Localization of salt-tolerant QTL in rice germination stage under different salinity concentrations

Yanning Wang · Liping Chen · Guiting Song · Tao Huang · Guangliang Wu · Jingai Tan · Peng Wang · Qin Cheng · Caijing Li · Qi Zhong · Shiyung Huang · Mengmeng Yang · Haohua He · Jianmin Bian

Abstract  Salt stress is an important abiotic stress, which has seriously affected the reproductive development of rice in many parts of the world. Therefore, it is particularly important to understand the genetic mechanism of salt tolerance in rice. In this study, we preliminarily located some quantitative trait loci (QTL) for root length, bud length, and survival percent under different salinity conditions (0, 100, 200 and 400 mM NaCl), using a population of chromosome segment substitution lines (CSSLs) constructed by Nipponbare and 9311. A total of 18 QTLs were identified, which explained the phenotypic variation of 4.76–37.59%, among which 13 QTLs were detected under salt stress condition. These salt tolerance related QTLs were divided into two categories, QTL expressed both under control and salt stress conditions (qSP3, qBL8), and QTL expressed just under salt stress condition (qBL3, qRL3, qSP4, qRL5, qSP7, qSP9, qRL10, qBL11-1, qRL11-1, qRL11, qSP12, qSP3, qSP4, qRL5, qSP7, qRL10, qRL10-1, qRL11, qRL11-1, qBL11, qBL11-1 and qSP12 were reported to be related with salt stress for the first time. These QTLs identified under salt stress may be valuable genetic factors for improving salt tolerance of rice by molecular markers technology, which will help to further understand the genetic mechanism of salt tolerance of rice.

Keywords  Rice · Salt stress · Root length · Bud length · Survival percent · QTL

Introduction

Rice is the staple grain crop in the world, feeding half of the world’s population (Lai et al. 2016; Pires et al. 2015; Shi et al. 2017). Salinization of land is a serious problem in agriculture, which is one of the major abiotic stress (Kumari et al. 2018). Due to unsustainable farming methods, poor irrigation methods (He et al. 2019; Li et al. 2019), sea level rise and improper use of fertilizers (Punyawaew et al. 2016; Yang and Guo 2018), most of the land and irrigated fields in the world are affected by salt stress (Pires et al. 2015), which severely affects the growth and development of crops (Shi et al. 2017). Rice is a glycophyte with different sensitivity to salt stress at different development stages (Rao et al. 2018; Wang et al. 2011). Salt stress has a serious effect on seed germination,
seedlings and reproductive development in the rice (Ganie et al. 2019). Therefore, the breeding of salt-tolerant rice varieties is an important target for breeders and also an effective method to reduce salt stress damage in rice (Lekklar et al. 2019; Shi et al. 2017).

The previous research showed that the salt tolerance of rice was controlled by many genes (Lekklar et al. 2019), and the related traits of salt tolerance were complex (Li et al. 2019). Mining and utilizing salt-tolerant genes/QTL is not only beneficial to the cultivation of salt-tolerant rice (Lin et al. 2004), but also have great significance for understanding the genetic mechanism of salt tolerance in rice (He et al. 2017; Wang et al. 2012b). With the development of molecular marker technology, genetic mapping has become a powerful tool to identify QTL/genes that control important complex agronomic traits (Mardani et al. 2014; Pandit et al. 2010). In rice, many QTLs of salt tolerance have been identified by genetic map, most of which were located on chromosomes 1, 2, 6 and 7, and a few are located on chromosomes 10 and 11 (Ammar et al. 2009; Zheng et al. 2015), but so far only a few salt tolerance genes have been cloned (Jahan et al. 2020). SKC1 is the first salt-tolerant gene successfully isolated by map-based cloning, which is located on chromosome 1 (Ren et al. 2005). SKC1 encodes a sodium transporter of HKT family (Li et al. 2017), which regulates Na+/K+ homeostasis under salt stress (He et al. 2019). Another salt-tolerant gene, DST, was obtained from salt-tolerant mutants by map-based cloning and located on chromosome 3 (Li et al. 2019). DST encodes a new zinc finger transcription factor, which negatively regulates the drought and salt tolerance of rice (Huang et al. 2009). HST1 is a newly identified salt-tolerant gene, which encodes a B-type response regulatory protein OsR22. HST1 may be involved as a transcription factor in regulating the expression of osmotic or ion transport related genes (Takagi et al. 2015). Although many QTLs for salt tolerance have been identified in rice, there are few studies on QTLs for salt tolerance under different salinity concentrations (Wang et al. 2012b), and the regulation mechanism of salt tolerance in rice is still unclear.

