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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 separately on a plant's foliage or onto its roots. We conducted experiments on chickpea model plants under ambient and elevated CO_2 levels, 412 and 850 ppm, that reflect current and future climate scenarios. We found that plants can uptake fire ash P only through their leaves, by a direct nutrient uptake from particles captured on their foliage, but not via their roots. 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 CO_2 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.

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 ecosystem (Mikhailova et al., 2019; Aciego et al., 2017; Chadwick et al., 1999; Goll et al., 2022; Gross et al., 2015, Palchan et al., 2018). 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; 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% of the fire ash particles are generated via high grassland and savanna fires in Africa whereas the rest are emitted from the Savana'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 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 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). 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).

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). 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 eCO_2 conditions, which are projected to 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. Chickpea served as our model plant and was grown under eCO_2 and 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 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 aCO_2 conditions as fire ash P is highly soluble and thus bioavailable. Finally, the role of foliar uptake pathway will be more dominant under eCO_2 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 After Germination (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 as directly on the foliage (-P+leaf ash) and 12 directly on the roots (-P+root 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.

2.2 Fire ash type

The fire ash was produced by bone-fire burning of branches and needles of coniferous trees that grow in Neve-Shalom Forest, Israel (31°82191 N, 34°98719 E). Later, the ashes were burned again in a furnace at 550°c for two hours to achieve complete combustion of the organic material. Complete combustion of organic material results in production and oxidation of volatiles or gases such as carbon dioxide (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 (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

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 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) 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 total P in fire ash was measured using ICP-MS (0.625%). P fractionation in the fire ash 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 analogues are presented in SI Table 1,4.

2.4 Fire ash application

Fire ash was applied manually on the plants in 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. Leaf area was determined in parallel trials whereas the chickpea 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 as per plant.

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. Same 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. The plants were rinsed in tap water, 0.1M HCl and three times in distilled water to remove any ash remains. Subsequently, the plants were dried in an oven at 65°C for 72 h and their dry weight was determined. Sample preparation for mineral analysis was conducted as follows: the dry plants were ground toa fine powder in a stainless-steel ball mill (Retsch MM400; Germany). The elements measurement performed by burning 1 g of the plant material in a 550°c for 4 hours, to get rid 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 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. 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). The plants were taken to Ben Gurion biogeochemistry lab to perform the holding capacity analysis. After dust and ashes application, the leaves were gently shaken for 10 sec and weighed. The differences between the weights before and after the ash application represent leave'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 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 d,f). Compared with the control plants, the biomass increased from 1.36 g to 2.14 g (i.e., growth of 57.0%) and P content from 0.96 mg to 1.45 mg (i.e., growth of 50.3%). In plants that received root application of fire ash there are no increases in biomass nor P content (Fig. 1c,e).

3.2 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. 2d,f). Compared with the control plants, the biomass increased from 1.50 g to 1.84 g (23.2%) and P content from 1.03 mg to 1.17 (12.6%). In plants that received root application of fire ash there are no increases in biomass nor P content (Fig. 2c,e).

3.3 Shoot nutrient status under eCO_2 conditions

To quantify the impact of eCO_2 conditions on plant's nutrient status, we divide the nutrients concentration averages in plants shoot in the control group of the eCO_2 by the concentration averages of the aCO_2 group (Fig. 3). We see that eCO_2 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.

3.4 Leaf surface properties

Leaf surface pH ranged from 1 to 1.3 with an average value of 1.18 (presented in 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).

