Research paper

Direct foliar acquisition of desert dust phosphorus fertilizes forest trees despite reducing photosynthesis

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Phosphorus (P) availability to forest trees is often limited by local soil conditions that increase its fixation to soil minerals. In certain regions, atmospheric-P inputs can compensate for low soil-P availability. Among atmospheric-P sources, desert dust is the most dominant. However, the effects of desert dust on P nutrition and its uptake mechanisms by forest trees are currently unknown. We hypothesized that forest trees that naturally grow on P-poor soils or soils with high soil-P fixation capacity can acquire P from desert dust deposited on their leaves via direct foliar uptake, bypassing the soil, thus promoting tree growth and productivity. We performed a controlled greenhouse experiment with three forest tree species: Palestine Oak (*Quercus calliprinos*) and Carob (*Ceratonia siliqua*), native to the NE edge of the Saharan desert, and Brazilian peppertree (*Schinus terebinthifolius*), native to the Atlantic Forest in Brazil, which is located on the western part of the trans-Atlantic Saharan dust route. To simulate natural dust deposition events, the trees had desert dust applied directly upon their foliage and were monitored for growth and final biomass, P levels, leaf surface pH and the rate of photosynthesis. The dust treatment increased the P concentration significantly by 33–37% in *Ceratonia* and *Schinus* trees. On the other hand, trees that received the dust displayed a 17–58% reduction in biomass, probably related to particle coverage of the leaf surface that inhibited photosynthesis by 17–30%. Overall, our findings show that direct P uptake from desert dust can be an alternative P uptake pathway for multiple tree species under P-deficient conditions, with implications for forest trees' P economy.

Keywords: foliar uptake, leaf surface, plant nutrition.

Introduction

Phosphorus (P) is an essential nutrient governing critical functions in plant metabolism, growth and productivity. Primary sources of P inputs to most terrestrial ecosystems include P released by chemical weathering of rock and atmospheric deposition of solid particles or precipitation. Estimates of P release by rock weathering range between 0.05 and 1.00 kg P ha^{-1} year^{-1}, whereas total P input from the atmosphere range between 0.07 kg ha^{-1} year^{-1} and 1.7 kg ha^{-1} year^{-1} (Newman 1995). Among atmospheric-P sources, desert dust is the most common (Okin et al. 2004, Aciego et al. 2017), about half

of which is generated in Africa's Sahara Desert and Sahel belt, whereas the rest is emitted from drylands in other continents (Middleton 2017). The African desert dust is transported across the Atlantic Ocean, and some follows north-east routes over the Mediterranean Sea and toward the Middle East (Prospero 1996).

In many ecosystems, P bioavailability is often limited by local environmental conditions. In the tropics, heavy precipitation and high temperatures promote intense soil weathering and P fixation to soil minerals. In contrast, in semi-arid regions, located at the margins of dust source areas and receiving large

quantities of dust inputs, water limitations generate weak weathering (Selmants and Hart 2008), and dust-derived P inputs tend to be large relative to soil-P reservoirs. Therefore, desert dust can be a relevant contributor to both wet and dry ecosystems' nutrient cycling (Mahowald et al. 2008, Myriokefalitakis et al. 2016) as the importance of dust-borne P depends on the dust deposition rate and the reservoir of total P in downwind ecosystems (Swap et al. 1992, Chadwick et al. 1999, Artaxo 2002).

The common rationale states that terrestrial plants acquire the bulk of their P from soils by direct root uptake or through symbiotic interactions with microorganisms such as mycorrhizal fungi (Smith and Read 2008). Atmospheric-P inputs sustain plant's primary productivity by replenishing soil-P pools (Chadwick et al. 1999, Okin et al. 2004, Cleveland and Townsend 2006, Pett-Ridge 2009, Eger et al. 2013, Gross et al. 2016, Aciego et al. 2017), via either direct dust deposit onto soils or throughfall. However, because soils often have high P sorption capacity, the released P from the dust-borne P compounds may be rapidly fixed by soil minerals in forms that are unavailable for plant uptake (Olander and Vitousek 2004, Vitousek et al. 2010). That is, plants would have to compete for the deposited P not only with each other and microorganisms but also with soil minerals, which would result in low utilization of dust-P.

In dense forests, tree canopies can increase atmospheric P deposited into the forest ecosystem by trapping large amounts of airborne particles on the leaves. As a result, the adsorption to a mature forest stand is three to four times greater than in an open field (Das et al. 2011, Runyan et al. 2013). Research by Uni and Katra (2017) found that forests in the semi-arid areas create a significant reduction in PM2.5/PM10 during dust events, further emphasizing the high efficiency with which forest trees trap airborne dust. This phenomenon is explained by the high surface area of the canopy and by the micrometeorological boundary layer effects increasing deposition (Baldocchi et al. 1988).

Foliar P uptake is a well-documented phenomenon for many plant types and given the high P adsorption of the foliage, it raises a question about the contribution of foliar P uptake to the total P budget of forest trees. Foliar P fertilization is an important agricultural technique to satisfy the nutritional needs of various crops when soil conditions limit nutrient availability or when the stage of plant growth, the internal plant demand and the environmental conditions interact to limit the delivery of nutrients to critical plant organs (Bukovac and Wittwer 1957; Koontz and Biddulph 1957; Mosali et al. 2006, Fernández and Brown 2013). Recent research in our lab by Gross et al. (2021) found that specific annual crops, only while enduring P deficiency, react to P-rich desert dust deposition by absorbing P from the dust directly via foliage, similar to a foliar fertilizer.

