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Research Article

Study on Provenance Variation in Phenotypic Traits and Salt Tolerance of *Ulmus pumila* Seeds

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Abstract

Ulmus pumila, as a pioneer tree species for afforestation in saline-alkali soils in northern China, exhibits drought and salt tolerance, rapid growth, and strong adaptability. It performs well in saline soils with salt content ≤0.45% and demonstrates significant effectiveness in soil improvement for coastal saline-alkali lands. However, research on the phenotypic-salt tolerance synergistic response patterns and comprehensive evaluation of *Ulmus pumila* seeds at the seed source scale remains limited. To select superior *Ulmus pumila* provenances suitable for saline-alkali land, this study examined seed trait characteristics of 11 geographical provenances, along with their germination performance and early seedling growth under salt stress [0 (CK), 0.3%, 0.6%, 0.9%, and 1.2% NaCl solutions], and assessed the salt tolerance of each provenance. The results revealed significant differences among provenances in 1,000-seed weight, longitudinal diameter, transverse diameter, and their ratio. The Tai'an provenance exhibited the highest 1,000-seed weight, while the Nanjing provenance showed the lowest. With increasing salt concentration, seed germination, seedling growth, and root development were significantly inhibited, with notable differences observed among provenances. Among these, the Linqu provenance demonstrated the strongest germination capacity and the most robust root development. Correlation analysis indicated that 1,000-seed weight was significantly positively correlated with germination capacity, and seedling biomass was highly significantly positively correlated with germination level and root development. Based on a comprehensive evaluation using the membership function method, the salt tolerance of the 11 provenances was ranked as follows: Linqu > Tai'an > Harbin > Xingtai > Xianyang > Baicheng > Baiyin > Changyi > Nanjing > Taiyuan > Liaocheng.

Keywords

Ulmus pumila, Provenance, Salt Stress, Seed Germination

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1. Introduction

Soil salinization has emerged as a critical global ecological constraint, impeding vegetation restoration and the sustainable utilization of land resources. Globally, saline soils cover approximately 954 million hm^2 [1], while China alone harbors 99.13 million hm^2 of saline-alkali land—equivalent to nearly one-quarter of its arable area [2-4]—posing a grave threat to agricultural productivity and ecological security. This challenge is particularly acute in coastal saline-alkali regions, where high salinity, elevated pH, and low fertility result in poor survival rates for conventional tree species [5, 6], a scarcity of suitable planting stock, and considerable difficulty in forest establishment. Nevertheless, forest ecosystems contribute indispensably to soil structure improvement, carbon-sink enhancement, and regional ecological stability. Their extensive root systems effectively anchor soil, mitigate erosion, and lower groundwater tables via biodrainage, thereby curbing surface salt accumulation. Consequently, promoting afforestation in saline-alkali areas is of paramount importance for safeguarding ecological security and fostering sustainable development [7].

Provenance selection represents a key strategy for acquiring appropriate planting materials in saline-alkali environments. For widely distributed tree species, spatial heterogeneity in precipitation, light, temperature, and soil properties—driven by variations in latitude, longitude, and altitude—has, over prolonged natural selection, fostered genetic differentiation among intraspecific populations, giving rise to geographic ecotypes with markedly divergent salt tolerances [8]. To date, significant provenance-specific differences in salt tolerance have been documented in species such as Ailanthus altissima [9], Populus euphratica [10], Elaeagnus angustifolia [11], Xanthoceras sorbifolium [12], and salt pine [13]. Seed phenotypic traits and their adaptive value constitute important criteria in provenance selection. Research has established a notable link between seed traits and salt tolerance, with seed size often positively correlated with tolerance capacity [14], and root plasticity serving as a key adaptive strategy during the seedling stage [15]. Evaluation of salt tolerance has evolved from single germination parameters to comprehensive assessments incorporating multidimensional indicators, including seedling root morphology and physiological responses. To overcome the limitations of single-indicator approaches, integrated methods such as the membership function and principal component analysis are now widely employed in screening salt-tolerant germplasm.

Ulmus pumila, a pioneering species for afforestation in northern China's saline-alkali lands, is valued for its drought resistance, salt tolerance, rapid growth, and broad adaptability [16]. It performs well on soils with salt contents ≤0.45% [17] and has demonstrated substantial soil-amelioration effects in coastal saline areas [18]. Under salt stress, U. pumila seedlings maintain ionic homeostasis through aboveground Na^+ translocation and K^+ accumulation [19], while relying on their antioxidant systems to alleviate oxidative damage [20]. The germination phase is particularly sensitive to salt stress [21]. Zhu et al. [22] reported that the salt-tolerance thresholds during germination varied significantly among 35 U. pumila families, ranging from 105.87 to 188.75 mmol/L. However, at the provenance level, few studies have systematically examined the coordinated responses between seed phenotype and salt tolerance, or performed comprehensive evaluations thereof. Against this background, the present study utilized seeds from 11 geographic provenances of U. pumila to: (i) systematically compare seed phenotypic traits; (ii) integrate multiple indicators, including germination dynamics and seedling root morphology under simulated salt stress, to reveal inter-provenance differences in salt tolerance; (iii) explore correlations between salt tolerance and seed traits; and (iv) apply the membership function method for a comprehensive salt-tolerance evaluation of each provenance. The findings are expected to provide a valuable reference for provenance selection in saline-alkali afforestation practices.

2. Materials and Methods

2.1. Experimental Materials

In 2023, a total of 217 germplasm accessions were collected, of which 11 were selected for in-depth investigation based on geographic representativeness, distinct latitudinal/longitudinal gradients, and preliminary screening for phenotypic extremes. From late April to early May 2024, mature seeds of *Ulmus pumila* were sampled from 11 geographically distinct provenances across China (Table 1). Upon return to the laboratory, seeds were air-dried in a cool, well-ventilated area. Damaged, insect-infested, shriveled, or unfilled seeds were discarded, and healthy seeds with intact morphology and uniform size were retained and stored at 4°C for subsequent analyses. For seed dimension measurements, 10 seeds per provenance were randomly selected in three replicates (i.e., 30 seeds per provenance in total). Longitudinal diameter (maximum length) and transverse diameter (maximum width) were measured using an electronic digital caliper with a precision of 0.01 mm, and the longitudinal-to-transverse diameter ratio was subsequently calculated. The 1,000-seed weight was determined using the 100-seed method: for each provenance, 100 clean, de-winged seeds were randomly sampled in eight replicates, weighed on an electronic analytical balance (accuracy: 0.0001 g), and the average value was converted to 1,000-seed weight. Table 1 Collection locations of seeds from different provenances of *Ulmus pumila*.

Table 1. Collection locations of seeds from different provenances of Ulmus pumila.

