Article

Natural Regeneration of *Morus alba* in *Robinia pseudoacacia* Plantation and the Mechanism of Seed Germination and Early Seedling Growth Restriction in the Yellow River Delta

Mengyao Wang [1], Xiangyuan Zhu [2], Wei Liu [1], Kexin Wang [1], Chunxia Tan [1], Guangfang Liu [1], Peili Mao [1,*], Banghua Cao [1,*], Bo Jia [1], Yuanxiang Pang [1] and Fucheng Jiang [3]

1   Key Laboratory of State Forestry Administration for Silviculture of the Lower Yellow River,
    Taishan Mountain Forest Ecosystem Research Station, Shandong Agricultural University,
    Tai'an 271018, China
2   Agricultural and Rural Bureau of Zhoucun District, Zibo 255000, China
3   Agricultural Production Department of Dongying Junmachang Group, Dongying 257000, China
*   Correspondence: maopl1979@163.com (P.M.); caobanghua@126.com (B.C.)

Abstract: There is a wide range of naturally regenerated *Morus alba* in the declining *Robinia pseudoacacia* plantation of the Yellow River Delta. It is important to clarify the key mechanism of natural regeneration of *M. alba* for the transformation of declining *R. pseudoacacia* plantation. According to the death density of *R. pseudoacacia*, the plantation of *R. pseudoacacia* was divided into nondeclining, moderately declining, and severely declining forests. The structural characteristics of adult trees and seedlings of *M. alba* in different decline degrees forest were investigated. A pot experiment was conducted to study the seed germination and early seedling growth of *M. alba* in saline alkali soil and nonsaline alkali soil under different soil salt contents and light intensities. The results showed that the natural regeneration of *M. alba* was obviously affected by the decline of *R. pseudoacacia* plantation. With the increase of decline degree, *M. alba* density and seedling density first increased and then decreased, and were the highest in the medium decline plantation. Under full light intensity, the vigor index of *M. alba* seeds and the biomass of seedlings were significantly greater than those of 25% full light intensity. The germination rate and germination index under 1‰ soil salt content were significantly lower than those under 3‰, but the biomass of seedlings was on the contrary. The 1000-seed weight, seed germination, and seedling biomass of moderately declining *R. pseudoacacia* plantations were close to those of nonsaline alkali land, while significantly higher than those of nondeclining plantations, but the germination index of moderately declining *R. pseudoacacia* plantation was higher than that of nonsaline alkali land. Therefore, the germination ability of maternal trees in saline alkali land was higher than that in nonsaline alkali land under salt stress.

Keywords: coastal saline–alkali land; plantation decline; seedling density; maternal tree habitat; seed quality

1. Introduction

Planted forests are an important component of global forest resources. With the rapid increase in the area of global planted forests in recent decades [1], they play increasingly important roles in timber production, environmental improvement, landscape construction, and climate change mitigation [2]. China has the largest area of planted forests in the world. However, the management of planted forests are difficult because of lacking effective and long-term scientific theoretical guidance and sustainable management technology systems suitable for different regions of planted forests. For a long time, plantation forest management has overemphasized and pursued short-term productivity and economic benefits, favoring artificial regeneration and homogeneous pure forest cultivation patterns, ignoring the natural succession and regeneration of planted forests [2], which has led to a

serious decline in many planted forests. Natural regeneration of planted forests is currently attracting attention and is being explored in terms of stand structure [3], litter fall density [4], seedling adaptation [5,6], and seedling establishment [7,8]. However, current studies have shown that the natural regeneration of planted forests and their near-naturalistic succession are difficult to achieve [2,9,10]. Therefore, the elucidation of natural regeneration limitation mechanisms of planted forests is of great importance for their sustainable management.

Seed quality determines the ability of seeds to germinate and the quality of seedlings, and is one of the key factors determining the success of natural regeneration [11,12]. The growing environments the maternal tree demonstrate significant influences on the quality of the seeds of the offspring, which is known as the maternal effect. The wide variety of environments experienced by maternal trees during seed production directly influences the characteristics (e.g., dormancy, longevity, etc.) of offspring seeds [13–15] and is considered to be an important determinant of natural regeneration [16]. Sionit and Kramer [17] found that exposure to water stress during the pod formation and filling stages of soybean led to a reduction in seed weight. The study of *Quercus brantii* found that the seedlings from drought-stressed maternal trees increased adaptability to drought [18]. The external temperature experienced by the parent plant also affects seed size [19]. Studies on annuals have found that drought stress experienced by grandparents and parents affects the performance of offspring [20]. Herman and Sultan [21] summarized the effects of the various environments experienced by the parent on the fitness of the offspring. For long-lived conifers, the variety of environments they experience provides a guarantee of offspring fitness [22]. Maternal effects can alter the adaptations of offspring in the short term and are more adaptable to changes in the external environment, especially in the context of global climate change, than genetic changes that can only occur over long periods of time in plants [11]. However, the duration and mode of action of the maternal effect is currently unclear.

Light intensity and soil salinity are important environmental factors that affect seed germination and seedling establishment of forests in coastal saline alkali land. During the stage of seed germination, light and salt stress have different effects. Generally, seed germination is not strongly related to light, but soil salinity has a significant effect on seed germination [23]. For non-salt-tolerant plants, seed germination is significantly inhibited as soil salt content increases [24,25], but for salt-tolerant plants, low salt concentrations have less effect on seed germination and even have some promotion [26,27]. During the seedling growth stage, light is the most important determinant of seedling understory growth and survival [6]. In order to intercept more light in the understory, plants increase the leaf biomass ratio and decrease the root biomass ratio [28]. As soil salinity increases, seedling growth is significantly inhibited. The root system is the first sensory organ of salt stress [29], and its biomass allocation increases, but root growth is significantly inhibited beyond the tolerance range [30]. A comparison revealed that plants may have opposing adaptation strategies when subjected to both low light and salt stresses. Therefore, it is important to explore the regeneration mechanisms under planted forests in coastal saline lands for the management of planted forests.

The Yellow River Delta is a typical global coastal saline land with shallow groundwater depth and high mineralization, and there are few tree species suitable for afforestation in this area. Monitoring and mastering of riparian vegetation biomass [31,32] and hydrology [33] is an important part of vegetation management. *Robinia pseudoacacia* forests planted in the 1970s and 1980s are the largest planted forests in the region, but they are now in severe decline and a large number of deaths have occurred. Yao et al. [34] found that *R. pseudoacacia* grew well when the groundwater depth was lower than 1.8 m during the low-water-level period. In winter, the groundwater level in some areas was lower than the sea level, and the incoming water from the Yellow River was relatively small, which caused seawater intrusion and increased the mineralization of groundwater, exacerbating the death of the *R. pseudoacacia* forest [34]. Therefore, the regeneration of *R. pseudoacacia* plantation has become an urgent demand. *Morus alba* is also an important silvicultural species in

the region [35] and is highly adaptable with strong tolerance to salt stress and drought stress [25,36]. Field surveys have revealed the widespread presence of naturally regenerated *M. alba* within *R. pseudoacacia* plantations in the region, but this phenomenon has not attracted enough attention. To reveal the natural regeneration pattern of *M. alba*, identify key limiting factors, and provide theoretical and technical support for the transformation of degraded *R. pseudoacacia* plantations, in this paper, we investigated the distribution characteristics of *M. alba* in *R. pseudoacacia* plantations with different degrees of decline, assessed their natural regeneration capacity, and analyzed the factors affecting the establishment of seedlings. At the same time, *M. alba* seeds in *R. pseudoacacia* forest and nonsaline alkali land were collected to study seed germination and early seedling growth under light intensity and salt stress, and to clarify the key influence mechanism of maternal tree habitat and environmental factors on seed germination and seedling establishment.

2. Materials and Methods

2.1. Study Area

The study was conducted in the Yellow River Delta area in the north of Shandong Province (37°35′~38°12′ N, 118°33′~119°20′ E). The region is a warm, temperate, semihumid continental monsoon climate zone. The average annual temperature is 11.9 °C, the average annual daily range is 10.7 °C, the average annual precipitation is 592.2 mm, the average annual evaporation is 1908.2 mm, and the average annual evaporation ratio is 3.22. The soil is mainly composed of fluvo aquic soil and saline soil. Tidal soil accounts for 44.46% of the total soil area in the region, and saline soil accounts for 50.88% of the total area in the region. The vegetation types in the area are few and simple, mainly herbs and shrubs, with few woody plants, and *Suaeda glauca*, *Phragmites australis,* and *Tamarix chinensis* are the main distribution species [37].