Most dust-P is found in the form of apatite, the most abundant phosphate mineral in desert dust, known to dissolve in acidic conditions (Harouiya et al. 2007). Since the leaf surface is usually characterized by a slightly acidic pH from leaf exudation of acidic compounds, the authors hypothesized that leaf acidity can increase dust-P availability to foliar uptake. This research was the first to investigate the matter and reveal the potential contribution of natural desert dust deposition. However, it is unknown whether these plant processes act at an ecological scale, and moreover in forests.

Despite the possible positive nutritional effects of desert dust deposition on foliage, research considering the physical coverage and shading of dust particles on leaves suggests several negative implications. The coverage itself on the plant canopy can reduce plant yield (Li et al. 2010) and in accordance with the variation of dust load, particle size, distribution of these particles and their chemistry, dust particle concealment was found to reduce photosynthesis rate and photosynthetically active radiation by up to 58% in specific plant species (Hirano et al. 1995, Sharifi et al. 1997) and to cause stomatal occlusion when lower surfaces were dusted (Zia-Khan et al. 2014). Consequently, adverse effects on plant growth and yield can be expected (Hatami et al. 2018). Considering the finding of Gross et al. (2021), we have basis to speculate that such dust effects may be less pronounced in relation to increasing plants' P internal demand.

Here we studied for the first time the effects of foliar desert dust-P on the growth and P nutrition of Mediterranean and tropical forest trees. We hypothesized that, similar to some annual crops, forest trees can acquire P from desert dust deposition on their leaves directly via foliar uptake, as an alternative route to root uptake from the soil, avoiding limits of soil-P availability. We projected that although the dust particle coverage on the leaf may restrict photosynthesis, the additional P absorbed will enhance tree growth. We conducted a greenhouse experiment on young trees of three key species, representing different forest type ecosystems and accessibility to desert dust: *Quercus calliprinos* and *Ceratonia siliqua* from the semi-arid Mediterranean mixed forest, and *Schinus terebinthifolius* from Brazil's tropical Atlantic Forest. While enduring either P limitation or P starvation, the trees were supplied with a desert dust analog via manual dispersion on their leaves and monitored for P concentration, biomass, leaf pH and photosynthetic carbon assimilation to unravel the potential role of dust in the P economy of these relevant tree species.

Materials and methods

Plant material and experimental design

In August 2020, *Quercus calliprinos* (Palestinian oak), *Ceratonia siliqua* (Carob) and *Shinus terebinthifolius* (Brazilian

peppertree) saplings were bought from a nursery at ages 7, 9 and 6 months respectively; their average height was 15 cm at the time. Sclerophyllous *Q. calliprinos* and *C. siliqua* both grow in the East-Mediterranean mixed forest, typically on rocky hillsides tolerant to drought conditions. *Quercus calliprinos* has a low growth rate as a small tree or large shrub (attaining an adult height of 5–18 m), whereas *C. siliqua* maintains a medium growth rate into a small-sized tree (adult height of 10–17 m). *Schinus terebinthifolius* is a small tree or large shrub (adult height of 7–10 m). It originates from the Atlantic Forest of Brazil, but a high growth rate and invasive nature allow it to thrive in all kinds of ecosystems: from dunes to swamps.

The saplings were uprooted from the original soil-bearing pots, roots were rinsed of remnant soil particles, and transplanted into perlite (perlite 212, particle size of 2 mm; Agrekal, HaBonim, Israel), an inert soilless growing media. Saplings were kept in controlled greenhouse conditions at the Weizmann Institute greenhouse facility (31.9038° N, 34.8080° E). Inside the greenhouse the saplings were subjected to natural lighting partially concealed by transparent white walls and roof. Overall, photosynthetically active radiation (PAR) averaged at 600 μmol m^{-2} s^{-1} during 10:00–15:00h along most of the experiment period. The temperature was kept at 25 $\pm$ 3 °C and relative humidity at 70%, and trees were sustained in 1.1-l pots. Despite possible differences in the actual nutrient requirements between the different tree species, saplings of all species received the same regular nutrient media containing the following elements: N (50 mg l^{-1}), P (3 mg l^{-1}), K (50 mg l^{-1}), Mg (30 mg l^{-1}), Fe (0.8 mg l^{-1}), Mn (0.4 mg l^{-1}), Zn (0.2 mg l^{-1}) B (0.4 mg l^{-1}), Cu (0.3 mg l^{-1}) and 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 $CaCl_2$. The micronutrients were supplied in EDTA (ethylenediaminetetraacetic acid) chelates as a commercial liquid fertilizer (Koratin, ICL Ltd, Beer Sheva, Israel). The saplings received fertigation four times a day via drip irrigation, for increasing time periods sustaining a modest nutrient deficiency (1 min allowing 0.13 l day^{-1}, then 2 min for 0.26 l day^{-1} and finally 3 min for 0.4 l day^{-1} per fertigation) up until the finalization of the experiment.

The saplings were harvested several months after the second dusting treatment (after 3.5 months for *Schinus* trees, and 2 months for *Ceratonia* and *Quercus* trees). The entire duration of the experiment, from tree purchase to tree harvest, continued over 7 months, from August 2020 to March 2021 for *Schinus*, and 8.5 months for *Quercus* and *Ceratonia*, from August 2020 to May 2021.

