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A Mathematical Model Predicts Salt Tolerance in Upland Rice at the Germination Stage

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Keywords: Salt tolerance evaluation; Mathematical model; Salt tolerance indicators; Germination; upland rice.

Keywords: GR: Germination Rate; MFV: Membership Function Value; MST: Moderate Salt Tolerance; RFW: Root Fresh Weight; RL: Root Length; SII: Salt Injury Index; SFW: Shoot Fresh Weight; SL: Shoot Length; SS: Salt Sensitive; HST: High Salt Tolerance STI: Salt Tolerance Index; TFW: Total Fresh Weight; , WST: Weakly Salt Tolerant.

Abstract

Objective: Soil salinization is an important abiotic stressor limiting crop yield. Screening of upland rice germplasm resources during germination to choose salt-tolerant varieties for cultivation on saline land has great potential to improve crop yields.

Results: Here, we measured the germination rate (GR), root fresh weight (RFW), root length (RL), shoot fresh weight (SFW), shoot length (SL), and total fresh weight (TFW) of 25 upland rice varieties under salt treatment of 0 or 150 mM NaCl at 10 days after sowing (DAS). Under the stress of 150 mM NaCl, the GR, RFW, RL, SFW, SL and TFW of the measured upland rice varieties decreased to different degrees. Through cluster analysis, the salt tolerance of the tested varieties was divided into four categories: five varieties showed high salt tolerance (HST), seven showed moderate salt tolerance (MST), six showed weak salt tolerance (WST), and seven showed salt sensitivity (SS). The established salt tolerance formula for upland rice (Y = (0.311 × STI of RFW) + (0.382 × STI of RL) + (0.239 × STI of SFW) + (0.388 × STI of SL) + (0.903 × STI of TFW) − 0.051) can used to assess the salt tolerance of every upland rice variety. With 150 mM NaCl treatment, TFW was a reliable indicator of the salt tolerance of upland rice. We then used this information to develop an equation for a salt tolerance index (STI) based on TFW that could predict the salt tolerance of any upland rice variety.

Conclusion: In this study, 25 upland rice varieties were distributed into four classes according to cluster analysis: five HST, seven MST, six WST and seven SS. We put forward a mathematical equation that can predict any salt tolerance of upland rice, and conclude that TFW is a reliable physiological indicator to evaluate salt tolerance of upland rice. Our method has the potential to greatly improve upland rice yields in saline–alkali land by enabling salt tolerance evaluation and breeding of salt-tolerant crops.

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Introduction

Soil salinization has become a global focus. Current data shows that ~1.125 billion hectares of arable land worldwide are contained too much salt, with saline soil accounting for about one-fifth of all irrigated land [1]. In addition, irrigated land is decreasing by 1–2% a year because of soil salinization; at this rate, 50% of arable land will be lost by 2050 [2]. However, the world's population is growing rapidly, and it is estimated that by 2050 it will up to 9.6 billion [3]. As a result, total grain output worldwide is expected to rise by 38% and 57% by 2025 and 2050, respectively, to maintain current food supply [4].

Saline soil is widely distributed in China, which has ~100 million hectares, mainly in the semi-arid and arid areas north of the Yangtze River [5]. With limited land resources threatening sustainable food production, saline land represents a huge potential reserve of land resources in China; the development and utilization of saline land would be an effective way to enlarge the amount of cultivated land and safeguard the food supply. Therefore, the use of saline land to increase agricultural yields is an important element of future food security that can be achieved only by a major breakthrough in the cultivation of salt-resistant crop varieties [6].

The damage of salt to crops directly manifests as ion toxicity and osmotic stress, which lead to oxidative stress and other secondary injuries [7], ultimately impairing crop growth and yield. In a high-salt environment, the excess salt in the soil prevents seeds from germinating and growing, making it hard for the roots to absorb water suck moisture and even causes water leakage from the plant, thus damaging the normal physiological metabolism of the plant. With increasing salt concentrations, excessive accumulation of Na^+ in the cytoplasm causes various types of damage, such as blocked protein synthesis, decreased enzyme activity, weakened photosynthesis, and accelerated accumulation of toxic substances [8], which can slow plant growth, decrease yield, and ultimately lead to death [9].

