Glycosyltransferase *OsUGT90A1* helps protect the plasma membrane during chilling stress in rice

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Author contributions

MRS and YS conceived the project and designed the experiments. YS, HP, YL, ZZ, and MRS performed the experiments, and SC generated transgenic rice plants. CC provided material and intellectual support. YS and MRS performed all data analyses and wrote the manuscript. All authors edited and approved the final version of the manuscript.

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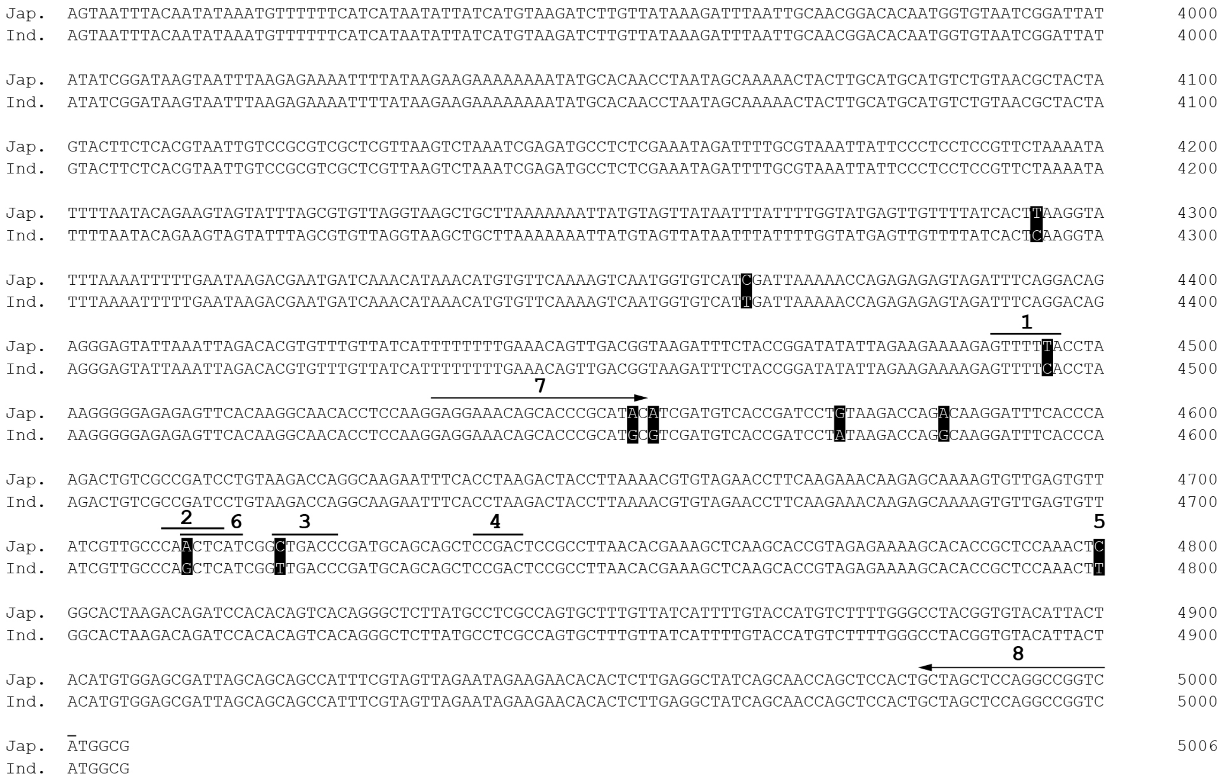

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Ind.  AGTAATTTACAATATAAATGTTTTTTCATCATAATATTATCATGTAAGATCTTGTTATAAAGATTTAATTGCAACGGACACAATGGTGTAATCGGATTAT    4000

Jap.  ATATCGGATAAGTAATTTAAGAGAAAATTTTATAAGAAGAAAAAAAATATGCACAACCTAATAGCAAAAACTACTTGCATGCATGTCTGTAACGCTACTA    4100
Ind.  ATATCGGATAAGTAATTTAAGAGAAAATTTTATAAGAAGAAAAAAAATATGCACAACCTAATAGCAAAAACTACTTGCATGCATGTCTGTAACGCTACTA    4100

Jap.  GTACTTCTCACGTAATTGTCCGCGTCGCTCGTTAAGTCTAAATCGAGATGCCTCTCGAAATAGATTTTGCGTAAATTATTCCCTCCTCCGTTCTAAAATA    4200
Ind.  GTACTTCTCACGTAATTGTCCGCGTCGCTCGTTAAGTCTAAATCGAGATGCCTCTCGAAATAGATTTTGCGTAAATTATTCCCTCCTCCGTTCTAAAATA    4200

Jap.  TTTTAATACAGAAGTAGTATTTAGCGTGTTAGGTAAGCTGCTTAAAAAAATTATGTAGTTATAATTTATTTTGGTATGAGTTGTTTTATCACTTAAGGTA    4300
Ind.  TTTTAATACAGAAGTAGTATTTAGCGTGTTAGGTAAGCTGCTTAAAAAAATTATGTAGTTATAATTTATTTTGGTATGAGTTGTTTTATCACTCAAGGTA    4300

Jap.  TTTAAAATTTTTGAATAAGACGAATGATCAAACATAAACATGTGTTCAAAAGTCAATGGTGTCATCGATTAAAAACCAGAGAGAGTAGATTTCAGGACAG    4400
Ind.  TTTAAAATTTTTGAATAAGACGAATGATCAAACATAAACATGTGTTCAAAAGTCAATGGTGTCATTGATTAAAAACCAGAGAGAGTAGATTTCAGGACAG    4400

Jap.  AGGGAGTATTAAATTAGACACGTGTTTGTTATCATTTTTTTTGAAACAGTTGACGGTAAGATTTCTACCGGATATATTAGAAGAAAAGAGTTTTTACCTA    4500
Ind.  AGGGAGTATTAAATTAGACACGTGTTTGTTATCATTTTTTTTGAAACAGTTGACGGTAAGATTTCTACCGGATATATTAGAAGAAAAGAGTTTTCACCTA    4500

Jap.  AAGGGGGAGAGAGTTCACAAGGCAACACCTCCAAGGAGGAAACAGCACCCGCATACATCGATGTCACCGATCCTGTAAGACCAGACAAGGATTTCACCCA    4600
Ind.  AAGGGGGAGAGAGTTCACAAGGCAACACCTCCAAGGAGGAAACAGCACCCGCATGCGTCGATGTCACCGATCCTATAAGACCAGGCAAGGATTTCACCCA    4600

Jap.  AGACTGTCGCCGATCCTGTAAGACCAGGCAAGAATTTCACCTAAGACTACCTTAAAACGTGTAGAACCTTCAAGAAACAAGAGCAAAAGTGTTGAGTGTT    4700
Ind.  AGACTGTCGCCGATCCTGTAAGACCAGGCAAGAATTTCACCTAAGACTACCTTAAAACGTGTAGAACCTTCAAGAAACAAGAGCAAAAGTGTTGAGTGTT    4700

Jap.  ATCGTTGCCCAACTCATCGGCTGACCCGATGCAGCAGCTCCGACTCCGCCTTAACACGAAAGCTCAAGCACCGTAGAGAAAAGCACACCGCTCCAAACTC    4800
Ind.  ATCGTTGCCCAGCTCATCGGTTGACCCGATGCAGCAGCTCCGACTCCGCCTTAACACGAAAGCTCAAGCACCGTAGAGAAAAGCACACCGCTCCAAACTT    4800

