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RESEARCH ARTICLE

Identification of Sri Lankan rice varieties having osmotic and ionic stress tolerance during the first phase of salinity stress

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Abstract: Salt tolerance of plants during the first phase of salt stress requires a combination of physiological traits conferring tolerance to both osmotic stress and ionic stress. Accordingly, the objectives of the present study were: (a) to screen a substantial number of varieties (102) from the Sri Lankan rice (*Oryza sativa*) germplasm and thereby identify varieties with osmotic and ionic tolerance during Phase I of salt stress development; and (b) to identify the physiological mechanisms that are responsible for osmotic and ionic tolerance. The 102 varieties tested included 51 traditional, 4 old-improved and 47 new-improved varieties, which were screened in nutrient solutions at 100 mM NaCl. Whole plant salt tolerance was quantified using relative leaf area (RL) and relative total dry weight (RW), i.e. leaf area and total dry weight at 100 mM Na^+ as ratios of their respective values at 1 mM Na^+, the unstressed control. Cluster analysis based on RL and RW enabled classification of Phase I salt tolerance of the screened varieties into five groups as, 'highly tolerant' (6 varieties), 'tolerant' (25), 'moderately tolerant' (32), 'susceptible' (30) and 'highly susceptible' (9). Capacity to maintain relatively high tissue water content, capacity for Na^+ exclusion at the root surface and root xylem and tissue tolerance to excess shoot Na^+ were identified as tolerance mechanisms of rice for salinity at Phase I. High shoot tolerance to Na^+ contributed to tolerance in 40 out of the 63 varieties identified as Phase I-tolerant to varying degrees. In comparison, high or medium capacity to maintain either whole plant or shoot relative water content contributed to tolerance in 48 varieties, while Na^+ exclusion at either of the two control points contributed to tolerance in 33 varieties. Based on the varietal phenotyping of the present study, suitable varieties can be selected: (a) for direct recommendation to areas of mild to transient salinity; (b) as parents in conventional breeding programmes to develop salt tolerant rice varieties; (c) for molecular biological studies to identify genes responsible for Phase I salt tolerance.

Keywords: Mechanisms of salt tolerance, Phase I salt tolerance, relative water content, salt-stress, sodium exclusion, tissue tolerance.

INTRODUCTION

Soil salinity, defined as the presence of excess salts in the soil solution in agricultural lands, is one of the major constraints to increase crop productivity throughout the world (Christiansen, 1982). Salinity is gradually spreading in the rice lands of Sri Lanka as well, both in the coastal regions and inlands (Sirisena & Herath, 2009). Spread of salinity has the potential to reduce national rice production significantly as rice is one of the most salt-sensitive crops (Maas & Hoffman, 1977; Munns & Tester, 2008). Agronomic measures such as improving field drainage, maintenance of 2 − 3 cm of standing water throughout the growing period, crop establishment by transplanting (Sirisena & Herath, 2009) and application of organic manure (Gamage *et al.*, 2009) can alleviate the adverse effects of soil salinity on the productivity of rice. However, identification of tolerant germplasm and breeding for salt-tolerance would be a better long-lasting solution to combat the growing threat of salinity. This is especially important for the Sri Lankan rice industry as national food security is intimately linked to the national rice production being able to keep abreast with the increasing population-driven demand. Therefore, identification of salt tolerant varieties with underlying tolerant mechanisms from the Sri Lankan rice germplasm with a view of using them in future breeding programmes is important.

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Blumwald and Grover (2006) identified two principal genetic approaches to the development of salt tolerant crop varieties: (a) exploitation of natural genetic variation within the germplasm of a crop species either through direct selection in saline environments or identification of quantitative trait loci (QTLs), which can subsequently be used with marker-assisted selection (Flowers *et al.*, 2000; Koyama *et al.*, 2001); (b) production of transgenic crop varieties by introducing new genes for salt tolerance or by altering the expression levels of existing genes (Borsani *et al.*, 2003; Munns, 2005; Blumwald & Grover, 2006). Both these genetic approaches require identification of salt tolerant genotypes/varieties within the germplasm of a given crop species. The Sri Lankan rice germplasm consists of more than 3000 accessions or varieties including about 2000 traditional types with too many repetitions and introductions from other countries with, close to 300 improved varieties that have been developed through plant breeding programmes initiated by the Sri Lankan Department of Agriculture from 1950s onwards, and about 800 unknown varieties (Dhanapala, 1996).

Development of salt tolerant varieties through conventional plant breeding would only require identification of relatively salt tolerant genotypes that can be used as parents in a breeding programme. However, molecular-based plant breeding requires not only identification of tolerant genotypes, but also elucidation of their mechanisms of tolerance, which could then lead to identification of genes responsible for those mechanisms. Finding new genes for salt tolerance requires precise phenotyping (Munns *et al.*, 2006), which means genotypes/varieties with demonstrated tolerance to salinity. The two-phase model as proposed by Munns (1993) and subsequently modified by Sümer *et al.* (2004) and Munns and Tester (2008), provides a physiological basis to identify salt tolerant varieties and their mechanisms of tolerance. This model, which has been validated through experimental data (Fortmeir & Schubert, 1995; Munns *et al.*, 1995), predicts that plants response to salt stress occurs in two distinct phases: (a) an initial phase (Phase I) of osmotic stress caused by reduced water uptake due to excess salts in the external soil solution, which is followed by; (b) the second phase (Phase II) of salt ion toxicity due to excess salts within the cells, tissues and organs. Accordingly, tolerance during Phase I of salt stress should include mechanisms to maintain tissue water status and thereby avoid the adverse effects of water stress on cellular processes and plant growth (i.e. osmotic tolerance). In contrast, tolerance in Phase II requires mechanisms to exclude excess salt ions from plant tissues, especially the young leaves and growing tissues (Flowers & Yeo, 1986; Munns, 2002; Tester & Davenport, 2003), mechanisms to sequester excess salts (Tester & Davenport, 2003) in the vacuole (Flowers & Yeo, 1988; Neumann, 1997; Munns *et al.*, 2006) or salt glands (Flowers *et al.*, 1990; Glenn *et al.*, 1999; Marcum, 1999) away from the cytoplasm where important physiological processes take place. Capacity for K^+/Na^+ discrimination and maintain ion homeostasis (i.e. maintenance of K^+:Na^+ ratio within favourable limits) (Jeschke, 1984; Gorham, 1993; Munns *et al.*, 2000; Koyama *et al.*, 2001) and increased tissue tolerance to excess salts are further mechanisms that may confer salt tolerance during Phase II (Cheeseman, 1988; Yeo *et al.*, 1990). While the initial two-phase model of Munns (1993) predicted only osmotic stress as induced by tissue water shortage to be present during Phase I, subsequent measurements (i.e. Sümer *et al.*, 2004) showed that salt ion toxicity could also be operating during Phase I, especially in salt-sensitive crops such as rice and maize.

Several mechanisms could contribute to confer tolerance to osmotic stress during Phase I. Capacity to maintain tissue water content thereby maintaining celluar turgor could prevent initial growth reductions caused by loss of turgor (Munns, 2002). Maintenance of tissue water status could also prevent abscisic acid (ABA)-induced longer term growth reductions (De Costa *et al.*, 2007). Salt-stress induced reductions in cellular growth have been shown to occur due to altered cell wall properties, namely, decreased cell wall extensibility (Cramer & Bowman, 1991; Neumann, 1993) and increased yield threshold (i.e. the minimum turgor pressure required for cell expansion) (Cramer & Bowman, 1991; Pritchard *et al.*, 1991). Therefore, the capacity to minimize the reduction of cell wall extensibility and the increase of yield threshold would minimize growth reduction during Phase I and thereby contribute to osmotic stress tolerance. As salt ion toxicity could also be operating during Phase I, mechanisms to tolerate ion toxicity such as salt exclusion, intracellular compartmentalization in the vacuole and increased tissue tolerance to excess salts would also contribute to Phase I salt tolerance (Tester & Davenport, 2003; Munns & Tester, 2008). Alternatively, atleast part of the excess salts that accumulate in tissues during Phase I could play a role in osmotic tolerance by contributing to turgor maintenance *via* osmotic adjustment (Greenway & Munns, 1980; Munns & Tester, 2008). Thus, the objectives of the present study were: (a) to screen a substantial number (at least 100) of varieties from the Sri Lankan rice germplasm and thereby identify varieties with osmotic and ionic tolerance during Phase I of salt stress development; and (b) to identify the physiological mechanisms that are responsible for osmotic and ionic tolerance.

METHODS AND MATERIALS

Varietal screening was carried out in ten rounds of experiments, each round using a different set of rice varieties (Table 1) over a period of 02 years from September 2007 – September 2009. In order to standardize varietal performance in different rounds, the known salt-tolerant variety At354 was used in every round as a standard check variety. Seeds were obtained from the Plant Genetic Resources Centre (PGRC) of the Department of Agriculture (DoA), Gannoruwa, Sri Lanka.

Plant material

Altogether 102 rice varieties were used in the varietal screening. These included three different types of varieties of varying maturity durations ranging from 2 ½ months to 5 – 6 months. The different types of varieties included 51 'traditional' varieties, 4 'old-improved' varieties and 47 'new-improved' varieties.

The 51 traditional varieties were selected from a germplasm collection of about 2000 traditional varieties that are maintained at the PGRC/

Table 1: Rice varieties used in the different rounds of varietal screening and their dates of planting and sampling.

Round	Date of planting (7-day old seedlings)	Date of Phase I sampling	Rice varieties screened
1	13.09.2007	03.10.2007	Bg750, At303, Bg94-1, Bg300, Bg304, At354†, Pokkali *(7 varieties)*
2	08.01.2008	28.01.2008	H4, Murungakayan 101, Pachchaperumal, Raththal, Nona Bokra, Pokkali, Dick Wee, Seeraga Samba, At354† *(7 varieties excluding At354 and Pokkali)*
3	22.04.2008	12.05.2008	Bg450, Bg380, Bg350, At353, Bw400, Ld66, Bg379-2, Bg352, Pokkali, At354† *(8 varieties excluding At354 and Pokkali)*
4	29.09.2008	19.10.2008	At401, H10, Bg407, Bw302, IR29, Bandara Haththewa, Periyakarappan, At354† *(7 varieties excluding At354)*
5	18.11.2008	08.12.2008	62-355, Bg34-8, Bg301, Bw272-6B, Bg276-5, Madathawalu, Dahanala, Kuruluthuda, Podi Wee A8, Bw78, Kalu Heenati (Warakapola), Kalu Heenati (PGRC), At354† *(12 varieties excluding At354)*
6	05.01.2009	25.01.2009	H7, Bg34-6, Bg357, Bg305, Bg250, Ld355, Ld356, At16, Bw351, Bg360, Bg359, Bw267-3, Bw266-7, At354† *(13 varieties excluding At354)*
7	02.04.2009	22.04.2009	Hetada Wee, Suwandel, Pola Al, Devaraddiri Weda Heenati, At86-1, At85-2, Bg745, Bg38, Bw452, At354† *(10 varieties excluding At354)*
8	19.04.2009	09.05.2009	Bw451, Bw453, Bg403, H9, At48-3, Bg400-1, MI273, Pokuru Samba, Beheth Heenati, Podi Niyan Wee, Goda Wee, At354† *(11 varieties excluding At354)*
9	16.07.2009	05.08.2009	Tetep, Sudu Bala Wee, Kahata Wee, Muthu Samba, Karayal, Hondarawalu 502, Mada Al (Kaluthara), Muhudu Kiriyal, Kalu Mudu Kiriyal, Kara Al, Mada Al, Moroberekan, Basmathie, Murunga, Kottiyaran, Kos Ata Wee, Keera Samba, Hathial, At354† *(18 varieties excluding At354)*
10	06.08.2009	26.08.2009	IR8, Heen Wee, Rathkarayal, Sinna Karuppan, Devaraddiri, Ptb16, Suduru Samba, Panduru Wee Kuru Wee, Kivul Handiran, At354† *(9 varieties excluding At354 and Devaraddiri)*
		Total	**102 varieties screened**

DoA, Gannoruwa, Sri Lanka. Those varieties, which gave indications of possible salt-tolerance based on information gained from traditional rice farmers and also the varietal names were selected. In addition, all traditional varieties that are currently being cultivated, eventhough in small extents by a limited number of farmers, were selected for screening. The traditional varieties are low-yielding (i.e. < 1 t ha^{-1}) and have a tall plant type with drooping leaves. Most of them are photoperiod-sensitive and almost all of them are susceptible to all major rice diseases present in Sri Lanka such as blast, bacterial leaf blight and sheath blight, while being less responsive to added inorganic nitrogen fertilizer (Abeysiriwardena, 2010).

The 'old-improved' varieties are a group of varieties, known in Sri Lanka as the 'H-series', that were developed in the 1950s and 1960s by improvement of the traditional varieties. The old-improved varieties also have a tall plant type with droopy leaves, but are moderately-resistant to the rice blast disease. They are less photoperiod-sensitive, more nitrogen-responsive and higher yielding (3 – 4 t ha^{-1}) than the traditional varieties.

The 'new-improved' varieties are the post-green revolution varieties that were developed during the period from late-1960s onwards. They are high-yielding (8 – 10 t ha^{-1} under optimum conditions), photoperiod-insensitive and have a dwarf plant type with comparatively more erect leaves. They are also highly responsive to added inorganic fertilizer and are resistant to major rice diseases such as rice blast and leaf blight. All the currently-recommended new-improved varieties were included in the present experiment.