In this study, a set of chromosome segment substitution lines (CSSLs), included 118 lines, derived from indica 9311 and japonica Nipponbare, were used to map and analyze the QTL for root length (RL), bud length (BL) and survival percent (SP) under different salinity concentrations at germination stage in rice. The aim of this study was to explore the genetic mechanism for salt stress tolerance and provide QTL for salt-tolerance rice varieties breeding by molecular-assisted selection (MAS) (Lai et al. 2016; Mardani et al. 2014).

Materials and methods

Plant materials

A set of CSSL population, included 118 lines, derived from 9311 and Nipponbare. 9311, an indica variety, was used as the recipient parent; Nipponbare, an elite japonica variety, was used as the donor.

Stress treatment and evaluation

Fourty filled and healthy seeds of parents and CSSLs were sterilized in 10% sodium hypochlorite solution for 15 min and then rinsed with distilled water for three times (Mardani et al. 2014; Shi et al. 2017). The seeds were soaked in distilled water for 3 days to germinate (Li et al. 2017; Wang et al. 2012b). Finally, 30 uniform germinated seeds were selected and placed in a petri dish with single-layer filter paper (Li et al. 2017). In the experimental group, the seeds were treated with 100 mM, 200 mM and 400 mM sodium chloride solution. In the control group, the seeds were treated with distilled water (0 mM NaCl condition). Each treatment has three replications (Wang et al. 2011). The treated seeds were cultured in an artificial climate chamber, maintaining a 14-h light/10-h dark cycle (27 °C/25 °C) and 80% relative humidity (Shi et al. 2017; Wu et al. 2020). The solutions were replaced everyday ensure that the concentration of sodium chloride solution and the volume of distilled water remain unchanged (Mardani et al. 2014). The RL, BL and SP of each line were measured and collected on seventh day (Basu et al. 2017).

Statistical analyses

Statistical analysis and QTL mapping of CSSLs population treated with different concentrations of sodium chloride were carried out by QTL IciMapping version 4.2 (Meng et al. 2015). The correlation
analysis between RL, BL and SP were conducted by SPSS.statistics.22 software.

Identification of QTL

Taking RL, BL and SP under different concentrations of sodium chloride treatment as indicators, QTL mapping for salt tolerance in rice germination stage was carried out on CSSLs population by QTL IciMapping version 4.2 (Meng et al. 2015), and LOD > 2.5 was selected as threshold to determine whether QTL existed (Zheng et al. 2015). QTL nomenclature refers to the method proposed by McCouch (Lai et al. 2016; Wang et al. 2011).

Results

Phenotypic variation of parents and CSSLs population

The values of RL, BL and SP of parents and CSSLs population under different salinity conditions are shown in Table 1. There is a significant difference in RL between 9311 and Nipponbare under 0 and 100 mM NaCl conditions, and the length of 9311 is significantly higher than that of Nipponbare (Fig. 1); There is a significant difference in BL between 9311 and Nipponbare under 0, 100 and 400 mM NaCl conditions, and the length of 9311 is significantly lower than that of Nipponbare (Fig. 1). There was no significant difference in SP under different salinity conditions. RL, BL and SP of CSSLs population showed continuous frequency distribution and transgressive segregation, which were consistent with the genetic characteristics of quantitative traits (Fig. 2).

Phenotypic correlation

Pearson correlation coefficients of three salt-tolerant traits RL, BL and SP under different salinity conditions are shown in Table 2. RL, BL and SP were significantly correlated at 200 and 400 mM NaCl ($p < 0.01$), although there was no correlation between RL and SP at 200 mM NaCl. There is no significant correlation between RL, BL and SP under control and 100 mM NaCl, although there is a correlation between RL and BL under 100 mM NaCl ($p < 0.05$).

QTL analysis

Under different salinity conditions, QTLs for three salt-tolerant traits are shown in Table 3, and the positions of these QTLs on chromosomes are shown in Fig. 3.

