REVIEW

Selection of Standard Rice Cultivars for Evaluating Cracking Resistance and Finding a Novel QTL Responsible for It

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Abstract

To breed rice cultivars with kernel-cracking resistance, we selected new standard cultivars for evaluation. Among 21 cultivars rated from "resistant" to "weak" in Tohoku, Hokuriku, and western Japan, we regarded "Ouu 431," "Ukei 1210," "Eminokizuna," and "Yamadawara" as resistant. We selected two resistant lines, namely, "IRSL 30" and "IRSL 37," as breeding materials from the chromosome segment substitution lines of "Itadaki" (*Oryza sativa* L.) × donor *Oryza rufipogon* and identified a major QTL, *qCR8-2*, responsible for cracking resistance by QTL analysis using F_4 individuals derived from "Itadaki/IRSL 30" and "Itadaki/IRSL 37." "Chugoku PL2," which was selected from the progeny of "Itadaki/IRSL 37," has *qCR8-2* in an "Itadaki" background. It had better palatability and a lower broken rice ratio during milling compared with "Itadaki." In this case, improved cracking resistance led to improved palatability and milling traits.

Discipline: Crop Science Additional key words: fissuring, head rice, high temperature, *Oryza rufipogon*, *Oryza sativa*

Introduction

Cracked rice kernels (Fig. 1) are regarded as damaged grains (MAFF 2001). They reduce the market value and increase the broken rice ratio during milling, which leads to a decrease in head rice recovery and diminished flavor. Kernel cracking is a major problem in rice production and postharvest processing. Relative humidity affects the development of cracking (Lan & Kunze 1996), and kernel cracking is caused by distortion in the endosperm caused by uneven moisture distribution due to repeated drying and wetting during the late grain-filling period, when the kernel hardens (Nagato et al. 1964). Cracking often follows harvest delays due to unstable weather, heavy rain, or high air temperatures after maturity (Arisaka 2002, Nitto et al. 2001), and head rice recovery decreases with a delay in harvesting time (Xangsayasane et al. 2018). Without adequate topdressing at the panicle formation stage of "Koshihikari," the percentage of cracked kernels (PCK) increases because

*Corresponding author: gome@affrc.go.jp Received 6 October 2023; accepted 19 December 2023. rachides and rachis branches withered rapidly and the daily range of panicle moisture content becomes wide (Kawaguchi & Houjou 2010). Improper drying during postharvest processing can lead to cracking (Itoh et al. 1974, Cnossen et al. 2003, Iguaz et al. 2006). High temperatures during the grain-filling stage also have a negative influence on kernel cracking and head rice recovery (Abayawickrama et al. 2017). PCK increases with an increase in average air temperature during the



Fig. 1. Grain cracking of "Itadaki," "IRSL 30," and "IRSL 37" in a soaking method (SM) highlighted by transmitted light Arrowheads denote the cracking positions.

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19 days after heading (Takahashi et al. 2002), and there is a high positive correlation between PCK and the average daily maximum air temperature during the 10 days after heading (Nagata et al. 2004).

Since 2000, many cases of kernel cracking caused by high air temperature during grain filling have been reported in Japan (Arisaka 2002, Nitto et al. 2001, Sakai et al. 2012, Sakaiya et al. 2012). Because air temperature in summer is expected to continue to increase (JMA 2017) and large-scale rice farm amalgamation makes it difficult to harvest at the ideal stage because of the concentrated heading spout caused by intense summer heat (Matsumura & Yamaguchi 2006), breeding rice cultivars with high kernel-cracking resistance is urgently required.