Experimental location, plant culture and experimental treatments

All 10 rounds of experiments were conducted in a rain-sheltered, ventilated planthouse at the Agricultural Biotechnology Centre, University of Peradeniya, (latitude 7° 15' 47 N, longitude 80° 36' 10 E, altitude 496 m above sea level). Plants were grown hydroponically in aerated nutrient solutions (Yoshida *et al.*, 1972). In all 10 rounds of experiments, seed germination, preparation of nutrient solutions and seedling establishment and plant management were done using the protocol described in De Costa *et al.*(2012). Briefly, seeds were germinated with moist filter paper and transferred to ¼ strength nutrient solutions in 3 L pots 01 wk after germination. Strength of the nutrient solution was increased in 25 % steps up to full strength at 2 d intervals.

In each round, the experimental treatment structure was a two-factor factorial with rice varieties and salt treatments being the two treatment factors. There were two salt treatments as 1 mM NaCl (un-stressed control) and 100 mM NaCl (salt-stress). Previous work as reported by De Costa *et al*. (2012) showed 100 mM Na^+ to be the optimum level of salt stress for screening rice germplasm for salt tolerance during the two phases of salt stress development. The experimental design was a completely randomized design with two replications. Each replicate of each variety had 09 plants. Salt treatments started a week after giving the full strength nutrient solution. The control treatment was maintained at 1 mM NaCl throughout. The salt-stress treatment started at 25 mM NaCl and was increased up to a final concentration of 100 mM in 25 mM steps at 2 d intervals.

Measurements

All measurements were carried out 24 h after increasing the salt concentration up to 100 mM Na^+. This was 20 d after transferring the 7 d old seedlings to nutrient solutions. Therefore, plant sampling and measurements in all varieties fell within the vegetative phase of the rice plant (i.e. between germination and panicle initiation).

Plant growth: In order to ensure that plant growth is measured during Phase I of salt stress development, as determined by De Costa *et al.* (2012), growth was measured 24 h after increasing the salinity up to 100 mM NaCl. Areas of the youngest fully expanded leaf and the next expanding leaf on the main culm were measured non-destructively in the control and salt-stressed treatments. Leaf area was estimated as 0.5 (leaf length × leaf width). A destructive sample of three plants was taken from each pot and their fresh and dry weights were measured.

Relative water content (RWC): Relative water content of the whole plant (RWCpl) was measured as the ratio between the plant water content (i.e. the difference between whole plant fresh and dry weights) and the respective whole plant dry weight. Similarly, shoot (leaf + culm) relative water content (RWCsh) was calculated by dividing the shoot water content (i.e. the difference between shoot fresh and dry weights) by the respective shoot dry weight.

Na^+ concentration in shoot and root: During sampling, the youngest fully expanded leaf and the next expanding leaf of the main culm and the root system were separated, dried and ground into a powder for Na^+ analysis. Shoot Na^+ concentration was measured on the youngest fully

expanded leaf and the next expanding leaf of the main culm while root Na^+ concentration was measured taking the entire root system as the sample. Na^+ ion extraction was done according to the general method for plant samples as described by Van Ranst *et al.* (1999). Na^+ concentration was measured using the flame photometer.

Calculation of the degree of salt tolerance: The degree of salt-tolerance of a given variety during Phase I of salt-stress development was quantified in terms of relative leaf area (RL) and relative total dry weight (RW). RL of each variety was calculated as the ratio between the area of the two leaves measured (i.e. the youngest fully-expanded leaf and the next younger leaf) under salt-stress (LAs) and the respective areas of the two corresponding leaves in the control treatment (LAc) (equation 1). Similarly, RW was calculated as the ratio between the total plant dry weight under salt-stress (Ws) and the corresponding total plant dry weight in the control (Wc) (equation 2). Higher values of RL and RW in a given variety would indicate relatively greater salt-tolerance at Phase I.

$$\mathrm{RL} = \frac{\mathrm{LAs}}{\mathrm{LAc}} \qquad ...(1)$$

$$\mathrm{RW} = \frac{\mathrm{Ws}}{\mathrm{Wc}} \qquad ...(2)$$

In order to establish possible relationships with the degree of salt tolerance, relative RWCpl (RRWCpl) was also calculated as the ratio between the respective RWCpl values under salt-stress (RWCpls) and the corresponding RWC in the control (RWCplc) (equation 3).

$$\mathrm{RRWCpl} = \frac{\mathrm{RWCpls}}{\mathrm{RWCplc}} \qquad ...(3)$$

Similarly, relative RWCsh was calculated as the ratio between the respective RWCsh values under salt-stress (RWCshs) and the corresponding RWCsh in the control (RWCshc) (equation 4).

$$\mathrm{RRWCsh} = \frac{\mathrm{RWCshs}}{\mathrm{RWCshc}} \qquad ...(4)$$

Quantification of Na^+ exclusion from the shoot: Na^+ exclusion from the shoot can occur at two points in its pathway from the soil solution to the leaves of a plant (Schubert & Läuchli, 1986, 1990). Part of the excess Na^+ in the external medium can be excluded at the root surface and thereby can be prevented from entering the root. Therefore, root Na^+ concentration (RtNa) in the salt-stressed treatment is a measurement of the degree of Na^+ exclusion at the root surface. In addition, Na^+ that has already entered the root can be prevented from reaching the shoot by being excluded from the root xylem at the xylem parenchyma. Accordingly, the ratio between shoot and root Na^+ (ShNa:RtNa) would constitute a measurement of the degree of Na^+ exclusion from the shoot at the root xylem parenchyma. ShNa:RtNa was calculated as,

$$\mathrm{ShNa} : \mathrm{RtNa} = \frac{\mathrm{ShNa}}{\mathrm{RtNa}} \qquad ...(5)$$

A higher ShNa:RtNa ratio would indicate a lower degree of Na^+ exclusion at the root xylem parenchyma and *vice versa*.

Pooling of growth data from different rounds of experimentation: Although all experimental rounds were conducted within a rain-sheltered planthouse at the same location, the meteorological conditions, in terms of maximum and minimum temperatures, solar radiation and pan evaporation rate, that were prevailing during different rounds of experimentation showed a certain degree of variation (reported later in the present paper). Therefore, there was a need to standardize the calculated *RL* and *RW* values before the data from different rounds of experimentation could be pooled and compared. Accordingly, all values of RL and RW of each variety were standardized by the corresponding values of At354 in the respective rounds. Therefore, the respective standardized relative growth parameters, RLst and RWst of a given variety, *i*, were calculated as follows (non-existence of variety x meteorological condition interaction effect was assumed);

$$\mathrm{RLst} = \frac{\mathrm{RL(i)}}{\mathrm{RL(At354)}} \qquad ...(6)$$

$$\mathrm{RWst} = \frac{\mathrm{RW(i)}}{\mathrm{RW(At354)}} \qquad ...(7)$$

The standardized relative growth parameters, as calculated by equations 5 and 6, of all varieties tested over 10 rounds of experimentation were pooled to be used in the data analyses for varietal classification based on salt-tolerance.

In contrast to growth measurements, which were highly influenced by the prevailing environmental conditions in the different rounds of experimentation,

relative RWC and shoot and root Na^+ concentration data were largely determined by the respective salt concentrations in the two experimental treatments (i.e. 1 and 100 mM Na^+), which did not vary between different rounds of experimentation. Therefore, there was no need to standardize the relative RWC and Na^+ concentration values in different rounds of experimentation. If at all, variations in environmental conditions would have only a minor influence on these two variables.

Data analysis

Analysis of variance: The variety, salt treatment and variety x salt treatment interaction effect on standardized relative growth parameters, relative water content and shoot and root Na^+ concentrations were tested for significance by analysis of variance (ANOVA). Means were separated using the Duncan's Multiple Range Test.

Cluster analysis: The primary objective of the present study was to classify the rice varieties that were screened into distinctly different groups based on their degree of salt-tolerance during Phase I of salt-stress development. This classification had to be done based on more than one measure of relative salt-tolerance such as the standardized relative leaf area (RLst) and standardized relative total dry weight (RWst). Cluster analysis (SAS Institute, 2008) was used for this purpose. Thus, 'Proc Cluster' procedure of the statistical software SAS (Version 8e) was used with 'method = complete' using RLst and RWst as the variables for clustering. Multivariate analysis of variance (MANOVA) was used to determine whether different clusters were significantly different based on the four multivariate test statistics (i.e. Wilks' Lambda, Pillai's Trace, Hotelling-Lawley Trace and Roy's Greatest Root) that are calculated by SAS.

Percentile points in the frequency distributions: In order to classify the varieties based on the magnitudes of their relative water content and root and shoot Na^+ concentrations, percentile points of frequency distributions of varietal means of RWCpl, RWCsh, RRWCpl, RRWCsh, ShNa, RtNa and ShNa:RtNa ratio were obtained using the SAS procedure 'Proc Means'.

RESULTS

Meteorological conditions during the different experimental rounds

Average meteorological conditions that prevailed during the 10 rounds of varietal screening are shown in Table 2. All temperatures (i.e. maximum, minimum and mean) remained within a range of 2 ^oC in all 10 rounds of the experimentation. Mean RH showed a wider range of variation from 66 % in round 6 to 80 % in round 1. With the exception of round 6, mean sunshine duration varied by about 1 hour among the rest of the experimental rounds. Pan evaporation rate, which reflects the net effect of temperature, RH and sunshine duration varied from 2.61 mm d^{-1} in round 4 to 4.70 mm d^{-1} in round 2. Number of days after transplanting at which 50 % tip burn of the youngest fully-expanded leaf was observed in the variety At354 (T_{50}) varied appreciably, between 45 days in round 3 and 63 days in round 8. The variation in meteorological conditions during the different rounds of experimentation could have influenced T_{50}, which can be considered as an index of the rate of salt-stress development. However, the absence of any significant correlations between T_{50} and any of the meteorological variables (data not shown) indicate that the influence of meteorological conditions on varietal response to salinity in different rounds was not systematic.

Plant growth during Phase I of salt-stress development

Leaf area

When the data obtained during Phase I (i.e. 24 hours after increasing salt stress up to 100 mM Na^+) from all 10 rounds of experimentation were analyzed, area of the two measured leaves showed highly significant ($p < 0.0001$) variation between varieties under both salt-stress and control treatments within each round (Table 3). The significant varietal variation of leaf area in the non-stressed control treatment (LAc) reflected the inherent variation in growth capacity of the tested varieties under optimum growing conditions (i.e. with adequate nutrients, but without excessive salts). On the other hand, the significant varietal variation of leaf area in the salt-stressed treatment (LAs) was caused by a combination of the varietal variation in salt-tolerance and the inherent varietal variation in growth capacity. Most of the varieties that showed high LAs were traditional and old-improved varieties, with *Nona Bokra*, *Seeraga Samba*, *Dick Wee* and H4 showing the highest values. Among the new-improved varieties, At401, Bw452, At48-3 and At86-1 had higher LAs. When the data under stressed conditions for all varieties were adjusted using the control, the relative leaf area (RL) also showed highly significant ($p < 0.0001$) variation between varieties (Table 3). RL of the standard check variety, At354, varied from 0.69 (in round 1) to 0.90 (in round 6) (Figure 1.a). This variation of RL was found to be statistically significant at $p < 0.05$

Table 2: Mean values* of major meteorological variables during different rounds of experimentation

Exp. round	Temperature† Max. T (°C)	Min. T (°C)	Mean T (°C)	Mean RH (%)††	Sunshine duration (Hrs)	Pan Evap.‡ (mm d^{-1})	T_{50} of At354‡‡
1	29.42	20.67	25.05	80.11	4.93	2.53	49
2	30.10	19.77	24.93	71.94	6.31	4.70	46
3	30.18	21.90	26.04	75.70	6.51	3.23	45
4	30.07	20.23	25.15	76.58	5.30	2.61	59
5	29.19	19.84	24.52	71.75	6.02	3.45	54
6	31.13	18.64	24.89	66.13	7.87	4.43	60
7	30.53	21.96	26.25	78.15	5.88	3.20	60
8	30.16	22.08	26.12	77.92	5.84	3.19	63
9	29.45	21.51	25.48	78.32	5.55	2.93	58
10	29.83	21.09	25.46	77.35	5.98	3.10	62

* - Each variable was averaged over the entire duration of the experiment (i.e. from transplanting until final Phase II sampling).

† - Max. T – Maximum temperature; Min. T – Minimum temperature; Mean T – Mean temperature; ††Mean RH – Mean relative humidity; ‡Pan Evap. – Pan evaporation rate;

‡‡T_{50} – Number of days after transplanting at which 50 % tip burn of the youngest fully-expanded leaf was observed in the variety At354.

