



Article Fine-Root C:N:P Stoichiometry and Its Driving Factors Are Different between Arbuscular and Ectomycorrhizal Plants in China

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Abstract: Fine roots are essential for terrestrial biogeochemical cycles. Mycorrhizal fungi's functions in regulating the uptake of carbon (C), nitrogen (N), and phosphorus (P) in plants are increasingly being recognized. However, the influence of mycorrhizae on Chinese plants' fine-root stoichiometry has not been considered. Herein, 772 plants with identified mycorrhizal types were divided into arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) types to investigate the differences in their fine-root stoichiometry and their driving factors. The results showed that the AM and ECM fine-root stoichiometries were significantly different (p < 0.001; p < 0.05). The AM plants' fine-root stoichiometry was mainly affected by the soil environment (8.76–90.12%), while ECM plants were more sensitive to climatic factors (23.51–52.41%). Further analysis showed that the mean annual temperature (MAT) was significantly correlated with AM plants' fine-root C and P and ECM plants' fine-root N and P. Mean annual precipitation (MAP) was significantly correlated with all AM plants' fine-root elements (p < 0.01) but was only negatively correlated with ECM fine-root P. It was concluded that the mycorrhizal type affects the response of the fine-root stoichiometry to climate and soil variations. Therefore, the mycorrhizal effect deserves attention when studying the relationship between plant nutrient uptake and environmental changes.

Keywords: fine root; stoichiometry; arbuscular mycorrhiza; ectomycorrhiza; climate; soil environment

1. Introduction

Ecological stoichiometry refers to the balance between various chemical elements in ecological interactions and organisms and is a method used to study the carbon (C), nitrogen (N), and phosphorus (P) concentrations of plants. The study of ecological stoichiometry is helpful for us to have a better understanding of ecosystem functions and the nutrient cycle. C, N, and P are the three most basic elements of plant life activities. C is a key structural factor in plants, and N and P are vital components of proteins and nucleic acids, which are also effective indicators of plant growth restriction in soil [1]. Thus, N and P are widely used to predict plant nutrient restriction [2,3] and the response to environmental stress [4]. C:N:P stoichiometry can reflect nutrient restriction in plants, which is a crucial index of nutrient decomposition [5]. Many studies have focused on the response of the leaf C:N:P stoichiometry to environmental changes at regional scales [6,7]; however, little is known about the fine-root C:N:P stoichiometry.

Fine roots are an important means for forest ecosystems to obtain nutrients, and their state changes are closely related to the C and N cycles in these ecosystems [8,9]. The fine-root C:N:P stoichiometry is a crucial factor affecting plant growth and soil nutrient



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Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). concentrations, and it can reflect the utilization of plant nutrients and the adaptability of plants to environmental changes [10]. The mean annual temperature (MAT) and mean annual precipitation (MAP) affect the elemental concentrations in plants by changing their distribution and structure, which are two vital climatic factors that affect species' stoichiometric patterns [11–13]. Because fine roots are very sensitive to environmental changes, it is crucial to understand the biogeochemical cycles to study fine roots' C:N:P stoichiometric characteristics and their responses to the MAT, MAP, and soil environment. Many previous studies have explored the relationships between fine-root C:N:P stoichiometry and the climate, soil nutrients, and plant functional groups [14,15], but whether different mycorrhizae influence the fine-root C:N:P stoichiometry has rarely been considered.

Mycorrhizae, the most extensive symbiosis between plant roots and soil mycorrhizal fungi [16,17], play a crucial role in maintaining biogeochemical cycles and ecosystem functions [18]. Most plants can coexist with mycorrhizal fungi to improve water and nutrient acquisition [19], especially in arbuscular mycorrhizae (AM) and ectomycorrhizae (ECM) [16]. In recent years, more and more studies have found that the functions of AM and ECM are different in ecosystems. Zhang et al. (2018) showed that ECM plants, which usually grow in poor soil, use nutrients more conservatively at a local or global scale [20]. Phillips et al. (2013) found that AM and ECM plants differ in their changing soil carbon and nutrient cycles [21]. Liu et al. (2020) found that AM and ECM caused differences in typical forest and swamp plant leaves' C, N, and P stoichiometric characteristics in the Greater Khingan Mountains [22]. However, it remains to be explored whether the mycorrhizal types affect the responses of the fine-root C:N:P stoichiometry to environmental changes at the Chinese national level.

China has a large-scale climate gradient, which essentially includes all plant types in the world [23,24]. Therefore, China provides an ideal place to study the effects of climate, soil, plant types, and mycorrhizal types on fine-root C:N:P stoichiometry. However, are the responses of plants' fine-root C:N:P stoichiometry to environmental change related to the mycorrhizal types in China? In this study, the differences in AM and ECM plants' fine-root C:N:P stoichiometry were analyzed in China, and the responses of AM and ECM plants' nutrient uptake to environmental changes were investigated. Based on this, the following hypotheses were proposed: (1) plants' fine-root C:N:P stoichiometry varies with the mycorrhizal type; (2) the effect of the mycorrhizal type on plants' fine-root stoichiometry is related to the climate or soil environment.