Jap.  GGCACTAAGACAGATCCACACAGTCACAGGGCTCTTATGCCTCGCCAGTGCTTTGTTATCATTTTGTACCATGTCTTTTGGGCCTACGGTGTACATTACT    4900
Ind.  GGCACTAAGACAGATCCACACAGTCACAGGGCTCTTATGCCTCGCCAGTGCTTTGTTATCATTTTGTACCATGTCTTTTGGGCCTACGGTGTACATTACT    4900

Jap.  ACATGTGGAGCGATTAGCAGCAGCCATTTCGTAGTTAGAATAGAAGAACACACTCTTGAGGCTATCAGCAACCAGCTCCACTGCTAGCTCCAGGCCGGTC    5000
Ind.  ACATGTGGAGCGATTAGCAGCAGCCATTTCGTAGTTAGAATAGAAGAACACACTCTTGAGGCTATCAGCAACCAGCTCCACTGCTAGCTCCAGGCCGGTC    5000

Jap.  ATGGCG                                                                                                  5006
Ind.  ATGGCG
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Fig. S1. SNP haplotypes of LOC_Os04g24110 promoter, coding region, and protein sequences in *JAPONICA* and *INDICA* reference subspecies. (a) The three SNPs in promoter region used for the haplotype analysis in Fig. 1b-c are labeled 2, 3, and 4. Arrows 7 and 8 indicate forward and reverse cloning primers for promoter amplification. Lines with number indicate potential transcription factor binding sites. The line labeled 6 shows a potential *ACTCAT* bZIP73 binding site. The line labeled 4 shows a potential *CCGAC* Low Temperature Response Element (LTRE) binding site.

b

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Jap.   ATGGCGGCGGCTGGTCACGATGTGCAGCTCCCCCACGTCGCCATCTTCCCGTTCATGGCCAGGGGCCACACCGTCCCGATGACCCACCTCGCCTGCCTTC    100
Ind.   ATGGCGGCGGCTGGTCACGATGTGCAGCTCCCCCACGTCGCCATCTTCCCGTTCATGGCCAGGGGCCACACCGTCCCGATGACCCACCTCGCCTGCCTTC    100

Jap.   TCCGCCGCCGCGGCCTCGCCACCGTCACCTTCTTCAGCACCCCGGGCAACGCGCCGTTCGTCCGGGGACAGCTCGACGACGACGTGGCCGTCGTGGAGCT    200
Ind.   TCCGCCGCCGCGGCCTCGCCACCGTCACCTTCTTCAGCACCCCGGGCAACGCGCCGTTCGTCCGGGGACAGCTCGACGACGACGTGGCCGTCGTGGAGCT    200

Jap.   TCCCTTCCCGGACCATGTCGTCGCCCGCGGCGCCGCGGAGTGCGTCGAGGCCCTCGACTCCCTGTTCCCCCTTCCGGCGTTCGTCGAGGCGGTGTCGGCG    300
Ind.   TCCCTTCCCGGACCATGTCGTCGCCCGCGGCGCCGCGGAGTGCGTCGAGGCCCTCGACTCCCTGTTCCCCCTTCCGGCGTTCGTCGAGGCGGTGTCGGCG    300

Jap.   CTCCGGCCGGGGCTGGAGGTGTCGCTCGCCGCCGCTCGGCCCCGCGTCGGCCTCCTCGTCGCCGACGCGTTCCTGCACTGGGCGCACGCCTCCGCCGCCG    400
Ind.   CTCCGGCCGGGGCTGGAGGTGTCGCTCGCCGCCGCTCGGCCCCGCGTCGGCCTCCTCGTCGCCGACGCGTTCCTGCACTGGGCGCACGCCTCCGCCGCCG    400

Jap.   CGCTCGGCGTCCCGACGGTGGCGTTCCTCGGCGGGAACATGTTCGCGACGATCATGCGCGACGTGATCCTCCGCGACAACCCGGCCGCCGCGCTGCTGTC    500
Ind.   CGCTCGGCGTCCCGACGGTGGCGTTCCTCGGCGGGAACATGTTCGCGACGATCATGCGCGACGTGATCCTCCGCGACAACCCGGCCGCCGCGCTGCTGTC    500

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Ind.   TGGCGGCGGCGGCGCCGAGGCGGCGACGTTCGCCGTGCCGGAGTTCCCGCACGTCCACCTCACGCTCGCCGACATCCCGGTCCCCTTCAACCGCCCGTCC    600

Jap.   CCGGAGGGTCCGATCATGGAGCTGAACGCCAAGCTATGGAAGGCCATCGCCGGCAGCAACGGCCTCATCGTCAACACCTTCGACGCCATGGAAGGCCGCT    700
Ind.   CCGGAGGGTCCGATCATGGAGCTGAACGCCAAGCTATGGAAGGCCATCGCCGGCAGCAACGGCCTCATCGTCAACACCTTCGACGCCATGGAAGGCCGCT    700

Jap.   ACGTCGAGCACTGGAACCGTGACCACCGCGCCGGCCCCAGGGCGTGGCCCATAGGCCCGCTCTGCCTCGCCCATGGCGGCACCGGCACCGGCACCGGCGC    800
Ind.   ACGTCGAGCACTGGAACCGTGACCACCGCGCCGGCCCCAGGGCGTGGCCCATAGGCCCGCTCTGCCTCGCCCATGGCGGCACCGGCACCGGCACCGGCGC    800

Jap.   CGTCGAGCCCTCATGGATGAAGTGGCTGGACGAGAAGGCGGCCGCCGGGAGAGCCGTGCTGTACGTGGCGCTCGGCACCGCCATGGCCATCCCGGACGCG    900
Ind.   CGTCGAGCCCTCATGGATGAAGTGGCTGGACGAGAAGGCGGCCGCCGGGAGAGCCGTGCTGTACGTGGCGCTCGGCACCGCCATGGCCATCCCGGACGCG    900
                                                          1
Jap.   CAGCTCAGGGAGGTCGCCGGCGGGCTGGAAGCCGCCGCGGCCGCGGGCGTCTACTTCCTGTGGGCCGTGCGCCCCAGCGACGCCGACCTCGGCGCCGGCT   1000
Ind.   CAGCTCAGGGAGGTCGCCGGCGGGCTGGAAGCCGCCGCGGCCGCGGGCGTCGACTTCCTGTGGGCCGTGCGCCCCAGCGACGCCGACCTCGGCGCCGGCT   1000

Jap.   TCGAGGAGCGCGTGGAGGGGCGAGGCATGGTGGTGCGGGAGTGGGTGGACCAATGGCGGATCCTGCAGCACGGCTGCGTGAGGGGCTTCCTCAGCCACTG   1100
Ind.   TCGAGGAGCGCGTGGAGGGGCGAGGCATGGTGGTGCGGGAGTGGGTGGACCAATGGCGGATCCTGCAGCACGGCTGCGTGAGGGGCTTCCTCAGCCACTG   1100

Jap.   CGGGTGGAACTCGGCGGTGGAGGGCGTCGCCGCCGGCGTGCCGCTGGCGGCGTGGCCGATGGGCGCCGAGCAGCCGCTCAACGCGATGCTCGTCGTCGAC   1200
Ind.   CGGGTGGAACTCGGCGGTGGAGGGCGTCGCCGCCGGCGTGCCGCTGGCGGCGTGGCCGATGGGCGCCGAGCAGCCGCTCAACGCGATGCTCGTCGTCGAC   1200