Later on, during the analysis we conducted an identical experiment on a group of P-starved *Ceratonia* saplings. All saplings were subjected to the same condition and performed in the same manner as described in the Materials and methods section, except that the P-starved group was treated with fertigation excluding P.

Dust origin and analysis

Prior to this experiment, we produced a dust analog from desert soil collected from a natural reserve in the southern Negev desert in Israel (30°32037.8″N 34°55017.0″E), considered to be within the desert belt of the Sahara. The dust analog was prepared by sieving the top soil layer of 1 cm to a dust particles size subjected to wind erosion (63 μm) (Guieu et al. 2010), following common procedures described by Stockdale et al. (2016) and Elad et al. (2018). Chemical and mineralogical properties of the dust analog were tested using X-ray fluorescence (XRF) spectrometer and X-ray powder diffraction (XRD), respectively, and are presented in Gross et al. (2021). The dust-P concentration was 4120 μg per g dust, of which 0.75% is labile P, 0.26% Fe-P, 66.7% Ca-P and 32.28%. The properties are comparable to that of Sahara and Middle Eastern dust samples that were previously captured in Israel and elsewhere (Scheuvens et al. 2013, Gross et al. 2016).

Foliar treatments

Saplings of each species were divided into two groups: one group treated with the desert dust analog (referred to below as dust) and a control group receiving no foliar treatment. Foliar dust treatments began after an acclimation period of 75 days for *Schinus* and 165 days for *Quercus* and *Ceratonia*, at the time *Schinus*, *Quercus* and *Ceratonia* reached an average height of 45, 24 and 50 cm, respectively. The dust was applied manually (as demonstrated in Figure 1), directly on the plant canopy, using a 63-μm sieve; the foliar treatment was given in two separate pulses 3 weeks apart, simulating the episodic nature of dust storms in the field. The dust mass added to the tree was equivalent to 100 g m^2, which is within the range of the average annual dust deposition in Central Israel reported in previous studies (Offer et al. 1998, Uni and Katra 2017). The actual mass supplied to each plant was calculated based on the leaf surface area of each species. Based on the average leaf area per tree (Schinus = 0.129 m^2 SE 0.011, *Ceratonia* = 0.1005 m^2 SE 0.027 and *Quercus* = 0.059 m^2 SE 0.022), the mass of dust applied per pulse (100 g m^2 in total divided into two application pulses) on each tree was 6.45 g per *Schinus*, 5.00 g per *Ceratonia* and 2.97 g per *Quercus* (so a total amount of 12.9 g, 10.0 g and 5.95 g, for each tree from each species, respectively). The sapling's leaf area index in the greenhouse was 5.6 for *Schinus*, 4.4 for *Ceratonia* and 2.6 for *Quercus*. Since the trees were young and generally small, by manual dusting we were able to disperse the dust on all leaves in a rather similar amount (as demonstrated in Figure 6), acknowledging some small amount of dust fell outside the tested experimental plot. Clearly, foliage distribution and exposure in the forest are less homogeneous than in our greenhouse experiment, and hence dust-P effects would be potentially smaller. Still, dust-P uptake from higher parts of tree crowns could be allocated to lower parts that are less exposed to dust deposition.

Before and after each dusting application, trees were sprayed gently with distilled water, assisting dust particle attachment to the leaf surface, and preventing dust suspension in the greenhouse air, or its transmission to saplings of neighboring trees. To prevent the dust from reaching the roots, the top surface of each pot was covered with thin plastic film for the entire duration of the experiment.

The dust treated groups had 12 replicates and the control had 24 replicates, resulting in a total of 36 trees per species, and 108 trees in total.

Photosynthesis analysis

To monitor carbon assimilation response to the dust particle coverage, we measured six leaves from six trees of each experimental group randomly after trees received the second pulse of foliar treatments. Measurements were made at midday using a Walz GFS-3000 photosynthesis system (Heinz Walz GmbH, Effeltrich, Germany), equipped with a lamp, set to a light intensity of 600 μmol m^{-1} s^{-1} (ambient natural lighting) at our greenhouse air temperature (25 $\pm$ 3 °C) and humidity (70%). According to ambient CO_2 levels, CO_2 was set to 400 p.p.m. Since leaf size was occasionally smaller than that of the specific instrument gas chamber, gas exchange rates were further calibrated to the actual leaf area by scanning measured leaves (via tabletop scanner: MFP-M477fdh, HP, CA, USA) and estimating projected leaf area using ImageJ software (Rueden et al. 2017) using threshold tool and area calculation.

Plant biomass

To remove the remains of dust from the exterior tissues of the tree organs, trees were rinsed sequentially in tap water, then in 0.1 M HCl for 5 min and finally in distilled water for 5 min as done previously (Gross et al. 2021). The biomass was then dried in an oven set to 65 °C for 48 h. Afterward, the dry biomass of each tree (root and shoot, separately) was weighed using a precision balance (Agentek, model MS105DU, Yakum, Israel).

P analysis

To measure plants' P concentration, the dry biomass of roots and shoots was first ground to fine powder using a stainless-steel ball mill (Retsch MM500 Vario; Hann, Germany), separately. In the case of the *Schinus* trees, all above- and below-ground organs were ground and included in the final fine powder used for P analysis. In the case of *Quercus* and *Ceratonia* trees, facing technical difficulties to grind the hardwood, we excluded the stem and hard root tissue and ground only two replicates of each species and treatment.