2. Materials and Methods

2.1. Data Compilation

In this study, the fine-root C, N, and P concentrations in plants and the environmental data of each plant, such as the mean annual temperature (MAT), mean annual precipitation (MAP), soil pH, and soil nutrients (C, N, and P concentrations), were obtained from the database built by Wang et al. (2019) [25]. We referred to Wang et al.'s (2006) [26], Hempel et al.'s (2013) [27], and Shi et al.'s (2020) [28] published literature to identify the mycorrhizal types of each species in the database and established a new database named the AM and ECM Plants Fine-Root C:N:P Stoichiometry Database in China, which contains the mycorrhizal types. First, it was ensured that all species in the database were not fertilized plants or potted or greenhouse plants. Second, we used a fine root diameter of <2 mm. Finally, considering the effect of the soil depth on fine-root nutrients, we selected the C, N, and P concentrations of the fine roots in the upper layer of 0–20 cm in the literature.

In the database, we classified 772 plants into AM and ECM types. AM and ECM plants were divided into herbaceous plants and woody plants according to their growth types to reveal whether the differences in AM and ECM plants' fine-root stoichiometry were related to the growth types. According to the growth characteristics and leaf shapes, plant types were further divided into trees, shrubs, graminoids, forbs, and conifers. Climatic factors included the mean annual temperature (MAT) and mean annual precipitation (MAP), and soil factors included the soil pH and C, N, and P concentrations. We explored the

differences in AM and ECM plants' fine-root stoichiometry and the effects of the plant types, climatic factors, and soil factors on them. According to the statistics, there were 564 AM plants in the database, including 118 trees, 79 shrubs, 358 herbs, and 9 lianas. There were 202 ECM plants, which included 191 trees, 11 shrubs, and 6 herbaceous plants. Because lianas are neither herbaceous nor woody and were few in number, they could not be classified as a subgroup. Please refer to Supplementary Data S1 for specific data.

2.2. Statistical Analysis

The differences in fine-root C:N:P stoichiometry between AM and ECM plants were analyzed by the Mann–Whitney U test. The differences in herbaceous and woody plants were analyzed in the same way. Under different mycorrhizal types, variation partitioning analysis (VPA) was conducted using the R software package "vegan". VPA analysis separates the total variances explained by different factors (climate, soil environment, plant types) into the independent effect of each factor and interactive effect of all factors. To better demonstrate the results, we performed a logarithmic transformation to test the relationship between environmental factors and fine-root stoichiometry in AM and ECM plants. Then, stepwise multiple regression analysis (SMR) was used to establish the relationship between environmental factors (MAT, MAP, soil pH, C, N, P concentration) and fine-root stoichiometry. We compared the R² of the best multiple regression model to evaluate the most influential environmental factors. All statistical analyses were conducted using the SPSS software (2012, ver. 22.0; SPSS Inc., Chicago, IL, USA) and R version 2.15.2 (The R Project for Statistical Computing, Vienna, Austria).

3. Results

3.1. Differences in AM and ECM Plants' Fine-Root C:N:P Stoichiometry

The C concentration of AM plants' fine roots was 443.43 mg g⁻¹ (Figure 1a), which was obviously lower than that of ECM plants (475.54 mg g⁻¹). The N and P concentrations of AM plants were 12.05 mg g⁻¹ and 1.01 mg g⁻¹ (Figure 1b,c), which were higher than those of ECM plants (9.89 mg g⁻¹ and 0.95 mg g⁻¹, respectively). AM and ECM plants' fine-root C:N and C:P also changed with fine-root C, N, P (Figure 1d,e). The C:N (69.16 mg g⁻¹) and C:P (757.97 mg g⁻¹) of ECM plants were higher than those of AM plants (43.04 mg g⁻¹, 565.54 mg g⁻¹). In our observations, the fine-root N:P of AM and ECM plants did not show a significant difference (Figure 1f).

3.2. Fine-Root C:N:P Stoichiometry in AM and ECM Plants Was Different under Different Life Forms

AM and ECM plants were further divided into woody and herbaceous plants (Figure 2). The result indicated that the fine-root C:N:P stoichiometry, under different mycorrhizal types, was closely linked to the plant life type. For fine-root C, C:N, and N:P in AM and ECM plants, there were prominent differences in both herbaceous and woody plants (Figure 2a,d,f), and the fine-root C and C:N in ECM plants (465.20 mg g⁻¹, 476.50 mg g⁻¹) was higher than that in AM plants (Figure 2a,d,f). However, the differences in the N concentration between AM and ECM plants were caused by woody plants, and the N concentration of AM woody plants was higher (1.61 mg g⁻¹). It could be seen that the differences in fine-root C:P between AM and ECM plants were caused by herbaceous plants (Figure 2e). However, the P concentrations of AM and ECM plants had no connection with the plant life forms (Figure 2c). It was concluded that the plant life forms were the main factors leading to the N and C:P differences between AM and ECM plants.



