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Title

Canopy processing of atmospheric dust creates a short-term phosphorus pathway in a tropical forest

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Abstract

Phosphorus (P) availability constrains productivity in many humid tropical forests, where highly weathered soils retain P in poorly available forms and external inputs are needed to offset long-term losses. Caribbean forests receive new P through trans-Atlantic Saharan dust and episodic African biomass-burning particles, however how this particulate P enters forest nutrient cycling remains poorly understood. Here, we examined the fate and uptake of particulate P in the Luquillo Experimental Forest, Puerto Rico, using a foliar dust-application experiment and soil incubations with mineral dust and wildfire ash. In soils, both materials increased P supply to ion-exchange membranes, but mineral dust-derived P was rapidly transferred into Fe- and Al-associated pools, whereas wildfire ash generated greater short-term P availability. On leaves, mineral dust exposure resulted in foliar uptake of dust-derived Fe and P, with P uptake quantified using Fe as a conservative anchor. Particles recovered from leaf surfaces contained more bicarbonate-extractable P than the applied dust, indicating that contact with leaves increased the lability of P remaining in deposited particles. Together, these findings identify two complementary canopy pathways: direct foliar uptake of dust-derived P and leaf-surface processing that increases the fraction potentially available for subsequent uptake, either from foliage or, following redistribution in throughfall, by roots. By revealing a pre-soil pathway for atmospheric P, our results highlight a process not explicitly represented in most terrestrial nutrient-cycle frameworks that may affect how models represent the biological availability of dust-derived P and its coupling to tropical forest carbon cycling.

1 Introduction

Phosphorus (P) availability strongly constrains productivity of humid tropical forests (Cunha et al., 2022; Reed et al., 2010; Vitousek et al., 2010; Vitousek and Sanford, 1986). These ecosystems develop on old, highly weathered soils in which primary mineral P sources are largely depleted (Vitousek et al., 2010; Walker and Syers, 1976), and ecosystem functioning and plant growth depends on efficient internal recycling within plant-soil systems (Turner, 2008; Turner et al., 2010). Despite tight recycling, P is continuously lost through leaching or progressively transformed into poorly available forms via sorption and occlusion onto iron (Fe) and aluminum (Al) minerals under acidic soil conditions (Quesada et al., 2010; Turner et al., 2010; Walker and Syers, 1976). These processes reinforce persistent P limitation and increase

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reliance on atmospheric deposition as a source of new P (Chadwick et al., 1999; Pett-Ridge, 2009; Vitousek et al., 2010; Wang et al., 2023).

Long-term Saharan dust transport across the Atlantic Ocean is recognized as a consistent external P source to the tropical forests of South and Central America and the Caribbean region (Neotropics; SWAP et al., 1992; Okin et al., 2004; Mahowald et al., 2008; Pett-Ridge, 2009; Das et al., 2013; Yu et al., 2015; Zan et al., 2025). Additional P may be supplied episodically by biomass-burning aerosols (Barkley et al., 2019; Descals et al., 2026; Holanda et al., 2023) although their magnitude and persistence are generally smaller and more variable than mineral dust inputs.

The prevailing framework treats atmospheric dust primarily as a geochemical input that replenishes forest P stocks after incorporation into soils (Aciego et al., 2017; Chadwick et al., 1999; Okin et al., 2004). Because dust-derived P is difficult to distinguish from the large background of soil P, its role in ecosystem nutrient cycling has been assumed to operate mainly over long timescales via soil processes (Okin et al., 2004). In addition, most P in mineral dust occurs in calcium phosphate minerals, which are generally considered to have low immediate bioavailability (Gross et al., 2015; Longo et al., 2014). In highly weathered tropical soils, however, newly released phosphate can be rapidly immobilized through sorption to Fe- and Al-rich mineral phases, potentially limiting its short-term biological availability (Hinsinger, 2001; Quesada et al., 2010). Thus, the ecosystem significance of atmospheric P deposition depends not only on the magnitude of the input, but also on its short-term partitioning among canopy, soil, and biological pools after deposition.

Forest canopies represent a large and chemically active interface between the atmosphere and the terrestrial biosphere. High leaf area index, canopy turbulence, and complex leaf architecture enhance particle interception relative to the projected ground area (Bridhikitti et al., 2024; Lawrence et al., 2007; Runyan et al., 2013; Uni and Katra, 2017). Empirical observations indicate that trees can accumulate substantially greater amounts of dust than adjacent open collectors, in some cases concentrating deposited material by approximately four- to six-fold relative to open areas(Runyan et al., 2013; Xu et al., 2026). As a result, atmospheric particles are redistributed across canopy and soil compartments: a fraction is transferred to the forest floor via throughfall and stemflow, a fraction is deposited directly onto exposed soil surfaces, and a fraction remains on foliage for variable residence times depending on rainfall dynamics and surface properties. These processes may alter the solubility and fate of dust-derived P

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before it enters the soil. Recent studies indicate that leaf surfaces can retain mineral dust and promote dissolution of sparingly soluble P-bearing minerals under mildly acidic surface conditions (Gross et al., 2021; Lokshin et al., 2024, 2026a; Starr et al., 2023). Yet research on atmospheric nutrient deposition remains largely soil-oriented and often overlooks canopy interception, leaf-surface processing, and potential uptake by leaves (Bauters et al., 2021; Goll et al., 2023; Hofhansl et al., 2010; Van Langenhove et al., 2020; Lawrence et al., 2007). Foliar nutrient uptake, widely used in crop fertilization (Bukovac and Wittwer, 1957; Fageria et al., 2009; Ishfaq et al., 2022; Wittwer and Teubner, 1959), provides a plausible mechanism by which a fraction of dust-derived P could enter biological cycling directly from leaf surfaces.

In soils, dust P may also dissolve gradually, but released phosphate can be rapidly immobilized through sorption to Fe and Al minerals, constraining its short-term biological availability Together, these contrasting canopy and soil processes suggest that leaf surfaces may act as a short-term biogeochemical processing zone for atmospheric P, rather than merely as a passive surface that intercepts particles before their transfer to soil.

Here, we examined the short-term fate of atmospheric particulate P in the Luquillo Experimental Forest, Puerto Rico, an ecosystem located downwind of the Saharan dust plume where African dust signatures have been documented in rainfall, soils, and biota (McClintock et al., 2019; Pett-Ridge, 2009). We combined a foliar dust application experiment with a soil incubation experiment to test whether deposited mineral dust follows different short-term trajectories on leaf surfaces and in highly weathered tropical soil. Specifically, we asked whether canopy exposure increases the labile fraction of dust-derived P, whether mineral dust and wildfire ash differ in their short-term contribution to soil P availability, and whether leaf elemental enrichment provides evidence for retention or partial incorporation of dust-derived material. Together, this approach allowed us to evaluate canopy processing as a potentially overlooked pathway in atmospheric P cycling.

2 Methods

2.1 Study site

The study was conducted in the Luquillo Experimental Forest (LEF), northeastern Puerto Rico (Weaver and Murphy, 1990). The Luquillo Mountains encompass approximately 11,000 ha of tropical forest spanning elevations from ~250 to 1,075 m a.s.l., with mean annual precipitation

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ranging from 2,500 to 5,000 mm due to strong orographic effects (Weaver and Murphy, 1990). Forest structure and nutrient dynamics are strongly influenced by recurrent hurricanes and rainfall-triggered landslides (Larsen and Simon, 1993; Scatena and Lugo, 1995). Our site was located near the USDA Forest Service Sabana Field Research Station (18.325224° N, −65.730755° W) at ~100 m a.s.l., with mean annual temperature of ~24 °C and precipitation of ~3,500 mm. The forest is relatively a-seasonal with no month receiving less than 200 mm of rainfall; however, a drier period often occurs in February and March (Minikaev et al. *in preparation*). Luquillo lies downwind of the Saharan dust plume and lacks major local particulate sources, making it ideal for dust-deposition studies (McClintock et al., 2019; Prospero and Lamb, 2003). Dust activity is highest in May–August (peak June–August) and can extend into Sept–Oct (Euphrasie-Clotilde et al., 2021, 2025). In Luquillo, dust deposition peaks in boreal summer and declines from mid-August as Sahel rainfall peaks (van der Does et al., 2020); dry deposition is approximately 53–73% and varies on average two-fold across 10 km area (McClintock et al., 2019; Torres-Delgado et al., 2021). Dust deposition is approximately 210 ± 70 kg ha−1 yr−1 (~21 ± 7 g m−2 yr−1; Pett-Ridge, 2009), while AeroCom model means are higher but uncertain (~590 ± 490 kg ha−1 yr−1 in 2006; (McClintock et al., 2019). Soils are highly weathered Ultisols/Oxisols developed on Cretaceous volcaniclastic parent material, rich in Fe/Al oxides, and characterized by strong P sorption (Barrow, 1983).

