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Linking fine root lifespan to root chemical and morphological traits—A global analysis

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Fine root lifespan is a critical trait associated with contrasting root strategies of resource acquisition and protection. Yet, its position within the multidimensional "root economics space" synthesizing global root economics strategies is largely uncertain, and it is rarely represented in frameworks integrating plant trait variations. Here, we compiled the most comprehensive dataset of absorptive median root lifespan (MRL) data including 98 observations from 79 woody species using (mini-)rhizotrons across 40 sites and linked MRL to other plant traits to address questions of the regulators of MRL at large spatial scales. We demonstrate that MRL not only decreases with plant investment in root nitrogen (associated with more metabolically active tissues) but also increases with construction of larger diameter roots which is often associated with greater plant reliance on mycorrhizal symbionts. Although theories linking organ structure and function suggest that root traits should play a role in modulating MRL, we found no correlation between root traits associated with structural defense (root tissue density and specific root length) and MRL. Moreover, fine root and leaf lifespan were globally unrelated, except among evergreen species, suggesting contrasting evolutionary selection between leaves and roots facing contrasting environmental influences above vs. belowground. At large geographic scales, MRL was typically longer at sites with lower mean annual temperature and higher mean annual precipitation. Overall, this synthesis uncovered several key ecophysiological covariates and environmental drivers of MRL, highlighting broad avenues for accurate parametrization of global biogeochemical models and the understanding of ecosystem response to global climate change.

absorptive root | fine root lifespan | leaf lifespan | root economics spectrum | root traits

Significance

Fine root turnover is an essential process controlling the uptake, conservation, and loss of nutrients, water, and carbon between plants and soils. As such, it is at the core of the recent but already well-known and hotly debated root economics space (RES) theory. Here, gathering an unprecedented dataset, we suggest that the current interpretation of the global RES axes needs to be partly reconsidered to account for the potential roles of the two axes in defining the fast–slow continuum in root strategies. We also demonstrate that there are major differences between plant above and belowground strategies for the longevity of leaf vs. root organs. Overall, our work provides a synthesis of root lifespan and its environmental and plant-related drivers.

Globally, fine root growth contributes to over 20% of terrestrial net primary productivity (1), yet the factors that control their turnover and persistence at broad spatial scales remain unresolved. Variation in fine root lifespan represents the conservation and allocation of plant carbon investments to support plant nutrient uptake, associations with soil microorganisms, and competition for soil resources and space (2–4). Moreover, fine root turnover represents a large input of C to soil and a primary driver of soil C formation (5). Unlike measurements of leaf lifespan (LL), direct measurements of fine root lifespan, such as assessments from minirhizotrons and rhizotrons, are sparse. The difficult and time-consuming nature of belowground observations has resulted in limited numbers of observations of fine root lifespan, and as such, the relationships of fine root lifespan with environmental factors and other plant traits are still poorly known (6).

Belowground, fine root traits are organized around several synthetic axes of variation that define plant economics strategies (the "root economics space", RES) (7, 8). First, a trade-off between high metabolism (represented by root N concentration; RN) and high investment in structural compounds (represented by root tissue density; RTD) is assumed to represent a gradient from roots with short lifespans and fast turnover but high rates of return on investment to roots with long lifespans and slower turnover but slower return on investment. However, this assumption only rests on limited data. Cross-species comparisons at local scales have revealed several traits that may relate to fine root lifespan. McCormack et al. (4) and Tjoelker et al. (9) provided evidence that root diameter (RD), specific root length (SRL), RN, and RTD may be good proxies for fine root lifespan. However, while other studies were generally consistent (10), such relationships vary across site locations and species sets, indicating a need for larger-scale assessments.