Figure 1. Differences in concentrations of C (a), N (b), P (c), C:N (d), C:P (e), and N:P (f) between arbuscular and ectomycorrhizal plants' fine roots. The red line denotes the median, the two white lines denote the 95% confidence interval, and the mean value is marked below. "ns" indicates that the difference is not significant. * p < 0.05; *** p < 0.001.

3.3. Relative Effects of Climate, Soil, and Plant Types on the AM and ECM Fine-Root C:N:P Stoichiometry

We further analyzed the relative effects of the climate, soil environment, and plant types on AM and ECM plants' fine-root stoichiometry to identify the factors that had the greatest relative influence on plant nutrient uptake. The climatic factors, soil environment, and plant types explained 17.64–90.26% and 2.43–61.10% of the AM and ECM plants' fine-root elemental traits, respectively (Figure 3). The independent effects of the soil environment on the AM fine-root C, N, P, and C:N were greater than those of climatic factors (2.73–11.28%) and plant types (-0.02-3.89%) (Figure 3a–d). Only fine-root C:P and N:P in AM plants were most sensitive to climate (23.86–37.81%), and the independent effect of climate (15.46–16.20%) was similarly greater than those of soil factors (3.77–9.11%) and plant types (-0.91-1.66%). The independent effect of climate explained 27.52%, 37.81%, 23.51%, 52.41%, and 50.88% of ECM plants' fine-root N, P, C:N, C:P, and N:P, respectively (Figure 3b–f), which was greater than the independent effect of the soil environment (2.73–11.28%) and plant type (-0.91-1.17%). However, only the fine-root C in ECM plants was mainly affected by the soil environment (5.45%) (Figure 3a).



Figure 2. Differences in fine-root C (a), N (b), P (c), C:N (d), C:P (e), and N:P (f) in woody and herbaceous plants associated with arbuscular and ectomycorrhiza. The red line denotes the median and the two white lines denote the 95% confidence interval. The number of samples is at the top, and the average is at the bottom. "*", "**", respectively, indicate a significant difference when p < 0.05, p < 0.01, p < 0.001, while "ns" indicates no significance.



Figure 3. Results of variation partitioning analysis for the effects (R^2 , %) of climate, soil, and plant type on AM and ECM plants' fine-root C (**a**), N (**b**), P (**c**), C:N (**d**), C:P (**e**), N:P (**f**), where red font represents AM plants and black font represents ECM plants. The red, green, and blue circles represent the independent effects of climate, soil, and plant types, respectively, and their interactions.

3.4. Climate and Soil Environment's Influences on AM and ECM Plants' Fine-Root C:N:P Stoichiometry

The C, N, P concentrations and their ratios in the fine roots showed the same or opposite patterns with the changes in climate (MAT, MAP) and soil (pH, C, N, P concentrations) (Figure 4a-i). The MAT, MAP, and soil pH explained 3.6%, 6.7%, and 13% of the fine-root C variation in AM plants, respectively (Table S1), while ECM plants' fine-root C had no linear relationship with MAT, MAP, and soil pH (Figure 4a,d,g). There were also significant differences between AM and ECM plants' fine-root N. Fine-root N in AM plants decreased significantly with the increasing MAP, while it had no obvious relationship with MAT and soil pH (Figure 4b,e,h). Fine-root N in ECM plants was negatively correlated with MAT (Figure 4b). AM and ECM plants' fine-root P significantly decreased with the increasing MAT and MAP (Figure 4c,f). MAT explained more changes in ECM plants' P, while MAP explained more changes in AM plants (Table S1). In addition, the P concentration of AM plants was positively correlated with the soil pH (Figure 4i). Only the AM fine-root C:N was negatively correlated with the soil pH (Figure S1g). Both AM and ECM fine-root C:P increased with the increasing MAT and MAP (Figure S1b,e, and the interpretation rate of fine-root C:P in ECM plants was higher than that in AM plants (Table S1). Fine-root N:P also showed the same pattern (Figure S1c,f), but MAT explained more changes in AM plants' fine-root N:P, and MAP explained more changes in ECM plants (Table S1). The P, C:N, C:P, and N:P of AM plants increased with the increasing soil P, C:N, C:P, and N:P, respectively (Figure 5a,d-f), and P, C:P, and N:P in ECM plants also demonstrated the same pattern with soil nutrients (Figure 5a,e,f). Although the variation trends were consistent, there were differences in the interpretation rate between AM and ECM plants (Table S2).



Figure 4. Trends in arbuscular mycorrhizal and ectomycorrhizal plants' fine-root C:N:P stoichiometry along MAT (**a**–**c**), MAP (**d**–**f**), and soil pH (**g**–**i**) gradients in China. The orange triangles represent AM plants and the black hollow circles represent ECM plants. The orange lines represent AM plants and the black lines represent ECM plants. The *p*-values are indicated at the top of each chart.

600

550

500

······ P>0.05

······ P>0.05





Figure 5. Correlations between the arbuscular mycorrhizal and ectomycorrhizal plants' fine-root C (a), N (b), P(c), C:N (d), C:P (e), N:P (f) and the corresponding soil C:N:P stoichiometry. The orange triangles represent AM plants and the black hollow circles represent ECM plants. The orange lines represent AM plants and the black lines represent ECM plants. The p-values are indicated at the top of each chart.

