Dear editor and reviewers,

We are happy to resubmit our paper “Direct foliar phosphorus uptake from wildfire ash“ (EGUSPHERE-2023-2617). 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 that the reviewers invested in reviewing our manuscript. The comments provided were insightful and constructive, contributing to the overall improvement of the paper. We have made a lot of effort to change the entire manuscript based on these comments. We conducted an additional experiment and are presenting new results from the sequential extraction of phosphorus (P) in leaves from four local trees. In addition, we have improved the introduction and hypothesizes, better clarified the methods, and strengthened the discussion section and toned down the conclusions. We are confident that the revised manuscript is now ready for publication in Biogeosciences.

Our responses to the reviewers are provided below in **bold.** For your convenience, following our responses, you will find the revised version of the manuscript with a “track changes” to make it easier for the reviewers to follow the changes we have made in the text.

*Both reviewers commented on our comparison to our second paper of Palchan et al which is in review. We were hoping the paper would be published by now but the war in Israel delayed the publication process. We attached the final version of the Palchan et al paper for the reviewers and editor eyes only. We are assured that Palchan et al paper will be published soon.

Reviewer 1

Major issues:

1. I really appreciate the sequential leach done of the wildfire ash, rather than just soluble and total. However, it is unclear how many samples were run to produce Figure S1. If it is only one, then I recommend at least 2 additional samples are run prior to publication to confirm that this sample is representative of P in fire ash. Please show all fire ash sample results in Fig. S1.

   R: We acknowledge the reviewer's comment. In response, we have sampled a new set of plants and conducted four additional ashing experiments to demonstrate that different ashed materials exhibit similar P fractionation. These results have been incorporated into Figure 1 in the main manuscript, as suggested by the reviewer.

2. Please include a summary of the P in fire-ash results as Fig. 1 in the main manuscript. The atmospheric community will be interested in the results and including this figure in the main manuscript will expand the impact of the work.
   R: We accept this suggestion. Thus, we added the Hedley sequence results of four ashed plant samples to the main manuscript in Figure 1.

3. Similarly, a results and discussion section for fire ash needs to be presented in the main text. Please also discuss how these results compare to previously published P contents and solubilities.

   R: Results and discussion on fire ash P are now presented in the main text. Our discussion includes comparisons to two highly relevant manuscripts, both released in the last few months: Wu et al. 2023 and Garcia et al. 2023 (P12 L354-360).

4. The discussion (especially section 4.3) needs clarification and expanding.
   R: The entire discussion was revised, better focused, and expended as the reviewer suggested (changed to section 4.4) (P13-14, L405-432)

<u>Minor issues:</u>

The manuscript contained a few careless errors that a thorough proof-reading would have caught prior to submission. For example, at one point the text refers to a figure that doesn't exist. I recommend thoroughly proofing the text prior to resubmission.

Abstract

Line 17: change particles to ash for clarity.

R: Changed accordingly (P1 L17)

Line 19: change "that reflect" to "which reflect"

R: Changed accordingly (P1 L19)

Line 20: This is a little confusing. Please rewrite for clarity – I think there is a way to only use the word "uptake" once in the sentence.

R: Changed accordingly (P1 L19)

Line 22: add "the" after In a future climate scenario

R: This sentence is changed from its original version to improve clarity (P1 L25)

Line 24: "with fire ash P being the sole nutrient absorbed by the foliage" – This is a very important finding, but it is unclear if it is P only (as opposed to other elements) or if it is fire ash P (as opposed to other aerosol types like dust).

R: The foliage exclusively absorbed P from the fire ash particles. We have adjusted the sentence accordingly. (P1 L21-22).

Line 25: I interpret your data as fire-ash P being a particularly efficient and important source of P. If you agree, please add to the last sentence of the abstract to highlight the significance of the results.

R: We have incorporated the suggested sentence into the text (P1 L31).

Introduction

The intro could benefit from providing some context for the importance of fire as a source of P, particularly to tropical soils that are extremely P-deficient. Even despite tropical soils being depleted in P, they are major carbon sinks, so understanding the biomass response to P deposition to these ecosystems is vital to estimating carbon fluxes accurately. I think a first paragraph around these ideas may highlight the importance of this works' findings and broaden readership.

R: This is an important note. The first paragraph has been revised to acknowledge the impact of fire-derived P deposition on biomass in phosphorus-limited tropical soils (P1 L37-38).

Line 33: P deficiency is particularly prevalent in tropical soils. Is it really prevalent globally?

R: You are correct; P deficiency is widespread, primarily in tropical soils but also in other regions. Several studies have reported global P deficiency, extending across various ecosystems beyond tropical climates. Examples include Vitousek et al. (2010), Hou et al. (2020), and others. We have modified the first paragraph of the introduction to emphasize this important point (P1-P2 L39-L43).

Line 34: It is my understanding that P is low in soils because it is leached from soils by precipitation or has been used by plants. The sentence currently reads as "P deficiency is prevalent globally due to its low bioavailability" which doesn't make sense. Please revise for clarity.

R: P limitation can arise from various factors, including low P concentration in the soil due to insufficient P in the bedrock or slow weathering, high leaching, or increased plant uptake. Additionally, P deficiency may result from its fixation to soil minerals, reducing its biological availability to plants. In tropical soils specifically, P deficiency is attributed to both low total P in the soil due to leaching and biological uptake, as well as high P fixation. We have revised the text to reflect these nuances (P1-P2 L39-L43).

Line 38: Savanna's should not be capitalized and should just be "savannas"
R: Corrected accordingly (P2 L47).

Line 37-39: The sentence that starts with "About 65%..." makes it sound like all fire ash particles originate from Africa. Please revise for clarity. I'm not sure what the authors are trying to say.

R: According to the literature, Africa is identified as the largest source of fire ash. We have revised the sentence based on this observation (P2 L46).

Line 48: Please do not cite a manuscript under review and take out this paper in the rest of your manuscript. It sounds like it may be accepted soon though. Hope that's the case!

R: We acknowledge the challenge of citing a paper that is not yet published. However, the work by Palchan et al. (in review) represents a written paper awaiting publication due to the complex political situation and ongoing conflict in Israel. This paper provides crucial insights that are highly relevant to our results, and it is anticipated to be published soon.

Line 55: There is literature showing that fire ash P is more soluble than dust from Barkley et al., 2019 and references therein). Please update this sentence to reflect this literature.

R: The Berkeley et al. (2019) paper is now included in the text. Also, we have added additional references from the literature that highlight the solubility of fire ash P Myriokefalitakis et al., 2016; Anderson et al., 2010; Wang et al., 2015 (P2 L63,69).

Line 61: These papers are ok to cite, but papers from 2014 and 2010 are pretty old in fire science – please add more recent references.

R: We have added a couple of newer papers, enhancing the content with the latest research findings (P2 L71).

Line 68: Please define eCO2 conditions. I also don't understand why the abbreviation e was chosen. Is there a more intuitive abbreviation that could be used? Does e stand for extreme? Define and explain.

R: The "e" is referring to elevated. It is described in the text. Corrected accordingly. (P2 L79).

Line 69: Please remove the comma.
R: Corrected accordingly (P2 L80).

Line 74: What is eCO_2 and aCO_2? This abbreviation should be explained. Is it "actual" and "extreme"?

R: The "a" refers to ambient and e to elevated. This is now clarified in the text and the sentence was corrected accordingly. (P3 L89).

Last paragraph in introduction (line 73):
Please exclude your hypothesis from this paragraph (sentence beginning on line 76 to end). It's confusing to read this because some of it is opposite of your results. To keep things clearer, please just say what the question is. For example: "…applied both directly to the foliage and to the roots to assess how plants use P from fire ash deposition".

We deleted the hypothesis and changed the paragraph accordingly. (P3 L84-94)

Line 91: Remove "had"
R: Corrected accordingly (P3 L113)

Line 103: Please add "day" instead of
D
R: Changed accordingly (P4 L125)

Line 108: as should say "ash"
R: Corrected accordingly (P4 L130)

Line 107: Please adjust grammar to say "At this stage, fire ash was applied directly on to the foliage of 12 -P plants…"

R: Corrected accordingly (P4 L129)

Line 111: What is bone-fire burning?

R: Corrected to a "The fire ash used in this study was produced by burning branches and needles of coniferous trees in a controlled bonfire setting". (P4 L139).

Line 113: Ash is also singular, so please say "Later, the ash was burned again…"

R: Corrected accordingly. (P4 L141).

Line 118: move sentences about Tables S1 and S2 to section 2.3 where you discuss the chemical composition methods.

R: Changed accordingly. (P4 L150).

Line 139: This sentence is repeated above. Remove the above one.

R: The specified sentence has been removed. (P5 L159).

Methods

Section 2.3:

It would be helpful to say give a sentence at the beginning of this section describing why each chemical analysis was chosen. For example, say something like "We performed X analysis to quantify total P and a sequential P leach to estimate the different fractions of P." Why was XRD performed? Why was ICP-MS performed? I imagine ICP-MS was done to determine a total P concentration while the sequential leaching was done to determine each P phase. Please state as such. What does each step of the sequential leach tell us? Which is most soluble?

R: An explanation sentence for each method has been added as well as the meaning of each step (P4 L156-158, L175).

Line 149: "two separate pulses" is confusing. I think you can just say twice or two times.

R: Corrected accordingly. (P5 L186).

Line 154: I understand following P deposition estimates from Gross et al. 2021 30 g/m2, but is this deposition rate reasonable for fires? Discuss why or why not. Even if it's not, I think it's ok because it's still important to be able to compare your results to another study.

R: While reliable data on fire ash deposition is limited, it is well-established that average global dust deposition exceeds that of fire ash (based on geographical location). Leveraging the abundance of reliable data on dust deposition, we opted to use dust deposition amounts as our reference for fire ash. This decision facilitates a meaningful comparison of our results with previous studies. It is essential to acknowledge that this may not precisely represent actual fire ash deposition. Therefore, we have included a brief discussion on this point (P5 L192-193).

Line 158: Please adjust the grammar. "The same amount of ash that was applied to the foliage was applied to the roots."

R: This sentence is changed from its original version to improve clarity (P6 L204).

Line 163: Change to "remaining ash" instead of "ash remains"

R: Corrected accordingly. (P6 L210).

Line 166: Should say "Elemental analysis was performed…" instead of "the elements measurement".

R: Corrected accordingly. (P6 L216).

