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Communication

Non-Linear Relationships between Fine Root Functional Traits and Biomass in Different Semi-Arid Ecosystems on the Loess Plateau of China

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Abstract: As a key soil carbon process, changes in plant root growth may have a dramatic impact on the global ecosystem's carbon cycle. Fine root functional traits and fine root biomass can be used as important indexes of plant root growth. Compared with the much better understood relationships between aboveground plant functional traits and aboveground biomass, knowledge on the relationships between fine root functional traits and belowground biomass still remains limited. In this study, plant fine roots in 30 abandoned lands, 9 woodlands, 29 alfalfa grasslands, 30 Caragana shrublands and 29 croplands were sampled at 0–20 and 20–40 cm soil depths in Zhonglianchuan, Yuzhong County, Gansu Province, China (36°02′ N, 104°24′ E), to clarify the characteristics of the relationships between fine root functional traits (e.g., diameter, specific root area (SRA) and specific root length (SRL)) and fine root biomass at 0–20 and 20–40 cm soil depths. The results showed that the relationships between the fine root functional traits and fine root biomass in these ecosystems were robust, allowing for the use of an allometric growth model at both 0–20 and 20–40 cm soil depths ($p < 0.05$). Specifically, the relationship between root diameter and fine root biomass was consistent with highly significant positive power, while highly significant negative power relationships of SRA and SRL with fine root biomass were observed ($p < 0.01$, except the root diameter–biomass models in the woodlands in the 0–20 cm soil layer ($p = 0.017$) and 20–40 cm soil layer ($p = 0.025$)). The results can provide some parameters for these terrestrial ecosystem process models. From this perspective, our study is beneficial in the construction of suitable strategies to increase plant biomass, which will help with the restoration of the semi-arid region of the Loess Plateau of China.

Keywords: root production; specific root length; specific root area; root diameter; allometry; semi-arid ecosystems

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1. Introduction

Plant functional traits are defined as "any trait which impacts fitness indirectly via its effects on growth, reproduction and survival" [1]. The trait difference between different plant species is an important part of plant functional diversity and plays an important role in theoretical research and modeling. The "resource economics trade-off strategy" among the plant functional traits is a landmark discovery in plant physiological ecology, and has become the main mechanism through which to explain the adaptation of different plants to environmental changes [2]. As an important component of plant functional traits, fine root functional traits are considered factors that reflect the ability of plants to compete for soil resources (e.g., root length and mass density) [3,4] and their growth rate (e.g., SRL) [3–5]. Based on the root economics spectrum (RES) [6–12], it may be hypothesized that fine root functional traits can be associated with fast resource acquisition or enhanced resource conservation—a trade-off between plant growth and survival [13]. However, due to the heterogeneity of soil environments and technological limitations, understanding of fine root functional traits is relatively behind that of the well-studied relationships in plant aboveground traits [13,14]. This limits the understanding of the relationship between above- and below-ground functional traits of plants and their adaptation to the environment [15].

There are two important implications of conducting research on fine root functional traits. On the one hand, it has been pointed out that approximately 40% of photosynthetic carbon fixation is allocated to fine roots (diameter < 2 mm) [16]. Therefore, the relationships between fine root functional traits (e.g., diameter, SRA and SRL) and fine root biomass may have important significance for predicting fluxes in the carbon cycle. On the other hand, previous studies have shown that factors affecting fine root functional traits include temperature [17,18], soil water status [19,20], root order [21], soil nutrient availability and resource allocation [22,23], and characteristics of soil microbial communities [24,25]. In addition, Wang et al. (2021) found that species differences affected root traits in the Loess Plateau [26]. For instance, in order to balance nutrient uptake when there are different availabilities of minerals in the rhizosphere, plants trigger fitness strategies such as enhancing root growth [27]. Some root traits (e.g., total root length, root diameter, and growth) are negatively affected by bulk density in compacted soil [28]. Soil pH may indirectly modulate the architecture of the root system by altering soil nutrient availability [29]. Accordingly, fine root functional traits can integrate environmental changes.

Plant biomass changes can be characterized using allometric growth models [30]. Plant allometric models are often constructed using the relationship between aboveground biomass and height or plant coverage [31]. Current studies on the relationship between fine root biomass and fine root functional traits have mainly focused on some common plants, such as wheat [32,33], alfalfa [34] and sugarcane [35], or specific ecosystems, such as deserts [36], forests [37] and crop ecosystems [38]. Studies of traits based on biomass models of root growth in semi-arid shrubs and forest ecosystems are still lacking. Additionally, the factors affecting fine root functional traits may change with soil depth [16]. Hence, establishing fine root functional trait–biomass models based on the relationships between fine root functional traits and fine root biomass in topsoil and subsoil in different ecosystems is of great scientific significance for predicting ecosystem adaptation to environmental changes, especially in semi-arid shrubs and forest ecosystems.