2.2. Experimental Design

2.2.1. Survey of *R. pseudoacacia* Planted Forests

Through fieldwork, the natural regeneration survey of *M. alba* was carried out in the *R. pseudoacaci* plantations in Shandong Yellow River Delta National Nature Reserve (A), Jiufenchang of Gudao Town (B), and Shenxiangou (C) (Figure 1). The planting spacing of *R. pseudoacaci* stands at the above three locations was 3 m × 4 m, and the stand characteristics were shown in Table 1. Based on the mortality density of *R. pseudoacacia*, the *R. pseudoacaci* plantations in the Jiufenchang was defined as an undeclined forest, Shenxiangou was defined as a moderately declining forest, and the reserve was defined as severely declining forest. Three randomly 20 m × 30 m sample squares were set up in each site. In each sample square, *R. pseudoacacia* and *M. alba* ≥ 1.5 m in height were defined as adult trees, and all trees were measured for diameter at breast height (DBH). Trees below 1.5 m in height were defined as seedlings and their height was measured. The number of dead *R. pseudoacacia* in the sample was also measured. Adult trees were classified into DBH sizes, with one diameter class for every 2 cm. Seedlings were divided into five height classes: 50–70 cm, 71–90 cm, 91–110 cm, 111–130 cm, and 131–150 cm. The soil was collected from 0–40 cm within the *R. pseudoacacia* forest and brought back to the laboratory. The soil salt content was measured by conductivity method. The pH value of soil was measured with a pH meter.

2.2.2. Collection of *M. alba* Seeds

In May 2019, mature *M. alba* fruits were collected from the Forestry Practice Base of Shandong Agricultural University in Tai'an (T), the *R. pseudoacacia* plantation in Jiufenchang (DW), and in Shenxiangou (DN). Among them, Tai'an was a typical nonsaline area. A total of 10 maternal trees were collected at each site. The *M. alba* fruits were repeatedly rubbed and rinsed five times, and the full seeds were selected and dried naturally. Using a thousand-seeds method, the 1000-seed weight per maternal tree was counted. The 1000-seed weight of T, DW, and DN was 1.99 ± 0.16 g, 0.98 ± 0.11 g, and 1.35 ± 0.14 g, respectively.
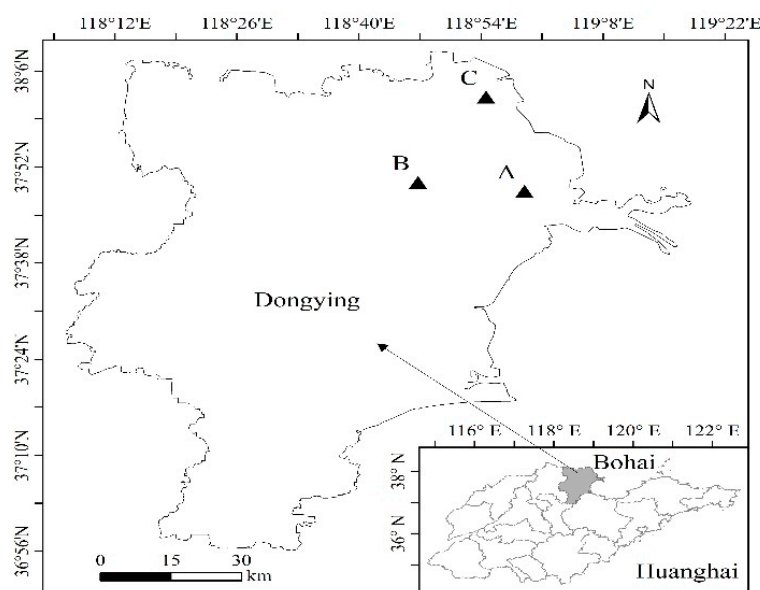
Figure 1. Geographical location of the study sites. A: Shandong Yellow River Delta National Nature Reserve; B: Jiufenchang of Gudao Town; C: Shenxiangou.

Table 1. Characteristics of stand structure of *Robinia pseudoacacia* plantation.

Indicators	Stand Age (Years)	Density of Standing Timber (Trees ha^{-1})	Average DBH (cm)	Dead Wood Density (Trees ha^{-1})	Soil Salinity (‰)	Soil pH
Jiufenchang	19	1033	8.33 ± 4.32	0	0.19	8.01
Shenxiangou	43	900	19.12 ± 2.88	100	0.21	7.92
Reserve	31	0	0	1200	0.23	7.86

2.2.3. Seed Germination and Seedling Growth Tests with Different Soil Salt Content, Light Intensity, and Maternal Tree Habitat

On 27 May 2019, seeds from different maternal tree habitats (T, DW, and DN) were taken separately and sown according to light intensity gradient (full light and 25% full light) and soil salt content (1‰ and 3‰), and five pots per treatment were sown with 50 seeds per pot. After the seeds were evenly spread on the soil surface, a thin layer of soil was covered to cover the seeds. Regular observations were recorded daily during the experiment to count the number of seeds germinated and watered regularly to keep the soil moist. The experiment ended on 5 November 2019. Three seedlings were selected from each pot, and then the seedlings were removed and divided into roots, stems, and leaves. After bringing it back to the laboratory, the root system was scanned by HP Scanjet 8200 scanner. The scanned images were then analyzed with Delta-T Area Meter Type AMB2 root parameter analysis software to obtain root length (RL, cm), root average diameter (RAD, cm), root surface area (RSA, cm^2), and root volume (RV, cm^3). The individual tissues were dried in an oven at 85 °C for 48 h. The dry weight was measured with an electronic balance (0.1 mg accuracy) and the seedling biomass (SB, root + stem + leaf mass, g), root biomass ratio (RMR, root mass/seedling biomass, g.g^{-1}), stem biomass ratio (SMR, stem mass/seedling biomass, g.g^{-1}), leaf biomass ratio (LMR, leaf mass/seedling biomass, g.g^{-1}), root shoot ratio (RSR, root mass/(leaf + stem biomass)), specific root length (SRL, total root length/root mass, cm.g^{-1}), and specific root surface area (SRA, total root surface area/root mass, cm^2.g^{-1}) indices were calculated.

Germination rate (Gr, %), mean germination time (MGT), germination index (Gi), and vigor index (Vi) were calculated as follows:

$$G_r = G_1/N \times 100 \tag{1}$$

$$\text{MGT} = \sum (D \times n_i) / \sum n_i \tag{2}$$

$$Gi = \sum (n_i / D) \tag{3}$$

$$Vi = S \times GI \tag{4}$$

where G_1 is the number of germination, N is the total number of tested seeds, n is the number of seeds germinating normally on each day, D is the number of days since seeds were placed in bed, G_t is the net germination number on each day, D_t is the corresponding germination day, and S is the dry weight of seedlings.

2.3. Data Analysis

Soil salt content, light intensity, and maternal tree habitat were used in a three-way ANOVA for the seed germination stage and seedling growth stage tests. The relevant data analyses were performed with SPSS 20.0 (SPSS Inc., Chicago, IL, USA) statistical analysis software, and multiple comparisons were performed. The test level was $p = 0.05$.

3. Results

3.1. Structural Characteristics of M. alba in the R. pseudoacacia Plantation

As seen in, Figure 2, *M. alba* were naturally distributed within the different declining *R. pseudoacacia* plantations. Within the nondeclining and severely declining *R. pseudoacacia* plantations, the density of adult *M. alba* were close: 633 and 656 trees ha^{-1}, respectively (Table 2). However, the density within moderately declining *R. pseudoacacia* stands was 7667 trees ha^{-1}, which was 12 times higher than both. Within the undeclined *R. pseudoacacia* forest, the DBH class structure was incomplete and the distribution showed a unimodal pattern, with the maximum density of 170 trees ha^{-1} at 8.1–10.0 cm DBH and 367 trees ha^{-1} at DBH greater than 8 cm. Within the severely declining *R. pseudoacacia* plantations, the diameter class structure was inverted-J-shaped, and the density was mainly distributed in the 2.1–12.0 cm DBH range with a density of 450 trees ha^{-1} and 222 trees ha^{-1} for DBH greater than 8 cm. Within moderately declining *R. pseudoacacia* stands, the diameter class structure was also inverted-J-shaped, with the largest number of diameter class 0–2 cm at a density of 4930 trees ha^{-1}, but none with the DBH greater than 8 cm.

