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Effects of Precipitation and Soil Moisture on the Characteristics of the Seedling Bank under *Quercus acutissima* Forest Plantation in Mount Tai, China

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Abstract: Natural regeneration is crucial for the development of sustainable forestry practices in light of the current global climate changes. In this paper, we compared the size distributions of *Quercus acutissima* seedlings in the understory of *Q. acutissima* forest plantations in Mount Tai in 2010 and 2017, studied the physiological and morphological responses of seedlings to the microenvironment, and explored the maintenance mechanisms of the seedling bank. The results showed that the density of understory seedlings in 2017 was only 61.63% of that in 2010, especially in the 20–40 cm height class. Between 2011 and 2016, the precipitation and soil water content were the highest in 2011, followed by 2013. The 2–4-year seedlings (height < 40 cm) were not significantly different in seedling biomass, biomass allocation, and root morphology (root total surface area, root volume, and root average diameter), and were significantly different in total root length, specific root length, specific root surface area, and nonstructural carbohydrate content of root, stem, and leaves. However, 5–6-year seedlings (height > 40 cm) showed the largest biomass. Principal component analysis indicated that altering root morphology, nonstructural carbohydrate, and biomass allocation played significant roles in the drought adaptation of seedlings in the understory. In conclusion, drought stress together with seedling adaptation influenced the dynamics of seedling bank in the understory of *Q. acutissima* plantations.

Keywords: seedling bank; seedling age; microenvironment; biomass allocation; nonstructural carbohydrates

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1. Introduction

Forest plantation has increased rapidly from 1990 to 2015 at the global scale, with a percentage increase from 4.06 to 6.95% of the total forest area between 1990 and 2015 [1]. The forest plantation plays an increasingly crucial role in timber production, environmental improvement, landscape rehabilitation, and climate change mitigation [2]. Natural regeneration is vital for sustainable forest management. Naturally regenerated forests have the advantages of better plant establishment, self-regenerated material, and high seedling densities [3,4]. However, improper management has made the planted forests unable to complete natural regeneration [5,6]. Stand structure [7], litter density and grass cover [8], seedling adaptation [9–11], stand management [12,13], and year-to-year variation in stand conditions [14] are considered to be vital factors affecting forest natural regeneration. The natural regeneration of plantations is a long-term and complex process affected by many factors. At present, the regeneration mechanisms of plantations are still poorly understood.

Sufficient seedling bank is the foundation of the success of natural forest regeneration [15–18]. The structure and composition of natural regeneration are closely related to environmental conditions under forest stands [8,19], including precipitation [20], air temperature [21], soil moisture [22], and soil temperature [14], which significantly affect the establishment and survival of tree seedlings. Long-term monitoring of tree seedlings revealed that the fraction of seedlings eventually reaching the sapling class is quite small due to high seedling mortality [14,23,24]. Therefore, Rey and Alcántara [24] suggested that seedling survival is a critical process for tree species recruitment. Abiotic factors, especially drought, are considered to be the main factors causing seedling death [24]. With the increase of seedling size, the proportion of non-photosynthetic tissues to total sapling biomass increases, as well as respiration costs [25–27]. The minimum light demands of tree species increased with increasing seedling size, which led to the decrease of shade tolerance [28,29]. Thus, the transformation from seedlings to saplings requires higher light intensity [29,30], which is one of the most important limiting factors under forest stands. In addition, Soto et al. [31] suggested that light and nitrogen interact to influence regeneration in old-growth Nothofagus-dominated forests in South-Central Chile. Therefore, the current understanding of the dynamics of seedling banks under forest remains very limited.

Nonstructural carbohydrates (NSC) storage is a fundamental process that allows organisms to meet variable demands for resources during their development and buffer environmental fluctuations in resource supply. NSC is mainly stored in the roots and stems of tree seedlings [32], and starch is its main component [25,33]. Under short-term drought stress, the NSC content of *Pinus massoniana* Lamb. seedlings increased rapidly, and the variation in NSC partitioning among organs was more highly significant than the variation in biomass partitioning [34]. However, the change of NSC in the roots of *Manihot esculenta* Crantz. was not significant [35]. In shaded forest understories, NSC in tree seedlings acts as a buffer during the periods of negative net carbon balance against herbivores and diseases [32], defoliation [36], and suddenly shade increases [37], etc. Under severe shading conditions, NSC in seedlings is greatly consumed [34,38], or little remains [38]. Similarly, reduced NSC reserve in the root system of *Populus tremuloides* Michx. and *P. balsamifera* L. seedlings during severe drought contributed to the root death of seedlings during the dormant season by compromising the frost tolerance of the root system [39]. Ivanov et al. [40] also found that critical exhaustion of the NSC reserves in the roots under water stress led to the greatest mortality of *Pinus sylvestris* L. seedlings. After the relief of drought stress, Tomasella et al. [41] suggested that preserving higher NSC content at the end of a drought can be important for the hydraulic resilience of trees. The survival of tree seedlings under the forest is a long-term process. With the continuous growth of tree seedlings, their NSC content gradually increases [28,42], which is considered conducive to their survival in the forest [36]. However, some studies have suggested that carbohydrate storage is not related to low-light survival for tree seedlings [42,43]. Myers and Kitajima [32] proposed that tree seedlings rely on NSC reserves to survive short-term periods of negative carbon balance under forest, thereby enabling net carbon gain over the long term. Therefore, the relationship between NSC and the survival of tree seedlings under forest has not yet achieved a unified understanding.

China has the largest forest plantation area in the world. For a long time, forest plantation management has paid much attention to short-term productivity and economic benefits but had ignored natural regeneration [2]. *Quercus acutissima* Carruth., a deciduous tree species belonging to *Quercus* in the Fagaceae family, is the main component tree of forest vegetation in warm temperate and subtropical regions of China. *Q. acutissima* is a pioneer tree in barren mountains and barren land, and an excellent tree species for soil and water conservation, with high ecological, economic, and landscape values. At present, there are few studies on the natural regeneration of *Q. acutissima* plantation, and the limiting mechanism is unclear. *Q. acutissima* has certain shade tolerance, and its seedlings rarely die under more than 12% full light [44]. Xue et al. [45] found there were a large number of seedlings in the secondary forest of *Q. acutissima*, but few saplings. To further explain the

restriction mechanism of the natural regeneration of *Q. acutissima* plantations, we studied the pure forest plantation of *Q. acutissima*, the main forest type of Mount Tai, and with the following aims: (1) to describe changes of the regeneration structure of *Q. acutissima* seedlings under the forest across a long-term period; (2) to explore the effects of the environmental factors on regeneration structure and seedling establishment; (3) to clarify the morphological and physiological adaptation with the increase of seedling age.

