Dear editor,

We are happy to resubmit our paper, “Foliar nutrient uptake from dust sustains plant nutrition” (egusphere-2024-2531). We were glad to see that the reviewers appreciate the importance of the work we have done. We thank the reviewers for the time and effort invested in reviewing our manuscript. The comments provided were insightful and constructive, contributing significantly to the overall improvement of the paper.

In response to the reviewers' comments, we have made substantial efforts to revise the manuscript. Specifically, we have improved the introduction, clarified the methods, strengthened the discussion section, and toned down the conclusions. Additionally, we have added a new table summarizing all the treatments and updated the previous Table 1 to provide a clearer and more comprehensive presentation of the data.

Our responses to the reviewers are provided below in **bold.** The revised submission includes a version of the paper with a “track changes” on to make it easier for the reviewers and editor to follow the changes we have made in the text (the line and page number in our responses refers to the track changes file only).

Referee #1:

Lokshin et al. show significant foliar nutrient uptake from desert dust and volcanic ash in chickpeas grown under elevated CO2 levels. Using neodymium isotope tracers, they quantified major acquisition of P, Fe, and Ni through leaves rather than roots. This study addresses an important knowledge gap in plant nutrition mechanisms under rising CO2 scenarios.

The experimental design used controlled greenhouse conditions with continuous CO2 fumigation, providing more stable CO2 concentrations compared to traditional Free-Air CO2 Enrichment (FACE) studies, which suffer from fluctuating daytime CO2 levels and nighttime CO2 shutoffs. Furthermore, FACE studies usually have low replication (n = 3) to save on CO2 costs. In contrast, the authors had 12 replicates, if I am not mistaken.

The authors' findings are important for understanding plant nutrition in a high-CO2 world, especially given concerns about declining nutrient content in crops. The research is informative about foliar supplementation as a method to maintain crop nutritional quality under elevated CO2 conditions.

The study has limitations, some of which can be addressed:

1. The shading effect of dust particles on photosynthesis was not fully controlled for, as no inert dust treatment was included to equalize light intensity between groups. While the authors mention this limitation in their discussion, they do not measure the size of potential shading impacts.

   R: Thank you for your comment. Our study is based on our pervious study that compared the effects of inert silicate dust, which lacks phosphorus, to desert dust with high phosphorus content (Gross et al, 2021, New phytologist). These set of experiments showed no impact of the shading

effect caused by the silica on chickpea growth. In another paper by our group (Starr et al., 2023) we examined the impact of foliar application of dust on several tree species, noting dust decreased photosynthesis in some species. To examine the shading effect in our study we assessed the effects of dust and ash on chickpea carbon assimilation (a photosynthesis metric) and found that the positive impacts of dust on biomass and phosphorus content outweighed the negative shading effects on photosynthesis. Based on your comment we have added a paragraph discussing this issue. (P19, L461-L474)

1. Statistical analysis is very limited. No statistical power for any of the tests is provided. The number of replicates is not even mentioned in Fig 5 legends for its error bars. The authors should clearly state the number of replicates in the text and all figures that use replicate numbers.

   R: Thank you for your comment. We have added statistical analysis and specified the number of replicates in the text (P10 L313-L317, P11 L346-L347, P12 L356-L358, P21 L511).

3) a few typos and errors easily fixable:

L64 “hidden hunger” is among key words and is relevant for this paper but the authors do not discuss the issue of hidden hunger and CO2 anywhere in the paper. Adding some discussion can be beneficial.

R: We deleted this key word (P2 L64).

L219 Formula has missing subscripts.

R: Changed accordingly (P9 L288).

L232 should be X-ray, not X ray.

R: Changed accordingly (P10 L308).

L281 Table 1 should be foliar-treated not foliar-trated.

R: The table was completely changed and now it is table 2. We corrected the spelling (P14 L366).

L343 and many other places references repeated twice such as (Hinsinger, 2001)(Hinsinger, 2001) –

R: Apologies. Technical problems. Corrected accordingly.

L378 Delete this phrase “Click or tap here to enter text.Click or tap here to enter text.

R: Apologies. Technical problems. Corrected accordingly.

L409 messed up font sizes with text in subscripts.

R: Changed accordingly (P21 L505-511).

Figures have text boxes that are barely readable due to tiny fonts.

R: Corrected accordingly (P20-P21 L499, L504).

