0	18.1
volcanic ash foliar-treated 412 ppm #2	2.14	1.74	0.81	2655	691	22032	6993	50	317	1.5	3.0	25.7
volcanic ash foliar-treated 412 ppm #3	1.41	1.00	0.71	2524	757	18830	8067	49	148	1.0	2.9	20.8
Discarded because plant did not grow/withered												
volcanic ash foliar-treated 412 ppm #5	1.83	1.30	0.71	2814	800	23818	7121	40	177	1.4	3.5	23.7
volcanic ash foliar-treated 412 ppm #6	1.92	1.49	0.78	2811	844	23122	7359	47	162	1.1	3.5	23.0
Discarded because plant did not grow/withered												
volcanic ash foliar-treated 850 ppm #2	2.22	1.85	0.83	2289	818	22549	6623	34	149	0.6	3.0	19.9
volcanic ash foliar-treated 850 ppm #3	2.82	2.48	0.88	2365	558	23525	6848	41	373	2.4	3.4	18.2
volcanic ash foliar-treated 850 ppm #4	2.40	2.19	0.91	2717	692	25778	7020	60	173	1.0	3.5	26.1
volcanic ash foliar-treated 850 ppm #5	1.89	1.38	0.73	2584	718	24440	6722	43	140	0.7	3.0	23.5
volcanic ash foliar-treated 850 ppm #6	2.78	2.37	0.85	2689	585	21384	7224	59	181	0.4	3.3	27.6
Control +P 412 #1	10.46	3.33	0.32	5138	2465	30660	9429	79	161.3	1.1	5.1	51.2
Control +P 412 #2	11.69	5.07	0.43	3729	2101	26096	7892	49	111.1	0.4	4.6	37.2
Control +P 412 #3	11.47	4.44	0.39	6540	2148	29291	9076	69	88.9	0.7	4.3	43.5
Control +P 412 #4	10.06	3.39	0.34	3322	1982	23933	6871	36	82.0	0.4	3.8	28.4
Control+P 412 #5	10.76	3.94	0.37	3415	1804	23800	6970	44	95.5	0.4	4.1	33.1
Control +P 412 #6	10.02	3.88	0.39	5147	2240	27966	8384	50	95.0	0.5	4.6	38.5
Discarded plant												
Control +P 850 #2	13.40	7.24	0.54	3759	2253	26837	7886	59	91.4	0.8	3.8	32.6
Discarded plant												
Control +P 850 #4	17.17	7.29	0.42	3202	2196	25021	8052	68	96.6	0.8	5.9	30.5
Control+P 850 #5	17.51	10.85	0.62	3633	2258	27403	8860	67	97.0	0.7	4.1	31.7
Control +P 850 #6	15.86	6.55	0.41	5488	2959	30362	11394	100	109.5	0.9	4.9	50.5
Fertilizers and dusts (ppm)												
+P fertilizer				1226	713	6000	11	76	151	0.4	5.6	50.1
-P fertilizer				1214	35	7808	7	70	136	0.4	5.1	47.5
Desert dust				6513	1387	8673	136081	245	12745	18.0	10.0	39.0
Volcanic ash #1				23534	1669	12514	64461	1097	63736	49.5	118.6	80.0
Volcanic ash #2				22648	1788	12056	61628	1066	61903	48.3	115.6	73.7

Physiological adaptations toward foliar uptake

The domesticated variety 'Zehavit' showed a strong response to the foliar treatment with up 35% increased biomass compared to the control group, whereas the wild variety CR934 showed up to 5% increases compared with the control group (Fig. 3a). The leaf pH of the Zehavit was 1.15 and of the CR934 it was 2.7 (Fig. 3b),

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trichome density, both glandular and non-glandular, were higher in the Zehavit compared to the CR934 (Fig. 3c-e). The exudates of oxalic, malic, and citric acids were significantly higher at the Zehavit in comparison to CR934 (Fig. 3f). The results indicate increased biomass, lower pH, higher trichome density, and higher exudate levels in the 'Zehavit' variety.