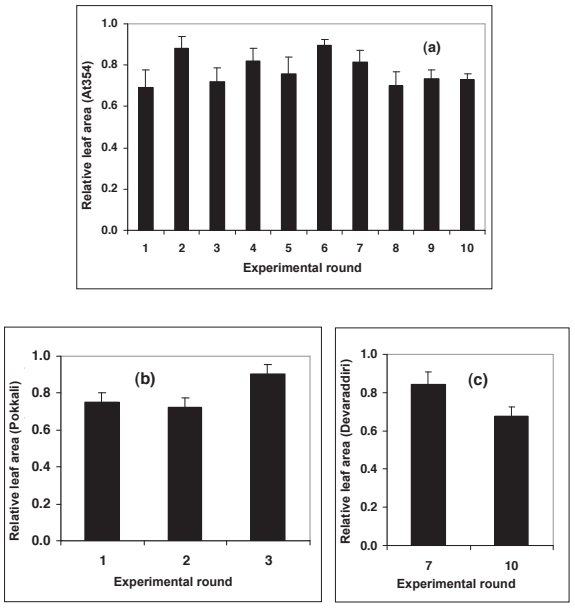

Figure 1: Variation of mean relative area of two selected leaves (i.e. the youngest fully-expanded and the next younger leaf) of rice varieties, At354 (a), Pokkali (b) and Devaraddiri (c), in the different rounds of experimentation. Each value is the mean of 12 replicate measurements.

based on the confidence limits in each round. Running an ANOVA on pooled data of At354 over different rounds was not allowed due to error heterogeneity among rounds. This was primarily due to the high coefficient of variation (CV = 27 %), which indicated the high within round variation of RL. Further analysis showed that mean leaf area of At354 in both the non-stressed control (LAc) and the salt-stressed treatment (LAs) showed a significant ($p < 0.05$) variation between different rounds of experimentation (data not shown). Furthermore, the two other varieties, which were grown in more than one experimental round (Table 1), i.e. *Pokkali* (in rounds 1, 2 and 3) and *Devaraddiri* (in rounds 7 and 10), also showed significant ($p < 0.05$) variation in their respective RL between different rounds of experimentation (Figures 1.b and c). *Pokkali* and *Devaraddiri* also showed a highly significant ($p < 0.0001$) variation in their LAc and LAs between different rounds (data not shown). Therefore, despite the absence of significance between-round variation of RL of At354, the RL values of all 102 varieties of the 10 different rounds of experimentation were standardized with the RL of At354 in the respective round.

Variation of the mean standardized relative leaf area (RLst) for the entire set of varieties screened is presented in Table 4. Altogether 38 varieties had RLst values,

Table 3: Variation of mean area of two selected leaves (i.e. the youngest fully-expanded and the next younger leaf) and mean total plant dry weight and their relative values with standard errors of different rice varieties under unstressed, control (1 mM Na^+) and salt-stressed (100 mM Na^+) conditions during Phase I of salt-stress development in different rounds of experimentation.

Variety	Leaf area (cm^2)				Relative leaf area (RL)		Total plant dry weight (g pl^{-1})				Relative total plant dry weight (RW)	
	Stressed		Control				Stressed		Control			
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Round 1												
At354	7.12	0.79	10.68	0.59	0.69	0.09	219	8	307	29	0.72	0.04
Pokkali	11.27	0.89	11.98	0.65	0.75	0.05	307	38	326	67	0.96	0.08
At303	9.17	0.95	10.75	0.84	0.75	0.11	307	28	280	9	1.09	0.07
Bg300	3.80	0.35	5.11	0.72	0.53	0.04	73	6	84	33	0.57	n.a.
Bg304	3.90	0.46	9.60	0.86	0.41	0.07	87	7	228	33	0.39	0.09
Bg750	10.53	0.90	11.25	1.65	0.68	0.09	249	21	279	30	0.91	0.17
Bg94-1	8.39	0.50	8.52	0.95	0.78	0.09	260	100	226	94	0.50	n.a.
Round 2												
At354	19.09	2.29	17.75	2.01	0.88	0.06	468	91	547	94	0.91	0.16
Pokkali	27.61	3.01	26.14	2.41	0.72	0.05	551	50	586	86	0.75	n.a.
Dick Wee	27.24	3.51	26.83	3.90	0.82	0.10	405	116	378	5	0.78	n.a.
H4	26.69	2.47	34.00	4.42	0.84	0.05	326	11	395	5	0.82	0.02
Murungakayan	23.05	2.04	21.37	2.82	0.83	0.08	316	71	415	52	0.80	0.27
Nona Bokra	30.99	3.42	34.15	4.50	0.94	0.05	436	47	355	9	1.12	n.a.
Pachchaperumal	23.76	2.62	31.60	4.01	0.66	0.06	390	24	647	44	0.60	0.00
Raththal	16.67	2.00	18.21	1.71	0.78	0.08	98	14	115	36	0.55	n.a.
Seeraga Samba	28.87	3.88	28.34	2.68	0.89	0.06	266	37	323	0	0.82	0.11
Round 3												
At354	13.52	1.03	19.57	1.35	0.72	0.07	509	143	678	81	0.79	0.30
Pokkali	19.69	1.37	21.42	1.40	0.90	0.05	668	98	644	105	1.05	0.03
At353	12.99	1.30	17.51	0.84	0.72	0.09	489	64	648	70	0.75	0.02
Bg350	10.39	1.07	13.15	0.83	0.77	0.09	437	39	408	30	1.07	0.02
Bg352	11.61	1.20	18.12	1.04	0.64	0.06	524	93	509	87	1.00	0.11
Bg379-2	7.71	0.74	10.12	0.73	0.70	0.07	262	64	334	14	0.79	0.22
Bg450	10.86	0.40	10.32	0.84	0.92	0.04	435	56	386	74	1.07	n.a.
Bw400	13.07	1.30	19.30	1.05	0.70	0.07	467	173	665	29	0.69	0.23
Bg380	14.81	1.51	16.98	1.01	0.67	0.08	632	143	671	67	0.93	0.12
Ld66	13.80	0.98	15.16	1.45	0.72	0.04	448	55	472	152	0.63	n.a.
Round 4												
At354	13.62	1.06	15.72	0.68	0.82	0.06	401	40	325	38	1.24	0.02
At401	18.93	0.83	18.66	0.83	0.94	0.06	514	4	622	81	0.84	0.11
Bg407	10.20	0.87	11.23	1.08	0.79	0.09	422	87	409	146	1.10	0.18
Bw302	13.53	1.12	11.82	1.02	0.79	0.09	592	91	411	6	1.24	n.a.
Bandara H	14.77	1.99	23.17	1.53	0.62	0.09	509	87	656	60	0.77	0.06
H10	18.59	1.48	21.49	1.40	0.76	0.07	520	26	668	28	0.78	0.01
IR29	9.89	0.92	11.10	0.86	0.80	0.10	291	32	359	83	0.83	0.10
Periyakarappan	21.49	2.04	27.67	1.34	0.73	0.06	688	145	964	16	0.71	0.14
Round 5												
At354	11.43	0.89	15.03	1.21	0.76	0.08	327	11	403	117	0.89	0.29
62-355	17.08	0.91	19.30	1.20	0.88	0.05	481	70	554	38	0.88	0.19
Bg276-5	9.58	0.80	14.81	1.18	0.68	0.06	244	62	313	69	0.77	0.03
Bg301	10.76	1.42	13.24	1.23	0.68	0.10	250	52	249	27	1.00	0.10
Bg34-8	11.30	1.21	11.88	1.04	0.85	0.04	263	95	222	54	1.00	n.a.
Bw272-6B	9.53	0.91	11.46	1.07	0.84	0.05	214	1	209	25	1.04	0.12
Bw78	4.08	0.45	8.50	0.86	0.53	0.08	80	9	162	2	0.49	0.05
Dahanala	11.60	0.50	12.86	1.39	0.82	0.05	278	12	287	46	0.80	n.a.

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Variety	Leaf area (cm^2)				Relative leaf area (RL)		Total plant dry weight (g pl^{-1})				Relative total plant dry weight (RW)	
	Stressed		Control				Stressed		Control			
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Kalu Heenati (W)	5.83	0.52	12.86	1.06	0.46	0.03	127	3	255	13	0.50	0.04
Kuruluthuda	13.25	1.53	8.94	1.60	0.85	0.10	350	84	189	56	1.09	n.a.
Madathawalu	10.42	0.50	21.09	1.63	0.52	0.04	217	18	555	87	0.41	0.10
Podi Wee A8	7.76	0.52	7.93	0.72	0.76	0.07	232	14	171	16	1.16	n.a.
Kalu Heenati (P)	13.00	0.70	18.71	1.56	0.70	0.06	310	4	431	147	0.81	0.27
Round 6												
At354	13.82	0.37	14.65	0.67	0.90	0.03	811	76	678	157	0.88	n.a.
At16	11.18	0.48	14.92	0.89	0.76	0.03	359	94	550	42	0.64	0.12
Bg250	15.44	0.68	19.33	1.39	0.86	0.06	678	11	803	n.a.	0.83	n.a.
Bg305	14.22	0.71	18.34	1.20	0.79	0.04	695	83	1006	82	0.72	0.12
Bg34-6	9.84	1.10	14.43	0.98	0.68	0.06	430	140	763	46	0.58	0.22
Bg357	12.82	0.47	13.66	0.69	0.88	0.05	724	1	851	111	0.87	0.11
Bg359	7.48	0.72	14.13	0.88	0.55	0.06	366	157	634	54	0.60	0.30
Bw266-7	10.21	0.60	14.38	0.71	0.72	0.05	498	19	636	116	0.81	0.18
Bw267-3	9.73	0.32	11.40	0.77	0.86	0.04	525	24	527	99	1.02	0.15
BW351	11.06	0.53	12.49	0.75	0.81	0.06	446	137	621	13	0.72	0.24
Bg360	9.02	0.17	8.53	0.61	0.90	0.04	328	64	527	n.a.	0.74	n.a.
H7	10.87	0.92	10.83	1.37	0.92	0.02	370	n.a.	450	n.a.	0.82	n.a.
Ld355	7.92	0.46	10.51	0.57	0.76	0.03	343	77	509	35	0.69	0.20
Ld356	11.24	0.82	15.14	1.07	0.77	0.06	469	10	714	54	0.66	0.06
Round 7												
At354	14.82	1.20	18.29	1.07	0.82	0.06	463	150	565	97	0.80	0.13
At85-2	10.84	1.39	19.76	1.83	0.46	0.05	346	15	871	150	0.47	0.17
At86-1	16.25	0.92	21.66	1.14	0.73	0.06	654	13	1075	104	0.63	0.13
Bg38	11.67	1.56	14.79	1.42	0.75	0.13	317	n.a.	331	n.a.	0.96	n.a.
Bg745	8.33	0.68	10.98	3.07	0.73	0.14	202	33	292	n.a.	0.58	n.a.
Bw452	16.85	1.51	19.17	1.78	0.84	0.06	555	58	690	17	0.80	0.06
Hetada Wee	24.93	2.01	27.17	1.62	0.90	0.06	748	130	678	73	1.09	0.07
Pola Al	13.71	1.71	11.51	1.36	0.86	0.12	386	n.a.	223	86	1.25	n.a.
Suwandel	16.29	1.59	26.29	2.26	0.65	0.07	660	159	694	76	0.94	0.13
Weda Heenati	10.50	1.00	13.59	1.19	0.65	0.10	253	46	267	66	0.62	n.a.
Devaraddiri	27.42	1.25	33.19	2.57	0.84	0.06	773	25	683	18	1.13	0.01
Round 8												
At354	18.03	1.69	26.73	2.03	0.70	0.07	543	0	752	23	0.74	0.00
At48-3	16.62	2.43	23.69	2.12	0.72	0.08	472	33	567	123	0.89	0.25
Bg400-1	8.41	0.73	11.34	1.44	0.79	0.08	163	2	189	30	0.89	0.13
Bg403	14.97	1.37	17.01	1.83	0.77	0.08	516	203	607	158	0.41	n.a.
Bw451	8.14	0.93	16.07	2.08	0.46	0.06	131	n.a.	412	12	0.31	n.a.
Bw453	14.65	1.37	25.60	1.18	0.57	0.05	372	130	729	149	0.50	0.08
Beheth Heenati	10.99	1.09	19.06	1.68	0.58	0.05	286	21	412	105	0.73	0.14
Goda Wee	16.07	1.14	19.93	1.75	0.71	0.05	415	40	453	74	0.96	0.24
H9	13.22	1.54	19.05	0.92	0.70	0.08	356	27	339	10	1.05	0.11
MI273	15.66	1.57	23.92	1.95	0.69	0.07	408	40	567	131	0.78	0.25
Podi Niyan Wee	17.10	0.92	18.36	2.05	0.69	0.07	416	64	314	48	0.97	n.a.
Pokuru Samba	12.01	1.71	15.56	1.77	0.69	0.11	353	156	286	31	0.77	n.a.
Round 9												
At354	16.60	1.14	13.06	0.88	0.73	0.04	223	16	231	12	0.97	0.12
Basmathi	5.89	0.99	7.86	2.23	0.31	0.07	161	69	85	.	1.08	n.a.
Hathial	16.99	1.87	21.99	1.68	0.78	0.10	379	32	355	41	1.07	0.04

