Interspecific differences in root foraging precision cannot be directly inferred from species' mycorrhizal status or fine root economics.

Abstract

Nutrient acquisition in plants can be represented by a suite of intercorrelated root traits such as root diameter, nitrogen content, root tissue density, and specific root length. However, it is unclear how a plant's ability to precisely forage for nutrients in a heterogeneous soil environment (i.e., the precision of placing roots into nutrient-rich areas) relates to these traits. Mycorrhizal symbiosis also affects the relationship between the fine root traits and root foraging precision because fungal hyphae may be used for foraging instead of roots. Hypotheses matching high root foraging precision with low mycorrhizal colonization or "fast" acquisitive strategies of plants have been raised based either on data from tree species or a limited number of herbaceous species.

To test these hypotheses, we compiled data quantifying the experimentally measured degree to which root biomass responded to patchy substrate nutrient concentrations (i.e., root foraging precision) for 123 herbaceous grassland species using a partial meta-analysis. We tested root foraging precision relationship with root traits involved in nutrient acquisition and mycorrhizal symbiosis (root diameter, specific root length, root tissue density, root tissue nitrogen content, and mycorrhizal colonization). The root foraging precision data came from four different pot experiments, and the trait data were extracted from publicly available trait databases. We used a phylogenetically informed approach in order to detect the degree of conservation of the relationships.

We found that root foraging precision was not significantly correlated with other fine root traits and mycorrhizal colonization. Thus, it appears unrelated to the main dimensions of the nutrient acquisition space of herbaceous species, namely acquisitive-conservative strategy and outsourcing of acquisition to the fungi. Also, we found only a very weak phylogenetic signal in root foraging precision of 123 species. Our results suggest that root foraging precision constitutes another distinct, evolutionarily independent dimension in herbaceous species' trait space.

Keywords

Mycorrhizal symbiosis, root foraging precision, nutrient patches, fine root traits, root economics, nutrient acquisition

Introduction

The distribution of nutrients in the soil is very heterogeneous at local spatial scales relevant to plant roots (Jackson and Caldwell 1993, Farley and Fitter 1999, Kreuzeder et al. 2018), and many plants respond to this heterogeneity by the preferential proliferation of roots into nutrient-rich patches (Drew 1975, Hutchings and de Kroon 1994). The proliferation mechanisms are based mainly on root biomass allocation and morphological changes of roots (Fransen et al. 1999, Hodge 2004, Giehl and von Wiren 2014). Such an allocation of resources into the proliferating roots helps the plant ensure higher nutrient acquisition (Hutchings and de Kroon 1994), which could be advantageous in plant competition for heterogeneous nutrient sources (Hodge et al. 1999, Wang et al. 2018). The ability to concentrate roots into favorable patches—root foraging precision—differs among species (Johnson and Biondini 2001, Grime and Mackey 2002, Cahill and McNickle 2011, Weiser et al. 2016). The differences in root foraging precision have been thought to be connected to plant growth rates and acquisitive strategies (Campbell et al. 1991, Aanderud et al. 2003, Kembel et al. 2008), or to the ability to outsource nutrients acquisition from roots to fungal hyphae by forming mycorrhizae (Cahill and McNickle 2011, Chen et al. 2018, Bergmann et al. 2020). The relationship of root foraging precision, plant growth and scale of foraging has been widely studied previously in the context of scale-precision trade-off of root foraging (Campbell et al. 1991, Aanderud et al. 2003, Rajaniemi and Reynolds 2004, Kembel et al. 2008, Reyes and Aguiar 2017). However, there being only a few comparative studies linking root traits or mycorrhizae to root foraging precision (Grime et al. 1997, Kembel et al. 2008, Eissenstat et al. 2015, Liu et al. 2015, Chen et al. 2016, Cheng et al. 2016), robust empirical testing of these linkages is lacking, especially in herbaceous species.

Previous studies suggest that the foraging strategy of plants is influenced by root diameter and mycorrhizal colonization. Species with thin roots are thought to forage more precisely with their roots than species with thicker roots, which instead rely more heavily on mycorrhizal symbiosis to forage for nutrients (Eissenstat et al. 2015, Liu et al. 2015, Chen et al. 2016, Cheng et al. 2016). This trade-off in root versus fungi hyphal foraging was observed mainly between arbuscular mycorrhizal tree species (precise root foragers with thin roots) and ectomycorrhizal tree species (worse root foragers with thick roots; Chen etal. 2018); however, the

relationship in herbaceous species is much less explored. Compared to the roots of the woody plants, roots of the herbaceous plants occupy different parts of the trait's spectra, and the relationships among traits are different. For example, herbaceous species have thinner roots than woody plants (with some exceptions) and rely less on mycorrhizal symbiosis with fungi (Ma et al. 2018).

Recently, Bergmann et al. (2020) proposed that root diameter and specific root length (SRL) may co-determine the "collaboration gradient", which describes the trade-off in mycorrhizal reliance that likely relates to root form. According to this, plant species with low root foraging precision would probably fit into the "outsourcing" part of the spectrum, defined by high root diameters, low specific root lengths (SRL), and high mycorrhizal colonization. But Bergmann et al. (2020) did not separate herbaceous and woody species among biomes in their study (trade-offs are shown for herbaceous and woody species together in separate biomes, or only for herbaceous species but across all biomes). Thus, it is not clear whether this trade-off would appear in the herbaceous species from one biome, specifically, grassland species. Although a negative correlation of root diameter and SRL can be found in herbaceous and woody species, the strength of this relationship differs between the groups (Ma et al. 2018). While changes in root diameter of woody species have only a limited effect on their SRL, even small changes in root diameter significantly impacted SRL in herbaceous species.

However, no major link between root foraging precision and SRL was found in 16 herbaceous grassland species (Kembel et al. 2008). Instead, they found root foraging precision to be positively associated with high root nitrogen concentration (N content) and those traits that hallmark acquisitive, "fast" plant life strategies (e.g., high respiration rates, short-lived tissues, high relative growth rates) in contrast to "slow" conservative ones (e.g., leaf and root longevity, leaf and root C:N ratio; Diaz et al. 2004, Reich 2014). This agrees with the theoretical prediction that precise root foraging should occur in species with low root tissue density (RTD) and high root N content (Chen et al. 2018). However, Kembel et al. (2008) found only a weak positive association between root foraging precision and specific leaf area (SLA), although SLA is usually strongly associated with the fast-slow continuum (Reich 2014, Weemstra et al. 2016).

To summarize, some influence of various root traits and mycorrhizal colonization on root foraging precision have been suggested, but the empirical evidence is mixed and primarily based upon either a few herbaceous species (Kembel et al. 2008) or woody plants only (Chen et al. 2018). To shed light on the determinants of root foraging precision, we assembled root foraging precision data for 123 herbaceous grassland species. We combine these with publicly available mycorrhizal colonization data (mycorrhizal status of plants – obligatory, facultative, or none; and intensity of mycorrhizal colonization) and root and shoot trait data (root diameter, N content, RTD, SRL, and SLA).

Because species share the evolutionary history of their traits (Felsenstein 1985), our study accounts for the phylogenetic relatedness of species to reveal its potential effects on the examined traits. For example, root diameter and mycorrhizal colonization and their interaction are strongly phylogenetically conserved (Ma et al. 2018). Other traits, namely N content, SRL, SLA, and RTD, show weaker phylogenetic conservation (Kembel and Cahill 2011, Kong et al. 2014, Valverde-Barrantes et al. 2017). Thus, the interaction of these traits with root foraging precision could be phylogenetically constrained. Moreover, the knowledge of phylogenetic conservation of root foraging precision is scarce and mixed, with no relationship found (Weiser et al. 2016) or with the signal of conservation in grasses (Kembel and Cahill 2005).

Specifically, this study's objectives were to test the following hypotheses:

1) In terms of collaboration trade-off, high root foraging precision for nutrients is more likely to occur in species with lower affinities for mycorrhizal colonization (or facultative or no mycorrhizal colonization) and thin roots (Chen et al. 2018), possibly in combination with high SRL (Bergmann et al. 2020).

2) Root foraging precision of nutrients is higher among species with acquisitive, "fast" plant life strategies (Kembel et al. 2008), which could be defined by high root tissue nitrogen content, low root tissue density, and possibly high SLA (Reich 2014, Weemstra et al. 2016).

3) Root foraging precision is not a phylogenetically conserved trait (Weiser et al. 2016), although lower root foraging precision has been noted in grass species previously (Kembel and Cahill 2005).

Materials and Methods

Foraging precision

We collected data about the root foraging potential of 123 herbaceous species from four different studies conducted between 2010 and 2017 (Belter 2014, Keser et al. 2014, 2015, Weiser et al. (2016 + unpublished data)). These studies represent a set of similar experiments that obtained the data necessary to calculate root foraging precision; however, we did not use a formal meta-analytic approach and asked individual authors for the data because the available datasets were few. In all studies, the individual plants were grown both in heterogeneous and homogeneous soil conditions, with the total nutrient supply not varying among treatments within a study. Although there were these commonalities between the studies, there were several methodological differences more fully described in the Supporting Information (Table S1), but also briefly highlighted below.

In each experiment, heterogeneous treatments were created by having the majority of the nutrient supply in only one half (Weiser et al.), one or two quarters (Keser et al. 2014, 2015), or within a small patch at the side of the pot (Belter 2014). (In the homogeneous treatments, the same overall amount of nutrients as in the heterogeneous treatments was mixed evenly throughout the pots, but data from the homogeneous treatments are not used here.) Two experiments used water drip irrigation to which dissolved fertilizer was added (Keser et al. 2015, Weiser et al.); the other two used slow-release fertilizer mixed in the substrate (Belter 2014, Keser et al. 2014).

At the end of the experiments, for each plant, the aboveground parts, as well as the belowground parts from the nutrient-rich and nutrient-poor patches of the heterogeneous treatments, were harvested separately, dried, and weighed. The biomass of roots from the nutrient-rich and -poor patches of the pots was used to calculate the root foraging precision of each plant (Table S1 in Supporting Information). Root foraging precision was calculated for each plant separately as:

$$log\left(\frac{root\ biomass\ in\ rich\ patch}{root\ biomass\ in\ poor\ patch}\right)$$

and the means of these values were calculated per species. Thus, even though the size of the patches differed among studies, the patches used for the calculation of root foraging precision of one species were the same size. The log-transformed ratios of the same size patches are comparable even if from studies with different patch sizes. For species present in more than one study (9 of 123 species), we used data from whichever study had the most replicates per species, to avoid pseudoreplicating data by using these species more times from different studies. Frequency and mean root foraging precision values from all studies are presented in the Supporting Information (Fig. S1). We used mean values of root foraging precision per species, which was shown previously to be relatively robust (Weiser et al. 2016). Context-dependent data of root foraging precision are not so common, but root foraging precision seems to be relatively stable across contrast in relative patch richness (Weiser et al. 2016, but see Lamb et al. 2004) or in different substrates volumes (Stiblíková and Weiser [unpublished]).

Root, shoot, and mycorrhizal traits

Plant root traits were extracted from the "Global root traits (GRooT) database" (Guerrero-Ramirez et al. 2021) and from the Alberta grassland plant trait database (Cahill 2020). The traits used here were: root diameter (62 species), nitrogen (N) content in roots (60 species), root tissue density (RTD; 66 species), and specific root length (SRL; 74 species). We used mean values of the traits per species calculated from the GRooT Full version using the GRooT aggregation R script to extract mean values. Trait means for species were calculated using values aggregated by study sites to account for potential pseudo-replication and variability in the data entries' resolution in GRooT (Guerrero-Ramirez et al. 2021). We treated the Alberta grassland plant trait data as a single study when merging it with the GRooT Full version dataset during our calculations of mean values. Ranges and dispersions of root trait data are summarized in the Supporting Information (Table S8a).