Line 167: Change "get rid of the" to "eliminate"

R: Corrected accordingly. (P6 L217).

Line 168: Delete "to achieve a clear solution".

R: Corrected accordingly. (P6 L218).

Line 179: Why only the P-deficient plants? Please discuss the reasoning.

R: PH measurements were conducted on P-deficient plants, excluding those treated with fire ash. The presence of the material on the leaf surface interferes with the physical contact between the flat surface of the pH electrode and the leaf itself. Additionally, we measured

the pH of P-sufficient plants, and the results were similar. This is now explained in the text (P6 L234-237).

Line 187: You can say “additional holding capacity analysis was performed at Ben Gurion University”

R: The sentence changed accordingly (P7 L242-L243).

Section 2.6: Reference for pH measurement available? Why was leaf pH measured? What does it tell us?

R: Yes, there are a several studies that reported similar acidic pH of chickpea leaves. References now added to the text (P6 L234). These measurements indicate the acidity of the leaf environment which promotes P dissolution in fire ash (see paper of Tiwary et al. (2022) now added to the text). This can provide insights into the foliar nutrient uptake mechanism as was shown in Gross et al. (2021). An explanation was added in the ‘Introduction’ section (P3 L85-L88).

Results

3.1:

- What is shoot? Is that the whole plant or the same as the root? Please define and explain why shoot biomass measurements are made for.
  R: The shoot refers to the aboveground part of the plants excluding the roots. An explanation has been added to the manuscript. (Methods, section 2.5, P6 L212-L214).

- There is no figure 1f or 1e. Please correct so the text refers to the correct figure.
  R: Corrected accordingly. (P7 L261-L264).

- Figures 1 and 2
  - These figures need to be explained. Please say that they are violin plots. What does the middle dash represent? What do the other dashed lines represent? It’s not standard dev because they are not the same on either side

of the center dashed line.

R: The dashed lines in the violin plots represent the median and the dotted lines the quartiles. We added this information in the figure legends (P10 L344-L345 and P11 L352-L353).

Please report the significance and what type of significance test was performed.

R: The significance is P<0.05, and the test used was the Tukey test. We added this information in the figure legends (P10 L344-L345 and P11 L352-L353).

3.2: Please make sure the text refers to the correct figures. There is no figure 2f or e.

R: Corrected accordingly (figures 2 and 3, P10, P11).

3.3: This paragraph is confusing. Please revise for clarity.

R: Whole section 3.3 was rewritten and clarified and changed to section 3.4 (P8 L272-283).

Line 208: Replace "Plant's nutrient status" to "the nutrient status of plant samples".

R: The sentence is changed from its original version for clarity (P8 L274).

Line 208-209: This is poorly worded and confusing, but a major result.

R: We reworked this section, providing detailed clarification of the calculation and explanations for the results (P8 L269-280).

Figure 3:

Remove interpretation from Figure 3 caption (second the last sentence)

R: Removed accordingly (changed to figure 4) (P12 L361).

The legend on the plot does not match the description of the legend in the caption. Please revise.

R: Corrected accordingly (figure 4).

Why was P not measured and provided on Fig. 3?

The plants were P-starved; therefore, the increase in P was assessed by calculating total P values. In this scenario, the P levels in the ionome cannot demonstrate changes in

concentration, as there were no variations due to the fact that all available P being directed toward plant growth. This is why figures 1 and 2 represent the total P values.

Discussion

Line 278: I think a better and stronger interpretation of your data is that direct foliar application of fire ash is directly beneficial to plants and increases biomass. The word “emphasizing” makes it sound like the results are not novel. Please link the fact that biomass increase to the plant taking up atmospheric carbon via photosynthesis.

R: We agree. The word 'emphasizing' has been changed to 'demonstrating.' Since the P-deficient plants were unable to grow, our results demonstrate that the increase in biomass is attributed to additional P directly taken up through the leaves from the fire ash particles. This P is the limiting factor for growth. Even the plants grown under elevated levels of CO_2 were unable to grow without sufficient P in their nutrition. The sentence has been modified to: 'Foliar application of fire ash under ambient CO_2 levels increased chickpea biomass and total P content compared to untreated control plants, demonstrating that foliar uptake of P from fire ash has a direct nutritional impact on plants, providing P for biomass growth and boosting photosynthesis’ (P12 L373-375).

Line 281: Please delete “… confirming out initial hypothesis that fire ash P is more bioavailable to plants” and remove any mention of the hypothesis. The authors could say here “emphasizing the importance of P for plant growth”.
R: Corrected accordingly. (P12 L379).

Line 281: Please delete “However, despite its projected bioavailability” and replace with something like “because there was no nutritional impact when fire ash was deposited on roots, we conclude the nutritional impact occurred exclusively through foliar uptake”
R: Corrected accordingly. (P12 L379-L380).

Line 282: Please delete the sentence that starts with “This discovery.” You do not need to discuss your initial hypothesis. You should instead refer to published literature – how are your results similar or dissimilar to previously published studies? Do your results challenge these studies?
R: Direct foliar uptake of P from fire ash particles has been overlooked, until now. Our

results represent the first instance in which fire ash particles were directly added to plants, thus definitively challenging the common perception that P is solely taken up through the roots from the soil, even in the case of atmospheric particle deposition. We have changed the sentence accordingly (P13 L394-L399).

Line 286: Imply should be implies.

R: Corrected accordingly (P12 L386).

Section 4.2: Connect to your results again. Do your results agree with other results from the Gross lab?

R: Yes, our results agree with the previous works of Gross et al. 2021 and Starr et al. 2023. We have added a short discussion and connected our results to their findings (P13 L405-408).

First sentence in 4.2: You do not need to repeat the same Gross et al. 2021 citation in the same sentence.

R: Additional citation was removed (section 4.2 changed to section 4.3).

I think you need a sentence like "our data showing low pH on plant leaves supports previous assertions that low pH may help facilitate P uptake on plant leaves".

R: Additional sentence was added: "As in previous studies, we also measured a highly acidic leaf surface environment (average pH value of 1.15) and a high dust holding capacity (average value of 15%), support previous assertions that low pH and high holding capacity may help facilitate P uptake on plant leaves" (P13 L405-408).

Section 4.3:

Delete discussion of your hypothesis (Line 310). Instead discuss why your results are unexpected based on current literature w/ citations.

R: The discussion of our hypothesis was removed, and the sentence was revised based on your comment (P13 L426-L428, L430-L435).

Line 308: Should contribution be content? I do not understand this sentence.

This section is generally pretty confusing.

R: This section has been rewritten and additional explanations were added (P13 L416-L428).

The results presented in Section 3.3 say that the eCO2 conditions reduced the conc of various elements, so the discuss section should discuss why. I feel like the discussion here is missing.

R: We expanded the discussion regarding the reasons for the nutritional reduction under elevated levels of CO_2 (P13 L416-L428).

Section 4.4

What is n.d. on line 328?

R: It is a mistake. Corrected accordingly (P14 L453).

Line 326: I think the current state thinking is that soluble nutrients like P are more quickly and easily used by the plants after deposition to the soil. Your results are interesting because they contradict that.

R: Your remark is correct; however, it's important to note that most of the P in fire ash particles is not soluble. Additionally, the soluble portions can interact with other minerals and/or microorganisms within the soil. When particles settle onto plant foliage, they may remain undisturbed and be partially dissolved by foliar organic acids such as oxalic, malic, and citric acids. We have clarified this in the text (P14 L457-L459).

Line 328: Delete “in accordance with the common view”

R: Changed accordingly. (P14 L455).

Line 238: Fire also releases N that contributes to N deposition… There is no current N limitation in terrestrial ecosystems because of anthropogenic emissions.

R: What we aimed to express is that anthropogenic pollution increases the concentration of nitrogen (N) in soils. Consequently, this elevation can lead to an imbalance in plant stoichiometry. The high phosphorus (P) concentration in fire ash could play a partial role in offsetting this anticipated stoichiometric imbalance. The sentence has been revised and clarified in the text (P14 L466-468).

Please discuss how your results inform biogeochemical models. What do the results say about the need for chemical transport model to capture the physics of deposition onto plant leaves? This means that modelers need to have accurate land type model inputs and need to account for surface roughness. Do models currently take deposition onto leaves into account?

R: It is an important observation. We have added a paragraph that underscores the significance of updating biogeochemical models (P15 L470-475).

SI:

1. Please redefine all abbreviations (except elemental symbols) in SI (e.g., XRF, etc.).
   R: The abbreviations were redefined.
2. Add longer descriptions of each table.
   R: Additional descriptions were added.
3. How many fire ash samples were analyzed? Figure S1.
   R: We conducted an additional experiment and analyzed four new samples of tree branches and leaves from four different trees to measure their P concentration and fractionation. See our responses to previous comments.

Reviewer 2

This paper is a nice illustration of the potential P-fertilising effect of ash deposited on plant surfaces. It has been known for a long time that P can be taken up by leaves, but this paper quantifies the importance of this P uptake for a crop species in an experimental setting. While the broader conclusions (that our future world will see more ash deposition and that this may make this biogeochemical pathway quantitatively more important than it has been) is true, I feel that the authors 'over-sell' the idea that it is going to be highly significant for plants. The experiment has done several things that maximise the effect of ash: high ash loads, complete burning of ash to remove organic residues, and importantly, choosing a species that is covered in hairs that contain high concentrations of acids, and that (being a legume) is quite responsive to P fertilisation. I would suggest that the conclusions are toned down.

R: We thank the reviewer for his comments. We have toned down the conclusions throughout the text.

I agree with (most of) the comments provided by Reviewer 1 and have avoided repeating the same points. Whilst this manuscript does not have many major issues, I believe that the cited manuscript (Palchan et al., in review) should have been made available to the reviewers. Everything indicates that this manuscript is a companion paper based on the same (or parallel experiment). The amount of data presented in this paper is not large. Whilst I have ticked the box 'minor revision', it is possible that a major revision that includes combining Palchan's manuscript to publish it as a single paper may be better advice.

