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Salt-Tolerance in Castor Bean (*Ricinus communis* L.) Is Associated with Thicker Roots and Better Tissue K^+/Na^+ Distribution

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Abstract: Soil salinity is a serious threat to agriculture worldwide. Castor bean (*Ricinus communis* L.) is an in-demand oilseed crop containing 40–60% highly valued oil in its seeds. It is moderately sensitive to salinity. Two glasshouse experiments were conducted to assess plant growth and ion tissue distribution in different castor bean genotypes under various salt stress conditions to explore their potential for cultivation on saline land. Experiment 1 evaluated the response of five castor bean genotypes to four salt treatments (0, 50, 100, or 150 mM NaCl) up to 91 days after sowing (DAS). Experiment 2 further evaluated two genotypes selected from Experiment 1 in 1 m deep PVC tubes exposed to 0, 100, or 200 mM NaCl treatment for 112 DAS (Experiment 2). Experiment 1 showed that salt addition (particularly 150 mM NaCl) reduced plant height, stem diameter, shoot and root dry weights, photosynthetic traits, and leaf K^+/Na^+ ratio while increasing the leaf Na^+ concentration of castor bean plants. Two genotypes, Zibo (Chinese variety) and Freo (Australian wild type), were more salt-tolerant than the other tested genotypes. In Experiment 2, salt-stressed Zibo flowered earlier than the control, while flowering time of Freo was not influenced by salt stress. The 200 mM NaCl treatment reduced the total root length and increased the average root diameter of both Zibo and Freo compared to the control. In addition, the 200 mM NaCl treatment significantly decreased total leaf area, chlorophyll content, and shoot and root dry weight of both castor bean genotypes by 50%, 10.6%, 53.1%, and 59.4%, respectively, relative to the control. In contrast, the 100 mM NaCl treatment did not significantly affect these traits, indicating that both genotypes tolerated salt stress up to 100 mM NaCl. In general, Freo had greater salt tolerance than Zibo, due to its higher average root diameter, lower Na^+ concentration, and higher K^+/Na^+ ratio in young leaves under salt conditions. In conclusion, genotype Freo is recommended for cultivation in saline soils and could be used to breed high-yielding and salt-tolerant castor bean genotypes.

Keywords: castor bean; salt tolerance; root traits; tissue ion distribution; leaf K^+/Na^+ ratio

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1. Introduction

Soil salinity refers to an excessive amount of dissolved inorganic salts or total soluble salts in soil to allow adequate plant growth [1]. Most crops do not thrive in saline-affected soils. Almost one billion hectares of agricultural land worldwide are affected by soil salinity [2]. More than one million hectares of agricultural land are severely salt-affected in south-western Australia. Consequently, agricultural productivity is reduced by $519 million per year, representing about 4.9% of the entire agricultural productivity [3]. Moreover, the salt-affected soil area is increasing each year due to natural salinization and increased irrigation, especially in arid and semiarid regions [4].

Excessive amounts of sodium chloride (NaCl) in the soil negatively affect plant growth by reducing root osmotic potential, creating specific ionic toxicity [5] and nutritional imbalances [6]. The presence of dissolved salts in soil reduces cell water potential, decreasing root water absorption and inhibiting plant growth. This is known as the osmotic effect [5]. Increasing Na^+ concentrations in cells can reduce the K^+/Na^+ ratio, disrupting plasma membrane permeability due to K^+ ion channel leakage to the surrounding solution [5,7]. High Na^+ will also disrupt the cationic balance by reducing the uptake of zinc, potassium, iron, calcium, and magnesium [8,9]. It is reported that enrichment of Na^+ in soil leads to soil alkalization [10]. Too much Na^+ in soil may affect soil structure, e.g., increasing the dispersion of soil aggregates, which may plug soil pores and impede water movement and soil drainage, as Na^+ is a much poorer flocculator than Ca^{2+} and Mg^{2+} due to its lower charge and larger ionic size in water [11].

Castor bean (*Ricinus communis* L.) is a perennial woody plant in the Euphorbiaceae family, indigenous to Ethiopia, Eastern Africa [12] with about 1.4 million tons of castor seeds produced globally in 2019 [13]. Castor bean is an oilseed crop containing 40–60% high value oil [14]. Castor oil is mainly used in engine lubricants, biofuels, and manufacturing. Ricin is a very interesting molecule remaining in the residual oilseed panel after oil extraction. It was experimentally observed that ricin could be promising in medicine, possibly to combat cancer [15]. Castor bean can survive in drought and saline environments due to its deep, extensive root system and fast growth pattern [16]. Castor bean grows well in arid and semiarid regions with limited water and often low to medium salt concentrations in soil [17]. However, some studies have classified castor bean as a moderately saline sensitive crop [18,19]. Jeschke and Wolf [20] reported that >40 mM NaCl reduced growth, suppressed branching, and reduced leaf size in castor bean. Salt stress (45 mM NaCl) inhibited the growth of castor bean variety 'BRS Energia' [19]. Salinity levels >71 mM NaCl significantly reduced the seed emergence rate, survival rate and seedling growth of castor bean [7]. Menon et al. [21] reported that seed yield of castor bean decreased by 66% and 82% with the increase in salinity to 100 and 150 mM NaCl, respectively, compared to the freshwater treatment. Pinheiro et al. [22] reported that 30 mM NaCl induced chlorophyll degradation and chlorosis in castor bean, reducing photosynthetic efficiency. In Würzburg, Germany, castor bean plants exposed to 160 mM NaCl survived and produced viable seeds due to some root and shoot physiological responses, including K^+ selective uptake in roots and translocation to young leaves, retaining Na^+ and Cl^- in older tissues, and increased K^+/Na^+ ratio in plant tissues [20].

Although the world production of castor bean increased at a rate of about 12,300 tons per year between 2000 and 2009, the production remains insufficient to meet the increase in demand [23]. The growth and production of castor bean are severely affected by high salinity in the irrigation water or in the soil [24]. Therefore, understanding the response of castor plants to salt stress is important for increasing castor bean production.

Although the impact of salt stress on different crops have been extensively studied, the underlying salt-tolerant mechanism of different castor bean genotypes involving root traits or ions distribution in response to salinity stress is still not well-understood. Therefore, in this study, we evaluated (1) how salt stress affects the morphological and physiological traits, shoot and root growth, and ion distribution of castor bean plants; (2) genotypic differences in castor bean in response to salt stress; and (3) possible mechanisms underlying castor bean tolerance to salt stress.

2. Materials and Methods

Two consecutive experiments were conducted, the first (Experiment 1) in 2018 and the second in 2020 (Experiment 2), in evaporatively-cooled glasshouses at The University of Western Australia, Crawley, Western Australia (31°93′ S, 115°83′ E, Mediterranean-type climate). The maximum/minimum/average air temperatures were 33/13/21 °C (Experiment 1) and 34/10/19 °C (Experiment 2). Mean relative humidity was 66% (Experiment 1) and 72% (Experiment 2) with 11–12 h of natural light duration.