Specific leaf area (SLA), an aboveground trait that is indicative of plant life history strategy along the fast-slow economics spectrum (Reich 2014, Weemstra et al. 2016), was collected from the LEDA Traitbase (Kleyer et al. 2008) for 91 species. The LEDA Traitbase contains mean values of the traits calculated per

study; we calculated weighted means from all records in the LEDA database for the given species with the number of replications (sample size) in the study as weights.

We collected mycorrhizal data from the "FungalRoot: Global online database of plant mycorrhizal associations" (Soudzilovskaia et al. 2020). We classified species solely noted as having arbuscular mycorrhiza (AM) associations as "obligatorily mycorrhizal" (55 species), species with both AM and non-mycorrhizal (NM) records as "facultatively mycorrhizal" (44 species), and species with only NM records as "non-mycorrhizal" (7 species). Seventeen species were missing in the database. We also extracted data about the intensity of mycorrhizal colonization from the same database, which was available for 60 species. The intensity of mycorrhizal colonization expresses the mean percentage of root system colonized by mycorrhizal fungi in a species (which we calculated across all records per species). These data ranged from 0 to 100%.

All data taken from databases and the compiled data on root foraging precision per species are provided in Table S2 in the Supporting Information.

Statistical analyses

Foraging precision and other root traits

Not all trait data were available for every species, and thus we performed a series of tests on different subsets of our data to test our hypotheses. First, to explore the relationship between root foraging precision and root diameter and SRL (collaboration trade-off) and root N content and RTD (fast-slow plant life strategies) in the multidimensional root functional trait space, we performed a phylogenetic principal component analysis (PCA) on 44 species. Mycorrhizal colonization intensity and SLA were not included in the analysis because the overlap in the species with available data was not as high (29), and we wanted to maximize the predictability of our model (for phylogenetic PCA with mycorrhizal colonization intensity and SLA see Fig. S3 in Supporting information). We standardized those traits used in the PCA to have a mean of 0 and standard deviation of 1 and estimated the phylogenetic signal using Pagel's lambda statistic(Pagel 1999). To test the relationships among root foraging precision and root traits (root diameter, SRL, N content,

and RTD), we usedphylogenetic canonical correlation analysis (CCA). All traits were standardized as in the previous model. We also used phylogenetic PCA axis loadings of the first three axes in the separate linear models to predict root foraging precision.

Second, we used phylogenetic linear models (Freckleton et al. 2002) to test the relationships of root foraging precision and each root trait separately due to low overlap among the datasets for individual traits (i.e., the number of species in the phylogenetic linear models in Table 1 – Df). For each model, we estimated the mean value (intercept) and the strength of the phylogenetic signal (Pagel's lambda; Pagel 1999). To test our hypotheses, we used the intensity of mycorrhizal colonization, mycorrhizal status, root diameter, SRL, N content, RTD, and SLA separately as predictors of foraging precision. We also included the study sources of our root foraging data (i.e., Belter 2014, Keser et al. 2014, 2015, Weiser et al.) as another predictor variable in our analyses (categorical with four levels) due to methodological differences among these studies and interactions between the two predictors (study source and trait). All predictors were tested using F-tests. To check the robustness of our results and evaluate the effect of phylogenetic signals, we also modeled all these relationships without phylogeny using linear regression and tested the effects of predictors using F-tests.

Trait relationships and mycorrhiza

It was hypothesized that the effects of root traits on root foraging precision could interact with mycorrhiza, but the data on AM colonization had an unfavorable overlap with the other trait data. Therefore, we modeled root foraging precision as a response to mycorrhizal status, root traits (diameter, N content, RTD, and SRL - each of these in turn separately), and their interaction using phylogenetic linear models as described above (section “Foraging precision and other root traits”). We excluded NM species from these analyses, as data from only one or two NM species were available for each model. The study sources of our root foraging data (i.e., Belter 2014, Keser et al. 2014, 2015, Weiser et al.) was also included as another predictor variable in our analyses, but we did not include its interactions with the other predictors due to the insufficient number of species at some levels. Again, to check the robustness of our results and to evaluate the effect of phylogenetic signals, we also modeled all these relationships without phylogeny using linear regression and tested the effects of predictors using F-tests.

In order to test whether the mycorrhizal collaboration trade-off and fast-slow trade-off are well represented in our dataset, we explored the phylogenetic correlations among the traits separately. That allowed us also to include the species for which we had only incomplete trait data. We computed correlations of root diameter, N content, RTD, SRL, the intensity of mycorrhizal colonization, and SLA with one another.

Phylogenetic structure of traits

To assess the phylogenetic signal for root foraging precision and each of our traits (root foraging precision, SLA, root diameter, N content, RTD, and SRL) separately, we again used phylogenetic linear models with estimation of the phylogenetic signal (Pagel 1999). The phylogenetic signal (lambda) in these models ranged from 0 to 1, where 0 corresponds to no phylogenetic signal and 1 to the Brownian motion evolution model. To explore the possible difference in root foraging precision between monocots and eudicots, we computed an unpaired two-sample t-test.

In all the analyses, SLA, root diameter, N content, and RTD were log-transformed; SRL was square-root transformed to correct for non-normality.

We fitted all models using R (R Core Team 2020. version 3.6.3) in Rstudio (RStudio Team 2020, version 4.0.3). For phylogenetic principal component analysis, we used the phyl.PCA functionfrom the phytools R package (version 0.7-70, Revell 2012); for phylogenetic canonical correlation analysis, we used phyl.CCA function from the same package. Phylogenetic correlation among traits was determined using phyl.vcv function, again from the phytools R package, and for phylogenetic linear models, we used the pgls function from caper R package (Orme et al. 2013, version 1.0.1). The phylogenetic tree used in all analyses was created with V.PhyloMaker R package using scenario 3 with mega tree GBOTB.extended as a backbone tree (Jin and Qian 2019). All images were created using R base graphics or the ggplot2 package (Wickham 2016 version 3.3.0).

Results

Root foraging precision and root traits

Root traits together with root foraging precision could be represented by three major principal components axes of functional trait trade-offs that described 85% of data variability in total (Fig. 1, Table S3 in Supporting Information). The first principal component in the data accounted for 33% of the variation and was associated with RTD and SRL (scores: RTD = 0.77, SRL = -0.89). Root foraging precision did not load heaviest on the first axis, but the second axis (to which root foraging precision is associated) accounted for an almost as high percentage of the variation (29%) as the first axis. In terms of the mycorrhizal collaboration trade-off the second principal component axis was associated with root foraging precision and root diameter (scores: root foraging precision = -0.66, root diameter = -0.86), but it was not related with SRL, as SRL was orthogonal to root foraging precision. According to the CCA (Table S3 in Supporting information), root diameter was positively correlated with root foraging precision, although the overall correlation of root foraging precision with all traits was weak (canonical correlation = 0.42) and not significant (p-value = 0.11). In terms of the fast-slow life strategy trade-off, the third principal component axis was associated with root foraging precision and N content (scores: root foraging precision = 0.41, N content = -0.84), but RTD was not much associated with root foraging precision on all axes. The negative correlation of root foraging precision and N content also occurred in CCA, but again, the overall correlation of root foraging precision and root traits was weak and not significant (p-value = 0.11). Further, the phylogenetic signal of the PCA and also the CCA, was weak ($\lambda = 0.285$). Root foraging precision was significantly affected by the principal component axis loadings of the second and third axes ($p < 0.001$ for PCA axis 2, $p = 0.03$ for PCA axis 3; Table S9 in Supporting Information).

We did not find individual traits (intensity of mycorrhizal colonization or mycorrhizal status, root diameter, SRL, N content, RTD, and SLA) to be significant predictors of the root foraging precision, regardless of whether phylogeny was included ($p > 0.05$, Table 1, Fig. 2, Fig. 3, Table S6 in Supporting Information). In all the phylogenetic linear models, there were significant differences in root foraging precision among study sources of the root foraging data, as each study dataset contained different species and methods ($p < 0.05$). However, the interaction of root traits and studies were non-significant in all the analyses ($p > 0.05$; Fig. S4 in Supporting Information); thus, all four studies were consistent in finding no associations among foraging precision and root traits.

Trait relationships and mycorrhiza

The interaction of root traits with the mycorrhizal status of plants did not affect root foraging precision (Table 2, Fig. 2). Only the interaction of SRL and mycorrhizal status was marginally significant as the predictor of root foraging precision ($p = 0.072$; obligatorily mycorrhizal species tended to have a slightly more negative relationship between SRL and root foraging precision in comparison with facultatively mycorrhizal species). The results of linear models of these relationships were the same regardless of the phylogeny signal (Table S7 in Supporting information).

In terms of representation of functional trait trade-offs in our data, we found a significant ($p < 0.05$) negative correlation between SRL and root diameter (-0.385), and SRL and RTD (-0.641). A significant positive correlation occurred between N content and RTD (0.359), N content and root diameter (0.614), and RTD and SLA (0.523; Table S4 in Supporting information). The intensity of mycorrhizal colonization did not correlate significantly with any trait.

Phylogenetic structure of traits

The overall phylogenetic signal in root foraging precision of 123 species is very weak and non-significant (Pagel's lambda 0.096 with 95% confidence interval [0, 0.487]; Table S5, Fig. S2 in Supporting Information). Also, the phylogenetic signal of root foraging precision is still non-significant even if taking into account that root foraging data come from four different studies ($\lambda = 0.084$, CI = [0, 0.384], $p(\lambda=0) = 0.119$). However, we found significant difference in mean root foraging precision between monocots and eudicots ($p < 0.001$, mean root foraging of monocots – 0.21, mean root foraging of eudicots – 0.55). For other traits, we found a significant phylogenetic signal in root diameter ($\lambda = 0.38$, CI = [0.026, 0.761]), N content ($\lambda = 0.53$, CI = [0.163, 0.814]), SRL ($\lambda = 0.51$, CI = [0.140, 0.810]), and marginally significant signal in intensity of mycorrhizal colonization ($\lambda = 0.43$, CI = [0, 0.744]) (Table S5 in Supporting information).

Discussion

Root foraging precision of the tested set of 123 herbaceous grassland species was not associated with mycorrhizal colonization or any of the expected fine-root traits, contrary to the hypotheses, which were derived from the results of recent studies (e.g., Kembel et al. 2008, Chen et al. 2018, Bergmann et al. 2020). Root foraging precision was not overall significantly phylogenetically conserved, which is consistent with Weiser et al. (2016); it is important to note, however, some of the data used here come from the latter study. Root foraging precision seems to be lower in monocots than eudicots, which partly agrees with Kembel and Cahill (2005). Adding a phylogenetic signal did not change the results of analyses testing the effect of root traits and mycorrhiza on root foraging precision.

Here we found no support for the hypothesis that there was a trade-off between root foraging precision and mycorrhizal symbiosis of plants accompanied with root diameter and SRL (Chen et al. 2018, Bergmann et al. 2020). Although foraging precision correlated positively with root diameter in multidimensional space, it was not significant. This is in contrast with studies on trees showing that species with low mycorrhizal colonization and root diameter have high root foraging precision, while highly mycorrhizal species with thick roots outsource their foraging to fungi hyphae (Eissenstat et al. 2015, Liu et al. 2015, Chen et al. 2016, Cheng et al. 2016). However, tree species with low foraging precision had ectomycorrhizal symbioses and good foragers arbuscular mycorrhizal symbioses; thus, the main difference appeared to be between mycorrhizal types (Chen et al. 2018). Our inability to conceptually replicate (Filazzola and Cahill Jr 2021) these prior studies could be due to nuances of study designs or may have biological explanation such as different life histories of trees and herbaceous species.

