Response of Fine-Root Traits of *Populus tomentosa* to Drought in Shallow and Deep Soil

Jianbiao Tan 1,2,*, Weichen Yu 1,2, Yang Liu 1,2, Youzheng Guo 1,2, Nan Liu 3, Haiman Fu 4, Nan Di 5, Jie Duan 1,2, Ximeng Li 6 and Benye Xi 1,2,*

1 Ministry of Education Key Laboratory of Silviculture and Conservation, Beijing Forestry University, Beijing 100083, China; t_jianbiao@bjfu.edu.cn (J.T.)
2 Key Laboratory for Silviculture and Forest Ecosystem in Arid- and Semi-Arid Region of State Forestry and Grassland Administration, Beijing 100083, China
3 Forestry Development Center of Donge County, Liaocheng 252037, China
4 Planning and Design Institute of Forest Products Industry, National Forestry and Grassland Administration, Beijing 100010, China
5 School of Ecology and Environment, Inner Mongolia University, Hohhot 010021, China
6 College of Life and Environmental Science, Minzu University of China, Beijing 100081, China

* Correspondence: benyexi@bjfu.edu.cn; Tel.: +86-10-6233-7055

Abstract: Understanding the response characteristics of fine roots to soil drought of different degrees is essential for revealing the ecological adaptability of trees to different water environments and diverse plant resource absorption strategies. This study focused on a Chinese white poplar (*Populus tomentosa*) plantation stand, which gradually experienced the process of deep soil drying. In 2019 and 2021, by measuring the fine-root length density (FRLD), mean root diameter (MRD), specific root length (SRL), and root tissue density (RTD) of 1920 root samples and continuously monitoring the soil water content (SWC) in 0–600 cm soil layers, we explored the response characteristics of fine-root distributions and morphological traits relative to soil drought of different degrees. The results showed that *P. tomentosa* primarily changed the fine-root vertical distribution rather than the total amount of fine roots for coping with soil drought of different degrees. Shallow soil drought induced more fine-root distributions in the deep soil layer, while drought in both shallow and deep soil further aggravated this trend. Shallow soil drought restrained shallow fine-root growth, yet deep soil drought promoted deep fine-root growth. The very deep fine roots (400–600 cm) were more sensitive to soil drought than shallow fine roots. The shallow soil drought significantly increased the SRL of very deep fine roots; in contrast, when deep soil drought also occurred, the MRD and SRL significantly increased and decreased, respectively. In addition, fine-root morphological traits exhibited significant vertical spatial and temporal variation. MRD increased and then decreased, and the RTD gradually decreased with depth, while SRL had an increased trend in the very deep soil layer (400–600 cm). When the rainy season came, MRD and SRL increased and decreased, respectively. In conclusion, when facing gradual deep soil drying, *P. tomentosa* will use a large range of rooting patterns to meet the water demand of the canopy. These patterns range from “drought tolerant strategies” by distributing more fine roots in the deeper soil layer where water is abundant to “drought tolerant strategies” by changing very deep fine-root morphological traits to improve water-absorbing and transporting efficiencies. Our findings provide insight into the ecological adaption strategy of tree root systems relative to soil drought of different degrees in arid and semi-arid regions and provide crucial theoretical support for developing water management technologies to cope with deep soil drying under climate change.

Keywords: poplar; soil drying; soil water content; fine-root distribution; fine-root morphology
1. Introduction

Under the background of global warming, precipitation decreases and soil evaporation increases, which causes an increase in the intensity and frequency of drought events in many parts of the world [1–3]. However, as the primary limiting factor of tree growth, water significantly affects forest ecosystems’ stability and multiple functions [4,5]. The root system is the main link between soil and plants, which usually accounts for 15% to 30% of the total tree biomass [6], performing functions such as anchoring, carbon storage, and the uptake and transport of water and nutrient resources [7,8]. However, due to the difficulty of observing and measuring the underground root system, the existing studies on drought stress’s effects on tree roots are still insufficient [9–12]. Fine roots are the most sensitive part of the root system relative to environmental changes. Because of its large absorption surface area and strong physiological activity [13,14], fine roots play a vital role in the absorption of plant water resources [15]. Therefore, understanding the response characteristics of fine roots to drought stress will help us elucidate the ecological adaptability of trees to different water environments and reveal diverse plant resource absorption strategies [16,17].

