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 Ssavannas'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~~After ~~g~~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~~h 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~~ wa~~sere~~ 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

160 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

165 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

170 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

175 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

180 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 analogue~~s~~ are presented in the supplement~~in~~, ~~SI~~ Table~~s~~ S1,S4.

2.4   Fire ash application

185 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

190 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

195 was applied in each application ~~pulse~~, between 35 and 45 DAG, resulting in a total of 3 g of as~~h~~ 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. Afterword~~s~~, 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 impact~~Same amounts and pulses of fire ash were applied to the roots~~. ~~After application, a~~ll 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 residues~~The plants were rinsed in tap water, 0.1M HCl and three times in distilled water to remove any ash remains~~. Subsequently~~Then,~~ 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 rid~~eliminate ~~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 ashes application, the leaves were gently shaken for 10 sec and weighed. The differences between the weights before and after the ash application represent leafve'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).

3.12   Shoot biomass and total P under aCO₂

Plants that received foliar application of fire ash show a significant increase in their biomass and P content (Fig. 12 db,fd). 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 3.23   Shoot biomass and total P under eCO₂

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).

300
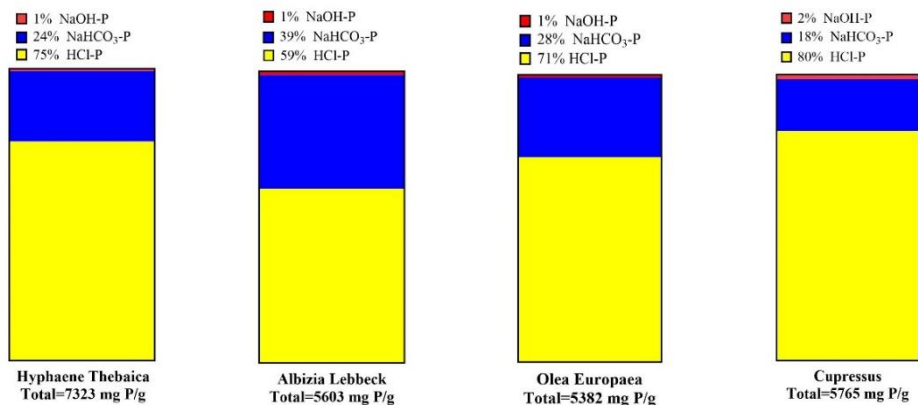
Figure 1: The fractionation of P in fire ash particles. Yellow color represents P fraction released by 1M HCl, blue color represents P fraction released by 0.5M NaHCO₃ and red color represents P fraction released by 1M NaOH. The average total P value of the four samples is 6018 mg P/g.
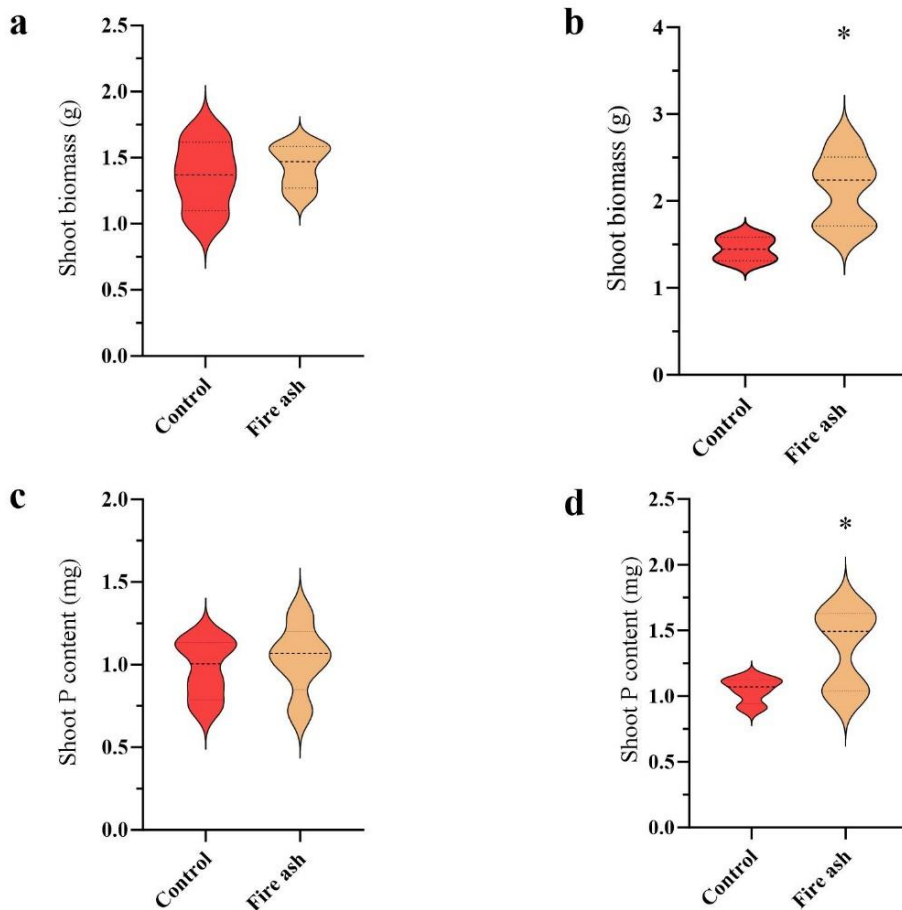
Figure 1 2 (a-d): The biomass and P content in chickpea plants that were grown under aCO₂ levels, after application of fire ash on roots in the substrate or to the foliage. Control plants with no ash application colored in red and while plants that were applied treated with fire ash are colored indicated 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.
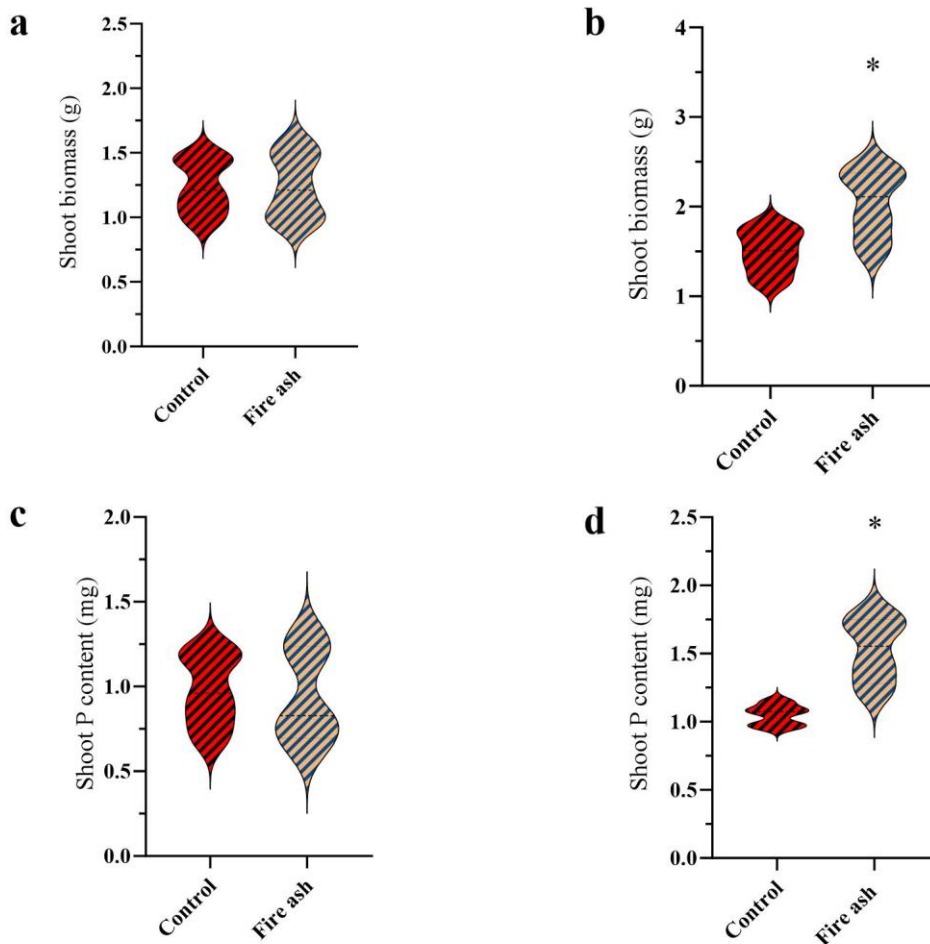
Figure 2 3 (a-d): The biomass and P content in chickpea plants that were grown under eCO₂ levels, after application of fire ash on rootsin the substrate or to the leavesfoliage. Control plants with no ash application colored in red, and plants that were applied with fire ash are colored in bright warmthbrown. (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