In addition to functional traits of fine roots identified at the local scale, there are likely additional drivers of fine root lifespan that may be increasingly important at the global scale including plant phylogenetic history, plant functional type, plant mycorrhizal type, as well as biogeography and climatic drivers. Plant phylogeny may affect fine root lifespan given the evolutionarily conserved nature of many root traits (3) and

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their role in shaping species distributions and diversity (11). For example, plant traits with less phylogenetic constraint may have a high rate of evolution (12) and thus be evolutionarily labile, which would, in turn, promote species diversity (13, 14). Likewise, there are differences in the life history strategies associated with different leaf habits, which may be associated with differences in fine root lifespan (deciduous vs. evergreen) (15). Different mycorrhizal types [ectomycorrhizal vs. arbuscular mycorrhizal (EM vs. AM)] (16) may also affect fine root lifespan by their impacts on root and plant nutrition and by their impacts on protection against herbivores and pathogens (17, 18). However, previous studies have not reported consistent differences in fine root lifespan being associated with mycorrhizal type (4, 19). Importantly, patterns of fine root dynamics across species have been linked to climatic variations. Higher temperature typically relates to higher root metabolic activity, greater free radical stress, and faster root aging and consequently shorter root lifespan (20). Still, these changes are often complex and species specific. Furthermore, severe drought often reduces the production of fine roots, and also alters fine root lifespan, but the responses are species specific and may depend on whether roots are grown in isolation or in competition with other plant species (21).

Not all fine roots have equivalent form and function, and recent efforts to understand root trait variation (including variation in fine root lifespan) have sought to categorize roots in ecologically meaningful ways. Traditionally, fine roots were defined based on diameter cutoffs (e.g., ≤2 mm) and are often considered as a homogeneous pool with mostly a resource acquisition function. However, comparisons of fine root traits, both within and across species, show that fine root orders are not homogenous (22). Plant roots have complex branching structures, that respond differently to soil resource changes (23) and with only the most distal roots (e.g., first- to third-order roots), being primarily engaged in resource acquisition (24). Several reports have now highlighted striking differences in fine root lifespan within the root branching hierarchy following the order-based classification (1). Xia et al. (25) found that an order increase in the fine roots of *Fraxinus mandshurica* was related to a 30.6% decrease in the mortality risk of fine roots. Gu et al. (26) found that the first two root orders of *Pinus sylvestris var. mongolica* have a 1.4-fold difference in root lifespan. As such, when comparing lifespan across fine roots of different species or environments, it is important to tailor the observations to a common pool of functionally similar roots (1).

Leaves and absorptive roots share the major role of acquiring resources for plant growth, which suggests that their structural and chemical defenses, as well as their metabolic activities might be coordinated (3, 27, 28). This could further translate into coordinated leaf and fine root lifespan (29), as lifespan is likely to be under the influence of similar traits above and belowground and lifespan is an important component of plant economics.

To understand the drivers of fine root lifespan at a large scale, we compiled the largest dataset of median fine root lifespan (MRL) to date using 98 observations on absorptive roots only, covering 79 woody species across 40 studies, to examine both abiotic [e.g., mean annual temperature (MAT) and precipitation] and biotic (root and plant traits, plant functional type, and mycorrhizal types) drivers of MRL. These 79 woody species included 48 genera from 28 families. In contrast to previous syntheses (7), we focused on studies that either explicitly or implicitly (e.g., minirhizotrons) focused on the absorptive fine root pool which represents the most metabolically active, resource acquisitive, and shortest-lived portion of the branched root system (30).

Our specific hypotheses were that:

(1) Fine root lifespan aligns with the acquisition-conservation axis of the RES;
(2) Plant functional types and environmental parameters influence fine root lifespan across sites;
(3) Fine root lifespan and LL are coordinated.

Results

High Variability of Fine Root Lifespan among Plant Species Globally. Across all 98 observations from 79 woody plant species, MRL ranged from 0.07 y to 1.8 y (27 d to 656 d, respectively), showing a 24-fold difference (*SI Appendix*, Fig. S1). We found large interspecific variation in MRL, including differences in species with different leaf habits (deciduous vs. evergreen), mycorrhizal types (AM vs. EM), and plant group (angiosperms vs. gymnosperms), but not with potential growth rate (fast vs. moderate vs. slow) (Fig. 1). Deciduous species (158 d) showed significantly shorter MRL than evergreen species (264 d) ($P < 0.01$, Fig. 1*A*). AM species