2.1. Experiment 1 (March to June 2018)

Experiment 1 comprised a completely randomized design with five castor bean genotypes (Wanneroo, Forrestdale, Freo, Wycombe, and Zibo), four salinity levels (0, 50, 100, and 150 mM NaCl represented by S0, S50, S100, and S150, respectively), and four replications. The range 0−150 mM NaCl was selected because, according to literature [7], the upper limit is beyond the salinity threshold that castor bean is able to tolerate. Wanneroo, Forrestdale, Freo, and Wycombe are Australian genotypes with good resistance to drought. Zibo is a Chinese genotype characterized by high yield (see Supplementary Table S1 for more detail). Seedlings were grown in non-draining plastic pots (250 mm diameter, 240 mm depth) with sealed bottom to avoid salt leaching, lined with a plastic sleeve to facilitate root harvest. The soil (10 kg) was a mixture of reddish-brown sandy clay loam [25] and brown river sand (3:1, *v*/*v*). The mixed soil consisted of 63.5% sand, 8.3% silt, and 28.3% clay. The sandy clay loam was collected from the topsoil (0–15 cm) of a field site at Cunderdin (31°64′ S, 117°24′ E), Western Australia. The soil contained 4 μg g^{-1} NH_4^+-N, 6 μg g^{-1} NO_3^--N, 46 μg g^{-1} P (Colwell), and 691 μg g^{-1} K (Colwell) with a pH of 6 ($CaCl_2$). The river sand was washed and air-dried before potting. The water content (*w*/*w*) at field capacity (i.e., freshly drained pot) was 24.5%.

The NaCl concentration in the nutrient solution was increased progressively by 25 mM each week from about one week after sowing until the final concentrations (0, 50, 100, 150 mM NaCl) were reached to avoid osmotic shock [26–29]. A diluted nutrient solution containing 7.3% N, 11% P, 28% K, 2.8% S, 0.21% Fe, 0.1% Mn, 0.08% B, 0.06% Zn, and 0.008% Mo, was applied weekly to each pot. The nutrient composition was based on the manufacturer's instructions of a compound fertilizer (Campbells Fertilisers, Australia). For the salinity treatments, 3.715 g pot^{-1} NaCl was added to each pot by adding NaCl to the nutrient solution and watering to field capacity to increase the salt concentration to 25 mM NaCl in the soil solution. For the non-saline control, pots were watered to field capacity with an equivalent volume of nutrient solution (no NaCl). For each pot, four seeds were planted, with the emerged seedlings later thinned to one plant per pot. The pots were maintained at field capacity by watering every 2–3 days to the required weight. The pots were rotated randomly each week to minimize spatial variability.

2.2. Experiment 2 (February to July 2020)

Two castor bean genotypes—Zibo and Freo—selected for Experiment 2 were relatively more salt-tolerant than the other genotypes in Experiment 1. The experiments adopted a completely randomized design with two castor bean genotypes (Zibo and Freo), three salinity treatments (0, 100, and 200 mM NaCl), and three replicates (18 PVC tubes in total). Plants were grown in PVC tubes (diameter: 150 cm, depth: 85 cm) lined with a plastic sleeve to facilitate root harvest. The tubes were filled with the same soil as in Experiment 1. The soil was watered to field capacity before sowing.

Salt stress was induced gradually to avoid salt shock, with 25 mM NaCl added every second day from 21 DAS until the pre-determined salinity level was reached. The saline treatments were implemented as per Experiment 1. Plants were watered manually with deionized water as needed, with a weekly application (100 mL) of dilute nutrient solution (see Experiment 1). Tubes were rotated randomly each week to minimize spatial variability. The seedling emergence date was noted.

2.3. Shoot Traits: Non-Invasive Measurements

In Experiment 1, final plant height, stem diameter, and photosynthetic traits were measured one day before harvest at the flowering stage (90 DAS). Plant height was measured from the base of the plant to the top leaf tip with a ruler. Stem diameter was measured on the thickest stem using a caliper. Photosynthetic traits, i.e., net photosynthetic rate (Pn), stomatal conductance (Gs), intercellular CO_2 concentration (Ci), and transpiration rate (Tr), were measured on the second most fully expanded leaf from the top using an LI-6400XT Portable Photosynthesis System (LI-COR, Lincoln, NE, USA).

In Experiment 2, plant height and stem diameter were measured weekly from 14 DAS until harvest at the flowering stage (112 DAS), using the same method as Experiment 1. The number of fully expanded leaves and leaf chlorophyll content were measured at 112 DAS. Leaf chlorophyll content was measured on the second-most fully expanded leaf from the top using a chlorophyll meter (SPAD 502Plus, Minolta Camera Co. Ltd., Osaka, Japan).

2.4. Shoot and Root Traits: Destructive Measurements

In Experiment 1, shoots were cut from the roots at the crown at 91 DAS, separated into leaves and stems, and oven-dried at 60 °C for five days to determine shoot dry weight. After shoot harvest, the plastic bag was removed from each pot and cut open to expose the roots and soil. The roots were carefully washed free of soil. Root samples were oven-dried at 60 °C for five days to determine root dry weight. The shoot and root dry weight ratio (S/R) was also calculated.

In Experiment 2, leaf area and shoot dry weight were measured at 112 DAS. The upper most and penultimate fully expanded leaves (young leaves) and remaining shoot parts (other upper plant parts) of each plant were sampled and the leaves were used for measuring leaf area with a leaf area meter (LI-3000, LI-COR Biosciences, Lincoln, NE, USA). After scanning, leaves and stems were oven-dried at 60 °C for five days to determine shoot dry weight. After shoot harvest, the plastic bag was removed from each tube and cut open to expose the roots and soil. The exposed roots in the soil columns were photographed. The soil was sampled in 0.2 m sections from the plant base. Root samples were recovered from each soil section after washing on a 1.4 mm mesh. Root samples were stored in plastic bags at 4 °C before being scanned at 400 dpi using an EPSON Perfection V800 photo scanner (Epson America Inc., Long Beach, CA, USA) and analysed for total root length and average root diameter using WinRHIZO Pro Software (v2009, Regent Instruments, Quebec, QC, Canada). After scanning, root samples were oven-dried at 60 °C for five days to determine root dry weight. The shoot and root dry weight ratio (S/R) was also calculated. Specific root length (SRL), an indirect measure of root system thickness, was measured by dividing total root length by total root biomass [30].

2.5. Plant Na^+ and K^+ Concentrations and K^+/Na^+ Ratios

For both experiments, the leaves of Zibo and Freo, being relatively more tolerant to salt stress than the other castor bean genotypes, were selected for measuring Na^+ and K^+ concentrations. The leaves were ground using a coffee grinder (Breville CG2B, Breville Pty. Ltd., Sydney, Australia) and Geno/Grinder® (SPEX SamplePrep, Metuchen, NJ, USA) to produce fine homogeneous powder. Ground samples (~100 mg) were added to 10 mL of 0.5 M nitric acid and shaken at 40 °C for two days before measuring leaf Na^+ and K^+ concentrations using inductively coupled plasma optical emission spectroscopy (ICP-OES) analysis, as described by [31]. The maintenance of high K^+ concentration and K^+/Na^+ ratios in shoots contributes to salt tolerance [32]. Leaf K^+/Na^+ ratios were calculated by dividing the respective K^+ concentration by Na^+ concentration.

