

Arbuscular mycorrhizal association regulates global root-seed coordination

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Abstract

Terrestrial plants exhibit immense variation in their form and function among species. Coordination between resource acquisition by roots and reproduction through seeds could promote the fitness of plant populations. How root and seed traits covary has remained unclear until our analysis of the largest ever compiled joint global dataset of root traits and seed mass. We demonstrate that seed mass and seed phosphorus mass scale positively with root diameter in arbuscular mycorrhizal (AM) plants, which depends on variation in root cortical thickness instead of root vessel size. These findings suggest a dual role of AM association in phosphorus uptake and pathogen resistance which drives the global root-seed coordination, instead of initially expected resource transport via root vessels as the main driver. In contrast, we found no relationship between root traits and seed mass in ectomycorrhizal plants. Overall, our study reveals coordination between roots and seeds in AM plants that is likely regulated by root-mycorrhizal symbiosis, and may be crucial in shaping global plant diversity and species distributions.

Main

Terrestrial plants vary greatly in their form and function to cope with heterogeneous natural environments, which contributes fundamentally to Earth's biodiversity¹⁻⁶. Substantial global variation in plant form and function has been shown to be captured by a two-dimensional space defined by above-ground plant traits critical to growth, survival, and reproduction, including leaf, stem, and seed traits¹. One dimension is related to plant size, consistent with the Corner's rules⁷, which state that larger plants are more likely to have larger leaves, stems, and seeds because they usually bear larger meristems⁸⁻¹⁰. The other dimension coincides with the leaf economics spectrum³, representing a trade-off between the capacity of rapid carbon acquisition in leaves and their investment cost^{3,8}.

Recently, studies have demonstrated that root traits also vary in a two-dimensional trait space^{2,6,11}. The first dimension represents a collaboration gradient for mycorrhizal symbiosis, ranging from "do-it-yourself" resource acquisition characterized by finer absorptive roots —to "outsourcing" of resource acquisition through mycorrhizal fungi associated with thicker absorptive roots and higher levels of mycorrhizal colonization⁶. The second dimension reflects a resource conservation gradient, highlighting a trade-off between acquisitive (high root nitrogen concentration) and conservative strategies (high root tissue density). This gradient has been suggested to align with the plant fast-slow economics spectrum^{6,7}, although the generality of coordination among plant size, economic spectrum, and mycorrhizal collaboration is still debated^{2,12}. Over evolutionary time, roots in coordination with above-ground

plant organs have enabled vascular plants to adapt to heterogeneous environments in diverse ways^{6,12,13}. For example, traits that represent the resource conservation dimension in the root economics space—such as root tissue density and root nitrogen concentration—often correlate with traits from the leaf economics spectrum, such as leaf nitrogen concentration and leaf mass per area¹². Notably, these economics traits vary independently from the size dimensions of the leaves, stems, and seeds^{1,13,14}.

While our understanding of the coordination between roots and above-ground organs has advanced in recent years^{2,6,12,13}, it remains uncertain whether, and if so, how and why roots are coordinated with seeds. More than two thirds of the world's plant species rely on seeds for reproduction, population maintenance, and establishment in new habitats^{15,16}. Seed mass is of particular importance for species' dispersal, seedling survival, and plant-animal interactions^{15,17,18}. Generally, larger seeds are dispersed by larger animals^{15,17} and produce seedlings with larger pathogen resistance and higher survival rates^{19,20}. Remarkably, terrestrial plants display a range of 13 orders of magnitude in seed mass^{1,15,16}. Examining how roots and seeds are coordinated is therefore a critical step toward fully understanding the global variation in plant form and function that support biodiversity on Earth.

Theoretically, roots and seeds are interconnected during at least two stages of the plant's life cycle. First, during the reproductive stage, seed formation depends on water, carbon, and mineral nutrients transported from vegetative organs, i.e., roots, stems, and leaves²¹. Therefore, seed size could be coupled with vessel size that is responsible for the matter transport efficiency during this stage. Such a relationship is

also suggested by Corner's rules. Alternatively, larger seeds have a greater demand of phosphorus (P) to support more cell division as larger seed develops. This will generate selective pressure for building thicker absorptive roots in larger-seeded plants to deploy more cortex-residing mycorrhizal fungi for more P acquisition²². Second, in the recruitment stage, the carbon and nutrients needed to establish initial vegetative organs (including the first roots, stems, and leaves) are derived primarily from the seed itself²¹. Larger seeds, which store more carbon and nutrients, face a higher risk of pathogen infection²³. In this context, producing thicker absorptive roots which are often enriched with mycorrhizal fungi that colonize the cortex^{6,24} could help enhance pathogen resistance²⁵. While some studies have reported a positive correlation between root diameter and seed size, they have focused on a limited number of species (primarily temperate non-woody species, possibly due to the difficulty of getting detailed root information for woody plants) and were based on restricted geographical sampling^{11,20,26-28}. Consequently, the global coordination between roots and seeds remains unclear. Here, we aimed to uncover this global coordination between roots and seeds, especially in terrestrial woody plants, and to elucidate the underlying mechanism.