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Variety	Leaf area (cm^2)				Relative leaf area (RL)		Total plant dry weight (g pl^{-1})				Relative total plant dry weight (RW)	
	Stressed		Control				Stressed		Control			
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Hondarawalu	7.47	0.99	12.38	1.24	0.64	0.11	159	8	202	53	0.85	0.26
Kahata Wee	7.70	0.88	10.51	1.28	0.71	0.08	153	13	158	4	0.97	0.06
Kalu Mudu Kiriyal	9.65	1.06	7.01	1.07	0.77	0.08	205	52	138	66	0.75	n.a.
Kara Al	8.29	0.66	10.19	1.40	0.67	0.13	142	0	283	10	0.50	0.02
Karayal	9.76	0.74	11.96	0.87	0.78	0.06	165	39	199	12	0.82	0.15
Keera Samba	7.26	0.69	8.31	0.80	0.80	0.08	140	20	131	12	0.85	n.a.
Kos Ata Wee	5.18	0.57	6.46	0.59	0.62	0.07	85	9	91	4	0.94	0.14
Kottiyaran	11.27	0.63	7.65	1.01	1.13	0.00	185	23	94	n.a.	n.a.	n.a.
Mada Al (Kaluthara)	4.83	0.76	8.67	1.31	0.39	0.09	92	24	109	36	0.47	n.a.
Mada Al	8.67	0.90	5.92	0.90	0.65	0.11	153	0	80	50	1.17	n.a.
Moroberekan	5.90	0.61	7.14	0.90	0.59	0.07	97	7	136	7	0.72	0.02
Muhudu Kiriyal	9.52	0.49	10.82	1.13	0.86	0.07	186	14	199	70	0.64	n.a.
Murunga	5.33	0.51	7.27	0.78	0.75	0.08	106	4	123	73	0.56	n.a.
Muthu Samba	7.90	0.46	7.08	0.93	0.80	0.07	122	16	102	30	1.05	n.a.
Sudu Bala Wee	10.32	0.89	10.60	1.24	0.80	0.11	288	87	162	22	0.88	n.a.
Tetep	10.05	0.43	10.20	0.86	0.90	0.06	225	20	237	35	0.96	0.06
Round 10												
At354	12.40	0.88	16.83	0.93	0.73	0.03	340	47	424	22	0.80	0.07
Heen Wee	11.82	0.51	14.35	1.36	0.83	0.06	268	39	279	52	0.97	0.04
IR8	9.57	1.53	14.19	1.52	0.43	0.09	231	100	321	62	0.27	n.a.
Kivul Handiran	13.36	0.76	18.42	1.00	0.75	0.06	310	9	412	57	0.77	0.13
Kuru Wee	5.50	0.70	9.56	0.91	0.58	0.06	115	27	174	49	0.67	0.03
Panduru Wee	15.01	1.75	15.90	1.99	0.73	0.02	353	n.a.	256	n.a.	n.a.	n.a.
Ptb16	11.04	1.84	13.38	1.47	0.67	0.11	217	n.a.	205	48	0.86	n.a.
Rathkarayal	5.25	0.75	10.09	1.20	0.49	0.07	116	n.a.	187	1	0.62	n.a.
Sinna Karuppan	16.23	0.92	24.61	1.56	0.68	0.05	328	17	722	59	0.47	0.10
Suduru Samba	9.21	1.65	15.10	1.47	0.64	0.09	142	n.a.	246	8	0.56	n.a.
Devaraddiri	11.61	1.17	15.17	1.08	0.68	0.04	287	71	353	1	0.81	0.20

Note: Stressed - 100 mM Na^+; Control - 1 mM Na^+; SE – Standard error of mean. Leaf area and total plant dry weight values are means of 12 and 6 replicate measurements, respectively. RL and RW are means of 2 replicate measurements. n.a. – SE is not available because only 1 replicate measurement was available.

which were greater than 1, showing that they had RL values, which were greater than the RL of At354. This indicated that leaf area growth of these varieties had a higher degree of tolerance to osmotic stress, which is the principal stress during Phase I of salt-stress development. The traditional rice variety, *Kottiyaran*, showed a substantially higher RLst than all other varieties, from which Bg450 and Tetep also showed RLst values greater than 1.2. Out of the 38 varieties, which had RLst > 1, there were 21 traditional varieties (out of the 51 tested), 2 old-improved varieties (out of 4) and 15 new-improved varieties (out of 47).

Total dry weight per plant

When the data obtained at Phase I from all 10 rounds of experimentation were analyzed within a round, the total plant dry weight showed a highly significant ($p < 0.0001$) variation between varieties under both salt-stress and control treatments within each round (Table 3). A higher total plant dry weight under salt-stress (Ws), indicates a combination of salt-tolerance and inherent genetic capacity for higher biomass growth. The varieties that had the highest Ws were *Hetada Wee*, Bg357, Bg305, *Periyakarappan*, Bg250, *Suwandel* and At86-1, which showed an approximately equal distribution between traditional and new-improved varieties. When the data for all varieties were pooled, the relative total dry weight (RW) also showed highly significant ($p < 0.01$) variation between varieties (Table 3). Similar to RL, RW of At354 also varied substantially between different experimental rounds from 0.72 in round 1 to 1.24 in

round 4 (Figure 2.a). This variation was found to be statistically significant at $p < 0.05$, based on confidence limits in each round. Running an ANOVA on pooled data of At354 over different rounds was not allowed due to error heterogeneity among rounds. Notably, *Pokkali* and *Devaraddiri*, the two other varieties, which were tested in more than one experimental round, showed significant ($p < 0.05$) between-round variation in RW (Figures 2.b and c). Furthermore, total plant dry weights of all three varieties showed a significant ($p < 0.05$) variation between different experimental rounds under both un-stressed and salt-stressed conditions (data not shown). Therefore, RW of the different rounds was standardized with the respective RW of At354 in each round.

Variation of the mean standardized relative total dry weight (RWst) for the entire set of varieties screened is presented in Table 4. Altogether 34 varieties had RWst values, which were greater than 1, showing that they had RW values, which were greater than the RW of At354. This indicated that the biomass growth of these varieties had a higher degree of tolerance to osmotic stress, which is the principal stress during Phase I of salt-stress development. The traditional rice variety, Pola Al, and the new-improved variety, At303, showed substantially

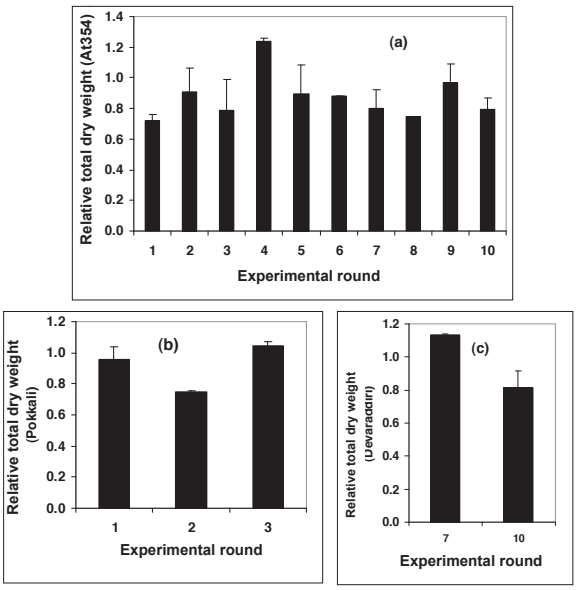

Figure 2: Variation of mean total plant dry weight of rice varieties, At354 (a), Pokkali (b) and Devaraddiri (c), in the different rounds of experimentation. Each value is the mean of 2 replicate measurements.

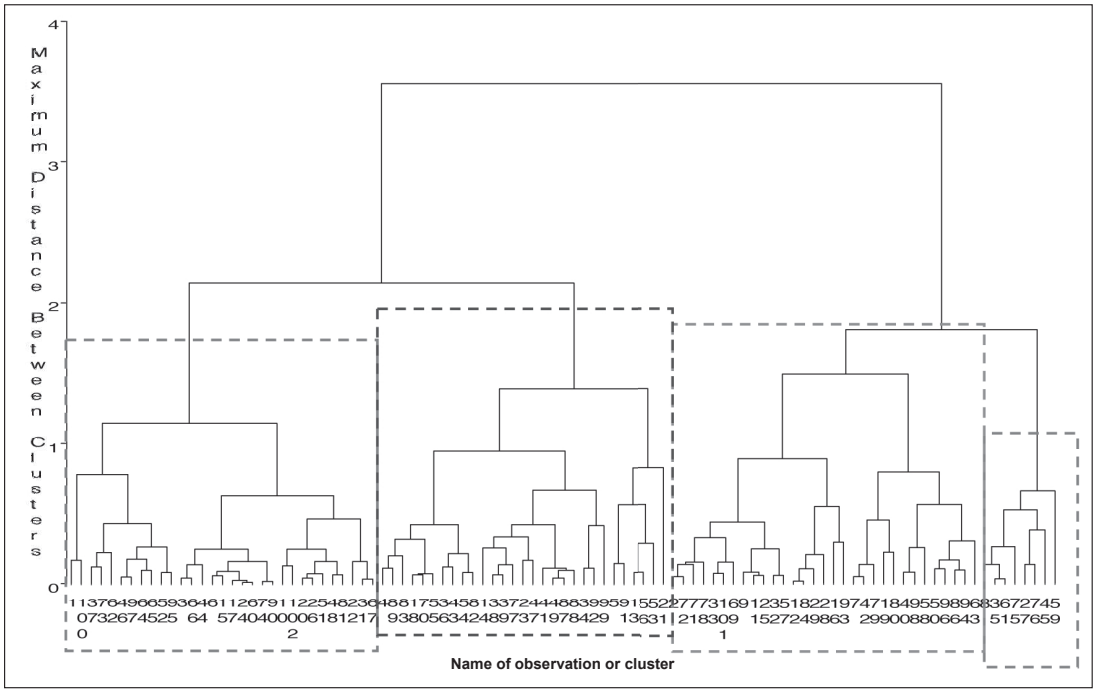

Figure 3: Dendogram of cluster analysis based on standardized relative total dry weight and standardized relative leaf area at Phase I of salt-stress development. Numbers, which should be read vertically, indicate different rice varieties (as given in Table 4) and squares identify the main clusters.

Table 4: Identified main and sub-clusters of varieties and their level of tolerance to salinity based on standardized relative growth performance during Phase I of salt-stress development

Var. No.†	Variety	Main cluster	Sub-cluster	Growth performance		Category of tolerance level
				RLst‡	RWst‡‡	
1	62-355	1	1	1.161	0.984	Moderately Tolerant Gr. 1
37	Bg360	1	1	1.001	0.845	Moderately Tolerant Gr. 1
46	Dahanala	1	1	1.084	0.891	Moderately Tolerant Gr. 1
52	H7	1	1	1.021	0.933	Moderately Tolerant Gr. 1
62	Kalu Mudu Kiriyal	1	1	1.046	0.775	Moderately Tolerant Gr. 1
64	Karayal	1	1	1.068	0.848	Moderately Tolerant Gr. 1
65	Keera Samba	1	1	1.093	0.873	Moderately Tolerant Gr. 1
73	Ld66	1	1	1.007	0.801	Moderately Tolerant Gr. 1
95	Seeraga Samba	1	1	1.013	0.904	Moderately Tolerant Gr. 1
97	Sudu Bala Wee	1	1	1.090	0.910	Moderately Tolerant Gr. 1
100	Tetep	1	1	1.224	0.990	Moderately Tolerant Gr. 1
3	At353	1	2	1.005	0.957	Moderately Tolerant Gr. 2
6	At354	1	2	1.000	1.000	Moderately Tolerant Gr. 2
10	Bg250	1	2	0.955	0.944	Moderately Tolerant Gr. 2
15	Bg357	1	2	0.985	0.984	Moderately Tolerant Gr. 2
17	Bg379-2	1	2	0.969	1.007	Moderately Tolerant Gr. 2
20	Bg407	1	2	0.958	0.887	Moderately Tolerant Gr. 2
22	Bw266-7	1	2	0.808	0.925	Moderately Tolerant Gr. 2
24	Bw302	1	2	0.966	0.999	Moderately Tolerant Gr. 2
26	Bw400	1	2	0.971	0.879	Moderately Tolerant Gr. 2
31	Beheth Heenati	1	2	0.832	0.979	Moderately Tolerant Gr. 2
44	Bw452	1	2	1.024	1.006	Moderately Tolerant Gr. 2
48	Dick Wee	1	2	0.935	0.853	Moderately Tolerant Gr. 2
51	H4	1	2	0.961	0.906	Moderately Tolerant Gr. 2
60	Kahata Wee	1	2	0.968	0.996	Moderately Tolerant Gr. 2
66	Kivul Handiran	1	2	1.018	0.967	Moderately Tolerant Gr. 2
67	Kos Ata Wee	1	2	0.845	0.974	Moderately Tolerant Gr. 2
74	MI273	1	2	0.981	1.044	Moderately Tolerant Gr. 2
81	Murungakayan	1	2	0.939	0.876	Moderately Tolerant Gr. 2
90	Pokuru Samba	1	2	0.979	1.036	Moderately Tolerant Gr. 2
102	Kalu Heenati(P)	1	2	0.924	0.906	Moderately Tolerant Gr. 2
4	At48-3	2	1	1.023	1.192	Tolerant
14	Bg352	2	1	0.895	1.270	Tolerant
18	Bg400-1	2	1	1.123	1.191	Tolerant
23	Bw267-3	2	1	0.954	1.162	Tolerant
34	Bg301	2	1	0.891	1.113	Tolerant
36	Bg34-8	2	1	1.123	1.115	Tolerant
38	Bg38	2	1	0.916	1.201	Tolerant
39	Bg380	2	1	0.929	1.180	Tolerant
41	Bg750	2	1	0.977	1.270	Tolerant
43	Bw272-6B	2	1	1.112	1.159	Tolerant
47	Devaraddiri	2	1	0.979	1.220	Tolerant
49	Goda Wee	2	1	1.009	1.284	Tolerant
54	Hathial	2	1	1.067	1.104	Tolerant
55	Heen Wee	2	1	1.140	1.214	Tolerant

