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ASSESSMENT OF GENOTYPIC VARIATION FOR SALT STRESS TOLERANCE AND RELATED CHARACTERISTICS AMONG SELECTED RICE CULTIVARS

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ABSTRACT

Rice is an important cereal and very sensitive to salt stress. However, information regarding the diversity of root traits and their response to salt stress is still limited because the studied cultivars do not fully cover a wide range of the total genetic diversity. In this study, we aimed to identify differences in tolerance, root morphological development, physiological characteristics, and yield components of selected rice cultivars under salt stress conditions. To this end, 56 cultivars from the Rice Diversity Research Set as well as five check cultivars were grown in a culture medium with 0 mM NaCl (control) or 50 mM NaCl (salt stress treatment). The dry shoot weight differed significantly between the stress and control treatments. Two cultivars were selected as salt tolerant and two others as non-salt tolerant. Salt stress did not affect the total root length of the two tolerant cultivars, but significantly increased the number of L-type lateral roots. The sodium content in the shoot of the two tolerant cultivars was lower than that of the two non-tolerant cultivars. Salt stress did not change the leaf water potential of the two tolerant cultivars and had a little influence on yield. These results suggested that the maintenance of water uptake due to the growth of the root system, mainly of L-type lateral roots, as well as the inhibition of sodium accumulation in the shoot were important mechanisms of salt tolerance that finally reflected in plant yield.

Keywords: Leaf water potential, L-type lateral root, Rice Diversity Research Set of germplasm, Salt stress, Sodium contents, Yield components

1. INTRODUCTION

The global climate change promotes the rapid deterioration of farmland soil worldwide. In Asia-Oceania, salt accumulation occurs in 8% of all arable lands [1]. Rice is the world's single most important food crop and a primary food source for more than a third of the world's population [2]. More than 90% of the world's rice is grown and consumed in Asia where 60% of the earth's people live. Rice accounts for 35 to 60% of the calories consumed by 3 billion Asians. Rice is very sensitive to salt stress [3]. The grain yield of rice is reduced by approximately 70–100% of its maximal yield performance due to salinity [4]. Therefore, salt tolerant cultivars are highly demanded by rice producers.

Previous studies identified genotypic differences in salt tolerance related to root development among rice cultivars [5-7]. However, information regarding the diversity of root traits and their response to osmotic stresses is still limited because the studied cultivars do not fully cover a wide range of the total genetic diversity. The Rice Diversity Research Set (RDRS) developed by the National Institute of Agrobiological Science (NIAS) allows the wide and comprehensive evaluation of genotypic diversity in rice [8]. Various studies have used cultivars from the RDRS to assess the genetic variation under various water stress conditions [9-13]. For instance, Uga *et al.* [12] analyzed anatomical and morphological traits under rainfed upland conditions and found differences in root characteristics between Japonica and Indica rice accessions, whereas Matsunami *et al.* [9] reported genotypic differences in the shoot and root biomass under soil moisture deficit conditions. However, no previous studies have used cultivars from the RDRS to investigate salt tolerance. Evaluating the genetic background and determining traits responsible for salt tolerance may provide novel information for improving breeding strategies and genetic analysis.

Salt stress is complex, since it comprises water deficit stress and sodium stress [14, 15]. The lateral root constitutes approximately 90% of the total length of the plant root system [16, 17], and its development has been indicated as an important adaptation factor to soil moisture changes [18-20]. Rice plants have two types of lateral roots: thick and long lateral roots with higher order branching (L-type) and thin and short lateral roots without higher order branching (S-type) [21, 22]. The different types of lateral roots vary in anatomy, developmental characteristics, carbon and nitrogen dynamics, developmental responses to various soil environments [18], and development regulation [23]. The L-type lateral roots tend to show sharper developmental responses to various soil moisture conditions [24, 25]. Toyofuku *et al.* [13] reported that the root-system development, especially of L-type lateral roots, involves genes responsible for dry matter production under osmotic stress. However, the function of the lateral root under salt stress remains unclear, and further research is necessary. Furthermore, the root characteristics of salt tolerant cultivars vary under stress conditions and thus, they need to be studied in relation to their genetic background [12].

In this study, we aimed to assess the genotypic variation in biomass production under salt stress using a wide range of genetically diverse cultivars from the RDRS. In addition, we studied the differences in the root morphological development, physiological characteristics, and yield components of selected tolerant and non-tolerant cultivars under salt stress.

2. MATERIALS AND METHODS

2.1 Plant culture

2.1.1 Experiment 1

In this study, we used 56 cultivars from the RDRS (Table 1), which developed by NIAS using data from a genome-wide restriction fragment length polymorphism survey of 332 accessions that selected based on the passport data of all stored collections and include 91% of all identified alleles [8]. Additionally, we used the salt-resistant cultivar Nona Bokra, the salt-sensitive cultivar IR28 [26, 27], and the drought-resistant cultivars IRAT109 [28-30], Azucena [31], and Dular [28, 32, 33] (Table 1).