2.6. Statistical Analysis

For each experiment, a two-way analysis of variance (ANOVA) using the R Agricole package in R version 3.4.3 [33] was performed to assess the effect of genotype, salinity treatment, and their interaction on growth, physiological traits, and Na^+ and K^+ concentrations in castor bean. Means were compared for significant differences using LSD at the 5% probability level. Principal component analysis (PCA) on photosynthetic traits of the five castor bean genotypes was performed by the Factoextra package in R version 3.4.0 [33].

3. Results

3.1. Experiment 1: Shoot and Root Traits

Genotype and salinity treatment had significant effects on plant height of castor bean (Figure 1). Control plants of Freo and Zibo were significantly taller than the other

genotypes (Figure 1). The plant height of Forrestdale and Wanneroo did not significantly differ between the salinity treatments and their respective controls. The 150 mM NaCl treatment significantly reduced plant height in Freo, Wycombe, and Zibo by 62.5%, 52.7%, and 31.0%, respectively, relative to their controls.

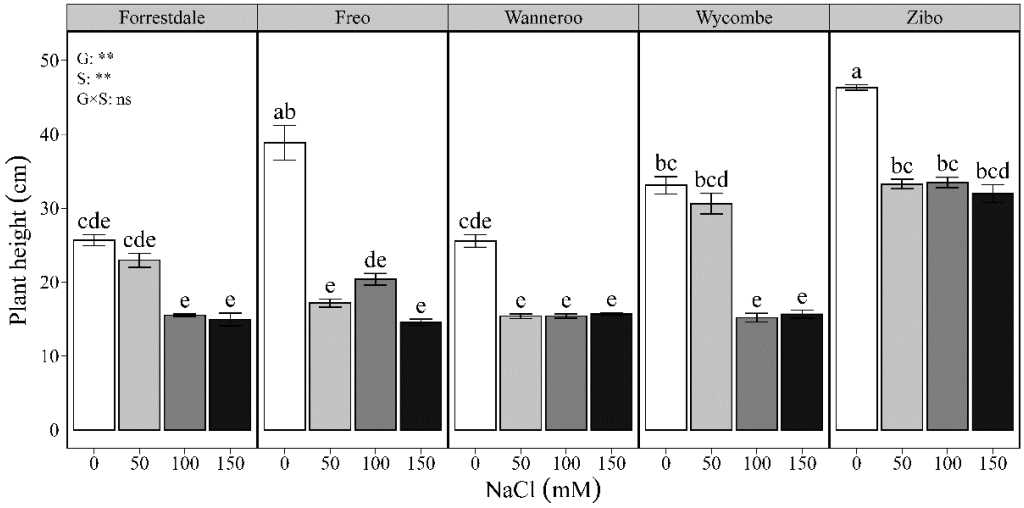

Figure 1. (Experiment 1) Plant height at 90 days after sowing of five castor bean genotypes subjected to different salinity levels. G and S represent genotype and salinity treatment, respectively. ** denote significance at the 0.01 probability level. ns denotes non-significance. Data are means of three replicates ± standard errors. Bars followed by different letters differ significantly at $p < 0.05$.

Salinity treatment significantly affected stem diameter of castor bean, with a significant genotype × salinity interaction (Figure 2). In general, stem diameter decreased with increasing salinity levels (Figure 2). For Forrestdale, Freo, and Wanneroo, the 100 mM and 150 mM NaCl treatments significantly decreased stem diameter, relative to the control, but not the 50 mM NaCl treatment. For Wycombe, the 150 mM NaCl treatment decreased stem diameter, relative to the control, but not the 50 and 100 mM NaCl treatments. For Zibo, stem diameter did not differ between the salinity treatments and the control.

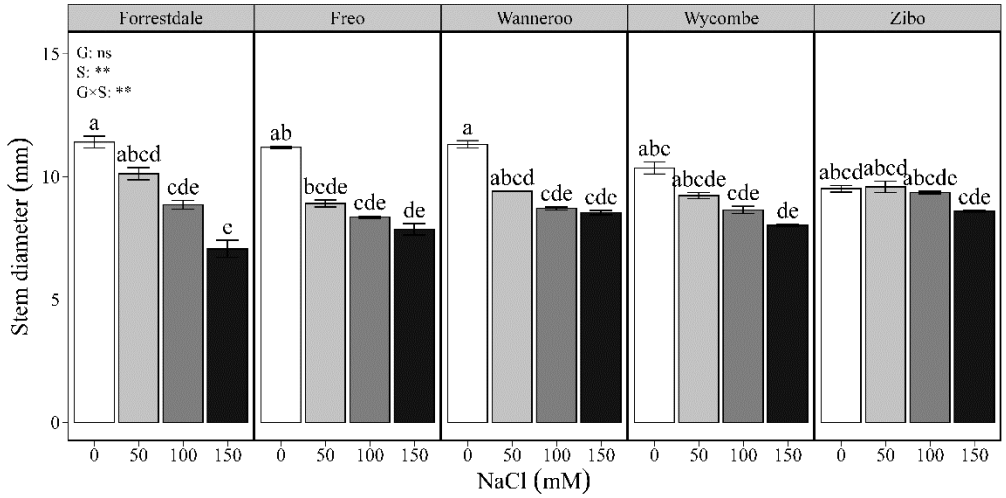

Figure 2. (Experiment 1) Stem diameter at 90 days after sowing of five castor bean genotypes exposed to four salinity levels. G and S represent genotype and salinity treatment, respectively. ** denote significance at the 0.01 probability level. ns denotes non-significance. Data are means of three replicates ± standard errors. Bars followed by different letters differ significantly at $p < 0.05$.

Salinity treatment significantly affected shoot and root dry weights of castor bean (Figure 3), with no significant genotype or genotype × salinity interaction. The 50, 100, and 150 mM NaCl treatments decreased shoot dry weight of Wanneroo by 27.3%, 44.4%, and 45.8%, respectively, relative to the control (Figure 3). Root dry weights in the 50, 100, and 150 mM NaCl treatments were reduced by 21.5%, 36.6%, and 44.1%, respectively, as compared to the control. Shoot and root dry weight ratio (S/R) was not affected by genotypes or salinity treatments.

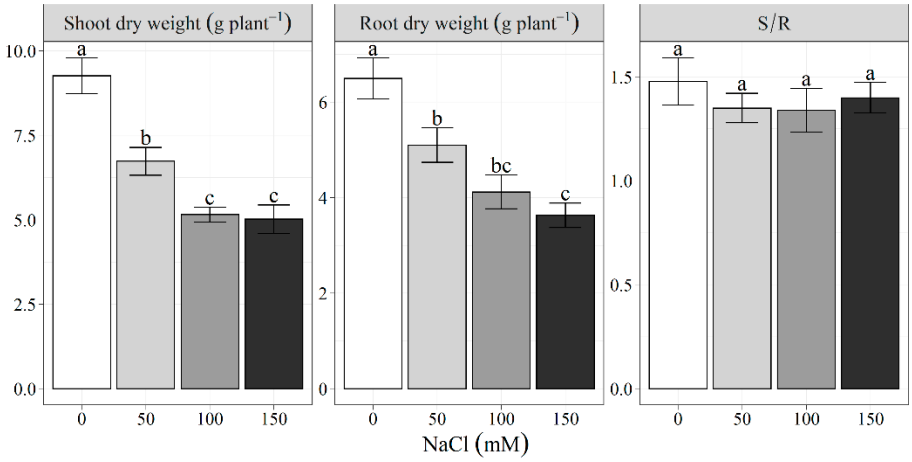

Figure 3. (Experiment 1) Shoot and root dry weights and their ratio (S/R) at 91 days after sowing of castor bean subjected to different salinity levels. Data are means of three replicates ± standard errors. Within each trait, bars followed by different letters differ significantly at $p < 0.05$.