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quartiles.
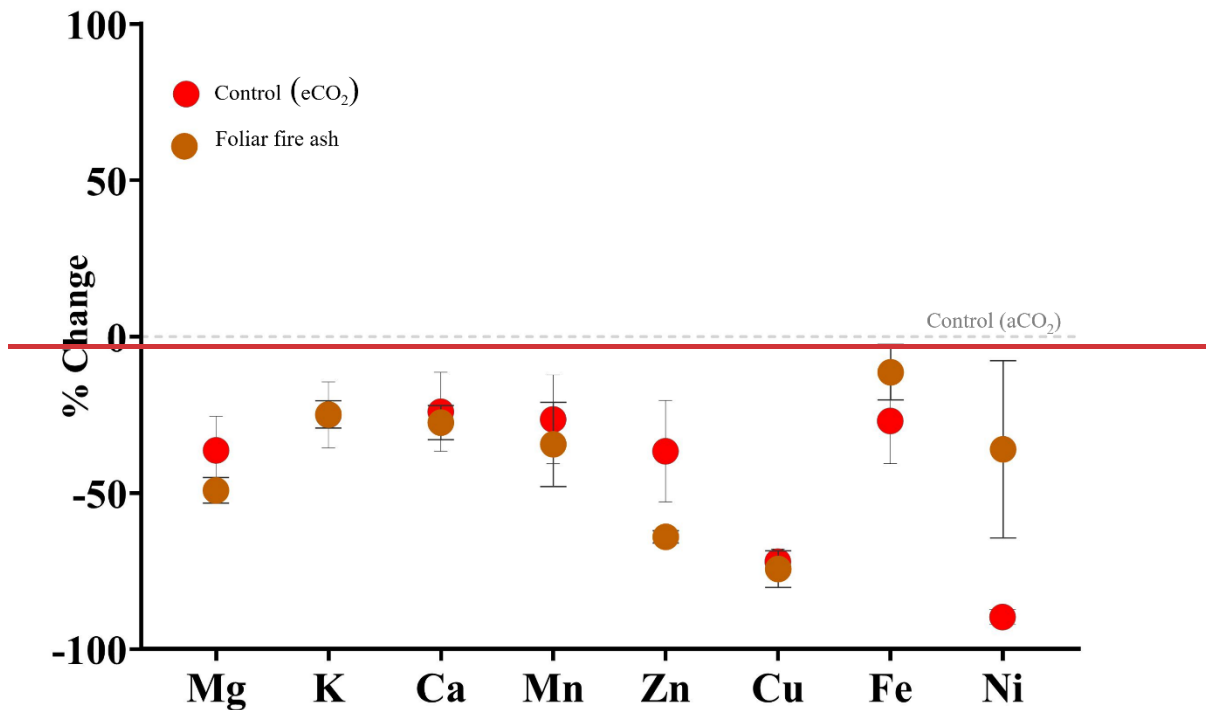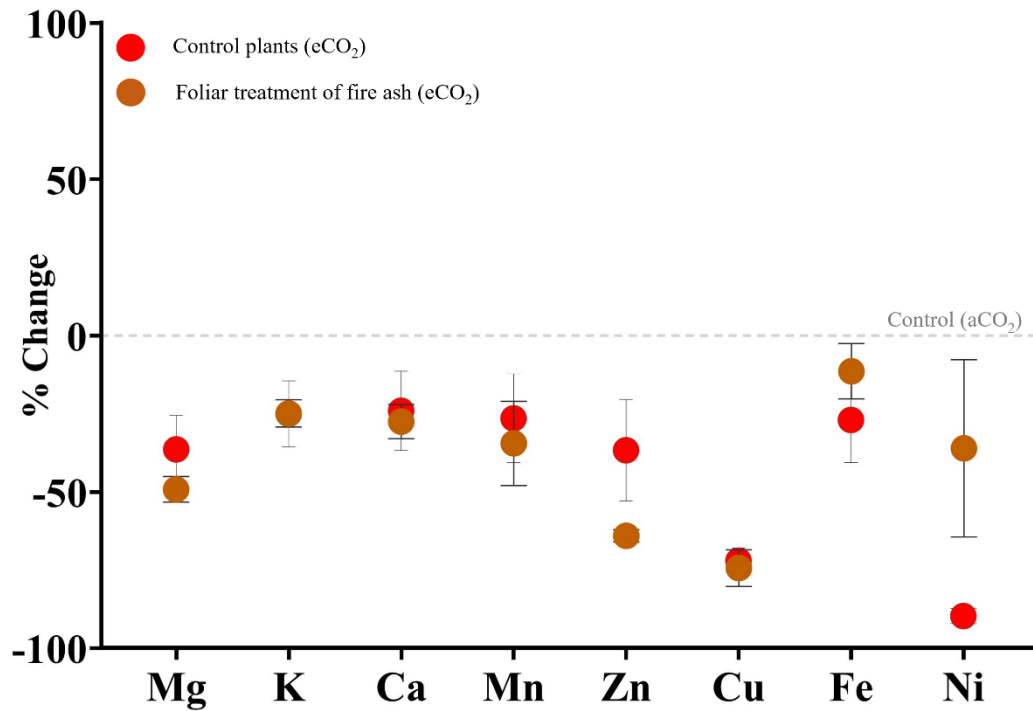
Figure ~~3~~ 4: **The % change in the nutrient concentration of plants that were grown under eCO$_2$ conditions in ~~comparison~~comparison to the plants that were grown under aCO$_2$ conditions. Red circles represent untreated control plants. Brown circles represent plants that received fire ash through foliar application. The dashed line represents the average values of the control plants grown under aCO$_2$ levels; the ~~v~~Values below the dashed line ~~represent~~indicate 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.~~1~~2 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 photosynthesis~~Foliar 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 uptake~~pathway.~~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 impl~~ies~~y 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 eCO₂ 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 other~~s~~ ~~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.~~5~~4   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~~~~o~~ur 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. ~~B~~auters 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 eCO₂ 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

