REVIEW

The use of floury endosperm mutants to develop rice cultivars suitable for dry milling

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Abstract

Starch is the major constituent of rice grains determining eating, cooking, and processing properties. While rice endosperm mutants with modified starch characteristics have provided valuable materials for elucidating the gene mechanisms involved in starch biosynthesis and grain development, their practical use in crop improvement has been rarely documented. In this review, we focus on the use of floury endosperm mutants with reduced grain hardness to breed rice cultivars suitable for dry milling. We describe the identification of "Suweon542", the original genetic source carrying *flo4-4* [formerly *flo7(t)*] which has been used to develop Korean rice cultivars specialized for dry-milled flour production. Molecular breeding efforts are highlighted in the development of "Garumi1" and "Garumi2", the floury endosperm rice cultivars with improved agronomic characteristics.

Keywords Rice · Endosperm · Dry milling · Flour · Mutation · Breeding

Introduction

Rice consumption in Korea has been sharply decreasing over the past four decades as the eating habits of the Korean people diversify with rapid economic growth. The per capita annual rice consumption in Korea recorded 61 kg in 2018, which is less than a half of 133 kg in 1980 (KOSIS 2019). As a result, overproduction of rice has been the major challenge in the Korean rice industry causing low market price, high storage cost, and stagnated income of rice growers. Despite the decrease in the total rice consumption, the amount of rice consumed as processed food (e.g., rice cake, bread, noodles, etc.) has been soaring in the recent years. While the total rice consumption in Korea decreased by 20% from 5.26 M tons in 2000 to 4.24 M tons in 2015, the amount consumed as processed food increased by 240% (from 180 to 610 thousand tons) during the same period (KOSIS 2019). Therefore, the government has been making policy and research efforts to invigorate the processed rice food industry and boost rice consumption in Korea.

The high cost of flour production is one of the main obstacles in scaling up processed rice food industry. Approximately 70% of rice used to manufacture processed food is utilized in the form of flour, of which the majority is produced using the wet milling technique (Kim 2013). To soften rice grains, wet milling involves the soaking and drying steps of rice before and after milling, consuming large amounts of water and energy (Chiang and Yeh 2002). While the dry milling technique mainly used for wheat flour production excludes the soaking and drying steps and can reduce the milling cost by 50–70%, the high grain hardness of regular rice cultivars causes high level of damaged starch in dry-milled flour and deteriorates end-use quality (Lee and Kim 2011; Leewatchararongjaroen and Anuntagool 2016; Kwak et al. 2017). This necessitates the development of rice cultivars with soft grain that pulverizes easily and is suitable for dry milling.

A number of endosperm mutants with modified starch structure have been identified and characterized in rice, providing valuable materials to elucidate the starch biosynthesis pathway (Nakamura 2018; Bao 2019). However, little information is available in terms of the practical use of the endosperm mutants in rice (Ashida 2014). In this mini review, we focus on the genetics and characteristics of the floury endosperm rice mutants, highlighting their utilization in molecular breeding to develop cultivars suitable for dry

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milling which would contribute to strengthening the processed rice food industry.

Floury endosperm mutants in rice

The term "floury" or "chalky" is generally used to describe soft, white non-translucent rice endosperm which breaks easily into powder due to the loosely packed starch granule structures (Satoh and Omura 1981; Kaushik and Khush 1991; Ashida et al. 2009). While some floury rice mutants referred to as "milky-white" exhibit the soft non-translucent characteristics in the entire endosperm area, others are partly floury and often classified as "white-core", "white-back", or "white-belly" that has the floury portion at the central, dorsal, or ventral area of the endosperm, respectively (Ashida et al. 2009). The non-translucent endosperm appearance of the floury mutants is similar to that of the "waxy" (glutinous) and "dull" (intermediate between waxy and non-waxy) mutants. However, when stained by I-KI solution, the endosperm of the floury mutants turns blue-black as regular translucent rice while the waxy mutants are not stained and the dull mutants show intermediate phenotype (Satoh and Omura 1981; Ashida et al. 2009). Also, the soft endosperm of the floury mutants is different from that of the waxy and dull mutants which shows high grain hardness as regular translucent rice (Satoh and Omura 1981). Recent reviews have provided extensive information on various types of rice endosperm mutants used for studying starch biosynthesis pathway (Nakamura 2018; Bao 2019). This review mainly focuses on the rice endosperm mutants classified as *flo* (floury), their characteristics, and potential use in breeding.