The current studies show that trees can adapt to water deficiency by using various strategies, such as increasing fine-root biomass and absorption surface areas, adjusting the fine-root distribution, or changing fine-root morphological and physiological traits [18–21]. However, the type of root ecological strategies trees use depends on the species, climate, and management measures [22–24]. For instance, Zou et al. [17] found that Chinese white poplar (Populus tomentosa) adapts to short-term soil water stress by adjusting fine-root distributions rather than changing fine-root morphological traits. Knutzen et al. [25] found that with the aggravation of soil drought, the root biomass of some beech (Fagus sylvatica) populations decreased, and the specific root area (SRA) increased; however, other populations only decreased root biomass or did not respond. Metcalfe et al. [26] found that the fine-root biomass, length, and surface area gradually decreased when soil moisture decreased, but the specific root length (SRL) and SRA showed the opposite trend in Amazon rainforests. Zhao et al. [27] found that intercropping improved the soil water status below 80 cm in depth and increased the deep fine-root biomass of apple trees (Malus domestica). Thus, according to existing research studies, we can only understand the potential response characteristics of tree roots relative to drought stress macroscopically. However, accurately predicting the actual drought response of specific tree species in a particular area is difficult. In addition, most existing studies are limited to shallow soil above 100 cm, but how the deep roots distributed below 100 cm respond to drought is poorly understood.

Stand water consumption will gradually increase with the aggravation of drought or the growth of trees. In addition, when the shallow soil water cannot meet the demand of tree transpiration, the roots will begin to absorb a large amount of water from the deep soil, which will cause a gradual transition from shallow to deep soil drought [28,29]. As a result, deep roots will be gradually subjected to drought stress, so some studies have begun to pay attention to the response characteristics of deep roots to soil drought. However, these studies have mainly focused on the Loess Plateau region of China and South America. For example, Zhao et al. [27] found that shallow soil drought increased both the shallow and deep fine-root biomass of apple trees, while Ma et al. [30] found that drought in both shallow and deep soil decreased the total amount of jujube (Ziziphus jujuba) fine-root biomass but increased its maximum rooting depth. Adriano et al. [31] found that soil drought enhanced root proliferation in the soil below 500 cm and increased the maximum rooting depth of orange trees (Citrus sinensis). Water uptake by deep roots plays a crucial role in the physiological activities of trees [32,33]. Increasing evidence shows that very few deep roots can make use of abundant deep soil water to help trees survive in drought periods in arid or seasonal arid areas [34–37]. However, observing and measuring deep roots is challenging, so most studies only measured the biomass rather than the morphological traits of deep roots, which hinders us from understanding the response of roots to environmental changes [38,39]. In addition, most existing studies are under the condition of shallow soil drought or drought in both shallow and deep soil, directly
analyzing the effect of soil drought stress on fine roots [17,27,40,41]. However, there are no studies on the changes in the response characteristics of fine-root functional traits during the transition from shallow to deep soil drought based on in situ measurements. A deeper understanding of this change will help us comprehensively reveal the drought-stress-adapting strategies of an entire root system of trees and predict changes in the structure and function of forests in the future.

P. tomentosa is an important native tree species in China. Due to its rapid growth, high timber quality, and excellent adaptability [42], it plays a vital role in constructing the timber forest and shelterbelt in the North China Plain. Our previous studies have shown that with the increase in stand age and tree water consumption in a P. tomentosa timber forest planted in the North China Plain, deep soil desiccation gradually appeared, resulting in severe deep soil drought [29]. This phenomenon brings significant challenges to the growth and health maintenance of P. tomentosa and other plantations in the North China Plain. In order to alleviate this problem, an understanding of the effects of deep soil drought on trees from the perspective of root ecology and the optimization of intensive cultivation technologies under deep soil desiccation are urgently needed. Therefore, we conducted a continuous study in a mature P. tomentosa plantation with respect to the gradual desiccation of deep soil to solve the following two scientific problems: (1) How does drought affect fine-root distributions during the transition from shallow to deep soil drought? (2) How do shallow and deep fine-root morphological traits respond to soil drought, and what are the differences in their responses? We have two hypotheses: (1) a shallow soil drought would induce more fine roots distributions in deep soil, and droughts in both shallow and deep soil would further aggravate this trend; and (2) compared with shallow fine roots, deep fine roots are more sensitive to soil moisture change and may adapt to soil drought stress by changing their morphological traits.

2. Materials and Methods

2.1. Experimental Site and Experimental Plantation

The experimental site is located in Gaotang County, Liaocheng City, Shandong Province (36.81° N, 116.09° E), which is representative of the Yellow River alluvial plain of North China (Figure 1). The climate in this region is dominated by warm-temperate semi-humid continental monsoons. The average annual temperature was 13.4 °C, the mean annual evaporation was 1880 mm, and the mean annual precipitation was 563 mm (1981–2010). This site has very flat terrain with an altitude of 30 m. The soil texture in the 0–140 cm soil layer is sandy loam, while silt loam layers and silt layers alternate in the 140–600 cm soil layer [29]. The groundwater level fluctuates relatively stably between 6 and 9 m depths [43].

The experimental plantation was established in April 2015 with the B301 clone ((P. tomentosa × P. bolleana) × P. tomentosa). The trees were 2 m apart within the rows and 3 m between rows at a density of 1666 trees ha⁻¹. At the time of the plantation’s establishment, the average height and diameter at the breast height (DBH) of trees were 3.0 ± 0.1 m and 3.7 ± 0.2 cm, respectively.