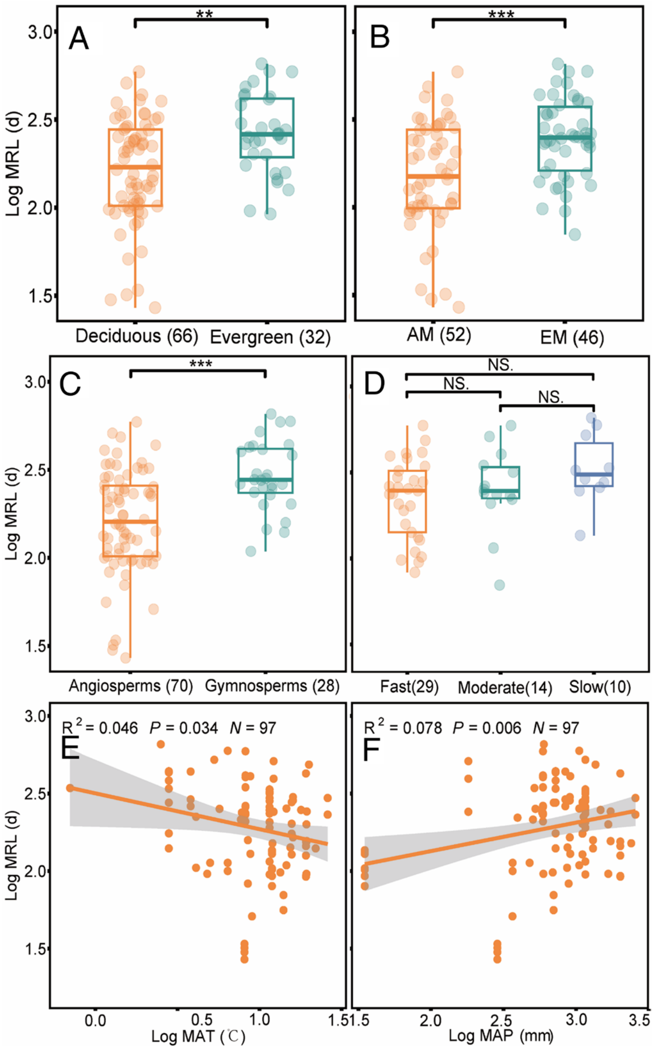

Fig. 1. MRL distribution based on (*A*) leaf habits, (*B*) mycorrhizal types (*C*) evolutionary group, and (*D*) plant growth rate, as well as the environmental drivers (*E*) MAT and (*F*) mean annual precipitation (MAP). AM: arbuscular mycorrhizal, EM: ectomycorrhizal. **$P < 0.01$, ***$P < 0.001$, NS: nonstatistically significant differences. The number within parentheses is the number of species. *N*: The number of independent data points.

(150 d) exhibited significantly shorter MRL than EM species (245 d) ($P < 0.001$, Fig. 1*B*). Gymnosperm species (321 d) exhibited significantly longer MRL than angiosperm species (197 d) ($P < 0.001$, Fig. 1*C*). Conversely, MRL was not significantly different between fast-, moderate-, and slow-growing species groupings but showed a trend toward slower-growing species having longer MRL (253, 286, and 364 d, respectively, Fig. 1*D*).

Different plant groups also differed in many of their functional traits which may have contributed to differences in MRL. For example, deciduous species displayed longer average SRL and RN and smaller RD and root carbon-to-nitrogen ratio (RCN) compared with evergreen species (*SI Appendix*, Fig. S2 *A–D*), although RTD was not significantly different between evergreen and deciduous species (*SI Appendix*, Fig. S2*E*). Fine roots of EM species had higher average RCN and longer SRL than AM species (*SI Appendix*, Fig. S2 *F* and *G*), but RD, RN, and RTD were not significantly different between EM and AM species (*SI Appendix*, Fig. S2 *H–J*). Angiosperms species displayed smaller RD and RCN and longer SRL compared with gymnosperms species (*SI Appendix*, Fig. S2 *K–M*). RN and RTD were not significantly different between angiosperms and gymnosperms species (*SI Appendix*, Fig. S2 *N–O*).

Across all species (*SI Appendix*, Fig. S3), there was a significant phylogenetic signal for MRL, as indicated by Blomberg's K statistic (*SI Appendix*, Table S1). This signal was lower than that of LL. All other traits, RD, RNC, RN, and SRL also displayed significant phylogenetic signals, except RTD.