Salinity treatment significantly affected net photosynthetic rate, transpiration rate, stomatal conductance, and intercellular CO_2 concentration (Table 1). Genotype had a significant effect on all photosynthetic traits. There was no significant genotype × salinity interaction for any photosynthetic traits. Averaged across genotypes, the 100 mM and 150 mM NaCl treatments decreased net photosynthetic rate by 35.4% and 58.5%, respectively, relative to the control (Table 1). Transpiration rate decreased with increasing salinity levels. Stomatal conductance and intercellular CO_2 concentration decreased with increasing salinity levels until 100 mM NaCl. Averaged across salinity treatments, Zibo had a relatively higher transpiration rate, stomatal conductance, and intercellular CO_2 concentration than Freo, but a similar net photosynthetic rate. Similarly, the principal component analysis showed that the first two principal components accounted for 98.6% of the total variance in the dataset and effectively discriminated Zibo for higher Tr, Gs, and Ci values, in contrast with Wycombe, Forrestdale, and Freo. In contrast, Wanneroo is characterized by higher Pn values (Figure 4).

3.2. Experiment 1: Leaf Na^+ and K^+ Concentrations and K^+/Na^+ Ratios

Leaf Na^+ concentration in Zibo increased with increasing salinity levels (Figure 5a). For Freo, there were no significant differences between salinity treatments and the control for leaf Na^+ concentrations. In the 100 mM and 150 mM NaCl treatments, Zibo had 1.5-fold and 7.9-fold higher leaf Na^+ concentration than Freo, respectively, indicating that Freo was able to reduce Na^+ concentration in leaf tissue compared to Zibo, thus showing a higher K^+/Na^+ ratio under salinity stress (Figure 5). For Freo and Zibo, leaf K^+ concentrations did not significantly differ between salinity treatments and the control (Figure 5b). Salinity treatments decreased the leaf K^+/Na^+ ratio in Zibo, relative to the control (Figure 5c), but had no effect on the leaf K^+/Na^+ ratio of Freo.

Table 1. (Experiment 1) Effect of salinity treatment on photosynthetic traits of five castor bean (*Ricinus communis* L.) genotypes grown in pots in a temperature-controlled glasshouse at 90 days after sowing.

Main Effect		Net Photosynthetic Rate ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	Transpiration Rate ($mmol\ H_2O \cdot m^{-2} \cdot s^{-1}$)	Stomatal Conductance ($mol\ H_2O \cdot m^{-2} \cdot s^{-1}$)	Intercellular CO_2 Concentration ($\mu mol\ CO_2\ mol^{-1}$)
Genotype	Forrestdale	11.0 ab	3.15 ab	0.21 ab	239 b
	Freo	10.9 ab	2.80 b	0.18 b	243 b
	Wanneroo	12.8 a	3.76 ab	0.25 ab	258 ab
	Wycombe	10.6 ab	3.30 ab	0.23 ab	254 ab
	Zibo	10.0 b	4.09 a	0.31 a	284 a
Salinity	0 mM	14.7 a	5.65 a	0.44 a	308 a
	50 mM	13.9 a	4.33 b	0.30 b	272 b
	100 mM	9.5 b	2.38 c	0.13 c	234 c
	150 mM	6.1 c	1.32 d	0.06 c	209 c
ANOVA					
Genotype		*	*	*	**
Salinity		**	**	**	**
Genotype × Salinity		ns	ns	ns	ns

Note: Main effects only (genotype and salinity) are reported because their interaction did not statistically significant. For each main effect, means followed by different letters differ significantly. *, $p < 0.05$; **, $p < 0.01$; ns, not significant.

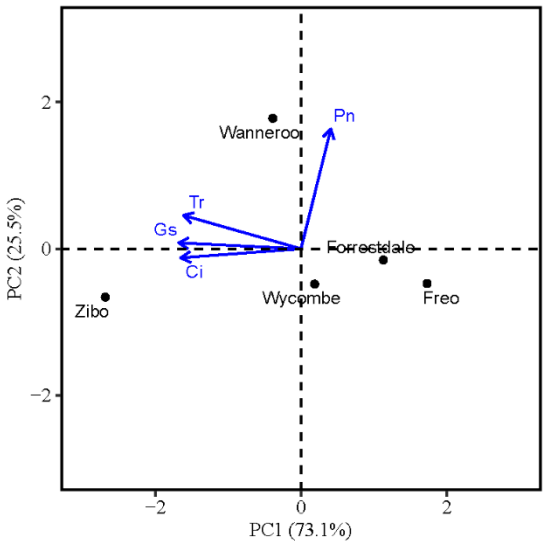

Figure 4. (Experiment 1) Principal component analysis (PCA) for the photosynthetic traits of different castor bean genotypes Pn, Gs, Ci, and Tr represent net photosynthetic rate, stomatal conductance, intercellular CO_2 concentration, and transpiration rate, respectively.

3.3. Experiment 2: Phenology and Shoot and Root Traits

Seedling emergence time for Zibo and Freo did not significantly differ between salinity treatments (Table 2). The number of fully expanded leaves did not significantly differ between genotypes in the same treatment or between the control and 100 mM NaCl treatment (Table 2). The 200 mM NaCl treatment produced significantly fewer fully expanded leaves than the control. In the 100 mM and 200 mM NaCl treatments, Zibo flowered and reached 50% anthesis earlier than the control plants (Table 2). Zibo matured earlier than Freo. Some salt-treated Zibo plants had started to produce seeds by 112 DAS. Neither the control nor salt-treated Freo had started flowering by 112 DAS (Figure 6).

At 112 DAS, the 200 mM NaCl treatment significantly reduced plant height in Zibo and Freo by 17.0% and 20.9%, respectively, while the 100 mM NaCl treatment did not affect plant height, relative to the control (Supplementary Figure S2). Stem diameter significantly differed between the 200 mM NaCl treatment and the control (Supplementary Figure S2). At 112 DAS, the 200 mM NaCl treatment significantly decreased stem diameter in Zibo

and Freo by 17.8% and 23.8%, respectively, relative to the control, while the 100 mM NaCl treatment did not affect stem diameter in Freo. Salt-treated Zibo had significantly smaller stem diameters than the control (Supplementary Figure S2).