Table 2. Characteristics of stand structure of *Morus alba* in the different declining *Robinia pseudoacacia* plantation.

Indicators	Density (Trees ha^{-1})	Chest Height Section Area (Trees ha^{-1})	Average Diameter at Breast Height (cm)	Seedling Density (Trees ha^{-1})
Jiufenchang	633	4.35	8.33 ± 4.32	No seedlings
Shenxiangou	7667	3.04	2.02 ± 0.10	467
Protected Areas	656	1.57	8.56 ± 3.91	26

The different declining *R. pseudoacacia* stands differed significantly in the number of *M. alba* seedlings (). No seedlings were found in the nondeclining *R. pseudoacacia* forests, and very few seedlings were found in the severely declining *R. pseudoacacia* forests, with a density of only 26 trees ha^{-1}. The density of seedlings within medium-declining *R. pseudoacacia* stands was 467 trees ha^{-1} and the distribution of plant height classes was unimodal. The maximum number of plants was 170 trees ha^{-1} at 91–110 cm plant height, after which the density decreased rapidly (Figure 3). Plant height was mainly distributed at 50–110 cm, accounting for 85.71% of the total number of seedlings (Figure 3).

3.2. Effect of Light Intensity and Soil Salinity on Seed Germination and Seedling Growth of M. alba Seeds

3.2.1. Seed Germination

The effect of light intensity on Gr, MGT, and Gi was not significant, the effect on Vi was significant (Table 3), and full light was higher than that of 25% full light (Figure 4). Soil

salt content had a significant effect on Gr and Gi, both being higher in 3‰ treatment than in 1‰ treatment, but not on MGT and Vi. Maternal tree habitat had a significant effect on Gr, MGT, Gi, and Vi. The Gr, MGT, and Vi of the DN habitat were not significantly different from those of the T habitat treatment but they were significantly greater than those of the DW habitat, and Gi of the DN habitat was significantly better than those of the T and DW habitat conditions (Figure 4). In terms of interaction, salinity and maternal tree habitat had a significant effect on Vi, and the interaction of light, salinity, and maternal tree habitat significantly affected Gr, MGT, Gi, and Vi. DN had a clear germination advantage in full light at 3‰ salt treatment, but the advantage was more pronounced in low light at 1‰ salt treatment (Figure 4).
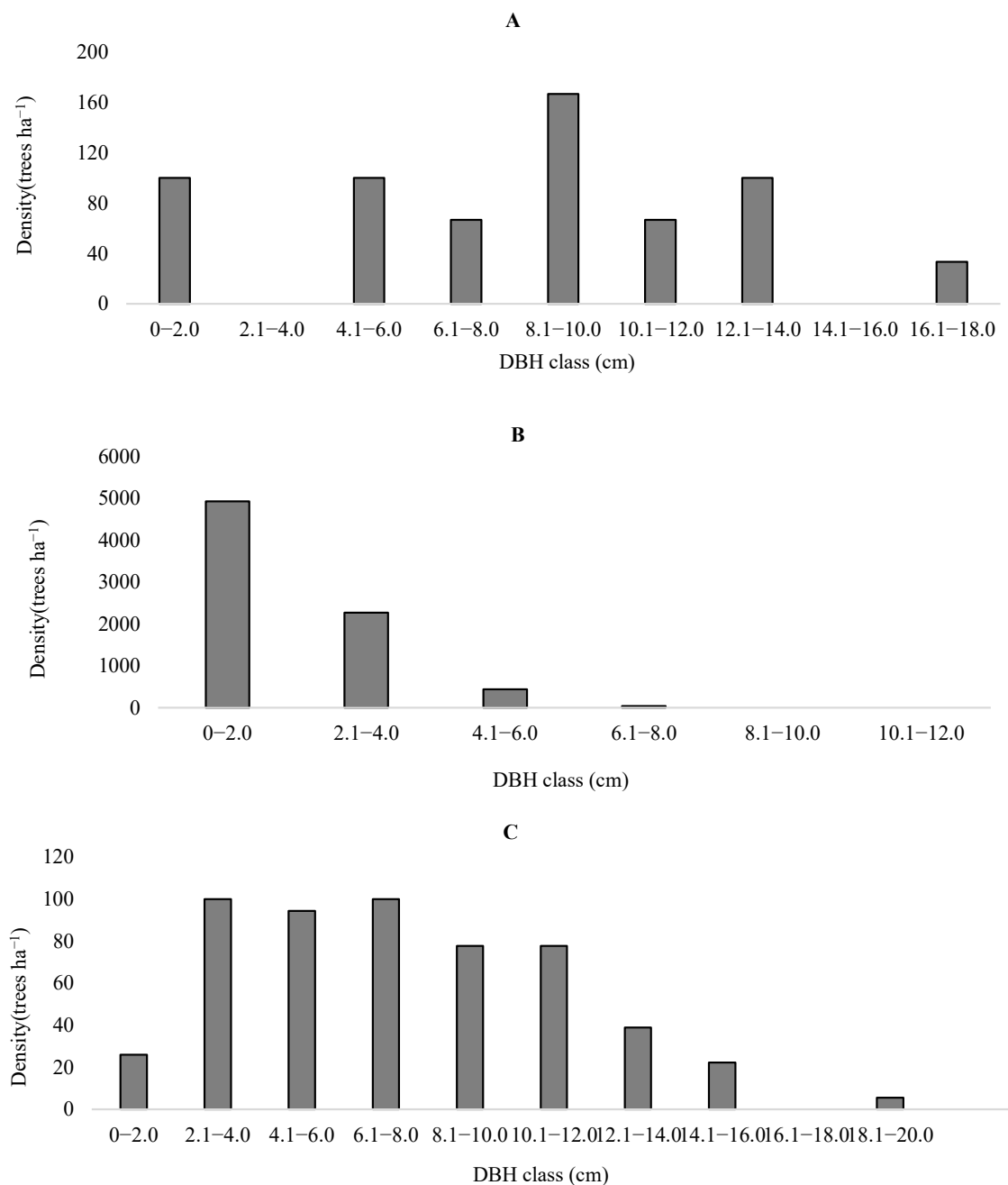

Figure 2. DBH class structure of *Morus alba* distributed in Jiufenchang (**A**), Shenxiangou (**B**), and reserve (**C**) *R. pseudoacacia* plantation.
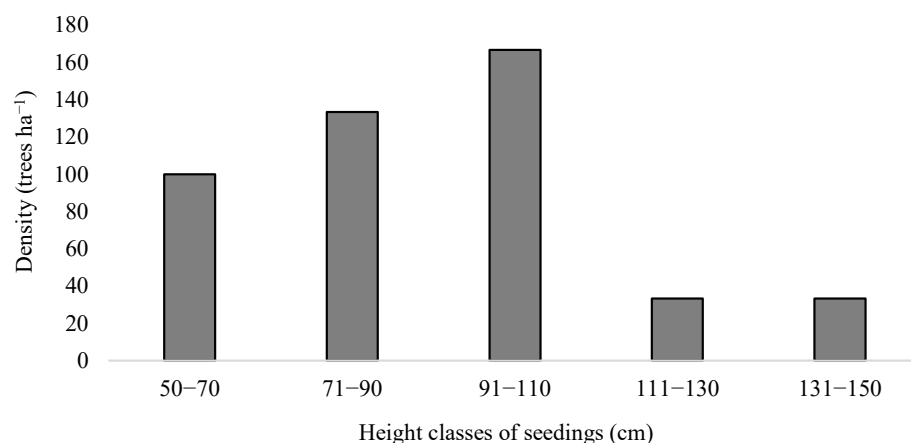
Figure 3. Distribution of height classes of *Morus alba* seedlings within the Shenxiangou *Robinia pseudoacacia* plantation.