470 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

475 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
480 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
485 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
490 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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6   References

Aciego, S. M., Riebe, C. S., Hart, S. C., Blakowski, M. A., Carey, C. J., Aarons, S. M., Dove, N. C., Botthoff, J. K., Sims, K. W. W., and Aronson, E. L.: Dust outpaces bedrock in nutrient supply to montane forest ecosystems, Nat Commun, 8, https://doi.org/10.1038/ncomms14800, 2017.

510

Barkley, A. E., Prospero, J. M., Mahowald, N., Hamilton, D. S., Popendorf, K. J., Oehlert, A. M., Pourmand, A., Gatineau, A., Panechou-Pulcherie, K., Blackwelder, P., and Gaston, C. J.: African biomass burning is a substantial source of phosphorus deposition to the Amazon, Tropical Atlantic Ocean, and Southern Ocean, Proc Natl Acad Sci U S A, 116, 16216–16221, https://doi.org/10.1073/pnas.1906091116, 2019.

515

Bauters, M., Drake, T. W., Wagner, S., Baumgartner, S., Makelele, I. A., Bodé, S., Verheyen, K., Verbeeck, H., Ewango, C., Cizungu, L., Van Oost, K., and Boeckx, P.: Fire-derived phosphorus fertilization of African tropical forests, Nat Commun, 12, https://doi.org/10.1038/s41467-021-25428-3, 2021.

Bigio, L. and Angert, A.: Oxygen Isotope Signatures of Phosphate in Wildfire Ash, ACS Earth Space Chem, 3, 760–769, https://doi.org/10.1021/acsearthspacechem.8b00216, 2019.