2. Materials and Methods

2.1. Study Area

The study area of Mount Tai lies in the middle of Shandong province, China, between Jinan City and Tai'an City. The climate is classified as the warm temperate continental monsoon zone, the average annual temperature is 12.6 °C, the frost-free period is 196 days, and the accumulated temperature greater than or equal to 10 °C is 3821 °C. The average annual precipitation is 758 mm and is concentrated from June to September. The soil type is mainly brown loam with a pH value of about 6.0 and a soil depth of 15~60 cm. Most of the vegetation in Mount Tai was planted in the 1950s and 1960s, with a total forest area of about 9490 hm^2 and a forest coverage rate of 81.5%. The main tree species include *Platycladus orientalis* (L.) Franco, *Q. acutissima*, *Robinia pseudoacacia* L., *Pinus thunbergii* Parl., *Pinus densiflora* Sieb. et Zucc., *Pinus tabuliformis* Carr., etc. [46,47].

2.2. Investigation of Q. acutissima Plantation

The investigation of *Q. acutissima* plantation was conducted in the Mountain Tai Forest Ecosystem Research Station of State Forestry and Grassland Administration (117°06′48.2″ N, 36°20′05.3″ E). The forest was planted in 1960 using 1-year-old seedlings. The plantation is a pure forest with an age of 60 years and an average altitude of 730 m. The permanent monitoring plot was established in 2010 with an area of 0.48 hm^2 (60 m × 80 m). Twelve 20 m × 20 m quadrats were set up in the plot. In each quadrat, we measured the diameter at breast height (DBH) for all trees with heights ≥1.5 m, which were defined as adult trees. Saplings and seedlings below 1.5 m in height were divided into eight height classes: <20 cm, 20–40 cm, 40–60 cm, 60–80 cm, 80–100 cm, 100–120 cm, 120–140 cm, and 140–150 cm. Adult trees were classified into DBH sizes, with one diameter class for every 5 cm. The permanent monitoring plot was reviewed in May 2017. The sampling and investigation methods in this paper referred to the forestry industry standard of the People's Republic of China issued by the State Forestry Administration (State Forestry Administration, 2011).

2.3. Measurement of Seedling Traits of Q. acutissima

On May 10, 2016, 19 seedlings with heights between 9 and 46 cm were selected in the *Q. acutissima* plantation. The height, diameter, and number of leaves of the seedlings were measured and collected. Then, each seedling was carefully excavated from the soil, and all the seedlings were sealed and stored in a fresh-keeping bag and brought back to the laboratory.

The age of seedlings was determined by counting the number of annual rings. These seedlings were divided into four groups according to their age: 2-year (I), 3-year (II), 4-year (III), and 5–6-year (IV). There were 3–9 seedlings in each group.

In the laboratory, the seedlings were divided into leaves, stems, and roots. The area of each leaf of each seedling was measured with a CI-202 portable laser leaf area meter (CID Inc., Washington, USA). After rinsing with clean water, these roots were scanned by HP Scanjet 8200 scanner, and the scanned images were analyzed by root parameter analysis software (Delta-T Area Meter Type AMB2) to obtain the length and surface area of roots. The roots, stems, and leaves of seedlings were dried at 80 °C until maintaining a constant weight. Then, the dry weight was weighed and recorded. After the dried samples of roots, stems, and leaves were pulverized, their concentrations of soluble sugar and starch were determined by anthranone–H_2SO_4 colorimetry, respectively [48]. Starch and soluble

sugars in each plant organ were added together to determine nonstructural carbohydrate concentration (NSC). All the seedling indices are shown in Table 1.

Table 1. Seedling characteristic indices, abbreviations, and units.

Seedling Characteristic Indices	Abbreviations	Units
Relative soil water content	RSWC	%
Seedling biomass (leaf + stem + root mass)	SB	g
Leaf mass ratio (leaf dry mass/total seedling dry mass)	LMR	$g\ g^{-1}$
Stem mass ratio (stem + petiole mass)/total plant mass	SMR	$g\ g^{-1}$
Root mass ratio (root dry mass/total seedling dry mass)	RMR	$g\ g^{-1}$
Specific leaf area (total leaf area/total leaf dry mass)	SLA	$cm^2\ g^{-1}$
Leaf area ratio (total leaf area/total seedling dry mass)	LAR	$cm^2\ g^{-1}$
Photosynthetic tissues/non-photosynthetic tissues (leaf mass/(stem + root mass))	P/NP	$g\ g^{-1}$
Total Root length	TRL	cm
Root volume	RV	cm^3
Root average diameter	RAD	mm
Root total surface area	RSA	cm^2
Specific root length (root length/dry root mass)	SRL	$cm\ g^{-1}$
Specific root area (root surface area/ dry root mass)	SRA	$cm^2\ g^{-1}$
Root soluble sugar	RSS	$mg\ g^{-1}$
Stem soluble sugar	SSS	$mg\ g^{-1}$
Leaf soluble sugar	LSS	$mg\ g^{-1}$
Root starch	RS	$mg\ g^{-1}$
Stem starch	SS	$mg\ g^{-1}$
Leaf starch	LS	$mg\ g^{-1}$

2.4. Monitoring Environmental Parameters under Q. acutissima Plantation

The environmental factors in the forest plot were measured from July 2011 to December 2016. The precipitation at 1.5 m in the forest was measured. The relative soil water content (RSWC) was measured at 10, 20, 30, and 40 cm depth of soil, respectively. The indices above were determined using a CR3000 automatic weather station (Campbell Scientific, Logan, UT, USA), which automatically recorded daily data every 10 min. Data were collected every month.