Seeds were germinated in petri dishes in the dark at 28°C for 3 d. During this period, the seminal roots of the germinating seedlings elongated approximately 1 cm with no differences among the cultivars. The seedlings were transplanted onto plastic nets (2.5 × 2.5 mm mesh; 16 seedlings per net) that placed in a beaker, which contained 1 L of the following nutrient solution: 1.5×10^{-3} M KNO_3, 1.0×10^{-3} M $Ca(NO_3)_2$, 2.5×10^{-4} M $NH_4H_2PO_4$, 5.0×10^{-4} M $MgSO_4$, 1.3×10^{-5} M Fe-EDTA, 2.3×10^{-6} M $MnCl_2$, 1.2×10^{-5} M H_3BO_3, 1.9×10^{-7} M $ZnSO_4$, 7.9×10^{-8} M $CuSO_4$, and 7.5×10^{-9} M $(NH_4)_6Mo_7O_{24}$. Distilled water was added every day, and the water level was maintained constant after transplanting. The solution was aerated by continuous bubbling (1,000 ml air min^{-1}) provided by an aerator (HPα 10000; NISSO, Japan). The bubbles did not travel as far as the root axis, and thus, they did not inhibit the growth of the root system [34]. The beakers were covered with heavy paper to exclude light and stimulate the growth of the root system. The plants were grown in a growth chamber at 28 ± 0.2°C with a 12-h photoperiod and a relative humidity of approximately 70% (MLR-350H; SANYO, Japan). The photon flux density of photosynthetically active radiation (PAR; 400–700 nm) at the top of each plant was 320 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

At 7 d after transplanting, 0 mM NaCl (control) or 50 mM NaCl (stress treatment; Maas and Hoffman [35]) was added in the culture medium.

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2.1.2 Experiment 2

Seeds of selected cultivars were allowed to germinate in petri dishes in the dark at 28°C for 1 d and then transferred to a greenhouse at Akita Prefectural University, Japan, at 25°C for 28 d. Next, each seedling was transplanted into a 1/2,000a Vagner pot filled with Andosol placed in a tank (92 cm × 184 cm × 41 cm), which contained 350 L of water. LP compound fertilizer (N: P: K = 8:8:8) of delayed release was added immediately after transplanting (12.5 g per pot) and at 56 d after transplanting (6.25 g per pot).

A total of 0 g of NaCl (0 mM NaCl; control) or 1,022 g of NaCl (50 mM NaCl; stress treatment) was added in each tank.

2.2 Measurements

2.2.1 Experiment 1

At 7, 8, 9, 10, and 14 d after transplanting, the top leaves were collected to measure the leaf water potential using thermocouple psychrometry with sample chambers (C-52; Wescor, South Logan, UT, USA) and a micro-voltmeter (HR-33T; Wescor) as described by [36].

At 14 d after transplanting, shoot and root samples were desiccated at 80°C for 2 d to measure the dry weight. The sample heated at 550°C for 6 h, and the ashes were dissolved in 1N HNO3 to measure the sodium concentration by inductively coupled plasma-spectrometry (OES Thermo ICAP 6000 SERIESR; Thermo Electron, Franklin, MA, USA).

Root samples were immediately fixed and stained in 0.1% (w/v) Coomassie Brilliant Blue G250 in 5% formaldehyde, 50% ethanol, 5% acetic acid (v/v) for 3 d. Images of the root system were captured using an image scanner (Epson Perfection V700 Photo scanner; Epson, Long Beach, CA, USA) at 1,200 dpi. The total length, total number of root tips, and average root diameter were measured by WinRHIZO (Regent Instruments Inc., Quebec, Canada). The number of L-type lateral roots and crown roots was counted by visual observation. The number of S-type lateral roots was calculated by subtracting the number of crown roots and L-type lateral roots from the total number of root tips.

2.2.2 Experiment 2

Plants were harvested at 160 d after transplanting, and the panicle number, spikelet number per panicle, fertility, and 1,000-grain weight were measured. Fertility was calculated using seeds of Indica and Japonica cultivars with specific gravity of 1.06 and 1.11, respectively [37].

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2.3 Data analysis

In Experiment 1, one cultivation examination was performed for each cultivar and each treatment. The data of dry weight and root morphological characteristics were the averages of five replications (five seedlings) and the data of leaf water potential and sodium content were the averages of three replications (three seedlings). In Experiment 2, each treatment was repeated in triplicate (three pots). The data of yield and yield components were the averages of three replications (three plants). Analysis of Student's *t*-test was performed using the statistical software Ekuseru-Toukei 2010 (Social Survey Research Information, Japan).

