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Comparative Physiochemical Mechanisms of Salt Tolerance between *Cornus florida* and *Cornus hongkongensis* subsp. *elegans* Based on Seed Germination and Seedling Growth

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Abstract: *Cornus florida* and *Cornus hongkongensis* subsp. *elegans* are potential species in saline-alkali areas for use as horticultural plants with high ornamental value. This work aimed to screen suitable tolerant dogwoods by comparing the responses of two dogwoods to salt stress according to phenotypic and physiochemical indicators on germination and seedling growth. For relieving seed dormancy, two pretreatments were performed on seeds, coded as T1 (soaked by gibberellic acid (GA₃) alone) and T2 (soaked by GA₃ with gradient salt concentrations of 0.2%, 0.3%, 0.4%, and 0.45%), and pretreated seeds were then germinated at the corresponding salt concentrations in pretreatment. As salt levels increased, the seed germination parameters decreased for both dogwoods, whereas the relative salt damage rate (SDR) significantly increased. While the growth of above-ground parts was significantly inhibited, that of underground parts changed little. Furthermore, the malondialdehyde content (MDA), superoxide dismutase activity (SOD), organic solutes (soluble sugar (SS) and proline (Pro)), and inorganic ions (K⁺, Na⁺, Ca²⁺) significantly accumulated in seedlings with increasing salinity levels, whereas K⁺/Na⁺ ratio decreased. Correlation analysis indicates that organic osmolyte (SS) and ion osmoregulation could be the main physiological mechanisms conferring salinity tolerance for both dogwoods. Compared with osmolytes, ion osmoregulation may be more critical for salt tolerance in the seedlings of the studied dogwoods. Collectively, the superior salt tolerance of *C. florida* to *C. hongkongensis* subsp. *elegans* suggests that the two species could be cultivated in saline areas with 0.3% and 0.2% salt levels, respectively.



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Keywords: salt stress; germination parameters; root length; organic solutes; inorganic ions

1. Introduction

Saline soils are distributed extensively across the world [1,2]. By 2050, salinization is predicted to cover about 50% of agricultural land [3]. In China, there are more than 34 million hm² of saline-alkali land and about 1 million hm² of coastal areas with the environment of salinization [4]. Salt stress harms plant survival, further reduces diversity, and distorts ecological balance in coastal areas [5]. For these problems, the use or cultivation of salt-tolerant species is the preferred strategy. Therefore, screening for more salt-tolerant ornamental species could not only enrich the diversity of plants, but also promote the coastal landscape and maintain ecological balance.

In saline areas, seed germination and early seedling establishment, being the start of the plant life cycle, are primarily threatened by salt stress through osmotic stress and ionic toxicity [6]. Salinity inhibition is not only reflected in descent of seed germination percentage [7,8], but also in morphological and physiochemical alteration of seedlings [9–12]. In response to salt stress, plants have formed systematic salt tolerance mechanisms that

include morphological adaptation [13–15], osmotic adjustment [16,17], ionic compartmentation [18], maintenance of membrane system integrity, and antioxidant defense systems [19,20]. Expounding the mechanisms of salt tolerance could be conducive to finding effective management strategies to mitigate salinity-induced detrimental effects on seed germination and early seedling establishment.

Dogwoods, with their petals of various colors and shapes, bright red berries, and colored leaves, form a cluster of ornamental tree species. They are classified into two groups, the East Asian group and the North American group, which are widely distributed in East Asia and North America, respectively [21]. Among these species, *Cornus florida* has a long history of wide cultivation in North America. Moreover, numerous cultivars with high ornamental value have been produced via hybrid and selection and then popularized in native areas [22]. In recent years, these cultivars have been successfully introduced to Korea and Japan, where they have also shown good performance [23]. Although the introduction of *C. florida* and its cultivars has also been attempted, they are less cultivated and are mainly planted in the coastal regions of China. In addition, *Cornus hongkongensis* subsp. *elegans*, which is native to Fujian, Jiangxi, and Zhejiang provinces in China, has good ornamental value and salt-stress resistance [4], making it a potential species for application in subtropical areas of China. Based on the field performance of two dogwoods on the Dafeng forest farm, Jiangsu, China, we speculated that *C. florida* may be superior to *C. hongkongensis* subsp. *elegans* in seed germination and seedling growth under salt stress. To explore the adaptivity of two dogwood species to a salt environment, we attempted to (i) ascertain the responses of the two species to salinity based on their seed germination and seedling growth performance and physiochemical traits, (ii) assess their salt tolerances by comparing their traits at various salt levels, and (iii) uncover how potential morphophysiological and biochemical determinants vary in response to salt stress at the whole-seedling level.

2. Materials and Methods

2.1. Seeds and Solution Preparation

Seeds of *C. florida* and *C. hongkongensis* subsp. *elegans* were sourced from locations in their natural distribution: Louisiana, USA and Lishui, Zhejiang, China, respectively. The 1000-seed weight of the *C. florida* and *C. hongkongensis* subsp. *elegans* samples used were 105 g and 61 g, respectively. The seed viabilities of both species were more than 80% by the tetrazolium (2,3,5-triphenyl tetrazolium chloride, TTC) test [24].

We used coarse salt particles of Yellow Sea origin, which are mainly composed of chlorine, sodium, sulfur, magnesium, calcium, potassium, carbon, bromine, strontium, boron, and fluorine, in the salt-stress treatments. Based on documentation on the coastal area, as well as the field performance of the two dogwoods on the Dafeng forest farm in Jiangsu, China, the salt solutions were set as 0.2%, 0.3%, 0.4%, and 0.45%, with distilled water as the control (CK).

2.2. Pretreatment and Germination of Seeds

Due to seed dormancy in dogwoods, pretreatment including hormonal soaking and cold stratification is necessary before germination testing. In brief, the experiment was divided into two steps: seed pretreatment (gibberellic acid (GA₃) soaking and cold stratification at 0–5 °C) and germination. In detail, seeds were pretreated with 500 mg·L^{−1} GA₃ with or without salt for 3 d; then, a mixture of seeds and sand (1:3, v/v) with suitable moisture was adjusted with 500 mg·L^{−1} GA₃ (with/without salt) and stratified at 0–5 °C for 60 d. Afterwards, the germination test was carried out with or without salt solutions.

The experiment was divided into three groups (CK, T1, and T2). For CK, salt solution was not added to the processes of seed pretreatment and germination. For T1, seeds were pretreated without salt, but salt solutions of different concentrations were added for the germination process. For T2, different salt treatments were consistent throughout seed pretreatment and germination (Table 1).

Table 1. Treatments for seed soaking, stratification, and germination under salt stress.