To extract the P from the dried and grounded plants A subsample of 100 mg from each grounded sample was used for ashing in 500 °C for 5 h transferred into a 50 ml tube, with 40 ml of 1 M HCl to each and placed on a laboratory orbital shaker for 40 min (mrc, model TOS-4030pd. Holon, Israel). Then, a subsample of 3 ml was transferred to 15 ml tubes and the pH of the solution was adjusted to a range of 5.5–6.5. The P in the solution was measured using the molybdenum blue spectroscopic method (Murphy and Riley 1962) using Tecan Infinite M200 Plate Reader (Tecan Group Ltd, Männedorf, Switzerland).

Leaf surface pH

Leaf surface pH was recorded prior to foliar treatments, 4 months after replanting, in the early morning hours, before evaporation of leaf exudes. The measurements were taken manually by attaching a portable pH flat electrode (HI-1413; HANNA pH instruments) onto the leaf surface, 1 leaf of each tree and 10 of each treatment.

Statistical analysis

Statistical analyses were performed with Jamovi, version 2.2.3. We used a set of general linear models to test differences among foliar treatments in P concentration, final dry biomass (3 treatments, 12–24 replicates of each) and carbon assimilation (3 treatments, 6 replicates of each) but not between the tree species. Significance was determined at $P \leq 0.05$. The significance of the differences between the foliar treatments was portrayed using post hoc Tukey test (Tukey's honest significant difference test).

Results

Phosphorus concentration and leaf surface pH

Despite the different characteristics of each species, the leaf surface pH measured was almost identical. Figure 2 shows all tree species demonstrate a moderately acidic pH of 4.6–4.8. In Figure 3a, the P concentration test demonstrates that all three tree species had higher P concentrations in response to foliar application of desert dust, in comparison with the control trees. Prominent differences were observed for *Ceratonia* and *Schinus* trees having 37 and 33% higher P concentration than the control, respectively. The *Quercus* trees showed only a modest non-significant increase of 12%.

The P concentrations in the roots of *Ceratonia* trees increased under the desert-dust treatment, indicating P absorbed via the foliage was later potentially transferred to other organs including those not exposed to foliar treatments.

Plant biomass and photosynthetic rate

The final biomass of dust-treated saplings was reduced compared with control plants for all tree species, decreasing by 58.4% for *Quercus*, 17.3% for *Schinus* and 32% (although not significant) for *Ceratonia* (Figure 4a). By integrating P concentration and biomass, we calculated the whole-plant P content (Figure 4b). Our calculation showed that only the *Schinus* had

Figure 1. Image of desert dust application on *S. terebinthifolius* trees' foliage.

Figure 2. pH of the leaf surface of *Schinus*, *Ceratonia* and *Quercus* trees.

an increase in the total P content of 11.8 mg (21.9%) per plant on average following the desert-dust application, *Ceratonia* P content did not change and *Quercus* showed a significant reduction of 55.2% in P content.

Photosynthetic net carbon assimilation averaged a range of 7.3–9.5 μmol CO_2 cm^{-2} s^{-1} under dust, compared with 9.7–12.3 for the control groups (Figure 5). Although photosynthesis was reduced by 17–30%, desert-dust coverage over the trees' foliage decreased the photosynthetic activity significantly only for *Schinus*.

Discussion

Effect of dust application on tree P concentrations

Two out of three tested tree species displayed higher P concentrations in response to foliar application of the desert dust analog (Figure 3a). Since the dust used in this experiment consisted of scarce amounts of labile P, roughly under 1% of the total P (Gross et al. 2021), the results imply some insoluble P fractions which are considered unavailable for plant uptake were dissolved on the leaf surfaces, as was shown before (Gross et al. 2021). Similar to dust-P, soil-P is also composed mostly of unavailable P fractions. Although foliar uptake is generally regarded as a passive process driven by the concentration difference between the leaf surface and the leaf interior (Eichert and Fernandez 2012), recent findings point out that foliar P uptake may be assisted by similar strategies to those used by plant roots. Plant roots operate a wide range of strategies and interactions to dissolve and mobilize insoluble P: symbioses with microorganisms (Smith and Read 2008), acidification of the rhizosphere and the release of phosphatase enzymes or P solubilizing short chain organic acid (Hinsinger 2001; Neumann and Römheld 2007; Nannipieri et al. 2011, Hofmann et al. 2016). Part of the P dissolution on the leaf could be attributed to the moderately acidic pH we measured on the surfaces of the leaves of all trees in our experiment (Figure 2) since most of the P in desert dust is bound to pH sensitive calcium (Ca) minerals (Andersson et al. 2016,
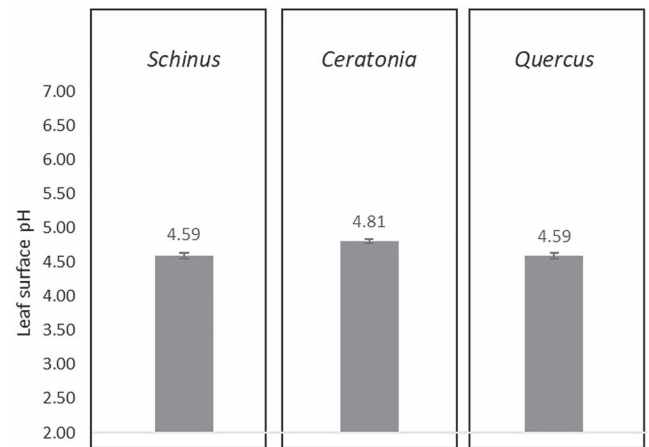
Gross et al. 2021) which dissolves as pH decreases. Furthermore, many plants also regularly release organic acid exudates to their leaf surfaces. Although their role is usually assigned to plant defense mechanisms against pathogens (Yoshida et al. 1997), according to Gross et al. (2021), these exudates promote P dissolution on the leaf itself. The phyllosphere may also play a role as in P-poor tropical forest, Mori et al. (2021) found that phyllosphere microorganisms allocate resources to obtain P in the trees' canopy.