2.2. Experimental Design

To form experimental stands with different soil moisture conditions, we designed two treatments from 2016 to 2021: no irrigation treatment (NI), in which trees only relied on rainfall, and full drip irrigation (FI), in which trees were irrigated whenever the soil matric potential dropped to −18 to −20 kPa. Treatment plots were arranged in a completely randomized block design, and each treatment consisted of five replicated plots. The treatment plot area was 432 m² and included 72 trees with 20 interior experimental trees in the measurement plot. The microenvironments, including elevation, slope, and soil profile, were almost identical across plots. In order to implement the irrigation treatment, a high-precision irrigation system (Netafim Co., Ltd., Tel Aviv, Israel) was laid out in the field, with the soil matric water potential monitored using tensiometers installed at 10 cm in depth and 15 cm from the dripper [44]. In FI, the stand was irrigated when the soil matric
potential under the dripper reached $-20$ kPa from Spring 2016 to September 2018. With the increase in stand age, the water consumption of trees increased gradually [29]. Therefore, the irrigation threshold of FI has been increased to $-18$ kPa since September 2018.

The development of this study depends on our previous research: (1) two treatments (NI and FI) with different soil moisture conditions in a shallow soil layer formed throughout continuous irrigation experiments from 2016 to 2019, and the soil water content (SWC) of the two treatments was continuously monitored; (2) the fine-root samples of the two treatments were obtained regularly in 2019; and (3) the phenomenon of deep soil desiccation in NI was observed in 2020 [29]. Therefore, we followed our plan to continue to sample fine roots regularly and to continuously monitor the SWC of two treatments in 2021. We investigated the soil drought effects of different degrees on the fine-root vertical distribution and morphological traits by SWC and fine-root data of 2019 and 2021. The rainfall of the experimental site in the growing season of 2019 and 2021 was 476 and 789 mm, respectively, and the irrigation amount of FI was 566 and 292 mm, respectively.

Figure 1. Geographic location of the experimental site in the North China Plain [yellow areas in (a,b)]. The boundaries of our experimental plantation are indicated by red color (c). The photo of our experimental plantation (d).
2.3. Soil Water Content and Root Measurement

In April 2019, when the stand was five years old, three sample trees with an average tree size were selected in each of NI and FI, and soil water content sensors (TSM640, Sinton Technology Ltd., Beijing, China) were installed at a 30 cm distance from each tree. Soil water content (SWC, cm$^3$ cm$^{-3}$) was automatically measured by these sensors for different depths (10, 30, 60, 100, 150, 250, 350, 450, and 550 cm) in a 0–600 cm soil profile at a frequency of every 30 min [45].

Soil cores were used to sample fine roots. A total of 1920 root soil core samples were obtained during the study period across nine sampling times: May, June, July, August, September, and October in 2019, and June, August, and October in 2021. At each sampling period, three to five trees in each treatment were selected for taking root samples. Sampling locations were set to be between rows and were at 30 cm distances from the trunk. The maximum sampling depth was 400 or 600 cm in 2019 and 600 cm in 2021, with sampling intervals of 20 cm (Table 1). The soil corer’s diameter was 11 and 8 cm for soil layers of 0–400 and 400–600 cm depth, respectively. All roots obtained from soil cores were manually washed using tap water with a sieve to separate the roots from soil particles and organic matter. Live roots were manually picked out and distinguished from dead roots by their lighter color and greater flexibility and resistance to breakage. Dead roots were discarded [17]. Live roots were then taken to the laboratory and kept in the fridge (−18 °C) until measured.

Table 1. Treatment, sampling locations, sample depth intervals, and depth of sampling events in 2019 and 2021.

<table>
<thead>
<tr>
<th>Year</th>
<th>Month</th>
<th>Treatment</th>
<th>Block</th>
<th>Interval (cm)</th>
<th>Depth (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2019</td>
<td>May, July, and September</td>
<td>NI, FI</td>
<td>1, 2, 4</td>
<td>20</td>
<td>600</td>
</tr>
<tr>
<td></td>
<td>June, August, and October</td>
<td>NI, FI</td>
<td>1, 2, 3, 4</td>
<td>20</td>
<td>400</td>
</tr>
<tr>
<td>2021</td>
<td>June, August, and October</td>
<td>NI, FI</td>
<td>1, 2, 3, 4, 5</td>
<td>20</td>
<td>600</td>
</tr>
</tbody>
</table>

NI, no irrigation; FI, full irrigation.

The fine roots (diameter < 2 mm) were identified by a Vernier caliper. We scanned these fine-root samples carefully without roots overlapping and crossing using an Epson Twain Pro high-quality scanner (Seiko Epson Inc., Suwa, Japan) at 400 dpi. WinRHIZO software (Regent Instruments Inc., Quebec, QC, Canada) was then used to measure the root mean diameter, surface area, volume, and root length. A total of 1920 fine-root samples were scanned, and then all fine-root samples were dried at 75 °C to a constant weight, and fine-root biomass was measured.