	CK	T1	T2
Seed pretreatment	GA ₃	GA ₃	GA ₃ + Salt solution(s) *
Germination	Distilled water	Salt solution(s) *	Salt solution(s) *
Number of treatments	1	4	4

* Contains 4 concentrations of salt solution: 0.2%, 0.3%, 0.4%, and 0.45%.

In total, nine treatments across the three groups (one in CK and four in both T1 and T2, respectively) were applied in the germination phase. Germination was carried out in a plastic box (L × W × H: 14 cm × 8.5 cm × 12 cm) filled with sand and kept at 25 °C and 24 h light for 28 d.

2.3. Estimation of Germination Parameters

Germination was determined based on the radicle extending by half of seed size. The standard for a normal seedling was when the cotyledons spread out. Germination parameters including germination rate (GR), germination potential (GP), germination index (GI), and related salt damage rate (SDR); seedling survival rate (SR) was measured according to Wang [25]. The corresponding formulas are as follows:

$$GR = \frac{\text{Germinated seeds in each treatment}}{\text{Total number of seeds}} \times 100\% \quad (1)$$

$$GP = \frac{\text{Total germinated seeds in each treatment at the germination peak}}{\text{Total number of seeds}} \times 100\% \quad (2)$$

$$GI = \sum \left(\frac{\text{Germinated seeds in each treatment in } t \text{ days}}{\text{Number of germination days corresponding}} \right) \quad (3)$$

$$SDR = \frac{GR_o - GR_i}{GR_o} \times 100\% \quad (4)$$

GR_o is the GR of CK, and GR_i is GR in each treatment.

$$SR = \frac{\text{Number of surviving seedlings}}{\text{Total number of seeds}} \times 100\% \quad (5)$$

2.4. Assessment of Seedling Growth Parameters

At the end of germination testing, 30 seedlings randomly selected from each replica were divided into two parts (the underground (root) and aboveground (stem and leaf)) to measure fresh weight (FW) separately. After de-enzyme treatment at 105 °C for 15 min, the sample was dried to a constant weight at 80 °C to obtain shoot and root biomass separately (dry weight, DW). At 0.45% salt concentration, SR of *C. hongkongensis* subsp. *elegans* was too low to attain seedling biomass.

The comprehensive evaluation value of salinity tolerance was calculated according to Li [26], where the original traits were SR, seedling height, root length, biomass of shoot, root, and the whole plant.

2.5. Determination of Biochemical Parameters

Seedlings from each replica were stored at −40 °C for determining malondialdehyde (MDA) and superoxide dismutase (SOD). The MDA contents were determined by the thiobarbituric reaction [27] via spectrophotometric analysis. Based on its ability to limit the photochemical reduction of nitro blue tetrazolium (NBT), the SOD content assay was implemented according to Singh [28].

Then, 0.5 g of fresh shoot samples were extracted and washed with 95% and 70% ethanol, respectively. The supernatants of extractions were obtained by centrifugation (at 3500 rpm for 10 min) for the determination of soluble sugar (SS) and proline (Pro) contents.

The colorimetric method for anthrone and sulphuric acid [29] and a sulfosalicylic acid assay [4] were employed to analyze SS and Pro measurement, respectively.

2.6. Measurement of Ion Deposition

The shoot samples were washed with distilled water. After drying to constant weight, all samples were crushed with a grinder [4]. Subsequently, a sifted (2 mm) dry sample of 0.2 g was mixed with 40 mL HCl (30%) and 5 mL HNO₃ in a muffle for 12 h, then boiled until it was colorless. The mixture was filtered and diluted with deionized water to 100 mL for further determination of the contents of Na⁺ (at 589.00 nm), K⁺ (at 769.90 nm), and Ca²⁺ (at 422.67 nm) via atomic absorption spectrometry (AA900T, Perkin Elmer Co., Waltham, MA, USA).

2.7. Data Analysis

Data were analyzed with a multi-factor analysis of variance for each variable, with treatment, species, and salt concentration as main fixed factors, followed by Duncan's multiple range test with treatment, species, or salt concentration. The absolute germination parameters of the two dogwood species were transformed into relative germination parameters. Pearson's correlation was used to analyze the correlations amongst all traits. All statistical analyses were conducted using SPSS version 21.0 (SPSS, Chicago, IL, USA).

3. Results

3.1. Effect of Salt Stress on Germination Parameters

Salt concentration, species, salt concentration × species interactions, and treatment had significant effects on all germinative parameters ($p < 0.05$). As salinity increased, GR, GP, GI, and SR decreased and SDR significantly increased for both dogwoods. In general, the characteristics of seed germination of *C. florida* were higher than those of *C. hongkongensis* subsp. *elegans*. For example, we found that the SR of *C. florida* was more than 50.00% at 0.3% salt level; however, this was found at 0.2% salt concentration in *C. hongkongensis* subsp. *elegans*. Regardless of species, seed germination in T1 was higher than it was in T2 (Figure 1). Furthermore, significant interactions in salt concentration × species were found for all measured parameters, indicating that the two dogwood species had divergent responses to salt stress. For example, at 0.45% in T1, GR still reached 71.87% in *C. florida*, whereas it dropped to 52.32% in *C. hongkongensis* subsp. *elegans*. At 0.45% in T2, GR in *C. hongkongensis* subsp. *elegans* was 29.6%, only half of that in *C. florida* (59.91%). A similar tendency was also observed in other measured indicators, except for SDR, which exhibited the opposite tendency (Figure 1).