The noticeable differences in P concentration range between the tree species (480–730 μg g^{-1} for *Schinus* and 820–1300 μg g^{-1} for *Ceratonia* and *Quercus*) are mostly ascribed to the natural differences between species attributes such as growth rate and internal P demand. However, the technical difficulty of grinding the hardwood of the *Quercus* and *Ceratonia* also mildly affected the magnitude of P concentration. In regard to this matter, the *Schinus* P concentration (Figure 3) represents the P in the entire tree, whereas the *Quercus* and *Ceratonia* P concentrations represent only the soft tissues. Analysis of selected hardwood samples shows that *Ceratonia* hardwood P concentration ranges between 640 and 740 μg g^{-1}, lower by 35% than that of the soft tissues, but *Quercus* hardwood P concentration ranges between 1000 and 1500 μg g^{-1}, higher by 18% than the soft tissue. The difference in trend between the P concentration in the hardwood of *Ceratonia* and *Quercus* is not crucial for our analysis of the dust impact on the sapling, but may give us insight into the P allocation strategies between the two tree species. *Ceratonia*, displaying a higher growth rate, maintains higher P concentration in the foliage, to support new growth, and *Quercus*, preserving more P in the hardwood as storage, is less dependent on external P sources.

Effects of dust application on tree total P content and biomass

All three tree species that received the dust treatment suffered from a reduction in their final biomass (Figure 4a) inversely
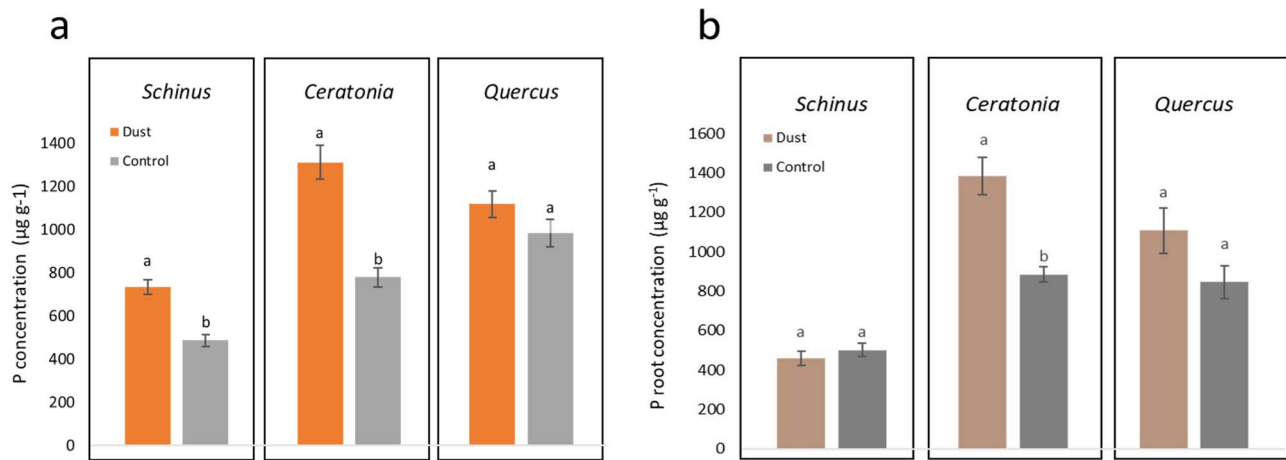
Figure 3. The effects of P-rich desert dust analog on (a) P concentration in the entire tree and (b) P concentration in the roots only. Letters represent statistically significant differences ($P < 0.05$) between treatments. Error bars represent the standard error.

corresponding to the P concentration increase, as displayed in Figure 3a. Thus, while P concentrations in *Schinus* and *Ceratonia* increased greatly with dust application, total plant P content increased mildly or stagnated, respectively (Figure 4b). We assume the antagonistic dust–leaf interactions limit the beneficial utilization of the dust-derived P. These findings are compatible with the conclusions of studies focused on the harmful aspects of natural or anthropogenic airborne particle matter on plants. Such studies found that dust disrupts several physiological and biochemical parameters. These include interference in photosynthesis and stomatal conductance (Hirano et al. 1995, Nanos and Ilias 2007, Chaturvedi et al. 2012, Shah et al. 2018), low chlorophyll content due to the high particle alkalinity (Singh and Rao 1981, Shukla et al. 1990), an increase in leaf temperature due to changes in leaf surface optical properties (Eller 1977, Sharifi et al. 1997, Wijayratne et al. 2009) or rather a decrease in leaf temperature due to dust's high albedo. These all relate to a diminution of the final plant biomass. Among aforementioned harmful effects of dust on tree foliage, we tested dust influence on photosynthesis as a comprehensive measurement indicating the interference in gas exchange via the following scenarios: (i) particles shading the leaf from PAR consequently reducing stomatal aperture and conductance and (ii) small particles clogging the stomata and physically hindering gas exchange. Figure 5 shows a moderate reduction, significant only in the case of *Schinus*, of the carbon assimilation rate. The substantial standard error, a repercussion of the large variability between leaves tested, as to their position on the tree, angle toward the light source and age, may have prevented explicit results on the matter of photosynthetic rate. However, the range of responses to dust among the tree species studied here leads us to presume that the disruption in carbon assimilation is not a singular factor restricting tree development under desert dust coverage. While only *Schinus*