2.5. Statistical Analysis

The precipitation effect was tested by a two-way ANOVA, with year and month as the sources of variations. The relative soil water content was tested by a three-way ANOVA, with year, month, and depth as the sources of variations. Seedling indices were analyzed by a one-way ANOVA. The responses of functional traits to height were compared, and multiple comparisons were made. The linear regression analysis of height and age was carried out using the excavated 19 seedlings. At the same time, the correlation analysis of each index was carried out. All the seedling indices were analyzed by principal component analysis (PCA). The test level was $p = 0.05$. All statistical analyses were conducted using R 4.1.2 for Windows.

3. Results

3.1. The Diameter Structure of Q. acutissima Plantation

The density of *Q. acutissima* adult trees in 2010 stands was 634 N ha^{-1}, with trees in the DBH class 2–5 cm accounting for 19.70%, 5–10 cm for only 3.44%, and 15–35 cm for 70.94%. In 2017, the density of adult trees was 675 N ha^{-1}, with trees in the DBH class 2–5 cm accounting for 14.81%, 5–10 cm for 0, and 15–35 cm for 77.78%. In 2017, compared with 2010, the density of trees in the DBH 2–5 cm decreased by 4.89%, 5–10 cm trees disappeared, and the density of 15–35 cm trees increased by 6.84% (Figure 1A).

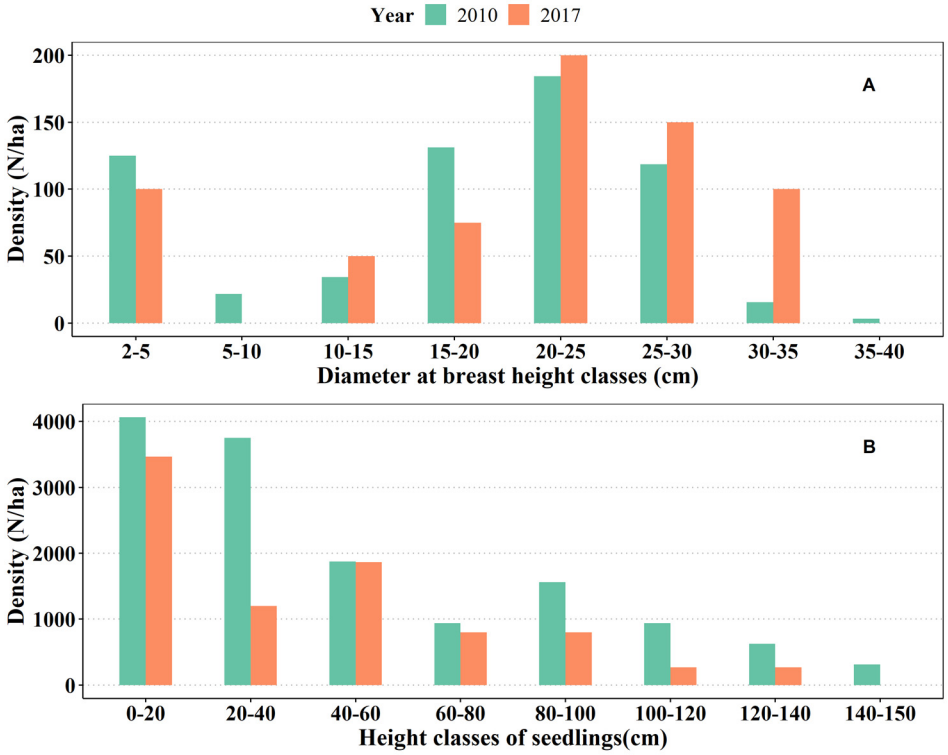

Figure 1. Distribution of diameter at breast height classes for adult trees (**A**) and distribution of height classes for seedlings (**B**) of *Quercus acutissima* in 2010 and 2017, respectively.

The height distribution of seedlings in 2010 and 2017 was pyramid-shaped (Figure 1B). The tree number reached a maximum in the height class 0–20 cm and 20–40 cm, and then gradually decreased as the height increased. Compared with 2010, the density of seedlings in 2017 was only 61.63% of that in 2010, showing a significant decrease. Moreover, seedlings of all height levels were reduced, especially at the height of 20–40 cm, which was only 32% of that in 2010. All seedlings at 140–150 cm disappeared in 2017. Regression analysis showed that there was a very significant linear relationship between height and age for seedlings with heights less than 46 cm ($F = 35.85$, $p < 0.01$, Figure 2).

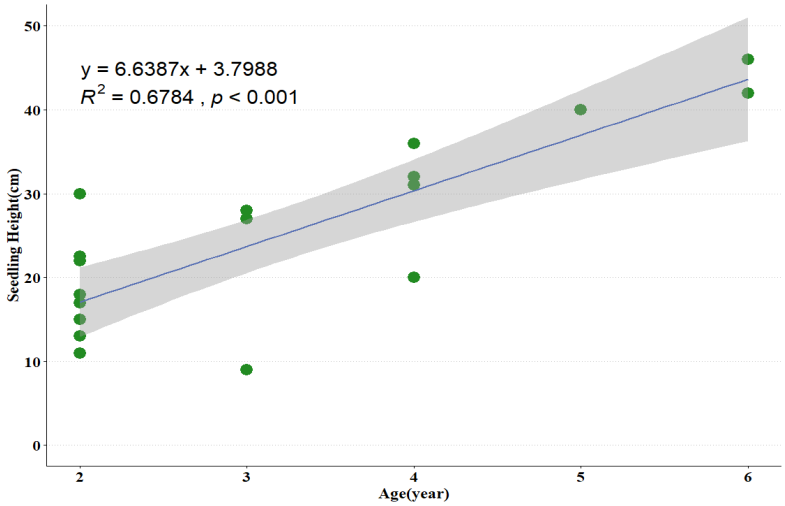

Figure 2. Linear regression between seedling height and age of *Quercus acutissima* seedlings.

3.2. Characteristics of Environmental Factors under Q. acutissima Plantation

3.2.1. Precipitation

There were significant differences in precipitation among different months (F = 11.34, $p < 0.01$) and years (F = 2.84, $p < 0.05$). With the increase of months, the precipitation first increased and then decreased, and was mainly concentrated between June and August each year (Figure 3). Among different years, precipitation in 2011 was the highest ($p < 0.01$), and precipitation in 2013 was significantly higher than that in 2016 ($p < 0.05$), and there was no significant difference in precipitation among other years ($p > 0.05$). During 2012 and 2016, precipitation in the same months fluctuated significantly among years (Figure 3).