We provide here the submitted paper of Palchan et al. for the reviewers and editor eyes only. Our paper describes the impact of fire ash on plants and differs from Palchan et al. which tests the impact of mineral particles like desert dust and volcanic ash which vary in their composition, source material and nature from combustion ash. Thus, merging our results with the data presented in Palchan et al. will generate a substantial amount of data, potentially overshadowing the specific effects of combustion ash on plants. We genuinely believe that the ecological importance and impact of combustion ash will interest a large number of readers, justifying a separate discussion and publication. It's important to note that the publication of the Palchan et al. paper has been delayed

partially due to the war in Israel. We believe that by spring both papers will be published and enable an appropriate comparison between the two papers. Palchan et al. article is expected to be published in the next couple of months. Once Palchan et al. paper will be published, we can ask the editorial committee of 'Biogeosciences' to change the citation status from 'in review' to the actual published paper. We promise that we will update once the paper is published.

L5: I suggest that the species (chickpea) is included in the title.

R: We thank the reviewer for his suggestion, however, we are certain now that the foliar uptake pathway is viable mechanism in other plants as we had published in other papers (Starr et al. (2023) and Gross et al. (2021)), where foliar nutrient uptake from atmospheric particles such as desert dust, was shown to occur in other crop and tree species as well. Thus, foliar nutrition from fire ash is probably applicable to other plant species. We are concerned that if we include the plant's name in the title, it will narrow down the true meaning of our article, which is broader than a single plant. Yet, we acknowledge the reviewer's remark and have added more mentions of the plant specie in the text in several places, and that chickpea is a plant with unique characteristics (P3 L85-L88 , P14 L448-L449).

L18 and L76: ash applied to the roots or rather to the soil surface?

R: The ash was applied to the perlite and gently mixed around the roots to enhance the physical contact between the roots and the particles, thereby increasing the chances of having a more significant impact. This is now explained throughout the text. For example (P1 L17, P3 L90).

L21: You have not demonstrated that plants cannot take up P through their roots. It didn't happen in your experiment, but it is the main pathway under normal circumstances. The way you formulate it here suggests that they don't.

R: **You are correct; the primary pathway for nutrient uptake is through the roots. However, our study focuses on the immediate (termed in the paper as "short time scale") impact of fire ash on plants. Our results indicate that in a short timescale, plants may not efficiently uptake P from fire ash via the root pathway, possibly due to low bioavailability or limited contact between fire ash particles and the roots. In contrast, the direct application of fire ash particles**

to the foliage enables extended and direct contact, increasing the likelihood of foliar P uptake. We have revised the paragraph to make it clearer based on your suggestion. (P1 L22-23).

L25: This is quite far extrapolated from one unique species to all plants. I'd add the word 'potentially' as a minimum and would suggest to tone this down.

R: The sentence is changed from its original version to town down the conclusions (P1 L21-29).

L68: "impair" is quite a strong word in "… impair plant's mechanisms of nutrient uptake …". "… reduce plant nutrient uptake …" may be appropriate?

R: We replaced 'impair plant's mechanisms of nutrient uptake' with 'reduce plant nutrient uptake' (P2 L80).

L68: explain that eCO2 and aCO2 are elevated and ambient CO2.

R: We added an explanation of eCO_2 and aCO_2 (elevated and ambient co2 levels). (P2 L79).

L77: "Fire ash impacts will be higher than that of other atmospheric sources due to the higher P concentrations and increased solubility in comparison to desert dust and volcanic ash". You cannot test this hypothesis as the experimental design does not include desert dush and volcanic ash treatments. This hypothesis seems to be formulated for the combined experiments of this paper and that of Palchan et al (in review) …

R: We removed this and other hypotheses in the introduction. We mentioned the comparison between fire ash and mineral dust in the discussion and refer to Palchan et at. And other papers. Please refer to our previous comment regarding Palchan et al. paper.

L108: fire ash, not fire as.

R: Corrected accordingly. (P4 L131).

L102: bonfire I assume?

R: You are right. Corrected accordingly. (P4 L139).

L113: further burning at 550 C reduces the ash to mineral-only ash, but is that the type of ash that is dispersed and deposited in the real world, or is that the less-completely burned ash?

R: In the real world, fire ash particles exhibit a wide range of burning completeness and temperatures, along with various types of organic matter, including stems, branches, leaves, fruits, needles, etc. In our attempt to describe and quantify the phenomenon, and recognizing the variability in real-world conditions, we wanted to establish a 'perfect' set of conditions. However, this is an important comment, and we added an explanation in the text (P4 L142-145).

L118: dispersion instead of erosion?

R: Corrected accordingly (P4 L149).

L155: "…whereas the chickpea grown in similar growing conditions." Change to "… in which the chickpea was grown …"

R: We replaced the sentences according to your suggestion. (P5 L194).

L156: 3 g of ash (not as)

R: Corrected accordingly. (P5 L195).

L157: "the ash was gently applied manually on the leaves". More detail is needed. Was it evenly spread, how did you avoid spillage? Did you touch the leaf or let the ash fall on it? Touching the leaf of chickpea damages hairs which release strong acids …

R: The application of fire ash particles was performed in the following manner: we placed the ash particles in a sieve with a 63-micron mesh size and spread the ash by gently shaking the sieve above each plant. Some particles were spilled during the process. Afterwards, the plants were left undisturbed with the settled ash particles on their foliage. The top of the pots was covered to prevent percolation of fire ash particles to the substrate. We added this explanation in the text (P5-P6 L196-L200).

L159: "applied to the roots". I strongly request different wording, e.g. soil surface, as I'm sure you didn't apply it to the roots in the way you applied it to the leaves. However, you may not like to use 'soil' for perlite. "Substrate" is an alternative option.

R: We replaced the wording 'applied to the roots' to 'applied to the substrate around the root system". This is now explained throughout the text. For example (P1 L17, P3 L90).

L162: "The plants were rinsed in tap water, 0.1M HCl and three times in distilled water to remove any ash remains." The HCl concentration seems very high, do you have evidence that this did not damage the plants? Do you also have (microscopic) evidence that all ash was effectively removed?

R: Before employing this washing method, we tested it extensively in our preliminary experiments. Additionally, this washing method was used in the work of Gross et al. (2021), where they applied desert dust to plants and microscopy was used to ensure that no damage occurred, and no excess of dust particles remained on the leaf surface. We added this explanation in the text (P6 L208-210).

L175: Not dust but ash.

R: Corrected accordingly (P6 L226).

L188: only ash, not dust?

R: Only fire ash. Corrected accordingly (P7 L243).

L189: leaf, not leave.

R: Corrected accordingly (P7 L245).

Figures 1 and 2: I think that these figures can be effectively combined. I would add Root biomass too. And I would prefer P concentration rather than P content. Differences in P content seem simply due to differences in biomass, but this can be verified by showing P concentration.

R: We did not detect changes in P concentration because any additional P was directed to biomass growth since the plants were P starved. Thus, the extra P taken up from fire ash particles is reflected by increased P content rather than P concentration.

The combination of Figures 1 and 2 would create an 8-panel figure, potentially complicating the understanding of the differences. Figures 1 and 2 depict two distinct growing settings with different CO_2 conditions. We believe that presenting them separately is a more representative way of illustrating the results.

Root biomass graph has been added to the supplementary file as figure S1 in the complementary.

L273: "The depletion of the plants nutrient status is caused by the downregulation of the roots system". This is an interpretation that should not be stated in the figure caption. Lower nutrient concentrations at eCO_2 are also due to 'dilution' by carbon-based compounds, including higher concentrations of non-structural carbohydrates.

R: We removed this interpretation from the figure caption. Since the control group, which was grown under elevated CO_2 conditions, did not show an increase in biomass, it indicates that the 'dilution' effect is not responsible for the nutrient reduction in this case. We acknowledge that the dilution affect is a major factor in many cases, and we discuss this in the text based on your suggestion. (P1 L23-L25, P13 L416-424).

L291: These results suggest that solubility tests examined by chemical extractions do not necessarily reflect actual biological availability and emphasize the importance of fertilization experiments with plants." I agree, but the result remains puzzling, and it's a pity that no attempts were made to look into this further. What was the pH in the perlite substrate? Was there evidence of the ash dissolving and being transported into the substrate? Were there roots throughout the substrate? Chickpea roots have the capacity to access P from poorly soluble salts, through the same mechanism that you propose for leaves.

R: This is an important observation. The tested plants exhibited an extensive root system, with an average root-to-shoot ratio of 50:50 and the pH of the substrate was around 7. Also, our aim was to study the immediate nutritional impact of fire ash particles right after deposition. Thus, the smaller physical contact between the fire ash particles than that of the leaves is an inherent property in field conditions and in our experimental system. Investigating the physiological response of roots following the application of fire ash and other atmospheric particles is an intriguing question that deserves dedicated research. We clarified this the text (P12 L389-L390).

L296: " … promotes the release of P solubilizing metabolites, such as malic citric and oxalic acids". As far as I know these compounds are contained in gland hairs, and only released when these break, rather than 'exuded'. Breakge may occur naturally, but I'd suggest that you comment on this rather than suggesting that these compounds are continuously exuded.

R: According to the work of Gross et al. (2021), chickpea plants sequester oxalic, malic, and citric acids from trichomes independently of their breakage. P-deficient chickpea plants increase the granular secretion by activating different strategies, for example increasing the

density of trichomes. However, we agree that fire ash application may physically break the glands and increase the exudate concentration. This is now mentioned in the text (P13 L403-L405).

L321: "Another possible factor could be the elevated pH level of the fire ash particles which may impact the chemical environment of the leaf surface." But your measurements demonstrate a highly acidic environment …

R: You are correct. The chickpea leaf environment is highly acidic; however, we did not measure leaf surface pH after the application of fire ash particles as the fire ash interferes with the pH measurements. Thus, we deleted this sentence from the text (P14 L443-L446).

Figure S1: why do the fractions not add up to 100%? Is that the soluble fraction that's missing? Why not include it?

R: We have added Figure S1 to the manuscript and incorporated four additional samples, as requested by Reviewer 1. The figure was changed based on your and reviewer 1 suggestion.