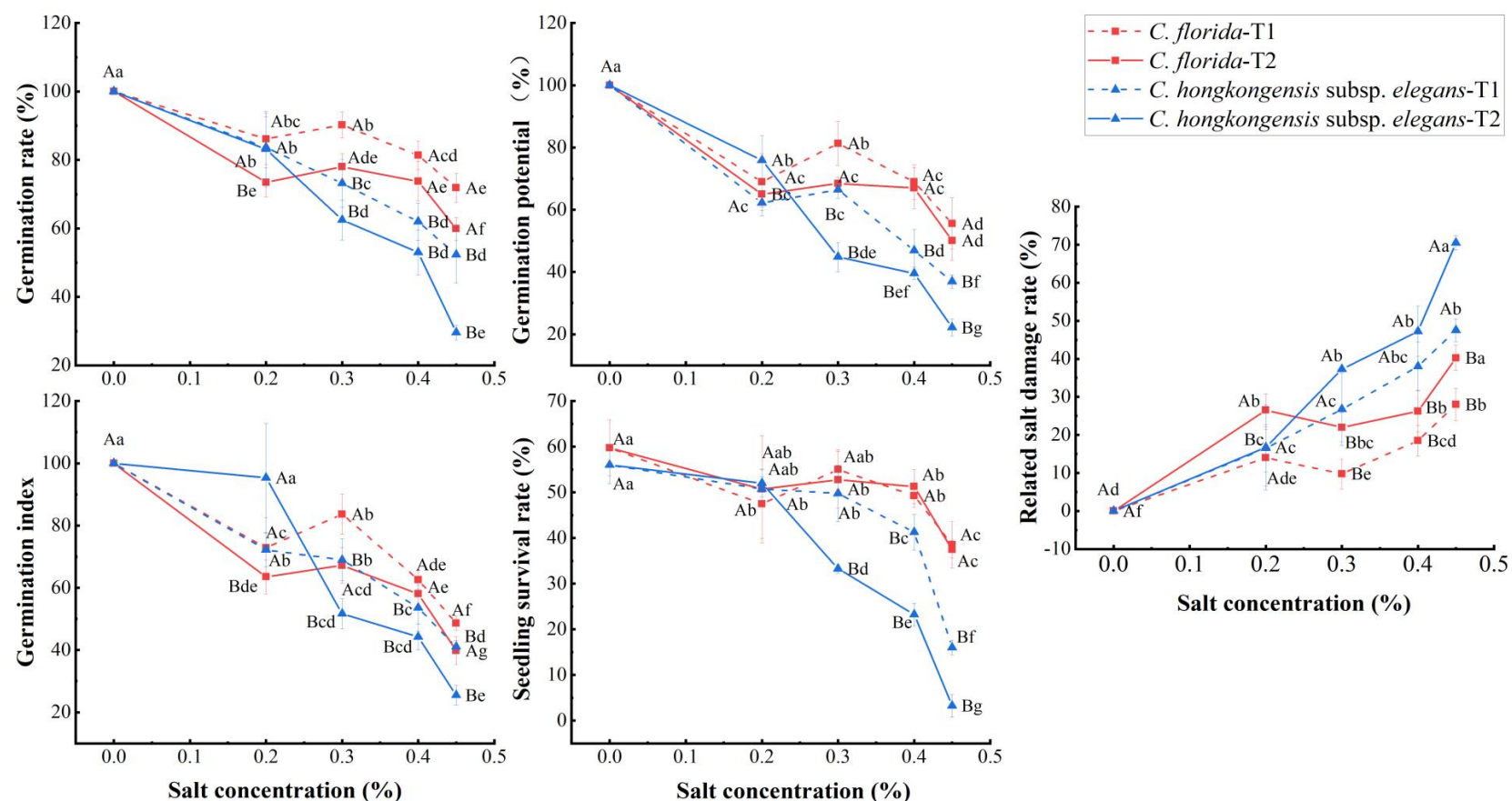


Figure 1. Effects of different treatments on germination parameters (germination rate (GR), germination potential (GP), germination index (GI), related salt damage rate (SDR)), and seedling survival rate (SR) of *Cornus florida* and *Cornus hongkongensis* subsp. *elegans*. Values are means of 4 independent replicates $\pm$ standard error. Different uppercase letters indicate the significant difference between species in the same treatment, and different lowercase letters indicate the significant difference among treatments for the same species according to Duncan's new multiple range test ($p < 0.05$). Meanwhile, germination parameters of CK were transformed to 100% (relative germination parameters), while those of salt treatments are expressed as relative germination parameters, which were calculated by multiplying the mean percentage increase in the relative germination parameters of CK compared with the absolute germination parameters.

3.2. Effect of Salt Stress on Seedling Growth Traits

Salt concentration exerted significant effects on all growth traits ($p < 0.05$) but not on root biomass for both species. As salinity increased, the seedling height decreased and root/shoot significantly increased, but the responsiveness to salt depended on species. At lower salt concentrations ($<0.4\%$), the seedling height of *C. hongkongensis* subsp. *elegans* significantly decreased, but there was no response in *C. florida*. Salt triggered the incrementation of root/shoot ratio for *C. florida*, especially at higher salinities (0.3 – 0.45%). However, the change was only significant at 0.45% salt level in T2 of *C. hongkongensis* subsp. *Elegans*. The root length of both dogwood species reduced insignificantly at 0.2 – 0.4% salt concentrations. Remarkably, this trait exhibited divergent responses between the two species at 0.45% , showing a sharp reduction in *C. hongkongensis* subsp. *elegans* but a slight change in *C. florida* (Table 2).

The shoot and plant biomass of *C. florida* showed no significant response to salt stress, but that of *C. hongkongensis* subsp. *elegans* were obviously inhibited by all salt levels (Table 3). Meanwhile, the root biomass in both dogwood species was not affected by salt treatments (Table 3). Overall, the inhibition response of growth performance to salt stress in *C. hongkongensis* subsp. *elegans* was greater than in *C. florida* for both the T1 and T2 treatments.

Table 2. Effects of different treatments on seedling height, root length, and root/shoot ratio of *C. florida* and *C. hongkongensis* subsp. *elegans*. Values are means of 3 independent replicates $\pm$ standard error. Different uppercase letters indicate the significant difference between species in the same treatment, and different lowercase letters indicate the significant difference among treatments for the same species according to Duncan's new multiple range test ($p < 0.05$), similarly for Table 3.