QTLs for root length

Seven QTLs were detected for RL (Fig. 3, Table 3). Under controlled condition, $qRL1$ and $qRL10-1$ were located on chromosome 1 and 10, with LOD values of 3.46 and 3.88, which explained 10.41% and 11.96% of phenotypic variation, respectively. Under the 100 mM NaCl condition, $qRL10$ was

| Table 1 | Phenotypic values of parents and CSSLs under different salinity conditions |
|----------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Treatments | Indices | Parents | CSSLs | Parents | CSSLs | Parents | CSSLs |
| | | RL | BL | SP | RL | BL | SP | RL | BL | SP | RL | BL | SP | RL | BL | SP |
| Water (control) | RL | 4.86 | 3.43 | 3.47 | 7.12 | 5.69 | 0.48 |
| | BL | 4.37 | 3.84 | 3.41 | 5.45 | 4.60 | 0.19 |
| | SP | 1.00 | 1.00 | 0.92 | 1.00 | 0.99 | 0.00 |
| 100 mM NaCl | RL | 2.27 | 1.54 | 0.61 | 2.12 | 1.30 | 0.11 |
| | BL | 3.09 | 2.69 | 1.45 | 3.70 | 2.83 | 0.13 |
| | SP | 1.00 | 1.00 | 0.88 | 1.00 | 0.99 | 0.00 |
| 200 mM NaCl | RL | 0.89 | 0.76 | 0.18 | 1.37 | 0.49 | 0.03 |
| | BL | 1.57 | 1.60 | 1.06 | 2.41 | 1.75 | 0.08 |
| | SP | 1.00 | 0.99 | 0.70 | 1.00 | 0.95 | 0.00 |
| 400 mM NaCl | RL | 0.00 | 0.00 | 0.00 | 0.24 | 0.04 | 0.00 |
| | BL | 0.45 | 0.75 | 0.00 | 1.11 | 0.24 | 0.05 |
| | SP | 0.94 | 0.94 | 0.00 | 1.00 | 0.13 | 0.02 |

$RL$ root length, $BL$ bud length, $SP$ survival percent
located on chromosome 10, with LOD value of 3.11, which explained 11.43% of phenotypic variation. Under the 200 mM NaCl condition, QTLs $qRL_{5}$, $qRL_{11}$, $qRL_{11-2}$ were located on chromosome 5 and 10, with LOD values of 3.15, 8.52 and 4.36, which explained the phenotypic variation of 4.76%-14.34%. Under the 400 mM NaCl condition, $qRL_{3}$ was located on chromosome 3, with LOD value of 5.70, which explained 19.93% of phenotypic variation.
QTLs for bud length

Four QTLs were detected for BL (Fig. 3, Table 3). Under controlled condition, $qBL8$ and $qBL11$ were located on chromosome 8 and 11, with LOD values of 5.13 and 2.92, which explained 15.84% and 8.63% of phenotypic variation, respectively. Under the 100 mM NaCl condition, there was no QTL detected. Under the 200 mM NaCl condition, QTLs $qBL8$ and $qBL11-1$ were located on chromosome 8 and 11, with LOD values of 2.56 and 3.58, which explained the phenotypic variation of 7.99% and 11.41%, respectively. Under the 400 mM NaCl condition, $qBL3$ was located on chromosome 3, with LOD value of 3.43, which explained 12.51% of phenotypic variation.

QTLs for survival percent

Seven QTLs were detected for SP (Fig. 3, Table 3). Under controlled condition, $qSP2$, $qSP3$ and $qSP7-1$ were located on chromosome 2, 3 and 7, with LOD values of 3.69, 4.31 and 15.31, which explained 7.07%, 8.46% and 37.59% of phenotypic variation, respectively. Under the 100 mM NaCl condition, $qSP12$ was located on chromosome 12, with LOD value of 6.26, which explained 19.61% of

---

Table 2 The correlation of tolerance indices under different salinity conditions

| Traits | Water (control) | 100 mM NaCl | 200 mM NaCl | 400 mM NaCl |
|--------|----------------|-------------|-------------|-------------|
|        | RL  | BL  | SP  | RL  | BL  | SP  | RL  | BL  | SP  | RL  | BL  | SP  |
| RL     | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   |
| BL     | 0.175 | 1   | 0.190* | 1   | 0.370** | 1   | 0.760** | 1   |
| SP     | -0.103 | -0.013 | 1   | -0.063 | -0.138 | 1   | -0.046 | 0.324** | 1   | 0.518** | 0.575** | 1   |