No.	Provenance	Longitude	Latitude
I	Tai'an	117.099589 E	36.155156 N
II	Changyi	119.283145 E	36.980915 N
III	Linqu	118.583316 E	36.418402 N
IV	Liaocheng	115.440342 E	36.580444 N
V	Xingtai	115.011530 E	37.016270 N
VI	Taiyuan	112.630437 E	38.025037 N
VII	Xianyang	108.091570 E	34.312348 N
VIII	Baiyin	104.959221 E	35.515161 N
IX	Harbin	126.634252 E	45.720355 N
X	Baicheng	122.839577 E	45.616417 N
XI	Nanjing	118.816814 E	32.078689 N

2.2. Experimental Design

In early May 2024, de-winged seeds from each provenance were surface-sterilized by immersion in a 3 g/L $KMnO_4$ solution for 10 min, followed by repeated rinsing with deionized water. The sterilized seeds were then soaked in deionized water at 35°C for 24 h, after which only fully imbibed (plump) seeds were selected for the salt-stress germination experiment. Germination was conducted on double-layer filter paper placed in 90-mm-diameter Petri dishes. NaCl solutions were prepared at five concentrations (0 [CK], 0.3%, 0.6%, 0.9%, and 1.2%, w/v), with five replicates per treatment. Both Petri dishes and filter paper were autoclaved prior to seed placement. For each dish, 20 mL of the corresponding NaCl solution was added, and 50 randomly selected seeds were evenly distributed on the filter paper. The dishes were then transferred to a constant-temperature illuminated incubator set at 25°C with a 12 h light/12 h dark photoperiod and incubated for 6 days. Seed germination was defined as visible radicle protrusion through the seed coat. Germination counts were recorded daily, and water loss was compensated by the weighing method to maintain stable salt concentrations throughout the incubation period.

At the end of the experiment, five uniformly growing seedlings were randomly selected from each Petri dish and gently rinsed with deionized water. After surface moisture was removed with filter paper, each seedling was separated into aboveground (cotyledons + stem) and belowground (root system) portions. Root traits—including total root length, root surface area, root volume, and average root diameter—were measured using a WinRHIZO STD 4800 root scanner. Subsequently, all samples were oven-dried at 80°C to constant weight, and dry mass was accurately determined using an analytical balance (precision: 0.0001 g). Based on the recorded data, the following parameters were calculated: germination rate, germination energy, mean germination time, germination index, vigor index, seedling biomass, root-to-shoot ratio, specific root length, and specific root surface area. The calculation formulas are as follows:

1) Germination rate (GR,%) = n/N × 100%
2) Germination energy (GE,%) = m/N × 100%
3) Mean germination time (MGT, d) = Σ(Gt × t)/ΣGt
4) Germination index (GI) = Σ(Gt/Dt)
5) Vigour index (VI) = S × Σ(Gt/Dt)

In the formulae, n is the total number of germinated seeds after the termination of germination; m is the number of seeds germinated during the first 3 days; N is the total number of tested seeds; Gt is the number of seeds germinated on day t; Dt is the corresponding germination time; and S is seedling dry weight.

6) Seedling biomass (SB, g) = above-ground dry weight + root dry weight
7) Root-shoot ratio (RSR) = root dry weight/above-ground dry weight
8) Specific root length (SRL, cm/g) = root length/root dry weight
9) Specific root surface area (SRA, cm^2/g) = root surface area/root dry weight

2.3. Salt-Tolerance Evaluation and Analysis

Relative value of each indicator (%) = treatment-group indicator mean/control-group indicator mean × 100%

SPSS 23.0 was used for cluster analysis and Pearson correlation analysis of the measured traits. Before cluster analysis, all traits were standardised using *Z*-scores. The correlation index was calculated using Formula (1) to determine evaluation indicators; the larger the correlation index, the stronger the representativeness of the indicator.

$$R_i^2=\sum r^2/(n-1) \quad (1)$$

where R_i^2 is the correlation index of each indicator in each category; n is the number of traits within each category; and r is the correlation coefficient between an item and other indicators within the same category.

Salt tolerance during the seed germination stage is regulated by multiple factors. Therefore, this study adopted the membership function method, combined with the weight of each indicator, to comprehensively evaluate salt-tolerance ability among different provenances. To objectively reflect the sensitivity of each provenance to NaCl stress, the relative values of each germination indicator were selected as the basis for evaluation. The relative values of the indicators were standardised using fuzzy mathematical membership functions: if a measured indicator was positively correlated with salt tolerance, the membership degree was calculated according to Formula (2); if it was negatively correlated, it was calculated according to Formula (3).

$$U(X_{ij})=(X_{ij}-X_{min})/(X_{max}-X_{min}) \quad (2)$$

$$U(X_{ij})=1-(X_{ij}-X_{min})/(X_{max}-X_{min}) \quad (3)$$

where U(*Xij*) is the membership degree of the jth indicator for the ith provenance; *Xij* denotes the measured value of the jth indicator for the ith provenance; and *Xmax* and *Xmin* denote the maximum and minimum values of the jth indicator, respectively.

The coefficient of standard deviation method was used to determine the weight of each indicator. The coefficient of standard deviation (*Vj*) was calculated according to Formula (4), and the weight (*Wj*) of each indicator was then obtained by normalisation according to Formula (5). Finally, the comprehensive evaluation value (D) of each provenance was calculated using Formula (6), and the salt tolerance of each *U. pumila* provenance was ranked according to the D value.

$$V_j=\frac{\sqrt{\sum_{i=1}^{n}(X_{ij}-\bar{X}_{ij})^2}}{\bar{X}_{ij}} \quad (4)$$

$$W_j=\frac{V_j}{\sum_{j=1}^{n}V_j} \quad (5)$$

$$D=\sum_{j=1}^{n}\left(U(X_{ij})\times W_j\right) \quad (6)$$

where *X̄ij* denotes the mean value of the jth indicator for the ith provenance; *Vj* denotes the coefficient of standard deviation of the jth indicator; *Wj* denotes the weight coefficient of the jth indicator; and *D* denotes the comprehensive evaluation value of each provenance.

2.4. Data Analysis

Data were organised using Excel 2016. One-way analysis of variance was performed using SPSS 23.0 statistical software, and Duncan's method was used for multiple comparisons and significance analysis. The significance level was set at 0.05. Figures were drawn using Origin 2024 software.

3. Results and Analysis

3.1. Differences in Traits of *U. pumila* Seeds from Different Provenances

Significant inter-provenance differences ($P < 0.05$) were observed in seed phenotypic traits, including longitudinal diameter, transverse diameter, aspect ratio (longitudinal/transverse diameter), and 1,000-seed weight among the 11 *Ulmus pumila* provenances (Table 2). The 1,000-seed weight ranged from 2.88 g to 7.76 g, with the Tai'an provenance exhibiting the heaviest seeds and the Nanjing provenance the lightest—the latter being significantly lower than all other provenances ($P < 0.05$). Overall, 1,000-seed weight displayed a clear increasing trend from southern to northern provenances. Longitudinal diameter ranged from 4.87 mm (Changyi) to 7.31 mm (Baiyin), while transverse diameter varied between 3.59 mm (Liaocheng) and 4.93 mm (Baiyin). The aspect ratio ranged from 1.30 to 1.59 across provenances, indicating an oval seed morphology. Notably, the Nanjing provenance exhibited the highest aspect ratio, which was significantly greater than those of all other provenances except Baiyin ($P < 0.05$), whereas the Xianyang and Harbin provenances recorded the lowest ratios.