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Fig. 1 Field experimental setup for foliar dust exposure in a tropical forest. Location of the study site at Sabana Field Research Station, Puerto Rico (top left), and representative images of the experimental setup in the understory (right and bottom panels). Leaves were enclosed within protective mesh chambers designed to retain applied dust particles while minimizing removal by rainfall, wind, and animal disturbance. The structures allowed natural environmental conditions (light, humidity, and air circulation) while isolating the foliar surface to quantify dust retention and uptake. The satellite image in the upper-left panel was obtained from Google Earth (image: Landsat / Copernicus; data from LDEO-Columbia, NSF, NOAA, SIO, U.S. Navy, NGA, and GEBCO; map data © 2021 Google). All field photographs were taken by the authors.

2.2 Dust and ash sources and characterization

Three particulate materials representing distinct atmospheric particulate inputs were used in this study. Atmospheric dust collected during expedition MSM104 onboard RV Maria S. Merian was obtained from a cellulose air intake filter during an open-ocean transit in the subtropical eastern North Atlantic(Zonneveld et al., 2021). This material represents mineral dust suspended in the marine boundary layer and transported from North African desert sources across the Atlantic Ocean, reflecting particles that have undergone atmospheric entrainment and long-range transport prior to deposition. A local desert dust analogue was collected from surface soils in the Negev Desert, Israel (30.888413° N, 34.787919° E), and used due to its

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compositional similarity to Saharan dust ('Desert soil dust'; Ridley et al., 2012; Gross et al., 2021). Finally, fire ash was collected following an extensive pine forest fire that lasted several days in early May 2025 near Newe Shalom, Israel (31.815151° N, 34.987202° E). This ash represents biomass-burning residues generated during large wildfires, a distinct atmospheric particulate source with chemical properties different from mineral dust ('Wildfire ash'). Mineral dust samples were air-dried, homogenized, and sieved to <63 µm prior to chemical analysis and experimental application, consistent with previous foliar dust-uptake experiments. Wildfire ash was air-dried and homogenized but sieved to <150 µm, because the ash material formed cohesive aggregates and could not be reproducibly passed through a 63 µm sieve without mechanically altering the sample. The <150 µm fraction was therefore used to remove coarse debris while retaining sufficient fine ash material for the soil incubation experiment.

The bulk elemental composition of all dust and ash materials was determined using X-ray fluorescence (XRF), and mineralogical composition was assessed using X-ray diffraction (XRD). Detailed elemental and mineralogical results are reported in Tables S1 and S2. The mineralogy, elemental composition, and P concentrations of both the Desert soil dust and Transatlantic dust fall within the range typically reported for Saharan dust in previous studies (Ridley et al., 2012; Gross et al., 2021; Lokshin et al., 2025). Likewise, the mineralogy and elemental composition of the wildfire ash are consistent with values reported for biomass-burning ash in previous studies (Bodí et al., 2014; Lokshin et al., 2024; tables S.1 & S2).

2.3 Dust deposition experiments

To compare the short-term fate of particulate P following deposition onto foliage or soil, we conducted separate foliar application and soil incubation experiments. The foliar experiment assessed direct acquisition of dust-derived P and changes in P lability following contact with leaf surfaces, whereas the soil experiment quantified short-term P availability and its partitioning among soil P pools.

2.4 Foliar dust application experiment

Foliar dust application was conducted in the forest during July 2025, corresponding to the local Saharan dust season (Euphrasie-Clotilde et al., 2021; McClintock et al., 2019), on two common woody species, *Miconia prasina* and *Manilkara bidentata*. M. *prasina* is a common understory

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shrub from a widespread tropical genus, whereas M. *bidentata* is a canopy tree species that was sampled here as accessible saplings in the understory. These species were selected because they are abundant in the Luquillo forest and representative members of the understory community, and their relatively small stature allowed direct access to foliage under field conditions without canopy disturbance. Because both species were sampled as accessible individuals in the understory, the experiment was designed to test short-term foliar processing under field conditions rather than to represent the full vertical structure of the forest canopy or the dust exposure of mature upper-canopy leaves.

Six individual trees of each species received dust treatment, while an additional six trees per species served as untreated controls. For each treated tree, four branches of comparable size and light exposure were selected: two branches received dust application and two remained untreated. The untreated branches served as within-tree controls, allowing us to account for variability among branches within the same tree and to compare this variability with that observed in fully untreated control trees. This design also helped distinguish treatment effects from natural heterogeneity in leaf nutrient concentrations, particularly for relatively immobile elements. In the control trees, two branches were selected and served as controls.

To standardize microenvironmental conditions and prevent disturbance during the experiment, selected branches were enclosed within protective structures (Fig. 1). Each enclosure consisted of a cylindrical frame (~30 cm diameter, ~50 cm length) constructed from flexible skeletal fencing and wrapped with transparent agricultural film. The enclosures were installed horizontally around the branches. These structures minimize disturbance from wind, rainfall splash, and wildlife while maintaining similar microclimatic conditions for both treated and control branches. In addition, they reduced direct rainfall wash-off and therefore extended particle residence time on leaf surfaces relative to natural open-canopy exposure. This design was used to maintain a controlled short-term exposure period and to allow detection of leaf-surface processing of deposited particles.

Leaf area per treatment branch was estimated using an elliptical approximation ($A = \pi \times L \times W / 4$). For *M. bidentata*, mean leaf dimensions were 25 cm (length) and 9 cm (width), yielding an average leaf area of 176.7 cm^2. With eight leaves per treated branch, the total treated leaf area was approximately 0.1414 m^2. For *M. prasina*, mean leaf dimensions were 15 cm × 5 cm, yielding 58.9 cm^2 per leaf. With sixteen leaves per treated branch, the total treated leaf area was approximately 0.0943 m^2.

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Dust was applied manually, in two pulses, using a fine sieve to achieve uniform coverage of leaf surfaces while minimizing loss to the surrounding environment. During the first pulse, Desert soil dust was applied at a rate of 3.5 g per treated branch for *M. prasina* and 7 g per treated branch for *M. bidentata*. Based on estimated leaf area, this corresponds to application rates of approximately 37 g m^{-2} for *M. prasina* and 49 g m^{-2} for *M. bidentata*. The second pulse was added four days after the first pulse, using Transatlantic dust, which was applied to both species at a rate of 3 g per treated branch, corresponding to approximately 32 g m^{-2} for *M. prasina* and 21 g m^{-2} for *M. bidentata*. The reduced application rate during the second pulse reflected the limited quantity of authentic trans-Atlantic dust available.

Cumulative foliar loading represented approximately 70 g m^{-2} of leaf area, equivalent to roughly three years of mean regional Saharan dust deposition in northeastern Puerto Rico (~21 g m^{-2} yr^{-1}; Pett-Ridge, 2009). This elevated loading was intentionally used as a concentrated short-term exposure to overcome background variability in leaf elemental composition and to test whether leaf surfaces can process deposited mineral particles. Pulsed application of two different dust types was used to simulate the episodic nature of dust inputs, which often originate from varying Saharan sources. Because the two dust materials were applied sequentially to the same treated foliage, the foliar experiment was used to evaluate the combined effect of mineral dust exposure on leaf surfaces rather than to quantify source-specific uptake from each dust type separately. The foliar application protocol followed procedures described in Lokshin et al. (2026). Foliar elemental responses were subsequently normalized to applied dust mass and treated leaf area (and, where relevant, exposure duration) to comparison with soil-mediated fluxes P uptake efficiency and facilitate comparison with soil-mediated fluxes. The experiment was terminated after seven days.

2.5 Elemental analysis of plant material

At harvest, residual particulate material was first removed from leaf surfaces using clean brushes for subsequent P fractionation analysis. Leaves were then exercised from each branch for elemental analysis. Tissues were washed in 0.1 M HCl and subsequently rinsed three times with distilled water to remove surface-adhered dust particles (Gross et al., 2021; Lokshin et al., 2026a). Samples were dried at 60 °C for 72 h to constant mass, and leaf dry mass was recorded. Dried leaf material was ground to a fine powder Approximately 1 g of dried, ground plant material was dry-ashed at 550 °C in a muffle furnace for 4 h (Tiwari et al., 2022a). The resulting

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ash was dissolved in 1 mL of concentrated HNO_3 to obtain a clear solution for elemental analysis.