Relationships of Fine Root Lifespan with Other Root Traits. Our principal component analysis (PCA) results were consistent with the classical representation of the multidimensional root economics spectrum along two major axes of variation (Fig. 2). The first, second, third, and fourth PC axes accounted for 39.54%, 27.19%, 20.65%, and 11% of the total variation, respectively (*SI Appendix*, Table S2). RD and SRL loaded heavily on opposite ends of the first axis with RD loading in the opposite direction of SRL (R = −0.66, $P < 0.001$, *SI Appendix*, Table S2 and Fig. S4). RN and RTD loaded heavily on opposite ends of the second axis with RN loading in the opposite direction of RTD (R = −0.28, $P < 0.05$, *SI Appendix*, Table S2 and Fig. S4). MRL loaded both PC1 and PC2 (*SI Appendix*, Table S2). SRL and RTD also loaded heavily on the third axis (*SI Appendix*, Table S2).

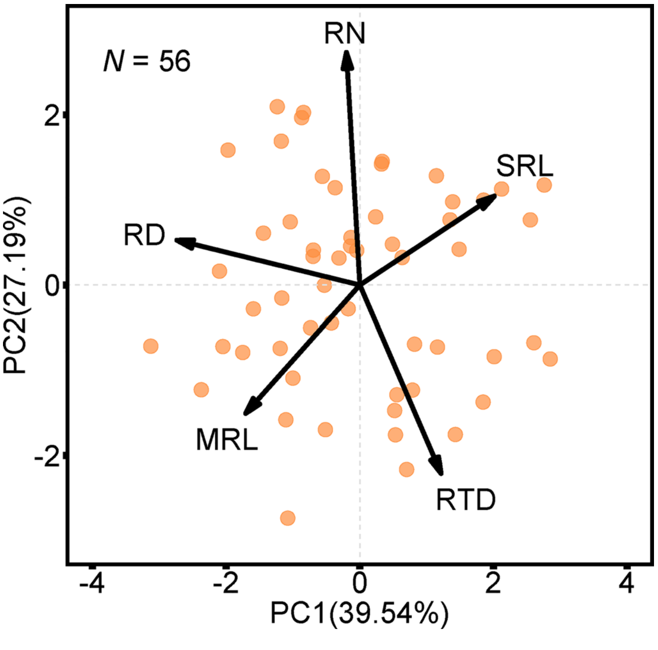

Fig. 2. PCA of key root traits representative of plant economic strategy, including MRL. RD: root diameter; RN: root N concentration; RTD: root tissue density; SRL: specific root length. Observations are species averages. *N*: The number of independent data points.

Across all species MRL increased linearly with RD (R2 = 0.435, $P < 0.001$, Fig. 3*A*) and RCN (R2 = 0.094, $P = 0.01$, Fig. 3*B*) and decreased linearly with RN (R2 = 0.105, $P = 0.007$, Fig. 3*C*). However, there was no significant correlation between MRL and RTD (R2 = 0, $P = 0.927$, Fig. 3*D*) and only a marginally significant correlation with SRL (R2 = 0.049, $P = 0.056$, Fig. 3*E*).

Fine Root Traits and Climate Variables as Predictors of Fine Root Lifespan. Comparing MRL across climate variables, we showed that MRL decreased with MAT (R2 = 0.046, $P = 0.034$, Fig. 1*E*) and increased with MAP (meanannual precipitation) (R2 = 0.078, $P = 0.006$, Fig. 1*F*).

Next, we selected RD, RN, RCN, MAT, and MAP as potential candidate variables to predict MRL through "dredge" analysis (31). The model averaging method was used to obtain the best overall model for predicting MRL (R2 = 0.47; *SI Appendix*, Fig. S5 and Table S3). In this final model, MAT and RN each had negative effects on MRL while RD and MAP had a positive effect.

Correlation of Fine Root Lifespan with LL. Across all species, MRL was not significantly correlated with LL ($P = 0.065$, Fig. 4). However, MRL and LL of evergreen species were significantly and positively correlated (R2 = 0.384, $P = 0.01$, Fig. 4*A*), but the MRL and LL of deciduous species were not correlated ($P = 0.37$, Fig. 4*A*). A lack of correlation between MRL and LL was also found when considering separately each dominant mycorrhizal type (AM species, $P = 0.55$; EM species, $P = 0.1$, Fig. 4*B*).