3. RESULTS

3.1 Experiment 1

Salt stress treatment inhibited the shoot and root growth in all cultivars, and genetic variations in plant growth were identified in the salt stress treatment. Salt stress tolerance was defined as the stress to control ratio (S/C ratio). The dry shoot weight S/C ratio (0.950–0.043) was significantly different than the dry root weight S/C ratio (1.020–0.230). Of all Indica cultivars, Jhona 2 showed the maximum shoot dry weight S/C ratio (0.950) and ARC 5955 the maximum root dry weight S/C ratio (1.020), whereas of all Japonica cultivars, Jaguary showed the maximum shoot and root dry weight S/C ratios (0.088 both; Table 1). Based on the shoot dry weight S/C ratio, we selected two salt tolerant cultivars, Jhona 2 (Indica cultivar) and Jaguary (Japonica cultivar), and two non-salt tolerant cultivars, Calotoc (Indica cultivar) and Padi Perak (Japonica cultivar). The latter two did not show the minimum shoot dry weight S/C ratio, and there were some cultivars those S/C ratio of the shoot were smaller than the non-salt tolerant cultivar that we selected. However, the growth of those cultivars was inhibited under a salt stress condition remarkably and we were not able to carry out a following experiment. Therefore, we selected 2 cultivars that were moderately weak in salt stress as non-salt tolerant cultivars.

Genetic variations in root morphological development were also identified in the salt stress treatment (Fig. 1). Ratul showed the maximum total root number S/C ratio (1.380) and Deng Pao Zhai the maximum total root length S/C ratio (1.445) as well as the maximum root surface area S/C ratio (1.214), whereas Chin Galay showed the minimum total root number S/C ratio (0.162) and Milyang 23 the minimum total root length S/C ratio (0.104) as well as the minimum surface area S/C ratio (0.120). The total root number, total root length, and root surface S/C ratios of Jhona 2 (selected salt-tolerant Indica cultivar) were 0.675, 1.050, and 0.965, respectively, whereas those of Jaguary (selected salt-tolerant Japonica cultivar) were 1.052, 1.118, and 0.863, respectively.

Differences in the morphological characteristics of tolerant and non-toletant cultivars are presented in Table 2. The total root length of tolerant cultivars did not change in the salt stress treatment compared with the control. The number of L-type lateral roots significantly increased by 4.08 times in Jhona 2 and by 1.52 times in Jaguary in the salt stress treatment. However, the number of crown roots and S-type lateral roots did not change in the salt stress treatment. The total root length significantly decreased by 0.48 times in Calotoc and by 0.31 times in Padi Perak in the salt stress treatment compared with the control. The number of crown roots and S-type lateral roots decreased significantly in the salt stress treatment, whereas that of L-type lateral roots did not change.

The sodium content in the shoot and root increased significantly in the salt stress treatment (Fig. 2). The sodium content in the shoot of tolerant cultivars was lower than that of non-tolerant cultivars in the salt stress treatment (Fig. 2-A). Specifically, the sodium content in the shoot of Jaguary and Jhona 2 was 3.2 mg g^{-1} DW and 2.8 mg g^{-1} DW, respectively, whereas that of Padi Perak and Calotoc was 9.7 mg g^{-1} DW and 6.6 mg g^{-1} DW, respectively. The sodium content in the root did not differ significantly among tolerant and non-tolerant cultivars in the salt stress treatment (Fig. 2-B). Specifically, the sodium content in the root of Jaguary and Jhona 2 was 2.2 mg g^{-1} DW and 2.6 mg g^{-1} DW, respectively, whereas that of Padi Perak and Calotoc was 4.2 mg g^{-1} DW and 1.7 mg g^{-1} DW, respectively.

Differences in the leaf water potential of Indica and Japonica cultivars in the salt stress treatment are shown in Fig. 3. The leaf water potential of the tolerant Indica (Fig. 3-A) and Japonica (Fig. 3-B) cultivars did not markedly change at 14 d after transplanting in the salt stress treatment compared with the control. However, the leaf water potential of the non-tolerant Indica and Japonica cultivars decreased at 8–14 d after transplanting in the salt stress treatment compared with the control.

3.2 Experiment 2

Differences in the yield and yield components of the selected tolerant and non-tolerant cultivars in the salt stress treatment are presented in Table 3. The spikelet number per panicle of all cultivars decreased significantly in the salt stress treatment compared with the control. However, the panicle number was not affected significantly in any cultivars. The fertility of non-tolerant cultivars decreased significantly in the salt stress treatment compared with the control. The average fertility S/C ratio of tolerant cultivars was 1.04 and that of non-tolerant cultivars was 0.74. The 1,000-grain weight of all cultivars decreased significantly in the salt stress treatment, except for that of Jhona 2. Additionally, the yield per plant of tolerant cultivars did not change in the salt stress treatment compared with the control, whereas that of non-tolerant cultivars decreased significantly. The average yield per plant S/C ratio of tolerant cultivars was 0.72, whereas that of non-tolerant cultivars was 0.38.

4. DISCUSSION

Previous studies showed that the shoot dry weight of rice plants is inhibited under salt stress conditions, and that the inhibitory degree in resistant cultivars is smaller than that in sensitive cultivars [38-40]. Similarly, the root length and root dry weight is inhibited under salt stress conditions [40], especially those of non-tolerant cultivars [41]. In the present study, we assessed the genotypic variation of rice cultivars selected from the RDRS in response to shoot and root biomass as well as root morphology under salt stress conditions (Table 1, Fig. 1). Changes in the root morphology greatly affected the shoot dry weight (Tables 1 and 2), revealing that the maintenance of root growth under salt stress conditions reflects on the shoot growth and yield performance.