Three working hypotheses

We proposed three alternative hypotheses in explaining the root-seed relationship (Fig.1):

(1) The Resource Transport Hypothesis. Based on Corner's rules⁷ and the Metabolic Theory of Ecology^{29,30}, we hypothesized that plants with larger seeds have

higher metabolic demand, requiring a larger-vessel root vascular system to support nutrient and water transport, overall higher carbon assimilation, and seed growth. Generally, soil nutrients are acquired by roots and mycorrhizal fungi. Nutrients, then, move into root vessels before being transported to seeds. If seed size is limited by nutrient transport via vessels rather than by nutrient acquisition, we predicted a positive correlation of seed size with root vessel diameter and root diameter given that roots with larger diameters generally have wider vessels^{24,31} (Fig. 1a).

(2) Mycorrhizal P Uptake Hypothesis. If seed size is primarily limited by nutrient acquisition especially P, we expected that plants with thicker absorptive roots, and hence more arbuscular mycorrhizal (AM) colonization, would be better able to meet the high P demand from producing larger seeds. Therefore, a positive correlation would be expected between root cortical thickness and seed P mass (where seed P mass = seed mass $\times$ seed P concentration); while ectomycorrhizal (ECM) roots, where there is no (or very little) contact between the root cortex and the soil solution (as the ECM fungal mantle completely or largely covers the roots), does not select for cortical area, ultimately resulting in the lack of above correlation. (Fig. 1b).

(3) The Pathogen Resistance Hypothesis. Although large seeds (usually with more internal nutrient reserves) can disperse over long distances, many still fall near the parent plant³²⁻³⁴, where soil pathogens to which a species is susceptible are likely to be more abundant. This phenomenon is known as the Janzen-Connell effect^{35,36}. A prerequisite for the Pathogen Resistance Hypothesis (but also for the Mycorrhizal P uptake mechanism) is that there is a differential relationship between seed size and

cortical thickness for AM and ECM (ectomycorrhizal) plants. Specifically, in AM plants, larger seeds tend to be associated with thicker absorptive roots with thicker cortices to allow for room for greater mycorrhizal colonization^{36,37} and enhanced pathogen protection^{25,37}, while no such relationship is expected in ECM plants because their absorptive roots are already encased in protective mycelial sheaths against pathogens^{38,39} (Fig. 1c).

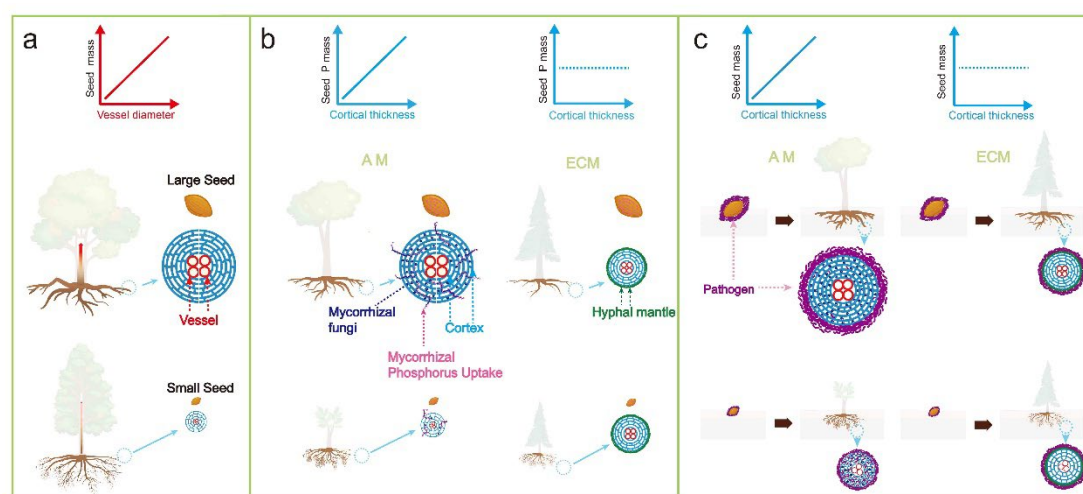


Figure 1 | Three hypotheses regarding the relationships between roots and seeds. a, Resource Transport Hypothesis: larger seeds are associated with thicker root vessels, enhancing nutrient transport efficiency to support seed growth. **b,** Mycorrhizal Phosphorus (P) Uptake Hypothesis: the development of larger seeds with greater P demand (i.e., from higher seed P mass) entails thicker root cortices which usually has more arbuscular mycorrhizal (AM) colonization, and hence more P uptake (solid pink filled circles) by AM fungi. In contrast, there is no such correlation in ectomycorrhizal plant species (ECM). **c,** Pathogen Resistance Hypothesis: predicts a positive relationship between root cortical thickness and seed mass. On the left half of panel (c), larger seeds of arbuscular mycorrhizal (AM) plant species (both woody and non-woody) are predicted to develop thicker root cortices, which attract mycorrhizal fungi to help defend roots against soil pathogens. This leads to a positive correlation between root cortical thickness and seed mass in AM plants. In contrast the right half of panel (c) predicts that ECM plant species, whose roots are protected by an ECM hyphal sheath, will show no correlation between root cortical thickness and seed mass.

Results and Discussion

A global dataset on roots and seeds

To test our hypotheses, we collected samples of roots, stems, leaves, and seeds from 660 woody plant species across 11 forest types in China, spanning climates from tropical to temperate regions (Extended Data Table 1). We measured seed traits including dry mass, length, and width and examined root anatomical traits such as cortical thickness, stele radius, vessel diameter, and vessel density, capturing key aspects of root morphology variation, specifically the mycorrhizal collaboration dimension. Additionally, we analyzed two classic traits within the root conservation dimension: root tissue density and root nitrogen concentration. Leaf traits, including nitrogen concentration and specific leaf area, were assessed to examine the leaf economics spectrum^{1,3,4}, along with mature plant height, as these traits are associated with seed construction and dispersal^{1,4}.