Elemental concentrations in plant material were determined by inductively coupled plasma mass spectrometry (ICP-MS; Agilent 8900cx, Agilent Technologies) at the Hebrew University of Jerusalem. The instrument was calibrated using multi-element standard solutions spanning 1 pg mL^{-1} to 100 ng mL^{-1} (Merck ME VI) and separate standards for major elements ranging from 300 ng mL^{-1} to 3 mg mL^{-1}. An internal standard solution containing 50 ng mL^{-1} Sc and 5 ng mL^{-1} Re and Rh was added to all samples and standards to correct for instrumental drift. Certified reference solutions (USGS SRS T-207 and T-209) were analysed at the beginning and end of each calibration sequence to verify analytical accuracy. Analytical precision was 3% for major elements and 2% for trace elements.

2.6 Soil dust experiment

To assess the impact of particulate deposition on short-term soil nutrient availability, a controlled pot incubation experiment was conducted using surface soils (top 10 cm) collected from the forest. Each pot contained 500 g (dry mass equivalent) of homogenized forest soil and had a surface area of 10 × 10 cm (0.01 m^2). Dust or ash was applied at a mass of 5 g per pot and gently mixed into the soil to simulate surface incorporation, corresponding to an areal loading of 500 g m^{-2}. This loading exceeds mean annual Saharan dust deposition to northeastern Puerto Rico (210 ± 70 kg ha^{-1} yr^{-1}, equivalent to ~21 g m^{-2} yr^{-1} (Pett-Ridge, 2009) and was intentionally used as a concentrated short-term addition to generate detectable changes in PRS-accessible nutrient fluxes.

Using the average dust P concentration reported in previous studies in the region (~1100 ppm), this corresponds to approximately 23 mg P m^{-2} yr^{-1} under typical deposition conditions. The elevated loading was therefore used to simulate a concentrated deposition pulse and ensure detectable short-term changes in soil nutrient flux. The experiment included four treatments, each consisted of six replicates: Trans-Atlantic dust, Desert soil dust analogue, Wildfire ash and an unamended control. Each day, 25 mL of deionized water whereas added to each pot to standardize soil moisture. After particulate addition, the incubation was run for seven days.

Plant-available nutrient supply was quantified using Plant Root Simulator (PRS®) probes (Western Ag Innovations Inc., Saskatoon, Canada). PRS probes consist of anion- and cation-

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exchange resin membranes mounted in a rigid plastic support that can be inserted directly into soil. Nutrients accumulate on the membranes over time, providing a time-integrated operational index of nutrient supply to an ion-exchange surface (Hangs et al., 2011; Ochoa-Hueso et al., 2023). This method provides a time-integrated measure of nutrient flux from the soil solution rather than an instantaneous estimate of extractable nutrient pools (Ochoa-Hueso et al., 2023).

For each pot, one anion and one cation PRS probe were inserted and deployed for six days. After retrieval, probes were rinsed with deionized water and processed according to the manufacturer's protocol. Adsorbed nutrients were extracted following Hangs et al. (2011) and quantified using inductively coupled plasma mass spectrometry (ICP-MS). Measurements from the anion and cation probes were combined as a single composite sample for each pot, representing the integrated nutrient flux during the deployment period. Nutrient fluxes were subsequently normalized to applied particulate mass and soil surface area to derive short-term soil P availability indices for comparison with canopy-processing responses. Full short-term PRS-accessible nutrient fluxes for all soil incubation treatments are presented in Table S3.

2.7 P fractionation of amended soils and recovered leaf-surface dust

P in amended soils, source dust and ash materials, and particulate material recovered from leaf surfaces was partitioned using a sequential extraction procedure adapted from the Hedley scheme (Mirabello et al., 2013) and modified for either tropical soils (Gross et al., 2016) or dust and arid materials (Gross et al., 2021). For each material, 0.5 g of sample was subjected to a series of increasingly aggressive extractants to operationally separate P pools according to relative lability and binding strength.

At the termination of the foliar dust application experiment, residual particulate material was gently brushed the upper and lower leaf surfaces using clean nylon brushes and collected into acid-cleaned tubes for subsequent laboratory P fractionation. Care was taken to avoid removal of leaf tissue. After particle recovery, leaf tissues were sequentially washed in three containers: distilled water, 0.1 M HCl, and distilled water again. Leaf samples were then dried at 60°C for 72 h before grinding and elemental analysis. This cleaning step was used to minimize the contribution of residual surface-adhered dust to the measured leaf elemental composition. The recovered particulate material was analyzed separately from the leaf tissue to assess changes in dust P partitioning during canopy exposure.

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The initial labile P extraction differed between soils and particulate materials. For amended soils, labile inorganic P was extracted using the Bray I method (Bray & Kurtz, 1945), which uses an acidic extractant composed of 0.03 M NH_4F and 0.025 M HCl designed to release readily available inorganic P associated with Fe and Al oxides in acidic soils. Soil samples were shaken with 30 mL of Bray I solution to quantify the labile inorganic P fraction. For source dust and ash materials, and for particulate material recovered from leaf surfaces, labile P was operationally assessed using 30 mL of 0.5 M $NaHCO_3$. Thus, Bray I was used for amended tropical soil samples, whereas bicarbonate extraction was used for dust, ash, and recovered leaf-surface particulate material.

The use of different initial extractants reflects the contrasting matrix properties of the analyzed materials. Bray I was used for the acidic, Fe- and Al-rich tropical soils because it is designed to estimate readily available inorganic P in such soils. In contrast, $NaHCO_3$ was used for source dust, ash, and recovered leaf-surface particulate material because these samples represent mineral particulate materials rather than acidic tropical soil matrices, and bicarbonate extraction provides an operational measure of the readily extractable P pool in dust and arid materials.

In the second step, exchangeable and sorbed P pools, typically associated with Fe and Al oxides, were extracted using 1 M NaOH for both dust and soil samples. In the third extraction step, 1 M HCl was used to target more strongly bound P phases, including Ca-associated P. The remaining solid residue was then completely digested using concentrated HNO_3 (65%) and HCl in a closed-vessel microwave digestion system (MARS-6; CEM Corp., USA) to quantify the residual P pool. P concentrations in the $NaHCO_3$, Bray I, NaOH and HCl extracts were determined using the molybdenum blue colorimetric method (Murphy and Riley, 1962) measured on a microplate photometer (Multiskan Sky; Thermo Scientific). This extraction sequence was used to compare shifts in operationally defined P pools in amended soils and in particulate material recovered after canopy exposure.

2.8 First-order estimation of potential dust-derived P incorporation using Fe enrichment

Detecting dust-derived P uptake in field experiments is inherently challenging. Unlike micronutrients such as Fe that tend to accumulate in leaf tissues (Page and Feller, 2015), P is highly phloem-mobile and can be rapidly redistributed to other plant organs following uptake (Arsic et al., 2025). As a result, changes in leaf P concentration at the site of deposition may

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remain small or undetectable even when net plant P acquisition occurs (Arsic et al., 2025; Lokshin et al., 2026a). In addition, plants in field conditions vary in initial size and grow under heterogeneous environmental conditions, which can obscure treatment-induced differences in biomass over short timescales. In a greenhouse, changes in biomass can be used to calculate total P uptake (Gross et al., 2021; Lokshin et al., 2025a). Because biomass changes could not be reliably quantified in field experiments, increases in total plant P could not be directly inferred from growth responses as in controlled experiments (Gross et al., 2021; Starr et al., 2023). To address this limitation, we used Fe as a conservative anchor element to estimate dust-derived P uptake. Fe is largely immobile in plant shoots (Page and Feller, 2015) and accumulates locally in leaves after deposition, allowing changes in Fe concentration to serve as a proxy for dust-derived foliar nutrient input and enabling estimation of associated P uptake (Lokshin et al., 2026).

To derive an empirical proportionality factor relating Fe enrichment to whole-plant P accumulation, we used data from a previously published controlled foliar dust experiment with Schinus terebinthifolius, a tropical tree species originating from the Atlantic coast of Brazil, a region that regularly receives Saharan dust (Starr et al., 2023). After a month, the entire plant was harvested and cleaned as described earlier. The trees were dried and their above and below ground biomass was determined. Then, the leaf Fe and P concentrations were measured as previously described and the total P and Fe in above ground biomass was calculated. The proportionality factor was calculated as:

$$k = \frac{\%\Delta P_{total}}{\%\Delta Fe_{total}} \quad (1)$$

where k is the proportionality factor between changes in P and Fe, $\Delta P\%$ is the percent change in total P content relative to controls, and $\Delta Fe\%$ is the percent change in total Fe content relative to controls. Percent changes were calculated from total element content, defined as element concentration multiplied by biomass. Using mean values from the greenhouse experiment, k = 0.464 (Fig. 3a). We applied this factor to the present field experiment as an approximate scaling relationship, while recognizing that it was derived from a different species under greenhouse conditions and may not capture species-specific variation in leaf surface traits, dust retention, or physiological responses. Detailed values for all variables, including ΔP, ΔFe, and derived parameters, are provided in Table S4.