Compared with Nona Bokra that is a salt tolerant cultivar [26, 27], two cultivars showed a higher shoot dry weight S/C ratio and 10 cultivars a higher root dry weight S/C ratio (Table 1). Since RDRS is a cultivar collection that covers the genetic diversity in rice worldwide [8]. Our results suggested the existence of highly salt-tolerant genetic resources.

The number of L-type lateral roots, which are longer and thicker, increased in salt tolerant cultivars in the salt stress treatment compared with the control (Table 2), results that were in agreement with those reported by Toyofuku *et al.* [13]. The L-type lateral roots account for an important portion of the total root length and surface area [16], and thus, an increased number of L-type lateral roots improve the water uptake under stress conditions. Previous studies showed that the development of L-type lateral roots is an important root trait related to drought tolerance [24, 25]. The water uptake is inhibited by salt stress, decreasing the leaf water potential [42, 43]. In the present study, the number of L-type lateral roots of tolerant cultivars increased in the salt stress treatment compared with the control. And the leaf water potential of non-tolerant cultivars decreased in the salt stress treatment compared with the control, whereas that of tolerant cultivars did not change significantly (Fig. 3). These results suggested that the L-type lateral roots contributed to the maintenance of the water uptake and the leaf water potential in salt tolerant cultivars under stress conditions. However, the underlying mechanism remains unknown, further research is necessary.

The sodium content in the shoot of tolerant cultivars was lower than that of non-tolerant cultivars in the salt stress treatment (Fig. 2). However, differences in the root were negligible among the cultivars. In rice, the photosynthetic rate, survival rate, growth rate, and shoot dry weight decrease with the increasing sodium content in the shoot [39, 44, 45], especially during early

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growth [4]. Some mechanisms of sodium transportation and accumulation were previously reviewed and showed that plant cells maintain a low cytosolic Na^+ level, while keeping a high level of K^+, which results in a high cytosolic K^+/Na^+ ratio that is preferable for vital cellular metabolic processes [46]. Salinity stress leads to Na^+ over-accumulation in the shoot, particularly in old leaves [46]. The restriction of Na^+ is critical for maintaining a high K^+/Na^+ ratio in the leaves of wheat [47]. OsHKT1;5 prevents Na^+ over-accumulation in rice by mediating Na^+ exclusion from xylem vessels and thus, protects against salinity stress [48]. A similar mechanism may occur in the root system [49, 50]. The root system of the salt tolerant rice cultivar Pokkari has apoplastic barriers that inhibit the flow of bulk water and dissolved solutes, resulting in the reduced uptake of Na^+ and increased survival rate [51]. However, further research is needed to elucidate the underlying mechanism of sodium uptake in salt tolerant cultivars.

In the present study, the yield of tolerant cultivars was not reduced significantly in the salt stress treatment compared with the control, whereas that of non-tolerant cultivars was reduced by approximately 40% (Table 3). These results suggested that salt tolerance at the seedling stage (Table 1) was positively related with yield performance at the reproductive stage, similarly as reported in previous studies [4, 6, 52]. The fertility of tolerant cultivars was also not influenced in the salt stress treatment compared with the control, whereas that of non-tolerant cultivars was markedly reduced (Table 3). Shereen *et al.* [53] showed that the inbred rice line that a decrease in fertility was little had a small decrease in yield in the 50-mM NaCl stress treatment. However, Makihara *et al.* [54] reported that different yield components are responsible for yield decrease in different salt sensitive rice cultivars under salt stress; for instance, the number of spikelets per plant in IR28 and Pokkali as well as the high sterility induced by white heads in Mangasa.

Salt stress is a combined stress, comprising osmotic stress and sodium stress [14, 15]. Toyofuku *et al.* [13] reported differences in osmotic stress tolerance among RDRS cultivars. The most salt tolerant cultivars Jhona 2 and Jaguary were ranked 26th and the 19th among the 59 cultivars under osmotic stress, respectively [13], whereas the most osmotic stress tolerant cultivars IR58 and Nipponbare were ranked 58th and 46th under salt stress. Therefore, different mechanisms are involved in salt stress and osmotic stress tolerance in rice.