Referee #2:

The paper shows that plants can absorb nutrients from deposited dust resulting in increased growth and that the relative benefit can be higher under elevated atmospheric CO_2 concentrations. Using Nd isotopes as tracers the authors were able to estimate the contribution of leaf uptake of individual nutrients. The paper thus delivers important and relevant data contributing to our understanding of the importance of dust deposition to plant nutrition, especially under increasing CO_2 levels.

However, I think that the paper needs improvement in several aspects, both in general terms and some specific aspects.

The following general aspects need clarification / improvement / discussion:

1. The authors follow a rather teleological approach when interpreting their results. This means they imply that plants induce changes in specific traits on purpose. Examples can be found throughout the paper, especially in the sections with the following headers: “Physiological adaptions toward foliar uptake” (l. 290), “Plant strategies for foliar mineral nutrient uptake” (l.337). I have some doubts about such postulates. First, evolution doesn’t follow a plan, and plants are unable to directly, deliberately “adapt” to their environment. They don’t have a “strategy”. Rather, certain plant traits happen to offer some advantages under specific conditions and are therefore selected during evolution. **Second**, in the present case, the cultivar showing improved nutrient uptake is the product of plant breeding, i.e. human intervention. This excludes that the plants themselves “adapted” or developed “strategies” to benefit from dust deposition. This obviously was the result of coincidence.

   R: Thank you for the comment. We changed the phrasing throughout the text according to this comment to a "neutral" phrasing. For example, “Plant strategies for foliar mineral nutrient

uptake" and "Plant strategies for foliar mineral nutrient uptake" changes to "Mechanisms Facilitating Foliar Nutrient Uptake" (P14 L372), and "Foliar mineral-nutrient uptake mechanisms" (P18 L421) accordingly. In addition, "These changes will derive plants to adapt and search…" changes to "These changes may lead to the selection of plant traits that facilitate alternative nutrient uptake pathways" (P3 L101).

2. **A.** The plants were treated with rather high dust doses. The amount of dust was higher than the final dry mass of plants, and the image in Fig. 1 illustrates that dust coverage was extreme. The authors mention that the dust coverage represents the average natural dust deposition in southern Israel during the entire growth period (l. 158/159). It is furthermore not clear whether the entire average deposition per m^2 was applied to a single plant or planting density was considered and values were corrected for the area covered by an individual plant. In any case, the relevance of this approach needs more attention and should be further discussed in the paper. **B**. Shading effects should also be discussed in more detail. The authors briefly refer to effects on photosynthesis. Light stress due to high light intensities, which can be expected in this region, may negatively affect plants and dust coverage could thus be beneficial. **C**. In this context: the conditions in the greenhouse (temperature and humidity regimes, light) should be given.

   R: A. We calculated the average foliar area of the chickpea pots, taking into consideration planting density, and correcting values for the area covered by an individual plants. These values were used to determine the total application mass. In total, the average application mass was 3 g per pot, simulating the total dust deposition per square meter over the growing season in southern Israel. This method was based on our previous studies (Gross et al, 2021, Starr et al, 2023, Lokshin et al, 2024). The picture in figure 1 was taken right after application and maybe misleading and with time, the amount of dust retained on the foliage is much lower than 3 grams, and the wet biomass of the plants is significantly higher than their dry weight. Therefore, while our application mass seems high, it was refined in many studies we have conducted to observe the impact of dust on plants without causing significant damage. We added explanation to the text (P6 L185-L194). B. We added a paragraph discussing the shading effect, its impact on photosynthesis rates, and the potential for light stress. See also our response to reviewer #1 (P19, L461-L474). C: We included the temperature, humidity, and light conditions (P4 L147-L149).

3. Some conclusions are too general and not justified by the presented results. In l.440/441 it is stated that "[…] we showed here that dust nutrient uptake via the foliar pathway in chickpea plants plays a major role in their nutrition". This implies that this is the case for all chickpea plants, wherever they grow worldwide. Please keep in mind that you conducted (i) only one experiment (ii) under rather artificial conditions (pot experiment, greenhouse, rather (unnaturally?) high dust doses) and (iii) foliar uptake was only relevant for one specific cultivar. Later (l. 452/453) you conclude that "[…] foliar nutrient uptake from natural dust will play a central role in eCO_2 earth […]. Again, I think that is a strong overinterpretation of your results for the above reasons.