The morphological traits analyzed in this study included the mean root diameter (MRD, mm), root tissue density (RTD, g cm$^{-3}$), and specific root length (SRL m g$^{-1}$). RTD was calculated by dividing the fine-root biomass by fine-root volume, while SRL was calculated as the fine-root length divided by fine-root biomass. The fine-root length density (FRLD, cm cm$^{-3}$) was calculated by dividing the fine-root length by the soil core volume (1900.7 or 1005.3 cm$^3$).

2.4. Data Analysis

To analyze the response characteristics of the fine-root traits of different vertical positions to the change in soil moisture, according to the heterogeneity of soil moisture of different depths, the soil profile was divided into four soil layers: 0–20, 20–200, 200–400, and 400–600 cm. In addition, according to the rainfall distribution, the growing season of *P. tomentosa* was divided into three seasons: before the rainy season (BRS, April to June), the rainy season (RS, July to August), and after the rainy season (ARS, September to October). The data of fine-root traits in the corresponding months of each season were averaged to analyze their seasonal dynamics. Then, the data of fine-root traits in the corresponding seasons of each year were averaged to analyze their interannual variation.
The effects of treatment and depth on fine-root morphological traits (MRD, SRL, and RTD), FLRD, and SWC were analyzed using repeated measures analyses. Treatment was the between-subjects factor, and depth was the within-subjects factor. A similar repeated measure analysis was used to assess the effects of the season and year on the above indexes. Before the analyses, the Kolmogorov–Smirnov and Shapiro–Wilk tests were used to verify whether the data of each variable met the assumptions of normality and homogeneity of variances. Because some FRLD data did not meet the assumptions of normality and homogeneity of variances, logarithmic conversion is carried out to satisfy the assumptions. Nevertheless, some data still did not meet the assumptions after conversion, so a non-parametric test (Friedman test) was conducted. The means of different levels were compared using the LSD test when the effect of a certain factor reached a significant level ($p < 0.05$). A correlation analysis was performed for the morphological traits of fine roots. Before the analysis, the Kolmogorov–Smirnov test was used to verify whether each variable’s datum met normality assumptions, and Pearson’s correlation analysis was performed for data that met normality; otherwise, Spearman’s correlation analysis was performed.

The repeated measures analysis and Friedman, Kolmogorov–Smirnov, and Levene tests in this study were performed in SPSS software (SPSS 25, IBM Inc., Chicago, IL, USA), and correlation analyses and graphing were performed in Origin software (Origin 2021, Origin Lab Corporation, Northampton, MA, USA).

3. Results
3.1. Soil Moisture Condition

Treatment had a pronounced effect on SWC, but the difference in SWC between the two treatments in each soil layer exhibited interannual variations. In 2019, only in the 0–20 cm soil layer was the SWC in FI significantly higher than that in NI ($p < 0.05$); however, in 2021, this advantage of FI also appeared in the 200–600 cm soil layers ($p < 0.05$) (Figure 2). The results indicate that, compared with FI, NI experienced a significant drought in the shallow soil layer in 2019, whereas FI experienced a significant drought in both shallow and deep soil layers in 2021 (Figure 2). In addition, in the 400–600 cm soil layer, the SWC in each of the two treatments in 2021 was significantly lower than that in 2019 ($p < 0.05$) (Figure S1).

The seasonal dynamics of SWC showed that, compared with FI, there was a significant drought in the shallow soil (0–20 cm) in NI in all seasons of 2019 ($p < 0.05$) (Figure 3). However, in 2021, NI showed significant drought in the shallow soil layer only before and after the rainy season, while it showed significant drought in the deep soil layer (200–600 cm) during the entire growing season ($p < 0.05$) (Figure 3).

![Figure 2](image_url)

Figure 2. Average soil water content (SWC) of the growing season (1 May–31 October) of two treatments in different soil layers in 2019 and 2021 (mean ± SE). NI, no irrigation; FI, full irrigation. * in the same soil layer indicates a significant difference ($p < 0.05$) among treatments, while ns indicates no significant difference ($p > 0.05$); different letters in the same treatment indicate a significant difference ($p < 0.05$) among soil layers, according to the LSD test.
3.2. Fine-Root Vertical Distribution

The fine-root vertical distribution patterns of the two treatments were relatively consistent in 2019 and 2021 (Figure 4). FRLD decreased sharply with depth in the 0–80 or 0–100 cm soil layers, yet it exhibited a uniform distribution rather than a significant change in depth in the deeper soil layer \((p > 0.05)\) (Figure 4).