.Plants generally show different sensitivities to salt stress at different developmental stages [10]. Seed germination is vital to plant growth and development and is highly affected by the surrounding environment. The germination stage of most plant seeds is sensitive to salinity [11]. For instance, with increased salt stress, the germination percentage and activity index of oat (*Avena sativa* L.) seeds gradually decrease, and the growth of radicle and germ slow, leading to a decline in yield [12]. Similarly, in soybean (*Glycine max* (Linn.) *Merr*.), salt damage can inhibit seed germination, affect nutrient growth, hinder the formation of root nodules, and significantly reduce soybean yield [13]. Therefore, increasing the GR under salt stress is the first requisite for planting crops in saline soil to increase yield.

Rice (*Oryza sativa* L.) is a vitally important crop and may play a critical role in solving the worldwide food crisis [14]. Rice is moderately salt sensitive; its growth is often restricted by drought and salinity. Drought can aggravate salt soil damage, and salt stress can inhibit water absorption, resulting in physiological drought. Rice cultivation in northern China is hampered by a shortage of fresh water resources and high cultivation costs, as the large areas of saline–alkali land in northern China are extremely short of fresh water resources. Upland rice, also known as land rice, is a type of cultivated rice that is tolerant of drought and salt [15]. Upland rice is sown by direct seeding, and water consumption during its whole growth period is only 20–30% of that of rice [16]. China has a long history of cultivation of upland rice, and diverse varieties exist. The unique physiological characteristics of upland rice are more suited to the arid and decertified areas of western and northern China than are those of other varieties. The promotion and cultivation of upland rice could not only boost local economic development, but also protect local ecological environments [17].

In the past few years, much work has been carried out to assess salt tolerance during rice germination [18,19]. The methods used have focused mainly on physiological indexes such as germination potential, GR, SL, RL, germination index and vitality index [15]; statistical methods such as clustering analysis and membership function method [20,21]; and biological approaches such as genome-wide association [22,23]. So far, little is reported about the evaluation of salt tolerance of upland rice. There is neither a unified method nor a reliable indicator to determine the salt tolerance of upland rice. Therefore, screening of upland rice germplasm resources for high salt tolerance and establishing reliable physiological indexes of salt tolerance are of great importance for breeding and cultivation of salt-tolerant upland rice in saline–alkali land, as well as for development and utilization of saline–alkali land in China to ensure food security.

In this study, we chose 25 widely cultivated upland rice varieties to evaluate and screen for salt tolerance during the germination stage. The evaluation methods include membership function, stepwise regression and cluster analysis. A mathematical model has been constructed, which can accurately predict the salt-tolerant ability of any upland rice variety during germination. We identified five HST, seven MST, six WST and seven SS varieties. Under 150 mM NaCl treatment, the membership function value (MFV) of the STI of TFW was shown to be a reliable index with which to determine the saline tolerance of upland rice during germination. These results hold great value for the cultivation of salt-tolerant upland rice varieties and the cultivation of saline–alkali land.

Materials and methods

Experiment materials

The seeds studied comprised 25 varieties of upland rice with different genetic backgrounds, which were kept in a refrigerator at a temperature < 4 °C before use.

NaCl treatment method

Healthy and uniform seeds (120 from each variety) were randomly chosen and soaked in distilled water for 24 hours to break dormancy. The seeds were incubated in 5% sodium hypochlorite solution for 30 minutes for disinfection and then washed with distilled water 3–5 times. Put the filter paper soaked with the corresponding solution on the 9 cm petri dish; each dish contains 20 seeds. NaCl solution mixed with 1/4 Hoagland's nutrient solution (pH 6.2) was used to impose salt stress, and control seeds were cultured with 1/4 Hoagland's nutrient solution. The upland rice seeds were cultured in an artificial climate chamber with relative humidity of 70%, the cultivation conditions were dark cultivation at 23 ± 3 °C for 10 h and light cultivation at 28 ± 3 °C for 14 h with a light intensity of 600 $\mu mol\ m^{-2}s^{-1}$.

Each treatment was repeated three times, and the corresponding solution was replaced every day. Record the number of germinated seeds every day at the same time after seed sowing. When the radicle emerged by 1 mm, the seed was considered to have germinated.