Ecosystems in arid and semi-arid regions are an important part of the carbon sink of terrestrial ecosystems [39], but they may be relatively fragile and sensitive to global changes [40]. In the Loess Plateau, alfalfa, Caragana and trees (e.g., *Populus tomentosa* Carr and *Betula platyphylla* Sukaczev) are widely used for vegetation restoration [41,42]. The increasing biomass of these plants is an important issue. It has been pointed out that fine root functional traits are related to the absorption capacity of fine roots [43,44]. Increased nutrient uptake efficiency contributes to plant biomass accumulation [45,46]. Hence, relationships between the fine root functional traits and fine root biomass in both topsoil and subsoil may help in constructing strategies to increase plant biomass, which is beneficial to the restoration of the semi-arid region of the Loess Plateau of China.

2. Materials and Methods

2.1. The Study Area

The sample sites were located in Zhonglianchuan, Yuzhong County, Gansu Province, China (36°02′ N, 104°24′ E; 2400 m above sea level). This region has a temperate semi-arid continental climate, with a mean annual air temperature of 7.4 °C [47], a mean annual rainfall of 305 mm occurring during the growing season (April–September) and a mean annual evaporation of 1300 mm [48]. The soil type is classified as Heima soil [49], which is the equivalent of Calcic Kastanozem in the FAO Taxonomy, and the landform is a Loess hilly area. The main dominant plant species are gramineous herbs, including *Agropyron cristatum*, *Leymus secalinus* and *Stipa capillata*, non-gramineous herbs such as *Artemisia frigida* and *Heteropappus altaicus*, leguminous herbs such as *Medicago sativa* L., *Oxytropis* and *Astragalus polycladus*, shrubs such as *Caragana korshinkii* Kom., and tree species including *Populus tomentosa* Carr, *Betula platyphylla* Sukaczev and *Prunus armeniaca* L. [48]. The contents of soil elements, pH and bulk density of five ecosystems is shown in Table 1.

Table 1. The soil properties in the five ecosystems. BD, soil bulk density; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus.

Ecosystem Type	pH	BD (g cm^{-3})	SOC (g kg^{-1})	TN (g kg^{-1})	TP (g kg^{-1})
Abandoned lands	8.44 ± 0.16	1.19 ± 0.14	9.29 ± 3.22	1.19 ± 0.38	0.61 ± 0.06
Woodlands	8.33 ± 0.19	1.14 ± 0.15	9.78 ± 4.52	1.27 ± 0.58	0.66 ± 0.05
Alfalfa grasslands	8.39 ± 0.20	1.24 ± 0.12	10.01 ± 3.80	1.38 ± 0.55	0.64 ± 0.05
Caragana shrublands	8.36 ± 0.23	1.16 ± 0.10	9.75 ± 3.39	1.56 ± 0.57	0.57 ± 0.04
Croplands	8.38 ± 0.20	1.26 ± 0.08	9.17 ± 3.93	1.24 ± 0.48	0.71 ± 0.10

Note: The values are arithmetic means ± standard deviations.

2.2. Research Methods and Sample Collection

In August 2022, we selected 30 abandoned lands, 9 woodlands, 29 alfalfa fields, 30 Caragana shrubs and 29 croplands according to the plant species in this area (Figure 1). The main dominant plant species were *Agropyron cristatum* (L.) Gaertn, *Setaria viridis* (L.) P. Beauv. and *Artemisia frigida* Willd. in the Abandoned lands. The 9 woodlands included 4 *Prunus armeniaca* L. lands, 3 *Populus tomentosa* Carr lands, 1 *Cupressus funebris* Endl. land, and 1 *Betula platyphylla* Sukaczev land. The Caragana shrubs were *Caragana korshinkii* Kom. The 29 alfalfa fields were *Medicago sativa* L. The 29 croplands included 9 corn fields, 9 potato fields, 3 buckwheat fields, 4 oat fields, 2 millet fields, 1 broomcorn field and 1 lily field.