Direct foliar phosphorus uptake from wildfire ash

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Abstract. Atmospheric particles originating from combustion byproducts (burned biomass or wildfire ash) are highly enriched in nutrients such as P, K, Ca, Mg, Fe, Mn, Zn, and others. Over long timescales, deposited wildfire ash particles contribute to soil fertility by replenishing soil nutrient reservoirs. However, the immediate nutritional effects of freshly deposited fire ash on plants are mostly unknown. Here we study the influence of fire ash on plant nutrition by applying ~~particles~~ ash separately on a plant's foliage or onto its substrate around the roots. We conducted experiments on chickpea model plants under ambient and elevated CO_2 levels, ~~412 and 850 ppm, that~~ which reflect current and future climate scenarios. We found that plants can ~~uptake~~ utilize fire ash P ~~only~~ and Ni through their leaves, by a direct nutrient uptake from particles captured on their foliage, but not via their roots~~.~~ both under ambient and elevated CO_2 levels. These results indicate that over a -short timescale, plants effectively uptake P from fire ash only via the foliage rather than the root pathway, possibly due to low bioavailability or limited contact between fire ash particles and the roots. According to many previous studies, elevated levels of CO_2 will reduce the ionome of plants, due to the partial inhibition of key root uptake mechanism, thus increasing the significance of foliar nutrient uptake in a future climate. ~~In a future climate scenario, foliar nutrient uptake pathway may be even more significant for plants, due to the partial inhibition of key root uptake mechanism. Our findings highlight the effectiveness of the foliar nutrient uptake mechanism under both ambient and elevated CO2 levels, with fire ash P being the sole nutrient absorbed by the foliage. These findings demonstrate the substantial contribution of fire ash to the nutrition of plants.~~ Furthermore, the role of fire ash is expected to increase in the future world, thus giving a competitive advantage to plants that can utilize fire ash P from the foliar pathway, as fire-ash P being a particularly efficient and important source of P.

1. Introduction

Atmospheric particles are a major source of macro and micronutrients such as phosphorus (P), iron (Fe), magnesium (Mg), calcium (Ca), potassium (K), manganese (Mn), zinc (Zn) and nickel (Ni) that are essential for terrestrial and marine ecosystems (Mikhailova et al., 2019; Aciego et al., 2017; Chadwick et al., 1999; Goll et al., 2022; Gross et al., 2015, Palchan et al., 2018). In terrestrial ecosystems, particularly the P-depleted Amazonian rainforest, the aeolian contribution of P is of special importance. The depletion of P in the Amazon is driven by processes such as leaching and plant uptake, coupled with the rapid fixation of P to soil minerals. Globally, P deficiency is prevalent due to insufficient P in the bedrock or slow weathering (Aciego et al., 2017), high leaching, or increased plant uptake ~~The aeolian contribution of P is especially important in terrestrial ecosystems since P deficiency is prevalent globally, primarily due to its low bioavailability in most soils~~ (Vitousek et al., 2010; Gross et al., 2016; Lynch, 2011; Cunha et al., 2022; Hou et al., 2020). Combustion byproducts from biomass burning ("fire ash") are among the most dominant atmospheric particles with global amounts of 750 Tg and can be deposited locally or transported remotely and supply nutrients even between continents (Barkley et al., 2019). ~~About 65%~~More than 50% of the fire ash particles are generated via high grassland and savanna fires in Africa whereas the rest are emitted from the ~~S~~savannas~~'s~~ in the Amazonian region or various drylands (Bauters et al., 2021; Yadav and Devi, 2019). For example, Barkley et al. (2019) have shown that African fire ash is wind transported and supplies up to half of the P deposited annually in the Amazon basin. Bauters et al. (2021) showed that biomass burning in Africa is a major contributor of P to nearby equatorial forests by atmospheric deposition. According to their findings, the actual deposition of fire ash is higher over the forest because of canopy complexity of the trees, pointing out the importance of the canopy trapping as a pathway for nutrient input into forest ecosystems. However, while the long-term impact of fire ash P reservoirs is well documented, the direct impact of freshly deposited fire ash on plant nutrition has been so far overlooked. Recent studies showed that atmospheric deposition of desert dust ~~and volcanic ash (two of the most dominant particles in the atmosphere besides fire ash) have~~ has a direct and immediate impact on plant's nutrition by foliar P uptake from particles that captured on their leaves (Gross et al., 2021; Starr et al., 2023, Palchan et al. in review), even though their P is found mostly in biologically unavailable forms (Gross et al., 2015; Longo et al., 2014; Zhang et al., 2018). These studies suggest that plants facilitate P uptake from dust by enhancing the dissolution of insoluble P bearing minerals via exudation of P solubilizing organic acids and acidification of the leaf surface area.

The nutritional impact of fire ash may be even higher than that of dust and volcanic ash as the concentration of P in fire ash particles can reach up to 10000 ppm, which is 5-10 times larger than in desert dust (Tan & Lagerkvist, 2011; Tiwari et al., 2022; Barkley et al., 2019). The knowledge regarding the bioavailability and chemical speciation of P in fire ash are still poorly resolved, yet, solubility is supposedly significantly higher than that of desert dust and volcanic ash, owing to P releasing chemical reactions that occur in high temperatures during biomass burning such as the high melting crystalline phases (calcium/magnesium potassium phosphates) during the combustion (Tan & Lagerkvist, 2011; Tiwari et al., 2022; Myriokefalitakis et al., 2016; Anderson et al., 2010; Wang et al., 2015).

The contribution of fire ash as a nutrient supplier is expected to further increase under almost all future climate scenarios as increased temperatures and drought frequency intensify fire weather conditions, which in turn, escalate the number of fires and their intensities (Liu et al., 2014, 2010;~~,~~ Pausas and Keeley, 2021;~~,~~ Canadel et al., 2021). Thus, understanding the actual nutritional impact of fire ash on plants becomes even more relevant. Furthermore, elevated levels of CO_2 generate a phenomenon known as the "CO_2 fertilization effect" which accelerates primary biomass production because of the increase in CO_2 assimilation by plants (Loladze, 2002; Myers et al., 2014; Gojon et al., 2022). The larger biomass of plants will increase their demand for P and other nutrients to sustain the stoichiometric imbalance caused by CO_2 fertilization, making alternative nutrient sources such as fire ash more important.

A recent study that examined the impact of desert dust and volcanic ash on plant's nutrition emphasized the dominant role of the foliar nutrient uptake pathway under elevated levels of CO_2 (eCO_2) conditions, which are projected to reduce plant ~~impair plant's mechanisms of~~ nutrient uptake from the root systems causing a reduction of plant nutrient status (Palchan et al., (in review)). Other studies documented that plants that grow under eCO_2

increase their efflux rates of soluble sugars, carboxylates, and organic acids such as oxalate and malate that promote the dissolution of nutrient-bearing minerals (Dong et al., 2021).

Here, we aim to study the immediate (i.e., several weeks) impact of fire ash on plant nutrition under current and future CO_2 levels. We used chickpeas as our model plants since these plants have a unique set of properties that enhance the dissolution of nutrients from leaves or roots, such as high secretion of organic acids that lower the pH of their leaf or soil surroundings and a high concentration of trichomes on leaves that help them retain particles on their surfaces (Gross et al., 2021; Starr et al., 2023; Yoshida et al., 1997).- The plants were grown under eCO_2 and ambient CO_2 (aCO_2) conditions in a greenhouse. The plants were supplied with fire ash as their sole P source, applied both directly to the foliage and to the substrate around the root system, to assess the P acquisition pathway that plants utilize from fire ash deposition. Additionally, we compare the impact of fire ash particles on plant nutrition to that of other atmospheric particles such as desert dust and volcanic ash. To further understand the impact of eCO_2 conditions on plants' ability to uptake nutrients, we grew chickpea plants under eCO_2, assessing the influence of fire ash P by applying it to the foliage and the substrate around the root system of the plants. Here, we aim to study the immediate (i.e., several weeks) impact of fire ash on plant nutrition under current and future CO2 levels. Chickpea served as our model plant and was grown under eCO2 and aCO2 conditions in a greenhouse. The plants were supplied with fire ash as their sole P source, applied both directly to the foliage and to the roots. We hypothesize that plants will be highly responsive to fire ash P, by increasing biomass and P uptake. Fire ash impacts will be higher than that of other atmospheric sources due to the higher P concentrations and increased solubility in comparison to desert dust and volcanic ash. The root P uptake pathway will dominate under aCO2 conditions as fire ash P is highly soluble and thus bioavailable. Finally, the role of foliar uptake pathway will be more dominant under eCO2 because of the impairment of mineral nutrient uptake via the root system and the increased organic acids exudation.

2 Experimental Design

2.1 Plant material

The experiments were performed on chickpea plant that served as our model plant in this research (Cicer arietinum cv Zehavit, a commercial Israeli kabuli cultivar). We used chickpea as a model plant because previous works had shown that chickpea positively responds to a foliar application of desert dust and volcanic ash (Gross et al. (2021), & Palchan et al. (in review)). The plants were grown at the Gilat Research Centre in southern Israel (31°210N, 34°420E) in a fully controlled glasshouse with inner division for two rooms 2x4 m, 4 m tall. At both rooms, the temperature was fixed at 25±3°C with relative humidity of 50-60%. The rooms were equipped with computer-controlled CO_2 supply system (Emproco Ltd., Ashkelon, Israel) that had automatically adjusted the CO_2 concentrations in the rooms. One room had CO_2 levels of 400 ppm (aCO_2) and in the other room CO_2 levels of 850 ppm (eCO_2) to simulate current and future earth CO_2 levels based on high emissions scenario (business as usual, SSP 8.5). Initially, 3 seeds per pot were sown in 54 pots filled with inert soilless media (perlite 206, particle size of 0.075–1.5 mm; Agrekal, HaBonim, Israel). After germination, plants were thinned to one plant per pot. All the pots were supplied with a nutrition solution (fertigation) containing the following elements: nitrogen (N) (50 mg L-1), P (3.5 mg L-1), K (50 mg L-1), Ca (40 mg L-1) Mg (10 mg L-1), Fe (0.8 mg L-1), Mn (0.4 mg L-1), Zn (0.2 mg L-1), boron (B) (0.4 mg L-1), Cu (0.3 mg L-1) and molybdenum (Mo) (0.2 mg L-1). The mineral concentrations were achieved by proportionally dissolving NH_4NO_3, KH_2PO_4, KNO_3, $MgSO_4$ and $NaNO_3$. The micronutrients were supplied in EDTA (ethylenediaminetetraacetic acid) chelates as commercial liquid fertilizer (Koratin, ICL Ltd). The location of each pot within the glasshouse was randomized at the beginning and changed every two weeks over the course of the experiment. The plants were dripped irrigated 4 times per day for 5 minutes, via an automated irrigation system from the germination stage. At 14 ~~D~~ day a~~A~~fter g~~G~~ermination (DAG), when plants were at early vegetative stages (two or three developed leaves), we changed the nutrient media for 42 of the pots to P-deficient media (P concentration of 0.1 mg L^{-1}) with similar concentrations for the other elements (-P). Visible P-deficiency symptoms (e.g., chlorosis of mature leaves, slight symptoms of necrotic leaf tips and an overall decrease in biomass accumulation) were observed after 35 DAG. At this stage 12 ~~of~~ -P plants were applied with fire -ash ~~directly~~ on the foliage (-P+leaf ash) and 12 ~~directly on~~ into the substrate near the roots (-P+~~root~~ ash to the substrate~~ash~~) while the rest served as control group (-P or +P). Overall, each group had six repetitions, resulting in a total of 54 pots grouped as follows: ~~-~~+P (control group), -P (control group), -P+leaf ash, -P + ~~root ash~~ash to the substrate.