Discussion

Root Lifespan–Trait Relationships in Relation to the Multidimensional RES. The RES synthesizes global species fine-root trait variation along two main axes: a belowground collaboration axis (reflecting a tradeoff between species with thick, highly mycorrhizal roots, and species with long SRL that are less reliant on mycorrhizal fungi for resource uptake) and an independent conservation axis (associated with a tradeoff between RTD prolonging MRL and RN) (7). Our PCA results align well with this multidimensional representation of the RES (Fig. 2). The position of MRL within this RES partly supports our hypothesis that MRL relates to the acquisition-conservation axis. However, MRL was directly only related to RN but not to RTD (Fig. 3 *C* and *D*), suggesting that the theoretical role of RTD in root protection by providing adequate structural and/or chemical protection against soil-borne pathogens (18) is only weakly related to observed MRL in soil, although several local scale studies have noted a significant relationship with RTD (10, 32, 33). Nonetheless, as expected, more metabolically active roots with higher RN (34) showed shorter lifespan, supporting the hypothesized trade-off between living fast and living long (3). In addition, the correlation between MRL and the RCN may not only be related to changes in RN but possibly also to a higher concentration of complex structural compounds such as lignin and suberin (35), effectively reducing their palatability to soil herbivores and increasing their resistance to soil pathogens.

In contrast to our expectation, root lifespan was also related to the collaboration axis of the RES, with MRL positively relating to RD, as well as negatively to SRL. The greater C investment per unit root length in roots with larger RD may be coupled with longer MRL to ensure a favorable nutrient and water return on