In contrast with the hypothesis of root foraging precision/fine root traits/mycorrhiza interplay (Chen et al. 2018), we did not find any of the relationships proposed. Although we did not find a correlation between root diameter and mycorrhizal colonization as proposed by Chen et al. (2018), a collaboration gradient defined by the negative correlation of root diameter and SRL (Bergmann et al. 2020) occurred in our data. Yet, we did not find a relationship between foraging precision and these two root traits.

Our results also did not support the hypothesis of high foraging precision being common among "fast weedy species" (Kembel et al. 2008), defined mainly by the high N content and low RTD (Bergmann et al. 2020) and possibly by high SLA (Reich 2014, Weemstra et al. 2016). However, we found a negative (but non-significant) correlation between foraging precision and N content in multidimensional space. Also, we did not detect the gradient of traits proposed by the fast-slow trade-off (N content, RTD, SLA). The lack of statistical support to the hypothesized relationships in our dataset suggests that root foraging precision could be controlled by suites of plant traits, such that in large samples, we may not expect a single trait to correlate. Root behaviors appear to be more complicated in fitting into trait-space than traditional static measures (Belter 2014) or aboveground plant behavior (Reich 2014).

We found no evidence that our lack of responses was due to insufficient data coverage. Specifically, we extracted from the GRooT an addition root trait dataset of all herbaceous species from similar conditions as species in our dataset (the filters used were non-woodiness, latitude from 23.5 to 66.5, and field experiments). We compared it with our root trait data, and both datasets showed similar data dispersion and range (Table S8 in Supporting Information). A less prominent fast-slow trade-off (described by N content and RTD) contrasts with the findings of Bergmann et al. (2020), who also used data from the GRooT database. However, they documented the gradient either on herbaceous species across all biomes or separately according to biome types (following the Köppen–Geiger classification) but without distinction of woodiness. Moreover, compared to the other biomes, the fast-slow trade-off in the continental biome (which covered a relatively large portion of our species) was less prominent (Bergmann et al. 2020). We found a reasonable negative correlation between the root diameter and SRL designing the trade-off of collaboration with mycorrhizal symbiosis (Bergmann et al. 2020). Nevertheless, our traits showed no direct links to the mycorrhizal colonization data, which contrasts with the mycorrhizal collaboration trade-off. The reason for this may be that for root diameter and SRL, we had a smaller range of the data coverage —we lacked species with high root diameter and low SRL, i.e., species that mainly outsource the nutrient acquisition to fungi, but these might be woody ectomycorrhizal species (Chen et al. 2018).

Besides the already mentioned correlations between traits, we also found a significant negative correlation between SRL and RTD and a significant positive correlation between SLA and RTD. According to the patterns suggested by the resource economics strategy theory (Reich et al. 1997), the aboveground SLA and belowground SRL should be correlated positively as representatives of "fast" plant acquisitive strategy, and both these traits should be negatively correlated with RTD, but this was not the case in our study. However, Kembel and Cahill (2011) also found complex relationships between these aboveground and belowground traits, showing that the relationships among traits may depend on environmental conditions and, thus, different selective pressures and constraints within and between communities.

In all analyses, the phylogenetic perspective on root foraging precision and root traits did not affect the results, and root foraging precision itself was not phylogenetically determined. Some of the other root traits in our dataset showed a strong phylogenetic signal, specifically root diameter, N content, SRL, and to a lesser extent, intensity of mycorrhizal colonization. SLA and RTD showed no phylogenetic signal. This partly agrees with the previous studies showing that root diameter together with mycorrhizal colonization is strongly phylogenetically conserved, followed by root N content, and then by SRL, SLA, and RTD, whose phylogenetic conservation is weaker (Kembel and Cahill 2011, Kong et al. 2014, Valverde-Barrantes et al. 2017, Ma et al. 2018). The reason for root traits not being as phylogenetically determined as in other studies could be the limited number of species in our study not covering the entire plant phylogeny. But even though the entire phylogeny is not covered, and the study did not involve tree species, the families to which some trees belong are still included in our study. The fact that we did not cover the conifers and other ancient groups could affect mainly finding the trade-off between root diameter and mycorrhizal colonization (Ma et al. 2018), which we did not detect.

Our results bring new insight into the relationship of root foraging precision and root traits of herbaceous species because we examined a higher number of solely herbaceous species than prior studies (Kembel et al. 2008, Chen et al. 2018). Because root foraging precision did not follow any previously proposed gradient of the nutrient acquisition space of herbs, we could suggest that foraging precision constitutes another distinct dimension in root trait space. Only some traits are subsumed into the fast-slow or mycorrhizal collaboration

trade-offs of plant life strategies, yet other traits might be important in nutrient acquisition in different contexts. Outside the experimental conditions, soil heterogeneity in terms of patch size, quality, and frequency differs among habitats, putting different emphasis on selecting traits that allow finding, reaching, and exploiting the patch in each of them. When the rich patches are scarce, transient in time, but relatively rich, such as those produced by small disturbances in dense stands, it might be quite rewarding to produce large networks of acquisitive structures to be close to the patch once it occurs. However, suppose the environment is resource-poor overall. In that case, the patches of the same relative contrast, size, and predictability as in the previous example can be exploited only locally, since the overall paucity of the environment prevents maintenance of the extensive network of acquisitive structures. Overall, the need to forage precisely and select on this ability independently of other fine root traits can be given by specific environmental factors in combination with different selective pressures on non-root traits (mycorrhizal symbiosis).

Our data also show only mixed support for the existence of fast-slow and mycorrhizal collaboration trade-offs (Diaz et al. 2004, Reich 2014, Bergmann et al. 2020). The inconsistencies in a different ordering of different sets of root traits suggest that root system organization is relatively poorly understood, and we lack a synthesis of the main traits of each of the axes proposed. This counters with knowledge of leaf traits space as they are relatively simple organs with less dynamic behaviors.

However, it is important to concede several limitations of the study. First, we used plant species mainly from temperate, continental, or arid regions; other regions (mainly tropical and subtropical) are understudied. Second, the study-specific setting of environmental and experimental conditions may vary in all data, but a single value is chosen to represent a species. Along environmental gradients, the fine-root traits vary unpredictably within a species (Weemstra et al. 2021), although we cared to select the fine root traits data sources to be as consistent as possible. In root foraging data, the effects of the environment are not studied enough. Thus, some uncertainty about data accuracy exists, which was a trade-off with their better availability through public databases. Despite using the databases, the available dataset was still somewhat sparse. The optimal but much more demanding way would be to measure the root traits together with root

foraging precision, or to standardize the protocols of data acquisition (Ottaviani et al. 2017, Freschet et al. 2021).

Despite the issues with the data, we believe in presenting true negative results here. This stems from the concordance of the four studies we used as root foraging precision data sources. We obtained primary data from individual authors, which enabled us to evaluate all available evidence. There were several methodological differences among the studies, which could affect the results and although the overall replication at the level of studies is relatively low (four studies), the trends were consistent among them. The studies could be considered true replicates because there is no overlap in species among the studies in the data used. We took inter-studies differences into account with a separate variable in the analyses, and it had no significant effect, so we believe that this was not the origin of the null results. Only SRL showed a weak signal in interaction with the study source of root foraging precision data, which means that species in different studies had a different relationship between SRL and root foraging precision, but this signal was relatively marginal.

Conclusion

This study aimed to detect the connection of root foraging precision in herbaceous species with their fine-root traits, SLA, or mycorrhizal symbiosis, but we did not reveal any relationship with these factors. Thus, root foraging precision probably performs on different root trait dimension independently of fast-slow or mycorrhizal collaboration trade-off. However, differences among herbaceous species in root foraging precision exist (Johnson and Biondini 2001, Grime and Mackey 2002, Cahill and McNickle 2011, Weiser et al. 2016). Similarly, species inhabiting contrasting environments differ in their root traits (Fort and Freschet 2020), yet the intraspecific response to contrasting environments is species-specific (Weemstra et al. 2021). Therefore, we suggest exploring the relationship between the root foraging precision and the environment more thoroughly. Namely, the current experiments on root foraging precision often overlook the root foraging of herbaceous plants in tropical areas; most of the studies from the tropics focus on tree species. Moreover, the context-dependency of root foraging precision should be studied more. Also, it should be noted that despite our current results, root foraging precision has been successfully linked to the overall

plant growth rate (with no signal of mycorrhizal symbiosis effect) (Grime et al. 1997, Weiser et al. 2016). It is also important to notice that the root foraging of plants can be separated into two main processes – first is the ability to find and detect the nutrient-rich patch, and second is the ability to exploit the patch (which was mainly covered by our study). The fine-root traits and trade-offs possibly do not operate similarly in these distinct processes.

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531

Table 1: Relationship of root, shoot, and mycorrhizal traits and root foraging precision. Each trait was tested separately. The strength of the phylogenetic signal in the relationship is expressed by Pagel's lambda (λ) with confidence interval (CI). The study variable indicates the origin of root foraging precision data and has four categories: Belter 2014, Keser et al. 2014, Keser et al. 2015, and Weiser et al. The number of species in analyses ranged from 60 to 99. Mycorrhizal status had two categories—obligatory and facultative. The non-mycorrhizal category was not included in the phylogenetic linear model, as there was missing data in the interaction with the author category, and the effect estimation procedure did not converge.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	λ	CI (λ)	p (λ=0)	Adj. R^2
Author	3	0.049	0.016	11.731	**< 0.001**	0.087	0, 0.499	0.255	0.251
SLA [log]	1	0.000	0.000	0.114	0.737				
Author * SLA	3	0.003	0.001	0.617	0.606				
Residuals	83	0.116	0.001						
Author	3	0.044	0.015	13.124	**< 0.001**	0.151	0, 0.566	0.231	0.388
Root diameter [log]	1	0.001	0.001	0.864	0.357				
Author * Root diameter	3	0.006	0.002	1.835	0.152				
Residuals	54	0.060	0.001						
Author	3	0.068	0.023	17.610	**< 0.001**	0.513	0, 0.872	1.000	0.481
N content [log]	1	0.004	0.004	2.795	0.101				
Author * N content	3	0.008	0.003	2.041	0.120				
Residuals	52	0.067	0.001						
Author	3	0.066	0.022	18.977	**< 0.001**	0.161	0, 0.528	0.130	0.447
RTD [log]	1	0.001	0.001	0.658	0.421				
Author * RTD	3	0.002	0.001	0.671	0.573				
Residuals	58	0.067	0.001						
Author	3	0.061	0.020	17.303	**< 0.001**	0.092	0, 0.404	0.195	0.424
SRL [sqrt]	1	0.001	0.001	0.952	0.333				
Author * SRL	3	0.009	0.003	2.590	0.060				
Residuals	66	0.077	0.001						
Author	3	0.063	0.021	13.616	**< 0.001**	0.049	0, 0.346	0.365	0.274
Mycorrhizal status	1	0.000	0.000	0.001	0.977				
Author * Myc. status	3	0.005	0.002	1.054	0.373				
Residuals	91	0.141	0.002						
Author	3	0.017	0.006	3.676	**0.018**	<0.001	0, 0.148	1.000	0.083
Mycorrhizal intensity	1	0.000	0.000	0.291	0.592				
Author * Myc. intensity	3	0.001	0.000	0.330	0.804				
Residuals	52	0.079	0.002						