To explore the global relationship between roots and seeds, we also compiled data from the Global Root Traits (GRooT) database⁴⁰ and other literature, incorporating 620 additional species with both root and seed traits data. Totally, this global dataset (our field-measured data plus those from GRooT database and literature) includes 239 plant families and spans two major mycorrhizal types (1023 arbuscular mycorrhizal plants and 142 ectomycorrhizal plants), three growth forms (331 herbs, 329 shrubs, and 636 trees), and diverse climatic zones (380 tropical plants, 450 subtropical plants, and 467 temperate plants) (Extended Data Fig. 1). This comprehensive dataset allowed us to investigate the universality of root-seed relationships.

The global root-seed coordination

Before analyzing the root-seed relationship using field-measured data, we first

210 explored the dimensions of the trait variation in roots, leaves, and seeds. This step was
211 necessary because if trait variations in those organs are different from those well-
212 documented in previous studies^{1,6,14}, the root-seed relationship derived from the field-
213 measured data might represent a specific case rather than a general pattern. The
214 results of principal component analysis (PCA) show that absorptive root traits align
215 with the two orthogonal dimensions: mycorrhizal collaboration gradient and the
216 conservation gradient (Fig. 2a)^{2,6}. In contrast, variations in above-ground plant traits
217 (Fig. 2b), consistent with Corner's rules, align with the established axes of the leaf
218 economics spectrum³ and plant size dimensions including mature plant height and
219 seed mass (Fig. 2c)¹. We also observed coordinated variation of the conservation
220 spectrum between above- and belowground traits, e.g., the closely aligned ordination
221 vectors for leaf and root N concentration (Fig. 2c).

222 We also found that, in both our field-measured trait study (Extended Data Figs. 2a,
223 b) and in the global dataset (Figs. 3a), seed mass is significantly and positively
224 correlated with the mycorrhizal collaboration gradient, particularly root diameter,
225 which represents the volume of the intraradical habitat for fungal partners⁶. However,
226 seed mass shows no relationship with the conservation dimension of roots (Fig. 2a).
227 This positive relationship between root diameter and seed mass holds consistently
228 across different climatic zones (tropical, subtropical, and temperate) and woody
229 species (trees and shrubs), with the effect being pronounced in AM plant species
230 (Extended Data Figs. 3a, d and 4a, d, g) and absent in ECM plant species. By
231 integrating our new data with existing literature, we demonstrate that the root

diameter-seed mass relationship is robust across plant growth forms, including woody and non-woody species (Extended Data Fig. 5). Moreover, this relationship remains consistent even after accounting for plant phylogeny (Extended Data Fig. 6).

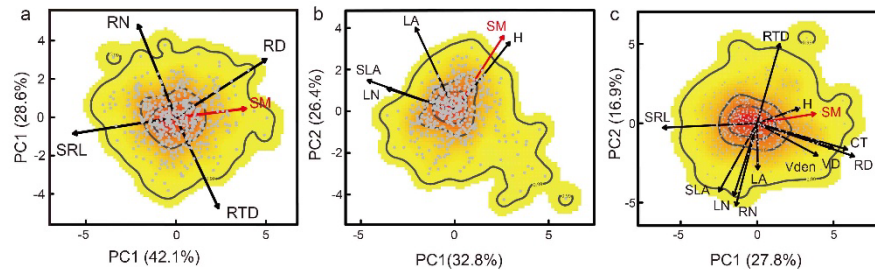


Figure 2 | Integration of seed mass within the above- and below-ground plant trait space.

Analyses were performed using our field-measured trait data: a, Seed mass and the four traits associated with the previously described two-dimensional root economics space (SRL, RTD, RN, and RD). b, seed mass, two traits associated with the plant size dimension (LA and H), and two traits associated with the leaf economics spectrum (SLA and LN). c, all traits from panels a and b, combined with root anatomical traits (CT, VD, and VDen). Color gradients indicate species occurrence probability within the trait space, with red indicating high occurrence and yellow indicating low occurrence. Contour lines correspond to the 0.25, 0.50, and 0.99 quantiles. Traits included in each dimension are: leaf economics spectrum (specific leaf area, SLA; leaf nitrogen concentration, LN); plant size (seed mass, SM; leaf area, LA; mature plant height, H); root economics space (root diameter, RD; specific root length, SRL; root tissue density, RTD; root nitrogen concentration, RN); and root anatomical (cortical thickness, CT; vessel diameter, VD; vessel density, VDen).