Jap.   GAGCTGCGCGTCGGGGTCAGGGTGCCGGTGCCGACGGCGATGGCGACGGGCGGGCACGGGGTGGTCGGGAGCGAGGTGATCGCGCGCGTGGCGAGGGAGC   1300
Ind.   GAGCTGCGCGTCGGGGTCAGGGTGCCGGTGCCGACGGCGATGGCGACGGGCGGGCACGGGGTGGTCGGGAGCGAGGTGATCGCGCGCGTGGCGAGGGAGC   1300
                                                    2                3          4
Jap.   TGATGATGATGGCCGGGGAGGGGAAGGGCGGCGGCGGCGGCGAGGAGGCGAGGAACGTCGCCGCGCTGGCGTCCAAGGCGCGAGAAGCGGTCGCCGAGGG   1400
Ind.   TGATGATGATGGCCGGGGAGGGGAAGGGCGGCGGCGGCGGCGAGGCGGCGAGGAACGTCGCCTCGCTGGCGTCGAAGGCGCGAGAAGCGGTCGCCGAGGG   1400

Jap.   CGGGTCGTCGTGGAAGGCGCTGGAGGAGATGGTTGCCACGCTCTGCCGCCCTGTTGAAGGAGATACACCGAAACCCACAAAATAANN                1487
Ind.   CGGGTCGTCGTGGAAGGCGCTGGAGGAGATGGTTGCCACGCTCTGCCGCCCTGTTGAAGGAGATACACCGAAACCCACAAAATAANN                1487
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c

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Jap.   MAAAGHDVQLPHVAIFPFMARGHTVPMTHLACLLRRRGLATVTFFSTPGNAPFVRGQLDDDVAVVELPFPDHVVARGAAECVEALDSLFPLPAFVEAVSA    100
Ind.   MAAAGHDVQLPHVAIFPFMARGHTVPMTHLACLLRRRGLATVTFFSTPGNAPFVRGQLDDDVAVVELPFPDHVVARGAAECVEALDSLFPLPAFVEAVSA    100

Jap.   LRPGLEVSLAAARPRVGLLVADAFLHWAHASAAALGVPTVAFLGGNMFATIMRDVILRDNPAAALLSGGGGAEAATFAVPEFPHVHLTLADIPVPFNRPS    200
Ind.   LRPGLEVSLAAARPRVGLLVADAFLHWAHASAAALGVPTVAFLGGNMFATIMRDVILRDNPAAALLSGGGGAEAATFAVPEFPHVHLTLADIPVPFNRPS    200

Jap.   PEGPIMELNAKLWKAIAGSNGLIVNTFDAMEGRYVEHWNRDHRAGPRAWPIGPLCLAHGGTGTGTGAVEPSWMKWLDEKAAAGRAVLYVALGTAMAIPDA    300
Ind.   PEGPIMELNAKLWKAIAGSNGLIVNTFDAMEGRYVEHWNRDHRAGPRAWPIGPLCLAHGGTGTGTGAVEPSWMKWLDEKAAAGRAVLYVALGTAMAIPDA    300
                        1
Jap.   QLREVAGGLEAAAAAGVYFLWAVRPSDADLGAGFEERVEGRGMVVREWVDQWRILQHGCVRGFLSHCGWNSAVEGVAAGVPLAAWPMGAEQPLNAMLVVD    400
Ind.   QLREVAGGLEAAAAAGVDFLWAVRPSDADLGAGFEERVEGRGMVVREWVDQWRILQHGCVRGFLSHCGWNSAVEGVAAGVPLAAWPMGAEQPLNAMLVVD    400
                                                       2     3
Jap.   ELRVGVRVPVPTAMATGGHGVVGSEVIARVARELMMMAGEGKGGGGGEEARNVAALASKAREAVAEGGSSWKALEEMVATLCRPVEGDTPKPTK.         495
Ind.   ELRVGVRVPVPTAMATGGHGVVGSEVIARVARELMMMAGEGKGGGGGEAARNVASLASKAREAVAEGGSSWKALEEMVATLCRPVEGDTPKPTK.         495
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Fig. S1. SNP haplotypes of LOC_Os04g24110 promoter, coding region, and protein sequences in *JAPONICA* and *INDICA* reference subspecies. (b) SNPs 1 and 4 in the LOC_Os04g24110 coding region were used for haplotype analysis in Fig. 1b-c. (c) Three non-synonymous amino acid changes resulting from three SNPs shown in (b) are highlighted with their corresponding numbers 1, 2, and 3.