2.2 Fire ash type

The fire ash in this study was produced by burning branches and leaves from five trees: *Hyphaene Thebaica, Olea Europaea, Albizia Lebbeck, Cupressus* and *Pinus*. Samples of *Hyphaene Thebaica, Olea Europaea, Albizia Lebbeck* were collected from the campus of Ben Gurion University (31° 15.680 N, 34° 47.964 E). The fire ash that was added to the plants was produced by burning branches and needles of coniferous trees (Cupressus and Pinus) in a controlled bonfire setting~~The fire ash was produced by bone-fire burning of branches and needles of coniferous trees~~. These branches and needles were collected from trees that grow in Neve-Shalom Forest, Israel (31°821~~91~~ N, 34°987~~19~~ E). Later, the ash~~es~~ was~~ere~~ burned again in a furnace at 550°c for two hours to achieve complete combustion of the organic material. In the real world, fire ash particles exhibit a wide range of burning completeness and temperatures, along with various types of organic matter, including stems, branches, leaves, fruits, needles, etc. In our attempt to describe and quantify the phenomenon, and recognizing the variability in real-world conditions, we wanted to establish a 'perfect' set of conditions. Complete combustion of organic material results in production and oxidation of volatiles or gases such as CO_2, carbon monoxide (CO), methane (CH_4) or nitrogen dioxide (NO_2), with only mineral residue remaining, i.e., “mineral ash” (Bodí et al., 2014). ~~.~~ The ash was processed through a set of sieves to achieve a particle size smaller than 63 µm, size subjected to wind ~~erosion~~ dispersion (Guieu et al., 2010). ~~The chemical and mineralogical properties of the fire ash are presented in Table S1 and S2 in the Supplement. The P concentration in our fire ash samples was 0.625%.~~ The chemical and mineralogical properties as well as P concentrations of our fire ash samples, resembles reported values in the literature (Bigio & Angert, 2019; Tan & Lagerkvist, 2011; Tiwari et al., 2022).

2.3 Fire ash chemical and mineralogical analysis

To validate the typical chemical, mineralogical, and elemental composition of our fire ash samples and ensure comparability with other studies, we conducted X-ray diffraction (XRD), X-ray fluorescence (XRF) as further explained. Mineralogical analysis of the fire ash was performed with ~~X-ray powder diffraction (~~XRD~~)~~ on 2 g of the fire ash using a Panalytical Empyrean Powder Diffractometer equipped with a position-sensitive X’Celerator detector. The chemical and mineralogical properties of the fire ash are presented in Table S1 and S2 in the Supplement.The data were collected in 2h geometry using Cu Ka radiation (k = 1.54178_A) at 40 kV and 30 mA. Scans were run over c. 15 min over a 2h range between 5° and 65° with an approximate step size of 0.033°. The phase analysis and quantification were performed using MATCH! 2.1.1 powder XRD analysis software with the PDF-2 crystallographic library (release year 2002) and WINPLOTR (September 2018 version) graphic tool for powder diffraction. We based the phase quantification on the relative intensity ratio method, which is determined by maximum intensity peaks relative to the corundum (Al_2O_3) maximum intensity peak (Hubbard & Snyder, 1988), using published intensity values for all identified phases. Elemental analysis was performed on 1 g of dried powder using an X-ray fluorescence (XRF)XRF spectrometer (Panalytical Axios X-ray system) with a single goniometer-based measuring channel consisting of a Super Sharp X-ray Tube with a rhodium anode operated at up to 60 kV and up to 50 mA at a maximum power level of 1 kW. The WDXRF used a beryllium (75 mm) anode tube window with different analysing crystals (LiF200 crystal, PE (002) crystal, Ge (111) crystal, PX1 synthetic multilayer monochromator, PX7 synthetic multilayer monochromator) to analyse the range of elements. The instrument is equipped with two types of detectors: a flow detector for longer wavelengths and a scintillation detector for shorter wavelengths. The chemical and mineralogical properties of the fire ash are presented in Table S1 and S2 in the Supplement. The total P and the total elemental analysis in fire ash was measured using ICP-MS (0.625%). We performed a modified Hedley scheme to assess P fractionation in the four fire ash samples was done using a sequential extraction procedure following a modified Hedley scheme (Mirabello et al., 2013) for desert soils and dust (Gross et al., 2016). Briefly, P was sequentially extracted from 0.1g of fire ash in four steps. First, the fire ash P was extracted with 30 ml of 0.5M $NaHCO_3$ (HCO_3-P, which reflects the dissolved and labile P, which is considered to have high bioavailability). In the second step, dust P was extracted with 1M NaOH (NaOH-P, considered as P that is loosely sorbed to Fe or Al oxides). In the third step, P was extracted with 1M HCl (HCl-P, considered as Ca-P complexes). The P in the extracts was measured using the molybdenum blue method (Murphy & Riley, 1962) in a microplate photometer (Multiskan Sky; Thermo Scientific). The chemical and mineralogical properties of the dust fire ash analogues are presented in the supplementin , SI Tables S1,S4.

2.4 Fire ash application

Fire ash was applied manually on the plants in two separate applications two separate pulses either on the foliage or on the roots. The first fire ash application was made after the first visual deficiency signs occurred, 35 DAG. Since there is limited data on the actual deposition of fire ash on terrestrial ecosystems, we followed the application doses of Gross et al. (2021). Briefly, Gross et al mimicked the yearly average amounts of dust deposition (January to April) in western Negev region, Israel -(Offer & Goossens, 2001; Uni & Katra, 2017), where the application dose was set to the equivalent value of 30 g m^{-2}, a typical dust deposition level during the major growth period. While this amount is not accurately representing the actual deposition of fire ash, it allows for a comparison of the impact of the two different atmospheric particles.. Leaf area was determined in parallel trials whereas the chickpea grown in which the chickpea was grown in similar growing conditions. Based on this, 1.5 g of fire ash was applied in each application pulse, between 35 and 45 DAG, resulting in a total of 3 g of ash per plant. The application of fire ash particles was performed in the following manner: we placed the ash particles in a sieve with a 63-micron mesh size and spread the ash by gently shaking the sieve above each plant, while part of the particles was spilled around the plants during the process. Prior to the application, the pot's surface was covered with nylon to prevent settling of ash particles to the root system. Afterwards, the plants were left undisturbed with the settled ash particles on their foliage. During foliar application of the fire ash, the ash was gently applied manually on the leaves while the pot surface was covered with nylon to prevent transport of ash particles to the root system. The same amount of ash that was applied to the foliage was applied to the substrate around the root area. Afterwords, ash particles were gently mixed around the roots to enhance the physical contact between the roots and the particles, thereby increasing the chances of having a more significant impactSame amounts and pulses of fire ash were applied to the roots. After application, all the surfaces of all the pots (-P foliar ash, -p root ash, -P and +P) were covered with nylon to equalize plants' conditions and minimize the effects of unrelated processes.

2.5 Plant biomass and elemental analysis

The plants were harvested 10 d after the last ash application, which was 55 DAG. Afterwards, we followed a cleaning method used in the study of Gross et al. (2021). Briefly, the plants were rinsed in tap water, 0.1M HCl, and three times in distilled water to remove any remaining ash residuesThe plants were rinsed in tap water, 0.1M HCl and three times in distilled water to remove any ash remains. SubsequentlyThen, the plants were dried in an oven at 65°C for 72 h and their dry weight was determined. Given that plant growth and alterations in plant ionome are evident through an increase in biomass, our examination focused on the above ground part of the plants (shoot), including stem, branches and foliage. Sample preparation for mineral analysis was conducted as follows: the dry plants were ground to a fine powder in a stainless-steel ball mill (Retsch MM400; Germany). Elemental analysis was performed The elements measurement performed by burning 1 g of the plant material in a 550°c for 4 hours, to get rideliminate of the organic material. The ashed plant material was subsequently dissolved using 1ml concentrated HNO_3 to achieve a clear solution. The solution was diluted with a double distilled water (DDW) to achieve a 1:100 dilution. The obtained solution was then measured by Agilent 8900cx inductive coupled plasma mass spectrometer at the Hebrew University (ICP-MS). 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 control plants, and dust root and foliage-treated plants and fire ash particles are given in tables S2-S4 in the supplement.

2.6 Leaf pH and Fire Ash Holding Capacity

Leaf pH was determined by analysis of P-deficient plants only. The pH was measured by manually attaching a portable pH electrode designed for flat surfaces (Eutach pH 150. P17/BNS Epoxy pH electrode with flat head for cream samples and surfaces, refillable) onto the surface of three or four leaves from each plant. pH recordings were taken once a week between the beginning of a P-deficient nutrition until the day before the termination of the experiment (Gross et al. (2021); starr et al. (2023), Yoshida et al., 1997) (Table S5 in the supplement). The measurement of leaf surface pH was made on P-deficient and P-sufficient plants, but not the fire ash treated plants because the presence of the material on the leaf surface interferes with the physical contact between the flat surface of the pH electrode and the leaf itself.

Fire ash holding capacity is a measure for the maximal mass of ash that can be held on the surface of a leaf after application of an excessive dose of ash and removing the free particles. This value was achieved by manually dispersing 1 g of ash on the adaxial surface of 0.5 g of fresh leaves, which were detached at the end of the experiment from 12 specially grown P-deficient and P sufficient plants that did not receive the ash treatment (additional plants). These plants were taken to Ben Gurion biogeochemistry lab to perform the ~~analysis of~~ holding capacity analysis ~~o perform the holding capacity analysis.~~. After ~~dust and~~ fire ash~~es~~ application, the leaves were gently shaken for 10 sec and weighed. The differences between the weights before and after the ash application represent leaf~~ve's~~ holding capacity (Gajbhiye et al., 2016).