Table 2. Seed traits (de-winged) of Ulmus pumila from different provenances.

Number	Provenance	Longitudinal diameter (mm)	Transverse diameter (mm)	L/D ratio	1000-seed weight (g)
I	Tai'an	5.76±0.70 bcd	4.23±0.47 bc	1.37±0.16 bc	7.76±1.14 a
II	Changyi	4.87±0.55 d	3.69±0.71 c	1.36±0.32 bc	6.04±0.73 bc
III	Linqu	5.34±0.39 cd	3.84±0.34 bc	1.40±0.12 bc	7.62±0.48 a
IV	Liaocheng	5.10±0.42 d	3.59±0.30 c	1.43±0.12 bc	4.88±0.73 c
V	Xingtai	5.10±0.87 d	3.64±0.56 c	1.41±0.18 bc	5.54±1.55 bc
VI	Taiyuan	6.41±0.81 b	4.92±0.72 a	1.32±0.18 bc	4.84±1.90 c
VII	Xianyang	5.38±0.91 cd	4.17±0.61 bc	1.30±0.16 c	7.02±0.53 ab
VIII	Baiyin	7.31±1.25 a	4.93±0.61 a	1.49±0.21 ab	6.8±0.62 ab
IX	Harbin	5.56±0.60 bcd	4.31±0.44 abc	1.30±0.11 c	6.03±1.10 bc
X	Baicheng	6.29±0.72 bc	4.50±0.50 ab	1.40±0.12 bc	6.36±0.48 ab
XI	Nanjing	6.29±0.69 bc	4.03±0.73 bc	1.59±0.26 a	2.88±0.79 d
Mean		5.80	4.18	1.40	5.95
F-value		13.672	12.572	4.658	8.617

Number	Provenance	Longitudinal diameter (mm)	Transverse diameter (mm)	L/D ratio	1000-seed weight (g)
P-value		<0.001**	<0.001**	<0.001**	<0.001**

Note: Different lowercase letters indicate significant differences among different provenances (*P*<0.05); ** indicates significance at the 0.01 level.

3.2. Effects of NaCl Stress on Germination of Different Provenances of *U. pumila* Seeds

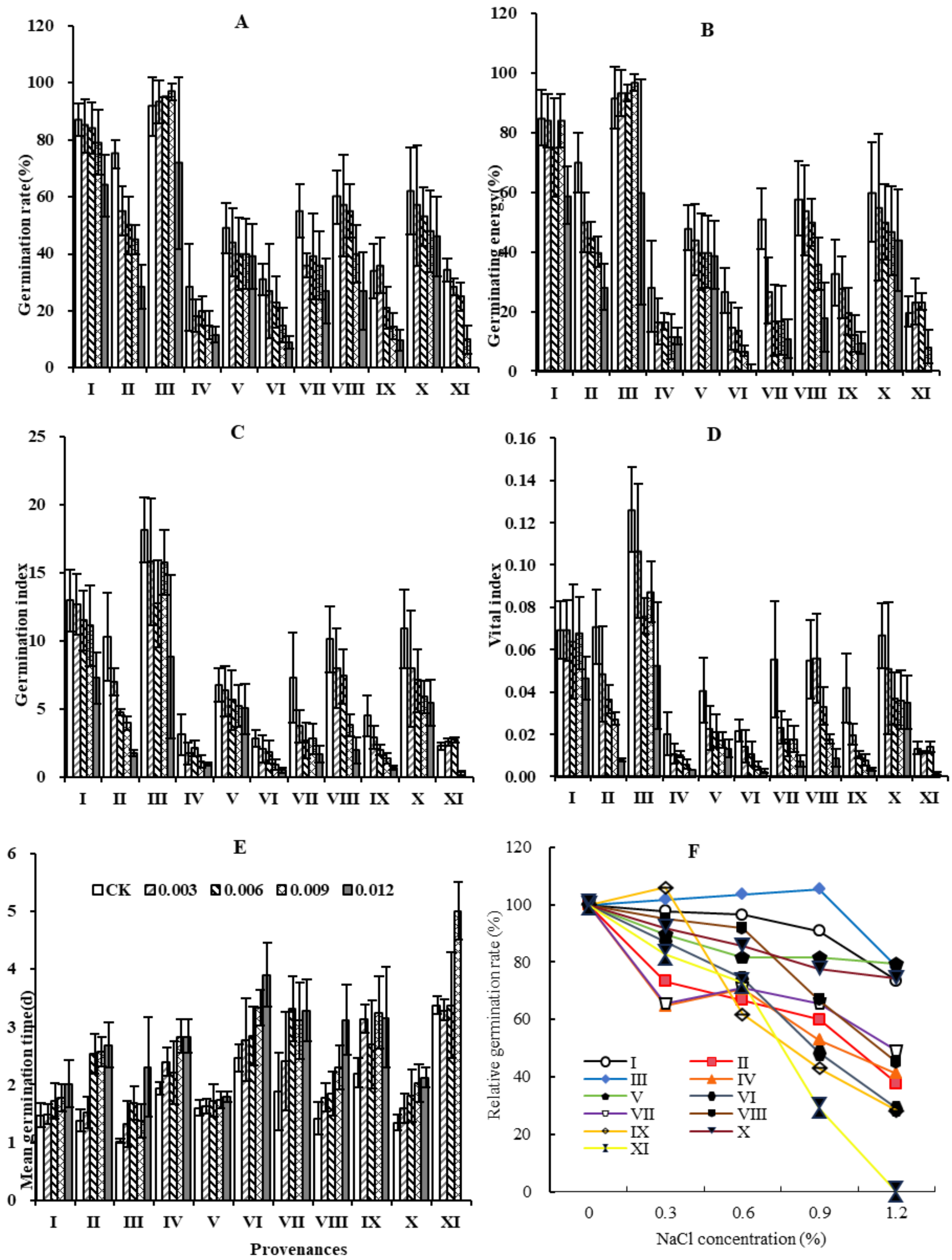


Figure 1. Changes in seed germination of different provenances of Ulmus pumila with increasing NaCl concentration.

Note: I, Tai'an; II, Changyi; III, Linqu; IV, Liaocheng; V, Xingtai; VI, Taiyuan; VII, Xianyang; VIII, Baiyin; IX, Harbin; X, Baicheng; XI, Nanjing. The same applies below.