Table 3. Three-factor variance analysis table of light intensity, soil salt content, and maternal tree habitat of *Morus alba* on seed germination and seedling growth. Gr: germination rate; MGT: mean germination time; Gi: germination index; Vi: vigor index; RMR: root biomass ratio; SMR: stem biomass ratio; LMR: leaf biomass ratio; RSR: root shoot ratio; SB: seedling biomass; RL: root length; RSA: root surface area; RAD: root average diameter; RV: root volume.

Indicators	Light (A)		Salt (B)		Maternal Tree Habitat (C)		A × B		A × C		B × C		A × B × C	
	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Gr	0.03	>0.05	5.26	<0.05	54.58	<0.01	0.01	>0.05	1.66	>0.05	0.90	>0.05	12.35	<0.01
MGT	0.87	>0.05	0.68	>0.05	14.85	<0.01	0.60	>0.05	0.41	>0.05	1.14	>0.05	5.76	<0.01
Gi	0.64	>0.05	9.86	<0.01	69.90	<0.01	2.09	>0.05	1.34	>0.05	0.84	>0.05	5.29	<0.01
Vi	8.76	<0.01	2.55	>0.05	24.16	<0.01	0.02	>0.05	1.55	>0.05	5.89	<0.01	4.21	<0.05
RMR	0.00	>0.05	1.56	>0.05	2.92	>0.05	5.10	<0.05	3.78	<0.05	0.50	>0.05	4.36	<0.05
SMR	1.95	>0.05	0.60	>0.05	1.19	>0.05	0.79	>0.05	2.93	>0.05	5.83	<0.01	0.40	>0.05
LMR	1.70	>0.05	1.48	>0.05	2.62	>0.05	2.96	>0.05	4.95	<0.05	6.41	<0.01	1.39	>0.05
RSR	0.00	>0.05	1.34	>0.05	2.72	>0.05	5.13	<0.05	3.65	<0.05	0.49	>0.05	4.10	<0.05
SB	46.61	<0.01	24.72	<0.01	34.83	<0.01	4.86	<0.05	10.96	<0.01	2.32	>0.05	2.06	>0.05
RL	1.60	>0.05	2.08	>0.05	9.02	<0.01	0.93	>0.05	2.20	>0.05	0.00	>0.05	0.71	>0.05
RSA	2.60	>0.05	1.22	>0.05	9.99	<0.01	1.48	>0.05	3.01	>0.05	0.07	>0.05	0.98	>0.05
RAD	1.13	>0.05	3.53	>0.05	2.40	>0.05	2.50	>0.05	2.49	>0.05	0.40	>0.05	0.15	>0.05
RV	3.71	>0.05	0.49	>0.05	10.46	<0.01	2.03	>0.05	3.94	<0.05	0.20	>0.05	1.24	>0.05

3.2.2. Seedling Biomass Traits

Light intensity, salinity conditions, and maternal tree habitat had nonsignificant effects on RMR, SMR, LMR, and RSR, and had a highly significant effect on SB (Table 3). For SB, the full light treatment was higher than that of the 25% full light treatment, the 1‰ salt treatment was higher than that of the 3‰ salt treatment, and the T habitat was not significantly different from the DN habitat but was significantly better than that under the DW habitat (Figure 5).

Light intensity × salinity conditions and light intensity × maternal tree habitat had a significant effect on RMR, RSR, and SB, and a nonsignificant effect on SMR and LMR. There was a significant interaction between salinity conditions and maternal tree habitat for SMR, but not for RMR, LMR, RSR, and SB, and the interaction of light intensity × salinity conditions × maternal tree habitat was significant for RMR and RSR, suggesting that seedling biomass allocation was influenced by a combination of factors.

3.2.3. Seedling Root Morphology

The effects of light intensity and salinity conditions on RL, RAD, RSA, RV, SRL, and SRA were all nonsignificant, while the parent tree habitat had no significant effect on RAD

and a highly significant effect on RL, RSA, and RV (Table 3). The light intensity × maternal tree habitat interaction had a significant effect on RV, while the other types of interaction had no significant effect on RL, RAD, RSA, and RV. The effects of maternal tree habitat on RL, RSA, and RV were all nonsignificantly different but were significantly greater in the T and DN habitat treatments than in the DW habitat treatment (Figure 6).
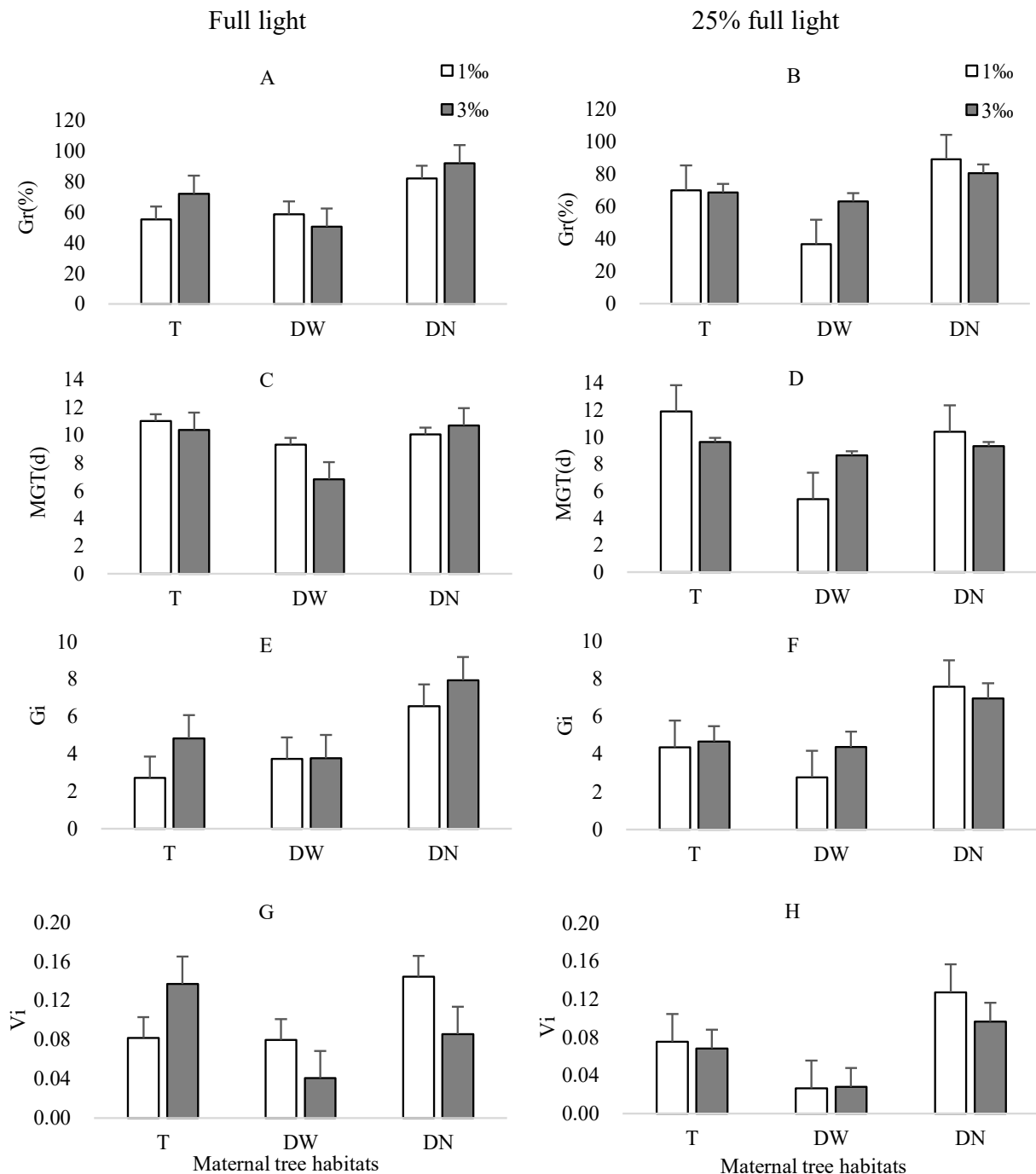