More than 16 mutants named *flo* have been reported in rice and 14 of them have been cloned (Table 1). Caution is required as some of the non-allelic mutants have been designated the same nomenclature, i.e., two non-allelic mutants each for *flo6* (Zhang et al. 2012; Peng et al. 2014) and *flo7* (Sheng et al. 2015; Zhang et al. 2016). Most of the *flo* mutants have been screened from the mutant populations induced by chemicals (MNU, EMS, SA), radiation (gamma ray), insertional mutagens (T-DNA, Tos17), or tissue culture owing to their abnormal grain appearance with white non-translucent endosperm which is different from the wild-type's translucent endosperm. The I-KI staining method is often used to distinguish floury mutants from waxy and dull mutants (Mo et al. 2013).

While the *flo* mutants including *flo(a)*, *flo6*, *flo10*, *flo12*, *flo13*, *flo14* and *flo16* exhibit the floury phenotype in most part of the endosperm except thin periphery, some are partially floury in the core (*flo5*, *flo8*, *flo15*) or peripheral (*flo7*) regions of the grain (Fig. 1). Interestingly, *flo4-1* and *flo4-4* [formerly *flo7(t)*], the allelic mutants of cy*OsP-PDK* (*Os05g0405000*), exhibit different floury endosperm

phenotype. While *flo4-1* carrying a T-DNA insertion between exon 3 and exon 4 is floury only in the core endosperm region (Kang et al. 2005), *flo4-4* with a missense mutation in exon 8 shows floury phenotype in most part of the endosperm except for the thin outer layer (Mo et al. 2013; Wang et al. 2018). Regardless of the extent of the floury phenotype within the endosperm, electron microscopy observations of the non-translucent endosperm area of the *flo* mutants reveal loosely packed starch granules with rounded shape that are different from the densely packed polyhedral starch granules observed in regular translucent endosperm (Fig. 2).

Major phenotype changes (e.g. grain weight, starch properties, etc.) observed in the *flo* mutants are summarized in Table 1. Most *flo* mutants exhibit significant decrease in grain weight mainly due to the altered endosperm starch structure with loosely packed granules that are different from wild-type's densely packed starch granules. Only two *flo* mutants, namely *flo5* (Ryoo et al. 2007) and *flo8* (Long et al. 2017), have comparable grain weight relative to wild-type while none of the *flo* mutants show increase in grain weight. Most *flo* mutants exhibit significant reduction in amylose content while a few, namely *flo6* (Zhang et al. 2012), *flo11* (Zhu et al. 2018), *flo13* (Hu et al. 2018) and *flo14* (Xue et al. 2019), show no significant change. Two exceptions are *flo5* (Ryoo et al. 2007) and *flo4-4* (Mo et al 2013), which have amylose content significantly higher than wild-type. Changes in other phenotypes including amylopectin chain length distribution, protein and lipid content, and plant height vary among different *flo* mutants (Table 1). While these mutants have provided invaluable materials to study the gene mechanisms involved in starch biosynthesis and grain development, their potential use in practical breeding has been rarely explored.

"Suweon542", a floury endosperm mutant suitable for dry milling

In Korea, "Suweon542" provided the original genetic source for developing rice cultivars suitable for producing dry-milled flour (Mo et al. 2013). Suweon542 is an elite rice line selected directly from a mutant population induced by sodium azide in the background of "Namil", a high-yielding non-glutinous Korean *japonica* cultivar. From over 5,000 mutant lines at M_8 generation, those with white non-translucent endosperm were visually screened. Waxy and dull mutants were excluded by I-KI staining. One line designated "Namil(SA)M2-1509-RGA-1-1-1-1" with floury appearance in the entire endosperm area was selected as a promising line, named Suweon542 and evaluated in yield trials and local adaptability tests. Compared to non-mutagenized Namil, Suweon542 was slightly taller and headed few days

Table 1 Floury endosperm mutants identified in rice and their major characteristics in comparison with wild-type