To determine the optimal NaCl concentration, a preliminary germination test was conducted. Eight upland rice varieties were randomly selected from the 25 varieties to be tested. A seven-concentration gradient of 0 (control), 50, 100, 125, 150, 175 and 200 mM NaCl in 1/4 Hoagland's nutrient solution (pH 6.2) was prepared; it was determined that 150 mM NaCl was the most suitable concentration for the experiment.

Determination of physiological parameters

The seeds of the 25 upland rice varieties of different genetic backgrounds were treated with 0 or 150 mM NaCl. Seed germination was observed every day from the second DAS, and the number of germinated seeds was recorded from 4 to 10 DAS. Upland rice seedlings with relatively uniform growth were randomly selected to measure SL and RL (cm) at 10 DAS. The TFW was obtained by summing SFW and RFW. The GR, STIs and salt injury indexes (SII) corresponding to the GR, RFW, RL, SFW, SL and TFW were calculated with the following equation:

GR (%) = (number of germinated seeds on 10th day/total number of tested seeds) × 100%;

STI = value of an indicator under salt stress/control value;

SII = 1 − STI

Evaluation of salt tolerance

Using the method of fuzzy comprehensive evaluation to evaluate the salt-tolerant ability of 25 upland rice varieties [24], the calculation formula of MFV is as follows:

$$X_i = (X_n - X_{min}) / (X_{max} - X_{min}) \times 100\%, \ i=1, 2, 3, \ldots, n$$

In the equation, X_i is the MFV of the STI of a certain index of an upland rice variety, X_n is the STI of a certain variety, X_{min} and X_{max} are the minimum and maximum values of an index STI of all varieties [25,26]. The mean MFV was the mean MFV of GR, RFW, RL, SFW, SL and TFW of each species. The salt tolerance of upland rice varieties can be evaluated on the basis of the mean MFV value of each physiological characteristic. The mean MFV value represents the saline tolerance of upland rice varieties.

Hierarchical clustering analysis of STI during germination

According to the method described by Wu et al, (2019), the 25 upland rice varieties were divided into HST, MST, WST and SS groups and a mathematical evaluation model was constructed as follows:

$$Y_i = \beta_1 X_{n1} + \beta_2 X_{n2} + \beta_3 X_{n3} + \beta_4 X_{n4} + \beta_5 X_{n5} + \mu, \ i=1, 2, 3, \ldots, n$$

In the equation, Y_i refers to the average MFV of a particular upland rice variety and X_{n1}–X_{n5} are the STIs of RFW, RL, SFW, SL and TFW of the nth upland rice variety, respectively. μ is the constant and β is the unstandardized coefficient.

Statistical analysis

Microsoft Office Excel 2003 was used to collect the data, and SPSS 22.0 software was used for cluster analysis, correlation analysis and multiple regression analysis. The membership function method was adopted.

Results

Determination of optimum salt stress concentration

To determine a suitable NaCl concentration, GRs of 8 upland rice varieties treated with 0, 50, 100, 125, 150, 175 or 200 mM NaCl were measured. With increasing NaCl concentration, GRs of all upland rice varieties showed a decreasing trend. The SII of GR under stress of different NaCl concentrations was calculated, and the functional relationship between SII and salt concentration was established by linear regression analysis (Figure 1). The salt concentration was 163.5 mM NaCl when the SII value decreased by 50% relative to the control value (0 mM NaCl). Therefore, we used 150 mM NaCl as the salt stress for subsequent experiments.

Correlation analysis of physiological indexes

RFW, RL, SFW, SL and TFW of upland rice varieties under salt stress decreased to different degrees compared with those of the control. Correlation analysis among different physiological parameters can reveal the degree of correlation between salt tolerance and these characteristics [27]. Therefore, we determined the RFW, RL, SFW, SL and TFW values of the 25 upland rice varieties under 150 mM NaCl (Supplementary Table S1) and calculated the STI of each characteristic (Supplementary Table S2). Correlation analysis of STI of physiological indicators under salinity stress was carried out to determine their relationship (Table 1). The STIs of RFW, RL, SFW, SL and TFW were positively correlated. Among them, STI of TFW related to STI of SFW strongly, with the correlation coefficient reaching 0.95, and the second strongest correlation is STI of SL and STI of SFW (0.92). The weakest correlation between STI of RL and STI of RL is 0.66.