**Correlation is significant at the 0.01 level
*Correlation is significant at the 0.05 level

Table 3 The QTLs for salt tolerance indices under different salinity conditions

| Treatment | Indices | QTL | Chr | Marker | LOD | Add | PVE (%) |
|-----------|---------|-----|-----|--------|-----|-----|---------|
| Water (control) | RL | $qRL1$ | 1 | chr1-bin5 | 3.46 | -0.56 | 10.41 |
| | | $qRL10-1$ | 10 | chr10-bin508 | 3.88 | -0.65 | 11.96 |
| | BL | $qBL8$ | 8 | chr8-bin428 | 5.13 | -0.48 | 15.84 |
| | | $qBL11$ | 11 | chr11-bin544 | 2.92 | -0.23 | 8.63 |
| | SP | $qSP2$ | 2 | chr2-bin127 | 3.69 | -0.01 | 7.07 |
| | | $qSP3$ | 3 | chr3-bin146 | 4.31 | -0.02 | 8.46 |
| | | $qSP7-1$ | 7 | chr7-bin378 | 15.36 | -0.04 | 37.59 |
| 100 mM NaCl | RL | $qRL10$ | 10 | chr10-bin501 | 3.11 | -0.21 | 11.43 |
| | SP | $qSP12$ | 12 | chr12-bin600 | 6.26 | -0.05 | 19.61 |
| 200 mM NaCl | RL | $qRL5$ | 5 | chr5-bin295 | 3.16 | 0.28 | 4.76 |
| | | $qRL11$ | 11 | chr11-bin593 | 8.52 | 0.17 | 14.34 |
| | | $qRL11-1$ | 11 | chr11-bin596 | 4.36 | -0.14 | 6.74 |
| | BL | $qBL8$ | 8 | chr8-bin428 | 2.56 | -0.23 | 7.99 |
| | | $qBL11-1$ | 11 | chr11-bin546 | 3.58 | -0.18 | 11.41 |
| | SP | $qSP7$ | 7 | chr7-bin370 | 6.64 | -0.05 | 22.55 |
| | | $qSP9$ | 9 | chr9-bin463 | 2.54 | -0.04 | 7.95 |
| 400 mM NaCl | RL | $qRL3$ | 3 | chr3-bin139 | 3.70 | 0.06 | 19.93 |
| | BL | $qBL3$ | 3 | chr3-bin139 | 3.43 | 0.22 | 12.51 |
| | SP | $qSP3$ | 3 | chr3-bin146 | 5.96 | 0.37 | 18.38 |
| | | $qSP4$ | 4 | chr4-bin211 | 3.50 | 0.14 | 10.28 |
phenotypic variation. Under the 200 mM NaCl condition, QTLs $qSP7$ and $qSP9$ were located on chromosome 7 and 9, with LOD values of 6.64 and 2.54, which explained the phenotypic variation of 22.55% and 7.95%, respectively. Under the 400 mM NaCl condition, $qSP3$ and $qSP4$ was located on chromosome 3 and 4, with LOD value of 5.96 and 3.50, which explained 18.38% and 10.28% of phenotypic variation.

**Discussion**

For breeders, it is a feasible way to cultivate salt-tolerant rice by aggregating salt-tolerant QTL Genes (Ganie et al. 2019). The detection of QTL is greatly promoted by using multiple related traits under different salinity concentrations (Wang et al. 2012b). In order to reveal the genetic control of salt tolerance at rice germination stage, 18 QTLs were identified on 12 chromosomes by using the newly constructed genetic map under different salinity conditions (0, 100, 200 and 400 mM NaCl).

**Comparison of the detected QTLs**

By comparing the chromosome positions of QTLs detected in our study with previously identified genes (QTLs) (http://qtaror.abr.affrc.go.jp/cgi-bin/gbrowse/Oryza_sativa/), we found that three QTLs in this study were close to the positions of several genes (QTLs) related to salt tolerance that have been mapped. For example, $qBL8$ located on chromosome 8 has the same chromosome interval as OsCPK21, which is involved in the positive regulation of abscisic acid and salt stress signal pathway (Asano et al. 2011). The $qSP9$ on chromosome 9 has the same chromosome interval as OsRNS4 (Zheng et al. 2014). The $qRL3$ located on chromosome 3 has the same chromosome interval as OsSUT1 and OsJAZ9. OsJAZ9 is involved in regulating potassium homeostasis, affecting Na$^+$/K$^+$ homeostasis and improving salt tolerance of rice (Siahpoosh et al. 2012; Wu et al. 2015). These coincidences indicate that QTL mapping results are reliable and accurate. Moreover, 14 QTLs ($qRL1$, $qSP2$, $qSP7-1$, $qRL10-1$, $qBL11$, $qSP3$, $qSP4$, $qRL5$, $qSP7$, $qRL10$, $qRL11$, $qRL11-1$ and $qSP12$) were detected for the first time, and the