Figure 4. Effects of light intensity and salinity on seed germination of *Morus alba* from different maternal tree habitats. T: seeds from nonsaline soil; DW: seeds from Jiufenchang in saline–alkali land; DN: seeds from Shenxiangou in saline–alkali land. (**A**): Gr, full light; (**B**): Gr, 25% full light; (**C**): MGT, full light; (**D**): MGT, 25% full light; (**E**): Gi, full light; (**F**): Gi, 25% full light; (**G**): Vi, full light; (**H**): Vi, 25% full light.
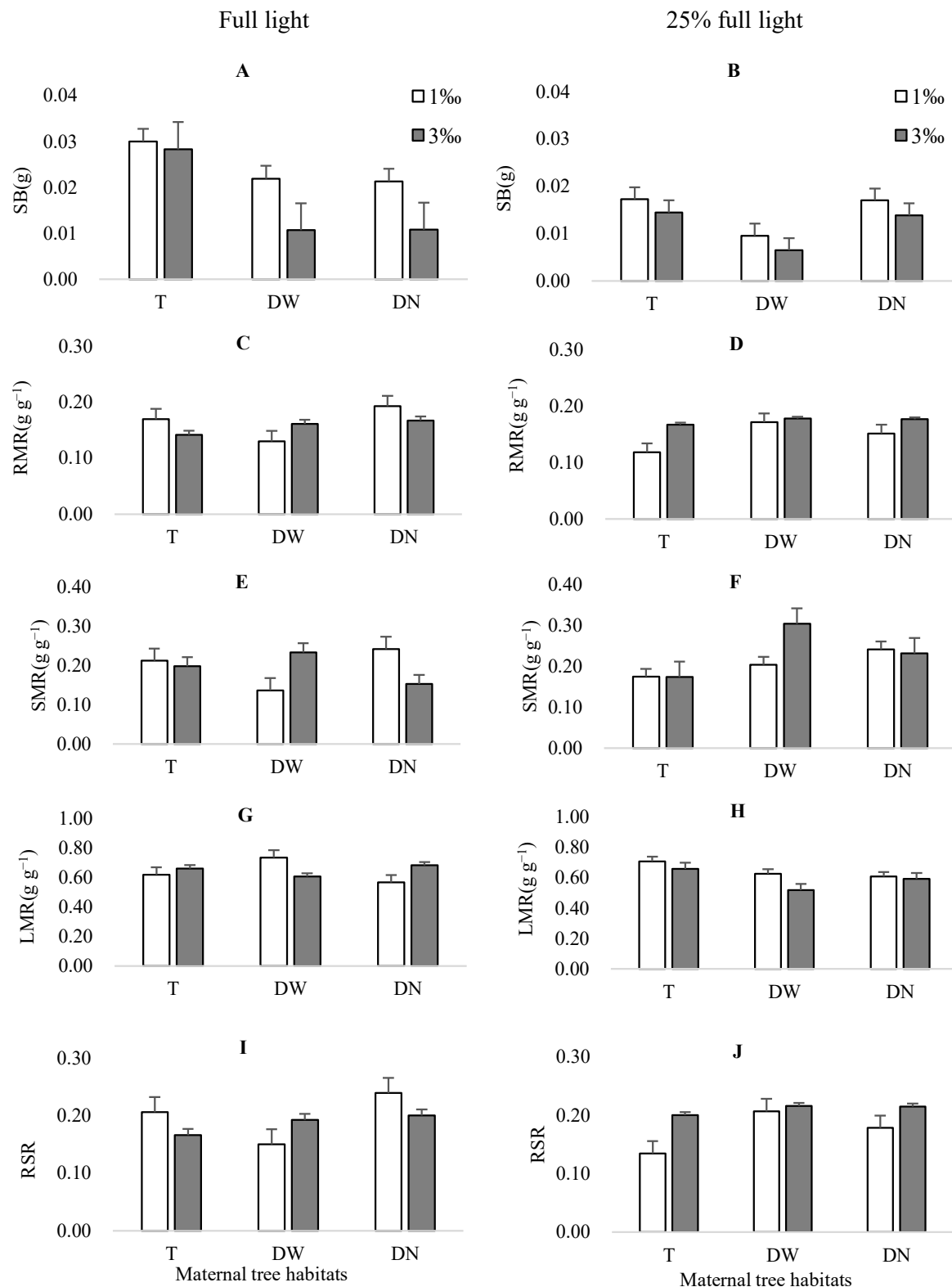
Figure 5. Effects of light intensity and salinity on biomass indices of *Morus alba* seedlings from different maternal tree habitats. T: seeds from nonsaline soil; DW: seeds from Jiufenchang in saline–alkali land; DN: seeds from Shenxiangou in saline–alkali land. (**A**): SB, full light; (**B**): SB, 25% full light; (**C**): RMR, full light; (**D**): RMR, 25% full light; (**E**): SMR, full light; (**F**): SMR, 25% full light; (**G**): LMR, full light; (**H**): LMR, 25% full light; (**I**): RSR, full light; (**J**): RSR, 25% full light.
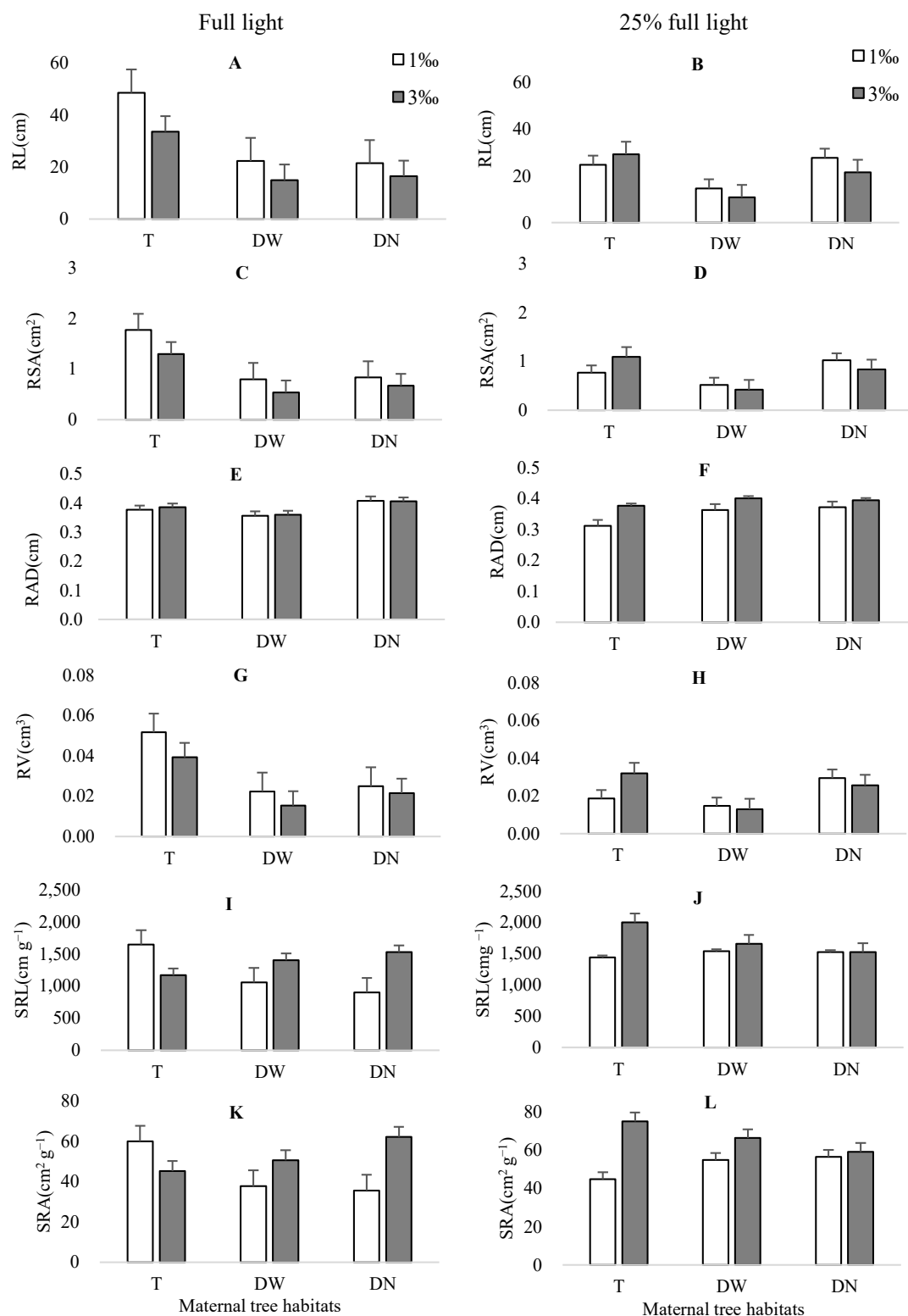
Figure 6. Effects of light intensity and salt content on root of *Morus alba* seedlings morphology from different maternal tree habitats. T: seeds from nonsaline soil; DW: seeds from Jiufenchang in saline–alkali land; DN: seeds from Shenxiangou in saline–alkali land. (**A**): RL, full light; (**B**): RL, 25% full light; (**C**): RSA, full light; (**D**): RSA, 25% full light; (**E**): RAD, full light; (**F**): RAD, 25% full light; (**G**): RV, full light; (**H**): RV, 25% full light; (**I**): SRL, full light; (**J**): SRL, 25% full light; (**K**): SRA, full light; (**L**): SRA, 25% full light.