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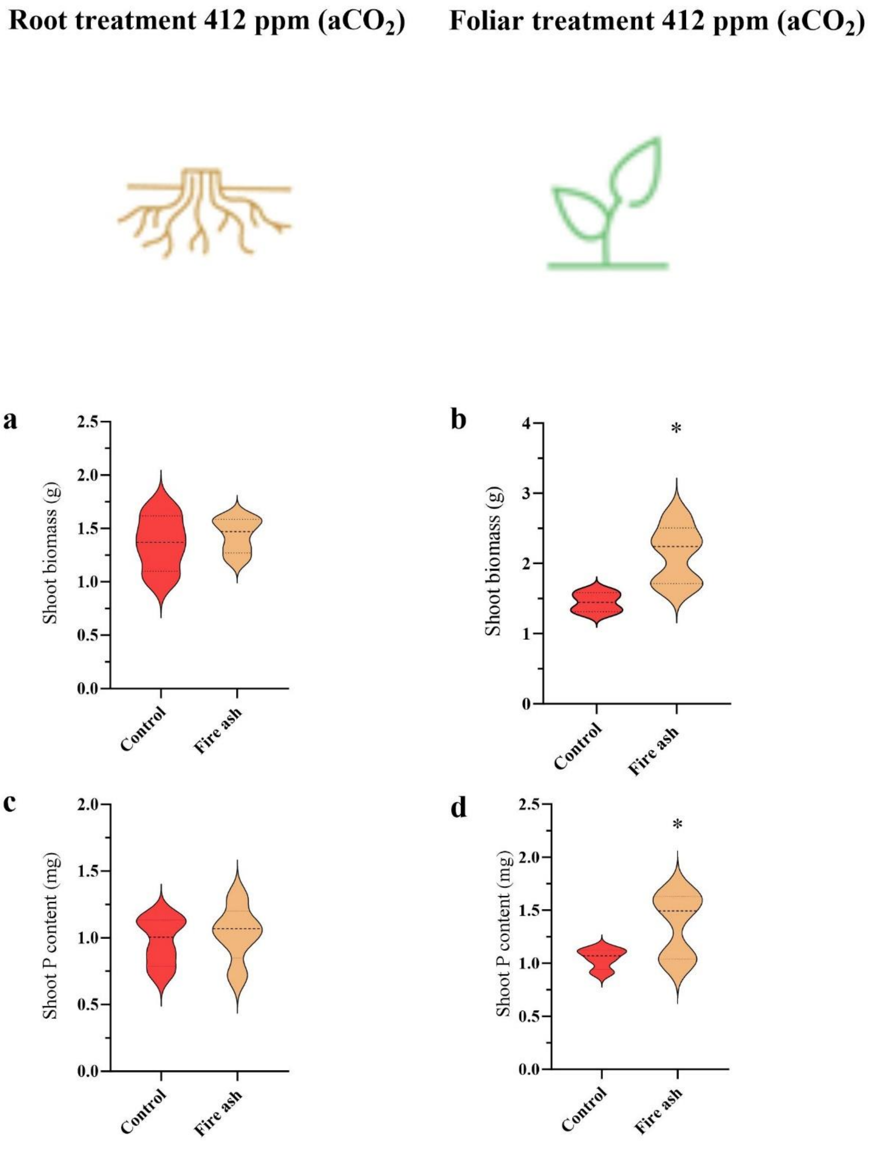

Figure 1 (a-d) The biomass and P content in chickpea plants that were grown under aCO_2 levels, after application of fire ash on roots or foliage. Control plants with no ash application colored in red and plants that were applied with fire ash are colored in bright warmth. (a,b) Shoot biomass of plants 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. Error bars represent standard deviations (n = 5).

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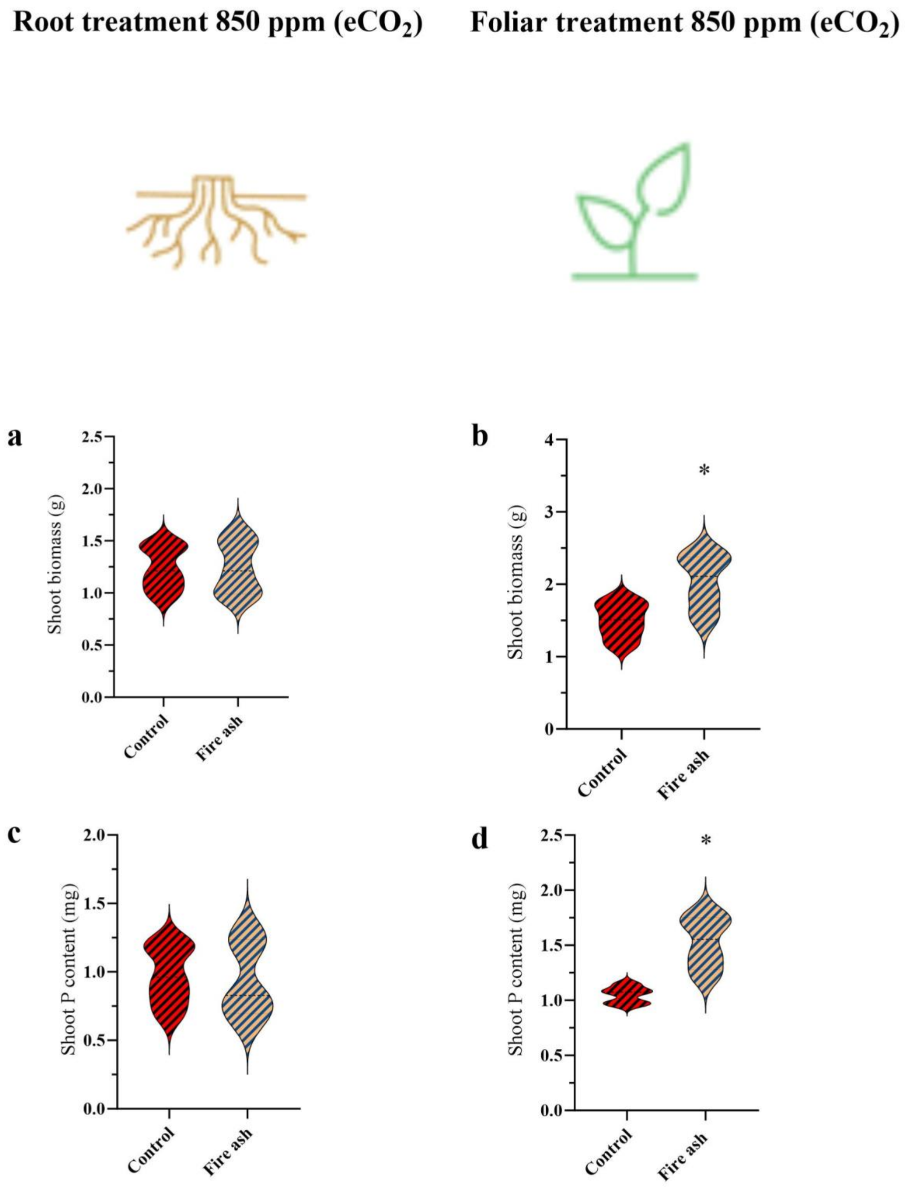