Analysis of variance (ANOVA) results (Table 3) revealed that both provenance and NaCl concentration had highly significant effects on all five germination parameters ($P < 0.01$). Overall, increasing NaCl concentration significantly suppressed all germination indicators: germination rate, germination potential, germination index, and vigor index decreased progressively, whereas mean germination time was prolonged. Specifically, germination rate declined from 54.85% (control) to 30.70% (1.2% NaCl), representing a 44.0% reduction; germination potential decreased from 51.91% to 25.70%, a drop of 50.5%; mean germination time was extended from 1.81 d to 2.74 d; germination index fell from 8.07 to 3.15, a reduction of 61.0%; and vigor index exhibited the sharpest decline, decreasing by 64.8% (from 0.0520 to 0.0183). Multiple comparisons indicated that, for germination rate, germination index, and vigor index, no significant differences were detected between the 0.3% and 0.6% NaCl treatments, nor between 0.6% and 0.9% for germination potential. In contrast, significant differences were observed between all other adjacent concentration levels, with each indicator decreasing progressively as concentration increased ($P < 0.05$). When NaCl concentration exceeded 0.9%, the relative germination rate of all provenances dropped markedly, suggesting that 0.9% NaCl represents the critical stress threshold for seed germination. Substantial inter-provenance variation in germination capacity was also observed. Across most salt treatments, the Linqu provenance consistently exhibited the highest germination rate, germination potential, germination index, and vigor index, along with the shortest mean germination time. In contrast, the Liaocheng, Taiyuan, and Nanjing provenances performed poorly across all indicators; notably, seeds from the Nanjing provenance completely failed to germinate under 1.2% NaCl.

Interaction analysis revealed that the provenance × NaCl concentration interaction had no significant effect on germination rate or germination potential, but exerted highly significant effects on mean germination time, germination index, and vigor index ($P < 0.01$). This interaction was primarily manifested as a rebound in germination performance of the Linqu provenance at 0.9% NaCl—characterized by shortened mean germination time and elevated germination and vigor indices—whereas the other provenances either continued to decline or approached stabilization. Based on the trend of relative germination rate across concentrations, the 11 provenances could be broadly categorized into three types: (1) "stable type" (Linqu), which was slightly promoted under low salt stress and rebounded near the critical concentration; (2) "slow-decline type" (e.g., Xingtai, Baiyin), showing a relatively gradual decreasing trend; and (3) "rapid-decline type" (e.g., Taiyuan, Liaocheng), with germination indicators deteriorating sharply as salt concentration increased.

3.3. Effects of NaCl Stress on Early Seedling Biomass and Root-to-Shoot Ratio of *U. pumila* from Different Provenances

Analysis of variance (Table 3) showed that NaCl concentration had extremely significant effects on early biomass and root-to-shoot ratio *($P<0.01$)*. Overall, total seedling biomass decreased continuously with the increase of NaCl concentration: the control mean was 0.0069, with respective reductions of 10.14%, 20.29%, 23.19% and 33.33% under 0.3%, 0.6%, 0.9% and 1.2% NaCl. The root-to-shoot ratio rose initially then fell, with a control mean of 0.2488, peaking at 0.2502 under 0.3% NaCl before decreasing to 0.1976 at 0.9% and 0.1702 at 1.2%.

Provenance also exerted extremely significant influences on early seedling biomass and root-to-shoot ratio (Table 3). Among the provenances, the biomass of seedlings in Changyi, Harbin and Xianyang was relatively high, while that in Xingtai and Nanjing was relatively low; In terms of root-to-shoot ratio, it was higher in Linqu, Changyi and Harbin, and lower in Tai'an and Xingtai. The interaction between provenance and concentration had a very significant effect on both seedling biomass and root-to-shoot ratio (Table 3), with distinct divergent response patterns (Figure 2). In Harbin, the biomass was the highest under control conditions, but decreased rapidly with the increase of NaCl concentration (a 48.39% reduction at 1.2% NaCl). In Changyi, it remained at a relatively high level between 0% and 0.9%.; In Tai'an and Linqu, the decline was moderate. In Baiyin, the biomass was significantly higher than the control at 0.3%, and in Xingtai, it decreased significantly by 31.75% at 0.3%. The Nanjing provenance was at a low level at all concentrations; For root-to-shoot ratio, Changyi and Linqu exhibited continuous declines with rising salinity. Harbin's ratio peaked at 0.6% then decreased; Tai'an's ratio increased significantly at 0.3% and remained elevated thereafter; Taiyuan showed negligible fluctuations, while Xingtai's ratio decreased markedly under high salinity.

Table 3. *Variance analysis of the effects of different provenances and NaCl concentrations on various indicators of Ulmus pumila during the germination period.*

	Provenance		NaCl concentration		Provenance×NaCl concentration	
	F	***P***	**F**	***P***	**F**	***P***
Germination rate	94.038	<0.001**	33.743	<0.001**	1.031	0.430

	Provenance		NaCl concentration		Provenance×NaCl concentration	
	F	*P*	F	*P*	F	*P*
Germination potential	90.631	<0.001**	31.333	<0.001**	1.344	0.100
Germination index	86.300	<0.001**	41.628	<0.001**	1.722	0.009**
Vigor index	63.890	<0.001**	44.664	<0.001**	1.757	0.008**
Mean germination time	48.731	<0.001**	38.800	<0.001**	2.041	0.001**
Biomass	19.034	<0.001**	41.894	<0.001**	2.812	<0.001**
Root-to-shoot ratio	26.632	<0.001**	18.485	<0.001**	3.217	<0.001**
Root length	17.036	<0.001**	105.099	<0.001**	4.592	<0.001**
Root surface area	5.924	<0.001**	13.036	<0.001**	1.450	0.056
Root volume	4.057	<0.001**	4.343	0.002**	0.985	0.503
Average root diameter	17.922	<0.001**	10.704	<0.001**	1.358	0.095
Specific root length	8.100	<0.001**	30.786	<0.001**	2.889	<0.001**
Specific root surface area	6.178	<0.001**	6.708	<0.001**	1.299	0.131

Note:** indicates significance at the 0.01 level.