4.1 Figures

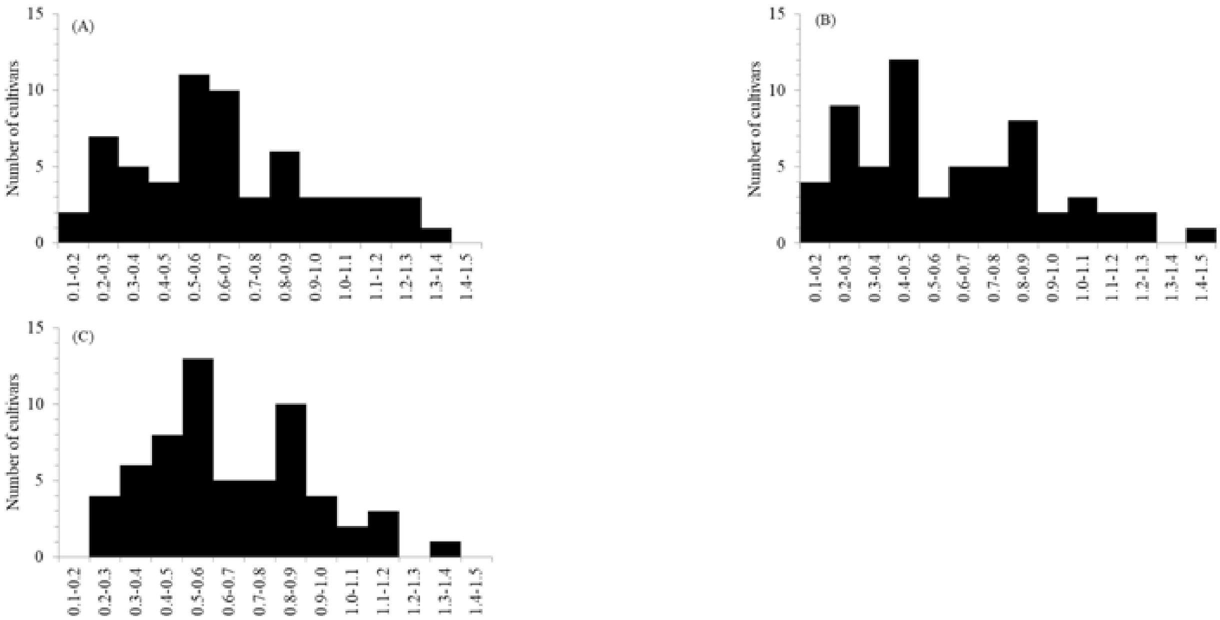

Fig. 1. Genotypic variation in the stress to control (S/C) ratio of total root number (A), total root length (B), and surface area (C) stress to control (S/C). The number of cultivars versus the S/C ratio is shown.

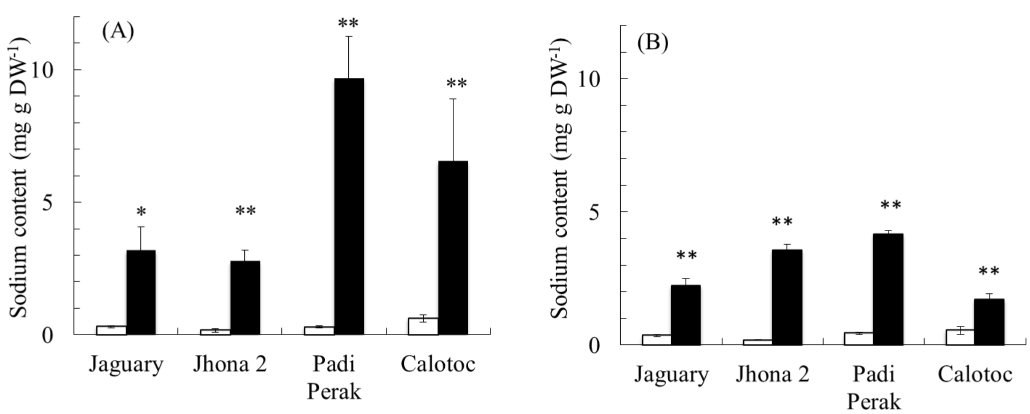

Fig. 2. Sodium content in shoot (A) and root (B) under salt stress (black bar) and non-stress conditions (white bar). Each value shows the mean ± standard error (n = 3). *, ** indicate significant differences between salt stress and non-stress conditions at $p < 0.05$ and $p < 0.01$.

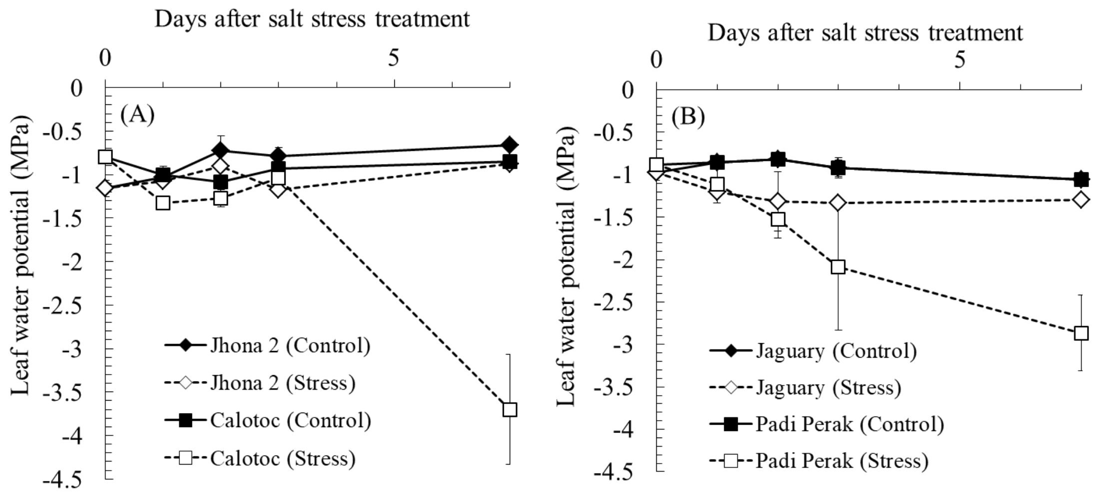

Fig. 3. Leaf water potential of Indica cultivars (A) and Japonica cultivars (B) under salt stress and non-stress conditions. Each value shows the mean ± standard error (n = 3).