---

**Fig. 3** Position of QTL for RL, BL and SP in CSSLs population under different salinity conditions
chromosome segment substitution lines harboring these QTLs also could serve as candidates for future fine mapping and positional cloning projects.

$qSP3$ and $qBL8$ were located in Chr3-bin146 and Chr8-bin428, respectively (Fig. 3, Table 3). These QTLs are highly repetitive and have been detected under two different salinity conditions. These QTLs with large phenotypic variation can be further studied. Although $qSP3$ and $qBL8$ were detected at different concentrations, the other QTLs were rarely co-located under different salinity concentrations. $qRL3$ and $qBL3$ controlling different traits were detected at the same chromosomal position, which may be related to the pleiotropy of QTLs, that is, QTLs of a certain segment on the chromosome act on multiple traits at the same time, which is common in rice (Lin et al. 2004). These QTL regions located in the same place are very useful for improving multiple salt stress traits at the same time (Lai et al. 2016).

QTLs related with salt stress

In this study, a total of 18 QTLs were located, of which 5 QTLs were detected just under control conditions and the other 13 QTLs were detected under salt stress. These 13 QTLs identified under the salt stress were connected with salt tolerance, and could be divided into two categories: first, QTLs were expressed in both control and salt stress conditions, but the expression level were different, such as $qSP3$ and $qBL8$, suggesting that the salt treatment significantly affected the expression level of the genes underlying these QTLs; second, QTLs were detected just under salt stress condition, such as $qBL3$, $qRL3$, $qSP4$, $qRL5$, $qSP7$, $qSP9$, $qRL10$, $qBL11-1$, $qRL11-1$, $qRL11$ and $qSP12$, which indicated that the genes underlying these QTLs were induced significantly after salt stress, when they were not normally expressed or expressed very lowly under control condition. The salt tolerance of rice was improved via a design-breeding approach according to the different expression ways of genes underlying these salt stress related QTLs.

Candidate genes for salt tolerance QTLs

For the new major QTLs responsible for salt tolerance, we conducted further candidate genes analysis of $qSP3$, $qSP4$, $qRL10$, $qBL11-1$, $qRL11$ and $qSP12$, whereas the interval for each QTL was less than 500 kb. The result showed that there were 198 putative genes underlying the six QTLs. Homologous analysis showed that 10 of the 198 putative candidate genes were closely related to previously characterized salt-tolerant genes (Asano et al. 2011; He et al. 2019; Huang et al. 2008; Siahpoosh et al. 2012; Toda et al. 2013; Wadekar et al. 2013; Wang et al. 2012a; Wu et al. 2015; Zhou et al. 2013) (Fig. 4, Table 4). The predicted candidate genes in this study will provide some reference for cloning salt-tolerant genes, although these candidate genes may need to be verified in the future. Interesting, the candidate gene $LOC_Os12g02200$ of $qSP12$ detected in our study codes for calcineurin-like phosphatase β subunit interacting protein kinase. Previous studies have shown that calcineurin β subunit interacting protein kinase family gene $OsCIPK31$ is involved in salt stress in rice (Piao et al. 2010). This result further indicates the rationality and reliability of candidate gene analysis, thus, the chromosome segment substitution lines harboring $qSP12$ represented a good candidate for $LOC_Os12g02200$ cloning under salt stress in the future.