showed a significant reduction in photosynthesis paired with 11% reduced biomass, *Quercus* demonstrated a mild to non-existent effect of dust on photosynthesis, but reduced biomass by 58% (Figure 4a). Observing the *Quercus* trees' unfavorable reaction to the dust treatment on final tree biomass raises questions as to the general sensitivity to substances applied on the leaves of specific species.

Our results differ from the findings of Gross et al. (2021) in which the same dust was applied to P-deficient crops. While the plant P concentrations in their study remained unchanged, the total plant P content was dramatically higher in the dusted plants in comparison with the un-dusted plants. This indicated that P extracted from dust was diluted within the growing biomass and rapidly utilized for plant development. In our case, the decrease in biomass effectively means there was less plant tissue to contain P and thus subtracting the nutritional contribution of dust should have resulted in lower P content compared with the control treatments. Hence, in the current experiment, we suggest that the slight increase in P content is indeed the outcome of P-rich dust contribution to foliar P uptake, but that P was not utilized efficiently due to dust-induced limiting factors.

Testing an alternative hypothesis to foliar uptake

Phosphorus analysis performed separately for roots and shoots showed that *Ceratonia* under dust treatment had a higher P concentration in the roots when compared with the control trees' roots (Figure 3b). At first glance, these data could confirm that P absorbed through the foliage was utilized and allocated to belowground organs. In the context of the trees' decrease in biomass following dust application, we speculated an alternative scenario: the rise of P concentration in trees treated with dust actually reflects an accumulation of root-acquired P in the roots, as restricted growth led to low P utilization. To test this alternative hypothesis, we conducted an additional similar
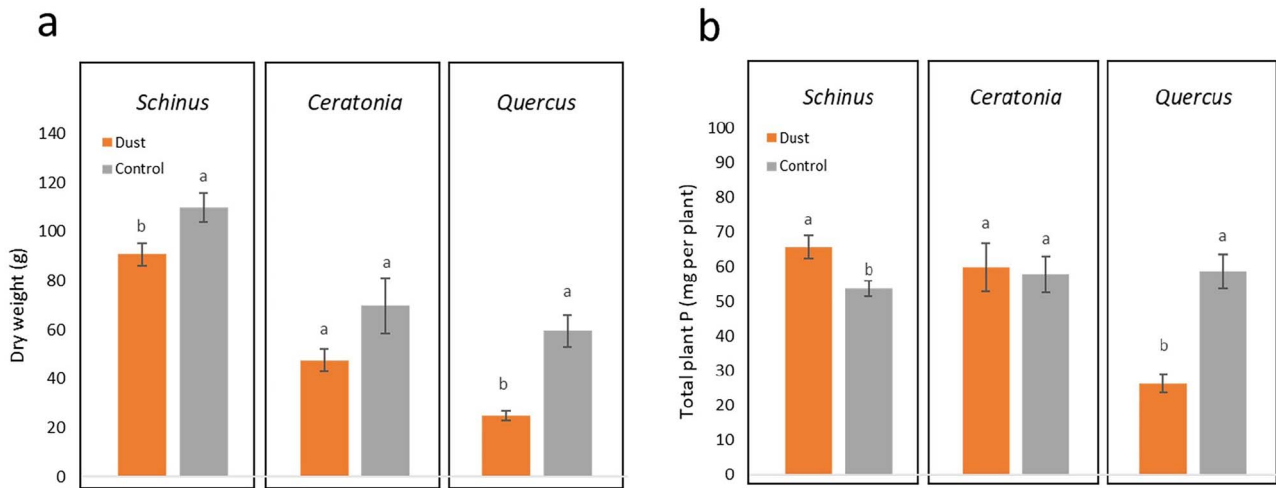
Figure 4. (a) Dry biomass of trees (g) and (b) total P content (mg per plant) in response to P-rich desert dust analog and control trees. Letters represent statistically significant differences ($P < 0.05$) between treatments. Error bars represent the standard error.
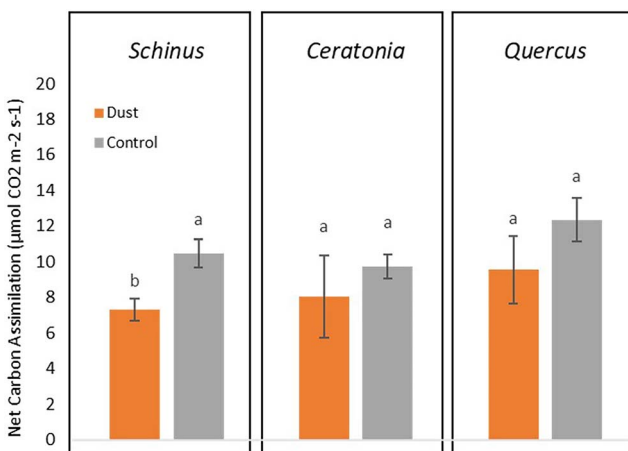

Figure 5. Photosynthesis described by leaf net carbon assimilation (μmol CO_2 cm^{-2} s^{-1}) of all three species with desert dust compared with control trees. Letters represent statistically significant differences ($P < 0.05$) between treatments. Error bars represent the standard error.