2.7 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.

3 Results

3.1 Fractionation of P in fire ash samples

Most of the P in fire ash that we produced from four different tree types was found in the HCl fraction (ranging from 59%-80%). The fraction of $NaHCO_3$-P ranged from 18%-39%. The NaOH-P fraction ranges from 1%-2%. The average total P ranges from 5382 mg/g to 7323 mg/g (Fig. 1).

3.~~1~~2 Shoot biomass and total P under aCO_2

Plants that received foliar application of fire ash show a significant increase in their biomass and P content (Fig. ~~1~~ 2 ~~d~~b,~~f~~d). Control plants had a dry biomass of 1.36 g, while the foliar treated plants had a dry biomass of 2.14 g, indicating an increase of 57.0%. Similarly, the P content increased from 0.96 mg to 1.45 mg, representing a growth of 50.3%. No increases in biomass or P content were observed in plants that received fire ash in the substrate (Fig. 2a,c).

~~Compared with the control plants, the~~ 3.~~2~~3 Shoot biomass and total P under eCO_2

Plants that received foliar application of fire ash show a significant increase in their biomass and P content (Fig. 3b,d). Control plants had a dry biomass of 1.50 g, while the foliar treated plants had a dry biomass of 1.84 g, representing an increase of 23.2%. Additionally, the P content rose from 1.03 mg to 1.17 mg, reflecting an increase of 12.6%. No increases in biomass or P content were observed in plants that received fire ash in the substrate (Fig. 3a,c).

3.~~3~~4 Shoot nutrient status under eCO_2 conditions

To quantify the impact of elevated eCO_2 conditions on the nutrient status of plant samples, we conducted a comparison between the ionome of chickpea plants grown under aCO_2 and those grown under eCO_2 levels for both foliar fire ash treated and untreated plants. The comparison was conducted as follows: the average value of each nutrient in plants grown under aCO_2 was calculated, and then each nutrient in individual chickpea plants grown under eCO_2 levels was expressed as a ratio relative to the average under aCO_2 conditions (eCO_2 plant$_{(each\ individual\ plant)}$/$aCO_2$ plant $_{(average\ of\ all\ the\ control\ plants)}$). ~~the impact of eCO2 conditions on plant's nutrient status, we divide the nutrients concentration averages in plants shoot in the control group of the eCO2 by the concentration averages of the aCO2 group (Fig. 3).~~ We observed that eCO_2 conditions led to a reduction in the concentrations of Mg, K, Ca, Mn, Zn, Cu, Fe, and Ni, ranging from 28.7% (Fe) to 90% (Ni). The foliar fire ash treated plants indicate a significant increase in the concentration of Ni, offsetting the reduction of the control untreated plants that was seen under eCO_2 from -90% to -60%, representing a 33% increase. No significant changes were observed for other nutrients (Fig. 4).~~We see that eCO2 conditions reduced the concentration of Mg, K, Ca, Mn, Zn, Cu, Fe and Ni in the range of 28.7 % (Fe) and 90% (Ni). Foliar fire ash application significantly increased the concentration of Ni (from -90% reduction to -60%, increase of 33%). No significant changes were found for other nutrients.~~

3.5 Leaf surface properties

Leaf surface pH ranged from 1 to 1.3 with an average value of 1.18 (~~presented in t~~Table S5 in the supplement). Fire ash holding capacity ranged from 0.07 g to 0.17 g with an average value of 0.13 g (presented in table S6 in the supplement). Fire ash holding capacity values were at the same order of magnitude as the values of desert dust and fire ash that were reported in Palchan et al. (in review).

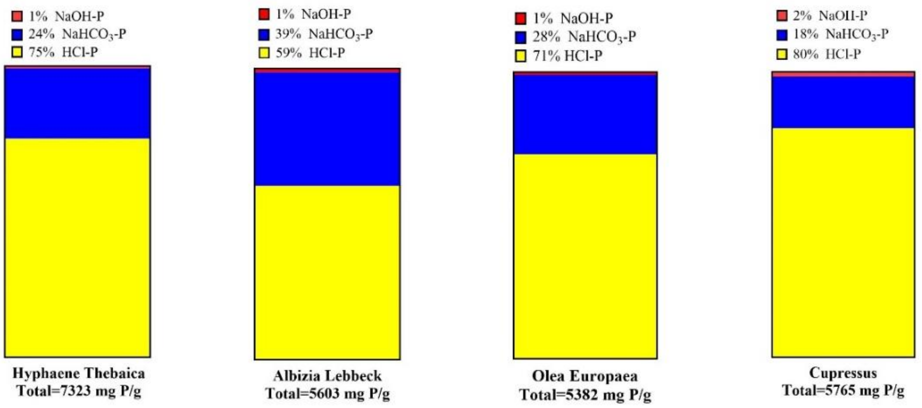


Figure 1: The fractionation of P in fire ash particles. Yellow color represents P fraction released by 1M HCl, blue color represents P fraction released by 0.5M $NaHCO_3$ and red color represents P fraction released by 1M NaOH. The average total P value of the four samples is 6018 mg P/g.

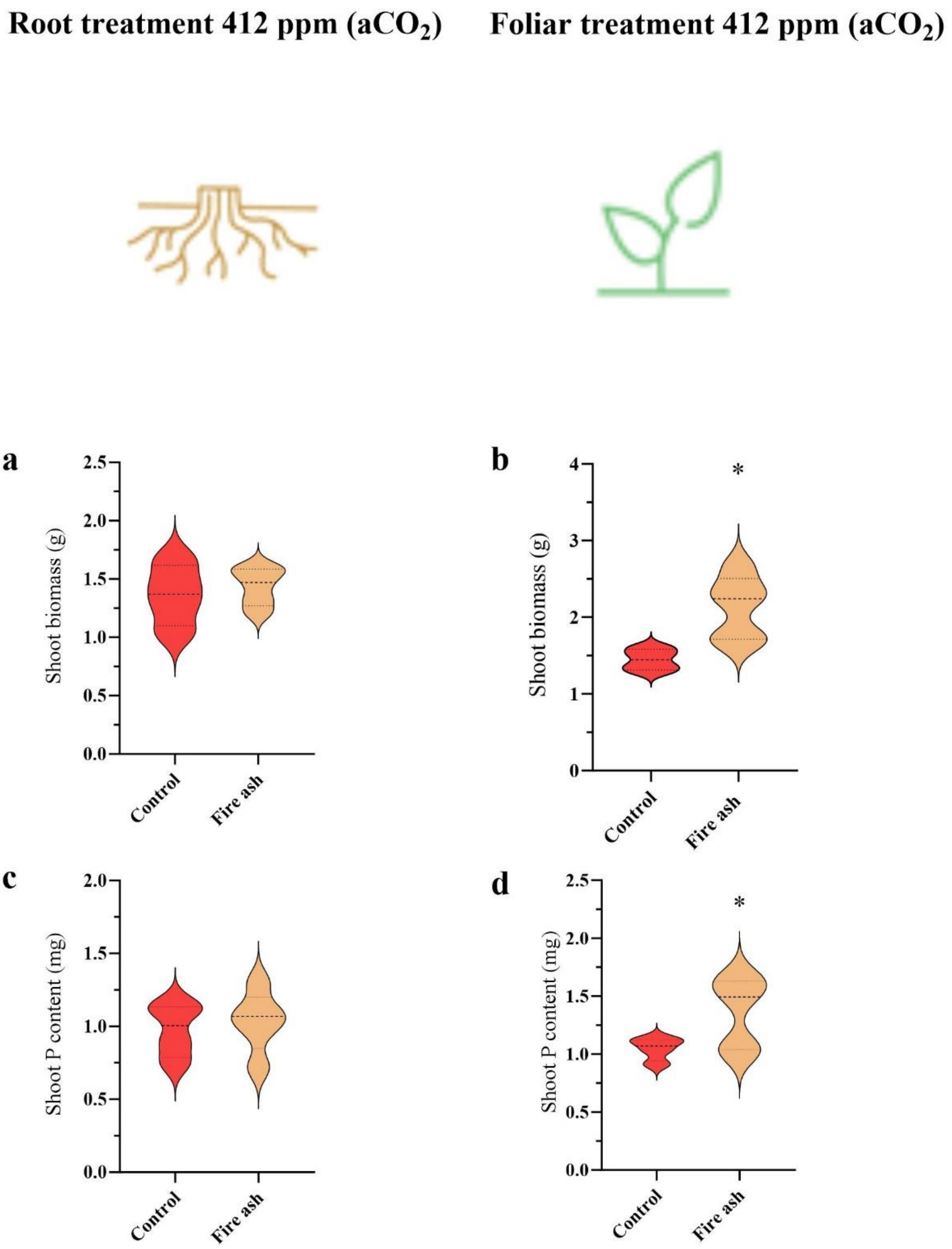


Figure ~~1~~ 2 (a-d): The biomass and P content in chickpea plants that were grown under aCO_2 levels, after application of fire ash ~~on roots~~in the substrate or to the foliage. Control plants with no ash application colored in red ~~and~~ while plants ~~that were applied~~treated with fire ash are ~~colored~~ indicated in a bright ~~warmth~~brown color. (a,b) Shoot biomass of plants that were applied with fire ash on their roots or their leaves. (c,d) P content of plants that were applied with

fire ash on their roots or their leaves. Asterisks represent statistically significant differences between bars (P<0.05, Tukey test). Error bars represent standard deviations (n = 5). The results are presented in a Violin plot, where the dashed line represents the median, and thin dotted lines indicate quartiles.