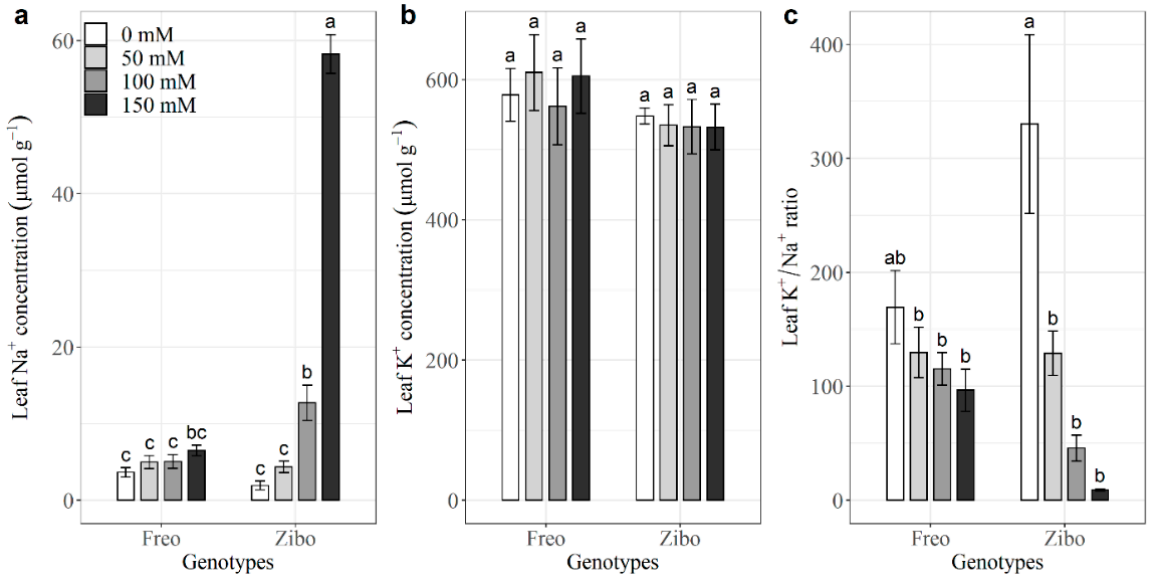

Figure 5. (Experiment 1) Leaf (**a**) Na^+ and (**b**) K^+ concentration, and (**c**) K^+/Na^+ ratio at 91 days after sowing of two castor genotypes (Freo and Zibo) exposed to four salinity levels. Data are means of three replicates ± standard errors. Bars followed by different letters differ significantly at $p < 0.05$.

Table 2. (Experiment 2) Time in days after sowing (DAS) to seedling emergence and 50% anthesis and shoot and root morphological traits at 112 DAS for two castor bean genotypes (Zibo and Freo) grown in a glasshouse under three salinity treatments (0, 100, and 200 mM NaCl).

Genotype	Treatment (mM)	Time to Seedling Emergence (Days after Sowing)	Time to 50% Anthesis (Days after Sowing)	No. of Fully Expanded Leaves	Total Leaf Area (cm^2)	Chlorophyll Content (mg m^{-2})	Specific Root Length (m g^{-1})	Average Root Diameter (mm)
Zibo	0	8.0 a	86.3 a	8.0 a	2419 a	56.1 a	3.6 a	0.56 c
	100	8.0 a	78.3 b	8.7 a	2162 ab	54.2 a	3.4 a	0.65 b
	200	7.3 a	78.0 b	6.0 b	1404 b	49.6 b	3.3 a	0.72 ab
Freo #	0	9.0 a	–	6.7 a	2853 a	54.8 a	3.2 a	0.63 b
	100	8.7 a	–	7.7 a	2631 a	52.4 a	3.0 a	0.65 b
	200	8.3 a	–	5.7 b	1231 b	49.5 b	3.5 a	0.79 a
ANOVA								
Genotype		**	–	ns	ns	ns	ns	*
Salinity		ns	**	**	**	*	ns	**
Genotype × Salinity		ns	–	ns	ns	ns	ns	ns

Note: Means followed by different letters differ significantly. *, $p < 0.05$; **, $p < 0.01$; ns, not significant. # Freo had not flowered by the harvest at 112 DAS.

Salinity treatment significant affected shoot dry weight of castor bean (Figure 7), with no significant difference between genotypes and no significant interaction of genotype × salinity interaction for shoot dry weight. The shoot and root dry weight ratio (S/R) was also not affected by genotypes or salinity treatments. The 200 mM NaCl treatment significantly reduced shoot dry weight by 53.1%, relative to the control (Figure 7), while the 100 mM NaCl treatment did not affect shoot dry weight.

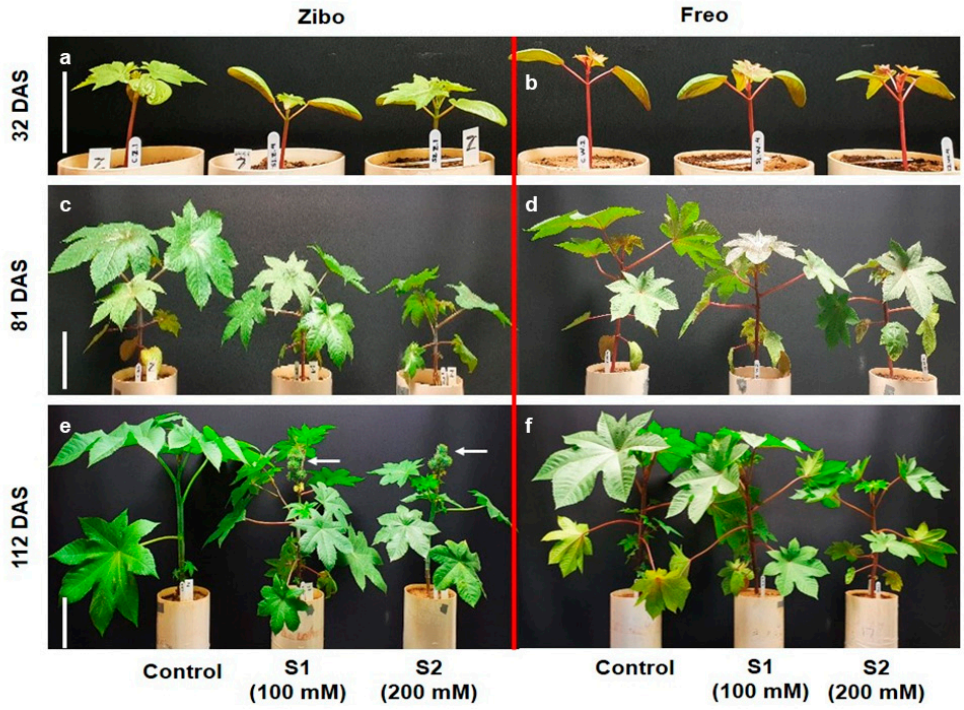

Figure 6. (Experiment 2) Shoot growth of castor bean genotypes Zibo (**a**,**c**,**e**) and Freo (**b**,**d**,**f**) under three salinity treatments (control, 0 mM NaCl; S1, 100 mM NaCl; and S2, 200 mM NaCl) at 32 (**a**,**b**), 81 (**c**,**d**) and 112 (**e**,**f**) days after sowing (DAS). White bars = 10 cm. Arrows in (**e**) indicate flowering and pod development in Zibo plants in the two salt treatments at 112 DAS.