There was an interannual variation in the relative fine-root vertical distribution pattern. In 2019, FRLD’s relative proportion of FI was higher than NI in 0–20 and 400–600 cm soil layers, while NI allocated more FRLD in the 20–400 cm soil layer (Figure 4a). Compared with 2019, the relative fine-root vertical distribution pattern of the two treatments in the 0–400 cm soil layers in 2021 did not change, while the trend in the 400–600 cm soil layer was the opposite (Figure 4). However, differences between the two treatments were not statically significant in any soil layer in two years \((p > 0.05)\) (Figure 4). In addition, the main fine-root distribution layer in FI was always the 0–20 cm soil layer for 2019 and 2021, while it was the 20–200 cm soil layer in NI (Figure 4). In the 200–600 cm soil layer, the proportion of FRLD allocated by NI (37%) was slightly higher than that of FI (35%) in 2019, whereas...
NI was obviously higher than FI in 2021 (NI: 46%; FI: 34%), but the difference was not statistically significant ($p > 0.05$) (Figure 4).

**Figure 4.** Vertical distribution of fine-root length density (FRLD) and relative FRLD proportion in different soil layers of two treatments in 2019 (a) and 2021 (b) (mean ± SE). * in the same soil layer indicates a significant difference ($p < 0.05$) among treatments, according to the LSD test.

Overall, there was no significant difference in the total FRLD between the two treatments (Figure 4). The total root length density of NI (3.0 cm cm$^{-3}$) was obviously lower than that of FI (4.4 cm cm$^{-3}$) in 2019, but the difference became minor in 2021 (NI: 7.6 cm cm$^{-3}$; FI: 8.1 cm cm$^{-3}$) (Figure 4). In addition, FRLD varied considerably between the two treatments (NI < FI; $p < 0.05$) in the shallow soil layer in 2019 (Figure 4a), whereas this phenomenon appeared both in shallow and deep soil layers in 2021 (Figure 4b). Specifically, the FRLD of NI was significantly lower than that of FI by 44% above 20 cm depth in 2019 ($p < 0.05$), but there was no difference below 20 cm depth ($p > 0.05$) (Figure 4a). Likewise, the FRLD of NI was consistently significantly lower than that of the FI above 20 cm depth in 2021 (45%, $p < 0.05$), but it was significantly higher than that of the FI in the 340–360, 400–420, and 440–460 cm soil layers ($p < 0.05$) (Figure 4b).

### 3.3. Fine-Root Morphological Traits

Soil drought did not affect fine-root morphology traits in the 0–400 cm soil layer in 2019 and 2021; however, it changed the fine-root vertical spatial variation pattern by significantly affecting fine-root morphological traits in the 400–600 cm soil layer and its interannual variation ($p < 0.05$) (Figures 5 and S2). In 2019, the vertical variation patterns of MRD (firstly increased and then decreased) and RTD (gradually decreased) of the two treatments were the same (Figure 5a,c). The SRL of NI was significantly higher than that of the FI in the 400–600 cm soil layer ($p < 0.05$), which caused the SRL of NI in this soil layer to be distinctly higher than that in other soil layers ($p < 0.05$) (Figure 5b).
Compared with 2019, the RTD of the two treatments did not change in any soil layer in 2021, so NI still did not change the vertical spatial variation pattern of RTD relative to FI in 2021 (Figures S2c and 5c). However, compared with 2019, the MRD of the two treatments decreased in the 0–400 cm soil layer in 2021; the MRD of NI and FI increased and decreased in the 400–600 cm soil layer, respectively, so the MRD of NI was higher than that of FI in this soil layer (p < 0.05) (Figures S2a and 5a). Furthermore, the MRD of NI in the 400–600 cm soil layer was significantly higher than the MRD in the 0–200 cm soil layer (p < 0.05) but close to the MRD in the 200–400 cm soil layer (Figure 5a). At the same time, compared with 2019, the SRL of the two treatments significantly increased in 2021 in the 0–400 cm soil layer (except for the SRL of FI in the 20–200 cm soil layer) (p < 0.05) (Figure S2b), but the SRL of NI did not increase as FI in the 400–600 cm soil layer (p < 0.05), so it was significantly lower than that of the FI in this soil layer (p < 0.05) and reached values close to that in the 0–400 cm soil layer (Figures S2b and 5b).

The seasonal dynamics of fine-root morphological traits were slightly affected by soil drought, and there was an interaction effect with respect to the treatment, depth, and year. In 2019, the MRD, SRL, and RTD of FI in the 20–600 cm soil layer had no noticeable variations during the entire growing season, but RTD in the 0–20 cm soil layer significantly
increased after the rainy season ($p < 0.05$) (Figure 6). Compared with FI, NI only changed the seasonal dynamics of fine-root morphological traits in the 0–20 and 400–600 cm soil layers: the MRD and SRL in the 0–20 cm soil layers significantly increased and decreased when the rainy season came ($p < 0.05$), respectively; at the same time, SRL and RTD in the 400–600 cm soil layer significantly decreased ($p < 0.05$) (Figure 6).