Cultivars differ in their kernel-cracking resistance (Hayashi et al. 2015, Nagata et al. 2004, Takita 2002). The resistance is typically evaluated using the late-harvest method (LH) (Horisue 1996). Two alternative methods are used: the soaking method (SM), in which dried panicles or unhulled rice harvested at maturity are soaked in water (Takita 1999); and the moisture absorption (MA) method, in which brown rice absorbs moisture under controlled laboratory conditions (Hayashi et al. 2015). Because PCK is affected by temperature, rainfall during grain filling, and fertilization, cracking resistance must be evaluated using standard cultivars that mature at similar times and conditions. Genetic information is also essential because DNA markers linked to genes or QTLs associated with cracking enable efficient selection without the influence of cultivation conditions.

We selected standard cultivars to evaluate cracking resistance and find new breeding materials (Nakagomi et al. 2019, 2020a). Using these standard cultivars, we found new breeding materials from chromosome segment substitution lines (CSSLs) of "Itadaki" (*O. sativa* L.) \times

donor *O. rufipogon* and identified a major QTL responsible for cracking resistance (Nakagomi et al. 2020b).

1. Selection of standard rice cultivars for evaluating cracking resistance

To select standard rice cultivars for evaluating kernel-cracking resistance, we tested cracking resistance at three breeding stations, the Tohoku Agricultural Research Center of the National Agriculture and Food Research Organization (TARC, NARO), the Western Region Agricultural Research Center (WARC, NARO), and the Fukui Agricultural Experiment Station, from 2015 to 2018 (Fig. 2 and Table 1; Nakagomi et al. 2019, 2020a). Cultivars of various maturity groups were selected based on previous reports (Watanabe & Kodama 1991, Nakagomi et al. 2012, Nagata et al. 2004, Takita 1992, 2002), and the data are shown (Table 2). We



Fig. 2. Locations of the three sites where standard cultivars were screened

Target region		Europeine antal aita			WARC		
Maturity group			TARC	Fukui Agricultural Experiment Station	Nomal transplanting	Early transplanting	
North part of co	ool region	(Tohoku Region)					
Early			2015-2017	—	2015-2017	—	
Medium			2015-2017	—	2015-2017	_	
South part of co	ool region	(Hokuriku Region)					
Early			2015-2017	2017	2015-2017	_	
Medium			_	2015-2017	2015-2017	_	
West part of war	rm region	(Western Region)					
Medium			_	2017, 2018	2015-2018	2016-2018	
Medium-to-l	ate		_	—	2015-2018	2016-2018	

Table 1. List of heading stage groups and experimental sites

TARC, Tohoku Agricultural Research Center; WARC, Western Region Agricultural Research Center