Hierarchical cluster analysis

Membership function analysis of the STIs of RL, SL, TFW, RFW and SFW was conducted to obtain the MFV and the average MFV of each index (Supplementary Table S3). The high average MFV represents the strong salt tolerance of the plants. The shortest distance method of Euclidean distance was used for clustering analysis of the average MFV value (Figure 2). When the Euclidean distance was 3, upland rice varieties were classified into four classes: HST, MST, WST and SS (Supplementary Table S4). Among the 25 upland rice varieties, there were five SST, seven MST, six WST and seven SS varieties (Figure 3).

Construction of mathematical equation and identification of a reliable indicator of salt tolerance

The mean MFV and STIs of each Physiological trait was analyzed by regression analysis and a mathematical model for evaluating the salt-tolerant ability was established. According to Table 2, the regression equation was established as follows: (Y_i = (0.311 × STI of RFW) + (0.382 × STI of RL) + (0.239 × STI of SFW) + (0.388 × STI of SL) + (0.903 × STI of TFW) − 0.051). Where the numbers 0.382, 0.388, 0.311, 0.239 and 0.903 represent the non-standardized coefficients of the STIs of the corresponding indexes, −0.051 is the random error term, Y_i indicates the salt-tolerant ability of a certain upland rice variety.

To verify the mathematical model could accurately reflect the salt tolerance of any upland rice variety or not, the Y values of 25 upland rice varieties were calculated and compared with the mean MFV (Table 3). The mathematical model was shown to be highly reliable. For example, in h12 was calculated to be 0.38, which was very close to its mean MFV 0.39. The Y value of h51 was 0.80, and the mean MFV was 0.80. These data indicate that the Y value and the mean MFV are very close.

The high average MFV value represents the strong salt tolerance of the plants. The average value of MFV is determined by several physiological parameters: RFW, RL, SFW, SL and TFW, so the STIs values of these parameters are closely related to the mean MFV value. In order to determine which of these physiological characteristics is the most reliable indicator, a linear model is fitted with the average MFV value and STI values of each indicator (Figure 4). In the linear model, the higher the correlation coefficient (R^2) value, the more relevant this indicator and the mean MFV value. Figure 4 shows that the mean MFV and STI of TFW have the highest R^2 value, which up to0.97; Followed by R^2 of the mean MFV and STIs of SFW, SL and RL respectively 0.92, 0.87 and 0.80; The mean MFV and STI of RFW have the smallest R^2 value of 0.73. The results are consistent with Table 2. Table 2 has shown that the mean MFV and STI of TFW also had the highest the non-standardized coefficient. We have shown that TFW can be considered a reliable index to represent the strength of salt tolerance.

To verify whether TFW can really represent the strength of salt tolerance of upland rice, three varieties were randomly selected from among each group: HST, MST, WST and SS. The TFW of each was measured at 0 and 150 mM NaCl at 10 DAS (Figure 5). With increasing salt tolerance (SS < WST < MST < HST), the inhibition of salt stress on upland rice variety growth and TFW decreased. Under the condition of 150 mM NaCl (A, a), salt-sensitive varieties hardly germinated, and the average TFW per plant was only 0.46 mg. TFW values per plant for weakly salt tolerant (B, b) and moderately salt-tolerant plants (C, c) were 1.45 mg and 4.66 mg per plant, respectively, whereas the average TFW per plant of highly salt-tolerant plants (D, d) was 11.77 mg.