Parameter		Seedling Height (cm)		Root Length (cm)		Root/Shoot	
Pretreatment	Salt Concentration (%)	<i>C. florida</i>	<i>C. hongkongensis</i> subsp. <i>elegans</i>	<i>C. florida</i>	<i>C. hongkongensis</i> subsp. <i>elegans</i>	<i>C. florida</i>	<i>C. hongkongensis</i> subsp. <i>elegans</i>
T1	0	7.35 $\pm$ 0.36 ^{Aa}	7.65 $\pm$ 0.54 ^{Aa}	4.13 $\pm$ 0.26 ^{Aabc}	4.67 $\pm$ 0.47 ^{Aa}	0.56 $\pm$ 0.04 ^{Ac}	0.61 $\pm$ 0.02 ^{Ab}
	0.2	7.33 $\pm$ 0.17 ^{Aa}	7.00 $\pm$ 0.18 ^{Aab}	4.23 $\pm$ 0.19 ^{Aabc}	4.20 $\pm$ 0.14 ^{Aa}	0.58 $\pm$ 0.03 ^{Abc}	0.60 $\pm$ 0.01 ^{Ab}
	0.3	7.20 $\pm$ 0.70 ^{Aa}	6.73 $\pm$ 0.77 ^{Bb}	4.43 $\pm$ 0.45 ^{Aab}	4.05 $\pm$ 0.25 ^{Aa}	0.62 $\pm$ 0.01 ^{Aab}	0.60 $\pm$ 0.03 ^{Ab}
	0.4	6.45 $\pm$ 0.48 ^{Abc}	6.43 $\pm$ 0.88 ^{Ab}	3.98 $\pm$ 0.33 ^{Abc}	4.15 $\pm$ 0.48 ^{Aa}	0.62 $\pm$ 0.01 ^{Aab}	0.64 $\pm$ 0.02 ^{Aab}
	0.45	6.48 $\pm$ 0.53 ^{Abc}	5.55 $\pm$ 0.48 ^{Bc}	4.00 $\pm$ 0.45 ^{Abc}	3.38 $\pm$ 0.50 ^{Bb}	0.62 $\pm$ 0.03 ^{Aab}	0.61 $\pm$ 0.04 ^{Ab}
T2	0.2	7.23 $\pm$ 0.33 ^{Aa}	6.65 $\pm$ 0.19 ^{Ab}	4.10 $\pm$ 0.14 ^{Aabc}	4.08 $\pm$ 0.17 ^{Aa}	0.57 $\pm$ 0.04 ^{Ac}	0.61 $\pm$ 0.02 ^{Ab}
	0.3	7.23 $\pm$ 0.26 ^{Aa}	6.70 $\pm$ 0.29 ^{Ab}	4.55 $\pm$ 0.30 ^{Aa}	4.15 $\pm$ 0.29 ^{Aa}	0.63 $\pm$ 0.02 ^{Aa}	0.62 $\pm$ 0.02 ^{Aab}
	0.4	6.90 $\pm$ 0.48 ^{Aab}	6.50 $\pm$ 0.52 ^{Bb}	4.28 $\pm$ 0.40 ^{Aab}	4.23 $\pm$ 0.54 ^{Aa}	0.62 $\pm$ 0.02 ^{Aab}	0.65 $\pm$ 0.04 ^{Aab}
	0.45	5.93 $\pm$ 0.45 ^{Ac}	4.43 $\pm$ 0.35 ^{Bd}	3.73 $\pm$ 0.22 ^{Ac}	3.00 $\pm$ 0.36 ^{Bb}	0.63 $\pm$ 0.04 ^{Aa}	0.68 $\pm$ 0.07 ^{Aa}

Table 3. Effects of different treatments on the biomass (dry weight) of shoot, root, and plant of *C. florida* and *C. hongkongensis* subsp. *elegans*.

Parameter		Shoot Biomass (g)		Root Biomass (g)		Plant Biomass (g)	
Pretreatment	Salt Concentration (%)	<i>C. florida</i>	<i>C. hongkongensis</i> subsp. <i>elegans</i>	<i>C. florida</i>	<i>C. hongkongensis</i> subsp. <i>elegans</i>	<i>C. florida</i>	<i>C. hongkongensis</i> subsp. <i>elegans</i>
T1	0	0.14 $\pm$ 0.02 ^{Aabc}	0.12 $\pm$ 0.01 ^{Aa}	0.04 $\pm$ 0.00 ^{Abc}	0.03 $\pm$ 0.00 ^{Aa}	0.18 $\pm$ 0.02 ^{Aab}	0.16 $\pm$ 0.01 ^{Aa}
	0.2	0.12 $\pm$ 0.01 ^{Abc}	0.10 $\pm$ 0.00 ^{Abc}	0.05 $\pm$ 0.00 ^{Aabc}	0.03 $\pm$ 0.00 ^{Ba}	0.17 $\pm$ 0.01 ^{Ab}	0.12 $\pm$ 0.01 ^{Bb}
	0.3	0.16 $\pm$ 0.01 ^{Aa}	0.10 $\pm$ 0.00 ^{Bbc}	0.05 $\pm$ 0.00 ^{Aabc}	0.03 $\pm$ 0.00 ^{Ba}	0.22 $\pm$ 0.02 ^{Aa}	0.12 $\pm$ 0.00 ^{Bb}
	0.4	0.13 $\pm$ 0.01 ^{Aabc}	0.09 $\pm$ 0.01 ^{Bbc}	0.05 $\pm$ 0.01 ^{Aab}	0.03 $\pm$ 0.00 ^{Ba}	0.19 $\pm$ 0.02 ^{Aab}	0.13 $\pm$ 0.01 ^{Bab}
	0.45	0.15 $\pm$ 0.00 ^{ab}		0.04 $\pm$ 0.00 ^{abc}		0.19 $\pm$ 0.00 ^{ab}	
T2	0.2	0.11 $\pm$ 0.02 ^{Ac}	0.09 $\pm$ 0.00 ^{Abc}	0.05 $\pm$ 0.00 ^{Aabc}	0.03 $\pm$ 0.00 ^{Ba}	0.16 $\pm$ 0.00 ^{Ab}	0.12 $\pm$ 0.01 ^{Bb}
	0.3	0.14 $\pm$ 0.01 ^{Aabc}	0.10 $\pm$ 0.01 ^{Bb}	0.04 $\pm$ 0.00 ^{Ac}	0.03 $\pm$ 0.01 ^{Aa}	0.18 $\pm$ 0.02 ^{Ab}	0.13 $\pm$ 0.01 ^{Bab}
	0.4	0.13 $\pm$ 0.01 ^{Aabc}	0.08 $\pm$ 0.00 ^{Bc}	0.05 $\pm$ 0.00 ^{Aabc}	0.03 $\pm$ 0.01 ^{Ba}	0.18 $\pm$ 0.01 ^{Ab}	0.12 $\pm$ 0.00 ^{Bb}
	0.45	0.11 $\pm$ 0.01 ^c		0.04 $\pm$ 0.00 ^{abc}		0.16 $\pm$ 0.01 ^b	

3.3. Effects of Salt Stress on Physiochemical Traits

Significant effects of salt concentrations on MDA content and SOD activity for both species were found, showing an upward trend with the rise of salt concentrations ($p < 0.05$). Salt concentration also had significant effects on SS and Pro content in both species ($p < 0.05$). The SS content of the two dogwoods significantly increased with the increase in salinity,

whereas no significant change was detected in the Pro content until salt levels of 0.3% and 0.4% in *C. florida* and *C. hongkongensis* subsp. *elegans*, respectively (Figure 2). Overall, the contents of MDA, SS, Pro, and SOD activity in *C. florida* were significantly higher than in *C. hongkongensis* subsp. *elegans* (Figure 2).