3.5. Stepwise Regression Analysis of Fine-Root C, N, P and Climate and Soil Environment in AM and ECM Plants

Figure 3 proves that the climate and soil environment were the main factors affecting AM and ECM plants' fine-root C:N:P stoichiometry. The R² of fine-root C in AM plants was 12.9%, which indicated that there were 12.9% changes in the response variable because of changes in the combination of MAP and soil pH. Soil pH, in these two control variables, was the most profound (50.27%, p < 0.001), while MAP was a secondary factor (49.74%, p < 0.01). The variation in AM plant N was 8.6%, mainly due to MAT (30.27%, p < 0.01), MAP (52.90%, p < 0.01), and soil pH (16.73%, p < 0.01). For ECM plants, the R² of fine-root N was 18.7%, which was higher than in AM plants. The variation in ECM plants' fine-root N was mainly attributed to MAT (25.11%, *p* < 0.05), MAP (47.76%, *p* < 0.05), soil pH (22.58%, p < 0.05), and soil C (4.55%, p < 0.05). The stepwise regression equation of fine-root P in AM plants screened three significant influencing factors, namely MAP (37.22%, p < 0.01), soil N (27.26%, p < 0.01), and soil P (25.51%, p < 0.01). Among the three significant influencing factors, MAP and soil P are particularly crucial, and this is also consistent with the results of Figures 4c and 5c. The fine-root P in ECM plants was explained by a set of factors including MAT (43.41%, *p* < 0.01), MAP (19.82, *p* < 0.01), soil pH (32.77%, *p* < 0.01), and soil P (3.40%, *p* < 0.01). MAP played an important role in predicting fine-root N, P, C:N, and C:P in AM plants (52.90%, 37.22%, 62.82%, 42.72%), while MAT was the greatest factor in predicting fine-root P (43.41%), C:P (67.91%), and N:P (59.82%) in ECM plants.

4. Discussion

The responses in terms of plant growth and development to environmental changes varied with the mycorrhizal types [29]. Shi et al. (2012) pointed out that mycorrhizae can not only affect the response of the forest ecosystem to climatic changes, but also participate in the C and P cycles in the ecosystem [30]. Vargas et al. (2010) showed that the response of the CO2 flux to temperature and precipitation changes in ecosystems was closely linked to the mycorrhizal types and plant types. AM plants were sensitive to precipitation and ECM plants were mainly affected by the temperature [31]. These studies highlight the vital role of mycorrhizae in plant growth. Therefore, in our research, we evaluated the differences in fine-root C:N:P stoichiometry and the effects of the climate, soil environment, and plant types on them under different mycorrhizal types.

Liu et al. (2020) found that fine-root C was not only related to life types but also to mycorrhizal types in the Greater Khingan Mountains [22]. The fine-root C in ECM plants was higher than in AM plants, which also led to the lower C:N and C:P of AM plants. The results were consistent with our research (Figure 1a,d,e). The fine-root N, P, and N:P of AM plants were higher than those of ECM plants (Figure 1b,c,f). Previous studies also exhibited that ectomycorrhiza, in terms of plant nutrient uptake, was more conservative than arbuscular mycorrhizae, so ECM plants had lower N and P concentrations [25,32]. The differences in the AM and ECM fine-root C:N:P stoichiometry were also related to the life types. Ning et al. (2017) found that woody plants' fine-root C was much higher than that of herbaceous plants when they explored plant leaves and fine-root C:N:P stoichiometries in the Horqin Sand Land [32]. Wright et al. (2004) found that the leaf N concentration per unit mass in herbaceous plants was greater than that in trees and shrubs [33]. Han et al. (2005) [24] and Tian et al. (2021) [34] found that the concentrations of N and P were obviously different among various groups. The N and P concentrations of herbaceous plants were significantly higher than those in woody plants, because fast-growing plants needed more N and P than slow-growing plants [35]. In this study, the AM plants were mostly herbaceous plants, while the ECM plants were mostly woody plants (Figure 2). The C and C:N of AM fine roots were significantly lower than those of ECM plants, especially woody plants (Figure 2a,d). The N, P, and N:P of AM herbaceous plants were higher than those of ECM herbaceous plants (Figure 2b,c,f), which supported the conclusions of the above studies.

Many previous studies have considered the effects of climate and latitude on plant nutrient uptake [36], but they have rarely considered the role of mycorrhizal types. In our research, we were the first to analyze the effects of the climate, soil environment, and plant type on the fine-root C:N:P stoichiometry in AM and ECM plants. Agren (2008) suggested that C, as a structural element of plants, has strong stability [37]. Chen et al. (2018) also showed that the C concentration of fine roots was not affected by the soil environment. However, the results of our research showed that both AM and ECM plants' fine-root C was affected by the soil environment (Figure 3a) [15], especially in AM plants. We attribute this inconsistency to the fact that the previous studies focused on local areas rather than the full spectrum of ecosystems in China. The fine-root N, P, and C:N in AM plants were mainly affected by the soil environment (soil pH, C, N, P) (Figure 3b–d), while ECM fine-root N, P, C:N, C:P, and N:P were more sensitive to climatic factors (MAT, MAP) (Figure 3b-f). This may be related to the characteristics of the host plants and the soil where they were distributed. For example, AM mycorrhizal types were mainly distributed in the tropics, while ECM plants were mainly growing in the temperate zone [38]. Due to a lack of relevant research, the specific reasons need to be further explored.