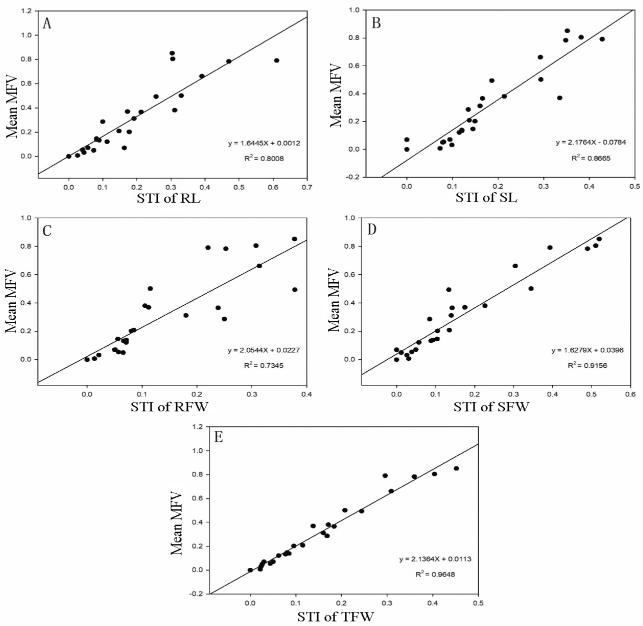

Figure 1: Selection of optimum salt concentration for evaluating salt-tolerant ability of 25 upland rice varieties. NaCl concentration was determined as the optimum salt concentration when the salt injury index (SII) of the Germination Rate (GR) was reduced to 50% of the control. Data in the figure are average germination rates of 8 upland rice varieties under each concentration of NaCl.

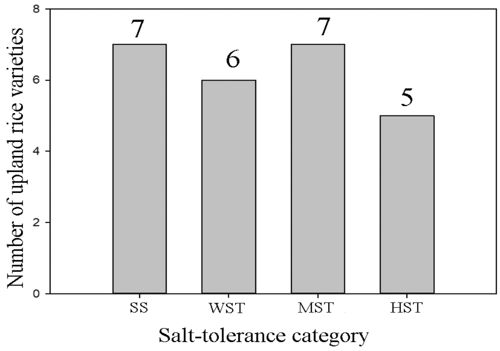

Figure 2: Hierarchical cluster analysis of the Membership Function Value (MFV) of 25 upland rice varieties under 150 mM NaCl stress.

HST: high salt tolerance; MST: moderate salt tolerance; WST: weak salt tolerance; SS: salt sensitive.

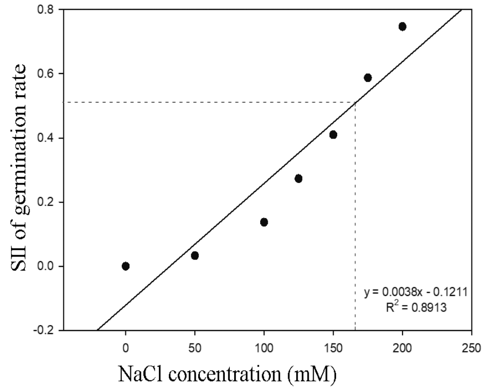

Figure 3: Number of 25 upland rice varieties with different salt-tolerance categories.

HST: high salt tolerance; MST: Moderate salt tolerance; WST: Weak salt tolerance; SS: salt sensitive.

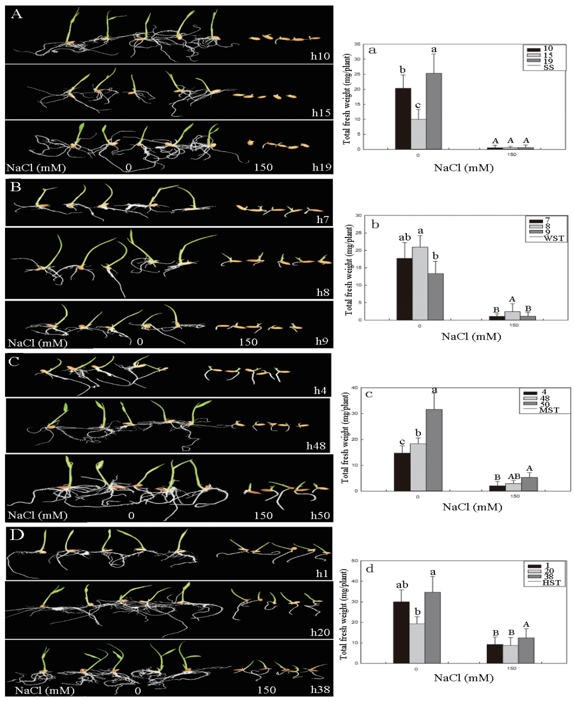

Figure 4: The linear fit between the STI of each physiological index and the mean MFV. (A): between STI of RL and mean MFV; (B): between STI of SL and mean MFV; (C): between STI of RFW and mean MFV; (D): between STI of SFW and mean MFV; (E): between STI of TFW and mean MFV.