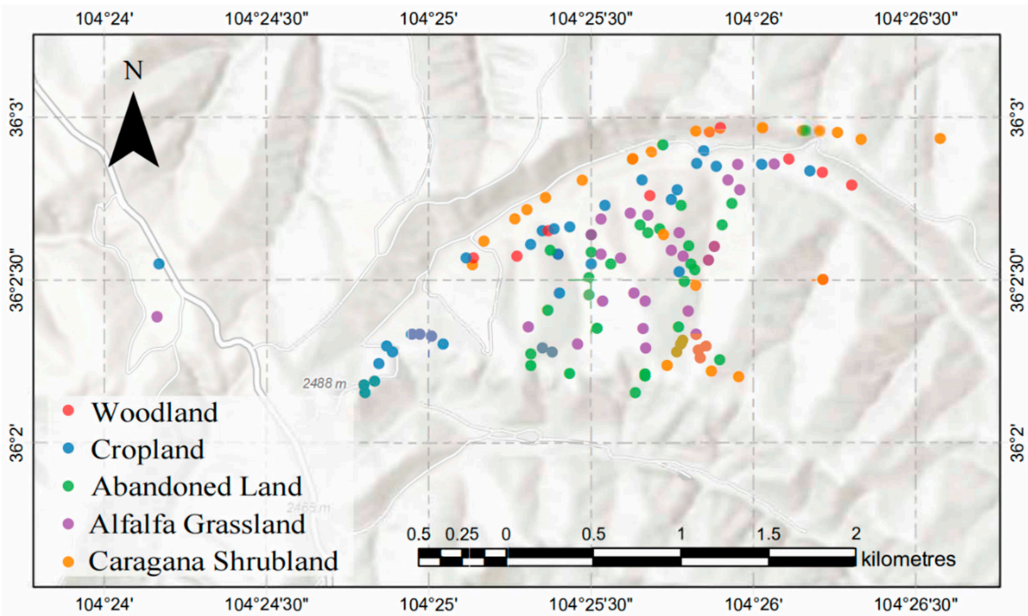

Figure 1. The sampling sites of this study on the Loess Plateau. The colors of the dots represent the corresponding ecosystems.

Fine roots (<2 mm in diameter) acquire essential soil resources and play an important role in ecological processes, such as the cycling of nutrients and carbon in terrestrial ecosystems [50,51]. Fine roots were obtained in different ecosystems. Since roots distribute differently with different soil depths [52,53], which may lead to differences in the relationships between fine root functional traits and biomass in different soil depths, a root core with a 4.2 cm inner diameter was used to sample the roots at 0–20 and 20–40 cm soil depths in each field. With the root core, two samples close to the well-grown dominant plant were taken and pooled into a composite sample in each field. In the laboratory, the samples were placed in a 0.15 mm sieve. The roots in the samples were carefully washed by wet sieving under gently flowing water to carefully remove the attached soil [54]. And then, fresh root samples were placed in water, and we selected roots that could pass through a 2 mm aperture sieve as "fine roots". The selected roots were placed completely flat without overlap and scanned in HP Root Scanner (HP Inc., Spring, TX, USA). The root images were saved in JPG format with a resolution of 300 dpi. Finally, the scanned root samples were dried in an oven at 70 °C to constant mass to obtain the root dry weight [55].

2.3. Fine Root Functional Traits

The scanned root area and root length were analyzed by the free software ImageJ (V2.3.0/1.53q) [56–58]. The analysis function of ImageJ gave the scanned root area and root length. Assuming that the root is a cylinder [59], the root diameter is calculated via "root scanned area = root length × diameter" (the upper and lower bottom areas of the cylinder are ignored).

Fine root biomass is calculated using the following formula [54]:

$$\mathrm{RB} = \mathrm{DW}/(2 \times \pi \times \mathrm{R}^2) \tag{1}$$

where RB is the fine root biomass (g m^{-2}); DW is the root dry weight (g); 2 represents the two samples taken with the root; R is the inner radius of the root core (0.021 m).

The SRL is calculated using the following formula [13]:

$$\mathrm{SRL} = \mathrm{L}/\mathrm{DW} \tag{2}$$

where SRL is the specific root length (m g^{-1}); L is the root length (m); DW is the root dry weight (g).

The SRA is calculated using the following formula [54]:

$$\mathrm{SRA} = \mathrm{SA}/\mathrm{DW} \tag{3}$$

where SRA is the specific root area (m^2 g^{-1}); SA is the root surface area (m^2); DW is the root dry weight (g).

2.4. Statistical Analysis

We modeled fine root functional traits and fine root biomass at both 0–20 and 20–40 cm soil depths in each of the five ecosystems. Under the prerequisite of $p < 0.05$, the optimal regression method was selected to establish the fine root functional trait (diameter, SRA and SRL)–fine root biomass models according to the R^2 values and the power function ($Y = a\,x^b$).