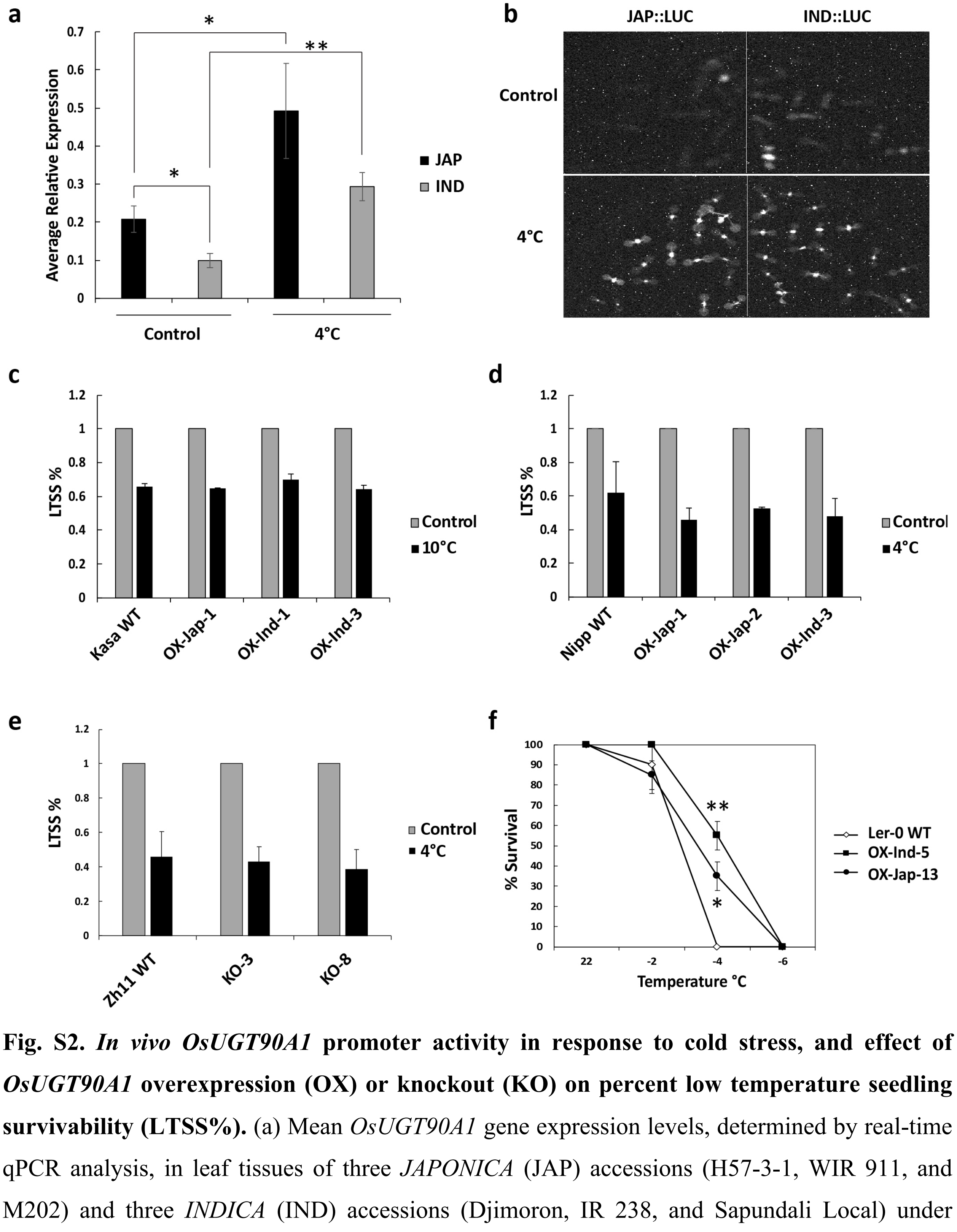

Fig. S2. ***In vivo OsUGT90A1*** **promoter activity in response to cold stress, and effect of** ***OsUGT90A1*** **overexpression (OX) or knockout (KO) on percent low temperature seedling survivability (LTSS%).** (a) Mean *OsUGT90A1* gene expression levels, determined by real-time qPCR analysis, in leaf tissues of three *JAPONICA* (JAP) accessions (H57-3-1, WIR 911, and M202) and three *INDICA* (IND) accessions (Djimoron, IR 238, and Sapundali Local) under 28°C/25°C control conditions and exposure to 4°C for 7 hrs. (b) *In vivo* real-time visualization of luciferase bioluminescent signals in transgenic Arabidopsis under standard growth condition (control) and after chilling treatment (4°C) for 3 hrs. JAP::LUC: a 500 bp *OsUGT90A1* promoter fragment from the *JAPONCA* accession KRASNODARSKIJ 3352 fused to LUC; IND::LUC: a 500 bp *OsUGT90A1* promoter fragment from the *INDICA* accession CAROLINO 164 fused to LUC. (c-e) Effect of *OsUGT90A1* OX and KO on LTSS% in wild type (WT) Kasalath (Kasa), Nipponbare (Nipp), and Zhong Hua 11 (ZH11) or OX and KO transgenic rice plants. Ind and Jap indicate that the *INDICA* or *JAPONICA* allele of *OsUGT90A1*, respectively, was overexpressed. (f) Whole plant freezing survival phenotypes of wild type (WT) and *OsUGT90A1* OX transgenic Arabidopsis plants. Ind- and Jap- indicate that the *INDICA* or *JAPONICA* allele of *OsUGT90A1*, respectively, was overexpressed.

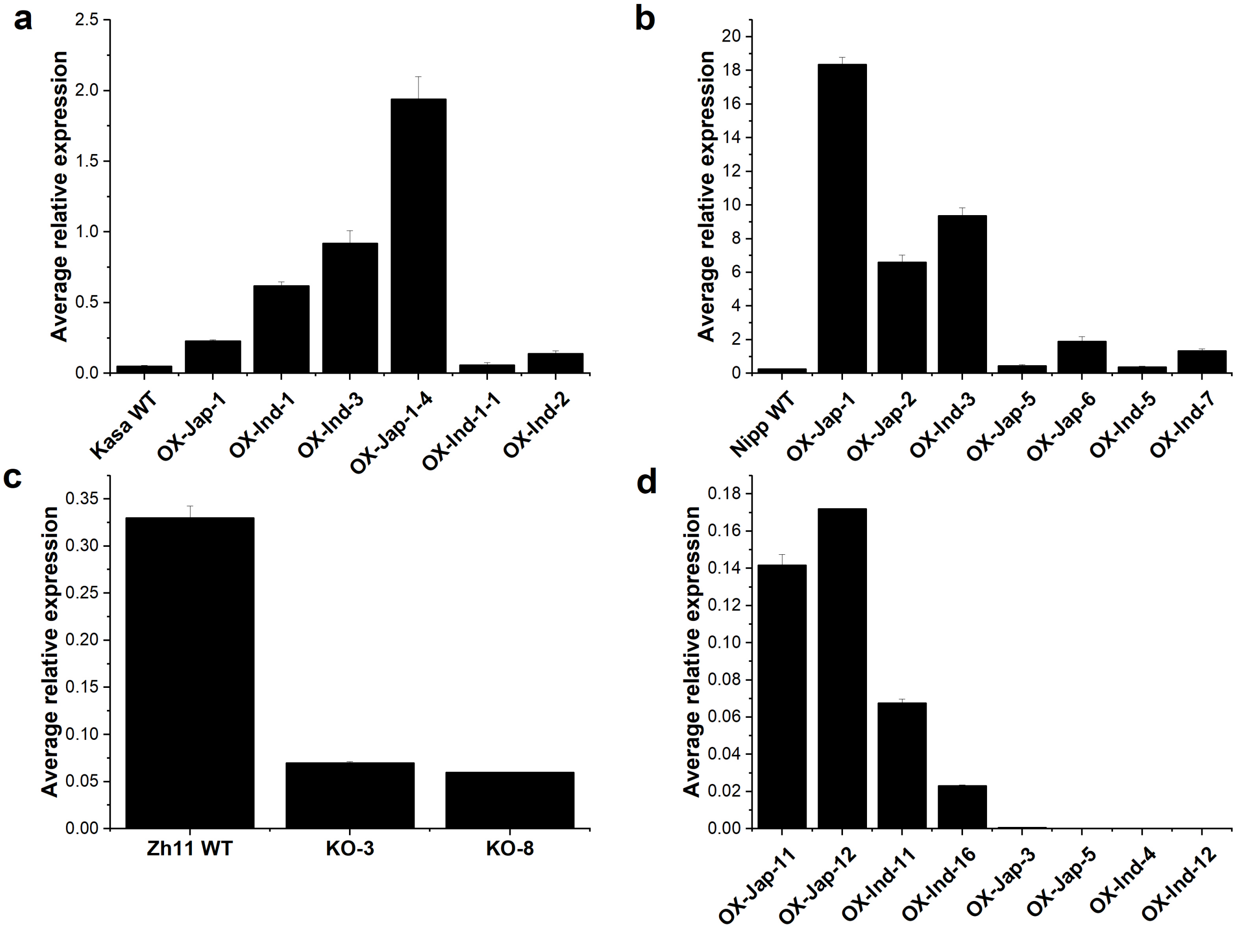

Fig. S3. Abundance of *UGT90A1* steady-state mRNA in individual transgenic rice and Arabidopsis plants used for analyses shown in Figs. 3-8, Fig. 10, and Fig. S4. The mean relative expression levels of *UGT90A1* in transgenic or wild type (except for heterologous Arabidopsis) plants are shown for: (a) Kasalath (Kasa) rice lines; (b) Nipponbare (Nipp) rice lines; (c) Zhong Hua 11 (Zh11) rice lines; and (d) Col-0 Arabidopsis lines.