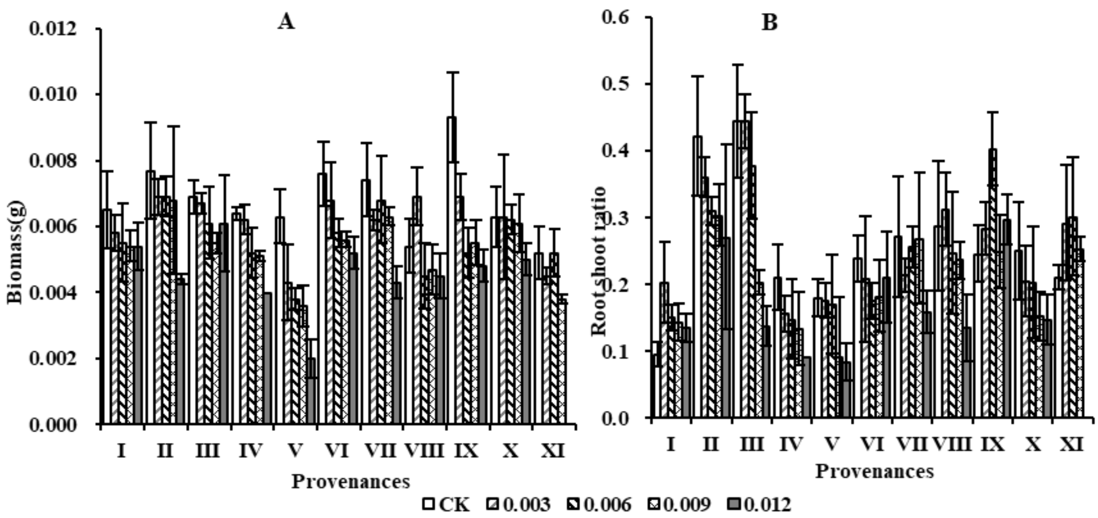
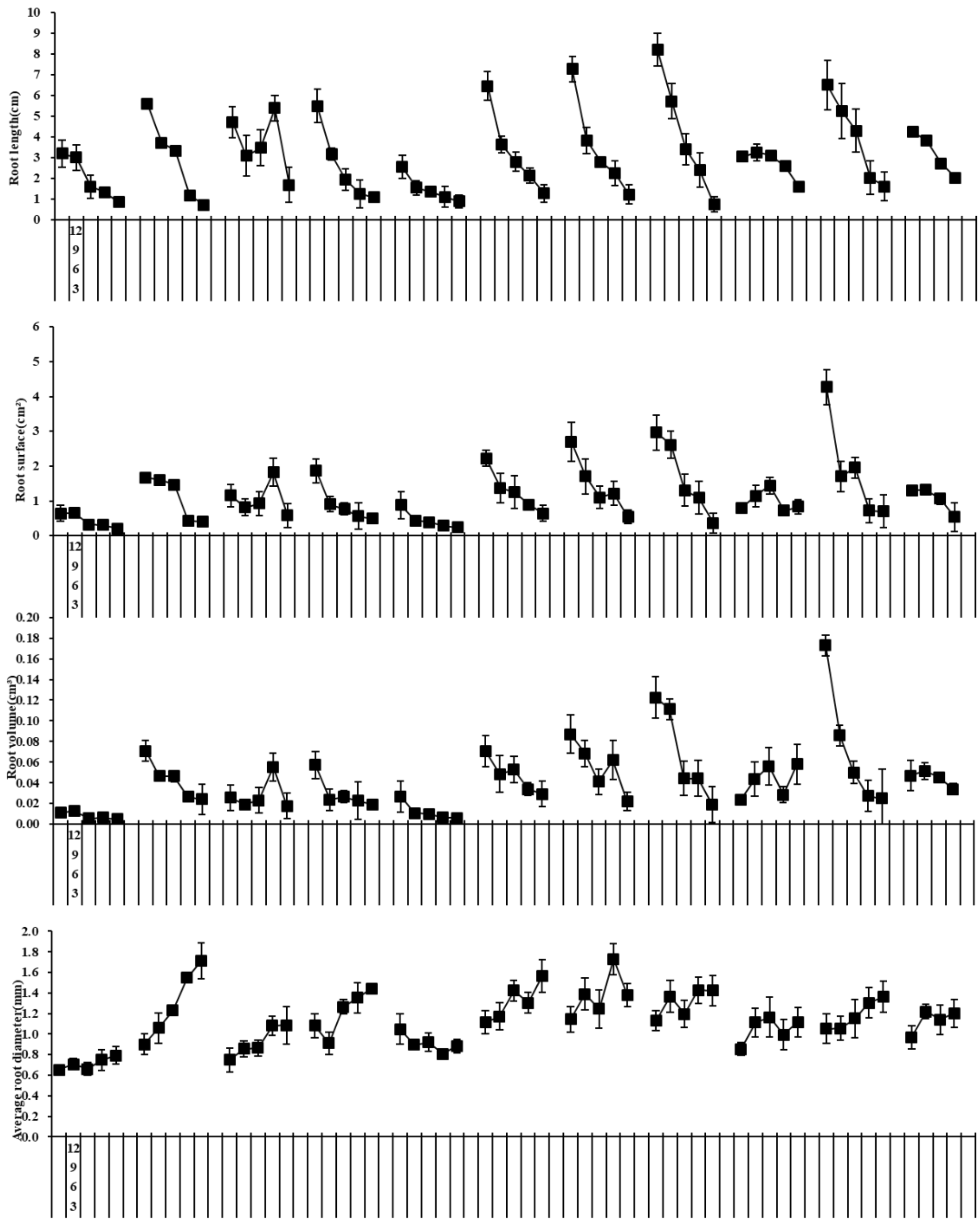


Figure 2*. Changes in early seedling biomass and root-to-shoot ratio of different provenances of Ulmus pumila with increasing NaCl concentration.*

3.4. Effects of NaCl Stress on Early Seedling Root Morphology of *U. pumila* from Different Provenances

Analysis of variance (Table 3) revealed that both provenance and NaCl concentration had highly significant effects on all six early seedling root morphological indicators ($P < 0.01$). The provenance × NaCl concentration interaction exerted highly significant effects on root length and specific root length, whereas no significant interaction was detected for the remaining root traits. All root parameters exhibited consistent trends in response to increasing NaCl concentration. Relative to the control, at 1.2% NaCl, root length, root surface area, root volume, specific root length, and specific root surface area decreased by 77.9%, 73.6%, 66.2%, 62.2%, and 54.3%, respectively, while average root diameter increased by 27.6%. Significant differences were observed between most adjacent concentration gradients for the majority of indicators, indicating a concentration-dependent inhibition of root growth under salt stress.

Substantial inter-provenance variation in root morphology was also observed across salinity levels. Under control conditions, the Baiyin, Baicheng, Xianyang, and Taiyuan provenances generally exhibited superior root parameters, whereas the Xingtai, Tai'an, and Harbin provenances showed relatively poor root development. This overall ranking among provenances remained largely stable with increasing salinity. However, at 0.9% NaCl, the Linqu provenance displayed a marked rebound in multiple root indicators—including root length, root surface area, root volume, specific root length, and specific root surface area—relative to its performance at 0.6% NaCl, and these values were highly significantly higher than those of all other provenances ($P < 0.01$). This interaction effect was primarily manifested in the Linqu provenance: its root length and specific root length increased remarkably from 0.6% to 0.9% NaCl (by 14.5% and 142.7%, respectively), whereas all other provenances continued to decline over the same concentration interval. Consequently, the pattern of inter-provenance differences shifted across salinity gradients, with Linqu exhibiting a distinctive response at the critical concentration.