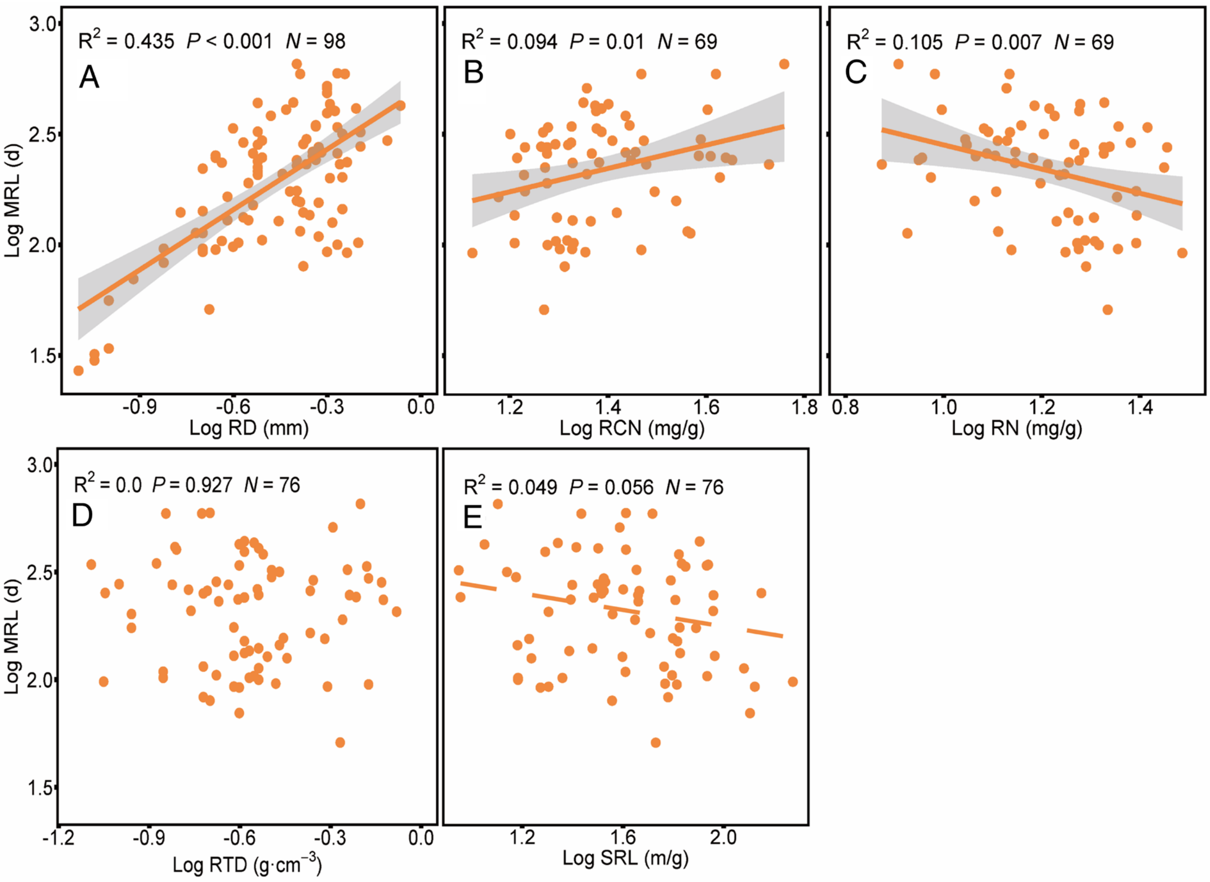

Fig. 3. Relationships between MRL and other root traits (*A–E*). RD: root diameter; RCN: root C: N ratios; RN: root N concentration; RTD: root tissue density; SRL: specific root length. *N*: The number of independent data points.

the higher C investment compared with roots of smaller RD (4). Thicker roots with larger cortex space for hosting fungi may also harbor more intensive association with mycorrhizal fungi, which can contribute to plant defense against pathogens and root survival in case of drought owing to better connection to soil residual water (36–38). In light of these results, we suggest that current interpretation of the global RES axes may need to be at least partly reconsidered to include the potential roles of both axes in defining the slow-fast continuum in root strategies.

Influence of Plant Functional Types and the Environment on Fine Root Lifespan. Our results indicate that MRL was significantly longer in evergreen species than in deciduous species (Fig. 1*A*). This may be due to historical differences in the respective growing environments of these two functional groups (2). Globally, evergreen species tend to inhabit less fertile and colder environments than deciduous species (2). The longer MRL of evergreen species reflects a "slower" ecological strategy that promotes carbon retention in fine root tissues, an ecological response to resource scarcity (3). Evergreen species also display thicker RD (on average, *SI Appendix*, Fig. S2*A*), representing higher carbon and nutrient investments, that may be compensated through longer period of resource capture (4, 29). In contrast, the shorter MRL of deciduous species is consistent with a "faster" soil foraging strategy (long SRL, *SI Appendix*, Fig. S2*C*) with higher metabolic rate (high RN, *SI Appendix*, Fig. S2*C*) to ensure rapid access to more abundant resources (3).

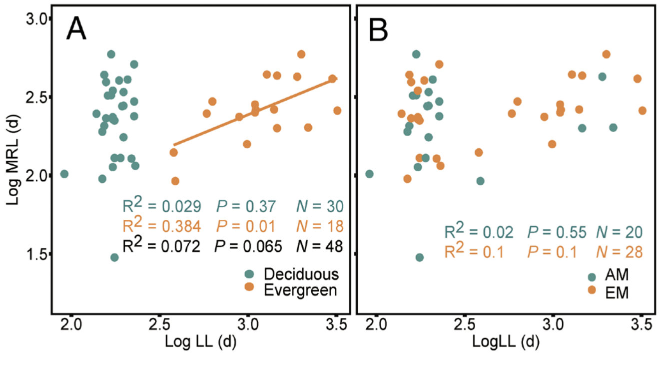

Fig. 4. Relationships between MRL and LL among evergreen or deciduous (*A*) and AM or EM forming (*B*) species. Statistics are reported for evergreen or deciduous; AM or EM; and across all species (black font) with regression lines displayed when significant. *N*: The number of independent data points.

We found that EM species exhibited longer MRL than AM species (Fig. 1*B*), possibly linked to their higher concentration of complex structural compounds than AM species (high RCN, *SI Appendix*, Fig. S2*F*, 18). Indeed, EM (angiosperm) species induce a physical and chemical barrier to prevent fungal penetration into the inner cortex via thickening of the exodermis walls that likely plays a protective role against pathogens (39). The EM fungal sheath production and the increase in fungal melanin content in EM root segments (40) may further protect roots against physical hazards and pathogen attack (41).