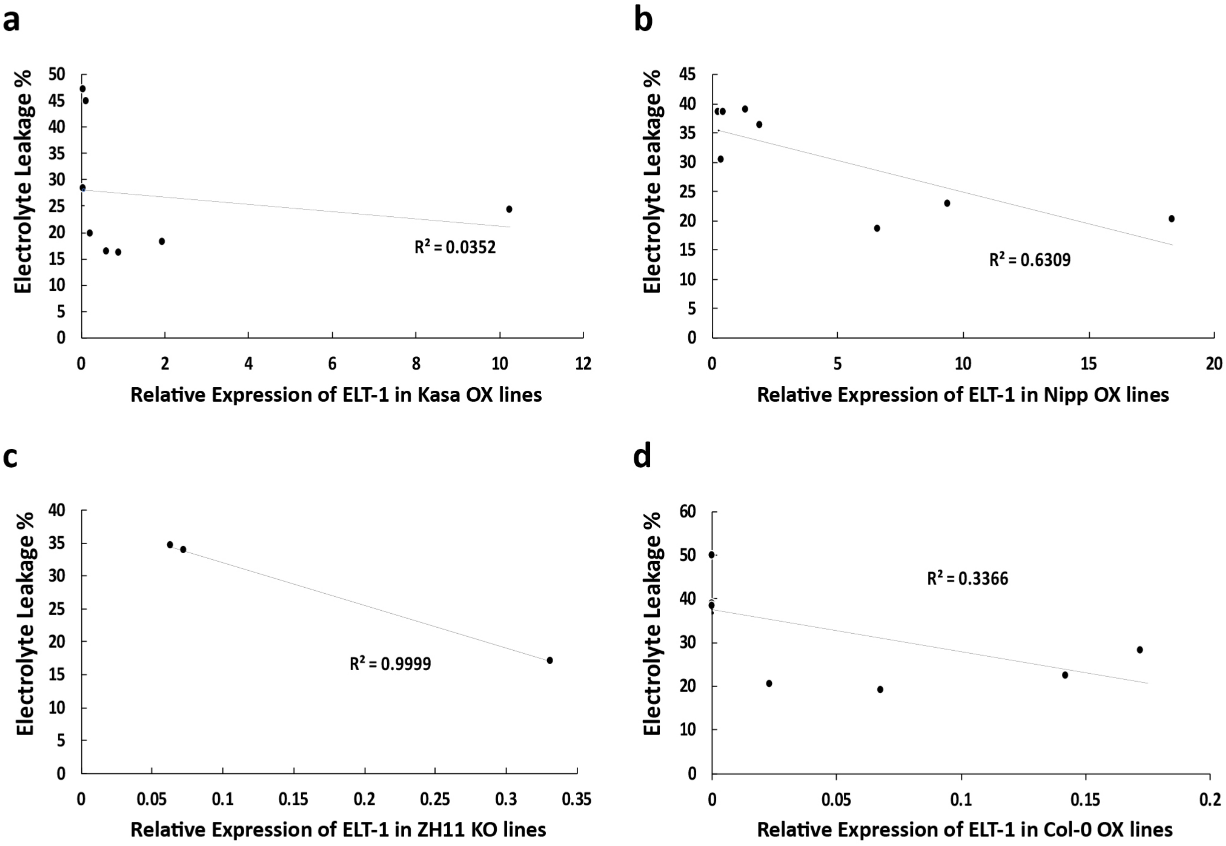

Fig. S4. Correlation of *OsUGT90A1* mRNA abundance with plasma membrane integrity in cold temperature stressed transgenic rice and Arabidopsis plants. Each dot represents an individual transgenic line in: (a) Kasalath (Kasa) rice; (b) Nipponbare (Nipp) rice; (c) Zhong Hua 11 (ZH11) rice; and (d) Col-0 Arabidopsis. Relative expression level of *OsUGT90A1* is shown on the x-axis and the corresponding median percent electrolyte leakage (%EL) as a measure of the degree of plasma membrane damage on the y-axis. Lines used in this figure are those both with significantly better than wild type %EL scores (Kasa: OX-Jap-1, Ind-1, Ind-3; Nipp: OX-Jap-1, Jap-2, Ind-3; Col-0: OX-Jap-11, Jap-12, Ind-11, Ind-16) and without significantly better than wild type %EL scores (Kasa: OX-Jap-1-4, Ind-1-1, Ind-2; Nipp: OX-Jap-5, Jap-6, Ind-5, Ind-7; ZH11: KO-3, KO-8; Col-0: OX-Jap-3, Jap-5, Ind-4, Ind-12).

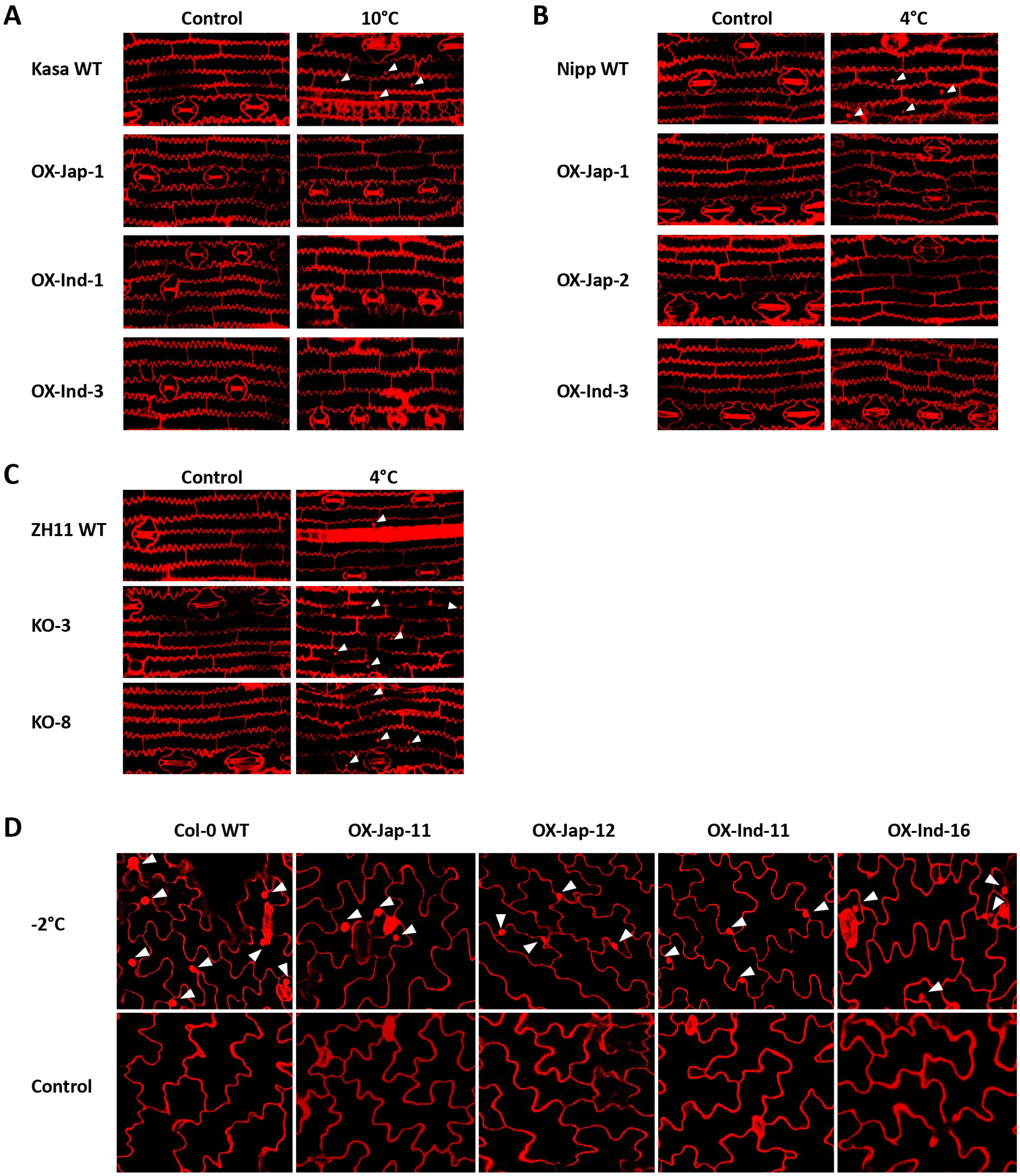

Fig. S5. Propidium iodide (PI) staining of wild type (WT) and *OsUGT90A1* overexpression (OX) and knockout (KO) transgenic rice and WT and OX transgenic Arabidopsis lines. (A-C) PI staining of the epidermal cell of leaf tissue in Kasalath (Kasa) OX, Nipponbare (Nipp) OX, and in Zhong Hua 11 (ZH11) KO lines under normal growth conditions (control) or with chilling stress. (D) PI staining of the epidermal cell of the leaf tissue in Col-0 OX lines under normal growth conditions (control) or with mild freezing stress. Damaged cells with PI-stained red nucleus are labeled by arrows. Ind and Jap indicate that the *INDICA* or *JAPONICA* allele of *OsUGT90A1*, respectively, was overexpressed.