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Var. No.†	Variety	Main cluster	Sub-cluster	Growth performance		Category of tolerance level
				RLst‡	RWst‡‡	
70	Kuruluthuda	2	1	1.114	1.213	Tolerant
77	Mada Al	2	1	0.884	1.205	Tolerant
82	Muthu Samba	2	1	1.087	1.081	Tolerant
83	Nona Bokra	2	1	1.065	1.235	Tolerant
87	Podi Wee A8	2	1	1.007	1.301	Tolerant
88	Podi Niyan Wee	2	1	0.983	1.309	Tolerant
89	Pokkali	2	1	1.053	1.161	Tolerant
92	Ptb16	2	1	0.913	1.078	Tolerant
99	Suwandel	2	1	0.795	1.175	Tolerant
5	At303	2	2	1.090	1.526	Highly Tolerant
13	Bg350	2	2	1.072	1.358	Highly Tolerant
21	Bg450	2	2	1.273	1.354	Highly Tolerant
53	H9	2	2	1.003	1.414	Highly Tolerant
56	Hetada Wee	2	2	1.100	1.371	Highly Tolerant
91	Pola Al	2	2	1.052	1.565	Highly Tolerant
2	At16	3	1	0.852	0.731	Susceptible Gr. 2
9	At86-1	3	1	0.895	0.793	Susceptible Gr. 2
11	Bg305	3	1	0.885	0.823	Susceptible Gr. 2
12	Bg34-6	3	1	0.755	0.655	Susceptible Gr. 2
16	Bg359	3	1	0.618	0.685	Susceptible Gr. 2
25	Bw351	3	1	0.907	0.822	Susceptible Gr. 2
28	Bw453	3	1	0.821	0.665	Susceptible Gr. 2
29	Bandara H	3	1	0.756	0.623	Susceptible Gr. 2
32	Bg276-5	3	1	0.891	0.866	Susceptible Gr. 2
33	Bg300	3	1	0.772	0.793	Susceptible Gr. 2
57	Hondarawalu	3	1	0.876	0.882	Susceptible Gr. 2
69	Kuru Wee	3	1	0.795	0.838	Susceptible Gr. 2
71	Ld355	3	1	0.842	0.781	Susceptible Gr. 2
72	Ld356	3	1	0.854	0.751	Susceptible Gr. 2
78	Moroberekan	3	1	0.801	0.739	Susceptible Gr. 2
84	Pachchaperumal	3	1	0.754	0.662	Susceptible Gr. 2
93	Rathkarayal	3	1	0.663	0.783	Susceptible Gr. 2
101	Weda Heenati	3	1	0.797	0.781	Susceptible Gr. 2
7	At401	3	2	1.141	0.680	Susceptible Gr. 1
19	Bg403	3	2	1.100	0.550	Susceptible Gr. 1
40	Bg745	3	2	0.898	0.725	Susceptible Gr. 1
42	Bg94-1	3	2	1.133	0.697	Susceptible Gr. 1
50	H10	3	2	0.924	0.629	Susceptible Gr. 1
58	IR29	3	2	0.969	0.674	Susceptible Gr. 1
63	Kara Al	3	2	0.911	0.518	Susceptible Gr. 1
79	Muhudu Kiriyal	3	2	1.167	0.661	Susceptible Gr. 1
80	Murunga	3	2	1.021	0.579	Susceptible Gr. 1
86	Periyakarappan	3	2	0.892	0.575	Susceptible Gr. 1
94	Raththal	3	2	0.883	0.609	Susceptible Gr. 1
96	Sinna Karuppan	3	2	0.931	0.590	Susceptible Gr. 1
98	Suduru Samba	3	2	0.880	0.701	Susceptible Gr. 1

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Var. No.†	Variety	Main cluster	Sub-cluster	Growth performance		Category of tolerance level
				RLst‡	RWst‡‡	
8	At85-2	4	1	0.562	0.583	Highly Susceptible
27	Bw451	4	1	0.656	0.415	Highly Susceptible
35	Bg304	4	1	0.597	0.546	Highly Susceptible
45	Bw78	4	1	0.698	0.550	Highly Susceptible
61	Kalu Heenati(W)	4	1	0.600	0.559	Highly Susceptible
75	Mada Al (Kaluthara)	4	1	0.533	0.490	Highly Susceptible
76	Madathawalu	4	1	0.690	0.454	Highly Susceptible
59	IR8	4	2	0.583	0.339	Highly Susceptible

† - The variety numbers are the same as those given in the dendogram (Figure 3).

‡ - Standardized relative leaf area at 100 mM Na^+

‡‡ - Standardized relative total plant dry weight at 100 mM Na^+.

higher RWst than all the other varieties, from which H9, *Hatada Wee*, Bg350 and Bg450 also showed RWst values greater than 1.35. Out of the 34 varieties, which had RWst > 1, there were 16 traditional varieties (out of the 51 tested), 1 old-improved variety (out of 4) and 17 new-improved varieties (out of 47).

RL and RW were highly-significantly ($p < 0.0001$) and positively correlated ($r = 0.582$). Similarly, RLst and RWst also showed a highly significant and positive correlation ($r = 0.569$, $p < 0.0001$).

Classification of varieties based on their degree of salinity tolerance at Phase I of salt-stress development

Cluster analysis based on RWst and RLst identified four main clusters (Figure 3 and Table 4). Within each of clusters 1, 2 and 3, only two sub-clusters could be identified. Cluster 4 had no sub-clusters. Multivariate analysis of variance (MANOVA) showed that both main clusters and sub-clusters were highly significantly different ($p < 0.0001$), with all four multivariate test statistics showing the same level of significance (i.e. $p < 0.0001$).

The main clusters and sub-clusters enabled a clear classification of varieties based on their degree of salt-tolerance during Phase I (Table 4). Varieties that could be classified as 'tolerant' were grouped into main cluster 2. Within this main cluster, the sub-cluster 2 contained six varieties, which could be categorized as 'highly tolerant' as both RWst and RLst had values, which were greater than 1, with RWst having values, which were substantially greater than 1. This sub-cluster contained two traditional (i.e. Hetada Wee, Pola Al), one old-improved (i.e. H9) and three new-improved varieties (i.e. At303, Bg350 and Bg450). Sub-cluster 1 of the main cluster 2 contained 25 varieties, which could be categorized as 'tolerant', with all RWst values being greater than 1, but not as high as those in the 'highly tolerant' sub-cluster. Majority of the 25 varieties within the 'tolerant' group had RLst values, which were greater than 1. This sub-cluster consisted of 13 traditional varieties and 12 new-improved varieties and included the known salt-tolerant varieties *Pokkali* and *Nona Bokra*. The traditional varieties *Devaraddiri* and *Kuruluthuda*, which are also known among farmers as relatively-tolerant, clustered into this group. The new-improved varieties in this sub-cluster included those from all maturity groups ranging from 2 ½ months (Bg750) to 4 months (Bg380 and Bg400-1).

Varieties that were grouped into two sub-clusters of the main cluster 1 could be categorized as 'moderately tolerant' as the majority of them had RLst and/or RWst values, which were close to one. All varieties in the sub-cluster 1, which were classified as 'moderately tolerant group 1', had RLst values greater than 1, but had RWst values lower than 1. This sub-cluster contained 11 varieties consisting of 7 traditional, 1 old-improved and 3 new-improved varieties. In comparison, only a few varieties that were clustered into sub-cluster 2 of the main cluster 1 had RLst or RWst values greater than 1. Varieties in this sub-cluster included At354, which has been used as the standard salt-tolerant variety in the present study. This sub-cluster, termed 'moderately tolerant group 2' included 21 varieties consisting of 9 traditional, 1 old-improved and 11 new-improved varieties.

Main cluster 3 contained varieties, which could be categorized as 'susceptible'. Two sub-clusters could be identified within this main cluster as well. One sub-cluster (sub-cluster 2), which included varieties that were classified as 'susceptible group 1' had RLst values greater than 0.8, but RWst values lower than 0.8. This sub-cluster contained 13 varieties including the known salt-susceptible variety IR29. The 12 varieties consisted of 7 traditional, 1 old-improved and 4 new-improved varieties. The other sub-cluster of main cluster 3 (i.e. sub-cluster 1) contained varieties, which had both RLst and RWst below 0.9. This sub-cluster was termed 'susceptible group 2' and included 18 varieties consisting of 7 traditional and 11 new-improved varieties.

Main cluster 4 contained 8 varieties, which had the lowest values of both RLst and RWst and were classified as 'highly susceptible'. This cluster consisted of 5 new-improved and 4 traditional varieties. Within this main cluster, the new-improved variety IR8 had an extremely low RWst value.

Whole plant and shoot relative water content

For both whole plant (RWCpl) and shoot (RWCsh) the relative water content, the variety × salt treatment interaction effect was found to be significant only in two experimental rounds, so that differential response of different varieties was evident only in these two rounds. The main effect of varieties on RWCpl and RWCsh were significant in six and five rounds, respectively. RWCpl showed significant ($p < 0.05$) reductions under salt stress in comparison to the unstressed control in 08 out of the 10 rounds of experimentation (Table 5), while RWCsh showed such significant reductions in six rounds. The frequency distributions of RWCpl and RWCsh showed that the respective percentile points under salt stress were always lower than their corresponding percentile points in the control (Table 6).

The relative RWCpl (RRWCpl, i.e. the ratio between RWCpl under salt stress and control) showed a significant ($p < 0.05$) variation among the 102 rice varieties tested (Table 7). The RRWCpl values ranged from 0.244 (in *Pokuru Samba*) to 1.041 (Bg352). Only three varieties (i.e. Bw351, Bg94-1 and Bg352) had RRWCpl values, which were greater than 1, indicating that the majority of varieties experienced a water shortage during Phase I of salt stress that was imposed in the present experiment. Similar to relative RWCpl, the relative RWCsh (RRWCsh, i.e. the ratio between RWCsh under salt stress and control) also showed a highly significant ($p < 0.001$) variation among varieties. RRWCsh ranged from 0.091 (*Kottiyaran*) to 1.119 (*Sinna Karuppan*), with 10 varieties showing values greater than 1. The percentile points in the respective frequency distributions of RRWCpl and RRWCsh are presented in Table 6. At the lowermost percentile points (i.e. 5th, 10th and 25th), RRWCsh values were considerably lower than the respective RRWCpl values. This meant that in the

Table 5: The levels of significance in analyses of variance of whole plant relative water content (RWCpl) and shoot relative water content (RWCsh) in the different rounds of experimentation

Trait/ source	df†	Round of experimentation									
		Exp. 1	Exp. 2	Exp. 3	Exp. 4	Exp. 5	Exp. 6	Exp. 7	Exp. 8	Exp. 9	Exp. 10
RWCpl											
Variety	101	ns‡	ns	ns	0.0101	ns	0.0019	0.0014	< 0.0001	0.0001	< 0.0001
Salt trt.	1	0.0369	ns	0.0070	ns	0.0018	0.0002	< 0.0001	< 0.0001	0.0401	< 0.0001
Var. x Salt trt.	101	ns	ns	ns	ns	ns	ns	ns	0.0016	ns	0.0359
CV (%)		16.40	14.39	10.77	9.93	16.01	7.17	7.01	7.00	15.83	5.23
RWCsh											
Variety	101	ns	0.0005	ns	ns	ns	0.0054	0.0002	< 0.0001	ns	0.0162
Salt trt.	1	ns	ns	ns	ns	0.0039	0.0016	0.0416	< 0.0001	0.0076	< 0.0001
Var. x Salt trt.	101	ns	ns	ns	ns	ns	ns	ns	0.0074	ns	0.0431
CV (%)		26.37	19.83	19.49	20.59	18.13	11.01	17.56	10.60	19.43	10.01

‡ns – Non-significant at p = 0.05.
†df – Degrees of freedom.
CV – Coefficient of variation.

varieties, which experienced greater reductions in plant water content during Phase I of salt stress development, those reductions occurred predominantly in the shoot rather than in the root. In contrast, at the uppermost percentile points (i.e. 90th and 95th), RRWCsh values were considerably greater than the respective RRWCpl values. This indicated that the varieties that were able to maintain their plant water content during Phase I did so predominantly by maintaining the water content of their shoots rather than in roots.

Correlations between RWC and measures of salt tolerance during Phase I of salt stress development

There was a highly significant positive correlation between RRWCpl and RRWCsh (Figure 4). With the exception of two weak correlations involving RRWCsh, whole plant and shoot RWCs did not show significant ($p = 0.05$) correlations with any measures of salt tolerance during Phase I (i.e. standardized or non-standardized relative total dry weights or relative leaf area). Even the two correlations involving RRWCsh, which were statistically significant, had very low correlation coefficients (i.e. 0.204 and 0.220) indicating a very low strength of the respective relationships with a high degree of scatter of data points (i.e. varieties). This also indicated the absence of a common mechanism of salt tolerance, which encompassed all the rice varieties that were tested in the present study. Therefore, the possible role of whole plant and shoot relative water contents in conferring salt tolerance during Phase I had to be elucidated by examining the respective relative water contents of individual varieties along with their respective tissue Na^+ concentrations, which provided indications about their capacities for Na^+ exclusion.