We found that MAT and MAP both influenced MRL. Warming significantly shortened MRL at a broad scale (Fig. 1*E*). The decrease in MRL at higher MAT may be the result of increased metabolic activity, buildup of free radicals, and faster root aging (20). For example, Jiang et al. (42) found that warming of 4 °C remarkably shortened MRL of Chinese fir in a field-scale warming experiment and that part of this negative effect may have been caused by an inadequate C supply to roots. Burton et al. (43) suggested that plasticity in MRL in northern hardwood forests may be regulated by carbohydrate supply from the shoot, with a reduced carbohydrate supply resulting in shorter MRL. Roots from plants growing at lower MAT had longer MRL, probably because fine roots tend to have lower respiration rates (44) and lower level of root activity at lower MAT. Variation in the response of MRL to changes in MAP likely depends on whether MAP strongly limits root growth. We found that an increase in MAP increased MRL (Fig. 1*F*). Higher MAP has also been associated with increased MRL in some tropical systems as MRL tends to increase during wet seasons and decrease during dry periods (45). However, excess MAP may reduce MRL as the high frequency of anoxic conditions in water-rich soil increases root stress and pressures from external factors, including soil pathogens and saprophytic fungi (20).

Correlation of Fine Root Lifespan with LL. In partial support for our third hypothesis, we showed that LL and MRL were positively correlated in evergreen species (Fig. 4*A*). Evergreen species often grow in environments with low soil nutrient or water availabilities (46). where increased LL and MRL prevent additional nutrient losses associated to root and leaf shedding (47). Coordinated ecological strategies above and belowground are thought to be critical for balancing the nutrient and carbon resource acquisition and losses and achieving optimal plant stoichiometry for cost-efficient growth and defense mechanisms (3, 27, 28). However, we were unable to demonstrate a correlation between MRL and LL among deciduous woody plants (Fig. 4*A*). This absence of clear trend is consistent with the few experiments comparing MRL and LL (48, 49). The only study to find a correlation between LL and MRL focused on grasses and savanna species (9), suggesting fundamental differences in the LL or MRL of herbaceous vs. woody species, or between different plant evolutionary lineages. Overall, the different environmental constraints faced by leaves and roots (50) may lead to different selection pressures for MRL and LL.

Interestingly, there was a distinctly weaker phylogenetic signal for MRL than that observed for LL (*SI Appendix*, Table S1), suggesting that MRL has undergone more change with evolution (12, 51). The emergence of colder and drier climate during the mid to late Cretaceous has been hypothesized as a cause of adaptation and root trait diversity in angiosperms (11, 52, 53). Angiosperm lineages may have the ability to evolve diverse types of roots quickly in various habitats that allow them to deal with changing environments. This further suggests that MRL and LL evolution may have been largely independent for angiosperm species, potentially leading to a lack of correlation between MRL and LL in this group.

The absence a of general trend between MRL and LL across all deciduous and evergreen species was largely due to a much lower difference between evergreen and deciduous species MRL (Fig. 4*A*) than observed for LL. The major difference in LL between deciduous and evergreen species is primarily driven by their strategies to cope with changing environmental conditions and optimize resource use for photosynthesis. Studies have shown that evergreen species have a longer LL than deciduous species owing to more conservative traits (i.e., thicker, denser, and with lower specific leaf areas) (54–56) implying more investment in structural integrity and/or defense against disturbances, especially in the context of resource constraint (55). Although LL is much more constrained in deciduous trees than in evergreens, in more productive locations, deciduous species have quick access to readily available resources (57), resulting in particularly short LL. In contrast to this large variation between deciduous and evergreen LL, the difference in MRL between the two types of plants is much smaller. As expected, MRL of evergreen species was significantly longer than that of deciduous species, but the magnitude of the difference was not comparable with that for LL. One potential explanation for this might be the inability of fine roots to reach very long lifespans in most soil conditions experienced globally. Most soils harbor a high diversity of microbial herbivores and pathogens that may benefit from the more constant abiotic conditions of the soil medium compared to the air. Acquisitive roots might more readily suffer damage to their cortex compared to their leaves, which may have less favorable conditions for microbial development. Moreover, turnover of acquisitive roots may be an adaptation for exchange of resources with the soil via interactions with soil microbes (58). More studies in natural settings are needed to understand the influence of soil properties, such as nutrient availability, soil texture, and density, on fine root lifespans.