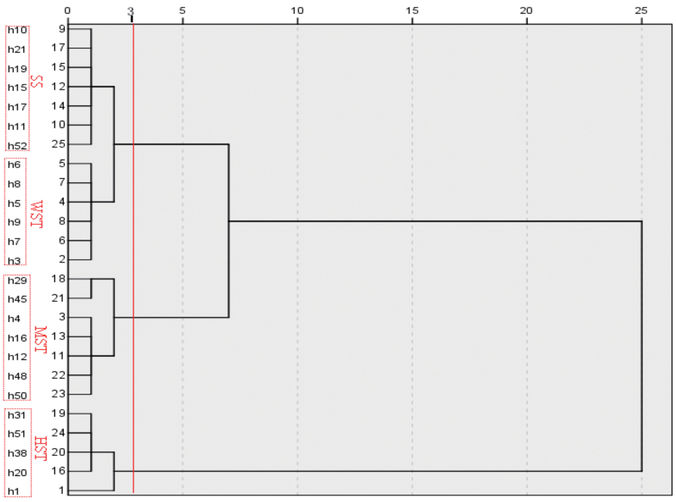

Figure 5: Growth status and total fresh weight of a plant of upland rice with different salt-tolerance categories treated with 0 and 150 mM NaCl. SS: A, a; WST: B, b; MST: C, c; HST: D, d. Data are means (n = 3) ± SD. Different letters indicate significant differences at P < 0.05.

Table 1: Correlative coefficients of physiological indexes (salt tolerance indices of root length (STI of RL), shoot length (STI of SL), root fresh weight (STI of RFW), shoot fresh weight (STI of SFW), and total fresh weight (STI of TFW)) of 25 upland rice varieties under 150 mM NaCl.

Indicator		STI of RL	STI of SL	STI of RFW	STI of SFW	STI of TFW
STI of RL	Pearson correlation	1	0.85**	0.66**	0.83**	0.82**
STI of SL	Pearson correlation	0.85**	1	0.68**	0.92**	0.88**
STI of RFW	Pearson correlation	0.66**	0.68**	1	0.70**	0.90**
STI of SFW	Pearson correlation	0.83**	0.92**	0.70**	1	0.95**
STI of TFW	Pearson correlation	0.82**	0.88**	0.90**	0.95**	1

*Correlation is significant at the 0.01 level

Table 2: Multiple regression analysis of salt tolerance index (STI) of each physiological index of 25 upland rice varieties under 150 mM NaCl.

Model	Unstandardized coefficients		Standardized coefficients	t	Significance
	μ or B	SE	β		
Constant	-0.051	0.007		-7.607	0.000
STI of RL	0.382	0.042	0.209	9.013	0.000
STI of SL	0.388	0.075	0.167	5.143	0.000
STI of RFW	0.311	0.262	0.130	1.185	0.250
STI of SFW	0.239	0.263	0.141	0.909	0.375
STI of TFW	0.903	0.571	0.416	1.748	0.097

* Where B stands for unstandardized coefficients(β). μ is the random error term. Mean MFV is the dependent variable, P<0.01.

Table 3: Validation of mathematical model for evaluating salt tolerance of upland rice under 150 mM NaCl.

Upland rice	STI of RL	STI of SL	STI of RW	STI of SW	STI of TW	Mean MFV	Y
h1	0.39	0.29	0.31	0.30	0.31	0.66	0.66
h3	0.08	0.14	0.06	0.10	0.08	0.15	0.15
h4	0.17	0.34	0.11	0.18	0.14	0.37	0.35