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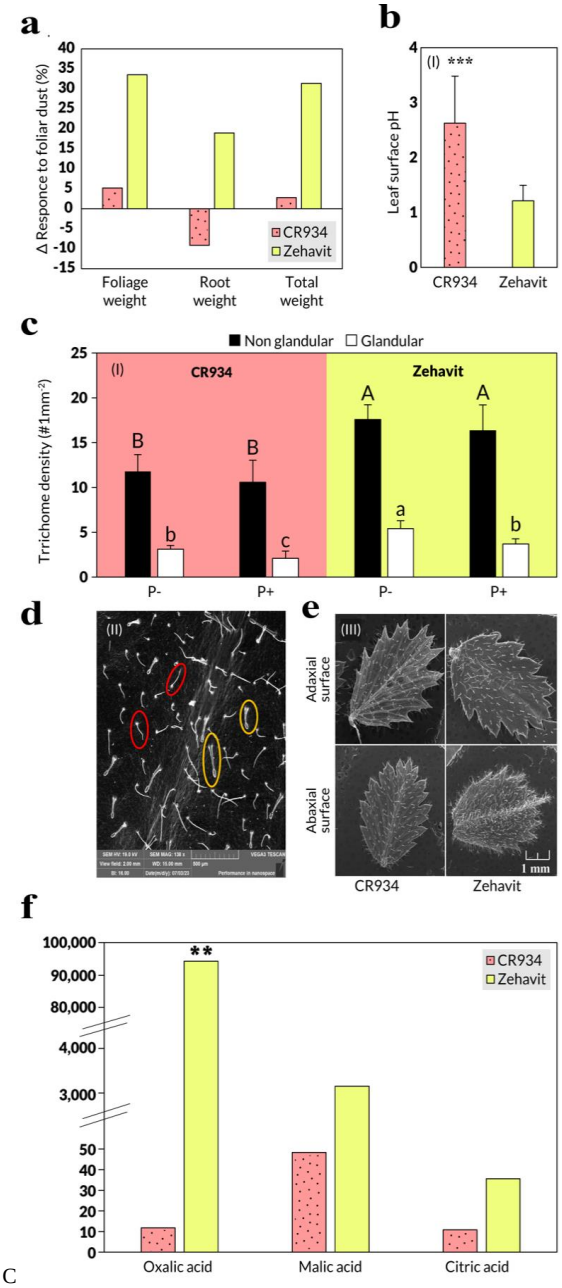

Fig. 3 Comparison of two chickpea varieties - CR934 (dotted, pink) and Zehavit (yellow) and their leaf properties under dust foliar fertilization. (a) Biomass and P uptake response to foliar dust P. Each column indicates the difference Δ (%) between the foliar dusted plants and the control untreated 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 non-Glandular (black column) and 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.

C

Nd isotopic analysis of the dusts, control plants and the treated plants

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 Nd to plants as an indirect measure of dust nutrient transfer (Fig. 4). The mineral dust

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analogues presented εNd values of 5 and -11 for the volcanic ash and the desert dust, respectively. Plant material εNd values of the control plants, that reflect the inheritance value (i.e., arising from the seed Nd isotope composition) was -0.3, desert dust treated plants were characterized with values of -8.8 to -5, and the volcanic ash treated plants were characterized with values of 3.4 to 4. Both treated plant groups are significantly different than the inheritance value of -0.3 characterizing the control group.