Target region	Calting	LH	SM	MA
Maturity group	Cultivar	(%)	(%)	(%)
North part of cool regio	n (Tohoku Region)			
Early	Year	2015-2017	2015-2017	2015, 2017
-	No. of experiments	6	6	3
	Ouu 431	15.5 a	39.3 a	42.8 ab
	Ukei 1204	33.5 ab	37.2 а	27.7 а
	Ouu 390	42.8 bc	48.4 ab	36.8 ab
	Hananomai	44.7 bc	41.5 a	38.7 ab
	Akitakomachi	55.5 cd	61.8 bc	61.7 ab
	Yumeakari	59.3 cd	64.9 bc	52.7 ab
	Tsugaruroman	68.9 d	75.0 с	57.5 b
Medium	Year	2015-2017	2015-2017	2015, 2017
	No. of experiments	6	6	3
	Ukei 1210	19.8 a	19.9 a	23.5 a
	Hitomebore	38.4 b	53.3 b	40.7 ab
	Haenuki	39.6 b	50.9 b	35.2 а
	Okiniiri	58.6 c	67.9 bc	57.8 bc
	Toyonishiki	66.8 c	79.8 с	64.0 c
	Yukigesvo	72.1 c	84.4 c	61.2 c
outh part of cool regio	n (Hokuriku Region)			
Early	Year	2015-2017	2015-2017	2015, 2017
5	No. of experiments	7	7	4
	Ouu 431	14.5 a	35.2 ab	41.6 bcd
	Etsunan 221	33.1 ab	22.1 a	22.6 a
	Hananomai	40.0 b	37.2 abc	35.9 ab
	Inabawase	41.0 b	53.3 cd	41.3 bcd
	Todorokiwase	43.5 bc	50.3 bcd	42.5 bcd
	Akitakomachi	51.8 bc	57.8 de	57.5 de
	Tsugaruroman	63.1 c	72.3 ef	55.5 cde
	Tovonishiki	63.2 c	72.5 Cl	65.6 e
Medium	Vear	2015-2017	2015-2017	2015-2017
Wiedrum	No. of experiments	6	5	4
	Eminokizuna	22.1 a	23.6 a	18.4 a
	Akisakari	38.5 ab	34.6 ab	22.5 a
	Hitomebore	37.1 b	48.7 ab	34.9 ab
	Haenuki	37.2 b	45.2 ab	36.6 ab
	Etsunan 222	45.5 b	45.4 ab	31.9 ab
	Koshihikari	51.4 c	51.4 b	40.3 h
est nart of warm regio	n (Western Region)	51.1 0		10.5 0
Medium	Year	2015-2018	2015-2018	2017, 2018
1110010111	No. of experiments	7	7	2
	Yamadawara	17.7 a	15.4 a	26.3
	Akibare	22.9 ab	21.9 ab	41.8
	Matsuribare	33.5 abc	37.0 bc	43.5
	Nipponbare	33.7 abc	33.0 ab	51.0
	Setonokagavaki	39.5 bc	33.2 ab	45.0
	Kinumusume	45.6 c	38.1 be	48.0
	Sakihikari	53.6 d	57.1 c	59.8
	Akidawara	69.7 de	70.0 d	61.3
	Vamahikari	79.8	69.5 d	65.2
Medium to lata	I alliallikali Voor	2015 2019	2015 2019	2017 2019
wiculuill-to-late	No. of experiments	2013-2018	2013-2018	2017, 2018
	Hinohikari	27.0 3	22.2 9	35.8
	Koganemasari	27.0 a 31.0 a	22.2 a	26.8
	Asominori	12.6 a	27.7 a 17.5 h	20.0
	Astron	72.0 a	τ/.J U	70.2
	Aokaze	65.1 b	61.0 c	70.3

Table 2. Average percentage of cracked kernels for the three evaluation methods (Nakagomi et al. 2019, 2020a)

LH, late-harvest method; SM, soaking method; MA, moisture absorption method

Values are the means of all experiments at each site for each year.

Means followed by the same letter within each heading group and method are not significantly different at the 5% level according to Tukey's test.

evaluated the cracking resistances of LH, SM, and MA. Plants of the trial cultivars were grown at each station according to the standard methods of each station. In LH, the panicles were harvested several days after maturity to achieve the same accumulated temperature from heading to harvest within each maturity group. After 5-12 panicles from each cultivar were harvested and air-dried, PCK was measured in 100-200 hulled grains that were \geq 1.8 mm thick by visual inspection with a TX-200 or TX-300 grain scope (Kett Electric Laboratory Co., Ltd., Japan). In SM (Nagata et al. 2013, Takita 1999), 5-12 panicles were harvested at maturity and air-dried. Unhulled grains with an adjusted moisture content of approximately 13% were soaked in water at 15°C for 1 h. After dehydration and air-drying, PCK was measured as in LH. In MA (Hayashi et al. 2015), hulled brown rice with an adjusted moisture content of approximately 12% was left to absorb moisture at 100% RH at an air temperature of 25°C for 5 h. PCK was measured as described for LH. LH was measured at each station, SM was performed at WARC, and MA was performed at Fukui using the materials harvested at each station.

The variations in heading date and average daily maximum temperature during the 10 days after heading were small in all maturity groups at all stations (SD: 0.94-2.08 days, 0.17°C-0.40°C; Nakagomi et al. 2019, 2020a). Therefore, the test conditions were suitable for the selection of standard cultivars. Despite differences in fertilization, air temperature, and rainfall among stations, positive correlations were observed among PCKs (Nakagomi et al. 2019, 2020a). The order of PCK among the trial cultivars obtained in this study was generally consistent with that reported in previous reports (Nagata et al. 2004, 2013, Nakagomi et al. 2012, Takita 1992, 2002). Therefore, we considered the data obtained here reliable and suitable for selecting standard cultivars.