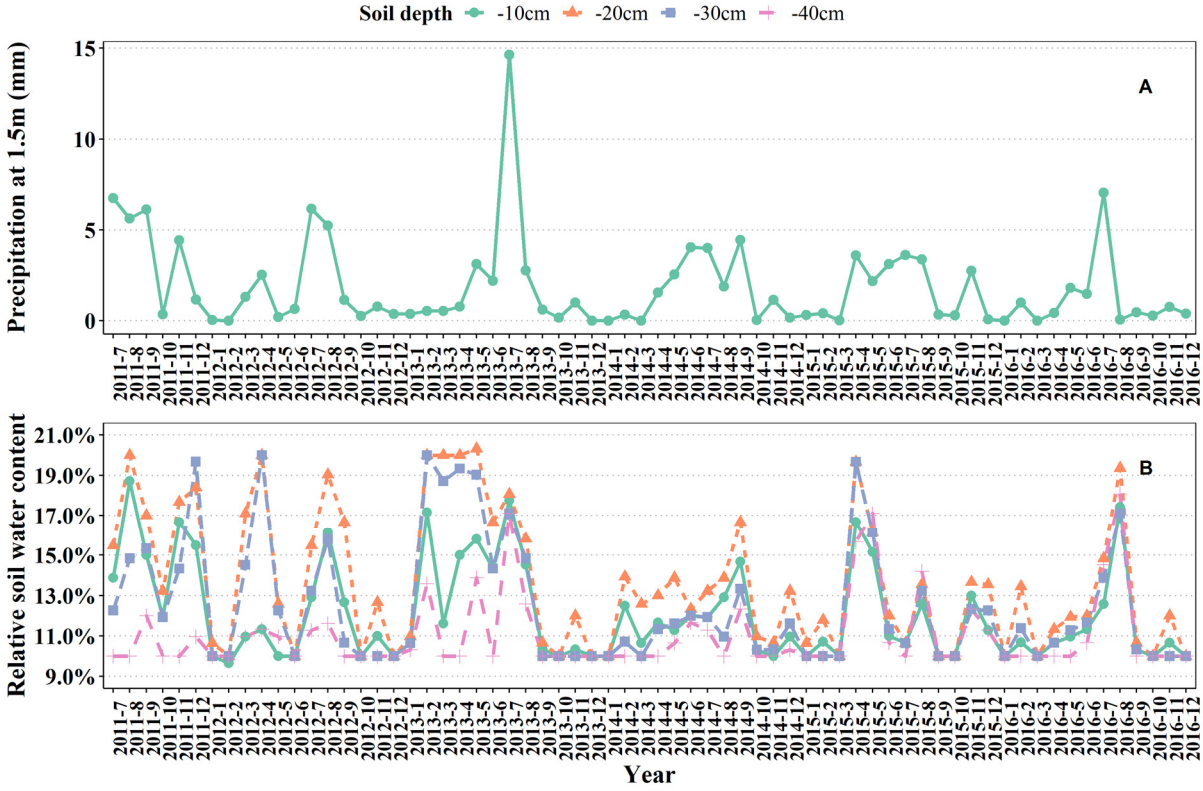

Figure 3. Variation of precipitation and relative soil water content in the *Quercus acutissima* plantation from 2011 to 2016. (**A**) Precipitation at 1.5 m; (**B**) relative soil water content.

3.2.2. Soil Moisture

The results of the analysis of variance showed that RSWC varied highly significantly between months (F = 146.82, $p < 0.01$), years (F = 163.09, $p < 0.01$), and soil depths (F = 285.73, $p < 0.01$). As the month increased, the RSWC changed in a bimodal pattern. The RSWC reached a peak in April and August, and reached a maximum in August. The RSWC declined to nadir in January, June, and October, and reached a minimum in January and October (there was no significant difference between January and October). Among years, RSWC was 2011 > 2013 > 2012≈2015 > 2014≈2016 ($p < 0.01$). Among soil depths, the order of RSWC was −20 cm > −30 cm > −10 cm > −40 cm.

3.3. Seedling Size Traits with the Increase of Age

Seedling age had a significant effect on height (F = 11.01, $p < 0.01$), ground diameter (F = 11.38, $p < 0.01$), and biomass (F = 18.60, $p < 0.01$). The height increased significantly with age (Figure 4A). Ground diameter and biomass showed no significant difference among age groups I, II, and III, and increased significantly at IV (Figure 4B,C).

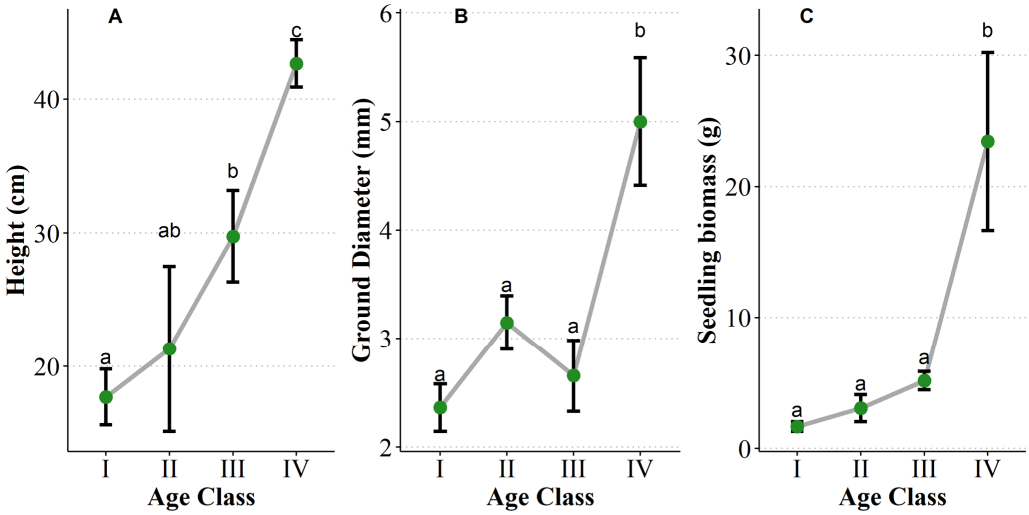

Figure 4. Changes of seedling biomass (**A**), ground diameter (**B**), and seedling biomass (**C**) with the increase of seedling age of *Quercus acutissima*. Different letters above error bars show significant differences.