Table 2: Relationship of root foraging precision and root traits in interaction with mycorrhizal status. Each root trait was tested separately. The strength of the phylogenetic signal in the relationship is expressed by Pagel's lambda (λ) with confidence interval (CI). The study variable describes the origin of root foraging precision data and has four categories: Belter 2014, Keser et al. 2014, Keser et al. 2015, and Weiser et al. The number of species in analyses ranged from 51 to 64. Mycorrhizal status had two categories—obligatory and facultative. The non-mycorrhizal category was not included in the phylogenetic linear model, as there was missing data in interaction with the author category, and the effect estimation procedure did not converge.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	λ	CI (λ)	p (λ=0)	Adj. R^2
Author	3	0.041	0.014	11.347	**< 0.001**				
Root diameter [log]	1	0.001	0.001	1.090	0.302				
Mycorrhizal status	1	0.002	0.002	1.923	0.172	0.224	0, 0.618	0.062	0.376
Root diameter * Myc. status	1	0.003	0.003	2.149	0.149				
Residuals	49	0.059	0.001						
Author	3	0.065	0.022	12.026	**< 0.001**				
N content [log]	1	0.003	0.003	1.691	0.200				
Mycorrhizal status	1	0.001	0.001	0.715	0.402	0.736	0, 0.939	0.169	0.394
N content * Myc. status	1	< 0.001	< 0.001	0.028	0.868				
Residuals	44	0.080	0.002						
Author	3	0.053	0.018	14.644	**< 0.001**				
RTD [log]	1	0.001	0.001	0.612	0.438				
Mycorrhizal status	1	< 0.001	< 0.001	0.002	0.966	0.225	0.010, 0.580	**0.033**	0.409
RTD * Myc. status	1	0.001	0.001	0.938	0.338				
Residuals	51	0.061	0.001						
Author	3	0.045	0.015	12.015	**< 0.001**				
SRL [sqrt]	1	0.002	0.002	1.483	0.228				
Mycorrhizal status	1	0.001	0.001	0.600	0.442	0.092	0, 0.497	0.318	0.362
SRL * Myc. status	1	0.005	0.005	3.655	0.061				
Residuals	57	0.072	0.001						

554

555

556 **Fig. 1**: Phylogenetic principal component analysis of root foraging precision (RFP) and root traits (root
557 diameter, N content, RTD, and SRL) for 44 species. We show the position of traits on the first and second
558 axes (a) and the first and third axes (b) with the proportion of variance explained next to the axes labels.
559 Each point represents a single plant species and is marked according to their mycorrhizal status (yellow
560 circle— obligatory mycorrhiza, green triangle—facultative mycorrhiza, black square – unknown
561 mycorrhizal status).

562

Fig. 2: Relationship of root diameter (a), SRL (b), the intensity of mycorrhizal colonization (c), N content (d), RTD (e), and SLA (f) with root foraging precision. Each plot contains the linear regression line (solid) and mean root foraging precision per all species (dashed), both after accounting for phylogenetic signals. Each point represents a single plant species and is marked according to their mycorrhizal status (yellow circle— obligatory mycorrhiza, green triangle—facultative mycorrhiza, blue diamond—no mycorrhiza). Values of traits are untransformed in original units; values of root foraging precision above 1 mean that plants create more roots in the nutrient-rich area, values below 1 mean that plants create more roots in the nutrient-poor area. We found no significant relationship between root foraging precision and root traits ($p > 0.05$).

576

577 **Fig. 3:** Relationship between root foraging precision and mycorrhizal status of 106 species. There was no
578 difference among obligatory, facultative, and non-mycorrhizal species in root foraging precision ($p > 0.05$),
579 regardless of whether phylogeny was included or not. The width of boxes is proportional to the number of
580 species in each mycorrhizal category. Each point represents one species. Values of root foraging precision
581 above 1 mean that plants created more roots in the nutrient-rich area; values below 1 mean that plants
582 created more roots in the nutrient-poor area.

583

(a)

SRL

RTD

N content

RFP

Diameter

PPC2 - 29 %

PPC1 - 33 %

(b)

RFP

RTD

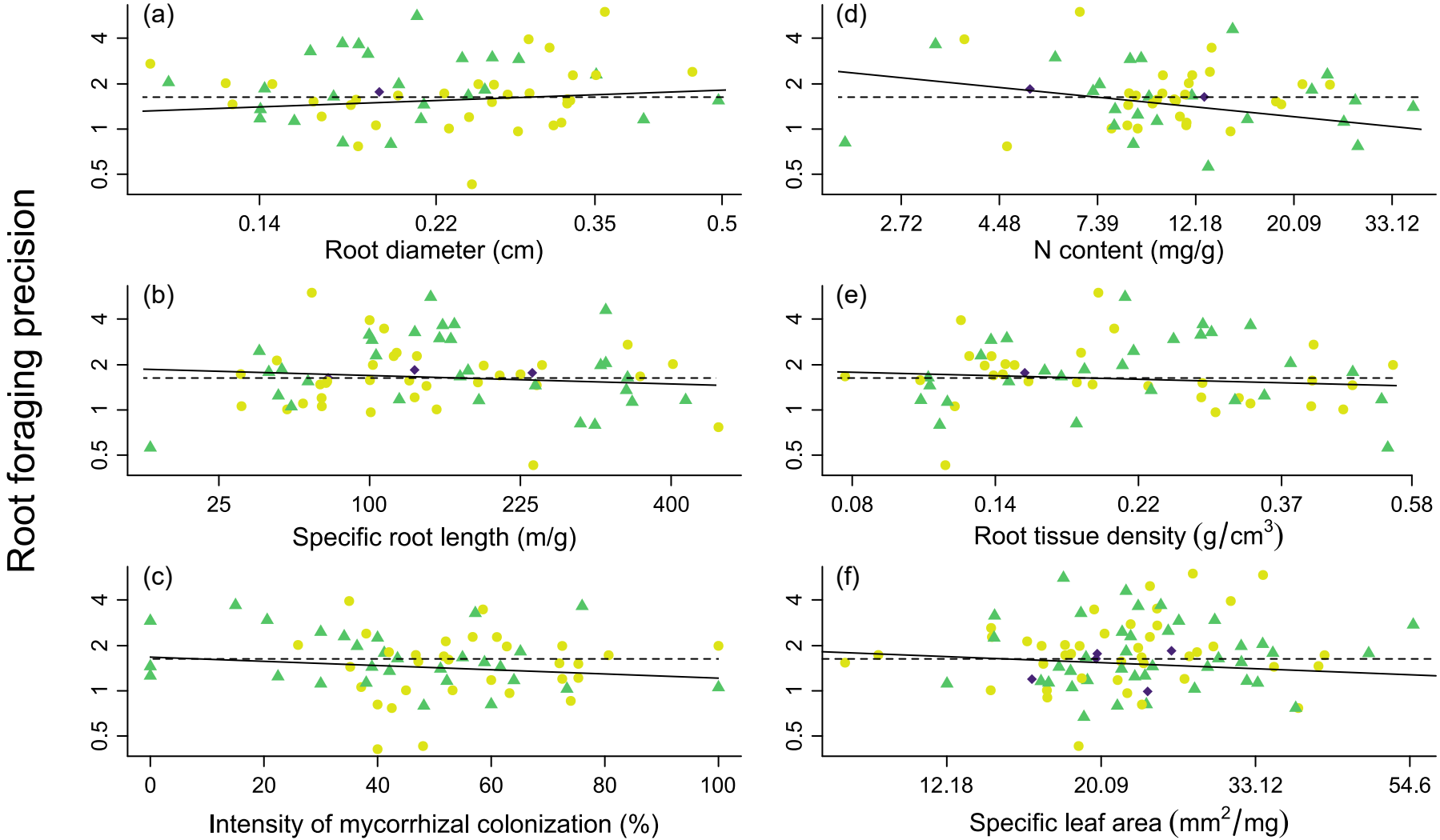
SRL

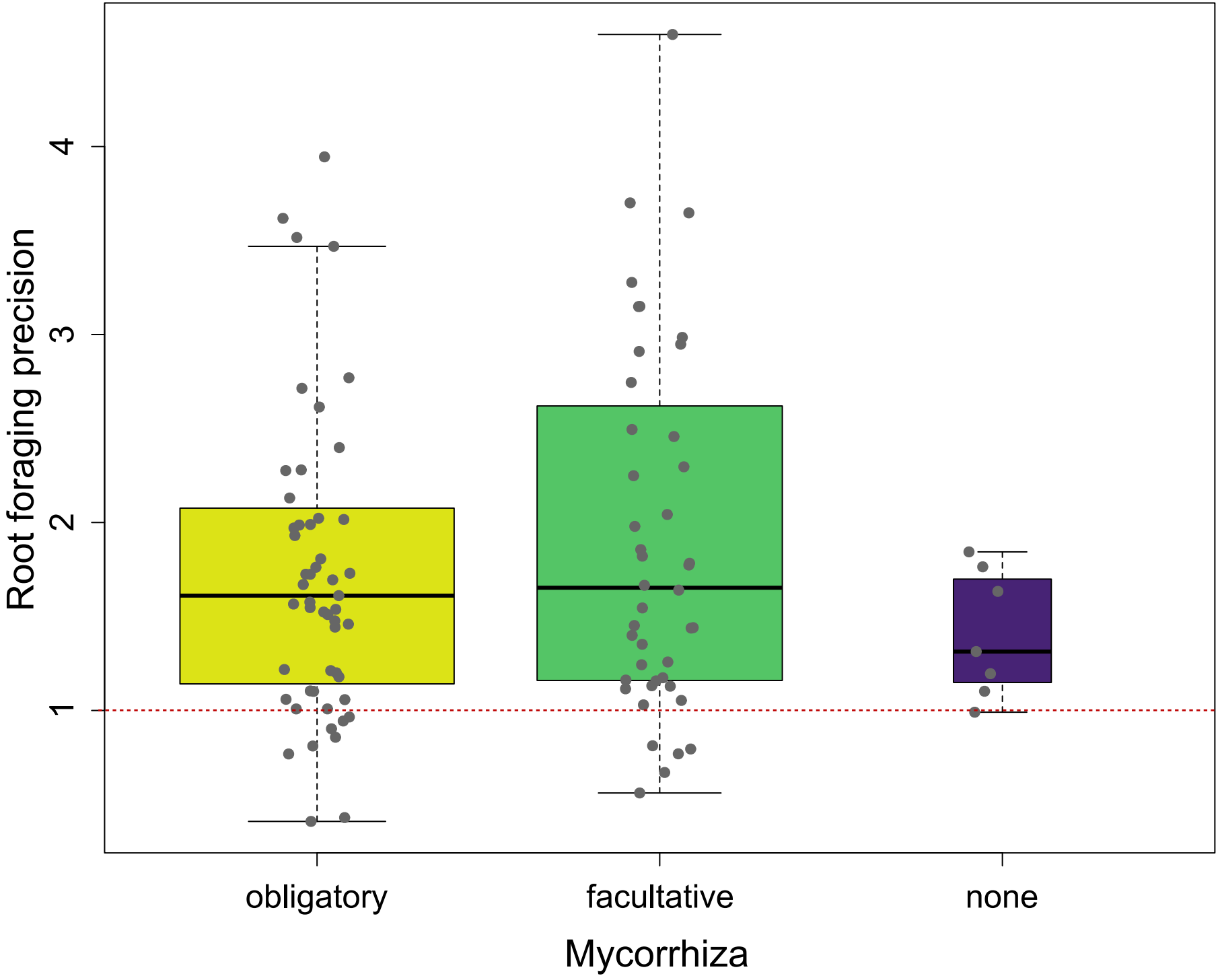
Diameter

N content

PPC3 - 23 %

PPC1 - 33 %


Root foraging precision
(a)
0.5
1
2
4
0.14
0.22
0.35
0.5
Root diameter (cm)
(d)
2.72
4.48
7.39
12.18
20.09
33.12
N content (mg/g)
(b)
25
100
225
400
Specific root length (m/g)
(e)
0.08
0.14
0.22
0.37
0.58
Root tissue density (g/cm3)
(c)
0
20
40
60
80
100
Intensity of mycorrhizal colonization (%)
(f)
12.18
20.09
33.12
54.6
Specific leaf area (mm2/mg)


Root foraging precision
1
2
3
4
obligatory
facultative
none
Mycorrhiza

Supporting Information

Table S1: Experimental designs of the four different root foraging precision studies (Belter 2014, Keser et al. 2014, Keser et al. 2015, Weiser et al.). The table shows similarities and methodological differences between studies. Plants were grown either in heterogeneous or homogeneous soil conditions, with the total nutrient supply not varying among treatments within a study.