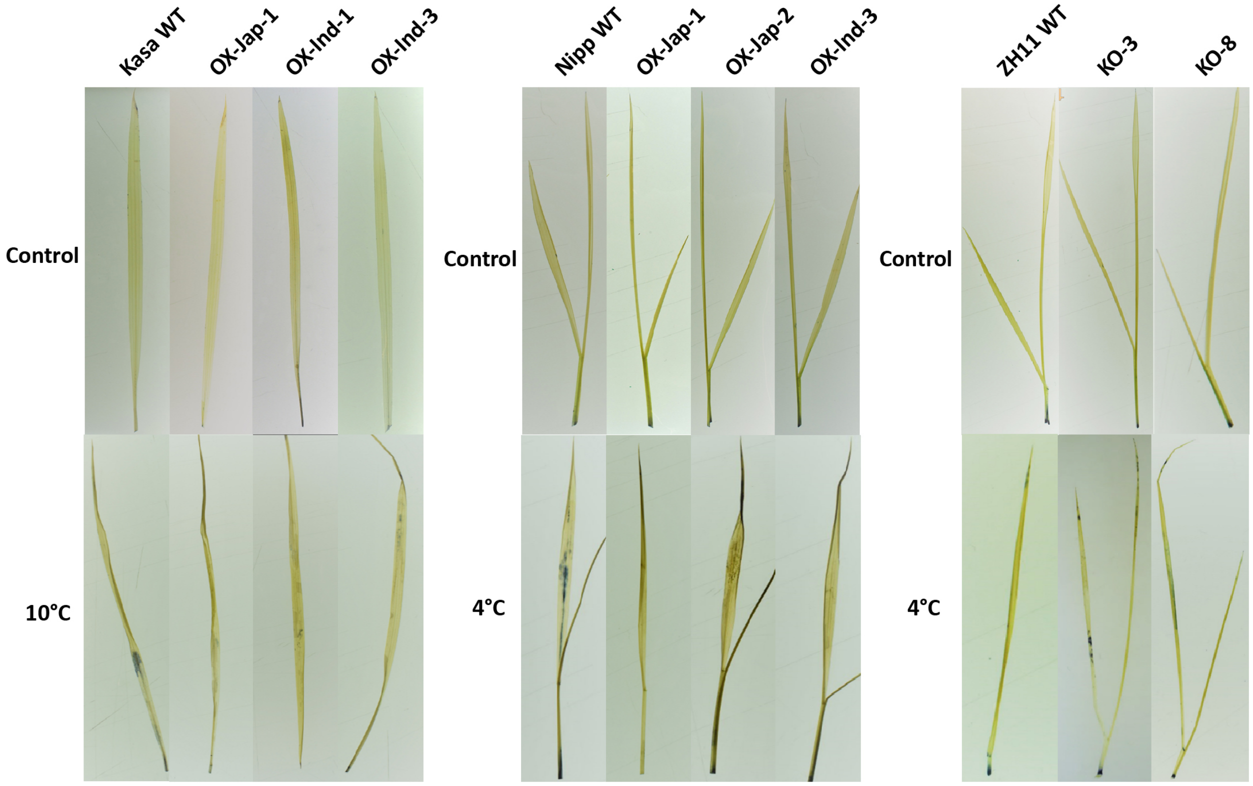

Fig. S6. Effect of *OsUGT90A1* overexpression (OX) and knockout (KO) on ROS scavenging activity under standard growth (control) or chilling stress conditions in transgenic rice. Nitro Tetrazolium Blue staining (blue) was used to qualitatively visualize the ROS $^{\bullet}O_2^{\cdot-}$ in leaves of wild type (WT) and OX lines in the Kasalath (Kasa; left) or Nipponbare (Nipp; middle) background, and of WT and KO lines in the Zhong Hua 11(ZH11; right) background. Ind and Jap indicate that the *INDICA* or *JAPONICA* allele of *OsUGT90A1*, respectively, was overexpressed.

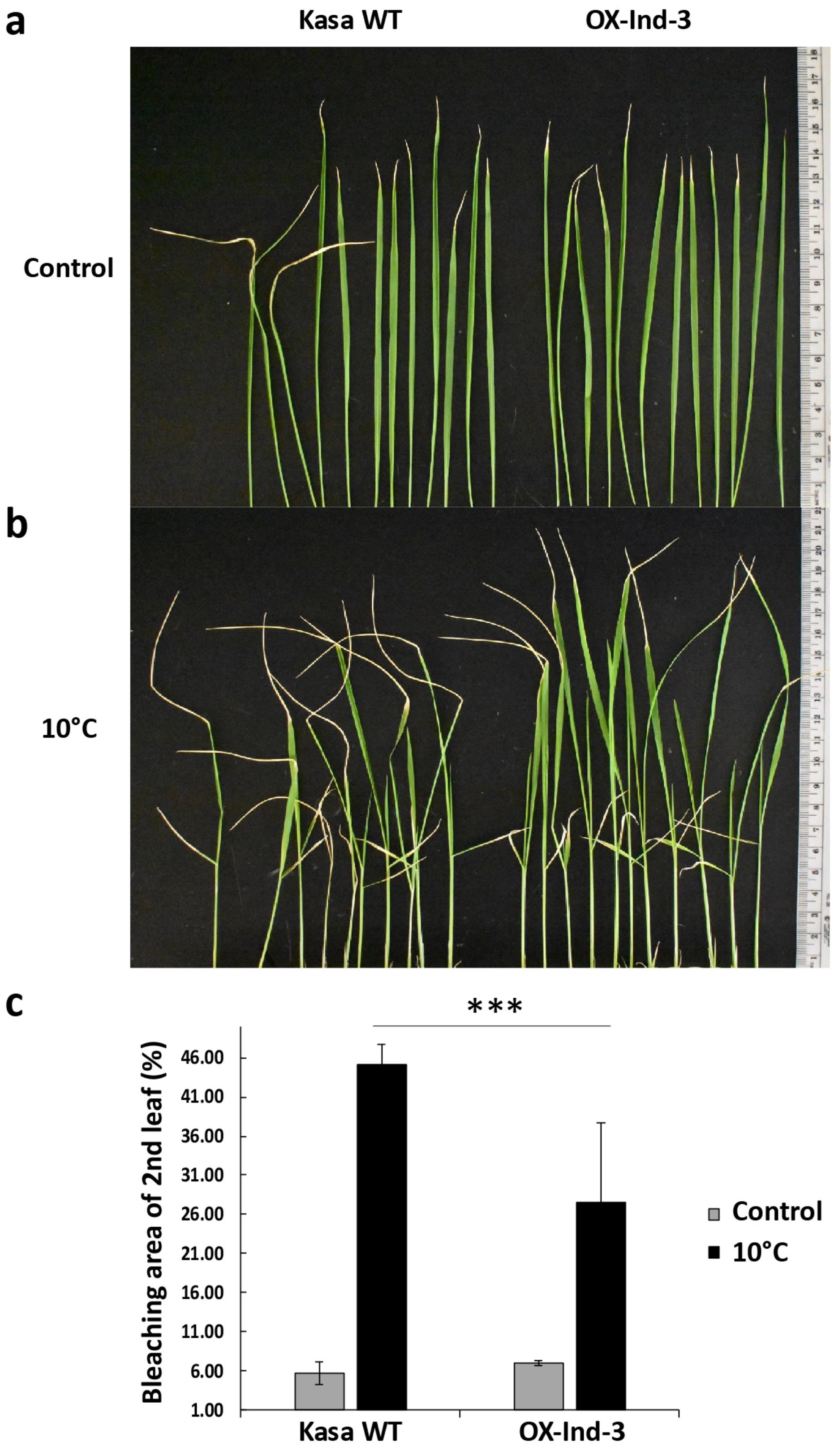
a
Kasa WT
OX-Ind-3
Control
b
10°C
c
***
Bleaching area of 2nd leaf (%)
46.00
41.00
36.00
31.00
26.00
21.00
16.00
11.00
6.00
1.00
Kasa WT
OX-Ind-3
Control
10°C