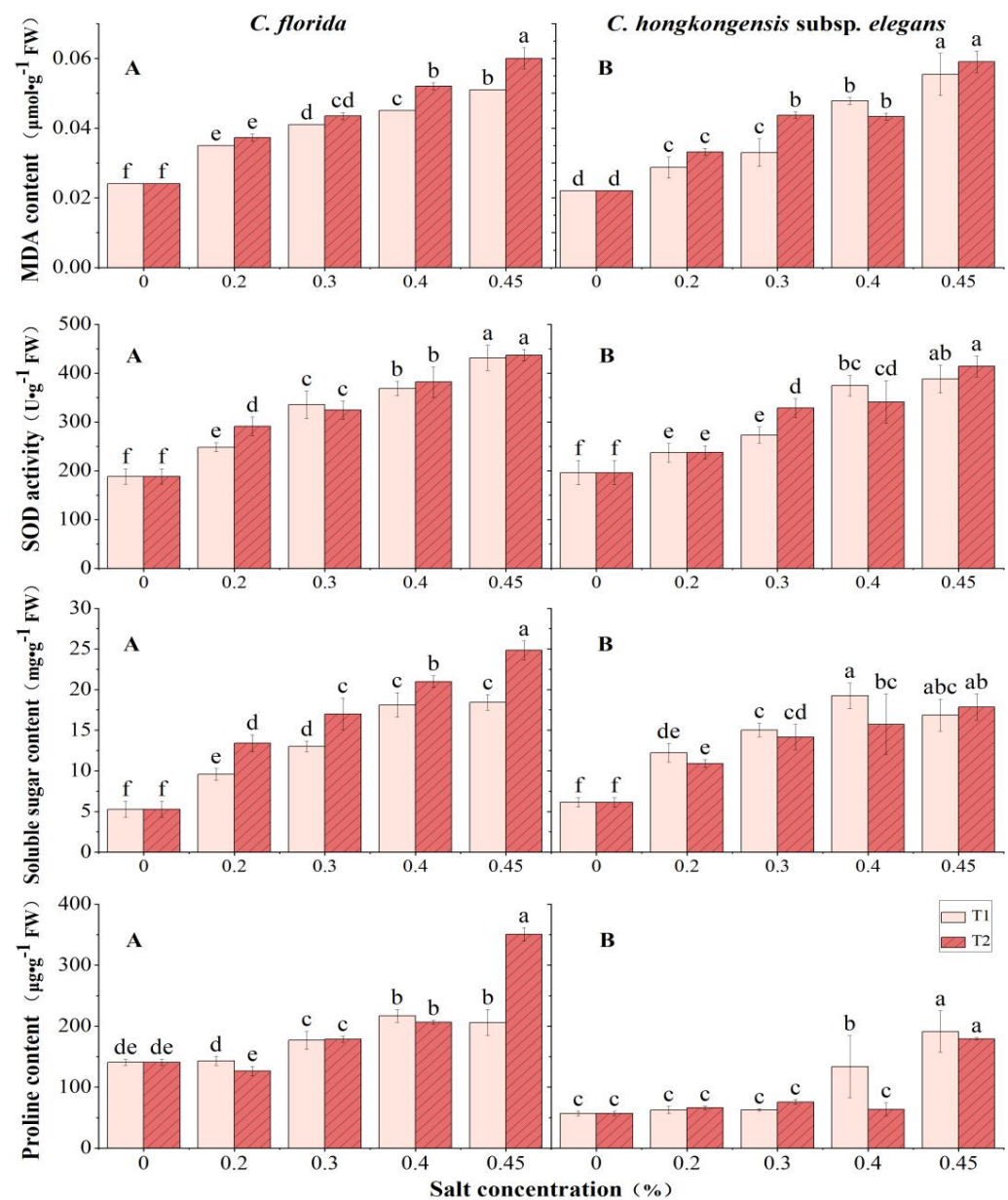


Figure 2. Responses of superoxide dismutase (SOD) activity, malondialdehyde (MDA), soluble sugar (SS), and proline (Pro) content in the shoot of seedlings of *C. florida* and *C. hongkongensis* subsp. *elegans* to salt stress. Different uppercase letters and lowercase letters indicate significant difference between species across different treatments and between treatments within each species, respectively, at $p < 0.05$ level. Each value is shown as the mean $\pm$ SD of four replicate measurements, as in Figure 3.

Figure 3 shows that salt stress had a significant effect on the accumulation of tested inorganic ions ($p < 0.05$). Predictably, increases in Na^+ were found in all stressed seedlings of both dogwood species as salt concentrations rose. Divergently, K^+ content remained stable in *C. florida*, but a certain increment occurred in *C. hongkongensis* subsp. *elegans* seedlings that were stressed by higher salt levels. Overall, K^+/Na^+ ratios in all stressed seedlings of both species were much lower than in CK; between salt treatments, the K^+/Na^+

ratio was stable in both dogwood species. Similar to the Na^+ content, rising tendencies in Ca^{2+} content occurred with the aggravation of salt stress in both dogwoods (Figure 3).