The accuracy of the model was tested by comparing the predicted and measured values of the model, taking the measured value as the independent variable, "x", and the predicted value as the dependent variable, "Y", and then we established the equation "Y = kx + b", in which the closer the value of "k" is to 1, the higher the accuracy of the model is, and "b" is a constant value [60]. For each of the five ecosystems, we randomly selected 70% of the data for modeling and the remaining 30% for model validation [61–63]. Statistical analysis was performed using IBM SPSS Statistics 20 (SPSS Inc., Chicago, IL, USA), and Origin 2015 (OriginLab OriginPro 2015, Northampton, MA, USA) was used for plotting.

3. Result

3.1. Root Functional Trait Model Based on Fine Root Biomass in Different Ecosystems

The relationships between fine root functional traits and fine root biomass were typically power functions. The relationship between diameter and fine root biomass was significantly positive ($p < 0.05$, Figures 2A,D,G,J,M and 3A,D,G,M) at the 0–20 and 20–40 cm soil depths. The relationships between SRA, SRL, and fine root biomass were significantly negative at the 0–20 and 20–40 cm soil depths ($p < 0.01$, Figures 2B,C,E,F,H,I,K,L,N,O and 3B,C,E,F,H,I,K,L,N,O).

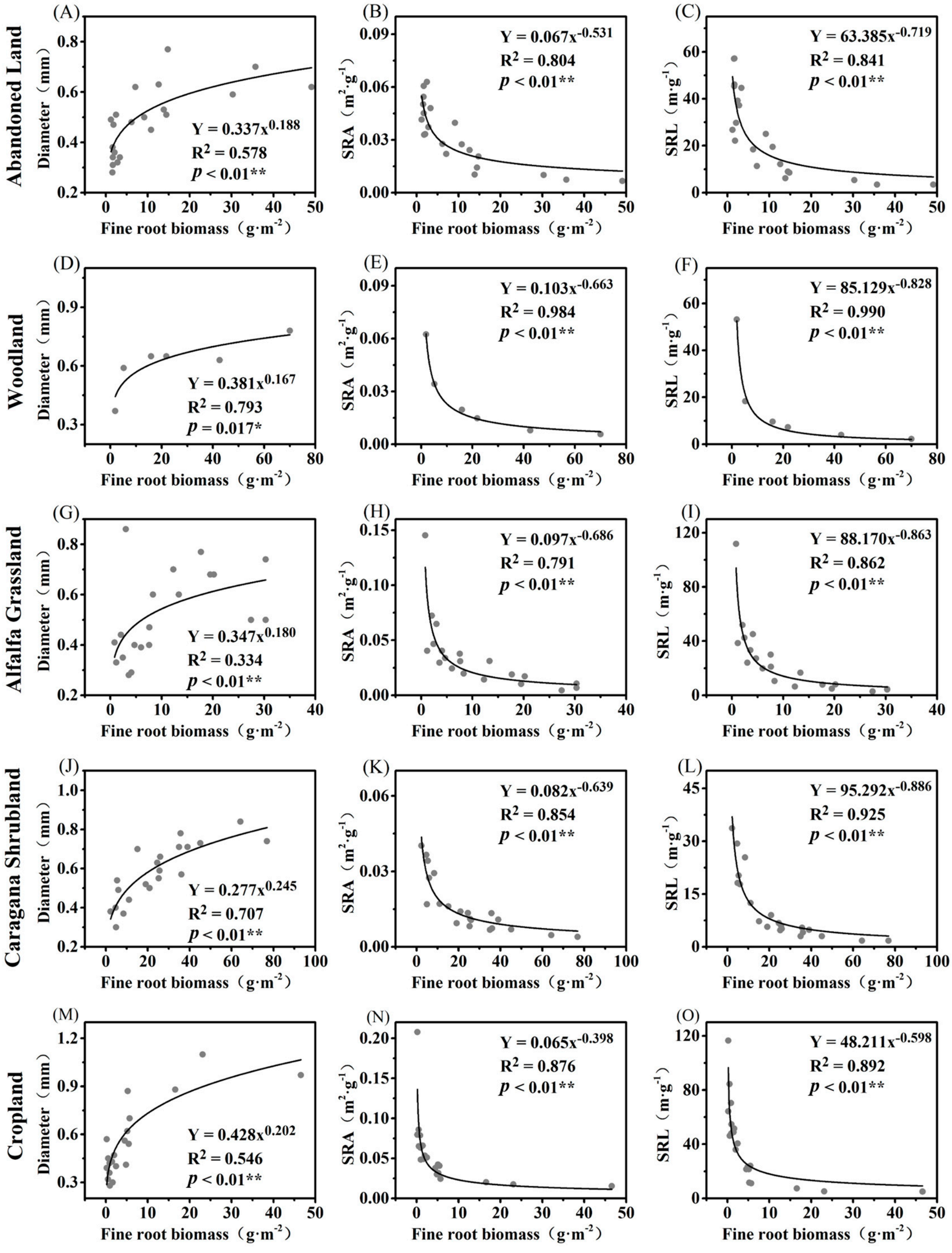

Figure 2. The subfigures (**A**–**O**) are the relationships between fine root functional traits and fine root biomass in different ecosystems at the 0–20 cm soil depth. SRL, specific root length (m g^{-1}); SRA, specific root area (m^2 g^{-1}). Significance is set at $p < 0.05$. "*" means $p < 0.05$ and "**" means $p < 0.01$.

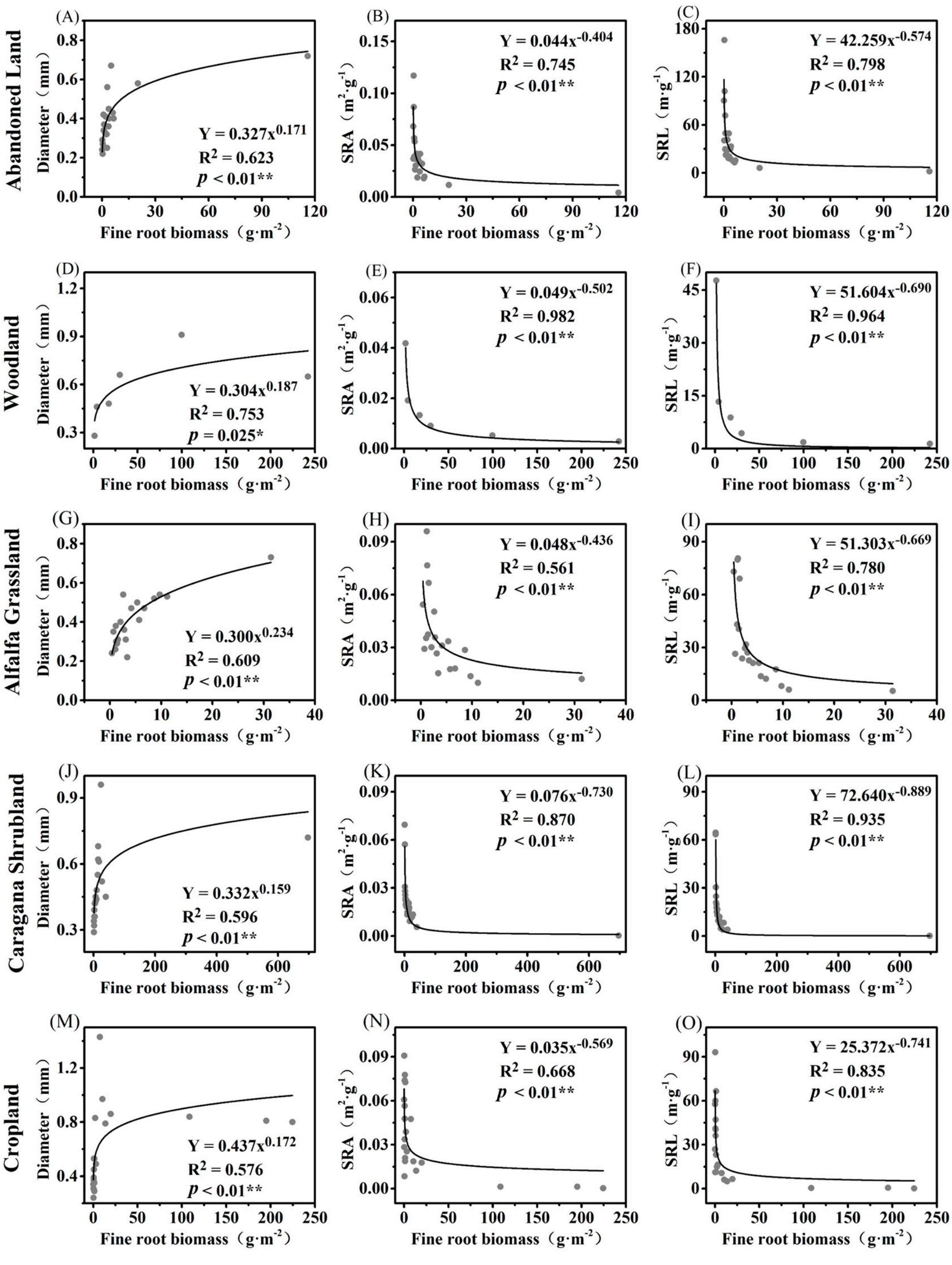

Figure 3. The subfigures (**A**–**O**) are the relationships between fine root functional traits and fine root biomass in different ecosystems at the 20–40 cm soil depth. SRL, specific root length (m g^{-1}); SRA, specific root area (m^2 g^{-1}). Significance is set at $p < 0.05$. "*" means $p < 0.05$ and "**" means $p < 0.01$.