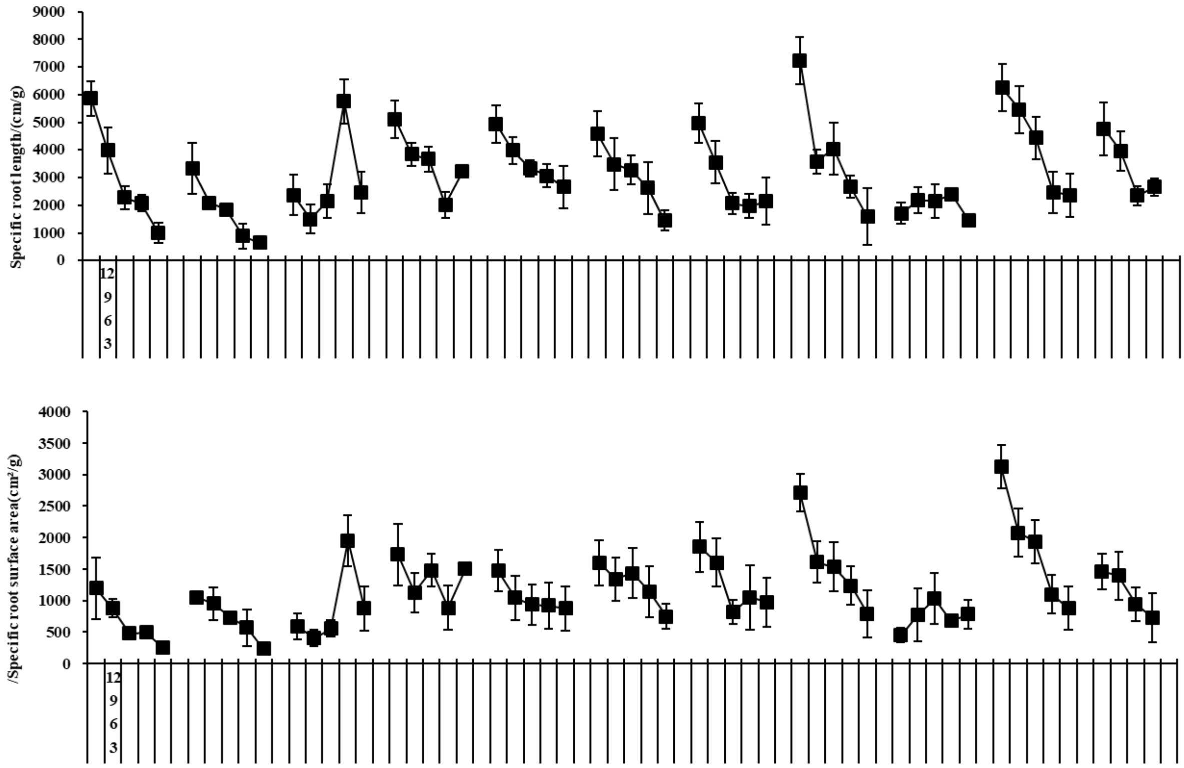


Figure 3. *Changes in early seedling root parameters of different provenances of Ulmus pumila with increasing NaCl concentration.*

3.5. Correlations Between Seed Phenotypic Traits and Germination Characteristics

As presented in Table 4, seed longitudinal diameter exhibited an extremely significant positive correlation with transverse diameter. The 1,000-seed weight showed a significant negative correlation with the length-to-diameter ratio but no significant correlation with transverse diameter. Notably, 1,000-seed weight was significantly positively correlated with germination rate and germination index, highly significantly positively correlated with germination potential and vigor index, and highly significantly negatively correlated with mean germination time. Regarding relationships between seed traits and root parameters, longitudinal diameter was significantly positively correlated with root length and average root diameter. Transverse diameter showed significant positive correlations with root length and root volume, and highly significant positive correlations with root surface area and average root diameter. The 1,000-seed weight was significantly positively correlated with root length. However, no significant correlations were detected between any seed phenotypic traits and seedling biomass.

Seedling biomass was highly significantly positively correlated with germination rate, germination index, and vigor index; significantly positively correlated with germination potential; and significantly negatively correlated with mean germination time. It also exhibited highly significant positive correlations with root-to-shoot ratio, root length, root volume, and root surface area. With respect to germination parameters and root traits, germination rate, germination potential, germination index, and vigor index were all highly significantly positively correlated with root length and specific root length, and highly significantly negatively correlated with average root diameter. Additionally, germination index was significantly positively correlated with specific root surface area, while vigor index showed a highly significant positive correlation with root surface area. Mean germination time was highly significantly negatively correlated with root length and specific root length, highly significantly positively correlated with average root diameter, and significantly negatively correlated with root surface area.

Table 4. *Correlation among various indicators of Ulmus pumila.*

Indicator	L	W	L/W	TKW	GR	GE	MGT	GI	VI	DWM	R/S	RL	RV	RSA	MRD	SRL	SRA
L	1.000																

Indicator	L	W	L/W	TKW	GR	GE	MGT	GI	VI	DWM	R/S	RL	RV	RSA	MRD	SRL	SRA
W	0.683**	1.000															
L/W	0.418**	-0.361**	1.000														
TKW	-0.079	0.176	-0.294*	1.000													
GR	0.019	-0.026	0.013	0.287*	1.000												
GE	-0.023	-0.069	0.004	0.347**	0.951**	1.000											
MGT	0.115	0.161*	0.001	-0.493**	-0.642**	-0.729**	1.000										
GI	0.025	-0.034	0.029	0.318*	0.914**	0.923**	-0.728**	1.000									
VI	0.037	-0.014	0.037	0.338**	0.879**	0.897**	-0.673**	0.926**	1.000								
DWM	0.054	0.122	-0.057	0.012	0.183**	0.155*	-0.131*	0.170**	0.354**	1.000							
R/S	0.095	0.075	0.044	0.073	0.065	0.074	0.028	0.098	0.203**	0.316**	1.000						
RL	0.194*	0.168*	0.050	0.296*	0.266**	0.264**	-0.29**	0.306**	0.383**	0.421**	0.361**	1.000					
RV	0.100	0.182*	-0.079	0.049	0.019	0.012	-0.065	0.047	0.099	0.231**	0.264**	0.570**	1.000				
RSA	0.156	0.210**	-0.042	0.118	0.112	0.108	-0.164*	0.157*	0.220**	0.287**	0.296**	0.753**	0.913**	1.000			
MRD	0.182*	0.276**	-0.081	-0.095	-0.395**	-0.422**	0.352**	-0.428**	-0.371**	-0.034	0.061	-0.029	0.410**	0.273**	1.000		
SRL	0.146	-0.001	0.213**	0.165	0.241**	0.248**	-0.355**	0.297**	0.240**	0.046	-0.169*	0.686**	0.426**	0.555**	-0.109	1.000	
SRA	0.127	0.137	0.021	0.098	0.096	0.092	-0.193**	0.122	0.124	0.036	-0.031	0.631**	0.792**	0.834**	0.306**	0.739**	1.000

Note: ** indicates significant correlation at the 0.01 level (2-tailed); * indicates significant correlation at the 0.05 level (2-tailed). L: Longitudinal diameter, W: Transverse diameter, L/W: Longitudinal/transverse diameter ratio, TKW: Thousand-kernel weight, GR: Germination percentage, GE: Germination energy, MGT: Mean germination time, GI: Germination index, VI: Vigor index, DWM: seedling biomass, R/S: Root-to-shoot ratio, RL: Root length, RV: Root volume, RSA: Root surface area, MRD: Mean root diameter, SRL: Specific root length, SRA: Specific root surface area.