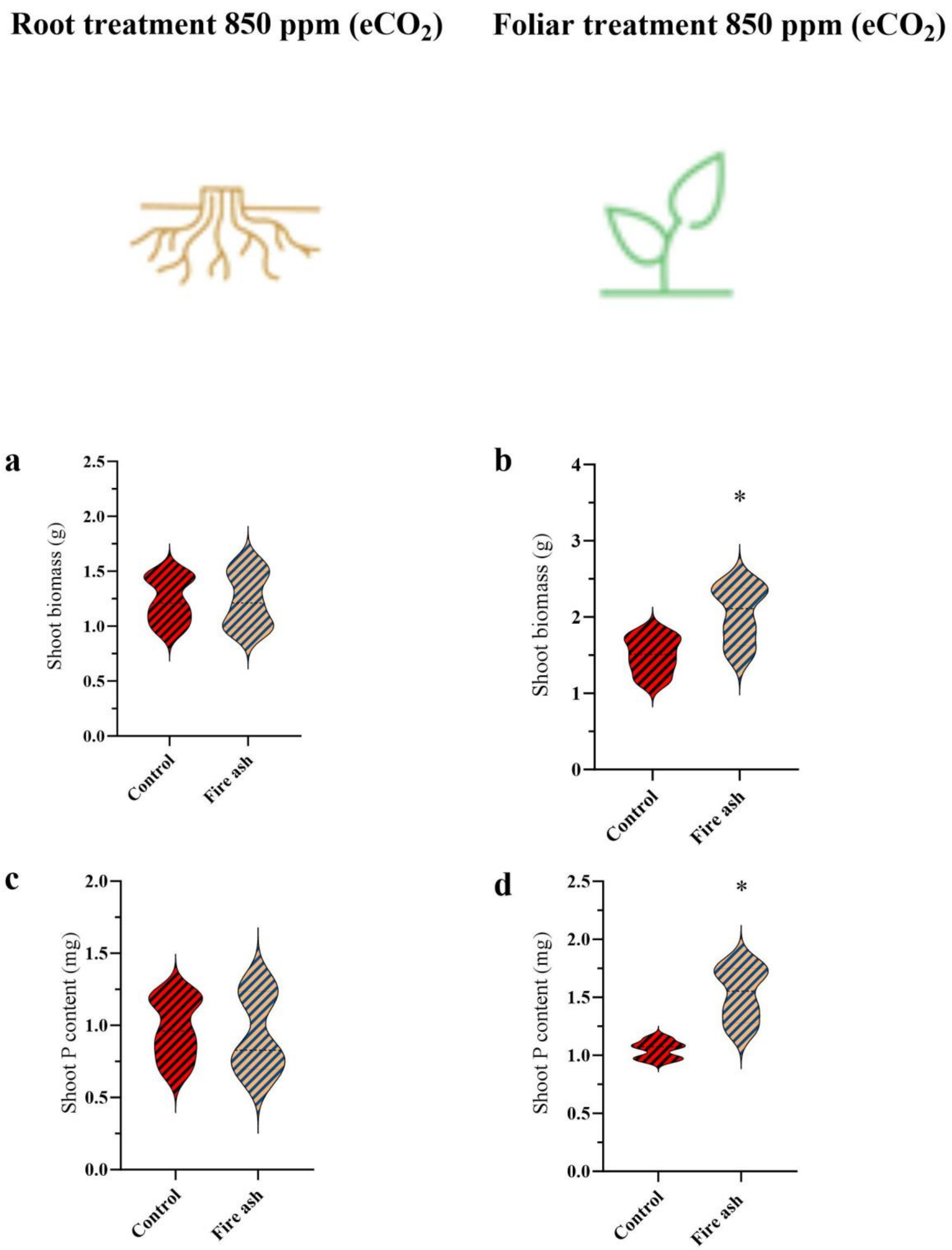
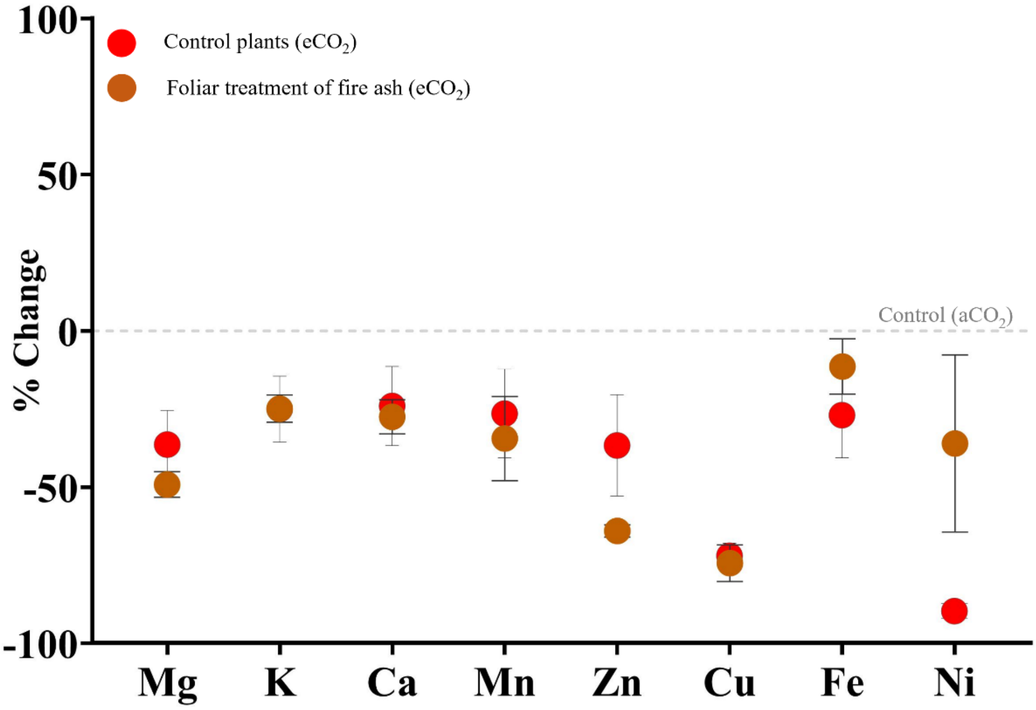


Figure ~~2~~ 3 (a-d): The biomass and P content in chickpea plants that were grown under eCO_2 levels, after application of fire ash ~~on roots~~in the substrate or to the ~~leaves~~foliage. Control plants with no ash application colored in red, and plants that were applied with fire ash are colored in bright ~~warmth~~brown. (a,b) Shoot biomass of plants that were applied with fire ash on their roots or their leaves. (c,d) P content of plants that were applied with fire ash on their

roots or their leaves. Asterisks represent statistically significant differences between bars (P<0.05, Tukey test). Error bars represent standard deviations (n = 5). The results are presented in a Violin plot, where the dashed line represents the median, and thin dotted lines indicate quartiles.



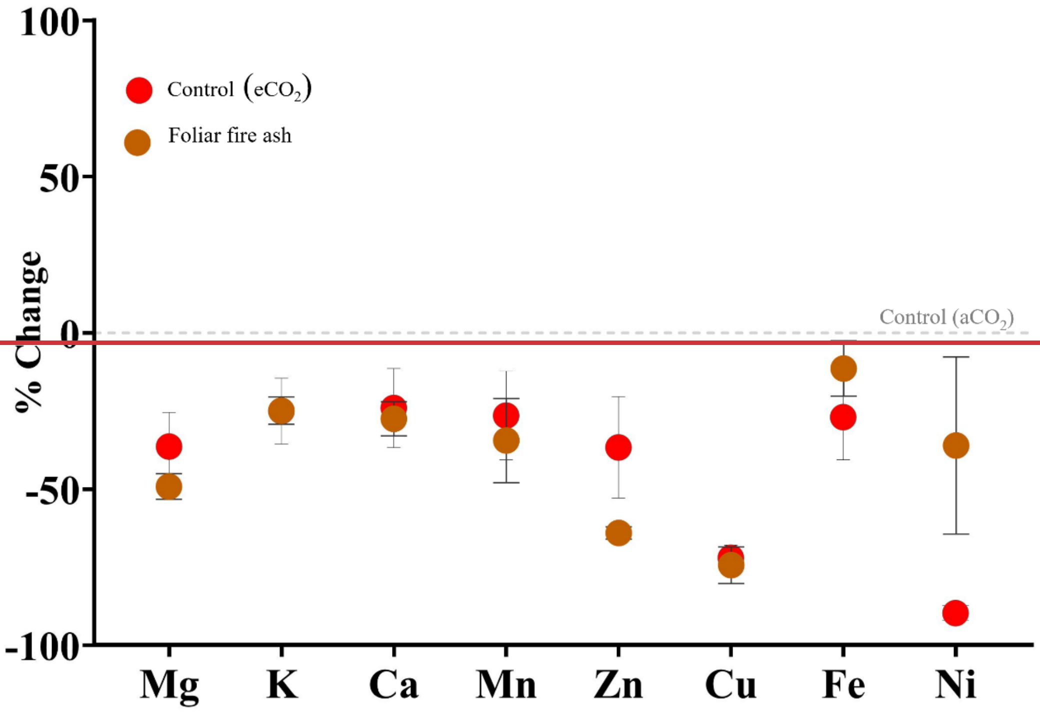


Figure 3 4: The % change in the nutrient concentration of plants that were grown under eCO_2 conditions in comparisoncomparison to the plants that were grown under aCO_2 conditions. Red circles represent untreated control plants. Brown circles represent plants that received fire ash through foliar application. The dashed line represents the average values of the control plants grown under aCO_2 levels; the vValues below the dashed line representindicate a decline in the respective nutrient under eCO_2 levels. The depletion of the plants nutrient status is caused by the downregulation of the roots system. Error bars represent standard deviations (n = 5).

4 Discussion

4.1 XRD, XRF and total P

The XRF, XRD, and total P values of the fire ash samples in our study are within the same order of magnitude as those found in the ash of Mediterranean Savanna forests (Sánchez-García et al., 2023). Also, the fractionation of P in the ashes aligns with fractionation reported in other studies (Wu et al., 2023). The results demonstrate fire ash exhibit a higher concentration of total P in comparison to soils, mineral dust or volcanic ash (Ranatunga et al., 2009; Tiwari et al., 2022; Starr et al., 2023)), with a significant percentage being in a soluble form (18%-39%). Yet, the majority of fire ash P is not readily soluble and is found in biologically unavailable form.