4. Discussion

4.1. Natural Regeneration of M. alba in R. pseudoacacia Plantation in the Yellow River Delta

M. Alba is one of the most important afforestation species in the Yellow River Delta, with a certain degree of salt tolerance, drought tolerance, and shade tolerance, and a strong adaptability. The *M. alba* covers a large area of cultivation in the region; the fruit is sweet and sour, birds like to eat it, and it may be carried by birds into the *R. pseudoacacia* plantation, where it sprouts and regenerates successfully under the proper circumstances, which is an important reason for the wide distribution of *M. alba* within the *R. pseudoacacia* plantation. A survey of *R. pseudoacacia* plantations suggested that the natural regeneration of *M. alba* was closely related to the degree of decline of the stand. Within the nondeclining *R. pseudoacacia* plantations in the Jiufenchang, the DBH class structure of *M. alba* was incomplete and there existed no seedling. *M. alba* is a light-demanding plant which requires high light intensity for natural regeneration. Natural regeneration of less shade-tolerant Quercus species also requires high light intensities for successful regeneration [3,38]. Therefore, the low light intensity within the forest is a crucial reason for the poor natural regeneration in the Jiufenchang. The *R. pseudoacacia* plantation in Shenxiangou is in moderate decline level, with a continuous *M. alba* DBH class structure, sufficient seedlings, and a population in a steady process of increase. The death of canopy *R. pseudoacacia* in this stand has improved the light environment within the stand and provided for successful regeneration of early *M. alba*. The high number of *M. alba* maternal trees in this stand and the large amount of fruit set provided an adequate source of seeds for natural regeneration. At the same time, *M. alba* densities of up to 7667 trees ha^{-1} significantly inhibited understory herbaceous growth. Numerous studies show that understory herbaceous vegetation is an important factor preventing natural regeneration [39,40]. The inhibition of herbaceous vegetation therefore increases the chances of seeds reaching the surface, facilitating seed germination and seedling growth, which is an important reason why *M. alba* with small seeds regenerates well in the Shenxiangou. The *R. pseudoacacia* plantations in the reserve are in serious decline, with all *R. pseudoacacia* plantations being dead and the adult *M. alba* with a growing DBH class structure, but with very few seedlings, only 26 trees ha^{-1}. The density of *M. alba* in this stand was only 656 trees ha^{-1}, the stand was not depressed, and herbs were present in large numbers, limiting seed germination and preventing natural regeneration. Therefore, the degree of decline of the *R. pseudoacacia* plantation, the number of *M. alba* maternal trees, and the growth of understory vegetation may be important factors influencing the success of natural regeneration of *M. alba* trees.

4.2. Comparison of M. alba Seeds in Saline Alkali Land and Nonsaline Alkali Land during Seed Germination and Early Seedling Growth

The germination rate, mean germination time, and vigor index of the DN habitat were not significantly different from the T habitat treatment and were significantly greater than those in the DW habitat, indicating that the maternal tree habitat had a significant effect on seed quality. The phenomenon has been found in both woody and herbaceous plants in different habitats and is thought to enhance the adaptive capacity of offspring [21]. The 1000-seed weight of *M. alba* was 1.99 ± 0.16 g for T and 1.35 ± 0.14 g for DN, both significantly greater than 0.98 ± 0.11 g for DW. Numerous studies show that seed size determines seed quality and is related to the nutrients contained within the seed [15,41,42]. Seed size is, therefore, a key indicator of seed quality in *M. alba*. González-Rodríguez et al. [11] also found that maternal tree effects significantly altered seed quality. However, Vivas et al. [43] suggested that it is the site condition and tree genotype of maternal tree which play important roles in offspring adaptation, rather than seed quality. The germination index of DN was significantly higher than that of T, indicating that its seed viability was significantly higher in the coastal saline zone. Yin [44] also found that the seed vigor of the introduced tree species *R. pseudoacacia* in the region was higher than that of nonsaline seeds. Thus, long-term salt stress in the Yellow River Delta enhances the salt tolerance of *M. alba* seeds, and seed size is not the only pathway, suggesting a complex mechanism of action for maternal

effects. There was no significant effect of maternal tree habitat on biomass allocation, which suggested similar adaptation patterns in biomass regulation. The differences in seedling biomass, root length, root surface area, and root volume were all not significant in the T and DN habitats compared to those in the DW habitat. Significant advantages of large seeds in seedling biomass and root development were also found in *Pinus thunbergii* [45] and *Quercus acutissima* [38]. In the understory, large seedling individuals improved survival rate [38,46]. Thus, long-term salt stress improves the ability of *M. alba* seeds to adapt to the soil salt stress, and the regulation of seed quality is one of the key regulation modes.

4.3. Effect of Light Intensity and Soil Salinity on Seed Germination and Seedling Growth of M. alba

In coastal saline areas, the seed germination and seedling growth within the forest are exposed to the combined effects of light intensity and soil salinity. This pot study showed no significant effect of light intensity on seed germination, germination index, and vigor index, indicating that *M. alba* germination is light-free. However, seedling biomass was significantly higher in full light than in 25% full light, indicating that *M. alba* is a light-demanding species. Under salt stress, 3‰ had a higher germination rate and germination index than 1‰. In May, when the mulberry seeds germinated, the statistical data for many years showed that there was little rainfall in the region [47]. Guo et al. [48] found that the soil water content in *R. pseudoacacia* forest in May was low and the soil salt content was high. The study of soil seed bank in this area found that the increase of soil salt content caused by the rise of groundwater level is an important factor to inhibit the germination of plant seeds [49]. Therefore, the high germination rate under 3‰ of soil salt content increased the possibility of successful seed germination. Salt stress germination tests on *M. alba* seeds in a light incubator exhibited that the difference in germination rate and germination index between 1‰ and 3‰ was not significant [25,50]. This may be related to the inconsistent environment for germination, but may also indicate that *M. alba* has a strong salt tolerance. Numerous studies show that the leaf biomass ratio increases and the root biomass ratio decreases with decreasing light intensity [51,52]; however, the root biomass ratio increases with increasing soil salinity [30]. Thus, the combined effect of multiple stresses may be an important reason for the lack of significant effects of light intensity and salt stress on biomass allocation. Drought also promotes increasing root biomass allocation in plants, but in contrast to light acclimation in the understory. Studies of understory seedling regeneration show that drought is the most important cause of seedling mortality [38,53]. Therefore, light intensity and soil salt content under *R. pseudoacacia* forest in coastal saline alkali land increase the complexity of adaptation of *M. alba* seedlings, which requires further research.