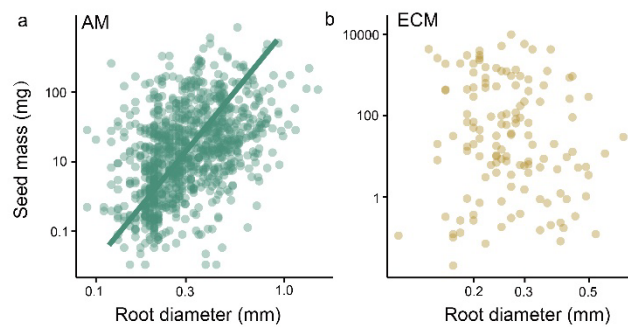


Figure 3 | Global relationship between root diameter and seed mass. Analyses were performed for arbuscular mycorrhizal (AM) (a) and ectomycorrhizal (ECM) plant species (b) using combined field-measured data and literature data. Global AM data show a significant positive correlation (a): Green filled circles; regression equation: $\log_{10}(y) = 6.23 \log_{10}(x) + 4.43$, $r = 0.45$, $P = 2.2 \times 10^{-16}$, $n = 983$. Both regressions are performed using the standardized major axis (SMA) regression. The scaling exponent for the AM plant species is 6.23 (95% confidence interval (CI) = 5.89–6.59) ($P = 1.32 \times 10^{-6}$; see the Method section). In contrast, no significant correlation was found for ECM plant species (b): Tan filled circles; $r = 0.11$, $P = 0.20$, $n = 131$. Significance was tested using a two-sided t -test. All data are plotted on logarithmic scales ($\log_{10}$) for both axes, with each point representing a single plant species.

Mechanisms of root-seed coordination

We explored potential mechanisms underlying the observed relationships between roots and seeds (Fig. 1). We found a relatively weak or no correlation between root vessel diameter and seed mass using field-measured data (Fig. 4a and Extended Data Fig. 3c). Conditional correlations analyses considering the significant relationship between cortical thickness and vessel diameter ($r = 0.52$, $P < 0.01$) showed no correlation between vessel diameter and seed mass ($r = 0.03$, $P < 0.54$) in AM plants. Remarkably, this correlation was also absent within each mycorrhizal type (Extended Data Figs. 3f and 4c, f, i), climatic zone (Extended Data Figs. 4c, f and i), and among tree and shrub species (Extended Data Fig. 3 c, f). This suggests that the positive relationship between root vessel diameter and seed mass, as expected by the Resource Transport Hypothesis, or the widely recognized Corner's rules, cannot fully explain

the observed positive relationship between root diameter and seed mass.

Although plant height was positively correlated with seed mass ($r = 0.32$, Extended Data Fig. 6), consistent with the empirical Corner's rules, its weak relationship with root vessel diameter ($r = 0.17$, Extended Data Fig. 6) likely limits the indirect pathway by which vessel traits might influence seed size. These findings may explain why the Resource Transport Hypothesis was not supported. Indeed, the weak correlation between plant height and root vessel diameter warrants further investigation.

In contrast to the root vessel diameter-seed mass relationship, we found a stronger positive correlation between root cortical thickness and seed mass, with a significant correlation in AM plants (green filled circles in Fig. 4b) but no such correlation in ECM plants (green open circles in Fig. 4b). Conditional correlation analysis further confirmed the positive correlation between cortical thickness and seed mass ($r = 0.24$, $P < 0.01$) in AM plants. This root cortex-seed relationship was consistent within each growth form (trees and shrubs) (Extended Data Figs. 3b and e) and climatic zone (tropical and subtropical) (Extended Data Figs. 4b, e and h) in AM plants, while it was absent in ECM plants.

The lack of a significant relationship between vessel diameter and seed mass in ECM plant species further challenges the universal applicability of the Corner's rules. In AM plants, thicker cortices are closely related to greater mycorrhizal colonization by providing more intraradical space for fungi symbiosis^{6,41}. These AM fungi could enhance phosphorus uptake for larger seed production. Consistent with the expectation of Mycorrhizal P Uptake Hypothesis, we observed a positive correlation

between cortical thickness and seed phosphorus mass ($r = 0.33$, $P < 0.05$) in AM plants and no correlation ($r = 0.001$, $P = 0.88$) in ECM plants. This suggests that the nutritional function of mycorrhizal association, particularly for commonly limiting nutrients such as P, potentially explains the root-seed relationship.

Since our field-measured data (Fig. 4, Extended Data Fig. 2a and c) were from mature plants and the Pathogen Resistance Hypothesis was originally based on seedling roots²¹, we also analyzed both mature and seedling roots for the same species, using field samples and literature data. This follow-up analysis showed a strong positive correlation in absorptive root diameter between the mature plants and their respective seedlings (Extended Data Fig. 7), indicating trait consistency over ontogeny. Several lines of evidence also support the Pathogen Resistance Hypothesis and Mycorrhizal P Uptake Hypothesis, which suggests that the resistance to soil-borne pathogens together with P uptake by symbiotic mycorrhizal fungi in root cortex may also regulate the root-seed relationship.