3.2. Test of the Regression Models

The slopes of the tested models for the three functional traits at a 0–20 cm soil depth in the abandoned lands were closest to 1, while R^2 values of abandoned lands were the highest among the five ecosystems, followed by Caragana shrublands, croplands (Figure 4), whereas R^2 values of Caragana shrublands were the highest among the five ecosystems, followed by croplands and alfalfa grasslands at a 20–40 cm soil depth (Figure 5). In the same ecosystem, the model of SRL–fine root biomass is best, followed by that of SRA and diameter, except for croplands at the 0–20 cm soil layer and alfalfa grasslands and Caragana shrublands in the 20–40 cm soil layer (Figures 4 and 5).

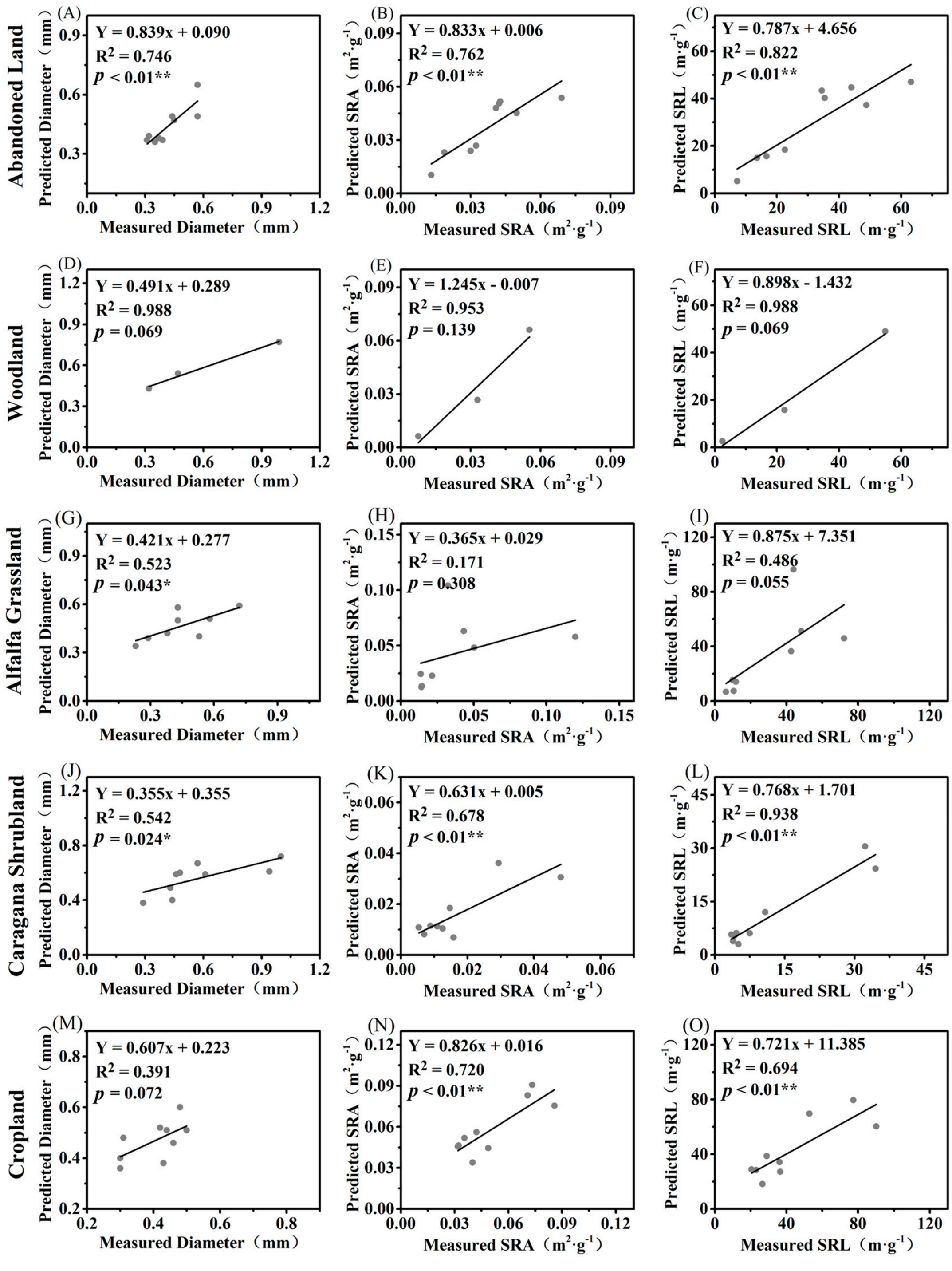

Figure 4. The subfigures (**A**–**O**) are the predicted and measured values of three fine root functional traits based on the non-linear relationships between fine root functional traits and fine root biomass in different ecosystems at the 0–20 cm soil depth. SRL, specific root length (m g^{-1}); SRA, specific root area (m^2 g^{-1}). Significance is set at $p < 0.05$. "*" means $p < 0.05$ and "**" means $p < 0.01$.