5. Conclusions

This paper shows that natural regeneration of *M. alba* within *R. pseudoacacia* plantation in the Yellow River Delta is widespread. The level of natural regeneration of *M. alba* trees is closely related to the degree of decline of *R. pseudoacacia* plantation. In the moderately declining Shenxiangou, the DBH class structure of both seedlings and large trees is consecutive and is of the growing type. However, in the nondeclining Jiufenchang, the large tree DBH class is inconsecutive and no seedlings were found. Within the severely declining protected forests, *M. alba* trees are consecutive at large diameter levels but have very few young seedlings. Therefore, the extent of *M. alba* regeneration is influenced by the stand structure of *R. pseudoacacia* plantation.

Maternal trees of *M. alba* in saline alkali land significantly influenced seed quality and seedling biomass. The germination index, seedling biomass, and root system characteristics of DN habitat were similar to those of Tai'an and significantly greater than those under DW habitat compared to seeds from nonsaline Tai'an, which was associated with the smallest seed weight per 1000 grains in DW. However, DN had a higher germination index than T,

improving the quality of seeds under salt stress. Therefore, thousand-seed weight can be used as a key indicator to evaluate the seed quality of mulberry in the Yellow River Delta.

In terms of environmental factors, light intensity had no significant effect on seed germination, but seedling biomass was significantly greater in full light than in 25% light penetration. Soil salinity significantly affected seed germination, and the germination capacity at 3‰ was higher than that at 1‰, which improved the adaptability to the change of soil salt content under *R. pseudoacacia* forest. However, the seedling biomass was lower than 1‰ at 3‰. Neither light intensity nor soil salinity had a significant effect on biomass allocation. The effects of light intensity and soil salinity indicate the complexity of the combined effect of multiple factors. Thus, the natural regeneration of *M. alba* trees in coastal saline *R. pseudoacacia* plantations is very complex. In the future, in order to clarify the natural regeneration dynamics of *M. alba*, it is necessary to establish long-term permanent sample plots and strengthen the monitoring of water resources in *R. pseudoacacia* forests.

Author Contributions: Conceptualization, P.M., B.J. and B.C.; formal analysis, M.W. and X.Z.; investigation, M.W., W.L., K.W., C.T., G.L. and Y.P.; resources, F.J.; data curation, X.Z.; writing—original draft preparation, M.W. and X.Z.; writing—review and editing, P.M., B.C. and K.W.; visualization, M.W.; supervision, B.C.; funding acquisition, B.C. All authors have read and agreed to the published version of the manuscript.

Data Availability Statement: Not applicable.

References

1. Payn, T.; Carnus, J.M.; Freer-Smith, P.; Kimberley, M.; Kollert, W.; Liu, S.; Orazio, C.; Rodriguez, L.; Silva, L.N.; Wingfifield, M.J. Changes in planted forests and future global implications. *For. Ecol. Manag.* **2015**, *352*, 57–67. [CrossRef]
2. Liu, S.; Yang, Y.; Wang, H. Development strategy and management countermeasures of planted forests in China: Transforming from timber-centered single objective management towards multi-purpose management for enhancing quality and benefits of ecosystem services. *Acta Ecol. Sin.* **2018**, *3*, 1–10.
3. Petritan, A.M.; Biris, I.A.; Merce, O.; Turcu, D.O.; Petritan, I.C. Structure and diversity of a natural temperate sessile oak (*Quercus petraea* L.)—European Beech (*Fagus sylvatica* L.) forest. *For. Ecol. Manag.* **2012**, *280*, 140–149. [CrossRef]
4. Pröll, G.; Darabant, A.; Gratzer, G.; Katzensteiner, K. Unfavourable microsites, competing vegetation and browsing restrict post-disturbance tree regeneration on extreme sites in the Northern Calcareous Alps. *Eur. J. For. Res.* **2015**, *134*, 293–308. [CrossRef]
5. Valladares, F.; Niinemets, Ü. Shade tolerance, a key plant feature of complex nature and consequences. *Annu. Rev. Ecol. Evol. Syst.* **2008**, *39*, 237–257. [CrossRef]
6. Valladares, F.; Laanisto, L.; Niinemets, Ü.; Zavala, M.A. Shedding light on shade: Ecological perspectives of understorey plant life. *Plant Ecol. Divers.* **2016**, *9*, 237–251. [CrossRef]
7. Szwagrzyk, J.; Szewczyk, J.; Bodziarczyk, J. Dynamics of seedling banks in beech forest: Results of a 10-year study on germination, growth and survival. *For. Ecol. Manag.* **2001**, *141*, 237–250. [CrossRef]
8. Guo, L.; Ni, R.; Kan, X.; Lin, Q.; Mao, P.; Cao, B.; Gao, P.; Dong, J.; Mi, W.; Zhao, B. Effects of Precipitation and Soil Moisture on the Characteristics of the Seedling Bank under *Quercus acutissima* Forest Plantation in Mount Tai, China. *Forests* **2022**, *13*, 545. [CrossRef]
9. Madsen, P.; Hahn, K. Natural regeneration in a beech-dominated forest managed by close-to-nature principles—A gap cutting based experiment. *Can. J. For. Res.* **2008**, *38*, 1716–1729. [CrossRef]
10. Agestam, E.; Ekö, P.M.; Nilsson, U.; Welander, N.T. The effects of shelterwood density and site preparation on natural regeneration of Fagus sylvatica in southern Sweden. *For. Ecol. Manag.* **2003**, *176*, 61–73. [CrossRef]
11. González-Rodríguez, V.; Villar, R.; Navarro-Cerrillo, R.M. Maternal influences on seed mass effect and initial seedling growth in four *Quercus* species. *Acta Oecol.* **2011**, *37*, 1–9. [CrossRef]
12. Domic, A.I.; Capriles, J.M.; Camilo, G.R. Evaluating the fitness effects of seed size and maternal tree size on *Polylepis tomentella* (Rosaceae) seed germination and seedling performance. *J. Trop. Ecol.* **2020**, *36*, 115–122. [CrossRef]
13. Mousseau, T.A.; Fox, C.W. The adaptive significance of maternal effects. *Trends Ecol. Evol.* **1998**, *13*, 403–407. [CrossRef] [PubMed]

14. Chen, D.; Yuan, Z.; Wei, Z.; Hu, X. Effect of maternal environment on seed germination and seed yield components of *Thlaspi arvense*. *Ind. Crop Prod.* **2022**, *181*, 114790. [CrossRef]

15. Adji, B.I.; Akaffou, D.S.; Reffye, P.D.; Sabatier, S. Maternal environment and seed size are important for successful germination and seedling establishment of *Pterocarpus erinaceus* (Fabaceae). *J. For. Res.* **2022**, *33*, 977–990. [CrossRef]

16. Galloway, L.F.; Etterson, J.R. Transgenerational plasticity is adaptive in the wild. *Science* **2007**, *318*, 1134–1136. [CrossRef]

17. Sionit, N.; Kramer, P.J. Effect of water stress during different stages of growth of soybean. *Agron. J.* **1977**, *69*, 274–278. [CrossRef]

18. Zolfaghari, R.; Dalvand, F.; Fayyaz, P.; Solla, A. Maternal drought stress on persian oak (*Quercus brantii* Lindl.) affects susceptibility to single and combined drought and biotic stress in offspring. *Environ. Exp. Bot.* **2022**, *194*, 104716. [CrossRef]

19. Mohamed, H.A.; Clark, J.A.; Ong, C.K. The influence of temperature during seed development on the germination characteristics of millet seeds. *Plant Cell Environ.* **1985**, *8*, 361–362. [CrossRef]

20. Herman, J.J.; Sultan, S.E.; Tim, H.K.; Riggs, C. Adaptive transgenerational plasticity in an annual plant: Grandparental and parental drought stress enhance performance of seedlings in dry soil. *Integ. Comp. Biol.* **2012**, *52*, 77–88. [CrossRef]

21. Herman, J.J.; Sultan, S.E. Adaptive Transgenerational pasticity in plants: Case studies, mechanisms, and implications for natural populations. *Front. Plant Sci.* **2011**, *2*, 102. [CrossRef] [PubMed]

22. Yakovlev, I.; Fossdal, C.G.; Skrøppa, T.; Olsen, J.E.; Jahren, A.H.; Johnsen, O. An adaptive epigenetic memory in conifers with important implications for seed production. *Seed Sci. Res.* **2012**, *22*, 1–14. [CrossRef]

23. Ahmed, M.Z.; Khan, M.A. Tolerance and recovery responses of playa halophytes to light, salinity and temperature stresses during seed germination. *Flora* **2010**, *205*, 764–771. [CrossRef]

24. Wang, D.; Jia, Y.; Cui, J. Research progress on effects of salt stress on plants and salt adaptability of plants. *Chin. Agric. Sci. Bull.* **2009**, *25*, 124–128.