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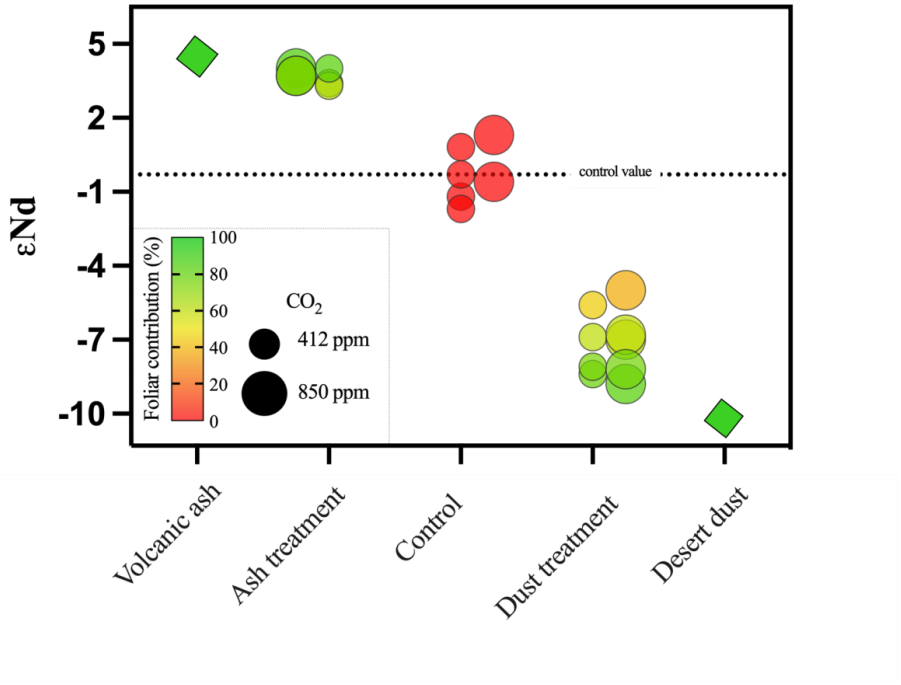

Fig. 4 Quantification of dust mineral-nutrient flux from the foliage. Radiogenic isotopic ratios of $^{143}Nd/^{144}Nd$ in the different sample groups (x-axis) expressed in εNd values. Diamonds represent the two applied mineral fractions of volcanic ash and desert dust; circles represent plants treated with the desert and volcanic 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.

Discussion

Foliar mineral-nutrients uptake

In our experiments, we simulated desert dust and volcanic ash deposition by manually applying them on chickpea plants (*Cicer arietinum cv 'Zehavit'*). The dust was applied separately either on the surface of the pot near the roots, or 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 total P content in the foliage-treated plants had increased, following dusts treatment, compared with the control group. In contrast, the root-treated plants did not show any increases in the biomass or P content, suggesting that over short timescales (i.e., several

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weeks), foliar uptake is the only nutrient uptake pathway from freshly deposited dust (Fig. 1c, e). These results were then replicated when a similar experiment was conducted with plants grown on sandy soil, in bigger pots (Fig. S1), emphasizing that our observations are not limited to the specific artificial experimental conditions in perlite (which may bias root behavior), but also apply for real soil conditions (Fig. S1).

Plant strategies for foliar mineral-nutrient uptake

Most of the P in the dusts is incorporated in the mineral lattice of minerals such as apatite (Dam et al., 2021), which is largely insoluble under the natural rhizosphere pH range (Hinsinger, 2001)(Hinsinger, 2001). Hence, P in volcanic or desert dust has low bioavailability for root uptake as was also shown in Lokshin et al, (2024a) with fire ash. On the leaf surface however, chemical, morphological, and microbial modifications may promote nutrient solubility and bioavailability and thus enable uptake through the leaf surface (Gross et al., 2021; Muhammad et al., 2019)(Gross et al., 2021; Muhammad et al., 2019). Examining two chickpea varieties with contrasting responses to dust application: wild variety CR934, and common domesticated variety Zehavit, we found a few properties that facilitate foliar P acquisition from dust **(**Fig. 3). These include structural, morphological, and chemical modifications that are comparable to those reported in the rhizosphere (Hinsinger, 2001)(Hinsinger, 2001). The foliar-uptake-efficient variety Zehavit has significantly more acidic leaf surface (pH ~ 1, Fig. 3b), and thus promotes both dissolution and mobility of P from the pH sensitive mineral apatite (Gross et al., 2015)(Gross et al., 2015), as well as other mineral-nutrients in the dust (Bradl, 2004; Gross et al., 2021; Muhammad et al., 2019)(Bradl, 2004; Gross et al., 2021; Muhammad et al., 2019). Additionally, a unique set of metabolites secreted from the leaf surface further facilitated the foliar uptake pathway in Zehavit. These include increased concentrations of oxalate and malate, which are known to release insoluble P in soils through anion exchange reactions (Lambers et al., 2019; Tiwari et al., 2022)(Lambers et al., 2019; Tiwari et al., 2022), and increased levels of sugars such as glucose and sucrose that may promote the activity of nutrient solubilizing microbes on the phyllosphere (Shakir et al., 2021)(Shakir et al., 2021) **(**Fig. 3f, fig. S2**).** We further found that Zehavit showed higher leaf trichome density on both leaf axial and adaxial sides (Fig. 3 c,d,e)**.** These trichomes facilitate the release of metabolites and promote adhesion of dust captured on leaf surfaces (fig. S3) (Gross et al., 2021)(Gross et al., 2021). 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 (Gross et al., 2021; Starr et al., 2023)(Gross et al., 2021; Starr et al., 2023). 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. Results of previous study with application of inert silicon powder on chickpea leaf surface indicate that the shading effect resulting leaf surface coverage with dust has low effect on plant growth and photosynthesis (Gross et al. (2021). Yet, the dust shading effect was more pronounced in several tree species (Starr *et al.*, 2023), suggesting the contrasting impact of coverage of the foliage should be considered.