Figure 6. Close-up image of the desert dust treatment on a *S. terebinthifolius* leaves.

experiment on an additional experimental group of *Ceratonia* saplings subjected to P starvation, expecting that the acute nutrient deficiency would resume despite the dust treatment. In contrast, the results show an increase in P concentration by 77 μg g^{-1} (16.4%) and total plant P content by 2.3 mg (43.4%) per plant on average (Figure 7) even though the trees had no other P source. In addition, a pronounced detraction in photosynthetic rate did not cause a reduction in tree final biomass (Figure S2b available as Supplementary data at Tree Physiology Online). This indicated that in the case of nourished trees, having another readily available P source in the soil, even if limited, the P-rich dust application is apparently more harmful to tree growth than it is useful for foliar nutrient uptake. In contrast, dust-P foliar uptake could be advantageous to

trees suffering from severe P starvation, which itself restricts photosynthesis and tree growth. These results agree with Gross et al. (2021), which showed that chickpea plants enduring P deficiency also responded to dust application with an increase in P and biomass.

Species-specific responses to dust application

Plant traits and physiological requirements such as leaf structure and biochemistry, growth rate, P requirements and adaptive strategies to cope with P scarcity shape their ability to collect particles from the air (Mo et al. 2015) acquire and utilize nutrients via direct foliar uptake from fertilizers (Eichert and Fernández 2012) and desert dust (Gross et al. 2021). For example, particle coverage is less detrimental to plants that exhibit physical protection structures, such as trichomes, compared with plants without such physical barriers (Kameswaran et al. 2019).

Summarizing the different responses of *Schinus*, *Ceratonia* and *Quercus* reveals a unique reaction of each species to
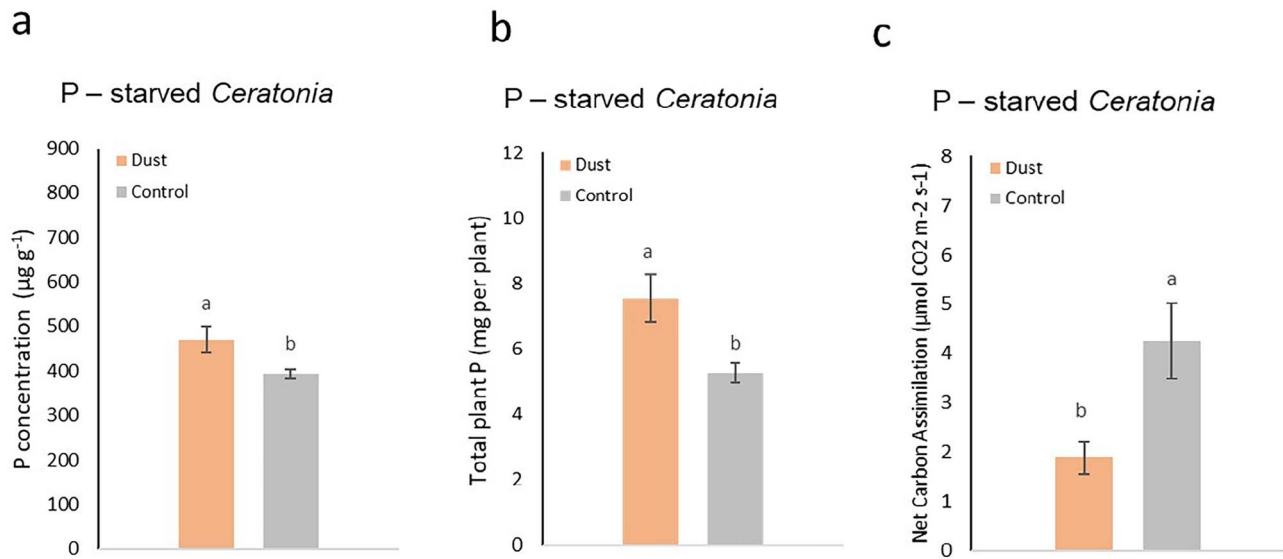
Figure 7. The effects of P-rich desert dust analog on P-starved *Ceratonia* trees: (a) tree P concentration, (b) total tree P content and (c) photosynthesis described by leaf net carbon assimilation (μmol CO_2 cm^{-2} s^{-1}). Letters represent statistically significant differences ($P < 0.05$) between treatments. Error bars represent the standard error.

Table 1. A summary of all three tree species reaction trends to dust foliar application, including P-starved *Ceratonia*.