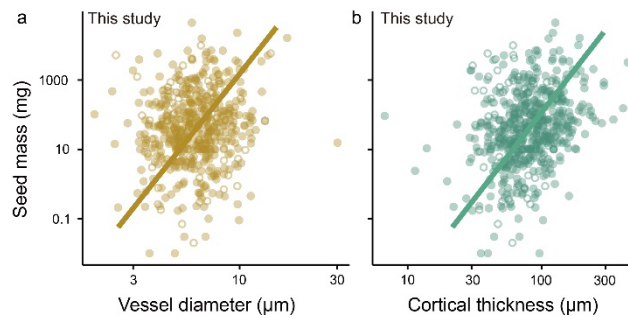


Figure 4 | Relationships between root anatomical traits and seed mass. The analyses were performed using our field-measured data. For arbuscular mycorrhizal (AM) plant species, seed mass is positively correlated with both vessel diameter (tan filled circles, **a**, $\log_{10}(y) = 7.34\log_{10}(x) - 4.14$, $r = 0.16$, $P = 1.45 \times 10^{-12}$, 95% CI = 6.71–8.04, $n = 458$) and root cortical thickness (green filled circles, **b**, $\log_{10}(y) = 4.81 \log_{10}(x) - 7.60$, $r = 0.33$, $P = 0.002$, 95% CI = 4.43–5.23, $n = 488$). Both regressions are performed using the standardized major axis (SMA) regression. In contrast, no correlation is observed for ectomycorrhizal (ECM) plant species (tan open circles, **a**, $r = 0.04$, $P = 0.77$, $n = 71$; green open circles, **b**, $r = 0.06$, $P = 0.62$, $n = 78$; regression lines not shown). Significance was tested using a two-sided *t*-test. Data are plotted on logarithmic scales ($\log_{10}$) for both axes, with each point representing a single plant species.

First, AM plants, particularly obligate AM species compared with non-mycorrhizal ones, tend to produce large seeds^{19,42,43}. These large seeds give rise to absorptive roots with larger diameters, which attract and sustain more mycorrhizal hyphae that, in turn, allow the plants to acquire more P and help fend off soil pathogens^{19,25} through secreting antagonistic compounds, enhancing immunity of host roots (even leaves³⁷), and/or competing for photosynthate or infection sites in cortical cells⁴⁴.

Second, previous studies^{36,45,46}, along with our integrated analysis, indicate that tropical and subtropical plant species potentially experience greater pathogen pressure than species in temperate regions. The higher levels of mycorrhizal colonization observed in tropical and subtropical roots, as compared to temperate ones (Extended Data Fig. 8a), may be a result of this geographic pattern of soil pathogens. The greater pathogen presence in more moist and warmer climatic zones can, in turn, select for

thicker root diameter and root cortex in these regions³¹, providing enhanced pathogen resistance likely through the above mechanisms by accommodating more mycorrhizal fungi within the cortex²⁵. Moreover, (sub-)tropical ecosystems are well-known to experience more prominent P-limitations than temperate ecosystems⁴⁷. Consequently, higher mycorrhizal colonization in thicker absorptive roots of (sub-)tropical plants could help meet the elevated P demands associated with producing larger seeds. These phenomena may explain the significant positive correlation between seed mass and both root diameter and cortical thickness (Figs. 3 and 4a).

Third, we note an increasing trend of soil fungal pathogen richness (potentially pathogen combinations or pathogenicity per tree species) from tropical to cold temperate regions in China⁴⁶ (Fig. 5 and Extended Data Figs. 8b-e). Alongside our root anatomical data, we further found strong positive correlations between root diameter, cortical thickness, and soil fungal pathogen richness in AM plants (Figs. 5a, c and Extended Data Figs. 8b, d), but not in ECM plants (Figs. 5b, d and Extended Data Figs. 8c, e). Therefore, the significant association between seed mass and the mycorrhizal collaboration dimension of the roots, particularly their role in pathogen defense, likely explains the independence of this dimension from the resource acquisitive-conservative strategy gradient in the previously described root economics space⁶. This relationship provides a novel perspective —well-supported by substantial empirical evidence —on the origins of the two-dimensional root economics space^{5,48}, and offers an interesting expansion on the relationship between chemical protection in roots and potential pathogen pressure⁴⁸.