4.2 Tables

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Table 1: Shoot and root dry weight and stress to control (S/C) ratios of 61 cultivars under salt stress and non-stress conditions.

		Shoot dry weight			Root dry weight (mg)		
Cultivar	Japonica/Indica	Control (mg)	Stress (mg)	S / C	Control (mg)	Stress (mg)	S / C
Jhona 2	Indica	74.90 ± 13.51	71.16 ± 10.33	0.950	19.74 ± 0.93	18.76 ± 0.61	0.950
Jaguary	Japonica	56.88 ± 2.21	50.05 ± 3.08	0.880	18.22 ± 2.93	16.03 ± 1.08	0.880
Nona Bokra	Indica	71.68 ± 3.60	62.36 ± 1.71	0.870	10.98 ± 0.46	8.89 ± 0.48	0.810
Khao Nok	Japonica	74.60 ± 17.67	62.66 ± 1.60	0.840	15.88 ± 1.66	13.34 ± 1.16	0.840
Tupa 121-3	Indica	56.86 ± 10.04	47.14 ± 1.01	0.829	28.42 ± 1.75	19.04 ± 0.67	0.670
Nepal 555	Indica	73.80 ± 17.70	60.03 ± 1.81	0.813	16.40 ± 0.38	11.64 ± 0.71	0.710
Jinguoyin	Indica	24.00 ± 8.91	19.50 ± 6.38	0.812	12.94 ± 1.14	6.08 ± 0.88	0.470
Vary Futsi	Indica	67.17 ± 8.70	53.63 ± 10.23	0.798	9.00 ± 0.51	7.65 ± 1.16	0.850
Azucena	Japonica	40.00 ± 7.92	31.67 ± 5.68	0.792	17.89 ± 2.72	10.02 ± 0.43	0.560
Ratul	Indica	63.83 ± 16.03	47.88 ± 1.53	0.750	11.28 ± 0.34	8.46 ± 0.90	0.750
Keikoba	Indica	52.00 ± 7.69	38.57 ± 8.86	0.742	10.76 ± 1.72	6.78 ± 1.46	0.630
Badari Dhan	Indica	70.20 ± 10.31	51.67 ± 1.16	0.736	11.82 ± 0.61	8.27 ± 0.59	0.700
ARC 7047	Indica	65.17 ± 9.60	46.67 ± 1.10	0.716	15.80 ± 1.08	11.85 ± 0.87	0.750
Khau Tan Chiem	Japonica	42.24 ± 6.83	30.00 ± 5.83	0.710	9.80 ± 0.43	7.64 ± 0.55	0.780
ARC 11094	Indica	40.20 ± 8.34	28.33 ± 6.83	0.705	14.60 ± 0.59	8.47 ± 0.61	0.580
ARC 7291	Indica	41.43 ± 11.17	29.08 ± 8.36	0.702	7.53 ± 0.30	5.35 ± 0.83	0.710
Urasan 1	Japonica	50.00 ± 12.03	32.50 ± 9.55	0.650	9.07 ± 0.66	5.89 ± 0.61	0.650
Rambhog	Indica	43.40 ± 2.04	28.20 ± 3.44	0.650	8.98 ± 1.20	6.10 ± 0.42	0.680
Dular	Indica	62.00 ± 11.56	38.86 ± 6.34	0.627	10.11 ± 6.03	4.35 ± 0.73	0.430
Kalo Dhan	Indica	29.57 ± 9.34	18.29 ± 1.09	0.618	11.31 ± 1.52	8.71 ± 0.74	0.770
CO 13	Indica	52.66 ± 7.24	32.08 ± 9.57	0.609	6.90 ± 1.26	1.86 ± 0.54	0.270
Khau Mac Kho	Japonica	53.00 ± 16.72	31.80 ± 12.45	0.600	12.10 ± 1.34	7.26 ± 1.08	0.600
Deng Pao Zhai	Indica	51.67 ± 7.85	29.71 ± 6.03	0.575	11.91 ± 1.02	5.24 ± 1.26	0.440
Hong Cheuh Zai	Indica	67.14 ± 9.01	38.57 ± 8.90	0.574	9.17 ± 0.95	7.43 ± 0.22	0.810
IRAT 109	Japonica	46.44 ± 2.39	26.00 ± 3.60	0.560	14.78 ± 0.78	6.35 ± 0.79	0.430
Neang Menh	Indica	50.50 ± 2.79	27.78 ± 3.76	0.550	8.89 ± 0.49	2.84 ± 0.99	0.320
Chin Galay	Indica	55.20 ± 0.49	30.20 ± 3.29	0.547	10.70 ± 1.00	5.35 ± 2.43	0.500
Dahonggu	Indica	35.80 ± 11.54	19.57 ± 5.93	0.547	13.64 ± 0.45	4.64 ± 0.30	0.340
Shwe Nang Gyi	Indica	45.50 ± 6.12	24.62 ± 8.34	0.541	8.78 ± 0.79	4.57 ± 0.53	0.520