Shoot and root Na^+ concentrations

When the data for all 10 rounds of experimentation were pooled, shoot and root Na^+ concentrations (i.e. ShNa and RtNa) showed a highly-significant variation between different varieties ($p < 0.0001$) and salt-treatments ($p < 0.0001$). In each of the varieties, ShNa and RtNa were significantly greater under salt-stress (i.e. at 100 mM NaCl) as compared to the respective un-stressed control (i.e. 1 mM NaCl). In addition, the variety × salt treatment interaction effect was also highly-significant ($p < 0.0001$). This indicated that the respective magnitudes of increases of ShNa and RtNa due to salt-stress were highly- significantly different among the

Table 6: Percentile points in the frequency distributions of whole plant and shoot relative water contents and shoot and root Na+ concentrations

		Percentiles of the frequency distribution						
Variable†	Mean	5th	10th	25th	50th	75th	90th	95th
RWCpl (1 mM Na^+)	6.28	4.86	5.15	5.60	6.37	6.94	7.42	7.69
RWCpl (100 mM Na^+)	5.56	4.17	4.70	5.13	5.57	6.04	6.33	6.63
RWCsh (1 mM Na^+)	4.38	2.48	2.65	3.29	4.32	5.17	6.07	6.46
RWCsh (100 mM Na^+)	3.81	2.22	2.36	3.02	3.77	4.53	5.42	5.66
RRWCpl	0.87	0.72	0.80	0.83	0.87	0.93	0.97	0.99
RRWCsh	0.83	0.58	0.66	0.77	0.86	0.93	0.99	1.06
ShNa (1 mM Na^+)	326.60	138.90	155.30	241.40	319.00	391.50	480.30	565.50
ShNa (100 mM Na^+)	650.40	229.70	278.50	399.20	548.70	869.90	1089.00	1472.90
RtNa (1 mM Na^+)	462.30	166.10	240.70	329.00	464.50	586.00	681.60	779.30
RtNa (100 mM Na^+)	1120.40	424.10	514.50	886.30	1117.30	1385.30	1594.90	1696.10
ShNa: RtNa (1 mM Na^+)	0.871	0.324	0.402	0.548	0.747	0.875	1.130	2.009
ShNa: RtNa (100 mM Na^+)	0.650	0.237	0.318	0.414	0.531	0.775	1.109	1.654

†RWCpl - Whole plant relative water content; RWCsh - Shoot RWC; RRWCpl - Relative whole plant RWC; RRWCsh - Relative shoot RWC; ShNa - Shoot Na^+ concentration (mmol Na^+ kg^{-1} dry weight); RtNa - Root Na^+ concentration (mmol Na^+ kg^{-1} dry weight); ShNa:RtNa - Shoot:root Na^+ ratio. All frequency distributions had 102 data points, which were the varietal means for each variable.

Table 7: Variation of relative whole plant (RRWCpl) and shoot (RRWCsh) relative water contents, shoot (ShNa) and root (RtNa) Na^+ concentrations and shoot:root Na^+ concentration ratio (ShNa:RtNa) at 100 mM Na^+ of different rice varieties during Phase I of salt-stress development.

Variety†			Na^+ Concentration (mmol Na^+kg^{-1} dry weight)		
	RRWCpl	RRWCsh	ShNa	RtNa	ShNa:RtNa
At303	0.813	0.767	169	385	0.441
Bg350	0.852	0.781	573	950	0.603
Bg450	0.850	0.885	355	913	0.389
H9	0.841	0.781	1613	716	2.253
Hetada Wee	0.796	0.911	988	1278	0.774
Pola Al	0.994	0.767	761	1278	0.596
At48-3	0.811	0.864	783	1305	0.597
Bg301	0.841	0.774	915	989	0.925
Bg34-8	0.765	0.619	1096	1464	0.760
Bg352	1.041	1.061	500	917	0.545
Bg38	0.782	0.542	281	140	2.009
Bg380	0.814	0.881	464	953	0.487
Bg400-1	0.845	0.868	620	1082	0.574
Bg745	0.841	1.032	372	217	1.708
Bg750	0.807	1.055	163	425	0.389
Bw267-3	0.908	0.810	448	1348	0.338
Bw272-6B	0.925	0.870	1006	1298	0.782
Devaraddiri	0.895	0.822	908	1080	0.931
Goda Wee	0.867	0.837	674	1172	0.574
Hathial	0.823	0.925	465	886	0.527
Heen Wee	0.847	0.839	761	794	0.959
Kottiyaran	0.744	0.091	420	1119	0.378
Kuruluthuda	0.605	0.507	870	1980	0.452
Mada Al	0.865	0.392	496	642	0.775
Muthu Samba	0.886	0.672	450	1133	0.399
Nona Bokra	0.914	0.720	295	1739	0.170
Podi Niyan Wee	0.928	0.789	843	1622	0.523
Podi Wee A8	0.924	0.858	1368	2724	0.504
Pokkali	0.848	0.868	353	569	0.625
Ptb16	0.838	0.678	968	1102	0.878
Suwandel	0.883	0.764	671	1595	0.419
62-355	0.841	0.933	870	1550	0.562
Bg360	0.930	0.888	481	1512	0.318
Dahanala	0.860	0.885	643	580	1.109
H7	0.878	0.979	633	1512	0.419
Kalu Mudu Kiriyal	0.935	0.680	510	888	0.576
Karayal	0.986	0.915	435	1123	0.388
Keera Samba	0.930	0.849	692	1279	0.557
Ld66	0.918	0.990	591	935	0.632
Seeraga Samba	0.936	0.759	264	554	0.479
Sudu Bala Wee	0.570	0.734	648	1048	0.618
Tetep	0.983	1.065	375	1069	0.353
At354	0.849	0.872	411	1371	0.340
Beheth Heenati	0.806	0.941	946	1272	0.746
Bg250	0.848	0.818	318	1457	0.220
Bg357	0.911	0.887	397	1675	0.237

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Variety†			Na^+ Concentration (mmol Na^+kg^{-1} dry weight)		
	RRWCpl	RRWCsh	ShNa	RtNa	ShNa:RtNa
Bg379-2	0.867	0.984	446	832	0.535
Bg407	0.954	0.888	423	1000	0.422
Bw266-7	0.928	0.828	535	1294	0.419
Bw302	0.915	0.816	267	1185	0.232
Bw400	0.806	0.925	482	909	0.537
Bw452	0.852	0.924	399	1504	0.267
Dick Wee	0.862	0.855	230	545	0.421
H4	0.913	0.792	202	250	0.828
Kahata Wee	0.930	0.689	360	1118	0.320
Kalu Heenati (P)	0.861	0.932	1640	1595	1.036
Kivul Handiran	0.899	0.965	965	1385	0.700
Kos Ata Wee	0.949	0.974	994	1100	0.903
MI273	0.845	0.956	616	1272	0.484
Murungakayan	0.887	1.010	230	436	0.527
Paduru Wee	0.901	0.621	693	797	0.869
Pokuru Samba	0.244	0.195	946	1419	0.666
At401	0.884	0.857	500	1551	0.322
Bg403	0.800	0.863	662	1490	0.449
Bg94-1	1.040	0.657	187	458	0.411
H10	0.978	1.035	384	837	0.458
IR29	0.989	0.917	438	514	0.911
Kara Al	n.a.	0.639	1512	1218	1.239
Muhudu Kiriyal	0.868	0.576	583	1133	0.522
Murunga	n.a.	0.760	411	1399	0.294
Periyakarappan	0.804	1.046	508	1109	0.460
Raththal	0.917	0.950	285	566	0.508
Sinna Karuppan	0.861	1.119	897	1098	0.828
Suduru Samba	0.802	0.866	1077	903	1.193
At16	0.844	0.802	513	1240	0.414
At86-1	0.941	0.991	779	1504	0.514
Bandara H	0.835	0.728	399	1000	0.404
Bg276-5	0.889	0.741	1006	1696	0.593
Bg300	0.730	0.848	282	479	0.601
Bg305	0.915	0.888	535	1620	0.330
Bg34-6	0.970	0.962	568	1294	0.449
Bg359	0.833	0.847	557	1077	0.517
Bw351	1.022	0.937	442	1620	0.274
Bw453	0.833	0.921	707	1371	0.517
Hondarawalu	0.824	0.804	541	1144	0.478
Kuru Wee	0.864	0.885	1473	1322	1.114
Ld355	0.951	0.914	333	1843	0.181
Ld356	0.982	0.971	1098	1457	0.755
Moroberekan	0.816	0.682	779	1100	0.710
Pachchaperumal	0.933	1.061	243	424	0.574
Rathkarayal	0.611	0.578	1618	1153	1.403
Weda Heenati	0.930	0.747	779	1322	0.590
At85-2	0.835	0.974	671	1533	0.438
Basmathi	0.876	0.890	1089	1117	0.986
Bg304	0.879	0.790	208	532	0.392

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Variety†			Na^+ Concentration (mmol Na^+kg^{-1} dry weight)		
	RRWCpl	RRWCsh	ShNa	RtNa	ShNa:RtNa
Bw451	0.855	1.059	1184	716	1.654
Bw78	0.802	0.910	1571	963	1.671
IR8	0.969	0.837	970	935	1.038
Kalu Heenati (W)	0.714	0.773	279	884	0.315
Madathawalu	0.897	0.897	915	1110	0.825
Mada Al (Kaluthara)	0.980	0.705	530	294	1.811
p*	0.0448	0.0001	< 0.0001	< 0.0001	<0.0001
CV (%)**	11.97	15.68	12.58	18.18	14.07

n.a. – Data not available

† – Each value is a mean of six replicate measurements

*p – Level of significance of the ANOVA (i.e. probability of observed varietal variation being due to random variation)

**CV – Coefficient of variation

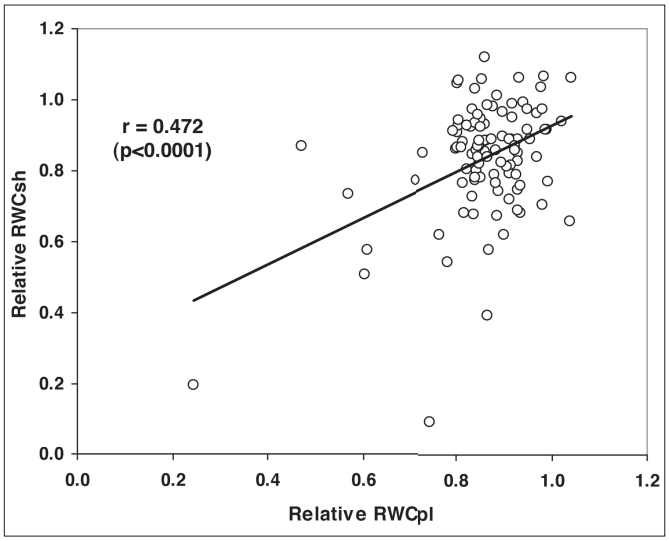

Figure 4: Correlation between varietal means of whole plant and shoot relative RWC of the 102 rice varieties during Phase I of salt stress development.

102 varieties tested in the present study. The respective ranges of ShNa and RtNa under salt-stress and control are presented in Table 8. The frequency distributions of ShNa and RtNa showed that both variables had substantially greater values under salt stress than in the control at all percentile points (Table 6). The highly significant ($p < 0.0001$) varietal variation in RtNa in both salt-stressed and un-stressed treatments showed that the varieties differed in their capacity to exclude Na^+ at the root surface by preventing Na^+ from entering the root tissue. RtNa was significantly ($p < 0.0001$) greater than ShNa under both salt-stressed and un-stressed conditions (Table 9), indicating that the root was able to exert a certain degree of control on Na^+ transfer to the shoot. However, the variety × plant part interaction effect on root and shoot Na^+ concentrations was highly significant ($p < 0.0001$), thus demonstrating significant varietal variation in excluding Na^+ from the shoot.

Table 8: Ranges of Na^+ concentrations in the shoot and root of the 102 varieties tested under salt-stressed (100 mM Na^+) and un-stressed (1 mM Na^+) conditions

Plant part	Treatment	Na^+ concentration (mmol Na^+ kg^{-1} dry weight)	
		Minimum (variety)	Maximum (variety)
Shoot	1 mM Na^+	104 (Bandara Haththewa)	797 (H9)
	100 mM Na^+	163 (Bg750)	1640 (Kalu Heenati-PGRC)
Root	1 mM Na^+	62 (Bg38)	892 (MI273)
	100 mM Na^+	140 (Bg38)	2972 (At353)

The ratio ShNa:RtNa, which is a measurement of the capacity of a given variety to exclude Na^+ from the shoot, showed a highly significant ($p < 0.0001$) variation between varieties and salt treatments. Interestingly, the mean (i.e. averaged across all 102 varieties) ShNa:RtNa ratio at 100 mM Na^+ (0.611) was significantly lower than that at 1 mM Na^+ (0.854). The frequency distribution of ShNa:RtNa ratio also showed that it was always lower at 100 mM Na^+ than at 1 mM Na^+ (Table 6). This indicated a greater capacity for Na^+ exclusion from the shoot when the plants are growing under a higher level of salinity. Conversely, the need for Na^+ exclusion from the shoot is lower when the plants are growing under very low levels of salinity, thus allowing a greater proportion of Na^+ absorbed by the root to reach the shoot resulting in a higher ShNa:RtNa ratio. However, there was a highly significant ($p < 0.0001$) variety × salt treatment interaction effect on ShNa:RtNa ratio, showing a significant variation between different rice varieties in their capacity for excluding Na^+ from the shoot. This was confirmed by the highly significant ($p < 0.0001$) varietal variation in ShNa:RtNa ratio at 100 mM Na^+, which ranged from 0.169 (in Nona Bokra) to 2.253 (in H9) (Table 7).