Fig. S7. Leaf bleaching (necrosis) phenotype of wild type (WT) Kasalath (Kasa) and *OsUGT90A1* overexpression (OX) Kasa lines, and quantification of necrotic sectors. (a) Leaf tip bleaching phenotype in the second leaf of 23-day-old seedlings grown under standard growth conditions (control). (b) Leaf tip bleaching phenotype in the second leaf of 23-day-old seedlings exposed to 10°C for two days and after one week of recovery growth. (c) Quantification of the median percent (%) bleached area of the 2^{nd} leaves shown in (a) and (b). Ind indicates that the *INDICA* allele of *OsUGT90A1* was overexpressed. ***: $P < 0.001$ (two-tailed Student's *t*-test).

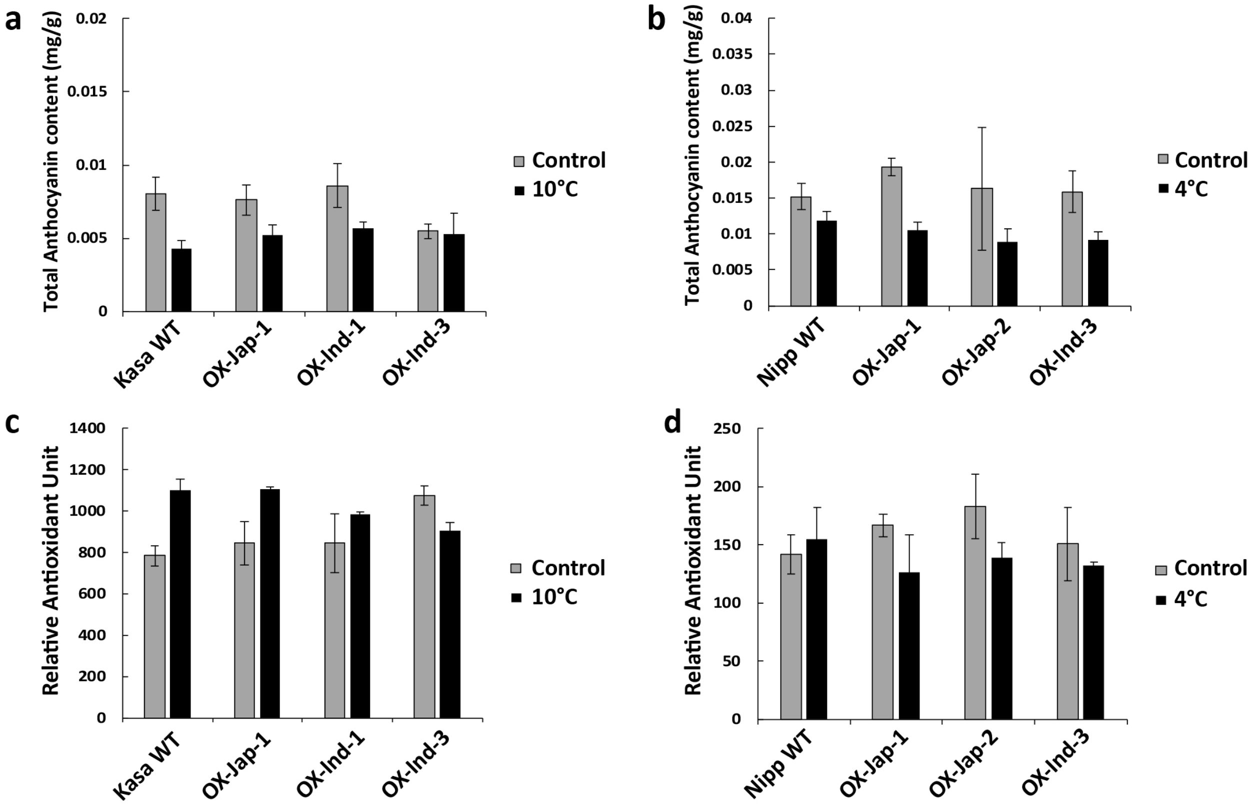

Fig. S8. Overall concentration and non-enzymatic antioxidant activity of total flavonoid/anthocyanin content extracted from leaf tissue of wild type (WT) and *OsUGT90A1* overexpression (OX) transgenic rice plants. (a) and (b), total flavonoid/anthocyanin content in leaf tissue of Kasalath (Kasa) and Nipponbare (Nipp) OX lines, respectively. (c) and (d), non-enzymatic antioxidant activity of flavonoid/anthocyanin extracts shown in (a) and (b) determined by the 2,2-diphenyl-1-picrylhydrazyl (DPPH) reduction assay.