3.4. Adaptation Traits of Seedlings with Increasing Age

3.4.1. Biomass Allocation

Variance analysis showed that seedling age had significant effects on LMR (F = 5.51, $p < 0.01$), RMR (F = 3.34, $p < 0.05$), LAR (F = 5.93, $p < 0.01$), and p/NP F = 5.15, $p < 0.05$), but not on SMR (F = 0.41, $p = 0.75$) nor SLA (F = 1.20, $p = 0.35$). There were no significant differences among age groups I, II, and III in LMR, LAR, and p/NP, but these indices all decreased significantly at IV (Figure 5A,E,F). As the age increased, the RMR decreased first and then increased significantly (Figure 5B).

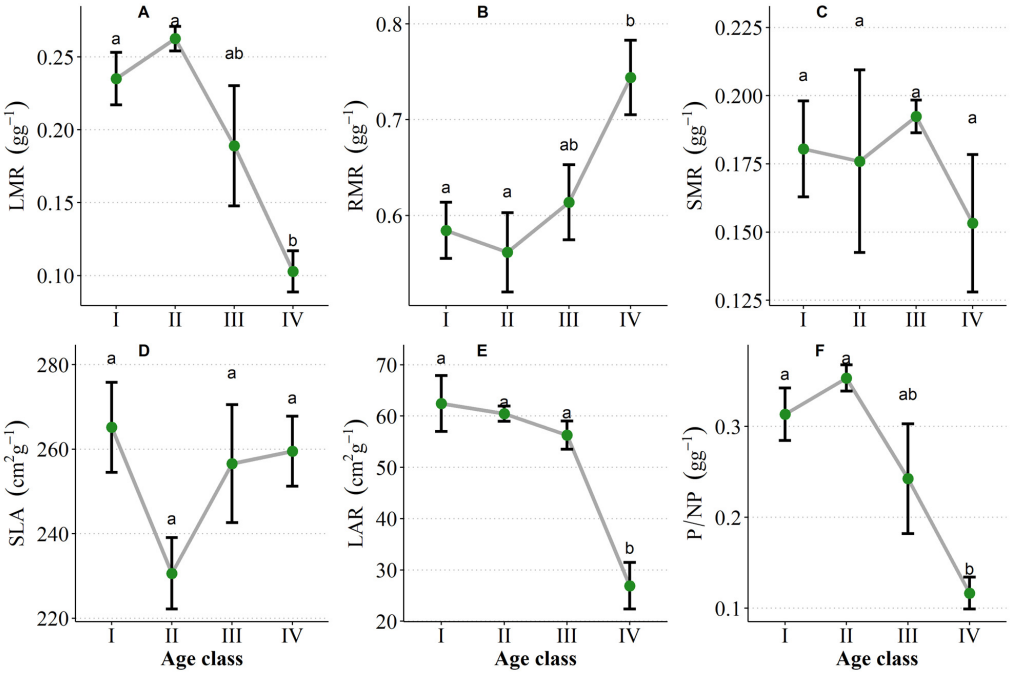

Figure 5. Changes of biomass allocation with the increase of seedling age of *Quercus acutissima*. (**A**) LMR, leaf mass ratio; (**B**) RMR, root mass ratio; (**C**) SMR, stem mass ratio; (**D**) SLA, specific leaf area; (**E**) LAR, leaf area ratio; (**F**) P/NP, photosynthetic tissues/non-photosynthetic tissues. Different letters above error bars show significant differences.

3.4.2. Root Traits

Seedling age had significant effects on total root length ($F = 4.74$, $p < 0.05$), root volume ($F = 34.64$, $p < 0.01$), average root diameter ($F = 82.42$, $p < 0.01$), and specific root length ($F = 7.19$, $p < 0.01$), but not on specific root surface area ($F = 1.35$, $p = 0.30$). With the increase of seedling age, root length continued to increase (Figure 6A), but specific root length and specific root surface area continued to decrease significantly (Figure 6E,F). However, RV and RAD showed no significant difference among I, II, and III, and increased significantly at IV (Figure 6C,D).

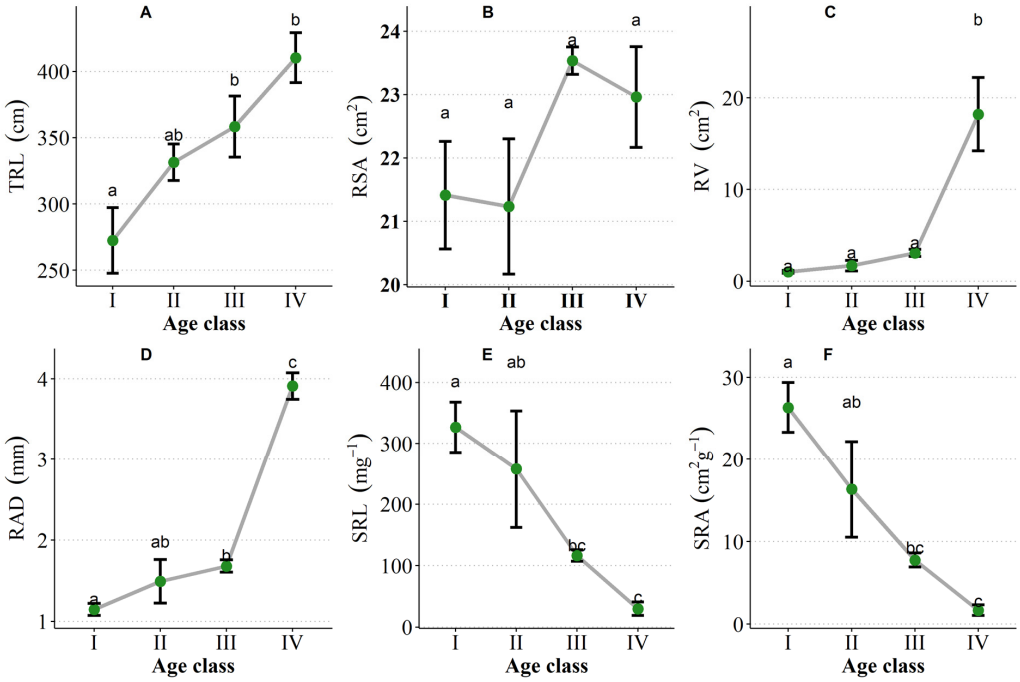

Figure 6. Changes of root traits with the increase of seedling age of *Quercus acutissima*. (**A**) TRL, total root length; (**B**) RSA, root total surface area; (**C**) RV, root volume; (**D**) RAD, root average diameter; (**E**) SRL, specific root length; (**F**) SRA, specific root area. Different letters above error bars show significant differences.