In the present study, Fe enrichment following dust application was calculated as:

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$$\%\Delta Fe = \frac{Fe_{dust} - Fe_{control}}{Fe_{control}} \times 100 \quad (2)$$

where Fe_{dust} is the Fe concentration measured in dust-treated leaves and $Fe_{control}$ is the mean Fe concentration in control leaves. Estimated potential dust-derived P incorporation was then calculated as:

where ΔP_{est} represents the estimated proportional increase in P associated with the observed Fe enrichment. Estimated post-treatment P concentration was calculated as:

$$\Delta P_{est} = k \times \%\Delta Fe \quad (3)$$

Estimated post-treatment P concentration was calculated as:

$$P_{dust,est} = P_{control} \times (1 + \frac{\%\Delta P_{est}}{100}) \quad (4)$$

where $P_{control}$ is the mean P concentration in control leaves and $P_{dust,est}$ is the expected P concentration following dust-derived enrichment. Dust-derived P mass per leaf sample was obtained as:

$$\Delta M_p(mg) = \frac{\Delta P_{est}(\mu g\ g^{-1}) \times leaf mass\ (g)}{1000} \quad (5)$$

where $\Delta M_P(mg)$ is the mass of P derived from dust uptake.

The Fe-derived $\Delta Pest$ value was applied uniformly to all replicate leaf samples of a given species, while variation in estimated P uptake among samples was driven by differences in measured leaf biomass. Fe outliers were identified using Tukey's interquartile range (IQR) method and excluded prior to calculation. This Fe-based approach provided a first-order estimate of potential dust-derived P incorporation associated with observed leaf Fe enrichment, while accounting qualitatively for the contrasting mobility of P and Fe within plant tissues.

To allow comparison among species and treatments, dust-derived P uptake was normalized to the mass of dust applied to the foliage. Apparent incorporation index was calculated as the mass of dust-derived P incorporated into leaf tissue divided by the mass of dust applied during the foliar application experiment. In addition, the fraction of bioavailable P contained in the deposited dust was estimated by comparing the calculated P uptake with the total P content of the applied dust:

$$Uuptake_{dust} = \frac{\Delta Mp}{M_{dust}} \quad (6)$$

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Where $Uuptake_{dust}$ is foliar uptake efficiency (mg P g^{-1} dust), ΔM_p is dust derived P mass incorporated into leaf tissue (mg) and M_{dust} is the total mass of dust applied to the foliage (g).

The bioavailable fraction of P in the dust was calculated as:

$$\%Bioavailability = \frac{Uaptake_{dust}}{P_{dust}} \times 100 \quad (7)$$

Where P_{dust} is the total P concentration in the applied dust (mg g^{-1}).

2.9 Statistical analysis

For the foliar dust application experiment, branches were sampled within individual trees, with two dust-treated and two untreated branches per treated tree. Branch-level values are shown in the figures to display within-tree and among-branch variability. However, individual trees were treated as the biological replicate units for statistical analysis. For each tree and treatment, branch-level measurements were averaged prior to statistical testing, yielding one dust-treated and one untreated value per tree. Differences between dust-treated and untreated branches were evaluated separately for each species using two-tailed paired t-tests. Fully untreated control trees were used to characterize background variation in leaf elemental composition and were compared with treated-tree values using two-tailed unpaired t-tests, with Welch's correction applied when variances were unequal.

Soil incubation treatments were compared using one-way analysis of variance (ANOVA) followed by Tukey multiple comparisons. When assumptions of equal variances were not met, Welch's ANOVA followed by Dunnett T3 multiple comparisons was used. Statistical significance was assessed at $\alpha = 0.05$. Data are presented as mean ± SD unless stated otherwise. All statistical analyses and figure preparation were performed using GraphPad Prism version 11.

3. Results

3.1 Particulate additions increase short-term PRS-accessible soil P

Addition of mineral dust or wildfire ash to tropical forest soil significantly increased short-term PRS-accessible P flux measured by ion-exchange resin membranes (Fig. 2). In the unamended control soil, P flux was extremely low and remained near or below the analytical detection

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limit. Both the desert soil dust and the trans-Atlantic Saharan dust produced similar responses, with mean PRS-accessible P fluxes of approximately 21 mg m^{-2} during the incubation period. In contrast, wildfire ash generated substantially higher P fluxes, with mean values of approximately 178 mg m^{-2}.

3.2 Leaf Fe enrichment indicates retention of dust-derived material

Because Fe is relatively immobile in plant tissues and tends to accumulate near sites of particle deposition, whereas P is mobile and can be redistributed within plants, leaf Fe enrichment was used as an indirect indicator of dust-derived material retained or partially incorporated into foliage. To derive a first-order relationship between foliar Fe enrichment and P accumulation, we used data from a previously published greenhouse foliar dust experiment with *Schinus terebinthifolius*. In that experiment, biomass of dust-treated plants increased significantly compared with controls. Leaf Fe concentrations increased substantially following dust application, while leaf P concentrations did not change significantly (Table S5). Total aboveground Fe and P contents were therefore calculated as element concentration multiplied by biomass. This analysis yielded an empirical proportionality factor in which increases in total P corresponded to 46.4% of the increase in total Fe.

We applied this Fe-based relationship to the foliar dust application field experiment as a first-order approximation of potential dust-derived P incorporation in *M. prasina* and *M. bidentata*. Following dust application, leaf Fe concentrations increased substantially in both species (Fig. 3b). Applying this conversion factor resulted in first-order estimated increases in leaf P concentrations of approximately 315 ppm in M. bidentata and 370 ppm in *M. prasina* relative to controls (Fig. 3c). Additional nutrient composition data for both species are provided in Tables S6 and S7.

3.3 Apparent short-term P response indices for canopy and soil pathways

To place the foliar and soil experiments on a common mass-normalized basis, we calculated apparent short-term P response indices relative to the amount of particulate material applied (Fig. 4a). For the soil pathway, PRS-accessible P fluxes were normalized to the mass of added mineral dust and soil surface area. The average value calculated from the desert source dust and trans-Atlantic Saharan dust treatments corresponded to 0.000727 mg P g^{-1} dust over the

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incubation period. For the foliar experiment, first-order estimates of potential dust-derived P incorporation, derived from the Fe-based calculation, were normalized to the amount of dust applied to foliage and treated leaf area. This yielded apparent foliar response indices of 0.257 mg P g^{-1} dust for *M. bidentata* and 0.1137 mg P g^{-1} dust for *M. prasina* (Fig. 4a). These values were normalized to the total P content of dust (1.1 mg P g^{-1} dust; Pett-Ridge, 2009) to estimate the biologically available fraction of dust-derived P. This corresponded to an average biological availability of approximately 16.85% for the foliar pathway and 0.066% for the soil-mediated pathway (Fig. 4b).

3.4 Changes in dust P fractionation following soil and canopy exposure

To investigate potential mechanisms influencing P availability following dust deposition, sequential P extractions were performed on soils and dust samples (Fig. 5). NaOH-extractable P increased following addition of dust or ash to soils (Fig. 5A). In the unamended control soil, NaOH-extractable P averaged 14.62 ± 2.49 µg g^{-1} but the addition of desert soil dust and trans-Atlantic Saharan dust increased NaOH-extractable P to 53.08 ± 10.11 µg g^{-1} and 37.44 ± 7.35 µg g^{-1} respectively. The highest values were observed following wildfire ash addition, with NaOH-extractable P reaching 58.12 ± 22.06 µg g^{-1}. Bicarbonate-extractable P was measured in dust samples before and after exposure on leaf surfaces (Fig. 5b). Initial bicarbonate-extractable P measured in the desert source dust ranged between 50.52 and 70.01 µg g^{-1}, while values in trans-Atlantic Saharan dust ranged between 33.37 and 69.33 µg g^{-1}. Dust particles recovered from leaf surfaces following the foliar dust application experiment showed significantly higher bicarbonate-extractable P (106.8 ± 22.3 µg g^{-1}) in comparison to initial levels in desert source dust or trans-Atlantic dust (ranging between 50.52 and 70.01 µg g^{-1} and 33.37 and 69.33 µg g^{-1}, respectively).