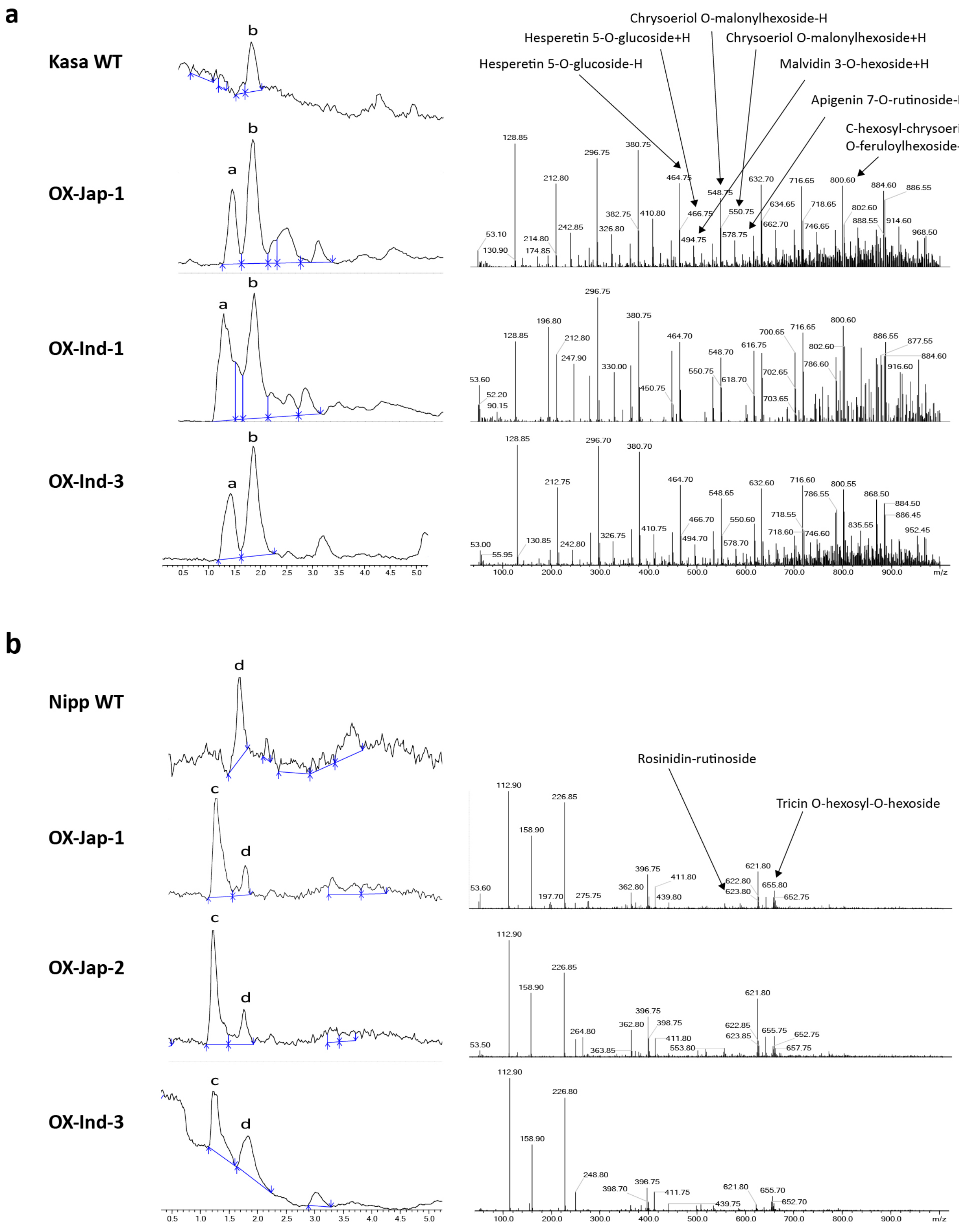

Fig. S9. Effect of *OsUGT90A1* overexpression (OX) on flavonoid/anthocyanin composition under chilling stress. (a) and (b), HPLC-MS assay determined specific flavonoid/anthocyanin composition groups (left) and compounds (right) in wild type (WT) or *OsUGT90A1* OX Kasalath (Kasa) and Nipponbare (Nipp) lines, respectively.

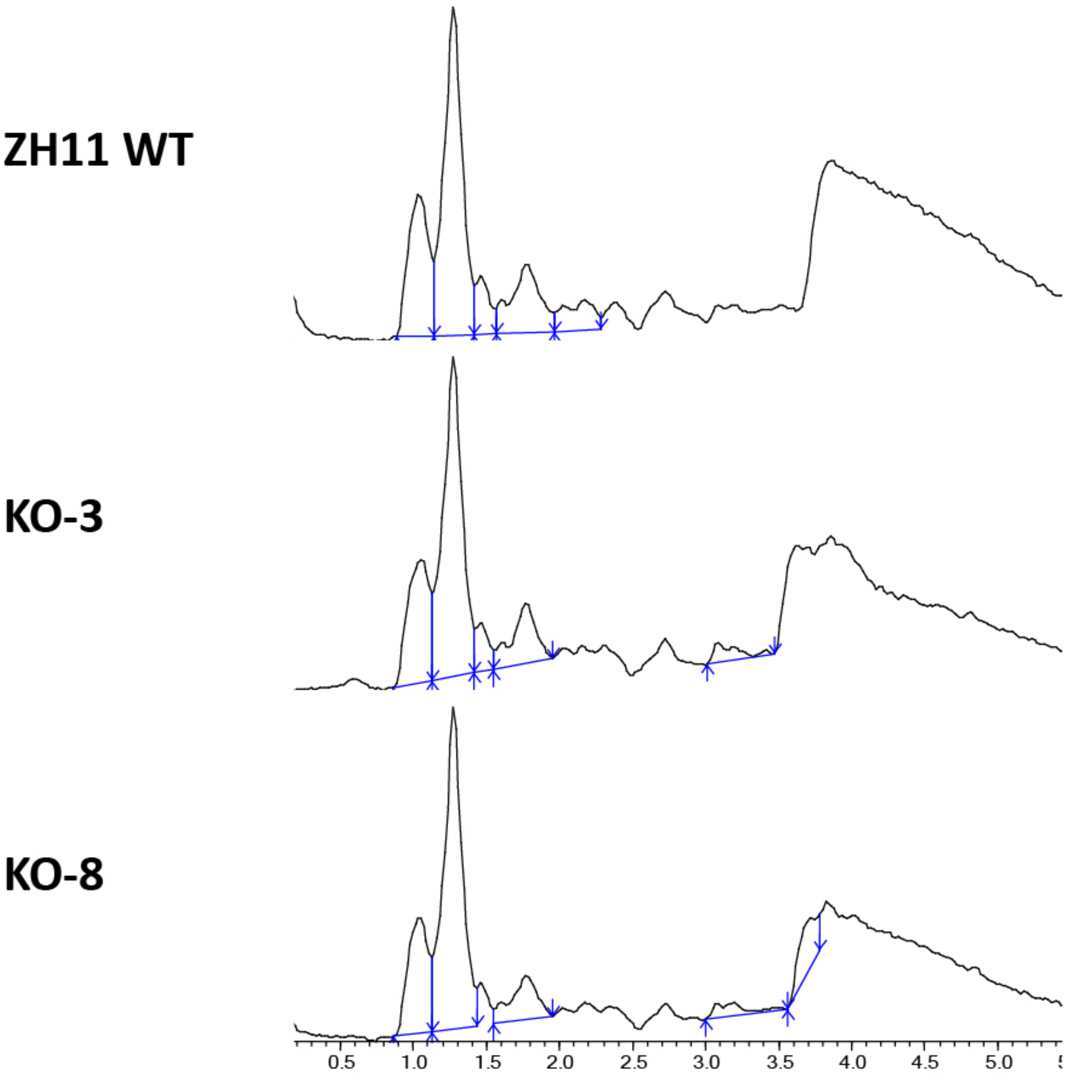

Fig. S10. Effect of *OsUGT90A1* knockout (KO) on flavonoid/anthocyanin composition under chilling stress. HPLC-MS assay determined specific flavonoid/anthocyanin composition groups in *elt1* KO mutants in the ZH11 background.

Table S1. Primer information

Gene	Forward (F) and reverse (R) primers	Purpose
OsUGT90A1	F: AGATCTACTTATTTTGTGGGTTTCGGTG R: GAATTCGCTCCAGGCCGGTCATG	Overexpression construct
OsUGT90A1	F: GGTACCGAGGAAACAGCACCCGCATAC R: GGATCCTGACCGGCCTGGAGCTAGC	promoter::LUC fusion
OsUGT90A1	F: CTCGAGCTCCACTGCTAGCTCCAG R: AGATCTTTTTGTGGGTTTCGGTGTATCTCCTTC	eGFP fusion protein
OsUGT90A1	GGCGACGACATGGTCCGGGA	Knockout construct
OsUGT90A1	F: AGATCTATGGCGGCGGCTGGTCA R: GAATTCACTTATTTTGTGGGTTTCGGTG	qRT-PCR
OsUGT90A1	F: ACCACTTCGACCGCCACTACT R: ACGCCTAAGCCTGCTGGTT	qRT-PCR
OsUBQ	F: ACCACTTCGACCGCCACTACT R: ACGCCTAAGCCTGCTGGTT	qRT-PCR