Conclusions. We analyzed global data on the fine root lifespan of woody species and explored its key drivers. We found that mycorrhizal type, leaf habit, and evolutionary group significantly influence fine root lifespan. Further, higher temperatures and lower precipitation are linked to a shortened fine root lifespan. Additionally, we were able to account for broad variation in fine root lifespan in our analysis and found that woody plant traits such as RD, root nitrogen, and root C:N ratio can help to understand part of the variability in fine root lifespan. Most importantly, our results shed light on the ecological interpretation of the recent and widely used RES proposed by Bergmann et al. (7) describing global diversity in root economics strategies. We demonstrate that root lifespan not only decreases with plant investment in root nitrogen but also increases with construction of larger diameter roots. Our findings also highlight the globally unrelated relationship between fine root and LL, emphasizing intrinsic differences in evolutionary adaptations between gymnosperm and angiosperms, and the relative independence of aboveground and belowground plant strategies with respect to lifespan.

Materials and Methods

Data Collection and Compilation. To build the largest global dataset of woody species fine root lifespan to date, we conducted an exhaustive literature search in the Web of Science (http://apps.webofknowledge.com) and China National Knowledge Infrastructure (http://www.cnki.net). Various keyword combinations were used for the search, including (root OR fine root) AND (lifespan OR life span OR longevity) AND (minirhizotron OR rhizotron). We then screened these articles according to the criteria: 1) the study included MRL and other root traits measurements (RD, RN, RCN, SRL, and RTD) on perennial woody plants (trees and shrub), and the relevant data could be extracted directly from the text, tables, figures, supplementary materials, or be freely available in dataset repositories; 2) reported MRL should be estimated on absorptive roots (order 1 to 3 roots); and 3) MRL was measured using the minirhizotron or rhizotron method. Noncompliant data were not collected. Missing data for the morphological and chemical fine root traits (RD, RN, RCN, SRL, and RTD) were completed using the FRED database (https://roots.ornl.gov) (59) and taking global species averages. Based on any two known data from RTD, SRL, and RD, another unknown data can be calculated from the formula $RD^2 = 4/(\pi \cdot RTD \cdot SRL)$. When multiple publications included the same data from a single study, the data were recorded only once. When the study included experiments at multiple locations, we considered them as distinct observations. The study locations are shown in *SI Appendix*, Fig. S6.

For all species, scientific names were cross-referenced with the Plants of the World Online database (https://powo.science.kew.org). We categorized each species into distinct leaf habits: deciduous and evergreen based on information from the TRY database (https://www.try-db.org). LL was also collected from TRY database, taking the species averages. We collected 48 observations of paired MRL and LL data (a subset of the original 98, but only including the ones that also reported LL). Woody species were categorized as AM and EM species (16) according to information in the FRED database. We categorized the potential growth rate of 53 species as fast, moderate, and slow based on available data on "growth rate" from the USDA plant database (https://plants.usda.gov).

Statistical Analyses. MRL and all other plant traits were log-transformed to ensure homogeneity of variance. ANOVA was used to compare variation in MRL and other root traits between leaf habit (deciduous vs. evergreen), mycorrhizal types (AM vs. EM), potential growth rate (fast vs. moderate vs. slow), and evolutionary group (angiosperms vs. gymnosperms). Since some of our trait data did not conform to the assumption of normality, the non-parametric correlation measure (Spearman's rank correlation analysis) was performed to analyze the linear correlations between MRL and plant traits using the corrplot R package. To estimate whether the combination of environmental and fine root traits can further improve our understanding of MRL, we determined the best model for predicting MRL. This was done by selecting candidate variables and using dredge function in the R package Multi-Model Inference to select the best-combined model for the dataset based on Akaike's Information Criterion (AIC) using the 69 observations for which all five additional traits were available (RD, RN, RCN, MAT, and MAP). When the best model and second best model differed by a the delta AIC < 4, we used a model averaging method.

Because MRL, RN, RCN, SRL, RD, and RTD were not measured on all species, to visualize the position of MRL within the root economics spectrum, we subset our full 98 observations covering 79 woody species to only include species with all five root traits (MRL, RN, SRL, RD, and RTD), which resulted in 56 species-level data for our PCA. To evaluate the phylogenetic influence on plant traits and their correlations, we tested Blomberg's K using the phytools R package. A value close to zero for Blomberg's K indicates phylogenetic independence, while a value close to 1 indicates increased similarity between closely related taxa (60). The statistical analyses were conducted in R 4.2.3 software.

Data, Materials, and Software Availability. All study data are included in the article and/or *SI Appendix*.

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