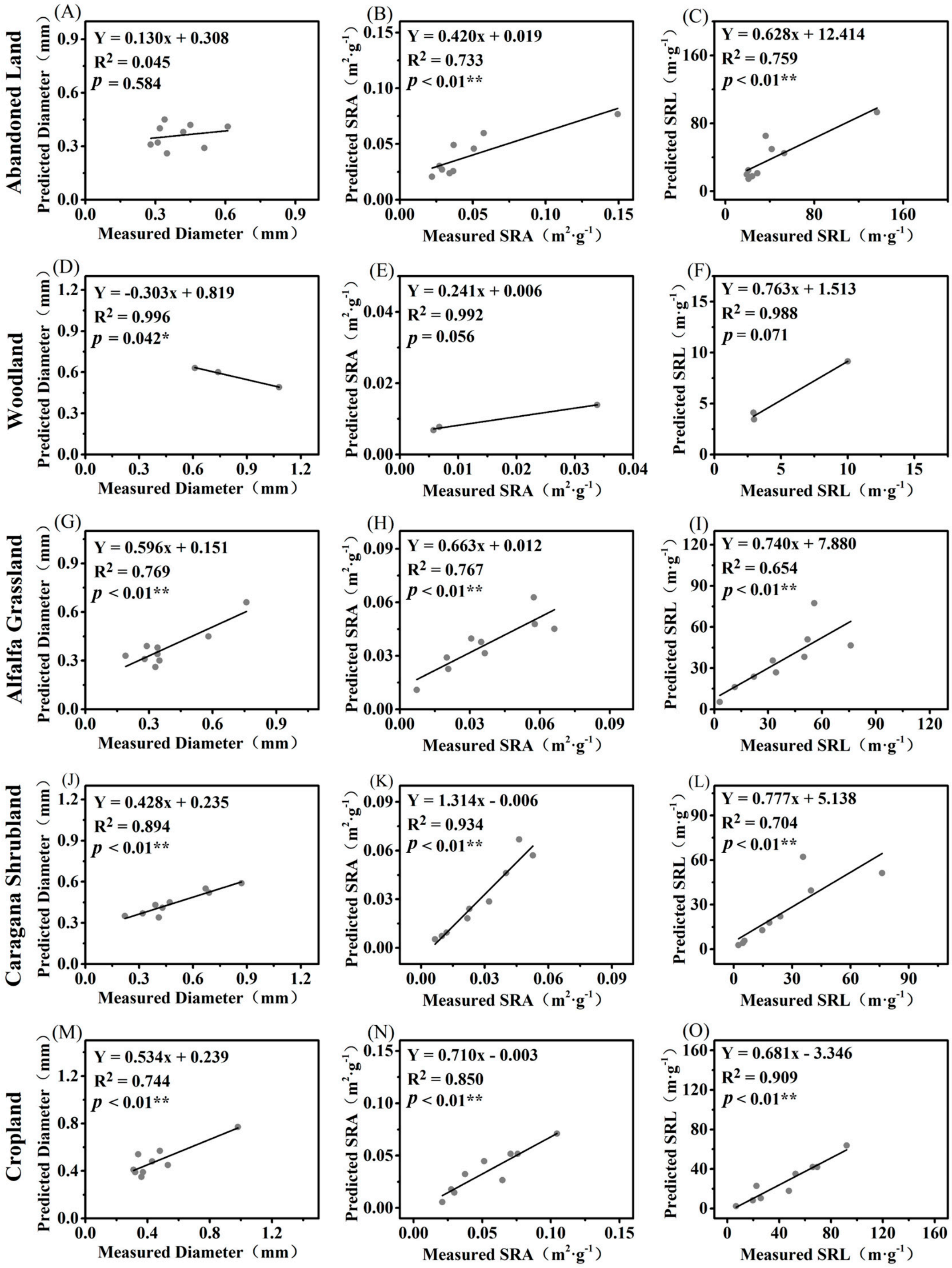

Figure 5. The subfigures (**A**–**O**) are the predicted and measured values of three fine root functional traits based on the non-linear relationships between fine root functional traits and fine root biomass in different ecosystems at the 20–40 cm soil depth. SRL, specific root length (m g^{-1}); SRA, specific root area (m^2 g^{-1}). Significance is set at $p < 0.05$. "*" means $p < 0.05$ and "**" means $p < 0.01$.

4. Discussion

Allometric growth describes the non-linear relationship between an organism's size and other properties, usually expressed as a power function [64,65]. Allometric growth relationships are common in forest ecosystems. For example, Peichl et al. (2007) studied an age sequence of four (2-, 15-, 30-, and 65-year-old) eastern white pine (*Pinus strobus* L.) forests in southern Ontario, Canada, and established age-specific allometric equations by using allometric relationships [66]. Ishihara et al. (2015) developed generic allometric equations for aboveground biomass and component (stem, branch, leaf, and root) biomass using large, compiled data sets of 1203 harvested trees belonging to 102 species [67]. Ma et al. (2020) established allometric growth models for the aridland shrub *Reaumuria soongorica*, including equations of above-ground biomass, branch biomass, foliage biomass and root biomass [68]. Many existing allometry models mainly focus on the prediction of above- and below-ground biomass [69–71] for specific species, limiting the range of trait variation. Accordingly, a major challenge is improving knowledge of root trait variation within and among species across diverse communities, ecosystems, and biological communities [72,73]. Our study focused on plant fine roots in different ecosystems, and robust allometric relationships between fine root functional traits and fine root biomass were observed. Different from the existing L-system [74,75], DyRoot [76], Root Typ [77] and other root models, the power function models established in our study focused more on fine root functional traits and fine root biomass, simply and intuitively reflecting the dynamic changes in the fine root functional traits following standing fine root biomass.

The plant economic spectrum (PES) hypothesis predicts that leaf and root traits evolved in coordination [13]. Therefore, there should be a correspondence between the leaf economics spectrum (LES) and RES [14,78,79]. For aboveground traits, allometric growth relationships have been reported in numerous studies, with power and logarithmic functions predominating [80–83], while linear relationships have also been shown [84]. The choice of functions also depends on the type of functional traits. For instance, Kong et al. (2019) showed an allometry-based nonlinear relationship between root tissue density and absorptive root diameter, while showing a linear relationship between stele radius and root tissue density [72].