h5	0.09	0.12	0.07	0.09	0.08	0.13	0.14
h6	0.18	0.15	0.08	0.11	0.10	0.20	0.21
h7	0.11	0.11	0.07	0.06	0.06	0.12	0.13
h8	0.15	0.14	0.09	0.14	0.11	0.21	0.22
h9	0.08	0.12	0.07	0.09	0.08	0.14	0.15
h10	0.07	0.08	0.07	0.01	0.03	0.05	0.05
h11	0.03	0.07	0.01	0.03	0.02	0.01	0.02
h12	0.31	0.21	0.11	0.23	0.17	0.38	0.39
h15	0.06	0.09	0.05	0.05	0.05	0.07	0.08
h16	0.21	0.17	0.24	0.14	0.18	0.37	0.37
h17	0.16	0.00	0.05	0.00	0.03	0.07	0.15
h19	0.04	0.10	0.02	0.03	0.02	0.03	0.04
h20	0.30	0.35	0.38	0.52	0.45	0.85	0.85
h21	0.04	0.08	0.06	0.04	0.04	0.05	0.06
h29	0.26	0.19	0.38	0.13	0.24	0.49	0.49
h31	0.61	0.43	0.22	0.39	0.30	0.79	0.78
h38	0.47	0.35	0.25	0.49	0.36	0.78	0.78
h45	0.33	0.29	0.11	0.35	0.21	0.50	0.49
h48	0.19	0.16	0.18	0.14	0.16	0.31	0.32
h50	0.10	0.13	0.25	0.08	0.17	0.29	0.29
h51	0.31	0.38	0.31	0.51	0.40	0.80	0.80
h52	0.00	0.00	0.00	0.00	0.00	0.00	-0.05

Discussion

There are four categories of salt tolerance based on average MVF values

The evaluation and selection of salt-tolerant varieties during seed germination are important to extending upland rice planting areas and improving yield. Under 150 mM NaCl treatment, GR, RFW, RL, SFW, SL and TFW of 25 upland rice varieties decreased to different degrees. Salt stress significantly inhibited growth of upland rice during the germination stage. In this study, 25 upland rice varieties were distributed into four classes according to mean MVF: Five HST, seven MST, six WST and seven SS.

TFW is a reliable indicator to represent the strength of salt tolerance

Seed germination is the first period of crop growth and development, and the saline tolerance at the germination stage determines population and yield [28]. Therefore, accurate, rapid and scientific evaluation of salt resistance in crops during the germination period is very important. GR, RFW, RL, SFW, SL and TFW are commonly used to assess the salt-tolerant ability of crops during germination [15]. Evaluation of salt-tolerant ability in crops, such as corn [29,30], rice (Oryza sativa L.) [18,19,31], and sorghum (Sorghum bicolor L.) [32,33], have been based on different indicators and methods. However, no consistent conclusion has been made regarding the key indicators of salt tolerance at the germination stage [15]. Therefore, a convenient, effective and reliable salt tolerance indicator would promote accurate evaluation of crop salt tolerance, as well as be instrumental in the development of salt-tolerant varieties. In this study, on the basis of integrative analysis of the stepwise linear regression analysis of the MFV and five physiological parameters, combined with correlation analysis, we have shown that TFW is a key indicator of salt tolerance and the STI of TFW can effectively and reliably represent the salt-tolerant ability of upland rice in the germination stage under 150 mM NaCl treatment. This conclusion will provide the basis for more efficient evaluation and prediction of the salt-tolerant ability of upland rice.

Mathematical model for predicting salt tolerance of upland rice

Salt tolerance in crops is a complex character related to many factors and under the control of multiple genes. The physiological characters related to salt tolerance were different in different genotypes. As a result, a single index cannot reflect the salt tolerance of crops comprehensively and accurately [34]. In this study, RFW, RL, SFW, SL and TFW of upland rice during germination were determined to evaluate salt tolerance. STIs of the physiological indicators were calculated, and the MFV of the STI and the mean MFV of each indicator were calculated. By combining the average MVF and STI values of each indicator, we obtained a regression equation: (Y_i = (0.311 × STI of RFW) + (0.382 × STI of RL) + (0.239 × STI of SFW) + (0.388 × STI of SL) + (0.903 × STI of TFW) − 0.051). This equation can be used to predict the saline tolerance of any upland rice variety.

Conclusions

In this study, the salt-tolerant ability of upland rice during germination was determined with 150 mM NaCl as the optimum salt concentration. Five HST, seven MST, six WST and seven SS varieties were screened. We put forward a mathematical equation that can predict any salt tolerance of upland rice. We conclude that TFW is a reliable physiological indicator to evaluate salt tolerance of upland rice. These results will be promoted the evaluation of salt tolerance of upland rice and help for the cultivation of salt-resistant varieties.

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