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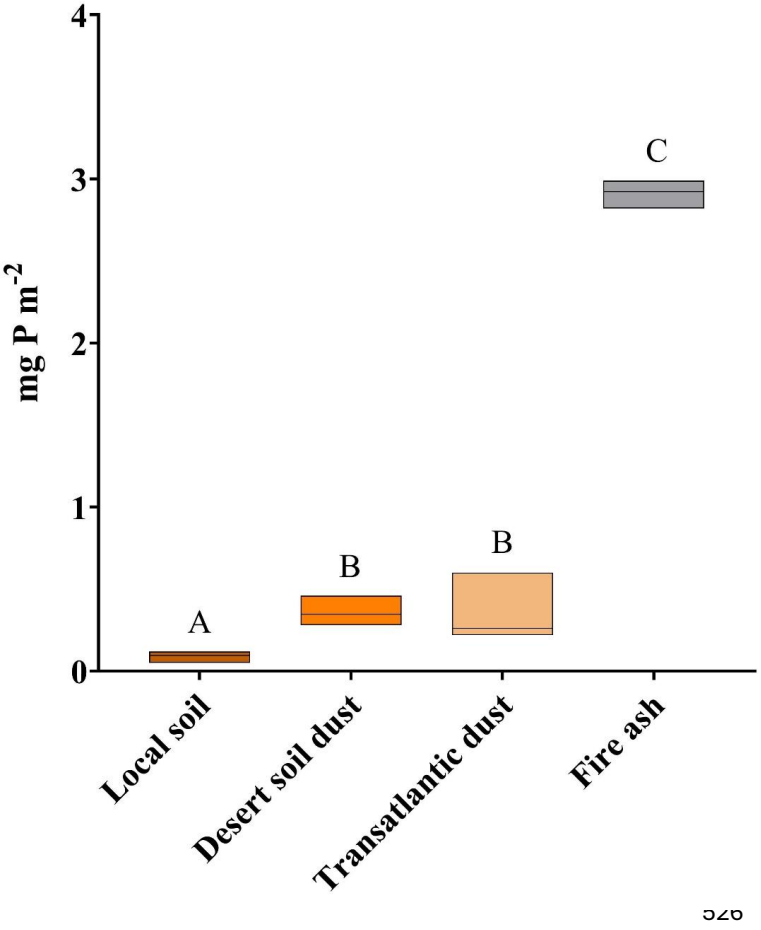

526

527 **Figure 2.** Bioavailable P flux measured using ion-exchange resin membranes (PRS probes)
528 during a 6-day soil incubation experiment following particulate amendment. Total bioavailable
529 P flux (mg P m^{-2}) is shown for local soil (control), desert dust, trans-Atlantic Saharan dust, and
530 wildfire ash treatments. Values represent time-integrated P supply to membranes over the
531 incubation period. Boxes indicate the interquartile range, center lines represent medians, and
532 whiskers denote the minimum–maximum range. Bioavailable P flux in the unamended local
533 soil remained extremely low and close to the analytical detection limit of the PRS method.
534 Different letters indicate significant differences among treatments (two-tailed t-test, $P < 0.05$).

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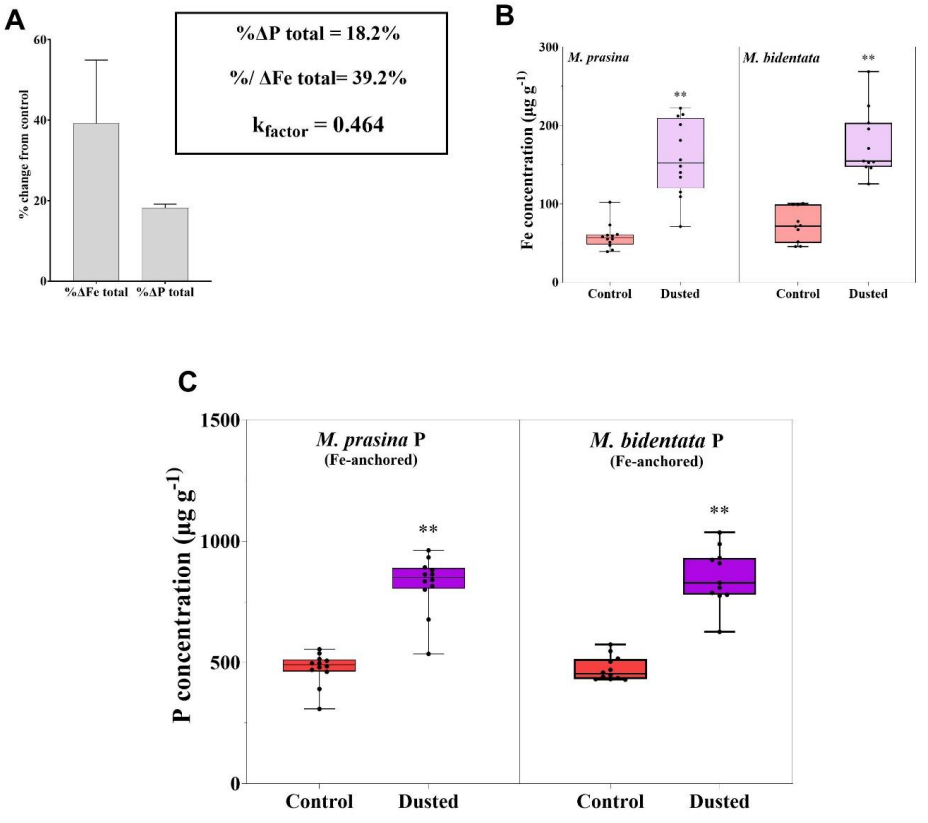

Figure 3. Estimation of dust-derived foliar P uptake using an Fe-anchored approach. (a) Calibration factor relating changes in total P and total Fe derived from a foliar dust application experiment on *S. Terebinthifolius (Starr et al., 2023)*. Total P increased by 18.2% and total Fe by 39.2% following dust application, yielding a conversion factor $k = \Delta P_{total}/\Delta Fe_{total} =$ 0.464. (b) Leaf Fe concentrations (µg g^{-1} DW) measured in control and dust-treated branches of *M. prasina* and *M. bidentata* following foliar dust application in the Luquillo Experimental Forest. (c) Estimated leaf P concentrations (µg g^{-1} DW) derived using the Fe-anchored conversion factor shown in panel A. Points represent branch-level measurements shown to visualize within-tree and among-branch variability. Statistical tests were performed on tree-level means, with individual trees treated as biological replicates. Boxes indicate interquartile range, center lines represent medians, and whiskers denote the minimum–maximum range. Asterisks indicate significant differences between control and dust-treated leaves (two-tailed t-test, $P < 0.05$).

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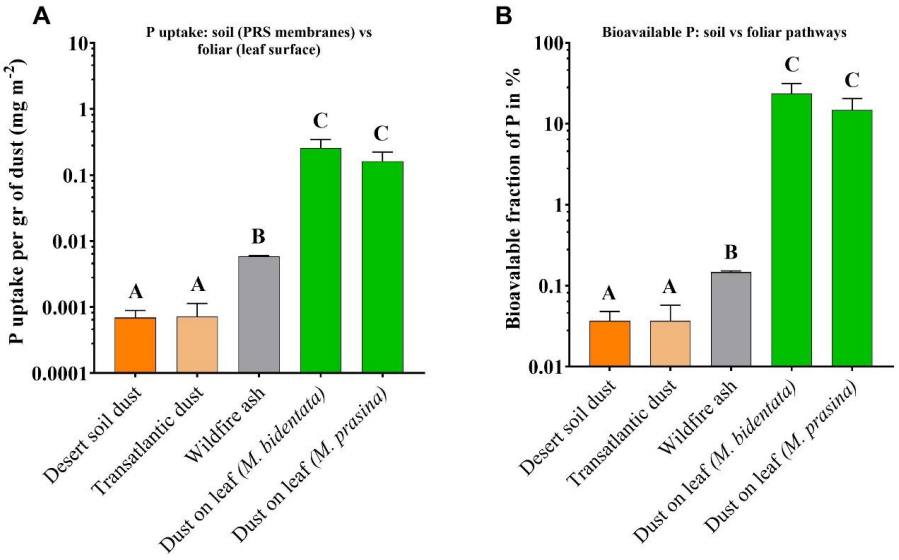

Fig 4. Efficiency of P acquisition from dust through soil and foliar pathways. (a) P uptake normalized to the amount of dust applied, expressed as P acquired per gram of dust per square meter (mg P g^{-1} dust m^{-2}). Soil-mediated uptake was calculated from PRS membrane measurements following addition of desert dust, trans-Atlantic Saharan dust, and wildfire ash. Foliar uptake was calculated from Fe-anchored estimates of P incorporation into leaves of *M. bidentata* and *M. prasina*. (b) Corresponding biologically available fraction of dust-derived P expressed as a percentage of total dust P. Dust P concentration was assumed to be 1100 ppm (1.1 mg P g^{-1} dust). Bars represent mean values ± SD. Different letters indicate significant differences among treatments (two-tailed t-test, $P < 0.05$).