Dust impact on plant nutrient status under eCO_2

Numerous studies reported that eCO_2 conditions reduce the concentrations of several nutrients in plant tissues such as Fe, Zn, Cu, Mn, Ni and others (Loladze, 2002; Fernando et al., 2014; Myers *et al.*, 2014; Gojon *et al.*, 2023). The reduction in shoot nutrient concentrations was also observed in our experiments (fig. 5). In accordance

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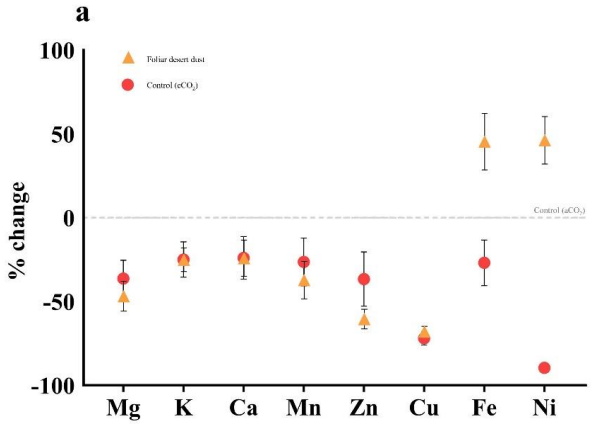
with previous knowledge (Loladze, 2002)(Loladze, 2002), plants that were grown under eCO_2 in our experiment showed a significant reduction of 10-50% in the concentrations of nutrients such as Mg, K, Ca, Mn, Zn and Fe, with even more significant reductions in Cu and Ni (72% and 90%, respectively), (Fig. 5). Although we did not observe statistically significant differences in biomass between control plants grown under aCO_2 and eCO_2 conditions (P = 0.4), the reduction in essential macro- and micronutrient concentrations may be partly explained by the effect of nutrient dilution. Another potential reason for the nutrient decline under eCO_2 could be related to reduced efficiency in mineral nutrient absorption through the root system (Gojon et al., 2023).Click or tap here to enter text.Click or tap here to enter text.. We found that foliar application of both volcanic and desert dust on plants that were grown under eCO_2 replenished their Fe and Ni concentrations (both essential micronutrients for plant growth and in the human diet) compared with the control group (fig, 5a,b). 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 increases returned Fe and Ni back to standard, nontoxic levels (Shahzad et al. 2018). These results emphasize that the role foliar uptake of atmospheric nutrients on the mineral nutrition level of plants will be greater under eCO_2 and offset the projected nutrient reduction driven by the dilution effect and the downregulation of the root's nutrient uptake pathway (Zhu et al., 2018)(Zhu et al., 2018).