520

Bodí, M. B., Martin, D. A., Balfour, V. N., Santín, C., Doerr, S. H., Pereira, P., Cerdà, A., and Mataix-Solera, J.: Wildland fire ash: Production, composition and eco-hydro-geomorphic effects, https://doi.org/10.1016/j.earscirev.2013.12.007, March 2014.

Chadwick, O. A., Derry, L. A., Vitousek, P. M., Huebert, B. J., and Hedin, L. O.: Changing sources of nutrients during four million years of ecosystem development, NATURE, 1999a.

525

Chadwick, O. A., Derry, L. A., Vitousek, P. M., Huebert, B. J., and Hedin, L. O.: Changing sources of nutrients during four million years of ecosystem development, NATURE, 1999b.

Cunha, H. F. V., Andersen, K. M., Lugli, L. F., Santana, F. D., Aleixo, I. F., Moraes, A. M., Garcia, S., Di Ponzio, R., Mendoza, E. O., Brum, B., Rosa, J. S., Cordeiro, A. L., Portela, B. T. T., Ribeiro, G., Coelho, S. D., de Souza, S. T., Silva, L. S., Antonieto, F., Pires, M., Salomão, A. C., Miron, A. C., de Assis, R. L., Domingues, T. F., Aragão,

530

L. E. O. C., Meir, P., Camargo, J. L., Manzi, A. O., Nagy, L., Mercado, L. M., Hartley, I. P., and Quesada, C. A.: Direct evidence for phosphorus limitation on Amazon forest productivity, Nature, 608, 558–562, https://doi.org/10.1038/s41586-022-05085-2, 2022.

Dong, J., Hunt, J., Delhaize, E., Zheng, S. J., Jin, C. W., and Tang, C.: Impacts of elevated CO2 on plant resistance to nutrient deficiency and toxic ions via root exudates: A review, https://doi.org/10.1016/j.scitotenv.2020.142434,

535

1 February 2021.

Du, E., Terrer, C., Pellegrini, A. F. A., Ahlström, A., van Lissa, C. J., Zhao, X., Xia, N., Wu, X., and Jackson, R. B.: Global patterns of terrestrial nitrogen and phosphorus limitation, Nat Geosci, 13, 221–226, https://doi.org/10.1038/s41561-019-0530-4, 2020.

540   Fu, H., Lin, J., Shang, G., Dong, W., Grassian, V. H., Carmichael, G. R., Li, Y., and Chen, J.: Solubility of iron from combustion source particles in acidic media linked to iron speciation, Environ Sci Technol, 46, 11119–11127, https://doi.org/10.1021/es302558m, 2012.

Gojon, A., Cassan, O., Bach, L., Lejay, L., and Martin, A.: The decline of plant mineral nutrition under rising CO_2: physiological and molecular aspects of a bad deal, Trends Plant Sci, https://doi.org/10.1016/j.tplants.2022.09.002, 2022.

545   Goll, D. S., Bauters, M., Zhang, H., Ciais, P., Balkanski, Y., Wang, R., and Verbeeck, H.: Atmospheric phosphorus deposition amplifies carbon sinks in simulations of a tropical forest in Central Africa, New Phytologist, https://doi.org/10.1111/nph.18535, 2022.

Gross, A., Goren, T., Pio, C., Cardoso, J., Tirosh, O., Todd, M. C., Rosenfeld, D., Weiner, T., Custódio, D., and Angert, A.: Variability in sources and concentrations of saharan dust phosphorus over the Atlantic Ocean, Environ 550   Sci Technol Lett, 2, 31–37, https://doi.org/10.1021/ez500399z, 2015.

Gross, A., Turner, B. L., Goren, T., Berry, A., and Angert, A.: Tracing the Sources of Atmospheric Phosphorus Deposition to a Tropical Rain Forest in Panama Using Stable Oxygen Isotopes, Environ Sci Technol, 50, 1147–1156, https://doi.org/10.1021/acs.est.5b04936, 2016.

Gross, A., Tiwari, S., Shtein, I., and Erel, R.: Direct foliar uptake of phosphorus from desert dust, New Phytologist, 555   230, 2213–2225, https://doi.org/10.1111/nph.17344, 2021.