Figure 6. The seasonal dynamics of MRD, SRL, and RTD of two treatments in different soil layers in 2019 and 2021 (mean ± SE). Different letters in the same treatment indicate a significant difference ($p < 0.05$) among seasons, according to the LSD test. BRS, before the rainy season; RS, the rainy season; ARS, after the rainy season.

Unlike in 2019, the fine-root morphological traits of FI in all soil layers significantly varied during the growing season of 2021 ($p < 0.05$) (Figure 6). Compared with FI, NI changed the seasonal dynamics of fine-root morphological traits in the 0–20 and 200–600 cm soil layers: the SRL and RTD in the 0–20 cm soil layers increased and decreased when the rainy season came ($p < 0.05$), respectively; MRD, SRL, and RTD in the 200–600 cm soil layer almost had no variation in the growing season ($p > 0.05$) (Figure 6).

3.4. The Relationship between Fine-Root Morphological Traits

Overall, there was a negative correlation between every two fine-root morphological traits ($p < 0.05$), but the relationship varied with treatments, depths, and years (Figure 7).
the 0–20 cm soil layer, the SRL of the two treatments significantly correlated with MRD in 2019; however, in 2021, the SRL of FI was not significantly correlated with MRD and RTD, while the SRL of NI significantly correlated with both RTD and MRD ($p < 0.05$) (Figure 7).

Figure 7. Correlation coefficients among fine-root morphological traits. * indicates a significant relationship between two traits ($p < 0.05$).

In the 20–600 cm soil layers, the SRL of the two treatments was almost affected by both MRD and RTD ($p < 0.05$), but the SRL of NI in the 400–600 cm soil layer in 2019 and the SRL of FI in the 200–400 cm soil layer in 2019 were not affected by RTD ($p > 0.05$) (Figure 7). In addition, the effect of MRD was greater than RTD on SRL (the correlation coefficient was higher) in the two treatments in each soil layer for two years (Figure 7).

4. Discussion
4.1. Effect of Soil Drought on Vertical Distribution

The fine root is the main absorption organ of water and a nutrient resource of plants, which is very sensitive to environmental changes and usually shows excellent plasticity [7,46,47]. Its vertical distribution determines the potential capacity of plants for water uptake and the
volume of available soil resources [48,49]. Consistent with the fine-root vertical distribution pattern reported by many previous studies [13,31,41], our study found that the FRLD in both treatments was concentrated in the shallow soil layer (0–20 cm) in both the five-year-old and seven-year-old *P. tomentosa* stand (Figure 4). Moreover, FRLD decreased sharply relative to depth in the soil layer above 100 cm, while it was uniformly distributed in the soil layer below 100 cm (Figure 4). Great resource availability, gas permeability, temperature, and rainfall capture occur at the surface; in addition, building and maintaining a root system in shallow soil consumes less energy [28,50]. Thus, to absorb soil water and nutrients efficiently, the fine roots of *P. tomentosa* are predominantly distributed in shallow soil. However, the soil environment in the deep soil layer was relatively stable, and the heterogeneity of soil water resources at different depths of the deep soil layer was relatively low, which may cause an even distribution of the fine roots of *P. tomentosa* in the deep soil layer. However, Zou et al. [17] found that shallow soil drought could change the fine-root vertical distribution pattern to the “S” type in both the four-year-old and five-year-old *P. tomentosa* stand. This is probably because their root sampling time took place in early spring (*P. tomentosa* has just experienced a long winter and spring drought, and its dormancy period has just ended).

Previous studies showed that when trees have a strong demand for deep soil water in the dry period, they will quickly initiate the proliferation of deep roots to find and absorb deep soil water. In addition, when aboveground organs stop growing during the dormant period, more carbon and water resources will be used for deep root growth to induce “material preparation” for the absorption and utilization of deep soil water in the following year [51,52]. The root sampling time in our study ranged from late spring to the end of the growing season. Consequently, soil drought may be alleviated when rainfall comes; moreover, the growth of aboveground organs consumes many carbohydrates, inhibiting the growth of deep underground roots. This may be a time regulation strategy adopted by trees to balance the allocation of resources and coordinate the growth of various organs with respect to using deep water efficiently [28].