Our results showed that climate and soil factors had the greatest influence on AM and ECM plants (Figure 3). Therefore, under different mycorrhizal types, we further studied the relationships between the fine-root elements and MAT and MAP. In our study, fine-root C, C:P, and N:P in AM plants were positively correlated with MAT and MAP (Figures 4a and S1B,C), but negatively correlated with N and P (Figure 4b,c). However, only fine-root P, C:P, and N:P in ECM plants changed significantly with MAT and MAP (Figures 4c,f and S1B,C). Our stepwise multiple regression analysis showed that MAP had a stronger effect on the C, N, P, C:N, and C:P of AM plants than ECM plants (Table 1), and the fine-root C, P, C:P, and N:P in ECM plants had stronger sensitivity to MAT changes (Table 1). This supported previous studies showing that AM plants were more sensitive to MAP changes, while MAT had the greatest influence on ECM plants [30,39]. In addition, Shi et al. (2012, 2021) obtained similar findings when studying the relationship between mycorrhizal types and leaf stoichiometry [39,40]. The fine root, as one of the plant organs, also showed the same patterns.

and pH).

Contribution of Predictor (%)									
Fine-Root Elements	Mycorrhizae	MAT	MAP	Soil pH	Soil C	Soil N	Soil P	Significance	R^2
С	AM	-	49.74	50.26	-	-	-	***	0.129
	ECM	25.95	33.87	35.27	-	-	1.30	ns	0.105
Ν	AM	30.27	52.90	16.73	-	-	-	***	0.086
	ECM	25.11	47.76	22.58	4.55	-	-	*	0.187
Р	AM	-	37.22	-	-	27.26	35.51	***	0.186
	ECM	43.41	19.82	32.77	-	-	3.40	***	0.464
C:N	AM	37.18	62.82	-	-	-	-	***	0.099
	ECM	31.20	48.71	18.45	-	-	1.44	***	0.316
C:P	AM	-	42.72	-	-	24.65	32.62	***	0.178
	ECM	67.91	3.40	12.48	-	-	16.21	***	0.455
N:P	AM	31.40	-	-	-	32.88	35.73	***	0.135
	ECM	59.82	23.02	9.82	-	-	7.34	*	0.207

AM: arbuscular mycorrhizae, ECM: ectomycorrhiza, MAP: mean annual precipitation, MAT: mean annual temperature. Significance levels: ns, non-significance; * p < 0.05; *** p < 0.001.

Both the soil pH and soil nutrients are vital factors that can affect plants' nutrient absorption [26,35,41,42]. Our results showed that the fine-root C, P, C:N, C:P, and N:P of AM plants were correlated with the soil pH, while those of ECM plants were not. This was contrary to a previous study that indicated that ectomycorrhizal plants were more sensitive to changes in soil pH [43]. This may have been caused by differences in species composition [44], and the specific reasons remain to be studied. Previous studies found that the C concentration in fine roots was not correlated with soil C, while P, C:N, and C:P in the fine roots were correlated with corresponding soil nutrients [15]. Our results were consistent with this study, as only fine-root P, C:P, and N:P in AM and ECM plants were positively correlated with the corresponding soil nutrients. This was related to the fact that AM and ECM plants have different N and P acquisition strategies [45]. In addition, this may also be related to the distribution of mycorrhizal fungi. AM plants tend to live in areas where N is abundant but P is deficient, while ECM plants tend to be distributed in areas where N is deficient [46,47].

Our study not only clarified the role of mycorrhizae in fine-root C, N, and P absorption, but also explored the responses of different mycorrhizal fine-root C, N, and P to MAT, MAP, soil pH, and C, N, and P concentrations. Many previous studies have also explored the relationship between the fine roots and soil layers, latitude, elevation, and soil communities [48,49]. The data that we had access to only included MAT, MAP, soil pH, and C, N, and P concentrations, so the influence of other soil factors, such as soil texture and soil type, on the fine-root stoichiometry remains to be explored. At the same time, in addition to the most widely studied C, N, and P, K, as the second most abundant element in plant photosynthesis, also deserves our attention [50].

5. Conclusions

There were differences in AM and ECM plants' fine-root C:N:P stoichiometry in China. Fine-root N, P, and N:P were significantly increased by AM plants, while the C concentration was decreased. The effects of plant types, climatic factors, and the soil environment on fine-root C, N, and P varied with the mycorrhizal type. Although the variation trends of fine-root N, C:P, and N:P in AM and ECM plants were consistent with those of MAT, MAP, and soil pH, they also showed great differences depending on the mycorrhizal types. AM plants were more sensitive to MAP changes. In summary, our results confirm that the

responses of fine-root C:N:P stoichiometries to environmental changes differ between AM and ECM plants in China.