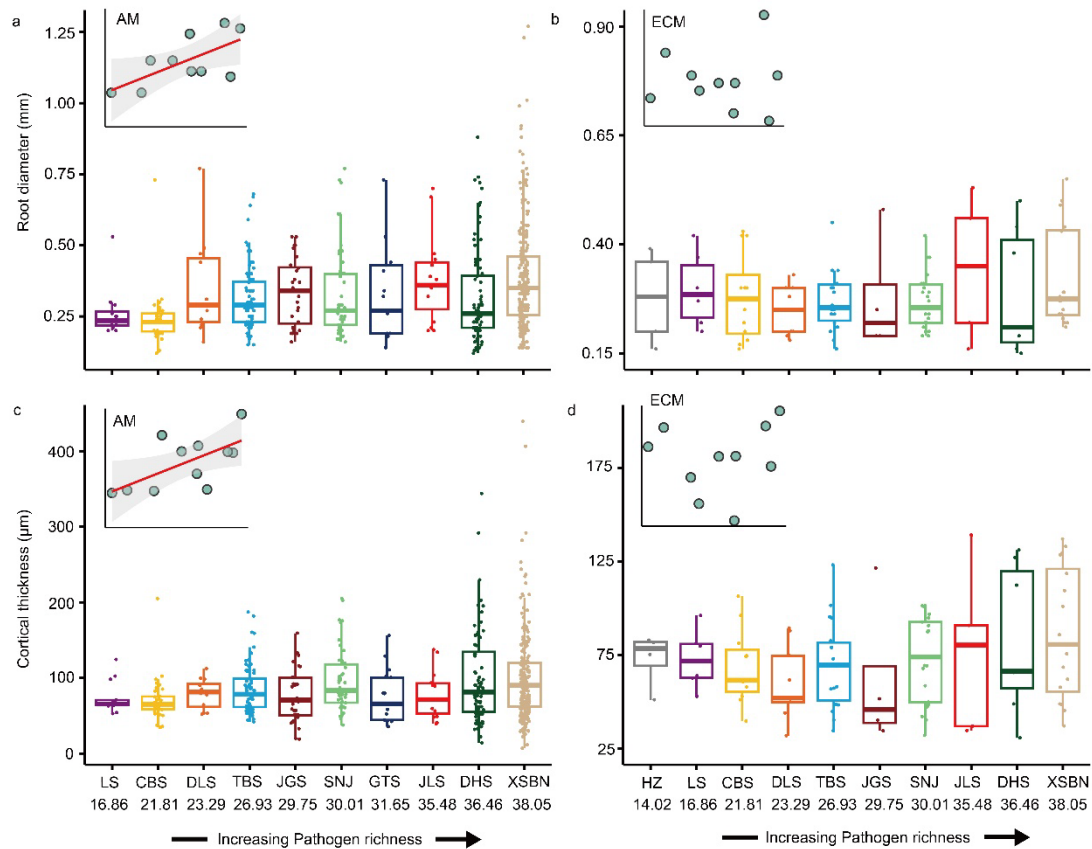


Figure 5 | Relationships between soil pathogen richness and root traits. Sampling sites in temperate forests include HZ, LS, CBS, DLS, and TBS; subtropical sampling sites include JGS, SNJ, GTS, JLS, and DHS; and tropical species were sampled in XSBN (see the Extended Data Table 1 for details of these sites). Panels (a) and (b) show box-plots of root diameter ($n = 535$, $n = 104$), while panels (c) and (d) show box-plots of cortical thickness for arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) plant species ($n = 535$, $n = 101$), respectively. For each plot, the sites are arranged in order of increasing soil fungal pathogen richness, with corresponding values (the number of Operational Taxonomic Units obtained by soil fungal sequencing) indicated below each sampling site. Pearson correlation indicates a positive correlation between soil fungal pathogen richness and both root diameter and cortical thickness in AM plant species (inset in panel a, $y = 0.005x + 0.16$, $r = 0.66$, $P = 0.04$; inset in panel c, $y = 0.005x + 0.16$, $r = 0.63$, $P = 0.03$). Shaded areas indicates 95% confidence intervals of the regression lines. In contrast, no significant correlations are observed for ectomycorrhizal (ECM) plant species (inset in panel b, $r = 0.04$, $P = 0.91$. inset in panel d, $r = 0.14$, $P = 0.69$). Significance was tested using a two-sided t -test. The inset figures show median values for root diameter and cortical thickness in each sampling site. Soil fungal pathogen richness data were sourced from literature reporting soil fungal pathogen patterns across forest sites in China⁴⁶, similar to our sampling sites. Box plots indicate the median value (solid line), 25th and 75th percentiles (box), and the data range (whiskers).

Our results further show no significant correlation of root diameter and seed mass with family divergence time, a proxy of evolutionary age (Figs. 6a, b). It suggests that

the environmental selection (e.g., increasing pathogen load and/or P limitation in habitats where thick-root species often grow) for this adaptive trait syndrome (i.e., thick absorptive roots accompanied with large seeds) may have always occurred within a specific divergence time, supporting effective mycorrhizal symbiosis and pathogen resistance.

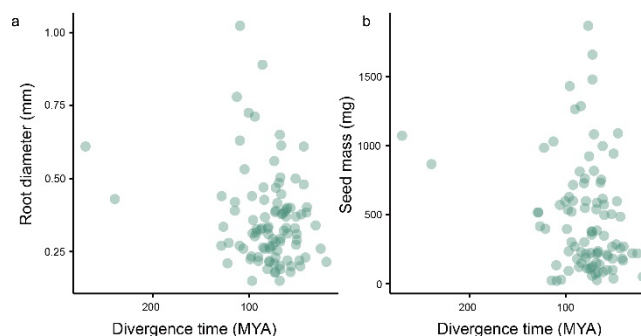


Figure 6 | Evolutionary trends of absorptive root diameter and seed mass. Spearman correlations are conducted using our field-measured data. Absorptive root diameter (**a**) and seed mass (**b**) are both no significant correlated with family divergence time (MYA, million years ago). Panel **a**, $r = 0.1$, $P = 0.319$, $n = 97$; panel **b**, $r = 0.19$, $P = 0.066$, $n = 93$. Significance was tested using a two-sided t -test.

We found that the positive relationship between root diameter and seed mass is stronger in non-woody plants than in woody plants (Extended Data Fig. 5), especially in temperate regions where most non-woody plants in the literature have been studied (Extended Data Fig. 9a). Non-woody plants typically exhibit lower mycorrhizal colonization rates than woody plants with the same absorptive root diameter⁴⁹, based on GRooT and literature data (Extended Data Figs. 9b, c). As a result, non-woody plants require larger-diameter absorptive roots than woody plants to achieve similar levels of mycorrhizal colonization, which facilitates both mycorrhizal P uptake and defense against soil fungal pathogens. While previous studies have reported differences in absorptive roots between non-woody and woody plants⁴⁰, our study is

the first to specifically explain the differences between non-woody and woody plants in terms of the root diameter-seed mass relationship, which could both be driven by mycorrhizal associations.