3.4.3. Non-Structural Carbohydrate (NSC)

There were significant differences in SSC ($F = 312.60$, $p < 0.01$) and SC ($F = 329.40$, $p < 0.01$) among different ages. With the increase of age, the SSC and SC of the root, stem, and leaf all increased significantly, and their orders were I < II < III < IV ($p < 0.01$, Figure 7). Organs also showed significant effects on SSC ($F = 631.57$, $p < 0.01$) and SC ($F = 543.37$, $p < 0.01$), respectively. There was no significant difference in soluble sugar between roots and stems ($p > 0.05$), which was significantly lower than that of leaves ($p < 0.01$). For starch, the root was significantly greater than that of the stem and leaf ($p < 0.01$), but there was no significant difference between the stem and leaf ($p > 0.05$).

3.5. Correlation Analysis of Seedling Traits

SB was negatively correlated with LMR, LAR, P/NP, SRL, and SRA, and positively correlated with RMR, TRL, RV, RAD, RSS, SSS, LSS, RS, SS, and LS (Figure 8). LMR, LAR, and P/NP were negatively correlated with RMR, TRL, RV, and RAD. RSS, SSS, LSS, RS, SS, and LS were negatively correlated with LMR, LAR, P/NP, SRL, and SRA, and positively correlated with RMR, TRL, RV, and RAD (the correlation between SS and RMR was not significant).

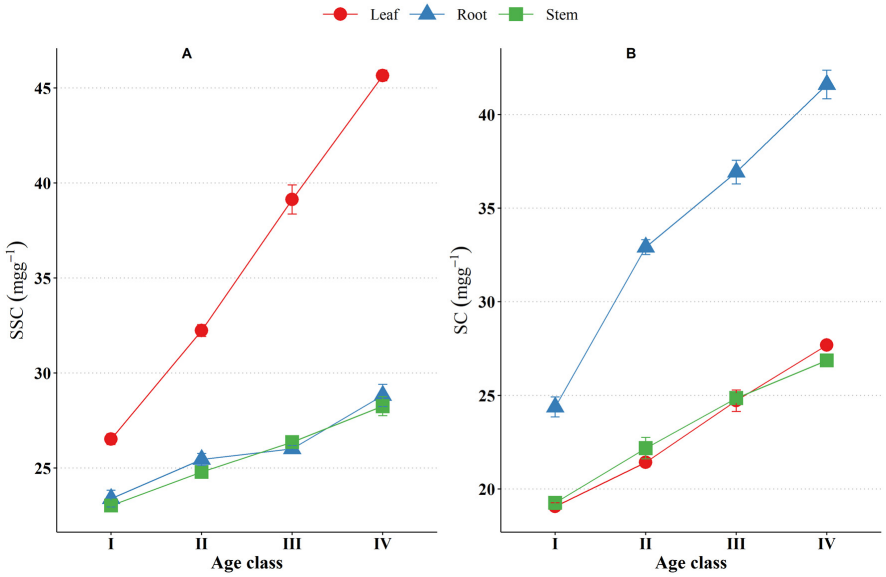

Figure 7. Changes of soluble sugar (**A**) and starch contents (**B**) in the roots, stems, and leaves with the increasing age of *Quercus acutissima* seedlings.