Table 9: Variation of mean Na^+ concentrations of the 102 varieties tested between shoot and root under salt-stressed (100 mM Na^+) and un-stressed (1 mM Na^+) conditions

Plant part	Mean Na^+ concentration† (mmol Na^+ kg^{-1} dry weight)		Duncan's critical range ($p = 0.05$)
	1 mM Na^+	100 mM Na^+	
Shoot	320.8†	619.3	19.9
Root	456.5	1135.0	42.0
Duncan's critical range ($p = 0.05$)	17.5	43.3	

†Each value is a mean of 102 varieties and two replicates

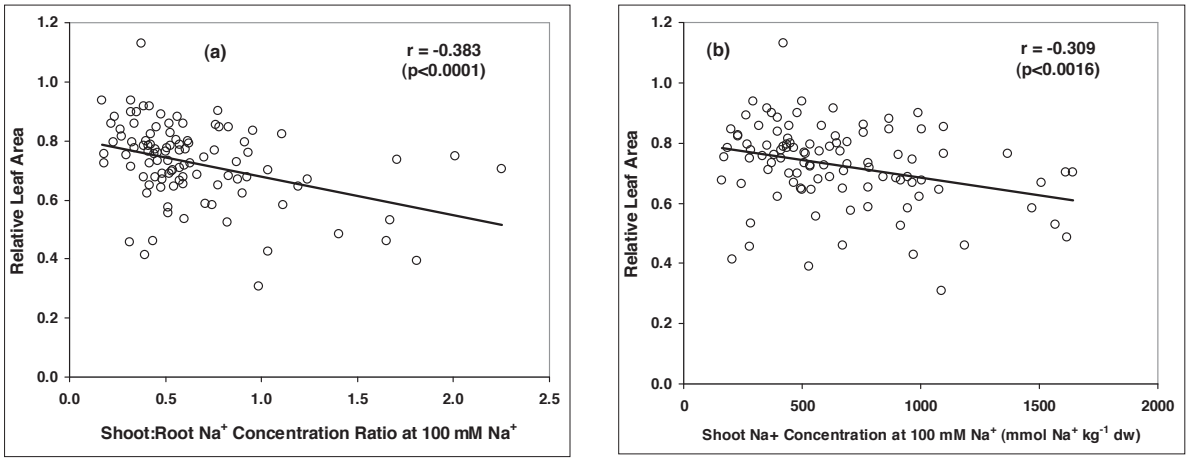

Figure 5: Correlations between relative leaf area and shoot:root Na^+ concentration ratio (a) and shoot Na^+ concentration (b) at 100 mM Na^+.

Correlations between shoot and root Na^+ concentrations and measures of salt tolerance during Phase I of salt stress development

Linear correlation analysis showed that the varietal means of ShNa:RtNa ratio at 100 mM Na^+ (i.e. in the salt stressed treatment) had highly significant ($p < 0.01$) negative correlations with relative leaf area (RL) and the standardized relative leaf area (RLst) (Table 10). As RL and RLst were the measures of salt tolerance (greater values indicating greater tolerance and *vice versa*), the above negative correlations meant that increasing the salt tolerance at Phase I required a lower ShNa:RtNa ratio (which indicate greater Na^+ exclusion from the shoot at the xylem parenchyma). Although shoot Na^+ concentration at 100 mM Na^+ also had significant or nearly significant negative correlations with RL and RLst, the correlation coefficients were lower than in the corresponding correlations with ShNa:RtNa. Interestingly, root Na^+ concentration at 100 mM Na^+ did not show significant correlations with any of the measures of salt tolerance. As expected, ShNa:RtNa ratio under salt stress was significantly positively correlated with the respective ShNa and negatively correlated with RtNa, while the different measures of salt tolerance were highly significantly positively correlated with each other (Table 10).

It can be noted that neither the ShNa:RtNa ratio nor ShNa under salt stress were significantly correlated with RW and RWst, which are more representative measures of salt tolerance than RL and RLst, because they measure the response of the whole plant to salt stress rather than just the response of the leaves. Furthermore, even the significant negative correlations between salt-stressed ShNa:RtNa, ShNa, RL and RLst had considerable scatter of data points as indicated by their relatively lower correlation coefficients, all of which were lower than -0.4 (Figures 5.a & b). Therefore, although the significant negative correlation between the ShNa:RtNa ratio under salt stress and RL indicated a significant role for Na^+ exclusion from the shoot at root xylem parenchyma in conferring salt tolerance during Phase I, the considerable scatter in the data points (which represent different

Table 10: Linear correlation matrix of shoot and root Na^+ concentrations (ShNa and RtNa), shoot:root Na^+ (ShNa:RtNa) at 100 mM Na^+ and different measures of salt tolerance during Phase I of salt stress development

	Linear correlation coefficient					
	ShNa	RtNa	RL	RLst	RW	RWst
ShNa:RtNa	0.569 *(< 0.0001)*	- 0.409 *(< 0.0001)*	- 0.383 *(< 0.0001)*	- 0.286 *(0.0036)*	- 0.187 *ns*	- 0.088 *ns*
ShNa	-	0.333 *(0.0006)*	- 0.309 *(0.0016)*	- 0.189 *(0.0566)*	- 0.095 *ns*	- 0.010 *ns*
RtNa		-	0.172 *ns*	0.123 *ns*	0.138 *ns*	0.112 *ns*
RL			-	0.886 *(< 0.0001)*	0.582 *(< 0.0001)*	0.454 *(< 0.0001)*
RLst				-	0.606 *(< 0.0001)*	0.569 *(< 0.0001)*
RW					-	0.884 *(< 0.0001)*

RL - Relative leaf area; RLst - Standardized RL; RW - Relative total plant dry weight; RWst - Standardized relative total plant dry weight. Probability of each correlation coefficient being equal to zero is given in parenthesis. ns - Correlation coefficient is not significantly different ($p = 0.05$) from zero. All correlations had 102 data points, which were the varietal means for each variable.

varieties) show that other mechanisms were also playing significant roles. Several other workers also have observed a lack of correlation between tissue Na^+ (and Cl^{-1}) concentrations and magnitude of growth under salt stress (Fricke, 2004; Hu *et al.*, 2007) or survival under salinity (Yeo *et al.*, 1990).

Possible mechanisms responsible for salt tolerance during Phase I of salt stress development

Based on the two-phase growth model of Munns (1993) and Munns and Tester (2008), three possible mechanisms can be identified as being responsible for salt tolerance during Phase I. Firstly, maintenance of higher relative water content under salt stress may confer salt tolerance during Phase I where water shortage is the principal stress factor. Secondly, Na^+ exclusion, both at the root surface and at the root xylem parenchyma, which would lead to a lower shoot Na^+ content under salt stress, could contribute to Phase I salt tolerance as Na^+ ion toxicity could also be present even at Phase I (Sümer *et al.*, 2004; Munns & Tester, 2008). Thirdly, tissue tolerance of excess shoot Na^+ could also play a role in Phase I salt tolerance. The presence or absence of the above mechanisms of salt tolerance was elucidated by examining the respective relative water contents and shoot and root Na^+ concentrations of individual varieties.

In classifying the extent of different mechanisms of Phase I salt tolerance, the percentile points of the frequency distributions of the relevant variables were used. The capacity to maintain plant and shoot water content under salt stress in the 102 varieties was classified as 'high', 'medium' or 'low' based on the frequency distributions of varietal means of RRWCpl and RRWCsh, respectively. Those varieties having RRWCpl or RRWCsh values greater than the 75th percentile were classified as having a 'high' capacity for maintenance of whole plant or shoot water content, respectively. Those having RRWCpl or RRWCsh values between the 75th and the 50th percentile points were classified into the 'medium' category, while those having RRWCpl or RRWCsh values lower than the 50th percentile were classified into the 'low' category. The respective capacities for Na^+ exclusion at the root surface and root xylem parenchyma were classified as 'high', 'medium' or 'low' using the frequency distributions of RtNa and ShNa:RtNa ratio, respectively (Table 6). Here, the varieties having RtNa and ShNa:RtNa values, which were lower than the 25th percentile were categorized as having 'high' capacities for Na^+ exclusion. Those having RtNa and ShNa:RtNa values between the 25th and the 50th percentile points were classified as having 'medium' capacity for Na^+ exclusion, while those with values greater than the 50th percentile were classified as having 'low' capacity. The tissue tolerance of excess shoot Na^+ of a given variety was also classified as 'high', 'medium' or 'low' by comparing its category of ShNa and the degree of overall salt tolerance of the variety as classified based on cluster analysis (Table 4). For this purpose, ShNa was also classified as 'high', 'medium' or 'low' based on the same ranges of percentiles as those used for classifying RRWCpl and RRWCsh. The decision scheme for classifying varieties based on their tissue tolerance of excess shoot Na^+ is given in Table 11.

Table 11: Decision scheme for classifying varieties based on their tissue tolerance of excess shoot Na^+

	Salt tolerance†	
Shoot Na^+ Concentration (ShNa, mmol Na^+ kg^{-1} DW)	Overall level of salt tolerance during Phase I (Table 4)	Level of tissue tolerance of excess shoot Na^+
High (ShNa > 549)	HT, T, MT1, MT2	High
	S1, S2, HS	No definite conclusion is possible
Medium (549>ShNa>279)	HT, T	High
	S1, S2, HS	Low
	MT1, MT2	No definite conclusion is possible
Medium/High (549>ShNa>500)	MT1, MT2	Medium
Low (<279)	HT, T, MT1, MT2	No definite conclusion is possible
	S1, S2, HS	Low

†HT - Highly tolerant; T - Tolerant; MT1 - Moderately tolerant (Group 1); MT2 - Moderately tolerant (Group 2); S1 - Susceptible (Group 1); S2 - Susceptible (Group 2); HS - Highly susceptible (based on Tables 4 and 7).

Table 12: Presence or absence of different mechanisms of salt tolerance during Phase I of salt stress development in the 102 individual varieties screened in the present experiment

Variety	Level of Phase I salt tolerance	Level of different mechanisms of salt tolerance				
		Na^+ exclusion at root surface	Na^+ exclusion at root xylem paren-chyma	Tissue tolerance of excess Na^+	Capacity to maintain plant water status	Capacity to maintain shoot water status
At303	HT	H	M	nd	L	L
Bg350	HT	M	L	H	L	L
Bg450	HT	M	H	nd	L	M
H9	HT	H	L	H	L	L
Hetada Wee	HT	L	L	H	L	M
Pola Al	HT	L	L	H	H	L
At48-3	T	L	L	H	L	M
Bg301	T	M	L	H	L	L
Bg34-8	T	L	L	H	L	L
Bg352	T	M	L	H	H	H
Bg38	T	H	L	nd	L	L
Bg380	T	M	M	H	L	M
Bg400-1	T	M	L	H	L	M
Bg745	T	H	L	nd	L	H
Bg750	T	H	H	nd	L	H
Bw267-3	T	L	H	H	M	L
Bw272-6B	T	L	L	H	M	M
Deva-raddiri	T	M	L	H	M	L
Goda Wee	T	L	L	H	M	L
Hathial	T	M/H	M	H	L	M
Heen Wee	T	H	L	H	L	L
Kottiyaran	T	L	H	H	L	L
Kurulu-thuda	T	L	M	H	L	L
Mada Al	T	H	L	H	L	L
Muthu Samba	T	L	M	H	M	L
Nona Bokra	T	L	H	nd	M	L
Podi Niyan Wee	T	L	M	H	H	L
Podi Wee A8	T	L	M	H	M	L
Pokkali	T	H	L	nd	L	M
Ptb16	T	M/L	L	H	L	L
Suwandel	T	L	M/H	H	M	L
62-355	MT1	L	L	H	L	H
Bg360	MT1	L	H	nd	H	M
Dahanala	MT1	H	L	H	L	M
H7	MT1	L	M/H	H	M	H
Kalu Mudu Kiriyal	MT1	M/H	L	M	H	L
Karayal	MT1	L	H	nd	H	M