Our results showed that soil drought had little effect on the total FRLD but affected its allocation in different soil layers. Specifically, the shallow soil drought in 2019 significantly inhibited the growth of shallow fine roots but had little effect on deep fine roots (Figure 4a); however, the drought in both shallow and deep soil layers in 2021 not only significantly inhibited the growth of fine roots but also significantly increased deep fine roots (*p* < 0.05) (Figure 4b). This finding is consistent with the first hypothesis of this study: shallow soil drought will induce more fine root distributions in the deep soil layer, while deep soil drought will further aggravate this trend. Our results partially agree with some previous studies. For example, Adriano et al. [31] found that orange trees without irrigation were rooted more deeply than trees with irrigation, and the fine-root biomass density of the former was higher than that of the latter below 500 cm. Ma et al. [30] found that the rooting depth of *Ziziphus jujuba* was greater without irrigation than with irrigation. In addition, Zou et al. [40] also found that drought stress could increase the rooting depth in a young *P. tomentosa* stand. Findings from the European temperate forests proved that even moderate drought altered the quantity and vertical distribution of fine roots in Norway spruce (*Picea abies* (L.) Karst.), a drought-sensitive and shallow-rooted species [53]. However, there is no study on how trees adjust the root vertical distribution pattern with gradual soil drought, especially during the transition from shallow to deep soil drought.

As an intense water-consuming species, *P. tomentosa* may adopt the “drought tolerant strategy” by distributing more fine roots in the soil layer with better moisture conditions to compensate for the limited water uptake in the soil layer with drought stress [28]. In this study, although soil drought stress was aggravated in 2021, the soil moisture condition in the deep soil layer was still more abundant than that in the shallow soil layer (Figure 2), which may stimulate fine roots to grow in the deeper soil layer to obtain more water and help trees resist drought stress and maintain growth vigor.
4.2. Effect of Soil Drought on Fine-Root Morphological Traits

When facing soil drought, besides adapting the “drought tolerant strategy”, trees also often adopt the “drought tolerant strategy” by changing their morphological traits (i.e., reduce MRD or increase SRL) to improve the water-absorbing efficiency in order to increase the water adsorption capacity [54,55]. Compared with adjusting the fine-root distribution, this strategy can also reduce the carbon cost for root system construction [28]. Our results indicate that the response of morphological traits of shallow and deep fine roots to soil drought was different. Soil drought did not affect any morphological traits in the 0–400 cm soil layer in 2019 and 2021, but in the 400–600 cm soil layer, the SRL of NI significantly increased in 2019 (p < 0.05), while the MRD and SRL of NI significantly increased and decreased in 2021 (p < 0.05), respectively (Figure 5a,b). The increase in the SRL of NI in the very deep soil layer (400–600 cm) may compensate for the decrease in fine-root proportion in this soil layer in 2019 (Figures 4a and 5b). However, with the aggravation of soil drought in 2021, the proportion of the fine roots of NI in the very deep layer increased (the relative FRLD was 5.96% and 19.20% in the 400–600 cm soil layer in 2019 and 2021, respectively), which meant that *P. tomentosa* might not need to increase water absorption by increasing absorption efficiency in this situation. This implies that deep soil drought would increase the diameter of the very deep fine roots in order to transport and explore relatively abundant deep soil water resources to compensate for the limited water absorption of fine roots in the shallow soil layer. However, regarding the impact of soil drought on fine-root morphological traits, the conclusion of previous studies was inconsistent [19]. For example, some studies found that soil drought increased the fine tree root SRL or SRA [26,56], decreased MRD [57,58], and increased RTD [57], yet most studies found that soil drought had little effect on tree fine-root morphological traits [17,31,59–61]. The contradiction in these results may be due to the different degrees of soil drought stress that trees suffer, and the characteristics of tree species may also explain this phenomenon. In addition, so far, there has been no research on the response of fine-root morphological traits in deep soil layers (>400 cm) to soil drought.

In addition, from the interannual scale, the MRD and SRL in each soil layer of the two treatments in 2021 were lower and higher than that in 2019, respectively (Figure S2a,b), which may be due to the increase in water consumption with the increase in stand age, and the degree of soil drought in almost all soil layers increased (Figure S1). This indicates that *P. tomentosa* not only adopts a “drought avoidance” strategy of shifting more fine roots to the deep soil with relatively abundant water resources to explore more abundant water resources, but also adopts a “drought tolerance” strategy of adjusting fine-root morphological traits to improve water absorption efficiency in order to meet the water demand of trees. Therefore, our results enlighten us that when studying the effects of soil drought on the morphological traits of plant roots, it is necessary to consider the degree of drought stress that plants suffer and comprehensively study the response of root systems in the entire root zone relative to soil drought. To summarize, the second hypothesis of this study needs to be modified: compared with shallow fine roots, very deep fine roots are more sensitive to soil moisture change and may adapt to soil drought stress by changing fine-root morphological traits. Besides changing the distribution and morphology of root systems, trees also respond physiologically to drought. For example, under drought conditions, Liu et al. [29] found that *P. tomentosa* trees reduced transpiration to alleviate water demand, and Liu et al. [45] found that hydraulic redistribution in roots appeared under extremely dry conditions, which allowed plants to maintain shallow root survival and activity by promoting root water recharge.