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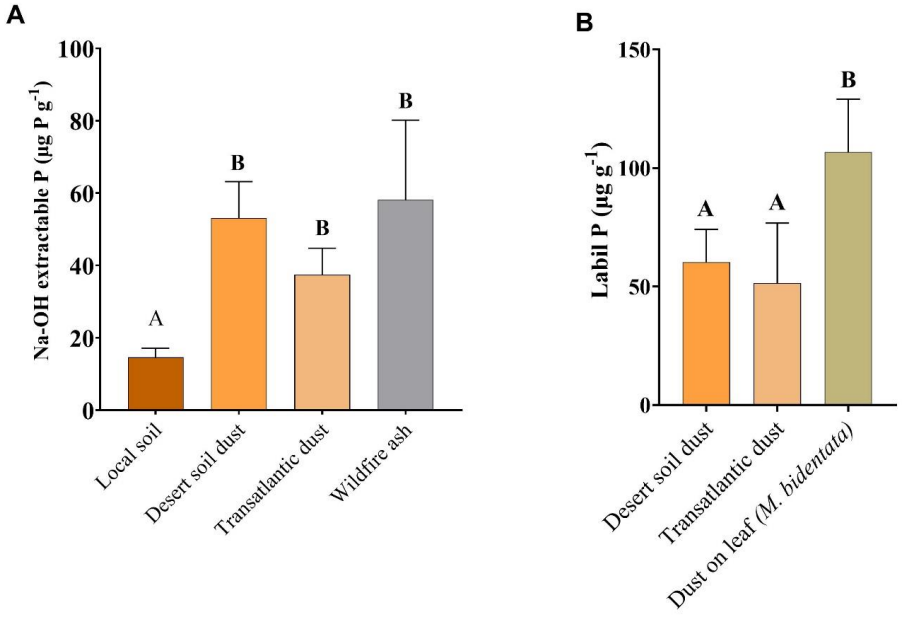

Fig 5. Changes in operationally defined P pools following soil and canopy exposure to dust. (a) NaOH-extractable P (µg P g^{-1}) measured in soil following addition of desert soil dust, trans-Atlantic Saharan dust, and wildfire ash compared with unamended local soil. NaOH extraction targets P associated with Fe and Al mineral phases. (b) Labile P (bicarbonate-extractable P; µg P g^{-1}) measured in dust samples before and after exposure on leaf surfaces of *M. bidentata* following the foliar dust application experiment. Bars represent mean values ± SD. Different letters indicate significant differences among treatments (two-tailed t-test, $P < 0.05$).

4 Discussion

4.1 Contrasting short-term fates of dust-derived P in canopy and soil compartments

Our results show that dust-derived P can follow contrasting short-term trajectories after deposition onto tropical forest canopy and soil surfaces. In the soil incubation experiment, mineral dust additions generated measurable PRS-accessible P fluxes, but sequential extraction

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indicated that much of the added P became associated with NaOH-extractable pools, consistent with rapid transfer to Fe- and Al-linked phases. dust recovered from leaf surfaces after canopy exposure showed an increase in bicarbonate-extractable P, used here as an operational measure of readily extractable P in recovered dust material, indicating that the foliar environment enhanced the labile fraction of deposited mineral dust. These findings suggest that the short-term fate of atmospheric P depends strongly on the compartment in which dust is processed. Rather than acting only as a passive interception surface, the canopy may function as a biogeochemical interface that alters dust P availability before particles are transferred to the forest floor.

4.2 Rapid immobilization limits short-term soil availability of dust-derived P

Our soil experiment showed that incorporation of dust into tropical forest soil generated measurable fluxes of plant-available P, whereas the native soil alone produced extremely low P fluxes that were close to the detection limit of the resin membranes. This confirms the strong P limitation characteristic of highly weathered tropical soils (Cunha et al., 2022; Lin et al., 2020; Wood et al., 2015). Much of the P in mineral dust is structurally bound within primary mineral phases such as apatite and other P-bearing minerals (Dam et al., 2021; Hudson-Edwards et al., 2014; Zhang et al., 2018), which are only sparingly soluble under the pH conditions typical of most natural soil and rhizosphere environments (Hinsinger, 2001). Soils in the Luquillo forest are strongly acidic, typically in the range of pH ~4–5, reflecting highly weathered, Fe- and Al-rich conditions (Mage and Porder, 2012; Vitousek et al., 2010). Such acidic environments are expected to enhance the dissolution of dust-derived P and increase its bioavailable fraction, consistent with experimental studies showing increased P release from mineral phases under low pH conditions (González-Olalla et al., 2024; Zhang et al., 2022; Sudeep et al., 2022). However, despite these favorable conditions for dissolution, we did not observe a corresponding increase in bioavailable P following dust addition. This suggests that any transient release of phosphate from dust is rapidly offset by re-adsorption onto Fe- and Al-rich mineral phases, which dominate sorption processes in highly weathered tropical soils (Chacon et al., 2006; Lin et al., 2020). Consistent with this interpretation, the increase in NaOH-extractable P following dust addition (Fig. 5a) indicates that released P was quickly transferred into Fe-associated pools, effectively buffering dissolved P and limiting its short-term biological availability. Such processes are well documented in tropical soils where

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dissolved phosphate is strongly sorbed to Fe and Al oxides, limiting its immediate biological availability (Gross et al., 2018; McGlynn et al., 2007). Experimental work in humid tropical forest soils has shown that P sorption occurs within hours and can retain most of the dissolved P even under variable redox conditions (Lin et al., 2020).

Previous studies have suggested that long-range atmospheric transport can increase P solubility through chemical aging of mineral dust, including exposure to acidic species such as nitric acid, sulfuric acid, and organic acids during atmospheric processing. Laboratory and modelling studies have shown that acidification of mineral aerosols can substantially enhance the release of bioavailable P from P-bearing minerals (Dam et al., 2021; Gaston, 2020; Korte et al., 2018; Nenes et al., 2011; Stockdale et al., 2016).

However, in our experiment we did not detect significant differences in bioavailable P after dust addition to soil between trans-Atlantic Saharan dust and locally sourced desert soil dust. This suggests that, at least for the materials examined here, long-range atmospheric transport did not produce a measurable increase in P bioavailability, which corresponds with recent reports on minimal transatlantic dust aging (Royer et al., 2025). One possible explanation is that intrinsic mineralogical differences among dust sources may exert stronger control on P release than atmospheric processing alone. Alternatively, as the transatlantic dust was collected only a few hundred km from the coasts of Africa, the time and magnitude of acid exposure during the relatively short atmospheric transport may be insufficient to substantially alter P solubility in comparison to dust that reaches Puerto Rico. In our study we applied dry dust to allow controlled residence time on leaf surfaces and to enable leaf-mediated dissolution without wash-off, yet rain-driven acidification can further enhance nutrient solubility in atmospheric particles (van der Does et al., 2020). Future studies should also incorporate wet deposition scenarios.

In contrast to dust, wildfire ash addition produced substantially higher PRS-accessible P flux in tropical soil, reflecting the enrichment of ash in readily soluble nutrients which are produced during biomass combustion in high temperatures (Goll et al., 2023; Lokshin et al., 2024) and likely its higher sensitivity to the acidic conditions in the soil (Tiwari et al., 2022a). These results suggest that wildfire ash deposition can represent an episodic but potentially important short-term source of bioavailable P to tropical forests soils. Although wildfire ash deposition is typically more spatially heterogeneous and less consistent than mineral dust inputs, its high nutrient solubility can generate intense short-term pulses of soil-available P, potentially

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accounting for emerging evidence of a substantial contribution of ash-derived P to tropical forest nutrient cycling (Barkley et al., 2019; Bauters et al., 2021; Descals et al., 2026; Goll et al., 2023).

4.3 Canopy processing creates a short-term labile P pathway

One plausible mechanism is acidification of the leaf surface by organic acids, which can promote the dissolution of P-bearing minerals in deposited dust; in chickpea, oxalic acid was observed together with a more acidic leaf-surface environment (Golan et al., 2025; Lokshin et al., 2026; Tiwari et al., 2022; Zhang et al., 2022).