On the basis of the PCK determined by LH, we selected 21 new standard cultivars rated from "resistant" to "weak" in the early and medium maturity groups in Tohoku and Hokuriku and in the medium and medium-to-late maturity groups in the western region (Table 3; Nakagomi et al. 2019, 2020a). As resistant standard cultivars, we selected "Ouu 431" and "Ukei 1210" in Tohoku, "Ouu 431" and "Eminokizuna" in Hokuriku, and "Yamadawara" in the western region. All new standard cultivars selected by LH, except "Ouu 431" and "Ukei 1210," could also be evaluated by SM and MA (Nakagomi et al. 2019, 2020a). Therefore, these methods were proven to be useful alternatives to LH.

2. Screening of highly cracking-resistant CSSLs and finding a QTL

To select highly resistant lines, we screened CSSLs derived from a cross between "Itadaki" (O. sativa ssp. japonica) and O. rufipogon as a donor (Hirabayashi et al., unpublished data) that may have unknown and unused traits that are useful for rice breeding (Nakagomi et al. 2020b). We selected two resistant CSSLs, namely, "IRSL 30" and "IRSL 37," using the new standard cultivars (Fig. 1 and Table 4; Nakagomi et al. 2020b). Their PCKs were much lower than the PCK of "Itadaki," which was as high as that of the slightly weak cultivar "Koshihikari" and as low as those of the resistant standard cultivars "Eminokizuna" and "Yamadawara." "IRSL 30" and "IRSL 37" had an O. rufipogon segment in the same region on Chr. 8 within the "Itadaki" background (Fig. 3; Nakagomi et al. 2020b). This result indicates that a QTL associated with kernel-cracking resistance derived from O. rufipogon is located on Chr. 8. To confirm the QTL position, we conducted QTL analyses with F₄ individuals

Table 3	. Standard	cultivars for	· assessing	cracking	resistance in	ı LH ((Nakagomi)	et al. 2019,	2020a)
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Ta	arget region	Evaluation							
	Maturity group	Resistant	Moderately resistant	Medium	Moderately weak	Weak			
N	orth part of cool region (Tohoku Re	gion)							
	Early maturity group	Ouu 431	_	Hananomai Ouu 390	Akitakomachi	Tsugaruroman			
	Medium maturity group	Ukei 1210	_	Hitomebore Haenuki	_	Toyonishiki Yukigesyo			
S	outh part of cool region (Hokuriku	Region)							
	Early maturity group	Ouu 431	_	Inabawase	Akitakomachi	Toyonishiki			
	Medium maturity group	Eminokizuna	_	Hitomebore Haenuki	Koshihikari	_			
И	est part of warm region (Western R	egion)							
	Medium maturity group	Yamadawara		Setonokagayaki Kinumusume	_	Yamahikari Akidawara			
	Medium-to-late group	_	_	Hinohikari	Asominori	Aokaze			