Our results showed that the vertical variation pattern of MRD and RTD in 0–400 cm soil layer (increased and decreased with depth, respectively) was consistent with that observed by Zou et al. [17] in a four-year-old *P tomentosa* stand (Figure 5a,c). Relative to the shallow soil, the longer vertical distance can increase the difficulty of transporting water from deep soil to the canopy. Thus, constructing thicker and lower RTD roots may be the best strategy to improve deep soil’s water-transporting efficiency and reduce the
root carbon cost, even though thicker roots may reduce the water adsorption capacity. Moreover, due to the gradual increase in SWC in the 0–400 cm soil layer (Figure 1), greater water availability in deep soil may not require greater root absorbing capacity as much as increased transport efficiency. However, with the further deepening of the soil layer, the MRD in the 400–600 cm soil layer began to decrease, and SRL did not change or increase, which may be because SWC decreased in this soil layer (Figures 2 and 5a,b). In addition, the very deep roots of trees need to overcome greater gravity to absorb and transport water, forcing fine roots to change their morphological traits in order to use water. Similar phenomena were also found in the study of the deep roots of other tree species. For example, Adriano et al. [31] found that the MRD and SRL of orange trees suddenly decreased and increased below 500 cm, respectively. Zhou et al. [41] also found that SRL in the very deep soil layer tended to increase.

The fine-root morphological traits exhibited significant seasonal variation, but soil drought had little effect on it. Overall, the MRD and SRL in the two treatments increased and decreased when the rainy season came, respectively (Figure 6). Perhaps it can be explained by the following two reasons: firstly, with the end of the fast-growing period of P. tomentosa (April–June) [62], the aboveground water demand for trees decreased; SWC increased when the rainy season came (Figure 3), so P. tomentosa did not need so many roots, particularly very fine roots with high water-absorbing efficiency for the uptake of water; secondly, the roots with high SRL or low MRD generally have a short lifespan [7,63], which means that some very fine roots might die in the rainy season.

4.3. Effect of Soil Drought on the Relationship between Fine-Root Morphological Traits

SRL is a key trait for characterizing the input–output ratio of the carbon and water absorption efficiency of the root, controlled by MRD and RTD. This study found that SRL was negatively correlated with MRD and RTD (Figure 7), which was consistent with the findings of [7,64]. However, the effects of MRD and RTD on SRL in different soil layers differed. Within two years, the SRL of the two treatments in the 0–20 cm soil was significantly affected by both MRD and RTD or only by MRD ($p < 0.05$), while the SRL in each soil layer of 20–600 cm was significantly affected by both MRD and RTD ($p < 0.05$) (Figure 7). In addition, the effect of MRD was greater in any soil layer. In a one- to five-year-old P. tomentosa stand, Zou et al. (2022) found that RTD was the main factor affecting SRL in the shallow soil layer, while MRD was the main factor in the deep soil layer, and SRL was not significantly affected by RTD in the deep soil layer. It can be observed that plants may adopt different strategies to control the utilization of soil resources per unit of root biomass (SRL) in shallow and deep soil layers, and strategies may change with respect to stand age.

5. Conclusions

A P. tomentosa plantation stand in the North China Plain that gradually experienced deep soil drying was taken as the research object in this study. By regularly measuring 1920 root samples and continuously monitoring the soil water content in the 0–600 cm soil layers for two years, the ecological strategies of fine roots for coping with soil drought of different degrees were researched.

We found that P. tomentosa did not promote the overall proliferation of fine roots but slightly reduced the total amount of fine roots and changed the fine-root vertical distribution. Shallow soil drought induced a more distribution of fine roots in the deep soil layer, while deep soil drought further aggravated this trend. Shallow soil drought restrained shallow fine-root growth, yet deep soil drought promoted deep fine-root growth. Secondly, very deep fine roots were more sensitive to soil drought than shallow fine roots, and they were adapted to drought stress by changing fine-root morphological traits. Shallow soil drought increased the SRL of very deep fine roots, while MRD and SRL increased and decreased, respectively, when deep soil drought occurred.
In conclusion, when facing gradual deep soil drying processes, *P. tomentosa* will use a large range of rooting patterns to meet the water demand of the canopy, and these patterns range from the “drought tolerant strategy”, which distributes more fine roots in the deeper soil layer where water is abundant, to the “drought tolerant strategy”, which changes very deep fine-root morphological traits to improve the water adsorption and transportation efficiency. Our findings provide insight into the ecological adaption strategy of tree root systems relative to soil drought of different degrees in arid and semi-arid regions and provide crucial theoretical support for developing water management technologies to cope with deep soil drying under climate change.

**Supplementary Materials:** The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f14050951/s1, Figure S1. Average soil water content (SWC) of the growing season (1 May–31 October) of two treatments in different soil layers in 2019 and 2021 (mean ± SE); Figure S2. Mean root diameter (MRD) (a), specific root length (SRL) (b), root tissue density (RTD) (c) of two treatments in different soil layers in 2019 and 2021 (mean ± SE).

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