Supplementary Materials: The following supporting information can be downloaded at: https: //www.mdpi.com/article/10.3390/agronomy13102512/s1. Figure S1: Relationship between the ratio of AM and ECM plants' fine-root C, N, P and MAT, MAP, soil pH. Table S1: Correlation coefficients of AM and ECM fine-root C:N:P stoichiometry with climate and soil pH. Table S2: Correlation coefficients of AM and ECM fine-root C:N:P stoichiometry with corresponding soil nutrients. Database S1: C, N, and P concentrations of species and corresponding MAT, MAP, and plant function groups.

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Data Availability Statement: The original contributions presented in the study are included in the article/Supplementary Materials; further inquiries can be directed to the corresponding authors.

Conflicts of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

References

- 1. Reich, P.B.; Oleksyn, J. Global patterns of plant leaf N and P in relation to temperature and latitude. *Proc. Natl. Acad. Sci. USA* **2004**, *101*, 11001–11006. [CrossRef]
- 2. Sperfeld, E.; Wagner, N.D.; Halvorson, H.M. Bridging ecological stoichiometry and nutritional geometry with homeostasis concepts and integrative models of organism nutrition. *Funct. Ecol.* **2017**, *3*, 286–296. [CrossRef]
- 3. Zeng, Q.; Lal, R.; Chen, Y. Soil, leaf and root ecological stoichiometry of Caragana korshinskii on the Loess Plateau of China in relation to plantation age. *PLoS ONE* **2017**, *12*, e0168890. [CrossRef]
- 4. Jing, M.M.; Shi, Z.Y.; Zhang, M.G.; Zhang, M.H.; Wang, X.H. Nitrogen and Phosphorus of Plants associated with Arbuscular and Ectomycorrhizas Are Differentially Influenced by Drought. *Plants* **2022**, *11*, 2429. [CrossRef]
- Elser, J.J.; Fagan, W.F.; Denno, R.F.; Dobberfuhl, D.R.; Folarin, A.; Huberty, A.; Interlandi, S.; Kilham, S.S.; McCauley, E.; Schulz, K.L.; et al. Nutritional constraints in terrestrial and freshwater food webs. *Nature* 2000, 408, 578–580. [CrossRef]
- Wu, S.W.; Shi, Z.Y.; Huang, M.; Yang, S.; Yang, W.Y.; Li, Y.J. Influence of Mycorrhiza on C:N:P Stoichiometry in Senesced Leaves. J. Fungi 2023, 9, 588. [CrossRef]
- Tian, D.S.; Reich, P.B.; Chen, H.Y.H.; Xiang, Y.Z.; Luo, Y.Q.; Shen, Y.; Meng, C.; Han, W.X.; Niu, S. Global changes alter plant multi-element stoichiometric coupling. *New Phytol.* 2018, 221, 807–817. [CrossRef]
- Li, M.; Huang, C.H.; Yang, T.X.; Drosos, M.; Wang, J.Z.; Kang, X.M.; Liu, F.L.; Xi, B.D.; Hu, Z.Y. Role of plant species and soil phosphorus concentrations in determining phosphorus: Nutrient stoichiometry in leaves and fine roots. *Plant Soil* 2019, 445, 231–242. [CrossRef]
- Fu, X.F.; Xu, C.H.; Geng, Q.H.; Ma, X.C.; Zhang, H.G.; Cai, B. Effects of nitrogen application on the decomposition of fine roots in temperate forests: A meta-analysis. *Plant Soil* 2022, 472, 77–89. [CrossRef]
- Guo, R.Q.; Xiong, D.C.; Song, T.T.; Cai, Y.Y.; Chen, T.T.; Chen, W.Y.; Zheng, X.; Chen, G.S. Effect of simulated nitrogen deposition on stoichiometry of fine roots on Chinese fir (*Cunninghamia lanceolata*) seedlings. *Acta Ecol. Sin.* 2018, 38, 6101–6110.
- 11. Reich, P.B. Global biogeography of plant chemistry: Filling in the blanks. New Phytol. 2005, 168, 263–266. [CrossRef]
- 12. Wright, I.J.; Reich, P.B.; Westoby, M. Strategy-shifts in leaf physiology, structure and nutrient content between species of high and low rainfall, and high and low nutrient habitat. *Funct. Ecol.* **2001**, *15*, 423–434. [CrossRef]
- 13. Xia, C.; Yu, D.; Wang, Z.; Xie, D. Stoichiometry patterns of leaf carbon, nitrogen and phosphorous in aquatic macrophytes in eastern China. *Ecol. Eng.* **2014**, *70*, 406–413. [CrossRef]
- Sardans, J.; Grau, O.; Chen, H.Y.H.; Janssens, I.A.; Ciais, P.; Piao, S.L.; Penuelas, J. Changes in nutrient concentrations of leaves and roots in response to global change factors. *Glob. Chang. Biol.* 2017, 23, 3849–3856. [CrossRef]
- 15. Chen, X.P.; Guo, B.Q.; Zhong, Q.L.; Wang, M.T.; Li, M.; Yang, F.C.; Cheng, D.L. Response of fine root carbon, nitrogen and phosphorus stoichiometry to soil nutrients in Pinus taiwanensis along an elevation gradient in the Wuyi mountains. *Acta Ecol. Sin.* **2018**, *38*, 273–281. [CrossRef]
- 16. Smith, S.E.; Read, D.J. Mycorrhizal Symbiosis, 3rd ed.; Academic Press: London, UK, 2008.