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Variety	Level of Phase I salt tolerance	Level of different mechanisms of salt tolerance: Na^+ exclusion at root surface	Na^+ exclusion at root xylem parenchyma	Tissue tolerance of excess Na^+	Capacity to maintain plant water status	Capacity to maintain shoot water status
Keera Samba	MT1	L	L	H	H	L
Ld66	MT1	M	L	H	M	H
Seeraga Samba	MT1	H	M	nd	H	L
Sudu Bala Wee	MT1	M	L	H	L	L
Tetep	MT1	M	H	nd	H	H
At353	MT2	L	H	M	L	H
At354	MT2	L	H	nd	L	M
Beheth Heenati	MT2	L	L	H	L	H
Bg250	MT2	L	H	nd	L	L
Bg357	MT2	L	H	nd	M	M
Bg379-2	MT2	H	L	nd	M	H
Bg407	MT2	M	M	nd	H	M
Bw266-7	MT2	L	M/H	M	H	L
Bw302	MT2	L	H	nd	M	L
Bw400	MT2	M	L	nd	L	M
Bw452	MT2	L	H	nd	L	M
Dick Wee	MT2	H	M	nd	L	L
H4	MT2	H	L	nd	M	L
Kahata Wee	MT2	L	H	nd	H	L
Kalu Heenati (P)	MT2	L	L	H	L	H
Kivul Handiran	MT2	L	L	H	M	H
Kos Ata Wee	MT2	M/L	L	H	H	H
MI273	MT2	L	M	H	L	H
Murunga-kayan	MT2	H	M	nd	M	H
Paduru Wee	MT2	H	L	H	M	L
Pokuru Samba	MT2	L	L	H	L	L
At401	S1	L	H	L	M	L
Bg403	S1	L	M	nd	L	L
Bg94-1	S1	H	H	L	H	L
H10	S1	H	M	L	H	H
IR29	S1	H	L	L	H	M
Kara Al	S1	L	L	nd	na	L

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Variety	Level of Phase I salt tolerance	Level of different mechanisms of salt tolerance: Na^+ exclusion at root surface	Na^+ exclusion at root xylem parenchyma	Tissue tolerance of excess Na^+	Capacity to maintain plant water status	Capacity to maintain shoot water status
Muhudu Kiriyal	S1	L	M	L	M	L
Murunga	S1	L	H	L	na	L
Periya-karappan	S1	M/L	M	L	L	H
Raththal	S1	H	M	L	M	H
Sinna Karuppan	S1	M/L	L	nd	L	H
Suduru Samba	S1	M	L	nd	L	M
At16	S2	L	H/M	L	L	L
At86-1	S2	L	M	nd	H	H
Bandara H	S2	M	H	L	L	L
Bg276-5	S2	L	L	nd	M	L
Bg300	S2	H	L	L	L	L
Bg305	S2	L	H	nd	M	M
Bg34-6	S2	L	M	nd	H	H
Bg359	S2	M	M	L	L	L
Bw351	S2	L	H	L	H	H
Bw453	S2	L	M	nd	L	M
Hondara-walu	S2	L	M	nd	L	L
Kuru Wee	S2	L	L	nd	L	M
Ld355	S2	L	H	L	H	M
Ld356	S2	L	L	nd	H	H
Moro-berekan	S2	M/L	L	nd	L	L
Pachcha-perumal	S2	H	L	L	H	H
Rath-karayal	S2	L	L	nd	L	L
Weda Heenati	S2	L	L	nd	H	L
At85-2	HS	L	M	nd	L	H
Basmathi	HS	L	L	nd	M	M
Bg304	HS	H	H	L	M	L
Bw451	HS	H	L	nd	L	H
Bw78	HS	M	L	nd	L	M
IR8	HS	M	L	nd	H	L
Kalu Heenati (W)	HS	H/M	H	L	L	L

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Variety	Level of Phase I salt tolerance	Level of different mechanisms of salt tolerance: Na^+ exclusion at root surface	Na^+ exclusion at root xylem parenchyma	Tissue tolerance of excess Na^+	Capacity to maintain plant water status	Capacity to maintain shoot water status
Madathawalu	HS	M/L	L	nd	M	M
Mada Al (Kaluthara)	HS	H	L	L	H	L

H - High; M - Medium; L - Low; M/H - Medium/high; M/L - Medium/low; H/M - High/medium. nd - No definite conclusion is possible; na - Data not available.

Coloured boxes contain the mechanisms identified as responsible for Phase I salt tolerance or susceptibility of each variety:
- High/medium capacity for Na+ exclusion or tolerance mechanisms responsible for salt tolerance at Phase I;
- Maintenance of whole plant or shoot water content responsible for salt tolerance at Phase I;
- Low capacity for Na+ exclusion or tolerance mechanisms responsible for susceptibility to salt stress at Phase I;
- Low capacity for maintenance of whole plant or shoot water content responsible for susceptibility to salt stress at Phase I.

Table 12 gives the overall picture of different mechanisms of salt tolerance that could be detected in the 102 individual rice varieties, based on the measurements taken in the present study. Out of the 63 varieties, which were moderately tolerant (MT), tolerant (T) or highly tolerant (HT) to salt stress at Phase I, high or medium capacity for Na^+ exclusion at the root surface, contributed to the tolerance in 17 varieties, while high or medium capacity for Na^+ exclusion at the root xylem parenchyma contributed to the tolerance in 18 varieties. High or medium capacity for Na^+ exclusion, at either of these two points contributed to Phase I tolerance in 33 out of the 63 varieties that showed tolerance. In comparison, tissue tolerance of excess shoot Na^+ contributed to Phase I salt tolerance in 40 out of the 63 tolerant varieties. High or medium capacity to maintain water content in the whole plant and shoot contributed to Phase I tolerance in 30 and 31 tolerant varieties, respectively (Table 12). Altogether, 48 out of the 63 varieties showed high or medium capacity for maintenance of whole plant or shoot water content.

Thirty nine varieties out of the 102 tested showed susceptibility to salt stress at Phase I. Out of these 39 varieties, lower capacity for Na^+ exclusion at the root surface and root xylem parenchyma was responsible for their susceptibility in 18 varieties, each with poor Na^+ exclusion capacity at either of the two points contributing to the susceptibility of 24 varieties altogether. Low tissue tolerance to excess shoot Na^+ contributed to Phase I salt susceptibility in 18 varieties, while the low capacity for maintenance of whole plant and shoot water content contributed to susceptibility in 17 and 19 varieties, respectively (Table 12).

It is notable that tolerance or susceptibility to salt stress at Phase I could be related to high or low capacities for Na^+ exclusion in 67 out of the 102 varieties tested. In comparison, high or low tissue tolerance to excess shoot Na^+ and high or low capacities to maintain whole plant or shoot water contents were related to the Phase I salt tolerance or susceptibility in 58 and 75 varieties, respectively. Out of the 63 varieties that showed Phase I salt tolerance, high or medium capacities in more than one tolerance mechanism contributed to their tolerance in 50 varieties. Similarly, low capacities in more than one mechanism of salt tolerance were responsible for the salt susceptibility of 29 out of the 39 susceptible varieties that were identified.

DISCUSSION

Identified varieties with Phase I salt tolerance

Reduction of leaf and whole plant growth is one of the main observable effects of salt stress during Phase I (Munns & Tester, 2008) and accordingly the capability to minimize growth reductions, as quantified by standardized relative leaf area (RLst) and standardized relative total dry weight (RWst), were used to measure the salt tolerance in the phase I of this study. The same

measures have been adopted in several other studies, which investigated Phase I salt tolerance in other crops as well (Fortmeier & Schubert, 1995; Munns *et al.*, 1995; De Costa *et al.*, 2007). Cluster analysis enabled the use of both RLst and RWst in classifying the degree of Phase I salt tolerance of the 102 rice varieties tested. In a recent comprehensive review, Munns & Tester (2008) stated that significant genetic variation within species may exist in the osmotic response to salinity, but this has not yet been documented. Therefore, the demonstration of significant genetic variation in osmotic tolerance within the rice germplasm is one of the major highlights of the present study.

Under actual field conditions, salt stress in Phase I is likely to occur in fields that are in the early stages of salinity development or in fields that experience transient salinity, particularly during relatively dry periods. These relatively mild levels of salinity could be present either in the top soil or sub soil. The varieties that have been identified as 'highly tolerant' or 'tolerant' in Phase I (Tables 4 and 12) can be used straightaway in breeding programmes aimed at developing varieties suitable for areas experiencing relatively mild or transient salinity. The three new-improved varieties in the 'highly tolerant' group (i.e. At303, Bg350 and Bg450), all of which have higher yield potentials as compared to old-improved and traditional varieties, along with other desirable features of tolerance to common pests and diseases, can be recommended for areas of mild or transient salinity. However, the two traditional varieties (*Pola Al* and *Hetada Wee*) and the old improved variety (H9), which were in the 'highly tolerant' group cannot be recommended for cultivation because of their comparatively lower yield potentials and susceptibility to major pests and diseases. Alternatively, they can be used in breeding programmes as parents of potential salt tolerant varieties. The considerable number of 'moderately tolerant' varieties can be recommended for cultivation in areas of mild or transient salinity if they possess a high enough yield potential along with other desirable features such as tolerance to pests and diseases, superior grain quality and tolerance to other abiotic stresses such as drought, heat and iron toxicity. The identified 'moderately tolerant' varieties may also be used in breeding programmes if they possess specific desirable features.

The varieties that were identified as 'susceptible' or 'highly susceptible' should not be recommended for areas with mild or transient salinity nor should they be used in breeding programmes aimed at increasing salt tolerance in rice. However, they may be selected for breeding programmes or recommended for fields with comparatively greater or longer-term salinity, if they possess tolerance to salinity during Phase II (i.e. ionic stress tolerance). This will be reported in a subsequent companion paper.

Mechanisms of salt tolerance during phase I

While tolerance to water stress-induced osmotic stress is the major stress factor operating during Phase I, it is highly likely that excess Na^+ toxicity was also a significant stress factor in this phase. This was evident by the ranges of shoot and root Na^+ concentrations in the present study that were within the ranges observed for rice (Garcia *et al.*, 1997; Yeo *et al.*, 1999), wheat (Munns & James, 2003) and maize (Fortmeier & Schubert, 1995; Sümer *et al.*, 2004) growing under salinity. Accordingly, results of the present study showed that maintenance of whole plant and shoot water status as well as mechanisms to avoid (Na^+ exclusion) or tolerate Na^+ toxicity (tissue tolerance) contributed to Phase I salt tolerance in the identified rice varieties. One or two of all these mechanisms could be observed in the six varieties that were identified as 'highly tolerant' (Table 12). For example, Na^+ exclusion at the root surface was responsible for the high tolerance in At303, whereas Na^+ exclusion at the root xylem parenchyma was responsible in Bg450. It was only these two varieties among the six 'highly tolerant' varieties that were able to maintain low shoot Na^+ concentrations. The other four highly tolerant varieties had high shoot Na^+ concentrations, which indicated that they had high tissue tolerance to shoot Na^+. It is possible that part of the excess Na^+ in the shoot may be acting as active solutes for osmotic adjustment and thereby maintain tissue turgor (Munns & Tester, 2008). Our observation that salt tolerant rice varieties can have both high and low shoot Na^+ concentrations agrees with the observations of several other workers (Yeo *et al.*, 1990; Tester & Davenport, 2003; Munns & Tester, 2008). For example, although H9 had high Na^+ exclusion capability at the root surface, it could not prevent shoot Na^+ reaching a high level because of the poor Na^+ exclusion capability at the root xylem. Therefore, it was the high shoot tolerance to excess Na^+ and possibly osmotic adjustment that conferred Phase I salt tolerance to H9. In addition to high shoot tolerance to excess Na^+, maintenance of whole plant water content contributed to the high Phase I tolerance of Pola Al.

High tissue tolerance to excess shoot Na^+ was the most prominent mechanism of tolerance (Table 12) among the 25 varieties in the 'tolerant' group. Osmotic adjustment using the excess shoot Na^+ may also have contributed to the observed Phase I tolerance. As in the 'highly tolerant' group, in this group also, capacity to maintain whole plant and/or shoot tissue water content was not a prominent mechanism of tolerance. Only one (i.e. Bg352)

out of the 25 tolerant varieties had both whole plant and shoot relative RWCs at high levels. In comparison, eight out of the 25 tolerant varieties and three out of the six highly tolerant varieties had both shoot and whole plant relative RWCs at low levels. On the other hand, the capacity to maintain comparatively higher tissue water content was more prominent in the 'moderately tolerant' group than in the 'tolerant' and 'highly tolerant' groups. Similarly, Na^+ exclusion was also more prominent in the 'moderately tolerant' varieties than in the 'tolerant' and 'highly tolerant' varieties. Schubert (1999), as cited in Sümer *et al.* (2004), showed that the capacities for Na^+ exclusion at the root surface and the root xylem in salt-stressed maize are genetically distinct. Schubert *et al.* (2009) demonstrated for maize, that it is possible to combine these two capabilities of Na^+ exclusion at the two anatomically and genetically distinct sites through conventional breeding to develop varieties with superior Na^+ exclusion. They also showed that such varieties with superior Na^+ exclusion capability could then be crossed with inbred lines showing osmotic tolerance to breed salt tolerant maize varieties, which show superior yield performance under saline conditions. This strategy can be adopted to breed new rice varieties with superior salt tolerance using varieties that were identified as having the different mechanisms in Phase I salt tolerance in the present study. Such a breeding programme based on physiological criteria could accelerate the development of salt tolerant rice germplasm in Sri Lanka.

Comparison between traditional and improved varieties in Phase I salt tolerance

Interestingly, Phase I salt tolerance was present in both traditional and improved varieties. There were four improved varieties among the six varieties identified as 'highly tolerant', while 12 improved varieties were among the 25 identified as 'tolerant'. Conversely, both traditional and improved varieties were equally represented among the 'susceptible' and 'highly susceptible' varieties. This indicates that the physiological mechanisms and their molecular genetic basis are present in both traditional and improved varieties. Accordingly, both these varietal groups, particularly the improved varieties with high yield potentials and resistance to major diseases, can be used in breeding programmes aimed at improving Phase I salt tolerance in the Sri Lankan rice germplasm.

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