Kaluheenati	Indica	74.33 ± 22.19	39.92 ± 2.01	0.537	25.37 ± 3.83	22.32 ± 2.58	0.880
Jena 035	Indica	43.52 ± 5.18	22.78 ± 2.64	0.523	11.08 ± 0.99	4.98 ± 1.09	0.450
Rexmont	Japonica	34.29 ± 7.17	17.83 ± 2.03	0.520	7.05 ± 0.98	3.67 ± 0.09	0.520
Anjana Dhan	Indica	27.29 ± 8.30	14.14 ± 1.12	0.518	14.27 ± 2.10	14.41 ± 1.07	1.010
Tupa 729	Japonica	47.21 ± 6.84	24.29 ± 4.23	0.514	7.50 ± 0.60	4.50 ± 0.61	0.600
ARC 5955	Indica	58.86 ± 11.33	30.00 ± 1.15	0.510	9.82 ± 1.09	10.02 ± 0.74	1.020
IR 28	Indica	30.44 ± 2.26	15.42 ± 1.91	0.507	5.68 ± 0.67	3.18 ± 0.67	0.560
Shoni	Indica	58.04 ± 15.63	29.02 ± 1.18	0.500	11.04 ± 1.75	5.52 ± 0.92	0.500
Deejiaohualuo	Indica	55.29 ± 9.21	27.14 ± 4.49	0.491	11.10 ± 0.84	5.44 ± 1.69	0.490
Hakphaynhay	Indica	29.98 ± 2.76	14.34 ± 1.17	0.478	13.88 ± 2.05	6.66 ± 0.91	0.480
Neang Phtong	Indica	49.40 ± 3.92	23.00 ± 2.83	0.466	12.90 ± 0.71	4.13 ± 0.14	0.320
Milyang 23	Indica	50.29 ± 5.79	22.86 ± 4.04	0.455	7.04 ± 0.61	3.17 ± 0.29	0.450
Muha	Indica	113.43 ± 11.57	51.29 ± 10.99	0.452	21.32 ± 2.38	11.94 ± 0.64	0.560
Basilanon	Indica	42.67 ± 12.23	19.24 ± 1.02	0.451	22.80 ± 0.47	18.70 ± 1.39	0.820
Lebed	Indica	67.88 ± 7.80	29.71 ± 7.40	0.438	12.96 ± 0.61	2.98 ± 0.37	0.230
Vandaran	Indica	80.57 ± 9.77	34.71 ± 5.68	0.431	11.01 ± 0.35	5.40 ± 0.71	0.490
Nipponbare	Japonica	40.20 ± 7.30	17.14 ± 6.54	0.426	11.55 ± 1.05	6.58 ± 0.41	0.570
Padi Perak	Japonica	44.08 ± 2.99	18.52 ± 1.00	0.420	14.20 ± 1.71	7.24 ± 0.66	0.510
Calotoc	Indica	64.14 ± 7.21	26.14 ± 6.26	0.408	15.90 ± 2.02	7.63 ± 1.34	0.480
Davao 1	Indica	51.63 ± 7.79	20.33 ± 6.00	0.394	7.43 ± 0.51	2.38 ± 0.93	0.320
Pinulupot 1	Indica	40.70 ± 8.39	16.01 ± 8.43	0.393	32.88 ± 2.40	13.15 ± 0.73	0.400
Qingyu(Seiyu)	Indica	67.20 ± 7.44	26.43 ± 9.73	0.393	14.12 ± 0.71	11.58 ± 0.96	0.820
Naba	Indica	21.58 ± 11.00	8.20 ± 5.87	0.380	8.28 ± 0.81	3.15 ± 0.67	0.380
Ma Sho	Japonica	49.50 ± 11.67	18.80 ± 1.00	0.380	12.38 ± 0.25	4.71 ± 1.16	0.380
Ryou Suisan Koumai	Indica	22.75 ± 7.24	7.91 ± 8.63	0.348	18.62 ± 4.36	12.29 ± 0.65	0.660
Surjamkhi	Indica	51.86 ± 10.79	18.00 ± 1.05	0.347	15.20 ± 0.58	8.66 ± 0.65	0.570
Nepal 8	Indica	22.86 ± 12.78	7.73 ± 6.33	0.338	19.03 ± 3.78	5.90 ± 0.69	0.310
Shuusoushu	Indica	31.40 ± 6.56	10.55 ± 8.79	0.336	13.12 ± 0.89	8.92 ± 0.63	0.680
IR 58	Indica	19.86 ± 8.89	5.76 ± 6.90	0.290	8.60 ± 0.47	2.49 ± 0.82	0.290
Asu	Indica	73.80 ± 5.88	21.29 ± 7.93	0.288	17.28 ± 1.70	15.89 ± 0.30	0.920
Tadukan	Indica	33.48 ± 4.83	6.57 ± 4.59	0.196	13.62 ± 0.96	7.08 ± 1.00	0.520
Kasalath	Indica	47.00 ± 6.90	2.00 ± 0.41	0.043	12.92 ± 1.32	4.13 ± 0.29	0.320

Each value shows the mean ± standard error (n = 5).