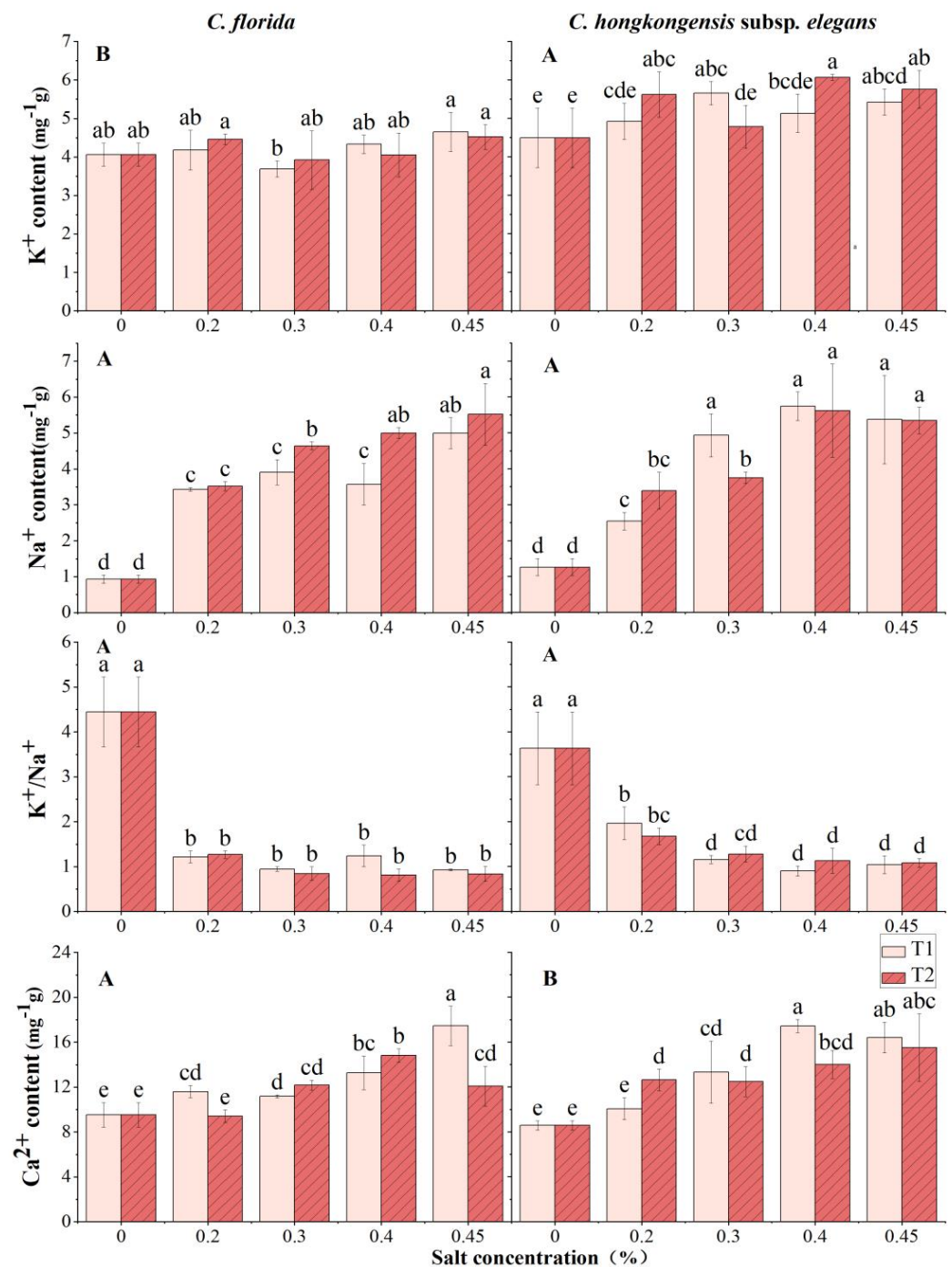


Figure 3. The changing patterns of K^+ , Na^+ , and Ca^{2+} contents and K^+/Na^+ ratios in the shoots of *C. florida* and *C. hongkongensis subsp. elegans* seedlings that were subjected to salt stress.

3.4. Correlations between Growth and Physiochemical Parameters

The SDR was negatively correlated with SR, seedling height, and root length. There was also a negative correlation between two growth parameters (seedling height and root length) among all physiochemical traits. Pairwise correlations of physiological indicators (MDA, SOD, SS, and Pro) were significantly positive (Figure 4). These correlations verified the consistency between phenotype and physiological response to salt stress.

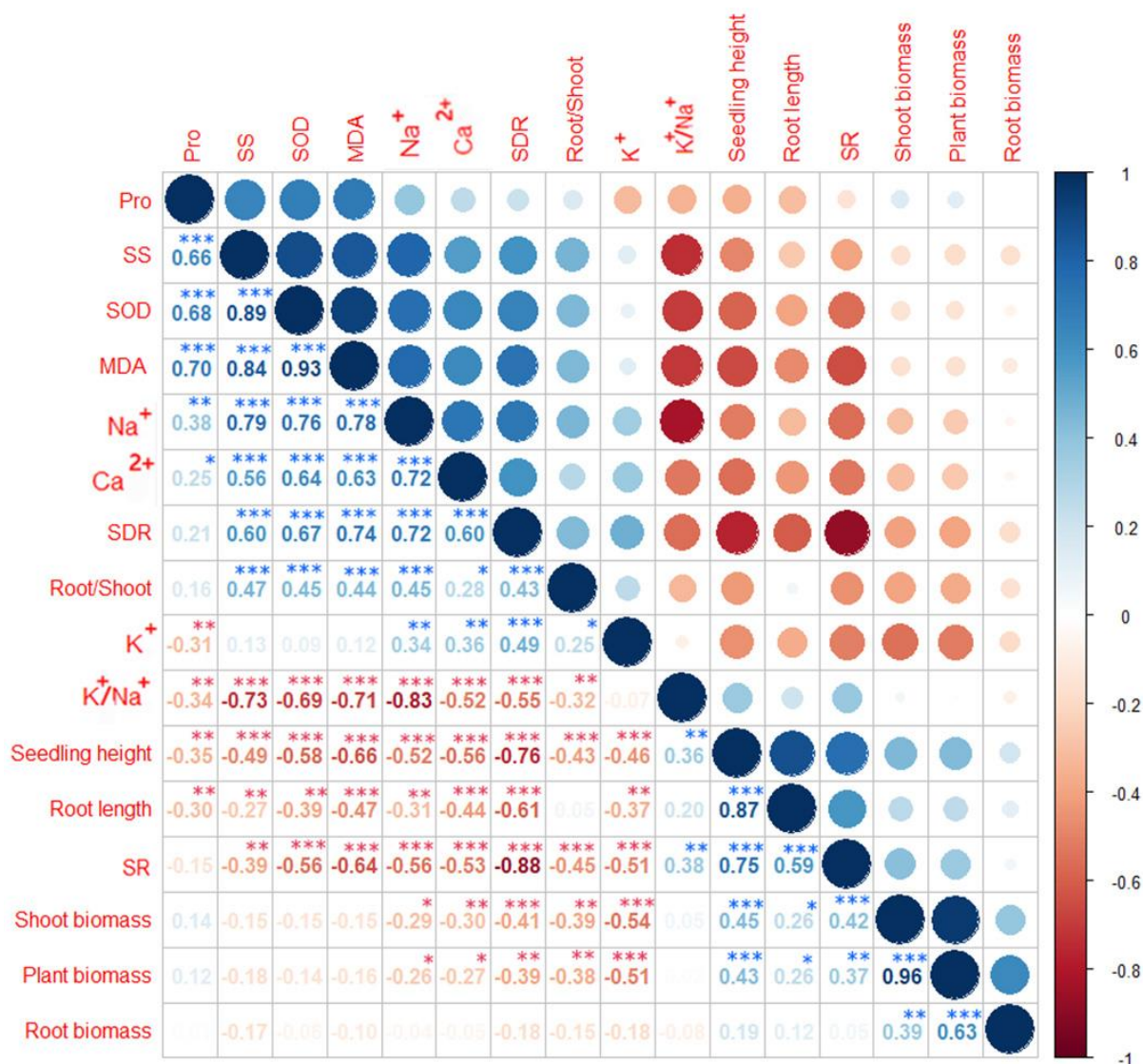


Figure 4. Correlation between seedling growth and physiological and biochemical parameters in seedlings of two dogwood species subjected to salt stress. Data in the boxes are the correlation coefficient. Red and blue represent positive and negative correlation, respectively. *, **, and ***: significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

3.5. Relationships between Salinity Tolerance with Variables

Salinity tolerance was significantly negatively correlated with SS and all tested inorganic ion contents. Among them, K⁺ content had the strongest responding determinant to salinity tolerance ($r = 0.333$, $p < 0.001$). Nonetheless, the correlations between salinity tolerance with SOD activity, Pro content, and K⁺/Na⁺ ratio were not significant (Figure 5).