3.6. Comprehensive Salt Tolerance Evaluation of *Ulmus pumila* Provenances at Germination Stage

NaCl stress exerted differential effects on the 13 germination-related indicators of *Ulmus pumila*, and no single parameter could adequately capture the comprehensive response to salt stress. To identify representative indicators for evaluating inter-provenance salt tolerance, correlation analysis was performed using the relative values of all indicators measured under 0.9% NaCl (Table 5), followed by intra-category ranking (Table 6). Based on these analyses, eight indicators were ultimately selected for salt-tolerance assessment: relative specific root surface area, relative specific root length, relative root surface area, relative germination index, relative germination rate, relative germination potential, relative mean root diameter, and relative root-to-shoot ratio. Using the membership function method, the 11 provenances were comprehensively ranked by their salt tolerance at the seed germination stage, from strongest to weakest, as follows: Linqu > Tai'an > Harbin > Xingtai > Xianyang > Baicheng > Baiyin > Changyi > Nanjing > Taiyuan > Liaocheng (Table 7).

***Table 5.** Relative indicators of different provenances of Ulmus pumila during seed germination under 0.9% NaCl stress.*

provenance	Relative germination rate (%)	Relative germination potential	Relative mean germination	Relative germination index (%)	Relative vigor index (%)	Relative biomass(%)	Relative root-to-shoot ratio (%)	Relative root length (%)	Relative specific root surface	Relative root volume (%)	Relative mean root diameter (%)	Relative specific root length (%)	Relative specific root surface
Tai'an	90.80	98.82	120.19	85.64	97.83	83.08	149.95	41.71	47.78	55.36	114.85	35.41	41.18
Changyi	60.00	57.14	185.55	38.55	38.84	88.31	71.91	20.71	26.50	37.11	171.49	26.88	54.27
Linqu	105.45	105.45	134.74	86.85	69.29	79.71	45.58	114.52	158.20	216.47	144.50	242.68	329.17
Liaocheng	52.94	41.18	146.55	37.50	29.21	79.69	63.56	22.70	30.28	39.75	125.02	39.35	50.94
Xingtai	81.63	83.33	109.41	77.15	42.75	57.14	50.42	43.29	32.55	24.25	77.15	62.09	62.40
Taiyuan	48.93	25.93	135.66	32.94	24.07	73.68	76.35	32.74	40.30	47.67	116.86	57.10	71.39
Xianyang	65.45	33.33	165.29	38.91	32.01	85.14	99.15	30.71	45.19	71.07	151.14	39.47	56.83
Baiyin	66.67	62.07	162.72	37.83	32.07	87.04	82.36	28.99	36.72	36.11	126.22	37.05	45.61
Harbin	42.94	38.18	147.58	31.00	18.62	59.14	101.47	85.18	90.97	121.89	116.12	139.62	150.61
Baicheng	77.42	78.33	151.36	54.28	54.42	96.83	60.77	30.91	16.95	15.66	123.90	39.43	35.19
Nanjing	29.13	41.67	148.10	14.49	9.63	73.08	120.54	47.41	41.38	71.86	124.11	55.73	49.69

***Table 6.** Correlation indices and ranking of indicators within each category.*

Classification	Indicator	Correlation index	Sort
1	Relative root surface area	0.451	3
	Relative root volume	0.419	5
	Relative specific root length	0.453	2
	Relative specific root surface area	0.532	1
	Relative root length	0.441	4
2	Relative germination rate	0.365	2
	Relative germination index	0.385	1
	Relative germination potential	0.352	3
	Relative vigor index	0.313	4
3	Relative mean germination time	0.261	2
	Relative mean root diameter	0.270	1
	Relative biomass	0.194	3
4	Relative root-to-shoot ratio	0.117	1

Table 7. Membership function values of relative indicators and comprehensive evaluation D values of different provenances of Ulmus pumila under.

Provenance	Membership function values under 0.9% NaCl treatment									
	Relative germination rate	Relative germination potential	Relative germination index	Relative root-to-shoot ratio	Relative root surface area	Relative mean root diameter	Relative specific root length	Relative specific root surface area	Comprehensive evaluation D value	Sort
Tai'an	0.808	0.917	0.983	1.000	0.218	0.400	0.040	0.020	0.423	2
Changyi	0.404	0.393	0.332	0.252	0.068	1.000	0.000	0.065	0.216	8
Linqu	1.000	1.000	1.000	0.000	1.000	0.714	1.000	1.000	0.876	1
Liaocheng	0.312	0.192	0.318	0.172	0.094	0.507	0.058	0.054	0.160	11
Xingtai	0.688	0.722	0.866	0.046	0.110	0.000	0.163	0.093	0.280	4
Taiyuan	0.252	0.000	0.225	0.295	0.165	0.421	0.140	0.123	0.179	10
Xianyang	0.476	0.093	0.337	0.513	0.200	0.784	0.058	0.074	0.238	5
Baiyin	0.492	0.454	0.323	0.352	0.140	0.520	0.047	0.035	0.222	7
Harbin	0.181	0.154	0.228	0.535	0.524	0.413	0.522	0.393	0.398	3
Baicheng	0.633	0.659	0.550	0.146	0.000	0.496	0.058	0.000	0.225	6
Nanjing	0.000	0.198	0.000	0.718	0.173	0.498	0.134	0.049	0.190	9
Weight	0.079	0.102	0.091	0.106	0.149	0.063	0.192	0.218		

4. Discussion

4.1. Inter-Provenance Salt Tolerance Variation of *U. pumila* and Its Association with Seed Traits

Geographically isolated provenances of *Ulmus pumila* have undergone divergent environmental filtering over their long-term distribution history, particularly with respect to soil salinity and climatic conditions, which has driven genetic differentiation in salt tolerance. Previous studies have confirmed that intraspecific genetic drift, mutation, and migration under heterogeneous habitats give rise to differential stress resistance among provenances of the same species [23]. Seed salt tolerance is closely linked to the soil salinity of provenance origins; populations originating from saline habitats tend to retain more salt-tolerant genes through natural selection [24-26]. In the present study, the Linqu provenance maintained a germination rate of 71.67% under severe 1.2% NaCl stress, whereas the Nanjing provenance completely lost germinability—a disparity that can be attributed to the native saline-alkaline soils of the Linqu region in Shandong Province. Differential germination responses to stress among ecotypes are shaped not only by edaphic and hydrological factors, but also by intraspecific genetic diversity and endophytic microbial communities [27]. Further research is warranted to elucidate the precise mechanisms underlying inter-provenance divergence in salt tolerance in U. pumila.