Although the entry pathway of P into leaf tissues is not fully resolved, trichome bases, stomata, cuticular pathways, and other hydrated surface structures have been proposed as potential routes for dissolved ion movement into leaves (Eichert & Fernández, 2023; Golan et al., 2025; Gross et al., 2021). Previous work has shown that a measurable fraction of nutrients contained in deposited dust particles can become associated with plant biomass following foliar exposure (Lokshin et al., 2026). The present experiment does not resolve the intracellular partitioning of dust-derived P, and the Fe-anchored estimates should therefore be interpreted as first-order approximations rather than direct measurements of foliar P uptake. Nevertheless, the combination of Fe enrichment, apparent P response indices, and increased bicarbonate-extractable P in recovered leaf-surface dust supports the conclusion that canopy exposure can enhance short-term dust-P availability.

When normalized to applied dust mass, the Fe-anchored apparent P response index was approximately 2.3-fold greater in M. bidentata than in M. prasina (0.257 versus 0.114 mg P g^{-1} dust, respectively). This difference may reflect species-specific variation in leaf traits that influence particle retention, dissolution, and potential nutrient transfer. Although *M. bidentata* is a canopy tree species and *M. prasina* is commonly associated with the understory (Pascarella et al., 2007; You and Petty, 1991), the individuals sampled in this study were accessible understory plants and therefore should not be interpreted as representing the full vertical canopy gradient. Variation in cuticle structure, trichome density, leaf wettability, surface roughness, and exudate chemistry can influence the retention and dissolution of deposited particles (Eichert and Fernández, 2023; Fernandez and Eichert, 2009; Sæbø et al., 2012). In addition, upper-canopy leaves may experience greater atmospheric particle interception, whereas understory foliage receives a canopy-filtered dust signal (Das et al., 2013; Uni and

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Katra, 2017). These factors highlight the need for future work that directly tests canopy-position effects and leaf functional traits across a wider range of tropical tree species.

The foliar pathway for wildfire ash-derived P was not tested in the present experiment. Previous studies indicate that P from wildfire ash can also become associated with plant tissues following foliar exposure (Lokshin et al., 2024b), suggesting that canopy processing may be relevant not only for mineral dust but also for episodic biomass-burning inputs. However, because ash and mineral dust differ strongly in chemistry, solubility, particle structure, and surface reactivity, foliar processing of ash-derived P in tropical forests should be treated as a hypothesis requiring direct experimental testing.

4.4 Interpreting short-term canopy and soil P response indices

When normalized to the total P content of the applied mineral dust, the canopy pathway corresponded to a short-term P response fraction of 16.85%, compared with 0.066% for the soil pathway (Fig. 4b). This large contrast shows that dust-derived P followed sharply different short-term trajectories in the canopy and soil compartments. On leaf surfaces, dust exposure produced Fe enrichment, estimated P incorporation, and increased bicarbonate-extractable P in recovered particles. In soil, mineral dust addition produced only a small PRS-accessible P response, while much of the added P was transferred into NaOH-extractable Fe- and Al-associated pools.

This comparison highlights the contrasting short-term partitioning of dust-derived P between canopy and soil environments. Canopy exposure maintained or enhanced a labile dust-P signal, whereas highly weathered tropical soil rapidly buffered dust-derived P into less immediately accessible pools. This interpretation is supported by the very low PRS-accessible P measured in unamended soil, the limited response to mineral dust addition, and the strong increase in Fe/Al-associated P following soil amendment (Figs. 2, 5a). It is further supported by the increase in labile P measured in dust recovered from leaf surfaces after canopy exposure (Fig. 5b).

The Fe enrichment and short-term dust-derived P response observed in the foliar pathway were not accompanied by detectable changes in biomass, leaf production, or overall plant growth during the seven-day field experiment, similar to findings from a recent Mediterranean field study (Lokshin et al., 2026). This contrasts with controlled experiments showing that foliar

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application of mineral dust P can stimulate plant P acquisition and biomass production under greenhouse or otherwise controlled conditions (Gross et al., 2021; Lokshin et al., 2025; Starr et al., 2023). This difference is consistent with the short duration and field setting of the present study, where growth responses are unlikely to be resolved over seven days and may require longer experiments, repeated deposition events, or more controlled environmental conditions.

Dust deposition can also influence leaf function through physical, non-nutritional effects, including surface shading and partial restriction of gas exchange by particle accumulation (Moradi et al., 2017; Starr et al., 2023; Lokshin et al., 2024a). Treated branches did not show visible symptoms of stress or chlorosis during the experiment, but physiological responses were not measured directly. Future experiments should combine nutrient tracing with photosynthesis, stomatal conductance, chlorophyll fluorescence, and inert-particle controls to distinguish nutritional effects from physical dust-coating effects.

Together, the canopy and soil response indicate that leaf surfaces can create a transient labile P pathway before atmospheric particles enter the soil, while highly weathered tropical soils can rapidly immobilize dust-derived P into Fe- and Al-associated pools. This contrast provides the central biogeochemical basis for interpreting canopy processing as an overlooked component of atmospheric P cycling in tropical forests (Avner Gross et al., 2021; Lokshin et al., 2025b; Starr et al., 2023).

4.5 Ecosystem-scale implications for tropical forest P cycling

The short-term canopy and soil response indices measured here are most useful when placed within the broader P-cycling context of the Luquillo forest. This comparison does not aim to close an ecosystem P budget, but rather to evaluate the potential magnitude of the experimentally observed canopy pathway relative to known internal recycling fluxes, external P inputs, and P losses within the same forest system.

P cycling in the Luquillo forest is dominated by internal recycling. Litterfall represents the largest internal P return, with published estimates of ~20–40 mg P m^{-2} $month^{-1}$ (Cuevas and Lugo, 1998; Heartsill-Scalley et al., 2007; Uriarte et al., 2015). Plant P uptake has been estimated at ~12–17 mg P m^{-2} $month^{-1}$ (Heartsill-Scalley et al., 2007; Pett-Ridge, 2009). Throughfall P fluxes are generally ~1–5 mg P m^{-2} $month^{-1}$, with episodic increases during dust

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events, and integrate direct atmospheric deposition, canopy leaching, and canopy exchange processes (Heartsill-Scalley et al., 2007; McClintock et al., 2019). External inputs are smaller than internal recycling fluxes but are important for the long-term balance of highly weathered tropical systems. African dust delivers ~23 mg P m^{-2} yr^{-1} to northeastern Puerto Rico (Pett-Ridge, 2009), while geogenic P inputs from rock weathering and saprolite-to-soil conversion are estimated at ~1.25 mg P m^{-2} yr^{-1} (Mage and Porder, 2012; Pett-Ridge, 2009). P losses from the system occur through leaching, estimated at ~0.66 mg P m^{-2} $month^{-1}$, and erosion, estimated at ~1 mg P m^{-2} $month^{-1}$ (Pett-Ridge, 2009).

Saharan dust transport to the Caribbean is strongly seasonal, with peak deposition during late spring and summer (Prospero et al., 2013; Yu et al., 2015). To place our short-term response indices within this seasonal context, we distributed the annual dust-derived P input of ~23 mg P m^{-2} yr^{-1} across the main dust-active period. This gives an estimated atmospheric dust-P input of ~7.66 mg P m^{-2} $month^{-1}$ during dust months. Applying the canopy response fraction measured in this study, 16.85%, gives a scenario-based canopy-associated dust-P flux of 1.29 ± 0.71 mg P m^{-2} $month^{-1}$ during a dust month. Applying the soil response fraction, 0.066%, gives a short-term PRS-accessible dust-P flux of 0.014 ± 0.0084 mg P m^{-2} $month^{-1}$ over the same seasonal framing.

These estimates suggest that the canopy-associated dust-P response is small relative to internal recycling, as expected, but comparable in magnitude to several external P fluxes that are important for long-term potentially meaningful relative to external P inputs and losses that influence the long-term ecosystem P balance. Applying the canopy response fraction of 16.85% directly to the annual atmospheric dust-P input of ~23 mg P m^{-2} yr^{-1} gives an estimated canopy-associated dust-P response of 3.87 ± 2.13 mg P m^{-2} yr^{-1}. This is approximately three times the estimated geogenic P input from rock weathering and saprolite-to-soil conversion of ~1.25 mg P m^{-2} yr^{-1}. During individual dust months, the canopy-associated response of 1.29 ± 0.71 mg P m^{-2} $month^{-1}$ is also comparable in magnitude to reported leaching losses of ~0.66 mg P m^{-2} $month^{-1}$, although these comparisons represent different processes and should not be interpreted as a closed P balance. In contrast, the short-term PRS-accessible soil response of 0.014 ± 0.0084 mg P m^{-2} $month^{-1}$ is much smaller, consistent with rapid immobilization of mineral dust-derived P into Fe- and Al-associated pools. Expressed relative to estimated plant P uptake, the canopy-associated dust-P response during dust months corresponds to up to ~8.5% of monthly plant P demand, whereas the short-term PRS-accessible soil response

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corresponds to ~0.1%. These percentages provide a seasonal magnitude comparison based on the experimental response indices, rather than a closed ecosystem uptake budget.