Study	Species information	Seed source	Duration of the experiment	Age of plants at the time of harvest	Pre-cultivation	Pots and patches	Planting	Fertilization	Root foraging precision (RFP)	Location
Belter 2014	18 species; common herbaceous species native to rough fescue prairie in Alberta, Canada	Seeds were collected from multiple plants in a native prairie in Alberta, Canada (53°05 N, 111°33 W); seeds were coldly stratified for two weeks	15 weeks	–	Seeds were germinated on the autoclaved mixture of sand and soil and watered daily	Circular 1.67-L pots with 3:1 mixture of sand and soil with a nutrient-rich patch in the heterogeneous treatment; the patch was placed on the side 3 cm from the pot center and had 2.5 cm in diameter	Plants were watered as needed to keep wet.	Fertilizer mixed in the substrate; nutrient-rich patch in heterogeneous treatment was created with 50% v/v composted cow manure, Sure-Gro Inc. In homogeneous trt., the same amount of fertilizer was mixed evenly in the pots	RFP was calculated from the dried biomass (weight) of roots in nutrient-rich patches and nutrient-poor patches taken from the opposite side of the pot in heterogeneous treatments (poor patches had the same size as a rich patch)	University of Alberta, Biological Sciences Rooftop, Edmonton, Alberta, Canada

Keser et al. 2014	12 species; herbaceous clonal species native to Europe and naturalized in Nort America (some of them invasive)	Ramets of species were collected from wild populations in Europe, each species from two populations at least 80 km apart	16 weeks	-	Collected wild ramets were planted in a greenhouse for about a year, the daughter ramets of similar sizes were used in the experiment (without rhizomes, stolons, or flowers)	Circular 60-L pots with 1:1 mixture of sand and agricultural soil with high clay content; pots were divided into 4 quarters (in heterogeneous treatment, two opposite quarters are nutrient-rich and the other two are poor)	-	Each pot received 135 g slow-release fertilizer (Osmocote Exact Standard 5-6M). Heterogeneous treatment: 67.5 g of fertilizer to the two nutrient-rich quarters and no fertilizer into the poor quarters. Homogeneous t.: 33.75 g of fertilizer into all four quarters	RFP was calculated from the dried biomass (weight) of roots in nutrient-rich quarters and nutrient-poor quarters of the pot; calculated only from roots (without separated clonal growth organs)	Greenhouse, Muri near Bern, Switzerland (46.55.1631N, 7.30.0853E)
Keser et al. 2015	22 species; herbaceous species native to Europe and naturalized in Nort America (some of them invasive)	Seeds from botanical gardens in Europe and commercial companies; seeds were coldly stratified for ten days	5 weeks	About 7 weeks	After cold stratification, seedlings were left for two weeks in the greenhouse and then replanted to the experimental pots	Square 1-L pots with a 1:1 mixture of sand and fine vermiculite; pots were divided into 4 quarters (in heterogeneous treatment, one quarter is nutrient-rich, and the other three are nutrient-poor)	Plants were fertilized three times per week through four syringes (drip irrigation) to the pot borders	Drip irrigation; heterogeneous treatment: 40 ml of a 1/2-strength and 40 ml of a 1/64-strength Hoagland solution in one and the other three pot quarters respectively; Homogeneous t.: 40 ml of a c. 1/8-strength Hoagland solution in all pot quarters	RFP was calculated from the dried biomass (weight) of roots in the nutrient-rich quarter and dried biomass of roots in the opposite nutrient-poor quarter of the pot; calculated only from fine roots (thick lignified roots were separated)	Greenhouse, University of Konstanz, Germany (N: 47°69'19.56", E: 9°17'78.42")

Weiser et al. (2016 + unpubl.)	71 species; perennial hemicryptophytes native to Europe, occurrence in mesic unshaded or moderately shaded habitats	Seeds were obtained from a commercial supplier (Planta Naturalis)	5 weeks	About 9 weeks	Seeds germinated in the greenhouse on clean sand for one month and were replanted to the experimental pots after approximately one and half months from the sowing	Circular 3-L pots with washed sand; pots were divided into two halves (in heterogeneous treatment, one half is nutrient-rich and the other nutrient-poor)	Plants were watered and fertilized two times per day through two syringes (drip irrigation) to the pot borders.	Drip irrigation; heterogeneous treatment: 0.2% fertilizer (Wuxal Super) in the nutrient-rich half and clear water in the nutrient-poor half. In homogeneous treatment, the same amount of fertilizer was supplied to the pots, 0.1% concentration to both halves of the pot.	RFP was calculated from the dried biomass (weight) of roots in nutrient-rich half and biomass of roots in nutrient-poor half of the pot	Greenhouse, experimental garden of the Faculty of Science, Charles University (50.069N, 14.425E)

Table S2: Complete dataset used in all analyses. Each species has the value of root foraging precision (log) and assignment of the root foraging study (Belter 2014, Keser et al. 2014, Keser et al. 2015, Weiser et al.). Information about the mycorrhizal status and intensity of mycorrhizal colonization for 106 and 60 species, respectively, were found in the "FungalRoot database" (Soudzilovskaia et al. 2020). We collected fine root traits data for our species from the "GRooT database" (Guerrero-Ramirez et al. 2021) and from the Alberta grassland plant trait database (Cahill 2020) – root diameter (62 species), nitrogen (N) content (60 species), root tissue density (RTD; 66 species), specific root length (SRL; 74 species). We collected shoot trait, specific leaf area (SLA; 91 species) from the LEDA Traitbase (Kleyer et al. 2008).

Species	Family	Root foraging precision	Study	Mycorrhizal status	Intensity of mycorrhizal colonization	Root diameter (cm)	N content (mg/g)	RTD (g/cm^3)	SRL (m/g)	SLA (mm^2/mg)
Aegopodium podagraria L.	Apiaceae	0.36	Keser 2014	facultative	62	-	-	-	-	28.36
Agrimonia eupatoria L.	Rosaceae	-0.40	Weiser	facultative	-	-	-	-	-	19.00
Agrostis capillaris L.	Poaceae	0.37	Weiser	obligatory	-	0.18	8.64	0.23	141.26	35.16
Achillea millefolium L.	Asteraceae	0.51	Weiser	facultative	55	0.24	11.94	0.17	169.02	19.12
Achillea ptarmica L.	Asteraceae	0.11	Weiser	facultative	30	-	25.90	-	-	12.19
Anthoxanthum odoratum L.	Poaceae	0.49	Weiser	facultative	44	0.17	9.60	0.11	344.30	29.37
Arctium minus (Hill) Bernh.	Asteraceae	1.26	Keser 2015	obligatory	-	-	-	-	-	24.07
Artemisia absinthium L.	Asteraceae	0.03	Weiser	facultative	73	-	-	-	-	27.18
Artemisia campestris L.	Asteraceae	0.01	Weiser	obligatory	45	-	9.06	-	52.77	16.85
Artemisia frigida Willd.	Asteraceae	0.06	Belter	obligatory	37	0.19	11.61	0.41	33.07	-
Artemisia ludoviciana Nutt.	Asteraceae	0.10	Belter	obligatory	-	0.32	11.63	0.33	60.69	-
Astragalus agrestis Douglas ex G. Don	Fabaceae	-0.86	Belter	-	-	-	25.48	0.53	17.60	-
Berteroa incana (L.) DC.	Brassicaceae	0.57	Weiser	none	-	0.19	-	0.15	237.00	19.83
*Bouteloua gracilis (*Kunth.) Lag. ex Steud.	Poaceae	0.10	Belter	-	60	0.19	13.81	0.44	37.46	-
Briza media L.	Poaceae	-0.21	Keser 2014	facultative	-	0.17	2.04	0.18	288.70	23.26
Bromus arvensis L.	Poaceae	0.57	Keser 2015	obligatory	40	-	-	-	-	18.22
Bromus benekenii (Lange) Trimen	Poaceae	-0.21	Weiser	obligatory	63	-	-	-	-	22.92
Bromus inermis Leysser	Poaceae	-0.04	Belter	obligatory	41	0.28	14.54	0.29	100.75	21.86
Bromus tectorum L.	Poaceae	0.58	Keser 2015	facultative	-	-	7.22	0.47	44.31	35.03

Carex leporine auct.	Cyperaceae	0.62	Weiser	facultative	-	0.14	-	0.18	50.21	-
Carex vulpine L.	Cyperaceae	0.49	Weiser	none	61	-	12.72	-	74.40	19.76
Centaurea jacea L.	Asteraceae	0.82	Weiser	obligatory	-	0.33	10.31	0.13	116.62	14.10
Centaurea stoebe L.	Asteraceae	0.70	Weiser	obligatory	0	-	-	-	-	-
Cerastium fontanum L.	Caryophyllaceae	1.07	Keser 2015	facultative	-	0.28	8.72	0.13	101.62	25.83
Cerastium glomeratum Thuill.	Caryophyllaceae	1.53	Keser 2015	facultative	-	-	14.70	-	318.00	21.77
Cirsium palustre (L.) Scop.	Asteraceae	1.73	Keser 2015	facultative	-	0.21	-	0.21	144.63	17.78
Cirsium vulgare (Savi) Ten.	Asteraceae	1.15	Keser 2015	facultative	-	0.18	-	0.28	99.71	14.22
Cynosurus cristatus L.	Poaceae	0.51	Weiser	obligatory	-	0.20	8.98	0.08	360.02	22.90
Dianthus armeria L.	Caryophyllaceae	0.89	Weiser	-	-	-	-	-	-	15.41
Dianthus carthusianorum L.	Caryophyllaceae	0.12	Weiser	facultative	-	-	-	-	-	16.94
Dianthus deltoides L.	Caryophyllaceae	0.18	Weiser	none	-	-	-	-	-	16.05
Echium vulgare L.	Boraginaceae	0.96	Weiser	obligatory	-	-	-	-	-	14.06
Elymus glaucus Buckl.	Poaceae	-0.12	Belter	-	-	-	10.40	0.49	28.61	-
Elymus lanceolatus Gould	Poaceae	0.20	Belter	-	-	0.22	-	0.31	94.78	-
Erigeron glabellus Nutt.	Asteraceae	-0.24	Belter	-	-	0.31	12.03	0.33	39.51	-
Erysimum crepidifolium Rchb.	Brassicaceae	0.65	Weiser	-	-	-	-	-	-	-
Euphorbia esula L.	Euphorbiaceae	0.55	Weiser	obligatory	-	-	-	-	-	41.42
Festuca hallii (Vasey)	Poaceae	0.35	Belter	-	42	0.20	7.28	0.58	51.91	-
Festuca rubra L.	Poaceae	0.30	Weiser	facultative	22	0.14	8.08	0.23	342.79	18.19
Filipendula ulmaria (L.) Maxim	Rosaceae	0.22	Weiser	facultative	75	-	9.07	0.35	48.63	22.40
Filipendula vulgaris Moench	Rosaceae	0.41	Weiser	obligatory	-	0.26	-	0.28	73.17	16.66
Gaillardia aristata Pursh	Asteraceae	-0.58	Belter	facultative	-	-	12.98	0.53	7.43	-
Galium album Mill.	Rubiaceae	1.00	Weiser	obligatory	47	0.10	-	0.41	344.42	24.09
Galium boreale L.	Rubiaceae	0.45	Weiser	obligatory	26	0.18	10.00	0.41	128.03	21.44
Galium verum L.	Rubiaceae	0.70	Weiser	obligatory	51	0.12	11.76	0.14	402.38	17.87
Geum rivale L.	Rosaceae	0.34	Weiser	facultative	-	-	36.88	-	-	21.46
Geum urbanum L.	Rosaceae	0.38	Weiser	obligatory	52	0.13	18.84	0.47	241.56	40.61
Glechoma hederacea L.	Lamiaceae	0.15	Keser 2014	facultative	-	0.21	15.85	0.10	419.53	32.20
Gypsophila paniculate L.	Caryophyllaceae	0.27	Weiser	none	-	-	-	-	-	-
Helianthemum grandiflorum (Scop.) DC.	Cistaceae	1.29	Weiser	obligatory	-	-	-	-	-	-