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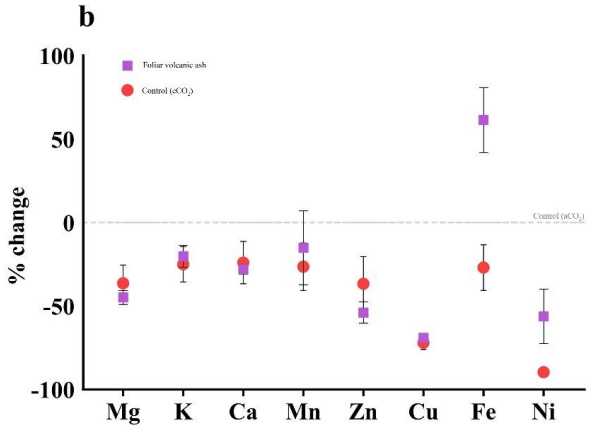

Fig. 5 Comparison of the % change in plant nutrient concentration under eCO_2 compared with aCO_2 control plants. The comparison was conducted as follows: the average value of each nutrient in plants grown under aCO2 was calculated, and then each nutrient in individual chickpea plants grown under eCO2 levels was expressed as a ratio relative to the average under aCO2 conditions (eCO_2 plant (each individual plant) /aCO_2 plant (average of all the control plants)). Changes in nutrient concentrations of the control eCO_2 plants (red circles) show that eCO_2 conditions deteriorate plant nutritional status 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.

Quantifying the contribution of foliar nutrient uptake from dust

Traditionally, radiogenic Nd isotopes serve as excellent tracers for sources of magmatic rocks (Stein and Goldstein, 1996)(Stein and Goldstein, 1996), sediment archives (Chadwick et al., 1999; Palchan et al., 2018)(Chadwick et al., 1999; Palchan et al., 2018), and water bodies (Farmer et al., 2019)(Farmer et al., 2019). Since Nd is found in high concentration in nutrient bearing minerals (Aciego et al., 2017; Arvin et al., 2017; Chadwick et al., 1999)(Aciego et al., 2017; Arvin et al., 2017; Chadwick et al., 1999), Nd isotopes were recently used to trace P sources in plant tissues, where it was shown that the contribution of dust outpaces the weathering of the local bedrock over geological time scales (Aciego et al., 2017; Arvin et al., 2017)(Aciego et al., 2017; Arvin et al., 2017). While the use of Nd isotopes to other elements such as P provides new knowledge on their sources, it should be done cautiously because different elements have differing speciation, uptake mechanisms, and transport kinetics in plant tissue. 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 its flux to plant tissue from dust. From this measurement we can approximate the flux of P, Fe and Ni via foliar pathway (Fig. 4). 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

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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. 4). However, Nd isotopes do not show the increased supplement of Fe and Ni in plants that were grown under eCO_2. Thus, more data on the relation between Nd and other nutrients uptake will advance its use in future studies to quantify the immediate contribution of freshly deposited dust on plants nutrition in field and lab experimental settings.

In conclusion, 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 on a short time scale than via the roots. Most of the P in the dust is incorporated in the mineral lattice of minerals such as apatite (Dam et al., 2021)(Dam et al., 2021), which is largely insoluble under the natural rhizosphere pH range (Hinsinger, 2001)(Hinsinger, 2001). 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 facilitate uptake through the leaf surface (Gross et al., 2021; Muhammad et al., 2019)(Gross et al., 2021; Muhammad et al., 2019). Thus, our findings highlight that dust serves as an alternative source of nutrients to plants from the foliage on short timescales of a few weeks. Furthermore, that foliar dust acquisition compensates for the reduction in nutrients such as Fe and Ni, induced by eCO_2 conditions (Gojon et al., 2023)(Gojon et al., 2023). The broader aspect of our findings emphasizes the central role of dust in plant nutrition through the foliar pathway and to global biogeochemical cycles. Our findings imply that the foliar nutrient uptake pathway from natural dust will play a central role in eCO_2 earth, and that this pathway may be a target for novel fertilization techniques to compensate for the expected decline in the crops' nutritional value.

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Author Contributions:

Conceptualization: DP, AG, RE

Dust sampling: AL, DA, AG

Methodology: DP, AG, RE

Investigation: AL, EG, SF

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Visualization: DP, AL, EG

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Project administration: DP, AG

Supervision: DP, AG, RE

Writing – original draft: DP, AG, AL, RE

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Availability Statement

All relevant data are included within the manuscript. No additional data, code, or software were used or are available beyond what is presented in the paper.

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