This comparison suggests that canopy processing is unlikely to dominate total P cycling in Luquillo, which is governed primarily by internal recycling. However, internal recycling redistributes P already present within the ecosystem and cannot replace P exported through leaching and erosion or transferred over longer timescales into occluded and strongly mineral-associated forms. Atmospheric dust and rock weathering provide new P that can partly offset these losses and long-term reductions in availability.

The significance of canopy processing therefore lies in how it may alter the fate of this new atmospheric input. Weathering-derived P must first be released from parent material and may subsequently be immobilized in highly weathered soils, whereas dust-P deposited directly on foliage arrives at a biologically active interface where some P may be taken up directly and contact with leaf surfaces may increase the lability of P remaining in deposited particles. This residual P may subsequently be redistributed in throughfall and become accessible to other canopy organisms or to roots after reaching the forest floor. Throughfall measurements quantify the P that reaches the forest floor after interacting with the canopy, but they do not isolate the fraction of deposited dust-P that may be retained, dissolved, transformed, or taken up at the leaf surface before redistribution. Throughfall therefore integrates these processes but cannot independently distinguish among foliar uptake, chemical transformation, canopy retention, and particle redistribution. The present estimates identify canopy processing as a potentially meaningful pre-soil pathway for atmospheric P, while its full importance at the scale of mature forest canopies remains to be quantified.

4.6 Implications for atmospheric P cycling and carbon–nutrient models

The results of this study suggest that forest canopies may function as reactive interfaces in atmospheric P cycling, rather than only as passive surfaces that intercept atmospheric deposition before transferring to the soil. Current representations of atmospheric nutrient inputs in ecosystem and Earth system models are largely soil-centered, with atmospheric P deposition commonly routed to soil nutrient pools before plant access (Chadwick et al., 1999; Okin et al., 2004). This structure is appropriate for many long-term nutrient-budget applications, but it does not explicitly represent either direct foliar uptake of atmospheric P or short-term chemical processing of atmospheric particles on leaf surfaces before their redistribution in throughfall.

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Canopy structure may further regulate this pre-soil processing step by controlling particle interception and residence time. High leaf area index, complex leaf architecture, and increased aerodynamic roughness can enhance particle capture, with canopy-level interception exceeding bulk deposition by several-fold in some systems (Runyan et al., 2013). Greater interception does not by itself demonstrate an increase in ecosystem-scale foliar P uptake. It does, however, increase the amount of atmospheric material contacting foliage and the opportunity for direct uptake, chemical transformation, temporary retention, and subsequent redistribution in throughfall.

This omission of these pathways may matter in highly weathered tropical forests, where the fate of newly deposited P depends strongly on the compartment in which it is first processed. In the soil, dust-derived P can be rapidly transferred into Fe- and Al-associated pools, limiting short-term accessibility (Jiang et al., 2019). On leaf surfaces, the same atmospheric material may experience a different chemical environment that increases the labile fraction of dust-derived P before it enters the soil system. In addition, the Fe-anchored estimates obtained here provide first-order quantitative evidence for direct foliar acquisition of dust-derived P. Models such as JULES-CNP, CLM-based C–N–P formulations, and ORCHIDEE-CNP already represent strong P constraints on tropical forest productivity and generally route atmospheric inputs through soil pools prior to plant access (Fleischer et al., 2019; Nakhavali et al., 2022; Sun et al., 2017; Goll et al., 2023). Incorporating foliar uptake and canopy-processing terms would not require assuming that foliar pathways dominate plant P acquisition, but would allow models to distinguish among atmospheric P taken up directly by foliage, P retained or chemically transformed on leaf surfaces and later redistributed, and P entering soil immobilization pathways.

Such a representation may also improve predictions under changing climate and land-use conditions. Dust emissions, transport pathways, and deposition patterns are expected to shift with climate change, land degradation, and desert expansion (Kok et al., 2023; Mahowald et al., 2008). Although foliar processing of ash was not tested here, biomass-burning aerosols may also provide episodic P inputs to tropical forests, particularly where fire regimes intensify or where long-range transport connects burning regions with P-limited ecosystems (Barkley et al., 2019; Bauters et al., 2021; Goll et al., 2023; Descals et al., 2026). At the same time, deforestation and canopy loss can reduce particle interception and thereby alter the fraction of atmospheric material retained and processed aboveground (Lawrence et al., 2007; De longe et al., 2008). Because tropical forest responses to rising CO_2 can be strongly constrained by P

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availability, changes in atmospheric P delivery and canopy processing could influence future carbon–nutrient feedbacks (Terrer et al., 2019).

The central implication is that atmospheric P may enter tropical forest nutrient cycling through two complementary pre-soil pathways: direct foliar uptake and leaf-surface processing that increases the lability of P remaining in deposited particles. The latter pool may remain available for subsequent uptake from foliage or, following redistribution in throughfall, by roots. Measurements of bulk deposition and soil P availability may not resolve these processes, whereas throughfall integrates multiple canopy effects but cannot by itself distinguish among foliar uptake, chemical transformation, and particle redistribution. Future work should quantify both pathways across canopy positions, tree species, dust loads, rainfall regimes, and particle types, and test how canopy-processed P is partitioned among foliar uptake, leaf retention, throughfall, stemflow, microbial processing, and soil immobilization. Representing these processes more explicitly could improve our ability to evaluate how atmospheric deposition contributes to tropical forest P cycling and to carbon–nutrient interactions in a changing world.

5 Conclusions

This study provides proof-of-concept evidence that tropical forest canopies can alter the short-term fate of atmospheric dust-derived P before deposited particles reach the soil. In the Luquillo Experimental Forest, foliar dust exposure resulted in uptake of dust-derived Fe and P, with P uptake quantified using Fe as a conservative anchor. In addition, particles recovered from leaf surfaces contained more bicarbonate-extractable P than the applied dust, indicating that contact with leaves increased the lability of P remaining in deposited particles. In contrast, mineral dust added to highly weathered tropical soil generated only a small PRS-accessible P response and was rapidly transferred into Fe- and Al-associated pools, whereas wildfire ash produced substantially greater short-term soil P availability.

These results show that atmospheric particulate P does not follow a single soil-mediated pathway after deposition. Instead, canopy exposure can promote two complementary pathways: direct foliar uptake of dust-derived P and leaf-surface processing that increases the pool of labile P remaining in deposited particles. This residual P may subsequently become available for uptake directly from leaf surfaces or by roots following redistribution to the forest floor in throughfall. By contrast, dust-derived P entering highly weathered tropical soils can be rapidly immobilized in less immediately accessible mineral-associated forms.

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Our findings therefore suggest that canopy contact may enhance the entry of atmospheric P into tropical forest nutrient cycling both through direct foliar uptake and by increasing P availability before particles reach strongly P-fixing soils. The ecosystem-scale importance of these pathways remains to be quantified across mature trees, canopy positions, species, and natural deposition events. Incorporating canopy processing into future field experiments, atmospheric deposition measurements, and coupled carbon–nutrient models may improve understanding of how dust and biomass-burning inputs influence tropical forest nutrient dynamics under changing climate, dust, and fire regimes.

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Data Availability Statement

The data supporting the findings of this study are available in the Supporting Information, tables, and figures during peer review. If the manuscript is accepted, the complete underlying dataset will be deposited in Zenodo and made publicly available with a persistent DOI prior to publication.

Conflict of Interest Disclosure

The authors declare there are no conflicts of interest for this manuscript

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Author contributions

A.L. conceptualized the study, conducted the field experiment, performed laboratory analyses, led data analysis, and wrote the original manuscript draft. A.G. conceptualized the study, supervised the research, contributed to experimental design and data interpretation, and reviewed and edited the manuscript. T.E.W. contributed to species selection, experimental design, field implementation, interpretation of the forest context, and manuscript development. J.-B. W. S. provided the trans-Atlantic dust samples, contributed to chemical analyses, and reviewed and edited the manuscript. E.H. contributed to laboratory sample preparation and chemical analyses. All authors contributed to manuscript revision and approved the final version.

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