Helictotrichon pratense (L.) Besser	Poaceae	-0.06	Weiser	obligatory	-	-	-	-	-	-
Heterotheca villosa (Pursh) Shinners	Asteraceae	0.15	Belter	-	-	0.22	12.65	0.33	65.30	-
Holcus lanatus L.	Poaceae	0.68	Weiser	facultative	36	0.20	7.47	0.21	312.00	31.62
Hypericum perforatum L.	Hypericaceae	-0.26	Keser 2015	obligatory	43	0.18	4.66	-	465.30	38.04
Hypochaeris radicata L.	Asteraceae	1.09	Weiser	facultative	-	0.26	5.96	0.14	151.77	-
Inula hirta L.	Asteraceae	0.16	Weiser	obligatory	60	-	-	-	-	21.19
Inula salicina L.	Asteraceae	0.18	Keser 2014	obligatory	73	0.24	-	0.32	70.68	26.31
Koeleria macrantha (Ledeb.) Schult.	Poaceae	0.01	Belter	obligatory	53	0.23	7.93	0.46	149.39	14.04
Koeleria pyramidata (Lam.) P. Beauv.	Poaceae	0.15	Weiser	facultative	-	0.40	-	0.31	185.64	16.53
Lathyrus pratensis L.	Fabaceae	0.44	Weiser	facultative	59	0.50	27.45	0.14	63.30	31.64
Leontodon hispidus L.	Asteraceae	0.53	Weiser	obligatory	52	0.27	11.54	0.13	204.91	26.73
Linaria repens (L.) Mill.	Plantaginaceae	0.91	Keser 2015	facultative	-	-	-	-	-	24.96
Linaria vulgaris Mill.	Plantaginaceae	0.16	Keser 2014	facultative	64	0.14	-	0.52	120.66	19.21
Lotus corniculatus L.	Fabaceae	0.83	Weiser	facultative	34	0.35	23.82	0.13	104.33	22.10
Luzula multiflora (Ehrh.) Lej.	Juncaceae	0.61	Weiser	none	-	-	5.24	-	132.06	25.23
Lychnis flos-cuculi L.	Caryophyllaceae	0.37	Weiser	facultative	0	0.22	-	0.11	240.16	23.72
Lychnis chalcedonica L.	Caryophyllaceae	0.10	Weiser	none	-	-	-	-	-	-
Lythrum salicaria L.	Lythraceae	1.31	Weiser	facultative	15	0.17	-	0.28	164.12	24.37
Lythrum virgatum L.	Lythraceae	-0.89	Weiser	obligatory	40	-	-	-	-	-
Malva sylvestris L.	Malvaceae	0.66	Weiser	obligatory	-	-	-	-	-	22.65
Melilotus latissimus Thuill.	Fabaceae	1.14	Keser 2015	-	-	-	-	-	-	-
Melilotus officinalis (L.) Pallas	Fabaceae	1.37	Keser 2015	obligatory	35	0.29	3.75	0.12	100.00	30.57
Myosotis arvensis (L.) Hill	Boraginaceae	0.71	Keser 2015	facultative	-	0.10	-	0.38	318.01	33.89
Myosotis scorpioides L.	Boraginaceae	0.57	Keser 2015	facultative	-	-	-	-	-	47.78
Nardus stricta L.	Poaceae	0.55	Weiser	obligatory	47	0.29	8.67	-	32.79	9.76
Persicaria maculosa S. F. Gray	Polygonaceae	1.15	Keser 2015	facultative	-	-	-	-	-	-
Peucedanum ostruthium (L.) Koch	Apiaceae	0.10	Keser 2014	obligatory	-	-	-	-	-	-
Phleum phleoides (L.) H. Karst.	Poaceae	0.37	Weiser	facultative	39	-	-	-	-	17.52

Plantago lanceolata L.	Plantaginaceae	0.54	Weiser	obligatory	81	0.23	10.28	0.14	225.10	17.88
Plantago major L.	Plantaginaceae	0.42	Keser 2015	obligatory	72	0.16	18.33	0.18	184.77	23.05
Plantago media L.	Plantaginaceae	0.69	Keser 2015	obligatory	73	0.25	20.97	0.14	247.05	18.73
Poa compressa L.	Poaceae	0.05	Keser 2014	facultative	100	-	8.04	-	54.79	18.28
Poa pratensis L.	Poaceae	-0.23	Belter	facultative	48	0.20	8.87	0.11	305.26	21.17
Potentilla recta L.	Rosaceae	0.69	Weiser	obligatory	100	0.14	-	0.54	102.17	16.56
Ranunculus acris L.	Ranunculaceae	0.82	Weiser	obligatory	57	0.35	11.97	0.12	133.81	23.52
Ranunculus arvensis L.	Ranunculaceae	0.59	Keser 2015	obligatory	42	-	-	-	-	27.40
Ranunculus bulbosus L.	Ranunculaceae	0.19	Weiser	obligatory	-	0.16	11.24	0.28	132.10	18.86
Rumex acetosa L.	Polygonaceae	1.08	Keser 2015	facultative	21	0.24	9.23	0.25	161.13	29.02
Rumex aquaticus L.	Polygonaceae	0.77	Weiser	-	-	-	7.74	-	-	24.32
Rumex crispus L.	Polygonaceae	1.29	Keser 2015	facultative	76	0.18	3.24	0.33	154.31	22.65
Rumex triangulivalvis (Danser) Rech. f.	Polygonaceae	0.32	Belter	-	-	-	-	-	-	-
Salvia pratensis L.	Lamiaceae	1.60	Weiser	obligatory	-	-	-	-	-	23.53
Sanguisorba minor Scop.	Rosaceae	0.87	Weiser	obligatory	38	0.46	13.09	0.18	118.72	20.31
Sanguisorba officinalis L.	Rosaceae	1.24	Weiser	obligatory	59	0.31	13.21	0.21	109.82	19.64
Saponaria officinalis L.	Caryophyllaceae	-0.01	Keser 2014	none	-	-	-	-	-	23.35
Scorzonera laciniata L.	Asteraceae	1.20	Weiser	-	-	-	-	-	-	18.31
Senecio aquaticus Hill.	Asteraceae	0.87	Weiser	-	-	-	-	-	-	25.33
Senecio erraticus Bertol.	Asteraceae	1.02	Weiser	-	-	-	-	-	-	-
Silene dioica (L.) Clairv.	Caryophyllaceae	-0.26	Keser 2014	facultative	-	-	27.81	-	-	37.72
Silene nutans L.	Caryophyllaceae	0.23	Weiser	facultative	0	-	-	-	-	23.15
Solidago missouriensis Nutt.	Asteraceae	0.46	Belter	obligatory	-	0.32	10.93	0.10	100.21	-
Sonchus arvensis L.	Asteraceae	0.90	Keser 2014	facultative	30	-	-	0.22	40.22	21.50
Stachys germanica L.	Lamiaceae	1.02	Weiser	obligatory	-	-	-	-	-	22.10
Symphyotrichum ericoides (L.) GL Nesom	Asteraceae	0.44	Belter	obligatory	-	0.33	11.02	0.15	73.84	-
Symphyotrichum falcatum (Lindl.) GL Nesom	Asteraceae	0.06	Belter	obligatory	-	0.31	8.60	0.12	70.79	-
Symphyotrichum laeve (L.) A. Löve et D. Löve	Asteraceae	0.39	Belter	obligatory	-	0.32	9.78	0.19	69.91	-
Tanacetum vulgare L.	Asteraceae	1.19	Weiser	facultative	57	0.16	-	0.29	132.23	18.81
Teucrium scorodonia L.	Lamiaceae	-0.10	Keser 2014	obligatory	-	-	-	-	-	16.87
Thalictrum flavum L.	Ranunculaceae	0.37	Weiser	-	-	-	-	-	-	26.10

Thalictrum lucidum L.	Ranunculaceae	-0.15	Weiser	obligatory	74	-	-	-	-	-
Thalictrum minus L.	Ranunculaceae	0.76	Weiser	obligatory	52	-	-	-	47.93	15.80
Tragopogon dubius Scop.	Asteraceae	1.79	Keser 2015	obligatory	-	0.36	6.75	0.19	65.31	27.03
Trifolium montanum L.	Fabaceae	-0.84	Weiser	obligatory	48	0.25	-	0.11	238.07	18.67
Trifolium pannonicum Jacq.	Fabaceae	0.11	Weiser	-	-	-	-	-	-	-
Trifolium pratense L.	Fabaceae	0.60	Weiser	facultative	65	0.26	22.00	0.16	175.98	21.78
Trifolium repens L.	Fabaceae	0.68	Weiser	obligatory	63	0.26	24.13	0.13	189.98	28.89
Verbascum phoeniceum L.	Scrophulariaceae	0.48	Weiser	obligatory	53	-	-	-	-	-
Verbena officinalis L.	Verbenaceae	0.81	Weiser	facultative	40	-	-	-	-	14.20
Veronica agrestis L.	Plantaginaceae	1.01	Keser 2015	facultative	-	-	-	-	-	55.20
Veronica hederifolia L.	Plantaginaceae	1.77	Keser 2015	obligatory	-	-	-	-	-	33.93
Veronica chamaedrys L.	Plantaginaceae	0.12	Keser 2014	facultative	38	0.15	10.00	0.11	349.97	33.36
Veronica spicata L.	Plantaginaceae	0.43	Weiser	obligatory	-	-	-	-	-	8.76
Veronica teucrium L.	Plantaginaceae	0.20	Weiser	obligatory	75	-	-	-	-	-

Table S3: Results of phylogenetic principal component analysis (pPCA) of 44 species and the position of root foraging precision and root traits (root diameter, N content, RTD, SRL) on first four axes (PCA 1-4), which described 97 % of the proportion of variance. The result of phylogenetic canonical correlation analysis (pCCA) of the same set of species (CCA 1), the canonical correlation was 0.42, and the p-value was 0.11. The lambda of both pPCA and pCCA was 0.285.

	PCA 1	PCA 2	PCA 3	PCA 4		CCA 1
Proportion of variance	0.33	0.29	0.23	0.12		-
Standard deviation	1.29	1.20	1.07	0.76		-
Root foraging precision	-0.33	-0.66	0.41	0.53		-11.57
Root diameter	0.29	-0.86	-0.26	-0.25		-8.36
N content	0.32	0.05	-0.84	0.43		8.08
RTD	0.77	0.39	0.39	0.23		2.96
SRL	-0.89	0.32	-0.20	0.08		-2.08

Table S4: Correlations of all fine-root traits, SLA, and intensity of mycorrhizal colonization. Phylogenetic correlation coefficients are in the upper triangle of the matrix; significant ones (P <= 0.05) are in bold. The numbers in the lower triangle (in grey) represent the number of species for which the correlation was tested.