Table 2: Root morphological traits of tolerant and non-tolerant cultivars under salt stress and non-stress conditions.

	Total root length (cm)			Number of crown root			Number of L-type lateral root			Number of S-type lateral root		
Cultivars	Control	Stress	S / C	Control	Stress	S / C	Control	Stress	S / C	Control	Stress	S / C
Stress tolerant												
Jhona 2	428 ± 140	450 ± 20 ns	1.05	12.4 ± 0.4	12 ± 0.5 ns	0.97	4.7 ± 1.1	19.4 ± 1.4 *	4.08	1694 ± 410	1131 ± 81 ns	0.67
Jaguary	981 ± 78	1097 ± 59 ns	1.12	11.5 ± 0.9	9.5 ± 0.9 ns	0.83	73.0 ± 3.3	111.3 ± 9.9 *	1.52	3383 ± 154	3528 ± 313 ns	1.04
Non-stress tolerant												
Calotoc	418 ± 42	202 ± 29 **	0.48	9.4 ± 0.5	2.2 ± 0.2 **	0.23	14.2 ± 2.7	12.9 ± 1.8 ns	0.91	1570 ± 295	566 ± 78 *	0.36
Padi Perak	485 ± 64	149 ± 47 **	0.31	10 ± 0.7	3.3 ± 0.6 *	0.33	56.1 ± 5.1	41.9 ± 11.6 ns	0.75	1684 ± 152	801 ± 222 *	0.48

Each value shows the mean ± standard error (n = 5).

*, ** indicate significant differences between salt stress and non-stress conditions at $p < 0.05$ and $p < 0.01$. ns, non-significant differences.

Table 3: Yield and yield components of tolerant and non-tolerant cultivars under salt stress and non-stress conditions.

	Yield (g/plant)			Panicle number			Spikelet number per panicle			Fertility (%)			1000-grain weight (g)		
Cultivars	Control	Stress	S / C	Control	Stress	S / C	Control	Stress	S / C	Control	Stress	S / C	Control	Stress	S / C
Stress tolerant															
Jhona 2	69 ± 5.9	50 ± 3.6 ns	0.73	31 ± 4.1	28 ± 2.7 ns	0.92	104 ± 3.6	89 ± 3.9 **	0.85	88 ± 2.2	91 ± 2.1 ns	1.04	25 ± 1.2	22 ± 0.7 ns	0.89
Jaguary	35 ± 3.3	25 ± 2.5 ns	0.70	15 ± 1.9	15 ± 1.5 ns	1.00	83 ± 2.0	65 ± 2.5 **	0.78	77 ± 2.3	80 ± 1.9 ns	1.04	36 ± 0.9	31 ± 0.6 *	0.86
Non-stress tolerant															
Calotoc	59 ± 3.5	22 ± 3.8 *	0.37	16 ± 1.9	15 ± 1.3 ns	0.90	146 ± 5.1	117 ± 6.4 **	0.80	78 ± 1.7	55 ± 2.8 **	0.72	17 ± 0.1	13 ± 0.7 **:	0.76
Padi Perak	32 ± 4.2	12 ± 0.9 **	0.38	12 ± 1.7	12 ± 1.3 ns	1.03	192 ± 12.3	139 ± 9.6 **	0.72	88 ± 2.0	67 ± 2.2 **	0.76	23 ± 1.2	19 ± 0.6 *	0.81

Each value shows the mean ± standard error (n = 3).

*, ** indicate significant differences between salt stress and non-stress conditions at $p < 0.05$ and $p < 0.01$. ns, non-significant differences

5. CONCLUSION

In the present study, we identified differences among the 61 rice cultivars related to salt stress tolerance and selected two tolerant and two non-tolerant cultivars to investigate their root morphology and performance. The number of L-type lateral roots increased, especially in tolerant cultivars in the salt stress treatment. Additionally, the sodium content in the shoot of tolerant cultivars was lower than that of non-tolerant cultivars, and the leaf water potential of the former did not change in the salt stress treatment compared with the control. Salt stress did not affect the yield or fertility of tolerant cultivars, but significantly decreased those of non-tolerant cultivars. These results showed that the maintenance of water uptake by the growth of the root system, mainly of L-type lateral roots, and the inhibition of sodium accumulation in the shoot were important mechanisms of salt tolerance and reflected on the maintenance of yield under salt stress conditions. However, further studies are required to gain insights into the underlying physiological and molecular mechanisms of salt stress tolerance in rice.

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