Guieu, C., Dulac, F., Desboeufs, K., Wagener, T., Pulido-Villena, E., Grisoni, J. M., Louis, F., Ridame, C., Blain, S., Brunet, C., Bon Nguyen, E., Tran, S., Labiadh, M., and Dominici, J. M.: Large clean mesocosms and simulated dust deposition: A new methodology to investigate responses of marine oligotrophic ecosystems to atmospheric inputs, Biogeosciences, 7, 2765–2784, https://doi.org/10.5194/bg-7-2765-2010, 2010.

560   Hou, E., Luo, Y., Kuang, Y., Chen, C., Lu, X., Jiang, L., Luo, X., and Wen, D.: Global meta-analysis shows pervasive phosphorus limitation of aboveground plant production in natural terrestrial ecosystems, Nat Commun, 11, https://doi.org/10.1038/s41467-020-14492-w, 2020.

Liu, X., Zhang, Y., Han, W., Tang, A., Shen, J., Cui, Z., Vitousek, P., Erisman, J. W., Goulding, K., Christie, P., Fangmeier, A., and Zhang, F.: Enhanced nitrogen deposition over China, Nature, 494, 459–462, 565   https://doi.org/10.1038/nature11917, 2013.

Liu, Y., Stanturf, J., and Goodrick, S.: Trends in global wildfire potential in a changing climate, For Ecol Manage, 259, 685–697, https://doi.org/10.1016/j.foreco.2009.09.002, 2010.

Liu, Y., Goodrick, S., and Heilman, W.: Wildland fire emissions, carbon, and climate: Wildfire-climate interactions, For Ecol Manage, 317, 80–96, https://doi.org/10.1016/j.foreco.2013.02.020, 2014.

570   Loladze, I.: Rising atmospheric CO_2 and human nutrition: Toward globally imbalanced plant stoichiometry?, Trends Ecol Evol, 17, 457–461, https://doi.org/10.1016/S0169-5347(02)02587-9, 2002.

Lynch, J. P.: Root phenes for enhanced soil exploration and phosphorus acquisition: Tools for future crops, Plant Physiol, 156, 1041–1049, https://doi.org/10.1104/pp.111.175414, 2011.

Masto, R. E., Mahato, M., Selvi, V. A., and Ram, L. C.: The effect of fly ash application on phosphorus availability 575   in an acid soil, Energy Sources, Part A: Recovery, Utilization and Environmental Effects, 35, 2274–2283, https://doi.org/10.1080/15567036.2010.533337, 2013.

Mikhailova, E. A., Post, G. C., Cope, M. P., Post, C. J., Schlautman, M. A., and Zhang, L.: Quantifying and mapping atmospheric potassium deposition for soil ecosystem services assessment in the United States, Front Environ Sci, 7, https://doi.org/10.3389/fenvs.2019.00074, 2019.

580   Myers, S. S., Zanobetti, A., Kloog, I., Huybers, P., Leakey, A. D. B., Bloom, A. J., Carlisle, E., Dietterich, L. H., Fitzgerald, G., Hasegawa, T., Holbrook, N. M., Nelson, R. L., Ottman, M. J., Raboy, V., Sakai, H., Sartor, K. A., Schwartz, J., Seneweera, S., Tausz, M., and Usui, Y.: Increasing CO2 threatens human nutrition, Nature, 510, 139–142, https://doi.org/10.1038/nature13179, 2014.

Offer, Z. Y. and Goossens, D.: Ten years of aeolian dust dynamics in a desert region (Negev desert, Israel):
585   Analysis of airborne dust concentration, dust accumulation and the high-magnitude dust events, J Arid Environ, 47, 211–249, https://doi.org/10.1006/jare.2000.0706, 2001.

Okin, G. S., Mahowald, N., Chadwick, O. A., and Artaxo, P.: Impact of desert dust on the biogeochemistry of phosphorus in terrestrial ecosystems, Global Biogeochem Cycles, 18, https://doi.org/10.1029/2003GB002145, 2004.

590   Palchan, D., Stein, M., Goldstein, S. L., Almogi-Labin, A., Tirosh, O., and Erel, Y.: Synoptic conditions of fine-particle transport to the last interglacial Red Sea-Dead Sea from Nd-Sr compositions of sediment cores, Quat Sci Rev, 179, 123–136, https://doi.org/10.1016/j.quascirev.2017.09.004, 2018.