	Root diameter	SRL	N content	RTD	Intensity of myc. colonization	SLA
Root diameter	1	**-0.385**	**0.614**	0.067	-0.014	-0.090
SRL	62	1	-0.243	**-0.641**	-0.049	0.180
N content	46	56	1	**0.359**	0.036	-0.236
RTD	60	66	**49**	1	0.263	**0.523**
Intensity of myc. colonization	40	46	**38**	41	1	-0.235
SLA	49	58	**46**	50	55	1

Table S5: Phylogenetic conservatism indices for SLA, fine-root traits, root foraging precision, and intensity of mycorrhizal colonization. Bold values indicate traits showing stronger phylogenetic signals than expected at random ($p < 0.05$).

	λ	CI (λ)	P (λ=0)
SLA	0	0, 0.218	1
Root diameter	0.377	0.026, 0.761	**0.029**
N content	0.528	0.163, 0.814	**<0.001**
RTD	0	0, 0.35	1
SRL	0.507	0.14, 0.81	**0.001**
Root foraging precision	0.096	0, 0.487	0.132
Intensity of mycorrhizal colonization	0.431	0, 0.744	**0.06**

Table S6: Linear regressions of the relationship of root foraging precision as predicted by SLA, root traits, or mycorrhiza in interaction with the origin of the root foraging precision (Study) without taking phylogeny into account. Root foraging precision comes from four studies with the same basic methodology but several differences (Belter 2014, Keser et al. 2014, Keser et al. 2015, Weiser et al.). Each trait was tested separately. Mycorrhizal status had three categories – obligatory, facultative, and non-mycorrhizal. The number of species in analyses ranged from 60 to 106. The results did not substantially differ from the same models accounting for phylogeny (Table 1).

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Study	3	7.108	2.370	12.529	**< 0.001**
SLA [log]	1	0.059	0.059	0.312	0.578
Study * SLA	3	0.308	0.103	0.543	0.654
Residuals	83	15.697	0.189		
Study	3	5.865	1.955	13.107	**< 0.001**
Root diameter [log]	1	0.180	0.180	1.208	0.277
Study * Root diameter	3	0.779	0.260	1.742	0.169
Residuals	54	8.054	0.149		
Study	3	7.212	2.404	18.504	**< 0.001**
N content [log]	1	0.201	0.201	1.550	0.219
Study * N content	3	0.591	0.197	1.516	0.221
Residuals	52	6.756	0.130		
Study	3	8.421	2.807	17.998	**< 0.001**
RTD [log]	1	0.084	0.084	0.541	0.465
Study * RTD	3	0.411	0.137	0.878	0.458
Residuals	58	9.045	0.156		
Study	3	8.241	2.747	17.265	**< 0.001**
SRL [sqrt]	1	0.257	0.257	1.615	0.208
Study * SRL	3	1.113	0.371	2.331	0.082
Residuals	66	10.501	0.159		
Study	3	8.869	2.956	14.670	**< 0.001**
Mycorrhizal status	2	0.097	0.048	0.240	0.787
Study * Myc. status	4	0.702	0.175	0.870	0.485
Residuals	96	19.346	0.202		
Study	3	2.261	0.754	3.676	**0.018**
Mycorrhizal intensity	1	0.060	0.060	0.291	0.592
Study * Myc. intensity	3	0.203	0.068	0.330	0.804
Residuals	52	10.661	0.205		

Table S7: Linear models of the root foraging precision in response to root traits and mycorrhizal status combined. Each root trait was tested separately. The study factor indicates the origin of root foraging precision data and has four categories: Belter 2014, Keser et al. 2014, Keser et al. 2015, and Weiser et al. The number of species in analyses ranged from 51 to 64. Mycorrhizal status had two categories—obligatory and facultative. The non-mycorrhizal category was not included in the models as there were missing data in interaction with the author category. The results did not substantially differ from the same models accounting for phylogeny (Table 2).

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Study	3	4.957	1.653	10.100	**< 0.001**
Root diameter [log]	1	0.227	0.227	1.389	0.244
Mycorrhizal status	1	0.196	0.196	1.199	0.279
Root diameter * Myc. status	1	0.384	0.385	2.350	0.132
Residuals	49	8.017	0.164		
Study	3	5.397	1.799	12.393	**< 0.001**
N content [log]	1	0.041	0.041	0.279	0.600
Mycorrhizal status	1	0.028	0.028	0.194	0.661
N content * Myc. status	1	0.025	0.025	0.171	0.682
Residuals	44	6.387	0.145		
Study	3	6.136	2.045	12.444	**< 0.001**
RTD [log]	1	0.036	0.037	0.222	0.640
Mycorrhizal status	1	0.004	0.004	0.026	0.872
RTD * Myc. status	1	0.069	0.069	0.418	0.521
Residuals	51	8.382	0.164		
Study	3	6.005	2.002	11.763	**< 0.001**
SRL [sqrt]	1	0.453	0.453	2.660	0.108
Mycorrhizal status	1	0.073	0.073	0.427	0.516
SRL * Myc. status	1	0.589	0.589	3.459	0.068
Residuals	57	9.700	0.170		

Table S8: The comparison of minimal and maximal values and first and third quartiles of fine-root trait data used in our study with data for all herbaceous species living in similar conditions found in the GRooT. To select species from the GRooT that live in similar conditions as the species in our dataset, we used non-woodiness, latitude from 23.5 to 66.5, and field experiments only as filters. The number of species for which we had data is written in the column "number of species".

	fine-root trait	minimal value	maximal value	1st quartile	3rd quartile	number of species
species in the study	root diameter	0.10	0.50	0.18	0.29	62
	N content	2.04	36.88	8.63	13.36	60
	RTD	0.08	0.58	0.14	0.33	66
	SRL	7.43	465.30	66.46	220.05	74
species from the GRooT	root diameter	0.11	0.94	0.15	0.41	164
	N content	2.07	28.70	8.02	12.41	219
	RTD	0.03	0.84	0.13	0.33	92
	SRL	2.79	433.50	22.64	88.70	294

Table S9: Phylogenetic PCA axis loadings of the first three axes as predictors of root foraging precision in linear models. Each axis loading was tested separately. The significant effects of axis loadings on root foraging precision are in bold. The number of species in the analyses was the same as their number in phylogenetic PCA (44 species; PCA with root foraging precision, root diameter, N content, RTD, and SRL). The PCA axis loadings contain scores of species on each of the PCA axis.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
PCA axis 1	1	0.550	0.550	2.849	0.099
Residuals	42	8.111	0.193		
PCA axis 2	1	3.958	3.958	35.350	**< 0.001**
Residuals	42	4.703	0.112		
PCA axis 3	1	0.918	0.918	4.978	**0.031**
Residuals	42	7.743	0.184		

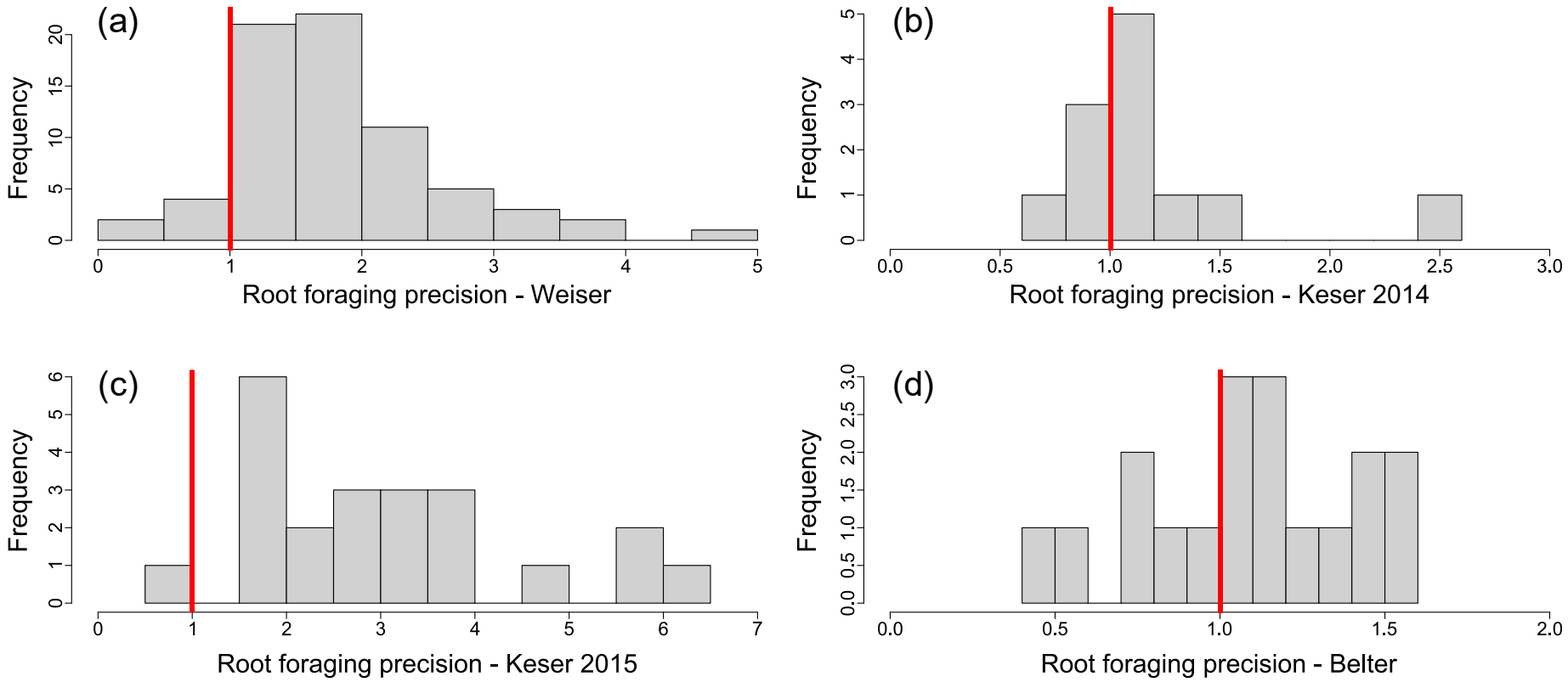


Fig. S1: Root foraging precision (biomass of roots in nutrient-rich part/biomass of roots in the nutrient-poor part) in four datasets used in our study (Belter 2014 (d), Keser et al. 2014 (b), Keser et al. 2015 (c), Weiser et al. (a)). Values of root foraging precision above 1 mean that plants create more roots in the nutrient-rich area; values below 1 mean that plants create more roots in the nutrient-poor area. Frequency indicates the number of species.