Conclusions

In summary, by analyzing the largest dataset on root traits and seed mass to date, we offer new insights into the connection between plant resource acquisition, reproduction by seeds, and pathogen protection in seedlings. Specifically, we found that large seeds are associated with thick absorptive fine roots. This link does not result from enhanced resource transport by larger vessel areas. Instead, it arises from a larger cortical area, supporting mycorrhizal symbionts that, in turn, help mycorrhizal P uptake and/or defense against soil pathogens and ultimately improve seedling survival and influences plant-soil feedbacks by affecting root morphology⁴⁹. Furthermore, this potential duality of function raises questions about the multifunctionality hypothesis by Newsham et al.⁵⁰, which posits a tradeoff between nutrient acquisition and pathogen defense, highlighting the need for more empirical studies to test this hypothesis. Our findings suggest practical applications in agriculture and forestry, such as selecting or cultivating AM plants with large seeds and hence thick absorptive roots to reduce the negative plant-soil feedback through their strong mycorrhizal association against soil pathogens. Importantly, this co-variation is strongly influenced by mycorrhizal type: it is present in AM plants but absent in ECM plants, likely due to an inherent difference in pathogen resistance between the two mycorrhizal types. The dual function of AM fungi in P uptake and

422 pathogen defense offers a fresh perspective on how above- and belowground plant
423 organs coordinate to shape whole plant life-history strategies and their adaptation to
424 heterogeneous environments. Understanding this coordination helps predict how plant
425 species will perform and distribute themselves in environments that differ in P
426 availability and pathogen load, particularly under global change. Finally, critical
427 experiments are needed in the future to dissect the dual role of AM association as well
428 as their relative contributions to the global coordination between root and seed traits.

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Methods

Study Sites: This study was conducted in 11 representative forest ecosystems across in tropical (1 site), subtropical (5 sites), and temperate regions (5 sites) in China. The tropical forest we sampled here is the typical forest and the hotspot of plant diversity in China. To get more generalization of the result in the tropical forest, we collected the largest number of plant species in this forest across all the 11 sampling sites. Detailed information on the sampling sites and the species number sampled can be found in Extended Data Table 1. We collected mature fruits and seeds of common woody plant species (trees and shrubs) from each site.

Sampling Approach and Trait Measurements: We first measured the height of each sampled individual. Following the methods of Schneider et al. (2021)⁵¹, we collected fruits and seeds⁵¹. For each plant species, more than three mature individuals were selected, and more than 50 mature fruits or seeds were collected from each plant individual, the number depending on how many fruits or seeds matured in the individual plant. For small-sized seeds, more than 100 seeds per plant species were collected. For species with limited or unavailable seed sources for collection, seeds were obtained from the Germplasm Bank of Wild Species in Southwest China. The fruit pulp or associated structures (*e.g.*, wind-dispersed appendages) were removed from each species, and seed size and dry weight were measured⁵². The dry mass of 30-50 seeds per species was measured (70°C, >72 hr); for small seeds, 100 seeds were measured, and for extremely small seeds, the weight per thousand seeds was used to calculate individual seed dry weight⁵¹⁻⁵⁴. For each species, we also collected at least

30 intact and undamaged leaves from the upper canopy to measure leaf morphological and chemical traits⁴. Leaf area (LA; cm²) was measured using a Li-3000C portable leaf area meter (Li-COR, Lincoln, NE, USA). Leaves were scanned, dried (60°C for 48 hr), and weighed to calculate specific leaf area (SLA; cm² g⁻¹). Leaves were then ground and analyzed for N concentration (LN%) using an elemental analyzer (IR-MS; Thermo Fisher Scientific, Waltham, MA, USA). Seed phosphorus concentration was measured for randomly selected 44 AM plant species and 28 ECM plant species following the Mo–Sb colorimetric method after digestion of the seed samples with H₂SO₄–H₂O₂⁵⁵.

Root samples were collected following established methods^{24,31,49}. Lateral roots were traced from the main root of each tree, and branches containing at least five root orders were selected. Surface soil was carefully brushed off, and a portion of each root sample was washed with deionized water and placed in FAA solution (9 ml 70% ethanol, 9 ml deionized water, 1 ml formaldehyde, and 1 ml acetic acid) for anatomical measurements. The remainder of the sample was stored on ice and transported to the lab for root morphological and chemical analyses^{24,31,49,56}.

In the laboratory, roots were cleaned with deionized water to isolate absorptive roots, specifically the 2-3 most distal root orders composed primarily of primary structures^{24,31,49,56}. Some absorptive roots were scanned using a root scanner (Epson Perfection V700 Photo scanner, Epson Company, Ltd, Japan), and root length, volume, and diameter (RD; mm) were calculated using WinRHIZO software (WinRhizo Pro 2007d software, Regent Instruments, Canada). The roots were then

dried (60°C for several days) and weighed to calculate specific root length (SRL; m/g) and tissue density (RTD; g/cm³). Another portion of the root sample was dried, ground, and analyzed for N concentration (Root N, %) using an elemental analyzer (IR-MS; Thermo Fisher Scientific, Waltham, MA, USA).

For each species, 15-20 first-order roots were selected from the FAA solution for anatomical analysis. The procedure involved dehydration with alcohol, clearing with xylene, embedding in paraffin, sectioning, and staining. Sections were photographed under a microscope (Olympus BX-63, Japan), and cortical thickness (CT; μm), vessel diameter (VD; μm), and vessel density (VDen; $\text{n } \mu\text{m}^{-2}$) were measured using ImageJ software (NIH Image, Bethesda, MD, USA)^{31,56,57}.