		2014-20	15			2015-20	17			2017			
	Heading	1,000-	PC	CK	Heading	1,000-	PC	CK	G	rain size		Maturity	
Line name	date (mo/d)	grain weight (g)	LH (%)	SM (%)	date (mo/d)	grain weight (g)	LH (%)	SM (%)	thickness (mm)	length (mm)	width (mm)	group	Evaluation
CSSLs													
IRSL 30	8/14	23.4	4.0	6.0	8/9	22.4	17.1	9.4	1.92	5.79	2.72	Medium	Resistant
IRSL 37	8/12	23.6	9.0	7.6	8/4	23.6	9.6	14.1	2.06	5.29	2.91	Early	Resistant
Recipient													
Itadaki	8/11	23.1	58.6	41.3	8/4	23.5	57.3	52.0	2.01	5.26	2.93	Early	Moderate to moderately weak
Standard cultivars													
Eminokizuna	_	_	-	-	8/3	20.1	36.0	23.9	1.98	5.12	2.74	Early	Resistant
Hitomebore	8/10	22.0	53.7	37.3	8/3	22.1	52.6	53.6	2.03	5.27	2.82	Early	Moderate
Haenuki	—	—	_	_	8/1	21.2	51.6	38.8	1.99	5.27	2.76	Early	Moderate
Koshihikari	8/9	21.6	68.7	45.3	8/1	21.5	74.9	52.7	1.98	5.12	2.89	Early	Moderately weak
Yamadawara	8/18	22.5	2.3	5.9	8/11	21.8	26.7	16.6	1.91	5.50	2.83	Medium	Resistant
Nipponbare	8/18	22.3	6.0	5.0	8/13	21.6	46.1	33.3	2.00	5.14	2.79	Medium	Moderate
Akidawara	8/17	21.5	51.7	34.6	8/12	20.5	74.2	63.7	1.97	4.96	2.74	Medium	Weak

Table 4. Evaluation of kernel-cracking resistance of IRSLs (Nakagomi et al. 2020b)

PCK, percentage of cracked kernels; LH, late-harvest method; SM, soaking method



Fig. 3. Graphical genotypes of IRSL 30 and IRSL 37 (Nakagomi et al. 2020b)

□ "Itadaki" genotype (homozygous); ■ "IRSL 30" or "IRSL 37" genotype (homozygous for *O. rufipogon*). Genetic typing was performed on the GoldenGate BeadArray platform (Illumina Inc., San Diego, CA, USA) using 768 SNP markers.

of "Itadaki/IRSL 30" and "Itadaki/IRSL 37" populations and detected a QTL associated with the PCK near marker RM5485 (24.07 Mbp) on Chr. 8 in both populations (Fig. 4 and Table 5; Nakagomi et al. 2020b), with PVEs of approximately 70%. The "IRSL 30" and "IRSL 37" genotypes decreased PCK. We named it *qCR* (*Cracking Resistance*) 8-2. This QTL was distinct from that detected in Chr. 8 in previous studies (Nakagomi et al. 2014, Pinson et al. 2013) because the locations of these QTLs did not overlap. A QTL associated with grain thickness was also detected near qCR8-2 in the "Itadaki/IRSL 30" population (Table 5). Grain thickness affects kernel cracking and PCK tends to increase with grain thickness (Nakagomi et al. 2012, Takita 2002). The "IRSL 30" grain was slightly thinner than the "Itadaki" grain (Table 4), but the "IRSL 30" genotype increased kernel thickness, and the QTL for grain thickness was not detected in the "Itadaki/IRSL 37" population (Fig. 4). These results indicate that qCR8-2 is a novel and essential QTL associated with the cracking resistance of "IRSL 30" and "IRSL 37" and is not associated with thinner grain thickness.

3. Palatability and milling traits of the new crackingresistant line

Cracked kernels increase the broken rice ratio during polishing and diminish the flavor of the cooked rice (Koide et al. 2001). However, it is not clear how cracking resistance decreases damage and the deterioration of flavors. We selected "Chugoku PL2" (Parent Line 2), a resistant line that has "qCR8-2" in the "Itadaki" background, from the progeny of "Itadaki/IRSL 37" and investigated its palatability and other polishing traits. The palatability traits "appearance," "stickiness," "umami and sweetness," and "overall" of "Chugoku PL2" harvested at maturity tended to be higher than those of the recipient "Itadaki" (Table 6). PCK in LH "Chugoku PL2" was 68 percentage points lower than that of "Itadaki" (Table 7). The head rice ratio was approximately 6 percentage points higher than that of "Itadaki" because less small pieces of broken rice fell through the sieve K. Nakagomi





The bars on the left of the chromosomes indicate the intervals above the LOD threshold values. Arrowheads denote the positions of the LOD peaks. White arrowheads indicate where values decreased in "IRSL 30" or "IRSL 37." Only chromosomes in which QTLs were detected are shown.