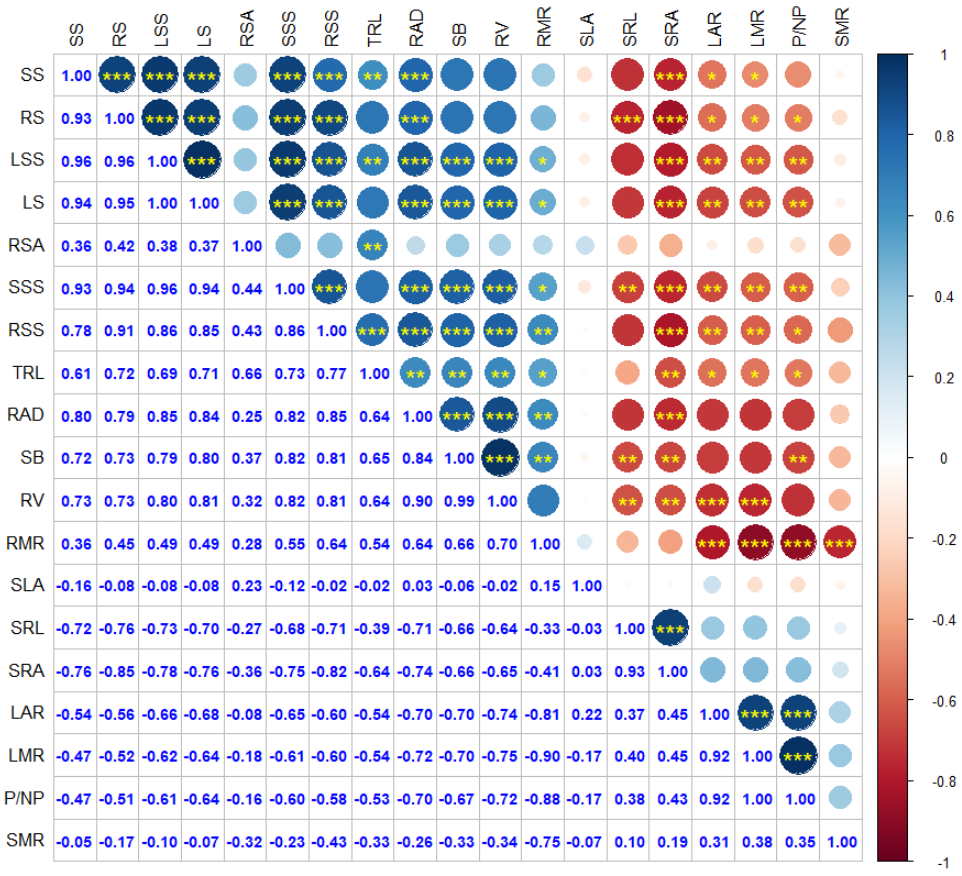

Figure 8. Correlations among seedling characteristics of *Quercus acutissima*. SB: seedling biomass; LMR: leaf mass ratio; RMR: root mass ratio; SMR: stem mass ratio; SLA: specific leaf area; LAR: leaf area ratio; TRL: total root length; RSA: root total surface area; RV: root volume; RAD: root average diameter; SRL: specific root length; SRA: specific root area; P/NP: photosynthetic tissues/non-photosynthetic tissues; RSS: root soluble sugar; SSS: stem soluble sugar; LSS: leaf soluble sugar; RS: root starch; SS: stem starch; LS: leaf starch. Significant code: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

The PCA incorporating seedling traits revealed that together, the first and second principal components represented 74.15% of the total variation (Figure 9). The first principal component (62.65%) was mainly related to seedling growth, including SB, NSC (SS, SSS, LSS, RS, SS, and LS), and root traits (RV, TRL, RAD, RSA, SRL, and SRA). The second principal component (11.5%) was associated with biomass allocation, including SMR, LMR, LAR, P/NP, SLA, and RMR.

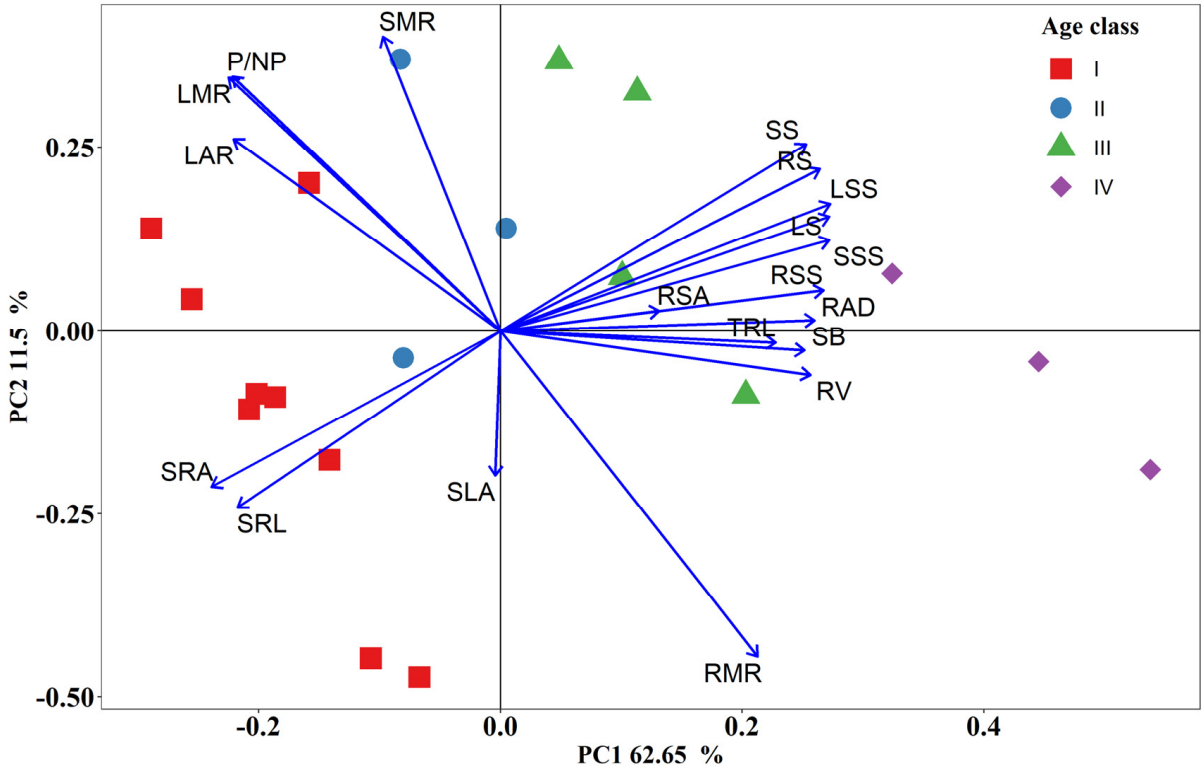

Figure 9. Principal component analysis of *Quercus acutissima* seedling trait. SB: seedling biomass; LMR: leaf mass ratio; RMR: root mass ratio; SMR: stem mass ratio; SLA: specific leaf area; LAR: leaf area ratio; TRL: total root length; RSA: total root surface area; RV: root volume; RAD: root average diameter; SRL: specific root length; SRA: specific root area; P/NP: photosynthetic tissues/ non-photosynthetic tissues; RSS: root soluble sugar; SSS: stem soluble sugar; LSS: leaf soluble sugar; RS: root starch; SS: stem starch; LS: leaf starch.

4. Discussion

Over the past decades, the predominant approach to studying successional dynamics has been to examine how community-level properties (e.g., diversity, biomass/carbon) vary over time and what factors influence their rates of change. Demographic rates of species can reveal mechanisms that underpin community assembly [49]. The seedling density of the *Q. acutissima* plantation in this paper was 14,063 N ha^{-1} in 2010 and 8667 N ha^{-1} in 2017. Thus, there were sufficient seedlings under the *Q. acutissima* plantation, which was related to the ability of shade tolerance in the seedling stage [44]. The size distribution of seedlings in 2010 and 2017 was pyramid-shaped, indicating that the seedling bank was relatively stable. Compared with 2010, the stand density changed little in 2017, but the seedling density decreased significantly, reaching only 61.63% of that in 2010. Several previous studies have suggested that low soil moisture caused by precipitation reduction is an important reason for limiting forest natural regeneration [20,50,51]. From 2014 to 2016, the relative soil water content in the *Q. acutissima* forest significantly and continuously decreased. Multiyear lags in tree drought recovery, termed 'drought legacy effects', are important for understanding the impacts of drought on forest ecosystems [52]. Thus, we thought that the decrease of seedling bank density was closely related to the drought for 3 consecutive years. However,