R: Thank you for the comment. We revised the phrasing to: we showed here that dust nutrient uptake via the foliar pathway in responsive chickpea plants play a significant role in their nutrition under P limited conditions" (P22 L537-L538), and "Our findings suggest that foliar uptake from natural dust could be a relevant pathway under future elevated CO2 conditions" (P22 L).

4. Please separate the (objective) presentation of results from (subjective) conclusions. Conclusions and interpretations should be restricted to the section "Discussion". In Figs. 1-3 the headings not only explain the results but contain your conclusions: Fig. 1 (l. 266-267) and Fig. 2 (l.275-276): "This implies that […], Fig. 3: "[…] rendering it as more fit to extract nutrients from dust particles".

   R: **Thank you for the comment. We separated the conclusions from the headings of Figs. 1-3.**

Specific remarks (from l.1 – 659):

l.34: Root uptake is for a long time no longer considered the "exclusive nutrition pathway" for plants (as also mentioned in the introduction). Please modify sentence accordingly.

R: Corrected accordingly (P3 L67).

l.82: "has bever been quantified before". I don't agree. A quick search in any database will deliver a whole bunch of respective papers.

R: As far as we know, this is the first attempt to quantify nutrient flux from dust via the foliage.

l.82-84: The cited literature on foliar uptake is outdated, and the citations are furthermore missing in the literature list. Please refer to more recent papers (latest edition of Marschner's textbook and references cited therein). You should also mention, at least briefly, the known pathways of foliar uptake and how nutrients bound in solid particles can be absorbed by leaves at all (nutrients in solid form are not available for uptake). In the discussion you explain how acids and sugar may increase availability, but the mechanisms proposed are rather vague and avoid direct explanations.

R: We have added information regarding foliar uptake in the 'Introduction' section, including citations from Marschner's 4th edition textbook and the references cited therein. Additionally, we revised the discussion to provide a more direct explanation based on Marschner's framework and others (P3 L86-L96, P18 L433-L438).

l.86: Please use more precise wording. Accumulation of C always exceeds the that of mineral nutrients.

R: We have added an explanation (P3 L100).

l.88: "These changes will drive plants to adapt and search for other nutrient uptake". See my general comment #1 above. Plant's IQ is rather low 😊

R: We changed the phrasing: "These changes may lead to the selection of plant traits that facilitate alternative nutrient uptake pathways" (P3 L102-L103).

l.90: typo. "…of macro…"

R: Corrected accordingly (P4 L105).

l.92: "…and for their dependent human and livestock nutrition". Weird sentence, please rephrase.

R: We deleted this part: "and for their dependent human and livestock nutrition" (P4 L107).

l.93: New paragraph starting with "In this experiment…"

R: Changed accordingly (P4 L109).

1.103: "...a non-responsive genotype": The meaning of this phrase is unclear at this point (later it becomes clear). Responsive to what?

R: Thank you for this comment. We have deleted this part from the introduction section.

l.114-116: Both sentences are grammatically incomplete, please rephrase. Again: the meaning of responsive is unclear at this stage.

R: Thank you for this comment. We have deleted this part from the introduction section.

l.118: Please specify the climatic conditions in the greenhouses (see comment #2 above).

R: We added the information regarding climatic conditions: "Temperature was fixed at 25 ± 3°C and relative humidity at 40–50%. Inside the greenhouse the saplings were subjected to natural lighting partially concealed by transparent white walls and roof. Overall, the Photosynthetically Active Radiation (PAR) levels were typical for the southern part of Israel during the months of September to November" (P5 L147-L149).

l.122: Typo: liter or litre

R: Changed accordingly (P5 L153).

l.126: Give composition of the nutrient solution and mode of application (intervals, how was it given, from above or below?)

R: We have added the nutrient solution and mode of application (P5 L154-L163).

l.128: "responsiveness". Again: what does it mean?

R: We provided additional details regarding the concept of responsiveness (P4 L135-L139).

l.133-137: Please give more details: how did you make sure that all plants uniformly received the same dose (3 g)?

R: Since dust application was performed manually, we cannot determine the exact amount of dust retained on the leaves with absolute precision. However, we ensured uniformity by applying the same dose (3 g) to all plants, correcting for the average area of the foliage in the pots. It is important to note that due to natural variability, more than 50% of the applied dust likely fell off the foliage during application, but efforts were made to distribute the dust as evenly as possible across all plants (P6 L185-L194).