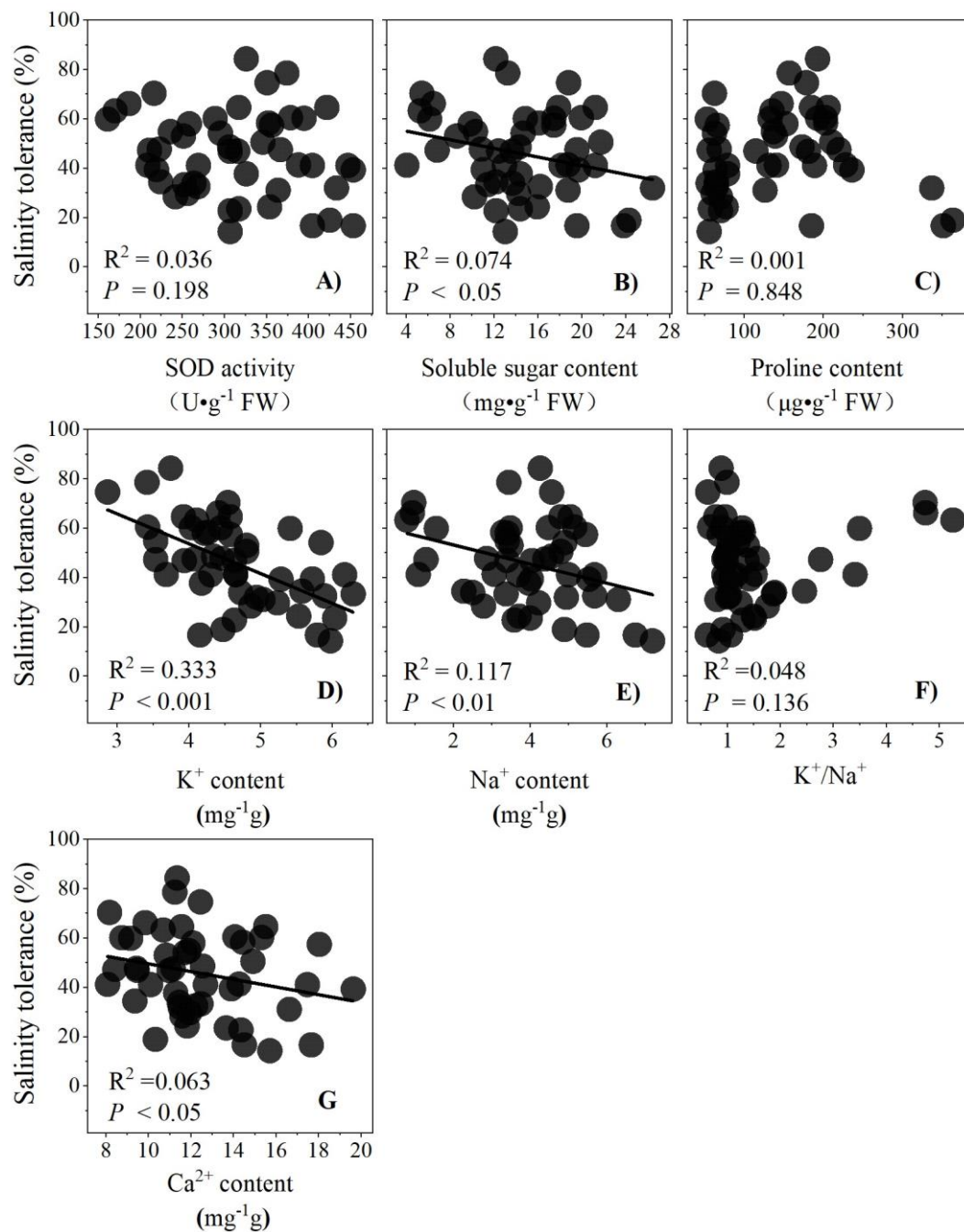


Figure 5. Relationships between salinity tolerance and assessed traits across different species and treatments. (A) SOD activity. (B) soluble sugar content. (C) proline content. (D) K^+ content. (E) Na^+ content. (F) K^+/Na^+ . (G) Ca^{2+} content.

4. Discussion

4.1. Salinity Inhibits Seed Germination and Seedling Growth in Two Dogwood Species, but *C. florida* Displays Better Salt Tolerance

Seed germination is sensitive to salt stress. For dormant seeds in natural conditions, dormancy release before germination will be delayed or destroyed in saline soil, which could weaken further germination [30]. The germination performance of these two dogwood species in response to salt stress provides substantial evidence in support of this conclusion (Figure 1).

Furthermore, osmotic stress and ion toxicity caused by salt stress usually delays seedling growth [7,8]. As shown in Figure 4, the SDR was negatively correlated with

SR, seedling height, and root length. In salt-stressed seedlings, the rate of expansion of tender leaves and shoot growth are inhibited by osmotic stress, and the aging rate of old leaves is accelerated when salt accumulates to toxic concentrations [13]. Publications in *Populus pruinosa*, *Elaeagnus angustifolia* L., etc. [31,32], and our results all proved this phenomenon. As presented in Tables 2 and 3, inhibited growth performances in the above-ground parts (i.e., seedling height and shoot biomass) worsened with increases in salt level. However, stable root growth in response to the increased salt levels (Tables 2 and 3) could maintain water and nutrient uptake from the soil to alleviate osmotic stress and nutritional imbalance [14,15]. Similar results have been obtained in red-osier dogwoods as well [10].

The responses of seedling growth to salt stress depend not only on salt level, but species as well. Whether for seed germination or seedling growth, *C. florida* demonstrated greater salt tolerance than *C. hongkongensis* subsp. *elegans* (Figure 1, Tables 2 and 3). The SR reached 50% and higher in *C. florida* at 0.3% salt level but in *C. hongkongensis* subsp. *elegans* at only 0.2%. This divergence in salt tolerance probably corresponds to their native habitats. *C. florida* originated in eastern North America, which covers numerous coastal salt marshes [22]. On the contrary, *C. hongkongensis* subsp. *elegans*, native to southeast China, mainly grows in mountain areas [33]. A similar phenomenon has been reported in wild soybean species. Among them, *Glycine tomentella*, as the only soybean growing in seaside habitats, shows the least sensitivity to salinity [34].