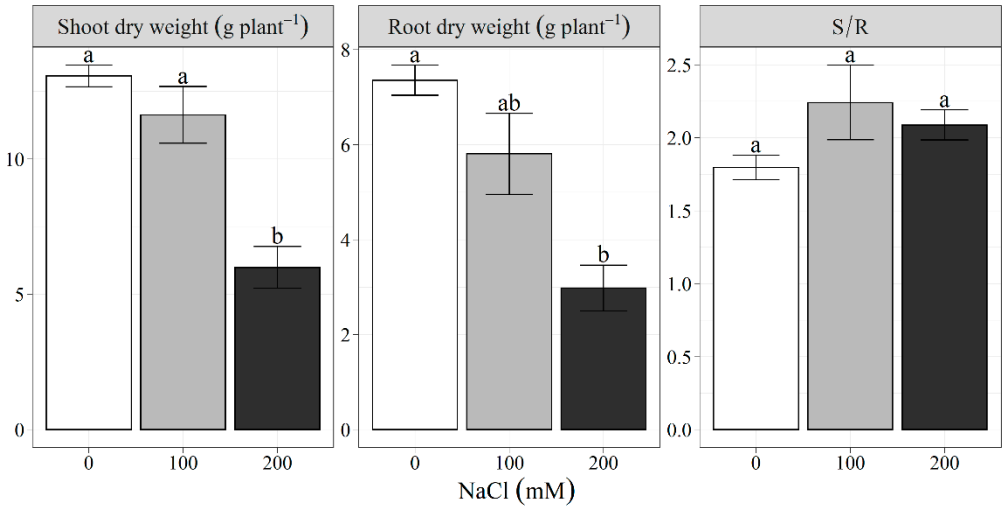

Figure 7. (Experiment 2) Shoot and root dry weights and their ratio (S/R) at 112 days after sowing of castor bean exposed to three salinity treatments (0, 100, and 200 mM NaCl). Data are means of three replicates ± standard errors. Bars followed by different letters differ significantly at $p < 0.05$.

Salinity treatment significantly affected total root length of castor bean plants, with no significant difference between genotypes and no significant interaction of genotype × salinity. The 200 mM NaCl treatment produced significantly less total root length than the control, while the 100 mM NaCl treatment did not significantly affect total root length (Figure 8). Specific root length did not significantly differ between the control and salt-treated plants or between genotypes (Table 2). Average root diameter increased significantly in the 100 mM and 200 mM NaCl treatments, relative to the control, but did not significantly differ between the two salt treatments (Table 2). Averaged across salinity treatments, Freo had a significantly higher average root diameter than Zibo. In terms of root length, the root

system of control plants comprised 70% fine roots (0–0.6 mm diameter) and 30% thick roots (>0.6 cm diameter), while salt-treated plants had about 55% fine roots and 45% thick roots (Figure 8). The 200 mM NaCl treatment significantly reduced root dry weight by 59.4%, relative to the control (Figure 7). Root dry weight did not significantly differ between the control and 100 mM NaCl treatment, with no significant difference between genotypes and no genotype × salinity interaction.

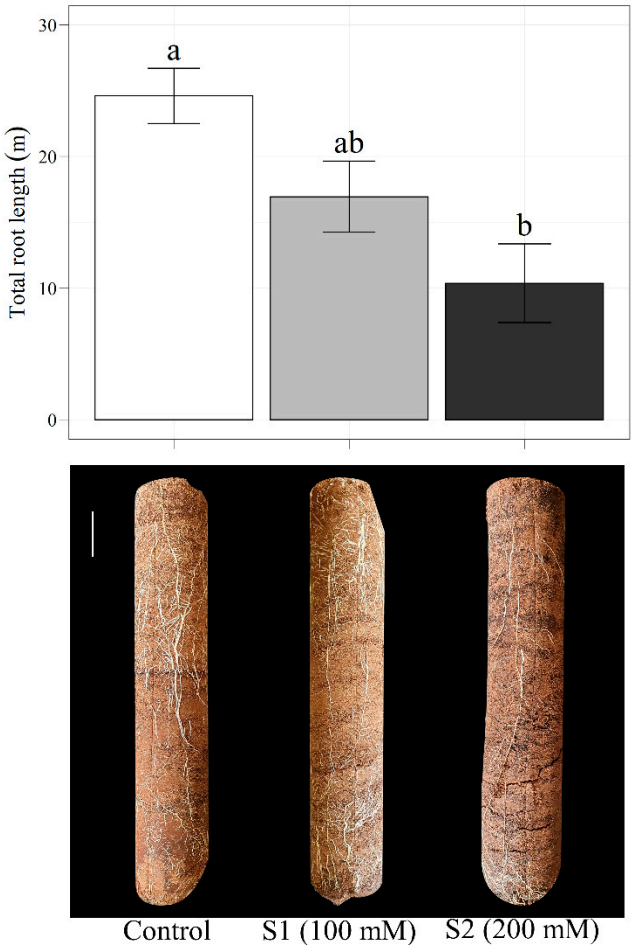

Figure 8. (Experiment 2) Total root length (**upper**) and soil columns with roots on the soil surface (**lower**) at 112 days after sowing of castor bean genotype Freo exposed to three salinity treatments (control, 0 mM NaCl; S1, 100 mM NaCl; S2, 200 mM NaCl). Data are means of three replicates ± standard errors. Bars followed by different letters differ significantly at $p < 0.05$. White bar denotes 10 cm scale.

Chlorophyll content did not significantly differ between Zibo and Freo within each treatment (Table 2). Regardless of genotypes, the 200 mM NaCl treatment significantly reduced chlorophyll content by 10.6%, relative to the control, but the 100 mM NaCl treatment did not differ from the control. Regardless of genotypes, the 200 mM NaCl treatment significantly reduced total leaf area by 50%, relative to the control (Table 2). On visual inspection, the salt treatments reduced leaf area on the uppermost and penultimate fully expanded leaves of both genotypes (Supplementary Figure S3). There was no significant genotype × salinity interaction for leaf area.

3.4. Experiment 2: Distribution of Na^+ and K^+ and K^+/Na^+ Ratios in the Leaves

In general, the two salt treatments produced higher Na^+ concentrations and lower K^+ concentrations in roots and other upper plant parts, respectively, than the control plants resulting in significantly lower K^+/Na^+ ratios (Table 3). For both genotypes, young leaves had significantly higher K^+/Na^+ ratios than other shoot parts (Figure 9 and Table 3).

On average, the 100 mM and 200 mM NaCl treatments produced 77% higher root Na^+ concentrations than the control, and 37% and 86% lower root K^+ concentrations and root K^+/Na^+ ratios, respectively, than the control (Table 3). In the 200 mM NaCl treatment, the Na^+ concentration in young leaves of Freo was 85.9% lower than that in Zibo, which indicated the ability of young leaf tissue in Freo to exclude Na^+ promoting the entrance of K^+ and sustaining a higher K^+/Na^+ ratio than Zibo (Figure 9). There was a significant genotype × salinity interaction for Na^+ concentration in other upper parts of castor bean plants (Table 3). Under the control and 100 mM NaCl treatments, Zibo and Freo had the similar Na^+ concentration in other upper parts, while under the 200 mM NaCl treatments, Freo had significantly lower Na^+ concentration in other upper parts than Zibo, which indicated that Freo was more resistant to salinity than Zibo.