1.139/140: "…harvested 10 days after the last dust application". You didn't mention so far that dust was applied twice and when the first application took place. This information is given later under the caption "Mineral dust material" (l.145). Please move the information given in l.157-163 to the general description of experimental design (l.133-136).

R: We moved this information to the general description of experimental design (P6 L185-L194).

1.125-142: The description of treatments is quite confusing. While reading I permanently had to do the math. Why don't you describe your experiment as a 2-factorial design with additional controls plants, n reps each. Think of presenting your design in a table.

R: We have added a table (Table 1) that summarizes all the different treatments (P6 L181).

l.152: Typo: monthS

R: Corrected accordingly (P5 L150).

1.157-163: The information given here is not about the materials themselves (as indicated by the heading) but about the mode of application. Move and merge, see comment above.

R: This part moved to the 'experimental design' part (P6 L185-L194).

1.166-167: Washing plants without using detergents and/or organic solvents may leave unabsorbed residues on the surface, even if the plain leaf surfaces appear clean. Scanning some random samples by SEM will not safely exclude contamination. Think of particles left in leaf axils or between trichomes. This will lead to a massive overestimation of nutrient uptake. Please consider this when discussing your results.

R: We appreciate the referee's comment regarding potential contamination from unabsorbed residues on the foliage. However, we adhered strictly to the established washing protocol described in Gross et al. (2021) and Lokshin et al. (2023a), which is designed to effectively remove any residual dust or ash particles from the plant surface. However, we agree that some particles may still be left on the leaves even after our washing procedure (which is a known problem in traditional plant studies also when roots are analyzed). We are not worried about the impact of particle contamination on phosphorus levels, as the P levels in the dust are smaller than in the plant. Thus, simple mass balance calculation shows that remains of few particles on the leaves will not cause a detectable overestimation. In addition, the amount of phosphorus dissolved from the dust using concentrated nitric acid is minimal, further confirming that any residual particles contribute negligibly to the measured phosphorus levels. Unlike P, Fe and Ni may be prone to overestimation as their levels in dust are much higher than in plant tissues. We address this concern in the revised text (P20 L495-L498)

Please give explanations (TRU, LN-spec, JNdi, BRC-2)

R: We have added explanations for TRU, LN-spec, JNdi, BRC-2 (P8,9 L267-L284).

l.219: missing subscripts

R: We added the missing subscripts (P9 L288).

l.281, Table 1: Please give data as means and standard deviation (or similar). Showing individual plant data makes this table rather confusing. Show macro element concentrations in % or mg/g rather than ppm. The value of 713 ppm P is very little for a P-fertilizer. I conclude that the data show the composition of the nutrient solutions, which should be indicated in the table.

R: Thank you for your remark. We have updated the table to reflect your suggestions, converting the values to averages and standard deviations. Macro-nutrients are now presented in mg/g, while micro-nutrients are given in µg/g. The values observed in the starved chickpea plants are typical for phosphorus-deficient chickpea, consistent with findings in Gross et al. (2021) and Lokshin et al. (2023a). Additionally, the nutritional composition of the nutrient solution and the applied dusts are included in the bottom section of Table 2 (P13 L363).

l.301, Caption Fig.3. Panel b: There are no cases of one or two asterisks, please remove. Panel e: “rendering it more fit to extract nutrients”. If consider this an unjustified speculation and not a direct conclusion from the shown results! Trichome density will probably affect retention of dust on leaf surfaces any may be involved in exudation. Both was not in focus of your study and therefore not shown. Furthermore, "extraction" of nutrients again implies

a deliberate action of plants (see above). BTW: The only purpose of figures/tables in the section "results" is to transport pure information, not interpretations! Panel f, y-axis: units are missing.

R: Thank you for this comment. We removed the interpretation sentence from the legend (P16 L391). We added the missing y-axis - the y-axis represents the ratio of the metabolite peak area to the peak area of ribitol, which was added as an internal standard in a fixed amount. This normalization ensures comparability between samples and accounts for variations in wet weight. Ribitol does not influence metabolite secretion but serves as a reference to standardize the data (P15 L381).

L.377/378: remove text.

R: We deleted the text.

L.428: "…of the seed". The value is also affected by root uptake of the seedling

R: We added a sentence explaining that the amount of Nd in the chemical fertilizers was negligible, meaning that all the Nd detected was derived from inheritance (P22 L525).

l.477: remove double citations throughout the paper (also in the list of references)

R: Apologies. Technical problems. Corrected accordingly.