In saline soil, the release of seed dormancy is subjected to salt stress. In our study, the germinative parameters and seedling growth in T2 were significantly lower than in T1 (Figure 1, Tables 2 and 3). It indicates that salt stress not only affects dormancy release, but also seed germination and seedling growth. To improve the survival and fast establishment of seedlings, the dormant seeds of salt-tolerant species should be treated with proper measures to ensure their survival under salt conditions. For integrated seed dormancy release, germination, and seedling growth, we suggest that dormancy be released in non-salt condition prior to sowing seeds in saline soil to speed up seed germination and further improve the survival and establishment of seedlings.

4.2. Accumulation of Soluble Sugar May Be an Adaptive Indicator to Salt Stress

In addition to morphological adaption, plants also undergo other physiological and biochemical adjustments, including in their antioxidant defense machinery and organic osmolytes, to better withstand oxidative stress and osmotic stress induced by salt stress [13,15,35].

Increasing salt damage may induce excessive reactive oxygen species (ROS) formation, leading to oxidative stress, lipid peroxidation, and loss of membrane integrity [36]. The MDA, as an indicator of membrane lipid damage, accumulates in large quantities under salt stress [37]. Significant accumulation of MDA in salt-stressed seedlings of both dogwood species indicated more serious oxidative damage in the membrane (Figure 2). In response to oxidative stress, the increased activity of antioxidant enzymes, including SOD, catalase (CAT), and peroxidase (POD), could detoxify ROS and improve plant adaptability in adversity [38,39]. The SOD acts as the “first line of defense” to cope with oxidative stress [40]. Although rising SOD with increasing salinity (Figure 2) indicated that it has some role in the adjustment of cell homeostasis, there was no significant correlation with salinity tolerance (Figure 5A), suggesting that it has a non-crucial role in dogwoods to resist salt stress. This has also been discussed in the context of some halophytes, for which more efficient mechanisms (e.g., compartmentation of Na⁺, accumulation of organic osmolytes) were speculated to help cope with salt load [13,41].

To promote osmotic adaptation to salt stress, plants tend to synthesize various osmolytes such as SS, Pro, and glycine betaine [42]. These solutes (e.g., SS) not only mitigate osmotic stress by keeping cellular turgidity but also act as osmoprotectants to alleviate oxidative damage in the cell membrane [16,17]. As documented in many plants [1,16,17], increased SS content was also found in our study (Figure 2). More importantly, it was negatively correlated with salinity tolerance (Figure 5B) and seedling growth traits (Figure 4).

The accumulation of SS allowed seedlings to survive and recover from high salinity; however, the synthesis of compatible solutes comes with an energy cost and involves a potential loss of plant growth [13]. A similar result under salt-stress conditions has also been observed in quinoa [12].

Meanwhile, the accumulation of Pro can alleviate ion toxicity and maintain intracellular ion homeostasis [43,44]. Controversially, Pro accumulation has been argued to be a salt tolerance mechanism or a negative consequence of salt damage under adverse conditions [45]. Some have suggested that Pro accumulation is a symptom of greater salt damage and has no effect on osmoregulation in rice, because Pro accumulated in greater quantities in salt-sensitive genotypes than salt-tolerant ones [46,47]. In contrast, others have found more Pro accumulation in salt-tolerant than in salt-sensitive rice lines and speculated that Pro accumulation could play an important role in osmotic adjustment [48]. In our study, the more salt-tolerant *C. florida* accumulated more Pro than *C. hongkongensis* subsp. *elegans*, supporting the claim that Pro accumulation may be an osmotic adaptation. Based on the rapid response of SS followed by Pro accumulation in these two dogwood species under salt stress (Figure 2) and the positive correlation between SS and Pro (Figure 4), we speculate that the salt-stressed seedlings alleviated osmotic stress by adjusting the content of these two osmolytes [49]. Meanwhile, the osmotic regulation mode of organic solutes in dogwoods may be that SS accumulates first and Pro is the later osmolyte [4].

4.3. Ion Osmoregulation May Be Critical for Salt Tolerance in Dogwood Seedlings

Inorganic ions also play important roles in regulating osmotic stress and maintaining ion homeostasis. Accumulated ions can maintain high cell water content and reduce transpiration when seedlings are faced with a lower water potential induced by high salinity [50–52]. Salt increased all measured ion content in the seedlings of the two species (Figure 3). High Na^+ accumulation in tissues, especially in leaves, is the cheapest form of osmotic adaptation [13], as exemplified in most plants [53,54]. Meanwhile, rising K^+ content with the increase in salt concentration indicates that Na^+ accumulation largely did not restrict the absorption of K^+ . This, however, seems to be counterintuitive. Due to the similarity of their physical and chemical properties, Na^+ and K^+ compete for binding sites in plasma membrane metabolism, so the increase in Na^+ should limit the absorption of K^+ [13,55]. However, maintaining high K^+ absorption under high salt stress, alleviating osmotic stress, has been reported in some halophytes [56]. The retention and increase in K^+ in both dogwood species was another indication of their extraordinary salt tolerance. The accumulation of Ca^{2+} (Figure 3) was also a manifestation of this effective prevention of K^+ leakage and improved salt tolerance in seedlings [57] and has been similarly verified in other dogwoods [4].

All measured inorganic ions were more closely correlated with salinity tolerance than the organic osmolytes (Figure 5), similar to previous results in salt-tolerant plants [12,58]. Compared to the greater energy cost required for the synthesis of organic osmolytes, it is cheaper and more profitable for seedlings to rely more on inorganic ions to participate in osmotic adjustment [59]. Therefore, it is essential to ensure ion osmoregulation and maintain ion homeostasis for salt tolerance in seedlings of our studied dogwood species.

5. Conclusions

In summary, *C. florida* demonstrated better salt tolerance than *C. hongkongensis* subsp. *elegans*. As salinity increased, the seed germination of both species decreased significantly. Meanwhile, the accumulation of organic (SS) and inorganic (K^+ , Na^+ , Ca^{2+}) substances might participate in osmotic adjustment together. Collectively, ion osmoregulation is supposed to be the main physiochemical mechanism of salt tolerance for both dogwoods during early seedling establishment. Thus, based on normal performances in *C. florida* at 0.3% vs. *C. hongkongensis* subsp. *elegans* at 0.2% salt level, we suggest that these two dogwoods could be candidate ornamental species for improved saline soil in coastal regions.

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