4.21 P uptake from fire ash under aCO_2 levels

Foliar application of fire ash under aCO_2 levels increased chickpea biomass and total P content compared to untreated control plants, demonstrating that foliar uptake of P from fire ash has a direct nutritional impact on plants, providing P for biomass growth and boosting photosynthesisFoliar application of fire ash under aCO2 levels increased chickpea biomass and total P content in comparison to untreated control plants, emphasizing its direct nutritional impact on plants. Chickpea plants were more responsive to fire ash in comparison to experiments with desert dust and volcanic ash from Palchan et al. (in review), demonstrating the importance of fire ash P for plant growth. confirming our initial hypothesis that fire ash P is more bioavailable to plants. However, because there was no nutritional impact when fire ash was deposited in the substrate area near the roots, we conclude the nutritional impact occurred exclusively through the foliar nutrient uptakepathway,despite its projected bioavailability, the direct nutritional impact occurred exclusively through the foliar uptake pathway. This discovery partially challenges our second hypothesis as no response was documented when fire ash particles were applied to the roots, even though the concentration and solubility of P and other nutrients in fire ash are considered higher in comparison to desert dust and volcanic ash (Bigio & Angert, 2019; Gross et al., 2015; Tan & Lagerkvist, 2011; Tiwari et al., 2022). The low bioavailability of fire ash P for root uptake impliesy that fire ash P is not fully soluble in the rhizosphere and maybe loosely attached to Ca, Fe or Al, that prevents its utilization (Masto et al., 2013; Qian et al., 2009; Tan and Lagerkvist, 2011; Santín et al., 2018). Another reason for the roots impairment in P uptake might be the insufficient physical contact between fire ash particles and the roots, even though the tested plants exhibited an extensive root system, with an average root-to-shoot ratio of 50:50 and the pH of the substrate was around 7, in the range of most alkaline soils. In contrast, plants foliage has a greater surface area that increases the direct physical contact between fire ash particles and plant tissues, thus creating a suitable condition for their partial solubilization. These results suggest that solubility tests examined by chemical extractions do not necessarily reflect actual biological availability and emphasize the importance of fertilization experiments with plants. It is difficult to compare our results with other studies because ~~the~~ direct foliar uptake of P from fire ash particles has been so far overlooked, until now. As far as we know, ~~O~~our results represent the first ~~instance~~experiment in which fire ash particles were directly added to plants, thus definitively challenging the common perception that P is solely taken up through the roots from the soil, even in the case of atmospheric particle deposition.

4.3~~2~~ Foliar nutrient uptake mechanism

Gross et al. (2021) and Palchan et al. (in review) have studied foliar nutrient uptake mechanisms and pointed out that the presence of trichomes facilitates the adhesion of dust captured on leaf surface and promotes the release of P solubilizing metabolites, such as malic citric and oxalic acids. In addition to the natural secretion of organic acids, the increased secretion may be enhanced as a result of the breakage of trichomes following the application of atmospheric particles on plants foliage~~.~~. As in previous studies, we also measured a highly acidic leaf surface environment (average pH value of 1.15) and a high fire ash holding capacity (average value of 15%), thus supporting the previous assertions that low pH and high holding capacity may help facilitate P uptake on plant leaves. The combination of leaf surface acidification ~~(pH values of the leaves are presented Table S5 in supplement)~~, secretion of organic acids and additional exudations combined with an increased trichomes density, enhances capture ~~foliar particles capture~~ and holding of particles, which in turn facilitates the foliar nutrient uptake in chickpea (chickpea leaves holding capacity of a fire ash particles are presented in Table S6 in the supplement).

4.4~~3~~ Foliar nutrient uptake under eCO_2 levels

In accordance with previous studies, growing chickpea plants under eCO_2 levels drove a significant reduction in nutrient status in comparison to plants that were grown under aCO_2 levels, despite receiving the same fertigation solution. The nutritional decline under eCO_2 mostly occurs due to the 'dilution' effect, where accumulation of carbon (C) exceeds that of mineral nutrients, and more importantly, because of a result of a partial inhibition of key root uptake mechanisms (Myers et al., 2014; Loladze, 2002; Gojon et al., 2022) ~~despite receiving the same fertigation solution~~. In our experiment the control group was grown under eCO_2 conditions and did not exhibit an increase in biomass. This indicates that the 'dilution' effect is not responsible for the nutrient reduction observed in our study and suggests that the primary reason for the nutritional reduction is likely the downregulation of transfer from roots to shoot or root uptake. As a result of the foliar application of fire ash particles, the nutritional reduction under eCO_2 was partially offset, leading to an increase in plants' Ni concentrations ~~In addition to increased P content, foliar application of fire ash under eCO_2 increased plants' Ni and moderately offset the reduction of Ni due to eCO_2 conditions~~ (Fig. 3). Yet, the nutritional contribution of foliar fire ash under eCO_2 levels was less prominent compared to the foliar application of desert dust and volcanic ash, which in addition to Ni also increased the concentration of Fe ~~Yet, its nutritional contribution under eCO_2 levels was less prominent in comparison to foliar application of desert dust and volcanic, which also offset the decline in Fe concentrations~~ (Palchan et al. (in review))~~. These results partially contradict our third hypothesis regarding the greater role of~~

~~foliar nutrient uptake from fire ash under eCO$_2$ levels~~. We anticipated that the foliage would ~~also~~ absorb additional nutrients, such as K, Ca, and Zn, which are present in higher concentrations in fire ash compared to desert dust and volcanic ash (T~~see SI t~~able S2). The absence of an impact of fire ash on chickpea Fe concentration contrasts with previous laboratory studies that demonstrated substantially greater Fe solubilities in combustion-derived aerosols compared to crystalline minerals~~The absence of an impact on chickpea Fe concentration challenges our projections considering that previous laboratory studies demonstrated the Fe solubilities of combustion-derived aerosols are substantially greater than those of crystalline minerals~~ (Schroth et al., 2009; Fu et al., 2012). One reason for the low response to fire ash Fe may be related to incomplete combustion which determines the bioavailability of mineral nutrients in fire ash which is mediated by combustion temperature and the presence of oxygen (Tan and Lagerkvist, 2011). In addition, ~~N~~natural forest fires exhibit varying combustion conditions, adding to the complexity of projecting the actual nutrient bioavailability of wildfires (Bodí et al., 2014). Thus, the actual availability of fire ash~~ P,~~ nutrients such as Fe, P, and others~~ nutrients~~ warrants further research, based on laboratory and field fertilization experiments at different combustion conditions. ~~Another possible factor could be the elevated pH level of the fire ash particles which may impact the chemical environment of the leaf surface and inhibit mineral solubilization. The direct effects of fire ash particles on plant physiology and morphology are mostly unknown.~~

4.54 Broader aspect

We recognize that in other plants, the phenomenon of foliar uptake might be less pronounced (Starr et al., 2023; Gross et al., 2021). in our opinion, selecting a suitable plant was essential to effectively demonstrate it. In a broader context, numerous articles have documented the contribution of wildfire ash to soil fertility through long-term processes, despite the fact that fire ash P contains a significant proportion of labile P ~~In a broader aspect, numerous articles documented the contribution of wildfire ash to soil fertility through long-term processes~~ (Bauters et al., 2021; Barkley et al., 2019; Bodí et al., 2014). The current perception dictates that fire ash nutrients are not immediately available to plants but rather interact with soil components and bind to minerals in the soil (Tiwari et al., 2022.; Chadwick et al., 1999; Okin et al., 2004). ~~. In accordance with the common view, O~~Our results demonstrated that in the time frame of a few weeks, the contribution of fire ash through the roots is negligible. I~~Yet, i~~n contrast, fire ash has an immediate nutritional significance to plants via foliar nutrient uptake pathway. It happens due to the foliar secretion of organic acids, such as oxalic and malic, which facilitate the dissolution of fire ash P. Bauters et al. (2021) emphasized that the canopy of the trees in African tropical forest capture P from biomass burning byproducts, which, upon settling on the ground with rain, contributed P to the nutrition of trees as was evident by larger and denser trees growth. We postulate that at least part of that fire ash P was taken up directly by the foliage. In a future world where the quantity and intensity of fires are expected to rise, alongside increasing demand for P due to the CO$_2$ fertilization effect, the contribution of fire ash to natural ecological systems will increase. The fact that the foliar uptake mechanism remains generally unaffected under eCO$_2$ suggests that this pathway may become crucial. Plants exhibiting the foliar nutrient uptake trait are more likely to benefit from fire ash fertilization in a future world. ~~Finally~~Another important contribution of fire ash~~,~~ ~~Fire ash~~ P deposition, is its potential to~~ can~~ alleviate the ecological stoichiometric imbalance ~~that stems from manmade~~resulting from anthropogenic nitrogen (N) pollution in soils~~deposition~~, which is expected to grow in the next decades (Liu et al., 2013) and disrupt plants and the ecosystem's function. Thus, fire ash may play a larger role in a world that shifts from N to P limitation ((Du et al., 2020) (Du et al., 2020). Currently, biogeochemical models do not incorporate foliar P uptake from fire ash and other atmospheric particles such as desert dust and volcanic ash. Given the substantial contribution of foliar uptake to plant nutrition from atmospheric deposition, it is imperative to include this process in global carbon and vegetation models. Such models should take into account canopy surface areas, canopy roughness, soil fertility and geographical distribution of atmospheric particles sources and sinks. This inclusion will lead to a more comprehensive description of the global P cycle.

5 Conclusions

We have conducted controlled experiments where we have grown chickpea plants under ambient and elevated CO_2 conditions. We fertilized the plants separately on foliage and roots with fresh fire ash and harvested the plants after 4 weeks. We then studied the plants elemental composition and reached the following conclusions:

- Freshly deposited fire ash has a direct impact on plant P nutrition only through the foliar nutrient uptake pathway and not via the root system.
- The root acquisition of a freshly deposited fire ash P, as well as other nutrients is limited, despite the high solubility of fire ash P.
- In general, P uptake from fire ash was higher than that of other natural atmospheric particles such as desert dust and volcanic ash.
- Foliar nutrient uptake from fire ash is sustained even under elevated CO_2 conditions, implying that the significance of foliar nutrient uptake from fire ash will increase in future climates. This is expected as the ionome of plants is anticipated to decrease, primarily due to the partial downregulation of the root's nutrient uptake mechanism. Foliar nutrient uptake from fire ash is maintained also under an elevated CO_2, suggesting that the role of foliar nutrient uptake from fire ash will be critical in a future climate as the ionome of the plants is expected to decrease, primarily due to partial downregulation of the root's nutrient uptake mechanism.

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Acknowledgments

A.L thanks financial support provided by and KKL climate team doctoral fellowship. We thank Dr. Yigal Erel and Ofir Tirosh for their support in ICP-MS analyses. The project was funded by the Israeli science foundation (ISF), grant number 144/19.

Author contributions

A.L performed the growing experiments, sample preparations, wrote the article along with input from all authors. D.P and A.G conceived and supervised the entire project.

Competing interests

The authors declare no competing interests.

Data availability

Source data for the main text, methods and supplementary information are provided as supplementary information tables.

Additional Information

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