We collected soil samples from Xishuangbanna Tropical Rainforest Nature Reserve, Dinghushan National Nature Reserve, Shennongjia National Nature Reserve, Jigongshan National Nature Reserve, Changbaishan National Nature Reserve, and Huzhong National Nature Reserve in the field according to the method described in Hu et al. (2019)⁴⁶. We obtained data on soil fungal pathogens through sequencing. Fungal functional guilds for fungal OTUs were also assigned using FUNGuild according to Tedersoo et al. (2014)⁴⁵ and Hu et al. (2019)⁴⁶.

The Global Dataset Collection: We obtained global data on fine root traits (including arbuscular mycorrhizal fungi colonization rates) from the GRooT database⁴¹. We obtained seed mass data from the TRY database⁵⁸ and from Carmona et al. (2021)². We also collected root and seed data not included in these databases from other published studies, including Wright et al., 1999; Siqueira et al., 2001;

Zangaro et al., 2005; Laughlin et al., 2010; Carmona et al., 2021; Mueller et al., 2024^{2,26-28,59,60}.

Mycorrhizal types of plants in both measured and collected datasets were determined based on published studies and mycorrhizal classification databases⁶¹⁻⁶⁶. For species whose mycorrhizal type was not confirmed in our databases and literature, we determined it through field observations during sampling and anatomical analysis of root paraffin sections. For a few plant species with the mycorrhizal type uncertain (15 species), we inferred the mycorrhizal type, as always done in previous studies, based on the predominant mycorrhizal type within the genus^{61,67}. Woody plants were classified into arbuscular mycorrhizal (AM, 757 species), ectomycorrhizal (ECM, 140 species), ericoid mycorrhizal (ERM, 4 species), non-mycorrhizal (10 species), or unknown (46 species). AM + ECM plant species were assigned to EM category based on their ability to diverge from the ancestral stage of AM⁶⁶. Non-woody plants were classified into AM (266 species), ECM (2 species), or unknown (29 species); AM + NM plant species were treated as AM, because AM is favored by natural selection in dual mycorrhizal associations⁶³. For plant species with mycorrhizal status undetermined, they were not included in the analyses of the impacts of mycorrhizal types (AM vs. ECM) on plant trait relationships.

Data Analysis: We conducted type II linear regressions using standardized major axis (SMA) to explore the bivariate plant trait relationships. The trait data were log₁₀-transformed before the SMA analysis to achieve normality. We used the “sma” function from the “smart” package to test the difference of the SMA slopes between

plant functional groups.

We first corrected species names and family information using The Plant List (<http://www.theplantlist.org>). Then, a phylogenetic tree was constructed using the “U.PhyloMaker” package⁶⁸, following the APG IV phylogenetic system⁶⁹ for all analyses. Based on this phylogenetic tree, we calculated Blomberg's K using the “Picante” package⁷⁰ to evaluate the phylogenetic influence on each trait; generally, a higher Blomberg's K indicates a greater phylogenetic influence⁷⁰. Next, we performed trait correlation analysis excluding phylogenetic effects using the “pgls” function in the “caper” package⁷¹ (Extended Data Fig. 6).

We conducted PCA using the “factoextra” and “funspace” packages to determine the major dimensions of trait variation among organs. Plant trait data were log₁₀-transformed and standardized before the PCA to meet the requirement of normal distribution and variance homogeneity, respectively. To visualize the probability of a given trait appearing in PCA space, we constructed two-dimensional kernel density plots with contours using the “funspace” package⁷² and added contour lines. The color gradient and contours correspond to the 0.25, 0.5, and 0.99 quantiles of the trait space, highlighting areas with the corresponding probability of trait occurrence. We also assess the evolutionary pattern of absorptive root diameter and seed mass using our field-measured data. Family-level values of root diameter and seed mass were assessed using “phytools” package and “anc.ML” function. All statistical analyses and data visualizations were performed using R (v.4.3.2; R Core Team 2023)⁷³.

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Data Availability:

The raw data in this study are available in Figshare (<https://doi.org/10.6084/m9.figshare.28300658>). Literature data were extracted from Global Root Trait database (<https://groot-database.github.io/GRooT/>)⁴⁰.

Code Availability:

The code utilized for this study is publicly available and is hosted in Figshare (<https://doi.org/10.6084/m9.figshare.28300658>).

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Author Contributions Statement

Q.Y. and D.K. conceived the idea. Q.Y. and B.G. completed the creation of figures. Q.Y., D.K., M.L. and P.B.R. conducted the statistical analyses. Q.Y., D.K., J.W., G.L. H.W. and Y.J. discussed and contributed to the final framework of this study. Q.Y and D.K. wrote the first draft of the manuscript with significant help from P.K., R.D.B., J.H.C.C., S.D., I.J.W. and J.A.H. Q.Y., B.G., M.L., Y.L., P.K., P.B.R., R.D.B., J.H.C.C., N.J.B.K., S.D., I.J.W., N.H., J.A.H., Y.P., Q.H., Z.L., Z.W., W.Y., J.D., Z.Y., H.W., C.P.C., O.V.B., D.L., J.C., H.Z., Y.Z., W.R., Y.Z., X.Y., G.F., J.W., G.L. and D.K. contributed to manuscript completion and revision.

Competing Interests Statement

Authors declare that they have no competing interests.