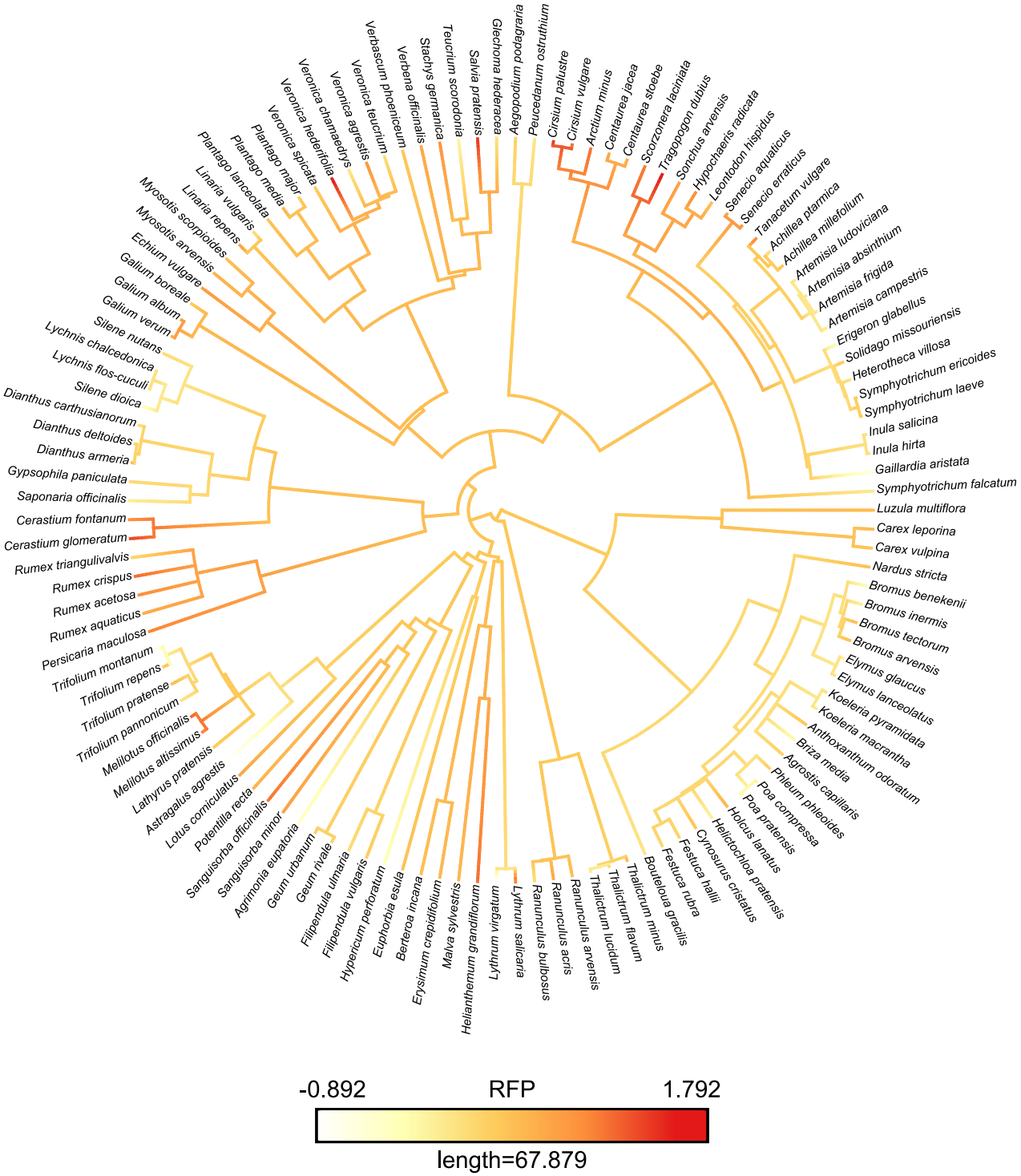


Fig. S2: Phylogenetic tree representing the overall evolutionary dependence of root foraging precision (RFP) on the dataset of 123 species. The phylogenetic signal in RFP was very weak (Pagel's lambda 0.096 with 95% confidence interval [0, 0.487]). We plotted the phylogenetic tree with function contMap from package phytools with ancestral states as maximum likelihood estimates based on a Brownian motion model of evolution estimated via function fastAnc (Revell 2012).

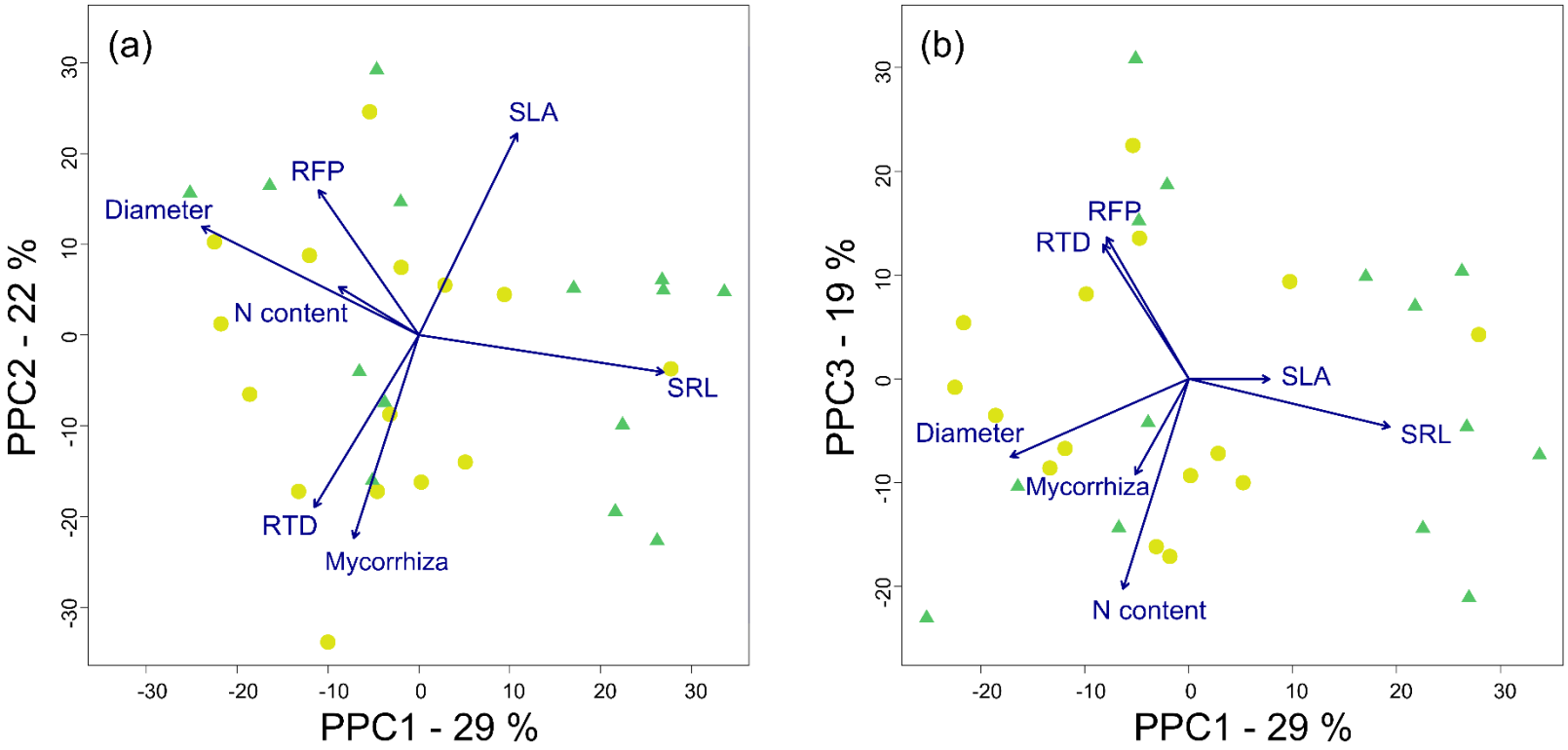


Fig. S3: Phylogenetic principal component analysis of root foraging precision (RFP) and root traits (root diameter, N content, RTD, SRL, SLA, and mycorrhizal colonization intensity) for 29 species. We show the position of traits on the first and second axes (a) and the first and third axes (b) with the proportion of variance explained next to the axe's labels. Each point represents a single plant species and is marked according to their mycorrhizal status (yellow circle— obligatory mycorrhiza, green triangle—facultative mycorrhiza).

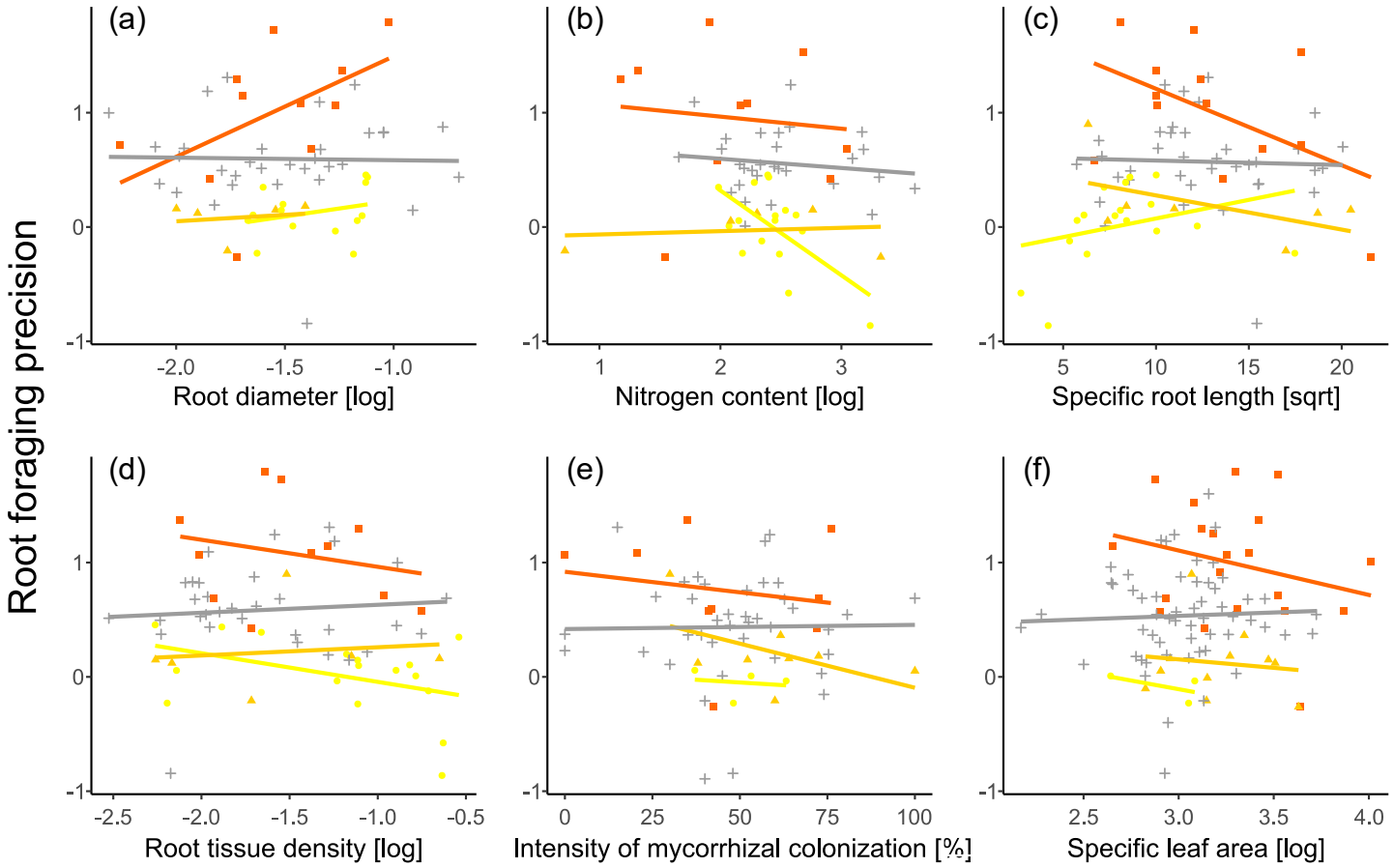


Fig. S4: Relationship of root diameter (a), N content (b), SRL (c), RTD (d), the intensity of mycorrhizal colonization (e), and SLA (f) with root foraging precision from each study of root foraging precision separately. Each point represents a single plant species and is marked according to the origin of root foraging precision data (Belter 2014 – yellow circle, Keser et al. 2014 – orange triangle, Keser et al. 2015 – red square, Weiser et al. – grey plus). Values of traits are transformed – root diameter, nitrogen content, root tissue density, and specific leaf area are log-transformed; specific root length is sqrt-transformed; the intensity of mycorrhizal colonization is in the percent. Values of root foraging precision above 0 mean that plants create more roots in the nutrient-rich area, values below 0 mean that plants create more roots in the nutrient-poor area. We found no significant relationship between root foraging precision and root traits, and the effects of root traits in interaction with the author of root foraging data were also non-significant ($p > 0.05$; see Table 1 in the main text).

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