Seed morphological traits constitute another key determinant of salt tolerance. Large seeds generally exhibit higher germination rates, and a significant correlation has been established between seed germination and seed size or weight. Large seeds tend to germinate earlier and more rapidly than small seeds [28-31]; however, contradictory findings have also been reported, suggesting that the effects of seed size may be context-dependent under abiotic stress [32, 33]. Our results demonstrated that 1,000-seed weight was significantly positively correlated with germination rate and germination index, highly significantly positively correlated with germination potential and vigor index, and highly significantly negatively correlated with mean germination time. Provenances with greater 1,000-seed weight (e.g., Tai'an and Linqu) exhibited superior salt tolerance, whereas the Nanjing provenance, which had the lowest 1,000-seed weight, ranked lowest in salt resistance. These findings are consistent with those of Li et al. [34], who detected a significant positive correlation between seed weight and salt tolerance in *Catalpa ovata*. Heavy seeds accumulate substantial storage reserves that supply energy for early germination [35] and enhance osmotic adjustment to counteract salt-induced water deficits [36]. Collectively, these observations suggest that 1,000-seed weight can serve as a core indicator for screening salt-tolerant provenances of *U. pumila*.

4.2. Salt Tolerance and Adaptive Strategies of *U. pumila* Seeds

Increasing NaCl concentration suppressed germination performance across all 11 provenances: germination rate, germination potential, germination index, and vigor index decreased progressively, while mean germination time was prolonged. This finding is largely consistent with previous reports [25, 37]. Germination was not significantly inhibited at NaCl concentrations below 0.6%, indicating that U. pumila seeds possess a certain degree of adaptability and salt tolerance—a conclusion that corroborates the findings of Liu [37] and Zhu et al. [22]. Notably, low-concentration NaCl exerted stimulatory effects on the germination of the Linqu and Harbin provenances. Specifically, the Linqu provenance achieved its highest germination rate (96.67%) at 0.9% NaCl, representing a 5.45% increase relative to the control. This promotion may be attributed to induced synthesis of osmoprotectants that help maintain cellular water potential [36], or to trace amounts of Na^+ acting as signaling molecules or enzyme cofactors that accelerate the catabolism of storage reserves [35]. For most provenances, germination parameters declined sharply once the NaCl concentration exceeded 0.9%. Previous studies have indicated that the inhibitory effect of high salt stress on seed germination is primarily associated with the toxic effects of salt ions [13, 36-40]. Salt exposure disrupts membrane integrity and physiological function, leading to metabolic disorders, reduced α-amylase activity, loss of seed vigor, and ultimately germination failure [41-43]. Correlation analysis revealed that germination rate, germination index, and vigor index were highly significantly positively correlated with seedling biomass in U. pumila, which is consistent with observations in sand-buried Pinus thunbergii [44]. Collectively, these results suggest that seed germination capacity under salt stress serves as a reliable indicator for evaluating salt tolerance in U. pumila.

Seedling growth is closely linked to root development [44]. Salt stress reduced root length, enlarged average root diameter, and decreased root surface area and volume, which aligns with findings in Robinia pseudoacacia [14]. Seedling biomass exhibited highly significant positive correlations with root-to-shoot ratio, root length, root volume, and root surface area. The inhibition of root development under salt stress significantly impairs water uptake capacity [14], and is therefore an important factor contributing to the reduced biomass observed among provenances. Notably, the Linqu provenance maintained stable root-to-shoot ratios under salt stress; at 0.9% NaCl, its root length, root surface area, and root volume increased slightly, with specific root surface area rising by 229.2%. Similarly, the Harbin provenance upregulated its root-to-shoot ratio under salinity. These findings suggest that optimized biomass allocation to roots and preservation of root functional integrity represent core adaptive strategies for U. pumila to cope with saline environments. Based on the combined performance in germination and seedling growth, 0.9% NaCl is identified as the critical salt-tolerance threshold for *U. pumila* seeds.

4.3. Comprehensive Salt Tolerance Assessment of *U. pumila* Provenances

Plant salt tolerance is a polygenic quantitative trait regulated by multiple interacting factors, necessitating comprehensive evaluation using multiple indicators [36]. Currently, a well-established and universally accepted evaluation system for plant salt tolerance remains lacking [45]. The membership function method integrates multiple key physiological indicators to objectively quantify the overall salt tolerance of different provenances. In this study, the Linqu and Tai'an provenances achieved high comprehensive values, making them priority candidates for ecological restoration in saline-alkaline lands. It should be noted, however, that this study only evaluated salt tolerance during the seed germination stage, and whether germination-phase performance accurately reflects whole-life salt resistance remains unclear. Future research should conduct long-term seedling and field trials, incorporate mixed salt stress treatments, and investigate the physiological and molecular mechanisms underlying salt tolerance at both seedling and mature stages, with the aim of refining the provenance selection system for salt-tolerant *Ulmus pumila*.

5. Conclusions

This study evaluated seed phenotypic traits, germination responses, and early seedling performance of 11 geographically distinct *Ulmus pumila* provenances under gradient NaCl stress. Significant inter-provenance differences were observed in all seed phenotypic traits, with 1,000-seed weight showing a significant positive correlation with salt tolerance. Increasing NaCl concentration generally suppressed seed germination and seedling growth, and 0.9% NaCl was identified as the salt-tolerance threshold for U. pumila seeds. Substantial variation in salt tolerance existed among provenances, with the Linqu provenance exhibiting the strongest tolerance, which was associated with its superior root plasticity. Based on comprehensive evaluation using the membership function method, the 11 provenances were ranked by salt tolerance at the germination stage as follows: Linqu > Tai'an > Harbin > Xingtai > Xianyang > Baicheng > Baiyin > Changyi > Nanjing > Taiyuan > Liaocheng.

Abbreviations

GR	Germination Rate
GE	Germination Energy

MGT	Mean Germination time
GI	Germination Index
VI	Vigour Index
SB	Seedling Biomass
RSR	Root-shoot Ratio
SRL	Specific Root Length
SRA	Specific Root Surface Area

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Conflicts of Interest

The authors declare that they have no competing interests.

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