Qian, Y., Miao, S. L., Gu, B., and Li, Y. C.: Effects of Burn Temperature on Ash Nutrient Forms and Availability from Cattail (Typha domingensis) and Sawgrass (Cladium jamaicense) in the Florida Everglades , J Environ
595   Qual, 38, 451–464, https://doi.org/10.2134/jeq2008.0126, 2009.

Ranatunga, T. D., Taylor, R. W., Bhat, K. N., Reddy, S. S., Senwo, Z. N., and Jackson, B.: Inorganic phosphorus forms in soufrière hills volcanic ash and volcanic ash-derived soil, Soil Sci, 174, 430–438, https://doi.org/10.1097/SS.0b013e3181b6deab, 2009.

Sánchez-García, C., Santín, C., Neris, J., Sigmund, G., Otero, X. L., Manley, J., González-Rodríguez, G., Belcher,
600   C. M., Cerdà, A., Marcotte, A. L., Murphy, S. F., Rhoades, C. C., Sheridan, G., Strydom, T., Robichaud, P. R., and Doerr, S. H.: Chemical characteristics of wildfire ash across the globe and their environmental and socio-economic implications, Environ Int, 178, https://doi.org/10.1016/j.envint.2023.108065, 2023.

Santín, C., Otero, X. L., Doerr, S. H., and Chafer, C. J.: Impact of a moderate/high-severity prescribed eucalypt forest fire on soil phosphorous stocks and partitioning, Science of the Total Environment, 621, 1103–1114,
605   https://doi.org/10.1016/j.scitotenv.2017.10.116, 2018.

Schroth, A. W., Crusius, J., Sholkovitz, E. R., and Bostick, B. C.: Iron solubility driven by speciation in dust sources to the ocean, Nat Geosci, 2, 337–340, https://doi.org/10.1038/ngeo501, 2009.

Starr, M., Klein, T., and Gross, A.: Direct foliar acquisition of desert dust phosphorus fertilizes forest trees despite reducing photosynthesis, Tree Physiol, 43, 794–804, https://doi.org/10.1093/treephys/tpad012, 2023.

610   Tan, Z. and Lagerkvist, A.: Phosphorus recovery from the biomass ash: A review, https://doi.org/10.1016/j.rser.2011.05.016, October 2011.

Tiwari, S., Erel, R., & Gross, A. (2022). Chemical processes in receiving soils accelerate solubilisation of phosphorus from desert dust and fire ash. European Journal of Soil Science, 73(4), e13270. https://doi.org/10.1111/ejsshttps://doi.org/10.1111/ejss. 13270

615   Uni, D. and Katra, I.: Airborne dust absorption by semi-arid forests reduces PM pollution in nearby urban environments, Science of the Total Environment, 598, 984–992, https://doi.org/10.1016/j.scitotenv.2017.04.162, 2017.

Vitousek, P. M., Porder, S., Houlton, B. Z., and Chadwick, O. A.: Terrestrial phosphorus limitation: Mechanisms, implications, and nitrogen-phosphorus interactions, Ecological Applications, 20, 5–15,
620   https://doi.org/10.1890/08-0127.1, 2010.

Wu, Y., Pae, L. M., Gu, C., and Huang, R.: Phosphorus Chemistry in Plant Ash: Examining the Variation across Plant Species and Compartments, ACS Earth Space Chem, 7, 2205–2213, https://doi.org/10.1021/acsearthspacechem.3c00145, 2023.

Yadav, I. C. and Devi, N. L.: Biomass burning, regional air quality, and climate change, in: Encyclopedia of
625   Environmental Health, Elsevier, 386–391, https://doi.org/10.1016/B978-0-12-409548-9.11022-X, 2019.

Yoshida, M., Cowgill, S. E., and Wightman, J. A.: Roles of oxalic and malic acids in Chickpea trichome exudate in host-plant resistance to Helicoverpa armigera. Journal of Chemical Ecology, 1997.

630

635

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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

645 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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