- 17. Averill, C.; Bhatnagar, J.M.; Dietze, M.C.; Pearse, W.D.; Kivlin, S.N. Global imprint of mycorrhizal fungi on whole-plant nutrient economics. *Proc. Natl. Acad. Sci. USA* **2019**, *116*, 23163–23168. [CrossRef]
- Sizonenko, T.A.; Dubrovskiy, Y.A.; Novakovskiy, A.B. Changes in mycorrhizal status and type in plant communities along altitudinal and ecological gradientsa case study from the Northern Urals (Russia). *Mycorrhiza* 2020, 30, 445–454. [CrossRef]
- Van der Heijden, M.G.A.; Martin, F.M.; Selosse, M.A.; Sanders, T.R. Mycorrhizal ecology and evolution: The past, the present, and the future. *New Phytol.* 2015, 205, 1406–1423. [CrossRef]
- Zhang, H.Y.; Lu, X.T.; Hartmann, H.; Kelle, A.; Han, X.G.; Trumbore, S.; Phillips, R. Foliar nutrient resorption differs between arbuscular mycorrhizal and ectomycorrhizal trees at local and global scales. *Glob. Ecol. Biogeogr.* 2018, 27, 875–885. [CrossRef]
- Phillips, R.P.; Brzostek, E.; Midgley, M.G. The mycorrhizal-associated nutrient economy: A new framework for predicting carbon-nutrient couplings in temperate forests. *New Phytol.* 2013, 199, 41–51. [CrossRef]
- 22. Liu, X.Y.; Hu, Y.K. Carbon, nitrogen and phosphorus stoichiometry in leaves and fine roots of typical forest swamps in the Greater Khingan Mountains. *Chin. J. Appl. Ecol.* **2020**, *31*, 3385–3394. [CrossRef]
- Fang, J.Y.; Song, Y.C.; Liu, H.Y.; Piao, S.L. Vegetation–Cclimate relationship and its application in the division of vegetation zone in China. Acta Bot. Sin. 2002, 44, 1105–1122.
- Han, W.X.; Fang, J.Y.; Guo, D.L.; Zhang, Y. leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China. New Phytol. 2005, 168, 377–385. [CrossRef] [PubMed]
- Wang, Z.Q.; Lv, S.Q.; Song, H.; Wang, M.C.; Zhao, Q.; Huang, H.; Niklas, J.K. Plant type dominates fine-root C:N:P stoichiometry across China: A meta-analysis. J. Biogeogr. 2019, 47, 1019–1029. [CrossRef]
- 26. Wang, B.; Qiu, Y.L. Phylogenetic distribution and evolution of mycorrhizas in land plants. Mycorrhiza 2006, 16, 299–363. [CrossRef]
- 27. Hempel, S.; Götzenberger, L.; Kühn, I.; Michalski Stefan, G.; Rillig Matthias, C.; Zobel, M.; Moora, M. Mycorrhizas in the central European flora: Relationships with plant life history traits and ecology. *Ecology* **2013**, *94*, 1389–1399. [CrossRef]
- 28. Shi, Z.Y.; Li, K.; Zhu, X.Y.; Wang, F.Y. The worldwide leaf economic spectrum traits are closely linked with mycorrhizal traits. *Fungal Ecol.* **2020**, *43*, 100877. [CrossRef]
- 29. Zhang, S.; Yuan, M.L.; Shi, Z.Y.; Yang, S.; Zhang, M.G.; Sun, L.R.; Gao, J.K.; Wang, X.G. The variations of leaf δ13C and its response to environmental changes of arbuscular and ectomycorrhizal plants depend on life forms. *Plants* **2022**, *11*, 3236. [CrossRef]
- Shi, Z.Y.; Wang, F.Y.; Miao, Y.F. Responses of forest net primary productivity to climate change in different mycorrhizal types. *Chin. J. Plant Ecol.* 2012, *36*, 1165–1171. [CrossRef]
- Vargas, R.; Baldocchi, D.D.; Querejeta, J.I.; Curtis, P.S.; Hasselquist, N.J.; Janssens, I.A.; Allen, M.F.; Montagnani, L. Ecosystem CO₂ fluxes of arbuscular and ectomycorrhizal dominated vegetation types are differentially influenced by precipitation and temperature. *New Phytol.* 2010, 185, 226–236. [CrossRef]
- Ning, Z.Y.; Li, Y.L.; Yang, H.L.; Sun, D.C.; Bi, J.D. Carbon, nitrogen and phosphorus stoichiometry in leaves and fine roots of dominant plants in Horqin Sandy Land. *Chin. J. Plant Ecol.* 2017, 41, 1069–1080. [CrossRef]
- 33. Wright, I.J.; Reich, P.B.; Westoby, M.; Ackerly, D.D.; Baruch, Z.; Bongers, F.; Chapin, T.; Cornelissen, J.H.C.; Diemer, M.; Flexas, J.; et al. The worldwide leaf economics spectrum. *Nature* **2004**, *428*, 821–827. [CrossRef] [PubMed]