Potential implication in rice salt tolerance breeding

Most of the QTLs previously located are based on recombinant inbred lines or backcross inbred line population (Luo et al. 2020; Wang et al. 2012b), and few of them use chromosome segment substitution lines. In this study, the population of CSSLs comprised of 118 lines, and each line of CSSLs population is homozygous with good stability. As the background of most receptor parents in multi-generation backcross is gradually covered by recurrent parents, the interference of genetic background is eliminated, and the accuracy of QTL detection is improved (Bian et al. 2010). Therefore, CSSLs carrying QTLs detected under salt stress is an effective resource for improving salt tolerance of rice (Bian et al. 2010). These markers are closely linked with rice salt tolerance QTLs (Lin et al. 2004), which will provide reference for rice salt tolerance breeding, contribute to the polymerization of rice salt tolerance QTLs, and realize high level of salt tolerance of rice.
Acknowledgements  We thank the anonymous referees for their critical comments on this manuscript. This research was supported grants (20192ACBL20017; 20192BCB23010) from Project of Science and Technology Department of Jiangxi Province, grant (GJJ170241) from Project of Science and Technology Department of Department of Education of Jiangxi Province and grant (201910410003) from National Undergraduate Training Program for Innovation and Entrepreneurship.

Fig. 4 Evolutionary tree of candidate genes and salt tolerance related genes

Table 4 Candidate genes related to salt stress

| QTL  | Putative genes | Gene name or annotation                                                                 | Reference genes |
|------|----------------|----------------------------------------------------------------------------------------|-----------------|
| qSP3 | LOC_Os03g21320 | Retrotransposon protein, putative, unclassified, expressed                             | OsJAZ9; OsTIFY11a |
|      | LOC_Os03g21480 | HAD superfamily phosphatase, putative, expressed                                       | DST             |
|      | LOC_Os03g21820 | Cell wall relaxation protein                                                           | OsCPK21         |
|      | LOC_Os03g21400 | Cytochrome p450                                                                         | DST             |
|      | LOC_Os03g21390 | None                                                                                   | OsHKT1          |
| qRL10| LOC_Os10g26190 | None                                                                                   | OsHAK21; qSE3   |
| qBL11-1| LOC_Os11g11090 | None                                                                                   | OsSLUT1         |
| qRL11| LOC_Os11g41890 | RNA recognition motif containing protein, putative, expressed                          | RSS3            |
| qSP12| LOC_Os12g02200 | Calcineurin-like phosphatase β subunit interacting protein kinase                      | SRWD4           |
|      | LOC_Os12g02170 | Retrotransposon protein, putative, SINE subclass, expressed                           | SRWD1           |
Funding This research was supported grants (20192AC81003; 20192CBB23010) from Project of Science and Technology Department of Jiangxi Province, grant (JG170241) from Project of Science and Technology Department of Department of Education of Jiangxi Province and grant (201910410003) from National Undergraduate Training Program for Innovation and Entrepreneurship.

Declarations

Conflict of interest The authors declare there are no conflicts of interest.