Table 5.	OTLs detected	using composite in	terval mapping a	nalvses (Naka	agomi et al. 2020b)
	C				

Population	Chr.	Trait	Nearest marker	Peak position (cM)	LOD	Additive effect	PVE	LOD threshold
Itadaki/IRSL30, F ₄	7	Heading date (day)	RM6852	15.40	12.40	2.08	47.3	2.33
		Grain thickness (mm)	RM1330-1	24.40	6.06	-0.02	32.5	2.40
		Grain width (mm)	RM1330-1	33.40	4.18	-0.02	17.9	2.36
	8	PCK (%)	RM5485	12.49	24.67	-24.32	69.6	5.79
			RM5485	26.49	8.23	-22.63	24.6	5.79
		Grain thickness (mm)	RM5485	12.49	11.70	0.02	44.7	2.40
		Grain length (mm)	RM5485	12.49	18.43	-0.05	72.4	12.0
			RM5485	24.49	19.60	-0.06	72.3	12.0
		1,000-grain weight (g)	RM5485	21.49	5.02	-0.97	33.8	4.75
		Heading date (day)	RM7556	9.49	3.13	-0.79	9.3	2.33
Itadaki/IRSL37, F ₄	8	PCK (%)	RM5485	12.14	23.4	-22.35	71.2	8.54

LOD, logarithm of odds; PVE, percentage of variance explained; PCK, percentage of cracked kernels

Table 6. Palatability of "Chugoku PL2" cooked rice

Line	Appearance (-3 to +3)	Aroma (-3 to +3)	Stickness (-3 to +3)	Umami and sweetness (-3 to +3)	Softness (-3 to +3)	Overall (-3 to +3)
Chugoku PL2	1.37	0.93	1.24	1.22	1.06	1.45
Itadaki	1.06	0.98	0.89	0.92	1.09	0.97

Rice harvested at maturity was tested in 2019 (21 evaluators) and 2020 (23 evaluators). Each score was rated in comparison with "Nipponbare" as a cultivar with average palatability (= 0). Higher scores indicate better appearance, aroma, umami, and sweetness; softer and stickier rice are better.

during milling, and the broken rice ratio of milled rice was much lower than that of "Itadaki." These results indicate that it is possible to improve palatability and milling traits at late harvest by improving cracking resistance by the introduction of qCR8-2. "Chugoku PL2" has poor agronomic traits such as long awns that seem to be derived from *O. rufipogon* and the same poor resistance to stress, such as high temperature, as

Line	PCK (%)	Head rice ratio (%)	Broken rice ratio (%)
Chugoku PL2	20.0	88.1	9
Itadaki	88.0	82.5	38

Table 7. Milling traits of "Chugoku PL2"

Late-harvested kernels \geq 1.8 mm thick with a moisture content of approximately 13% were used for tests in 2020. All tests were conducted in duplicates. The percentage of cracked kernels (PCK) was visually investigated using 150 kernels on a TX-200 (Kett Electric Laboratory Co., Ltd., Japan). The head rice ratio was calculated as the weight of the milled rice remaining on the sieve after milling 150 g of brown rice for 100 s in white-rice mode in a Magic Mill (SKM-5B, SATAKE Corp., Japan) \div 150 g. The broken rice ratio was investigated using 10 g of milled kernels over a sieve of the milling machine.

"Itadaki." Therefore, our next target is to develop cultivars with not only cracking resistance but also good agronomic traits.

Acknowledgements

This study was partially supported by grants from a project commissioned by the Ministry of Agriculture, Forestry and Fisheries of Japan (BGW1105). The author would like to thank the staff at WARC, TARC, and the Fukui Agricultural Experiment Station for their assistance.

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