Recognition of the non-linear relationship between fine root functional traits and fine root biomass can help us understand the trade-offs among fine root functional traits [67]. Different plant species have different root growth strategies; thus, their fine root functional traits are also different [72,85]. We established fine root functional trait–biomass models in both topsoil and subsoil in different ecosystems (Figures 2 and 3). By checking the prediction results of the power function models (Figures 4 and 5), we found that the measured values of the three fine root functional traits of the five vegetations were basically in good agreement with the predicted values at both 0–20 and 20–40 cm soil layers, indicating that the simulation accuracy of fine root functional trait–biomass models established in these soil layers was robust.

The differences in the accuracy of the models, especially the observed deviations from the perfect fit in the five ecosystems, may be related to the diversity of species, topographic, edaphic factors and the spatial variability of roots in the site [86]. Combined with the differences in soil resources of the five ecosystems (Table 1), it was inferred that the deviations may be related to BD, TN and TP, which is consistent with some reports [27,28]. Moreover, Comas et al. (2005, 2010) emphasized that root growth varies due to plant (e.g., developmental stages) and environmental factors [87,88]. Roybal et al. (2019) found that the relationships between root traits and environmental conditions (e.g., temperature and soil moisture) were highly variable among species [89]. Hence, how the site properties (e.g., soil resources, anthropogenic activities) affect the relationships between fine root functional traits and root production and the R^2 values of the models should be the focus of future research to further explain the observed deviations.

5. Conclusions

The results showed robust allometric relationships between fine root functional traits and fine root biomass. The relationships between fine root functional traits and biomass indicate important differences based on ecosystem type and root traits chosen for analysis in a semi-arid region. Accordingly, such results can help inform future efforts to model belowground traits at the plant and ecosystem scales.

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Data Availability Statement: The data presented in this study are available upon request from the corresponding author.

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