	Schinus	*Ceratonia*	P-deficient *Ceratonia*	*Quercus*
P concentration	↑	↑	↑	—
Photosynthesis	↓	—	↓	↓
Final dry biomass	↓	↓	↑	↓
P content	↑	—	↑	↓

Black arrows refer to significant results ($P < 0.05$), whereas gray arrows to insignificant results. The dash mark represents no reaction to dust application.

desert dust deposition (Table 1). Our results suggest that *Schinus* trees can benefit from absorbing dust-P through the leaves if the dust load itself does not obstruct photosynthesis. The absolute amount of dust deposition is of importance. Both P concentration and content were elevated post-dust application, while carbon assimilation and final dry biomass decreased mildly. Parameters that may support these results are the vigorous growth rate of *Schinus* trees which enhances its rapid P utilization. The fast-growing *Schinus* trees, although not subjected to P-starvation treatment, seem to have developed P deficiency throughout the experiment, supporting the prominent increase in both P concentration and P content. Physiological adaptations of trees from the P-poor tropical Atlantic Forest of Brazil (where *Schinus* originated) may also play a role in *Schinus* trees' response to desert dust. It has been shown that some plant species originating from places with infertile landscapes have a high P-sorption proficiency, efficiently remobilizing P from senescing leaves to maximize P utilization (Lambers et al. 2010). We speculate that such abilities may be useful, especially in the case of foliar uptake.

The sclerophyllous *Ceratonia* and *Quercus* trees responded differently. They are both adapted to low rainfall by sensitive regulation of gas exchange (Tenhunen et al. 1981, Lapidot et al. 2019, Rog et al. 2021) and display a lower growth rate. The *Ceratonia* P concentration increased, while biomass decreased, so P content stagnated. The main cause of the reduction in biomass was not the restriction of gas exchange. The additional experiment on P-starved *Ceratonia* trees (Figure 7) showed that the utilization of P for biomass development depends on the internal P demand of the tree. *Quercus* trees displayed the most unfavorable response. Although P concentration in the soft tissue remained unchanged, the dramatic decrease in biomass and leads us to presume no absorption of P through the leaves. Zavišić and Polle (2017) showed that different soil-P availability does not necessarily affect the P concentration in tree leaves, as some tree species rely mostly on P storage in the coarse roots. Dirks et al. (2019) showed that unlike *Schinus* and other fast-growing tree species, *Q. calliprinos* P-use economy is independent to a certain degree of environmental P availability, and mainly focused on maintaining a stable P concentration in

plant tissues. According to these findings, and in relation to our experiment, we can assume that if *Quercus* trees achieve foliar dust-P absorption, this would not necessarily result in biomass increment.

Although our data show that for *Quercus* and *Ceratonia* photosynthesis was not significantly reduced, previous studies on *Quercus* trees demonstrated otherwise. A study by Moradi et al. (2017) tested the effects of heavy dust deposition on three *Quercus* species. Using SEM microscopy coupled with IRGA gas exchange analysis, they discovered that the stomatal pores were occluded with small dust particles, thus explaining the lower gas exchange rates. Other potential destructive influences such as an increase in leaf temperature, or sensitivity to particle alkalinity, were not tested in the course of this experiment, yet leaf temperature in *Q. calliprinos* is already higher than in four other Mediterranean forest tree species (Lapidot et al. 2019). We conclude desert dust had an impairing effect on *Quercus* tree prosperity.

Both *Ceratonia* and *Schinus* responded to dust-P, even though the first originates on the desert's outskirts in the Mediterranean and Middle East naturally receiving 40–210 g m^2 year^{-1} of atmospheric dust deposition (Ganor and Foner 2001, Uni and Katra 2017), whereas the second originates in north-east South America, receiving a dust mass of only 1–20 g m^2 year^{-1} (Swap et al. 1992, Zhao et al. 2013, Yu et al. 2015, Herbert et al. 2018). Hence, we speculate different forest tree species, regardless of the native ecosystems in which they evolved, are able to utilize dust-P via the canopy.

Conclusions

The elevated P concentration and content after desert dust application present in *Schinus* and P-starved *Ceratonia* species partially proves our hypothesis of forest trees' ability to harvest P directly from the atmosphere and dissolve insoluble P sources, similar to roots. Trees suffering from P deficiency (such as P-starved *Ceratonia*, and *Schinus*, which developed P deficiency throughout the experiment) can benefit from this nutritional addition for growth and development. However, dust application had an overall harmful influence on trees that were capable of satisfying P nutritional needs via root uptake. In the case of *Ceratonia* and *Quercus* trees receiving satisfactory P fertigation to the roots, photosynthesis was possibly restricted by the coverage of the heavy dust load on the leaf surface. Ultimately, this created a tradeoff between contributing to the tree's P nutrition and lowering the efficiency of photosynthesis rate.

The attempt to reflect the conclusions from our greenhouse experiment to natural forest ecosystems requires the acknowledgement of several notable differences. The forest trees used in our experiment originate from locations where annual dust intake, dust-P concentrations and deposition frequencies vary spatially between and within these ecosystems. In our experiment, we applied a uniform dust dose of 100 g m^2 to all three tree species, in just two pulses 3 weeks apart, resulting in a much heavier dust load, possibly limiting photosynthesis to a greater extent than in natural conditions. Leaves are generally able to acquire nutrients dissolved in a liquid solution (Eichert and Fernández 2012), and not a solid substance such as dust particles. In the field, trees experience precipitation and dew cycling, dissolving the dust particles from the leaf surface and eventually washing them off. In our experiment we applied only occasional gentle spraying of distilled water, possibly sustaining dust particles partially undissolved on the foliage for a longer time span than that occurs in the field. Another considerable difference between the field and the greenhouse is the PAR intensity, which is lower indoors. Considering the constraints of the experimental setup (heavier dust load, lack of moisture, reduced solar radiation and more), we would expect that dust-induced limiting effects are less pronounced in the field.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online. All processed data is available within this paper. Raw data supporting the findings of this study are available from the corresponding author S.M. on request.

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