Table 3. (Experiment 2) K^+ and Na^+ concentrations and K^+/Na^+ ratios in root and other upper plant parts (excluded young leaves) of two castor bean genotypes (Zibo and Freo) grown under three salinity treatments in a glasshouse.

Genotype	Treatment (mM)	Na^+ (μmol g^{-1} Dry Weight)		K^+ (μmol g^{-1} Dry Weight)		K^+/Na^+ Ratio	
		Root	Other Parts	Root	Other Parts	Root	Other Parts
Zibo	0	52 b	13.0 d	497 a	1205 a	16.3 a	178 b
	100	217 a	69.6 c	292 b	877 b	2.4 b	22 c
	200	265 a	196.0 a	300 b	1039 ab	2.0 b	9 c
Freo	0	61 b	4.4 d	505 a	1190 a	16.5 a	225 a
	100	217 a	104.0 c	372 b	1118 ab	3.1 b	19 c
	200	317 a	157.0 b	305 b	1021 ab	1.7 b	11 c
ANOVA							
Genotype		ns	ns	ns	ns	ns	**
Salinity		**	**	**	*	**	**
Genotype × Salinity		ns	**	ns	ns	ns	**

Note: Means followed by different letters differ significantly. *, $p < 0.05$; **, $p < 0.01$; ns, not significant.

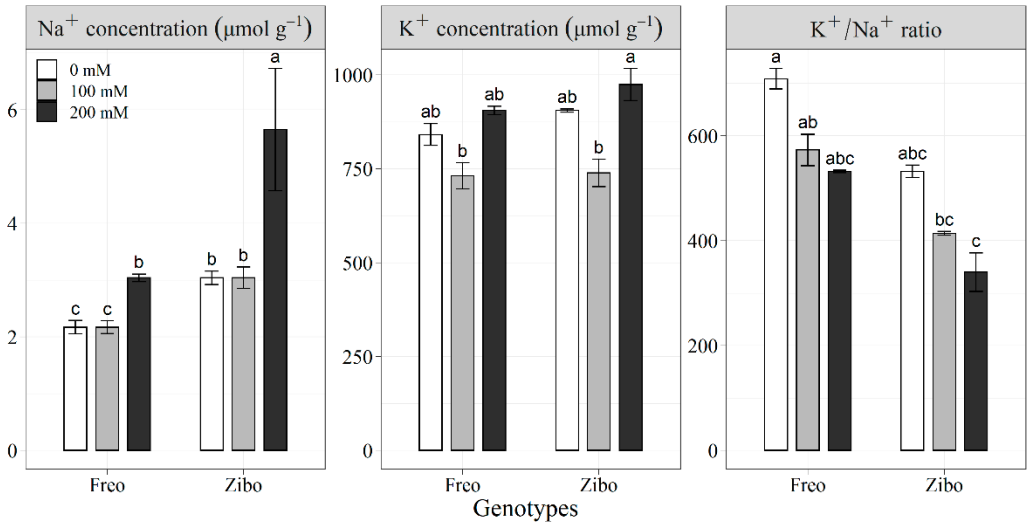

Figure 9. (Experiment 2) Na^+ and K^+ concentration, and K^+/Na^+ ratio in young leaves at 91 days after sowing of two castor genotypes (Freo and Zibo) exposed to three salinity levels. Data are means of three replicates ± standard errors. Bars followed by different letters differ significantly at $p < 0.05$.

4. Discussion

4.1. Salinity Effects on Phenology and Shoot-Related Traits

Soil salinity is a limiting factor for castor bean growth and development [7,19,34,35]. Experiment 2 revealed the extent to which castor bean genotypes Zibo and Freo can tolerate salt stress in soil. The upper salinity threshold (200 Mm NaCl) of both genotypes is higher

than that of wheat (60 mM NaCl) and barley (80 mM NaCl), the most saline-tolerant cereal crop [36].

In Experiment 2, salt-treated Zibo reached 50% anthesis eight days earlier than the control (Table 2). This phenomenon was also reported in maize by Leila et al. [37]. Unlike Arabidopsis and most other plants where flowering time is delayed by salt stress [38], castor bean plants have adapted by flowering earlier and completing their life cycle before the salt level adversely affects the growth [39]. Lima et al. [40] reported that castor bean plants irrigated with sodium water flowered 3.5 days earlier than those irrigated with calcium water. This was also confirmed by [41], who suggested that the plants regulate their physiology to survive under salt stress by accelerating the vegetative growth and entering quickly into the reproductive stages (flowering and podding).

In Experiment 2, the seedling emergence date did not significantly differ between treatments as the salt stress was applied at 21 DAS, after seedling emergence. In Experiment 1, the salinity treatments reduced plant height in Freo, Wycombe, and Zibo, relative to the control. Similarly, Wang et al. [29] suggested that decreased shoot height in maize induced by salt stress was associated with the impaired cell wall extensibility [42]. Jiao et al. [43] reported that 100 mM NaCl significantly reduced plant height in castor bean genotype ZiBi 5.

In Experiment 2, the 200 mM NaCl treatment significantly reduced stem diameter in Freo, relative to the control, with no effect in the 100 mM NaCl treatment (Supplementary Figure S2). High salt concentrations can restrict water absorption by reducing soil osmotic potential and cell turgor, which are implicated in stem diameter reduction [44]. In Experiment 2, castor bean treated with 200 mM NaCl had significantly fewer fully expanded leaves than the control. In another study, the number of fully expanded castor bean leaves declined linearly with increasing salinity levels [34]. Wang et al. [29] reported that salt stress reduced leaf number in maize, suggesting that a reduced leaf number equates to a decline in the emergence of new leaves which may be associated with osmotic stress.

In Experiment 2, the 200 mM NaCl treatment significantly reduced chlorophyll content in both genotypes, relative to the control (Table 2). In another study, 200 mM NaCl reduced chlorophyll content in castor bean, reducing photosystem efficiency [24]. Li et al. [45] reported that 200 mM NaCl damaged the photosynthetic apparatus of castor bean leaves. As expected, the photosynthetic traits, namely net photosynthetic rate, stomatal conductance, intercellular CO_2 concentration, and transpiration rate, significantly decreased in the 150 mM NaCl treatment in Experiment 1, relative to the control (Table 1). Salt stress can induce stomatal closure, reducing leaf gas exchange and intercellular carbon dioxide, and suppressing photosynthesis and plant growth [46]. Leaf transpiration rate significantly declined in response to limited water absorption by roots under salinity stress [44]. In Experiment 2, total leaf area significantly decreased in both genotypes in the 200 mM NaCl treatment, relative to the control (Table 2). Jiao et al. [43] found that 100 mM NaCl added from 10 DAS significantly reduced leaf area in castor bean seedlings by 30 DAS. Shoot growth declined in castor bean grown under 50–200 mM NaCl, subsequently reducing shoot dry weights [47]. In Experiment 1, the 150 mM NaCl treatment significantly decreased shoot dry weight of Forrestdale, Wanneroo, and Wycombe, but not Zibo or Freo, relative to the control. Moreover, Janmohammadi et al. [48] reported that 50 mM and 100 mM NaCl treatments reduced shoot dry weight of castor bean, relative to the control. The reduced shoot growth of castor bean could be attributed to water shortages due to increased osmotic potential or sodium toxicity under salt stress [32] or the diminished supply of nutrients due to restricted root growth, and thus decreased availability and uptake of essential minerals [49].