References

Ammar MHM, Pandit A, Singh RK, Sameena S, Singh NK (2009) Mapping of QTLs controlling Na+, K+ and Cl− ion concentrations in salt tolerant indica rice variety CSR27. J Plant Biochem Biotechnol 18(2):139–150
Asano T, Hakata M, Nakamura H, Aoki N, Komatsu S, Ichikawa H, Hirochika H, Oh sugi R (2011) Functional characterisation of OsCIPK21, a calcium-dependent protein kinase that confers salt tolerance in rice. Plant Mol Biol 75(1–2):179–191. https://doi.org/10.1007/s11103-010-9717-1
Basu S, Giri RK, Benazir I, Kumar S, Rajwanshi R, Dwivedi SK, Kumar G (2017) Comprehensive physiological analyses and reactive oxygen species profiling in drought tolerant rice genotypes under salinity stress. Physiol Mol Biol Plants 23:837–850
Bian JM, Jiang L, Liu LL, Wei XJ, Xiao YH, Zhang LJ, Zhao ZG, Zhai HQ, Wan JM (2010) Construction of a new set of rice chromosome segment substitution lines and identification of grain weight and related traits QTLs. Breed Sci 60(4):305–313. https://doi.org/10.1270/jsbbs.60.305
Ganie SA, Molla KA, Henry RJ, Bhat KV, Mondal TK (2019) Advances in understanding salt tolerance in rice. Theor Appl Genet 138:851–870
He X, Li L, Xu H, Xi J, Xu Z (2017) A rice Jacalin-related mannose-binding lectin gene, OsJRNL, enhances Escherichia coli viability under high salinity stress and improves salinity tolerance of rice. Plant Biol 19(2):257
He Y, Yang B, He Y, Zhan C, Cheng Y, Zhang J, Zhang H, Cheng J, Wang Z (2019) A quantitative trait locus, qSE3, promotes seed germination and seedling establishment under salinity stress in rice. Wiley-Blackwell Online Open 97(6):1089–1104
Huang J, Wang MM, Bao YM, Sun SJ, Pan LJ, Zhang HS (2008) SRWD: a novel WD40 protein subfamily regulated by salt stress in rice (Oryza sativa L.). Gene 424(1–2):71–79. https://doi.org/10.1016/j.gene.2008.07.027
Huang XY, Chao DY, Gao JP, Zhu MZ, Shi M, Lin HX (2009) A previously unknown zinc finger protein, DST, regulates drought and salt tolerance in rice via stomatal aperture control. Genes Dev 23(15):1805–1817. https://doi.org/10.1101/gad.1812409
Jahan N, Zhang Y, Ly Y, Song M, Guo L (2020) QTL analysis for rice salinity tolerance and fine mapping of a candidate locus qSL7 for shoot length under salt stress. Plant Growth Regul 90(1):307–319
Kumari R, Kumar P, Sharma VK, Kumar H (2018) Seedling stage salt stress response specific characterization of genetic polymorphism and validation of SSR markers in rice. Physiol Mol Biol Plants 25(2):1–13
Lai Y, Cheng J, Wang Z, Zhang H, He Y (2016) Identification of QTLs with additive, epistatic, and QTL × seed maturity interaction effects for seed vigor in rice. Plant Mol Biol Rep 34:160–171
Lekklar C, Pongpanich M, Suriya-arunroj D, Chinponganich A, Tsai H, Comai L, Chadhawan S, Bubooocha T (2019) Genome-wide association study for salinity tolerance at the flowering stage in a panel of rice accesses from Thailand. BMC Genom. https://doi.org/10.1186/s12864-018-5317-2
Li N, Sun J, Wang J, Liu H, Zheng H, Yang L, Li X, Zou D, Virk P (2017) QTL analysis for alkaline tolerance of rice and verification of a major QTL. Plant Breed 136:881–891
Li N, Zheng H, Cui J, Wang J, Zou D (2019) Genome-wide association study and candidate gene analysis of alkalinity tolerance in japonica rice germplasm at the seedling stage. Rice 12(1):24
LinHX, ZhuMZ, YanoM, GaoJP, LiangZW, SuWA, Hu-XH, RenZH, ChaoDY (2004) QTLs for Na+ and K+ uptake of the shoots and roots controlling rice salinity tolerance. Theor Appl Genet 108(2):253–260
Luo X, Deng H, Wang P, Zhang X, Li C, Li C, Tan J, Wu G, Wang Y, Cheng Q, He H, Bian J (2020) Genetic analysis of germinating ability under alkaline and neutral salt stress by a high-density bin genetic map in rice. Euphytica 216(7):1–12. https://doi.org/10.1007/s10681-020-02623-9
Mardani Z, Rabiei B, Sabouri H, Sabouri A (2014) Identification of molecular markers linked to salt-tolerant genes at germination stage of rice. Plant Breed 133(2):196–202
Meng L, Li H, Zhang L, Wang J (2015) QTL IciMapping: integrated software for genetic linkage map construction and quantitative trait locus mapping in biparental populations. Crop J 3(3):269–283
Pandit A, Rai V, Bai S, Sinha S, Kumar V, Chauhan M, Gautam RK, Singh R, Sharma PC, Singh AK (2010) Combining QTL mapping and transcriptome profiling of bulked RILs for identification of functional polymorphism for salt tolerance genes in rice (Oryza sativa L.). Mol Genet Genom 284(2):121–136