the responses of seedlings of different sizes were significantly different. The seedling density in the height class 0–20 cm in 2010 was similar to that in 2017. Rodríguez-García et al. [22] suggested that the significant variables that best explained the total seedling and viable seedling density were the spring and autumn precipitation of the year prior to establishment. During 2014 and 2016, the higher precipitation and soil water content of the *Q. acutissima* forest in April, May, and June may have contributed to seedling establishment. However, the seedling density in the height class 20–40 cm decreased more sharply in 2017 than in 2010, which was related to the significant decrease of relative soil water content from 2014 to 2016. Our results are consistent with the conclusions drawn by Rey and Alcántara [24]. For the seedlings taller than 40 cm, the decrease of density in 2017 was more obvious than that in 2010. Their death may have been related to the increase of minimum light demand with the increase of seedling size [29]. Many studies have shown that the conversion rate from seedlings to saplings is very low due to the insufficient relative light intensity under the forest for long-term survival [14,23,24,53]. Studies on the natural regeneration of *Quercus* have suggested that higher light intensity is necessary for successful regeneration [16,54]. Therefore, the microenvironment in the forest and the adaptability of seedlings with different sizes are important factors determining the dynamics of the seedling bank.

The critical process for natural regeneration is seedling survival [24]. It was found that the decrease of *Q. acutissima* seedling density in the height class 20–40 cm was significant, and their age was less than 5 years. Ammer et al. [53] suggested that the chances of a seedling surviving intraspecific competition for *Fagus sylvatica* L. were strongly determined by its dominance ranking within the first 5 years after establishment. From 2014 to 2016, the relative soil water content in the forest was significantly lower than that in other years, and the 2–4-year seedlings experienced this stage or part of it. There were no significant differences in biomass, biomass distribution, RSA, and RV among 2–4-year seedlings, indicating that their growth was significantly inhibited. Root production would decrease at severe soil drought [55,56]. In particular, *Pinus taeda* L. ceased root growth between −0.3 and −1.2 MPa [57]. Furthermore, severe drought increased physical soil resistance, which is assumed to restrict root growth [58]. Although there was the highest soil water content at −20 cm and −30 cm, it it may have been difficult for the seedling roots of *Q. acutissima* to grow to this depth under severe drought stress. However, no significant differences in biomass allocation were found among 2–4-year seedlings. Sinz et al. [17] showed that the biomass allocation of *Fraxinus pennsylvanica* Marsh. seedlings did not change significantly. The biomass and RMR of 5–6-year seedlings increased significantly, which may be related to the fact that these seedlings experienced a more suitable soil water content in 2013, making their roots grow to a suitable soil depth. Ammer et al. [53] suggested that the older seedlings showed stronger adaptability under the forest. Therefore, the environmental variability in the *Q. acutissima* forest was a vital factor affecting the growth and survival of seedlings under the forest.

Morphological and physiological adaptation is an important way for seedlings to persist under the forest. TRL and RAD of *Q. acutissima* seedlings aged 2 to 4 years increased significantly. Correlation analysis showed that seedling biomass was significantly positively correlated with TRL and RV. The increase of root length fostered water uptake from the soil under drought stress [55,56]. The coarsening of roots was conducive to the storage of more NSC [59]. It was also found that NSC was positively correlated with RAD. Gaucher et al. [25] thought that allocating more NSC to the root system was conducive to the survival of *Acer saccharum* Marsh.seedlings under the forest. With the increase of age, the starch and soluble sugar of *Q. acutissima* seedlings increased significantly in the roots, stems, and leaves, consistent with the results of Lusk and Piper [28]. The increase of NSC did not improve the respiration of seedlings [60], and it was more sensitive than the changes of morphological indices [34]. We also found that the NSC of *Q. acutissima* seedlings aged 2 to 4 years changed more rapidly than morphological indices. Because there was a significantly positive correlation between seedling biomass and NSC indices,

the increase of NSC content improved the survival of *Q acutissima* seedlings under the forest. For 5–6-year seedlings, RMR, TRL, RV, and RAD increased significantly, and the root morphological responses were more sensitive. Walters et al. [61] and Gaucher et al. [25] suggested that higher allocation to the roots favored long-term survival under the forest. Principal component analysis showed that root characteristics and NSC content were closely related to seedling growth. Therefore, the increase of root input and NSC content, as well as the regulation of biomass distribution, were the main ways for *Q. acutissima* seedlings to adapt to the variable environment under the forest.

5. Conclusions

The natural regeneration of plantations is a complex and long process, and the adaptability of seedlings under the forest is one of the key foundations for its successful regeneration. In the sample plot of the *Q. acutissima* plantation, the seedling bank was sufficient and stable, which was closely related to its shade tolerance. Compared with 2010, the seedling density decreased significantly in 2017. The most significant reduction in seedling density was observed for seedlings below 40 cm in height (seedling age $\leq$ 4 years), which is a critical stage for the natural regeneration of *Q. acutissima*.

During 2014 and 2016, precipitation decreased significantly, and SWC continued to decrease. The growth of 2–4-year seedlings was almost stagnant, and the regulation function of biomass distribution for themselves disappeared. Furthermore, their root growth was slow, which affected their root distribution in the 20–30 cm soil layer with the highest RSWC. Therefore, drought stress was the direct cause of the disappearance of 2–4-year seedlings. For those with seedling heights higher than 40 cm (seedling age $\geq$ 5a), which had root systems distributed in the appropriate soil depth, their growth was less affected. With the increase of age, the regulation ability of root morphology, NSC, and biomass allocation increased, which was the main way for *Q. acutissima* seedlings to adapt to drought stress in the understory. Therefore, as an important factor limiting the establishment of seedlings, drought stress together with seedling adaptation influenced the dynamics of the seedling bank in the understory of *Q. acutissima* plantations.

In future research, to provide theoretical support for the sustainable management of *Q. acutissima* plantations, we should strengthen the monitoring of environmental changes in the plantation, explore limiting mechanisms of seedling growth, and put forward reasonable management measures for natural regeneration.

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