4.2. Salinity Affects Root-Related Traits

In Experiment 2, the 200 mM NaCl treatment significantly inhibited root growth in both genotypes, particularly total root length and root dry weight (Figures 7 and 8). The root length of Iranian castor bean declined significantly at 50 mM salt stress and even more

so at 200 mM [48]. Presotto et al. [50] reported reduced root dry weights in castor bean genotypes with increasing sodium concentrations, which is presumably associated with the salinity tolerance mechanism developed by castor bean to reduce excess toxic sodium ion absorption [34].

In Experiment 2, salt stress significantly increased the average root diameter of both castor bean genotypes, relative to the control (Table 2 and Figure 8), suggesting that salt-treated castor bean had fewer fine lateral roots than the control. Similarly, Sá et al. [34] reported that salinity reduced root surface area, i.e., the root system generally had thicker roots with fewer fine lateral roots. Salt stress could enhance the suberization and thickening of the root endodermis, increasing root diameter [51]. Indeed, in terms of root length, the root system of control plants comprised 70% fine roots (0–0.6 cm diameter) and 30% thick roots (>0.6 cm diameter), while salt-treated plants had around 55% fine roots and 45% thick roots. In general, salinity inhibits lateral root initiation and reduces fine lateral root numbers [49]. Castor bean tends to have larger root diameter but lower total root length in the 200 mM NaCl treatment to resist salt stress.

4.3. Distribution of K^+ and Na^+ in Alleviating Salt Stress

In Experiment 2, root and shoot Na^+ concentrations significantly increased with increasing salt level in both genotypes (Table 3). Zibo and Freo successfully limited Na^+ translocation from roots to shoots, retaining most of Na^+ in the roots (Table 3). In general, both genotypes had higher K^+ concentrations than Na^+ concentrations in root, indicating selective root uptake of K^+ over Na^+. However, in the presence of salt, root K^+ concentrations significantly declined, relative to the control, due to competition between Na^+ and K^+ ions for the same cation channels in cell membranes to enter cells as Na^+ and K^+ ions have a similar ionic radius and hydration energy [52,53]. Hence, salt-treated castor bean had significantly lower K^+/Na^+ ratios than control plants (Table 3). Zhou et al. [7] reported significant reductions in K^+/Na^+ ratios in all castor bean parts, particularly the roots.

In Experiment 2, both genotypes actively translocated K^+ into young leaves and retained Na^+ in older shoot parts, such as stems and old leaves to maintain higher K^+/Na^+ ratios in young tissues. Jeschke and Wolf [20] also found that castor bean selectively translocated K^+ to young shoot parts while sequestering vacuolar Na^+ and Cl^- in older tissues as a salinity tolerance mechanism. Salt-sensitive species like Lupinus albus did not maintain this kind of non-uniform ion distribution under salinity stress, which led to Na^+ toxicity [54]. These results suggest that the ability to maintain a high K^+/Na^+ ratio in young leaves is associated with the salinity tolerance mechanism developed by Zibo and Freo to survive high salt stress.

4.4. Genotypic Differences in Response to Salt Stress

The salt tolerance of *Ricinus communis* L. varies between genotypes [55]. In Experiment 1, Zibo showed better salt tolerance than the other genotypes with no significant differences in stem diameter between the salt treatments and the control (Figure 2). Salt stress increased leaf Na^+ concentration and decreased leaf K^+/Na^+ ratio in Zibo but did not affect these traits in Freo, indicating that Freo was more salt-tolerant than Zibo (Figure 5). In Experiment 2, the response of stem diameter to salt stress at 112 DAS supported the greater salt tolerance of Freo than Zibo, as 100 mM NaCl significantly decreased the stem diameter of Zibo but not Freo (Supplementary Figure S2). The higher salt-tolerance capacity of Freo could be attributed to its larger average root diameter under salt stress than Zibo (Table 2), suggesting greater robustness and accumulation of reserves, which would enhance plant resistance to salt conditions [8].

Genotypic differences between Zibo and Freo in response to salt stress could be explained further by Na^+ and K^+ distribution and K^+/Na^+ ratio in different plant organs. Significantly lower Na^+ concentration in young leaves in Freo than in Zibo under high salinity level enhanced salt tolerance in Freo (Figure 9). Turner et al. [56] also reported that

salt sensitivity in chickpea was strongly related to higher Na^+ concentrations in young leaves and seeds, and limiting excessive Na^+ accumulation in young tissues is important for salt tolerance in plants. The significantly higher K^+/Na^+ ratio in young leaves of Freo than Zibo could be responsible for the greater salt tolerance in Freo, as maintenance of a high K^+/Na^+ ratio in plant cytosol is an important factor for salt tolerance in plants [57]. Wang et al. [29] also reported that a salt-tolerant maize genotype maintained a higher K^+/Na^+ ratio than a salt-sensitive genotype.

5. Conclusions

Salt stress decreased the plant height, stem diameter, photosynthetic traits, shoot and root dry weights, and leaf K^+/Na^+ ratio and increased the leaf Na^+ concentration of castor bean relative to the control. Salt-stressed Zibo plants flowered earlier than the control. Salt stress reduced the total root length and increased the average root diameter in castor bean. The greater salt tolerance of Freo than Zibo could be attributed to its higher average root diameter, selective uptake of K^+, and exclusion of Na^+ in young leaves under salt stress. The findings of this study enhance our understanding of salinity tolerance mechanisms in castor genotypes. Salinity tolerance is associated with thicker roots, lower Na^+ and higher K^+ concentrations, together with a higher K^+/Na^+ ratio in young leaves. These traits can assist breeding programs and the production of castor bean in Western Australia. Future studies should investigate root and shoot Cl^- concentrations, as well as yield and yield components at the flowering/maturity stages in castor bean for a more comprehensive understanding of the physiological responses under soil salinity. Follow-up studies will incorporate more genotypes in a wide range of field environments.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/agriculture11090821/s1, Table S1: Seed characteristics of castor bean genotypes used in this study, Figure S1: (Experiment 1) Plant growth of five castor bean genotypes exposed to four salinity treatments (S0, 0 mM NaCl; S1, 50 mM NaCl; S2, 100 mM NaCl; S3, 150 mM NaCl) at 90 days after sowing (DAS), Figure S2: (Experiment 2) Plant height and stem diameter at 112 days after sowing of two castor bean genotypes (Zibo and Freo) exposed to three salinity treatments (0 mM NaCl (control), 100 mM NaCl, and 200 mM NaCl), Figure S3: (Experiment 2) The (i) upper most and (ii) penultimate (ii) fully expanded leaves at 112 days after sowing of two castor bean genotypes (Zibo and Freo) exposed to three salinity treatments (control, 0 mM NaCl; S1, 100 mM NaCl; S2, 200 mM NaCl). White bars denote 10 cm scale.

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