25. Zhang, G.Y.; Tan, J.Z.; Liu, M.J. Effects of salt stress on mulberry seed germination and physiological and biochemical characteristics of seedlings. *Acta Sericologica Sin.* **2004**, *02*, 191–194.

26. Zhang, T.Y.; Sheng, J.; Wang, R.Y.; Li, H.Y.; Yang, Y.F. Effects of saline alkali stress and temperature on seed germination of *Artemisia selengensis*. *Acta Agrestia Sin.* **2019**, *27*, 581–588.

27. Cheng, L.; Li, Z.; Han, Z.; Shi, X. Response of seed germination of *Aralia salina* to temperature, light and salt drought stress. *Pratacultural Sci.* **2015**, *32*, 961–966.

28. Sendall, K.M.; Reich, P.B.; Lusk, C.H. Size-related shifts in carbon gain and growth responses to light differ among rainforest evergreens of contrasting shade tolerance. *Oecologia* **2018**, *187*, 609–623. [CrossRef]

29. Cavalcanti, F.R.; Santos Lima, J.P.M.; Ferreira-Silva, S.L.; Viegas, R.A.; Silveira, J.A.G. Roots and leaves display contrasting oxidative response during salt stress and recovery in cowpea. *J. Plant Physiol.* **2007**, *164*, 591–600. [CrossRef]

30. Mao, P.; Zhang, Y.; Cao, B.; Guo, L.M.; Shao, H.; Cao, Z.; Jiang, Q.; Wang, X. Effects of salt stress on eco-physiological characteristics in *Robinia pseudoacacia* based on salt-soil rhizosphere. *Sci. Total Environ.* **2016**, *568*, 118–123. [CrossRef]

31. Lama, G.F.C.; Crimaldi, M. Assessing the role of Gap Fraction on the Leaf Area Index (LAI) estimations of riparian vegetation based on Fisheye lenses. In Proceedings of the 29th European Biomass Conference and Exhibition, Marseille, France, 26–29 April 2021; pp. 1172–1176. [CrossRef]

32. Crimaldi, M.; Lama, G.F.C. Impacts of riparian plants biomass assessed by UAV-acquired multispectral images on the hydrodynamics of vegetated streams. In Proceedings of the 29th European Biomass Conference and Exhibition, Marseille, France, 26–29 April 2021; pp. 1157–1161. [CrossRef]

33. Pirone, D.; Cimorelli, L.; Del Giudice, G.; Pianese, D. Short-term rainfall forecasting using cumulative precipitation fields from station data: A probabilistic machine learning approach. *J. Hydrol.* **2023**, *617*, 128949. [CrossRef]

34. Yao, L.; Liu, G.; Liu, Q.; Fei, L. Remote sensing monitoring the health of artificial *Robinia pseudoacacia* forest. *Geomat. Inf. Sci. Wuhan Univ.* **2010**, *35*, 863–867.

35. Ke, Y. *Study on Salt Resistance of Mulberry and its Application in Saline Alkali Land*; China Academy of Forestry Sciences: Beijing, China, 2008.

36. Cheng, J.L.; Duan, J.L.; Wang, N.; Xiao, L.Y. Effect of polyethylene glycol simulated water stress on mulberry seed germination and physiology. *J. Anhui Agric. Sci.* **2006**, *24*, 6420–6422.

37. Zhang, J.; Xing, S.; Sun, Q.; Chi, J.; Song, Y. Study on flora resources and its features in Yellow River Delta region. *Res. Soil Water Conserv.* **2006**, *13*, 100–102.

38. Mao, P.; Kan, X.; Pang, Y.; Ni, R.; Cao, B.; Wang, K.; Zhang, J.; Tan, C.; Geng, Y.; Cao, X.; et al. Effects of forest gap and seed size on germination and early seedling growth in *Quercus acutissima* plantation in Mount Tai, China. *Forests* **2022**, *13*, 1025. [CrossRef]

39. Diaci, J.; Adamic, T.; Rozman, A. Gap recruitment and partitioning in an old-growth beech forest of the Dinaric Mountains: Influences of light regime, herb competition and browsing. *For. Ecol. Manag.* **2012**, *285*, 20–28. [CrossRef]

40. O'Brien, M.J.; O'Hara, K.L.; Erbilgin, N.; Wood, D.L. Overstory and shrub effects on natural regeneration processes in native Pinus radiata stands. *For. Ecol. Manag.* **2007**, *240*, 178–185. [CrossRef]

41. Baskin, J.M.; Lu, J.J.; Baskin, C.C.; Tan, D.Y.; Wang, L. Diaspore dispersal ability and degree of dormancy in heteromorphic species of cold deserts of northwest China: A review. *Perspect. Plant Ecol. Evol. Syst.* **2014**, *16*, 93–99. [CrossRef]

42. Larios, E.; Búrquez, A.; Becerra, J.X.; Venable, D.L. Natural selection on seed size through the life cycle of a desert annual plant. *Ecology* **2014**, *95*, 3213–3220. [CrossRef]

43. Vivas, M.; Zas, R.; Sampedro, L.; Solla, A. Environmental maternal effects mediate the resistance of maritime pine to biotic stress. *PLoS ONE* **2013**, *8*, e70148. [CrossRef]
44. Yin, K. *Effects of the Age of Mother Tree and Site Conditions on the Salt Resistant Germination of Robinia Pseudoacacia Seeds*; Shandong Agricultural University: Tai'an, China, 2019.
45. Mao, P.; Guo, L.; Gao, Y.; Qi, L.; Cao, B. Effects of seed size and sand burial on germination and early growth of seedlings for coastal *Pinus thunbergii* Parl in the Northern Shandong Peninsula, China. *Forests* **2019**, *10*, 281. [CrossRef]
46. Quero, J.L.; Villar, R.; Marañón, T.; Zamora, R.; Poorter, L. Seed-mass effects in four Mediterranean quercus species (Fagaceae) growing in contrasting light environments. *Am. J. Bot.* **2007**, *94*, 1795–1803. [CrossRef] [PubMed]
47. Liu, C. *Characteristics of Temporal and Spatial Variation of Water Recourse in the Yellow River Delta under Conditions of Climate Change*; Nanjing University of Information Science & Technology: Nanjing, China, 2012.
48. Guo, L.; Cao, B.; Mao, P.; Li, Z.; Hao, M.; Wang, T.; Jiang, F. Fine root vertical-seasonal distribution of *Robinia pseudoacacia* in relation to abioticfactors in a chronosequence in coastal saline alkali land of the Yellow River Delta, China. *Turk. J. Agric. For.* **2021**, *45*, 750–765. [CrossRef]
49. Feng, L.; Liu, J.T.; Han, G.X.; Zhang, Q.H.; Peng, L. Effects of grounder level fluctuation on characteristics of soil seed banks in coastal wetlands of the Yellow River Delta. *Acta Ecol. Sin.* **2021**, *41*, 3826–3835.
50. Huang, H.; Fu, J.; Cao, B.; Zhao, W.; Mao, P.; Wang, T.; Hao, Y.; Zhang, X.; Tan, H. Effects of salt stress and temperature on seed germination and seedling growth of mulberry. *J. Southwest For. Univ.* **2021**, *41*, 30–37.
51. Poorter, L. Growth responses of 15 rainforest tree species to a light gradient: The relative importance of morphological and physiological traits. *Funct. Ecol.* **1999**, *13*, 396–410. [CrossRef]
52. Bloor, J.M.G.; Grubb, P.J. Morphological plasticity of shade-tolerant tropical rainforest tree seedlings exposed to light changes. *Funct. Ecol.* **2004**, *18*, 337–348. [CrossRef]
53. Rey, P.J.; Alcántara, J.M. Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): Connecting patterns of seed dispersal to seedling establishment. *J. Ecol.* **2000**, *88*, 622–633. [CrossRef]