- 34. Tian, D.; Yan, Z.B.; Fang, J.Y. Plant ecological stoichiometry and its main hypotheses. *Chin. J. Plant Ecol.* **2021**, 45, 682–713. [CrossRef]
- Gusewell, S. N:P ratios in terrestrial plants: Variation and functional significance. New Phytol. 2004, 164, 243–266. [CrossRef] [PubMed]
- 36. Yuan, Z.Y.; Chen, H.Y.H. Global-scale patterns of nutrient resorption associated with latitude, temperature and precipitation. *Glob. Ecol. Biogeogr.* **2009**, *18*, 11–18. [CrossRef]
- Ågren, G.I. Stoichiometry and nutrition of plant growth in natural communities. *Annu. Rev. Ecol. Evol. Syst.* 2008, 39, 153–170. [CrossRef]
- Pate, J.S.; Stewart, G.R.; Unukovich, M. 15N natural abundance of plant and soil components of a Banksia woodland ecosystem in relation to nitrate utilisation, life form, mycorrhizal status and N2-fixing abilities of component species. *Plant Cell Environ*. 1993, 16, 365–373. [CrossRef]
- 39. Shi, Z.Y.; Hou, X.G.; Chen, Y.L.; Wang, F.Y.; Miao, Y.F. Foliar stoichiometry under different mycorrhizal types in relation to temperature and precipitation in grassland. *J. Plant Ecol.* **2012**, *6*, 270–276. [CrossRef]
- 40. Shi, Z.Y.; Xu, S.X.; Yang, M.; Zhang, M.G.; Lu, S.C.; Chang, H.Q.; Wang, X.G.; Chen, X.N. Leaf Nitrogen and Phosphorus Stoichiometry are Closely Linked with Mycorrhizal Type Traits of Legume Species. *Legume Res.* **2021**, *44*, 81–87. [CrossRef]
- 41. Sun, J.; Liu, B.Y.; You, Y.; Li, W.P.; Liu, M.; Shang, H.; He, J.S. Solar radiation regulates the leaf nitrogen and phosphorus stoichiometry across alpine meadows of the Tibetan Plateau. *Agric. For. Meteorol.* **2019**, *271*, 92–101. [CrossRef]
- 42. Ma, Y.Z.; Zhong, Q.L.; Jin, B.J.; Lu, H.D.; Guo, B.Q.; Zheng, Y.; Li, M.; Cheng, D.L. Spatial changes and influencing factors of fine root carbon, nitrogen and phosphorus stoichiometry of plants in China. *Chin. J. Plant Ecol.* **2015**, *39*, 159–166.
- 43. Lv, S.C.; Shi, Z.Y.; Zhang, M.G.; Yang, M.; Wang, X.G.; Xu, X.F. Differences of ash content in leaves of different mycorrhizal types and their responses to climate change. *Ecol. Environ. Sci.* **2020**, *29*, 35–40. [CrossRef]
- 44. Broadley, M.R.; Willey, N.J.; Wilkins, J.C.; Baker, A.J.M.; Mead, A.; White, P.J. Phylogenetic variation in heavy metal accumulation in angiosperms. *New Phytol.* 2001, 152, 9–27. [CrossRef] [PubMed]
- Bunn, R.A.; Simpson, D.T.; Bullington, L.S.; Lekberg, Y.; Janos, D.P. Revisiting the "direct mineral cycling" hypothesis: Arbuscular mycorrhizal fungi colonize leaf litter, but why? *ISME J.* 2019, *13*, 1891–1898. [CrossRef]

- 46. Cornelissen, J.H.C.; Aerts, R.; Cerabolini, B.; Werger, M.; van der Heijden, M. Carbon cycling traits of plant species are linked with mycorrhizal strategy. *Oecologia* 2001, 129, 611–619. [CrossRef]
- 47. Read, D.J.; Perez-Moreno, J. Mycorrhizas and nutrient cycling in ecosystem-a journey towards relevance? *New Phytol.* **2003**, 157, 475–492. [CrossRef]
- 48. Han, W.X.; Fang, J.Y.; Reich, P.B.; Woodward, F.I.; Wang, Z.H. Biogeography and variability of eleven mineral elements in plant leaves across gradients of climate, soil and plant functional type in China. *Ecol. Lett.* **2011**, *8*, 788–796. [CrossRef]
- 49. Bennett, J.A.; Maherali, H.; Reinhart, K.O.; Lekberg, Y.; Hart, M.M.; Klironomos, J. Plant soil feedbacks and mycorrhizal type 467 influence temperate forest population dynamics. *Science* 2017, 355, 181–184. [CrossRef]
- 50. Sardans, J.; Penuelas, J. Potassium: A neglected nutrient in global change. Glob. Ecol. Biogeogr. 2015, 24, 261–275. [CrossRef]

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