Figure 2 (a-d) The biomass and P content in chickpea plants that were grown under eCO_2 levels, after application of fire ash on roots or leaves. Control plants with no ash application colored in red, and plants that were applied with fire ash are colored in bright warmth. (a,b) Shoot biomass of plants 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. Error bars represent standard deviations (n = 5).

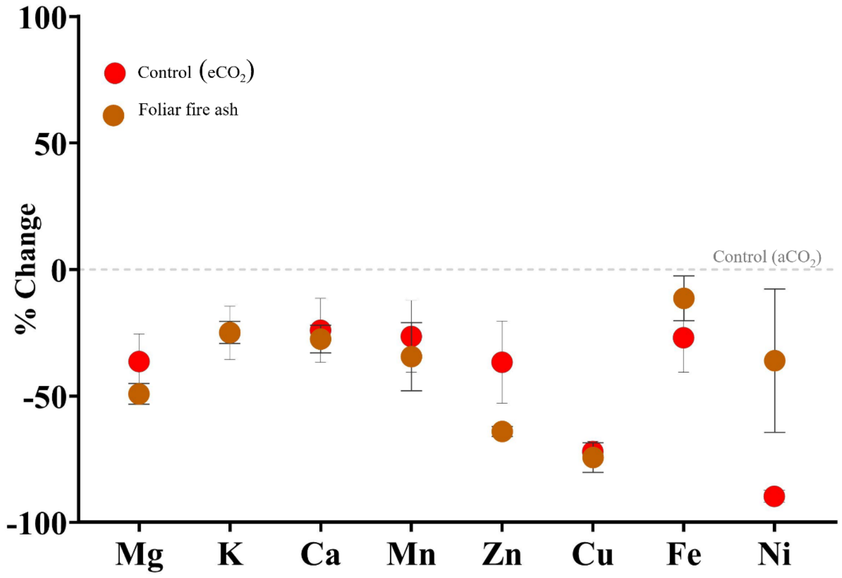

Figure 3 The % change in the nutrient concentration of plants that were grown under eCO$_2$ conditions in comparison the plants that were grown under aCO$_2$ conditions. Red circles represent untreated control plants. Brown circles represent plants that received fire ash through foliar application. Values below the dashed line represent 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 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 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), confirming our initial hypothesis that fire ash P is more bioavailable to plants. However, 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 imply 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. 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.

4.2 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 (Gross et al., 2021; Starr et al., 2023). 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 foliar particles capture and holding, which in turn facilitates the nutrient uptake in chickpea (chickpea leaves holding capacity of a fire ash particles are presented in Table S6 in supplement).

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 (Myers et al., 2014; Loladze, 2002; Gojon et al., 2022) despite receiving the same fertigation solution. 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, 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 (see SI table 2). 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). 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, Fe, and other 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.

4.4 Broader aspect

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., n.d.; Chadwick et al., 1999; Okin et al., 2004). In accordance with the common view, our results demonstrated that in the time frame of a few weeks, the contribution of fire ash through the roots is negligible. Yet, in contrast, fire ash has an immediate nutritional significance to plants via foliar nutrient uptake pathway. 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, Fire ash P deposition can alleviate the ecological stoichiometric imbalance that stems from manmade N 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)).

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 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 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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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.

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