Piao HL, Xuan YH, Park SH, Je BI, Park SJ, Kim CM (2010) Characterisation of OsCPK21, a calcium-dependent protein kinase that confers salt tolerance in rice. Theor Appl Genet 120(4):851–870
Punyawaew K, Suriya-arunroj D, Siangliw M, Thida M, Lanceras-Siangliw J, Fukuji S, Toojinda T (2016) Thai jasmine rice cultivar KDML105 carrying Salttol QTL exhibiting salinity tolerance at seedling stage. Mol Breed 36(11):150
Rao PVR, John O, Kumar SP (2018) Identification of QTLs for salt tolerance traits and prebreeding lines with enhanced salt tolerance in an introgression line population of rice. Plant Mol Biol Rep 36:695–709
Ren ZH, Gao JP, Li LG, Cai XL, Huang W, Chao DY, Zhu MZ, Wang ZY, Luan S, Lin HX (2005) A rice quantitative trait locus for salt tolerance encodes a sodium transporter. Nat Genet 37:1141–1146
Shi Y, Gao L, Wu Z, Zhang X, Wang M, Zhang C, Zhang F, Zhou Y, Li Z (2017) Genome-wide association study of salt tolerance at the seed germination stage in rice. BMC Plant Biol 17(1):92
Siahpoosh MR, Sanchez DH, Schlereth A, Scofield GN, Furhank RT, van Dongen JT, Kopka J (2012) Modification of OsSUT1 gene expression modulates the salt response of rice Oryza sativa cv. Taipei 309. Plant Sci 182:101–111. https://doi.org/10.1016/j.plantsci.2011.01.001
Takagi H, Tamiru M, Abe A, Yoshida K, Uemura A, Yaegashi H, Obara T, Oikawa K, Kanzaki E, Mitsuoka C, Natsume S, Kosugi S, Kanzaki H, Matsumura H, Urasaki N, Kamoun S, Terauchi R (2015) MutMap accelerates breeding of a salt-tolerant rice cultivar. Nat Biotechnol 33(5):445–449. https://doi.org/10.1038/nbt.3188
Toda Y, Tanaka M, Ogawa D, Kurata K, Kurotani K, Habu Y, Ando T, Sugimoto K, Mitsuda N, Katoh E, Abe K, Miyao A, Hirochika H, Hattori T, Takeda S (2013) RICE SALT SENSITIVE3 forms a ternary complex with JAZ and class-C bHLH factors and regulates jasmonate-induced gene expression and root cell elongation. Plant Cell 25(5):1709–1725. https://doi.org/10.1105/tpc.113.112052
Wadekar HB, Sahi VP, Morita EH, Abe S (2013) MKRN expression pattern during embryonic and post-embryonic organogenesis in rice (Oryza sativa L. var. Nipponbare). Planta 237(4):1083–1095. https://doi.org/10.1007/s00026-012-1828-2
Wang Z, Wang J, Bao Y, Wu Y, Zhang H (2011) Quantitative trait loci controlling rice seed germination under salt stress. Euphytica 178(3):297–307
Wang H, Zhang M, Guo R, Shi D, Liu B, Lin X, Yang C (2012a) Effects of salt stress on ion balance and nitrogen metabolism of old and young leaves in rice (Oryza sativa L.). BMC Plant Biol 12(1):194–194
Wang Z, Cheng J, Chen Z, Huang J, Bao Y, Wang J, Zhang H (2012b) Identification of QTLs with main, epistatic and QTL × environment interaction effects for salt tolerance in rice seedlings under different salinity conditions. Theor Appl Genet 125(4):807–815. https://doi.org/10.1007/s00122-012-1873-z
Wu H, Ye H, Yao R, Zhang T, Xiong L (2015) OsJAZ9 acts as a transcriptional regulator in jasmonate signaling and modulates salt stress tolerance in rice. Plant Sci 232:1–12
Wu G, Deng H, Yu M, Cai Y, Zhou D, Tan J, Yu J, Luo X, Tong S, Wang P, Zhang X, Li C, Li C, Wang Y, Cheng Q, He H, Bian J (2020) Genetic analysis of rice seed recovery under low-temperature conditions using a new CSSL population with a high-density genetic map in rice. Mol Breed. https://doi.org/10.1007/s11032-020-01189-7
Yang Y, Guo Y (2018) Unraveling salt stress signaling in plants. J Integr Plant Biol 60(09):58–66
Zheng J, Wang Y, He Y, Zhou J, Li Y, Liu Q, Xie X (2014) Overexpression of an S-like ribonuclease gene, OsRNS4, confers enhanced tolerance to high salinity and hyposensitivity to phytochrome-mediated light signals in rice. Plant Sci 214:99–105. https://doi.org/10.1016/j.plantsci.2013.10.003
Zheng H, Zhao H, Liu H, Wang J, Zou D (2015) QTL analysis of Na+ and K+ concentrations in shoots and roots under NaCl stress based on linkage and association analysis in japonica rice. Euphytica 201(1):109–121
Zhou J, Wang F, Deng P, Jing W, Zhang W (2013) Characterization and mapping of a salt-sensitive mutant in rice (Oryza sativa L.). J Integr Plant Biol 55(6):504–513. https://doi.org/10.1111/jipb.12048

Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.