Mutant	Chr	Gene	Gene ID	Wild-type (mutagen)	GW	AC	Amylopectin CLD	Other traits	References
flo-1	5	–	–	Kinmaze (MNU)	–	↓	–	–	Kaushik and Khush (1991)
flo-2 [*flo2*, *flo(a)*]	4	*FLO2*	*Os04g0645100*	Kinmaze (MNU) Hwacheong (MNU) Taikeng 8 (EMS)	↓	↓	9–21↓, 22–38↑, ≥ 38↓	PC↓	Kaushik and Khush (1991) Kawasaki et al. (1996) She et al. (2010) Qiao et al. (2010) Wu et al. (2015)
flo-3(t)	4	–	–	Shiokari (gamma ray)	–	–	–	–	Maekawa (1985) Kinoshita and Takahashi (1991)
flo4	5	cy*OsPPDK*	*Os05g0405000*	Dongjin (T-DNA) Hwayoung (T-DNA, Tos17)	↓	↓	=	PC↑, LC↑	Kang et al. (2005) Ryoo et al. (2007)
flo5	8	*SSIIIa*	*Os08g0191433*	Dongjin (T-DNA) Hwayoung (T-DNA)	=	↑	6–8↓, 9–15↑, 16–20↓, 22–29↑, ≥ 30↓	–	Ryoo et al. (2007)
flo6	1	*AGPL2*	*Os01g0633100*	Nipponbare (EMS)	↓	=	–	PC=	Zhang et al. (2012)
flo6	3	*FLO6*	*Os03g0686900*	Nipponbare (tissue culture)	↓	↓	6–8↑, 9–15↓, 16–40↑	PH↓, PC↑, LC↑	Peng et al. (2014)
flo7(t) (*flo4-4*)	5	cy*OsPPDK*	*Os05g0405000*	Namil (SA)	↓	↑	–	PH↑, PC↓	Mo et al. (2013) Wang et al. (2018)
flo7	12	–	–	Nipponbare (tissue culture)	↓	↓	–	PH↑	Sheng et al. (2015)
flo7	10	*FLO7*	*Os10g0463800*	Nipponbare (T-DNA)	↓	↓	6–7↓, 8–14↑, 15–55↓		Zhang et al. (2016)
flo8	9	*Ugp1*	*Os09g0553200*	Dianjingyou1 (MNU) Ningjing3 (MNU)	=	↓	7–9↑, 10–13↓, 14–16↑, ≥ 17↓	PH↓, PC=, LC↑	Long et al. (2017)
flo9	9	–	–	N22 (gamma ray)	↓	↓	–	Lethal, LC↓	Liu et al. (2018)
flo10	3	*FLO10*	*Os03g0168400*	N22 (MNU)	↓	↓	–	PH↓, PC↑, LC↑	Wu et al. (2019)
flo11	12	*Hsp70cp-2*	*Os12g0244100*	N22 (gamma ray)	↓	=	=	LC=	Zhu et al. (2018)
flo12	10	*AlaAT1*	*Os10g0390500*	Dianjingyou1 (MNU)	↓	↓	6–8↑, 12–17↓	PH↓, PC↑, LC↑	Zhong et al. (2019)
flo13	2	*NDUFA9*	*Os02g0816800*	Ninggeng 3 (EMS)	↓	=	–	Lethal	Hu et al. (2018)
flo14	3	*NPPR3*	*Os03g0728200*	Dianjingyou1 (MNU)	↓	=	–	Lethal	Xue et al. (2019)
flo15	5	*GLYI7*	*Os05g0230900*	W017 (MNU) Koshihikari (radiation)	↓	↓	6–13↑, 14–56↓	PH↓, PC↑, LC↑	You et al. (2019)
flo16	10	*CMDH*	*Os10g0478200*	N22 (gamma ray)	↓	↓	6–10↑, 11–12↓, 13–14↑, 15–48↓	PH↓, PC↑, LC↑	Teng et al. (2019)

AC amylose content; *CLD* chain length distribution; *EMS* ethyl methanesulfonate; *GW* grain weight; *LC* lipid content; *MNU* N-methyl-N-nitrosourea; *PC* protein content; *PH* plant height; *SA* sodium azide

↑ increase; ↓ decrease; = no change; – not available

later. Although Suweon542 had significantly higher number of spikelets (155 per panicle) than Namil (117 per panicle), its brown rice yield was 5.67 t/ha, 6% lower than that of Namil (6.00 t/ha) mainly due to the low weight of the floury grains.

Compared to Namil, the grain hardness of Suweon542 was reduced by 56%, indicating that the soft grains of Suweon542 would be easily pulverized during dry milling and produce good quality flour (Mo et al. 2013). Dried-milled flour of Suweon542 showed damaged starch content of 4.9%, 47% lower than that of Namil (9.2%), and its particle size distribution was highly similar to commercial wheat flour produced by dry milling. End-use qualities of the dry-milled and wet-milled Suweon542 flour were compared for various processed food products including bread, noodles, beer, rice cake and confectionery. The panel tests
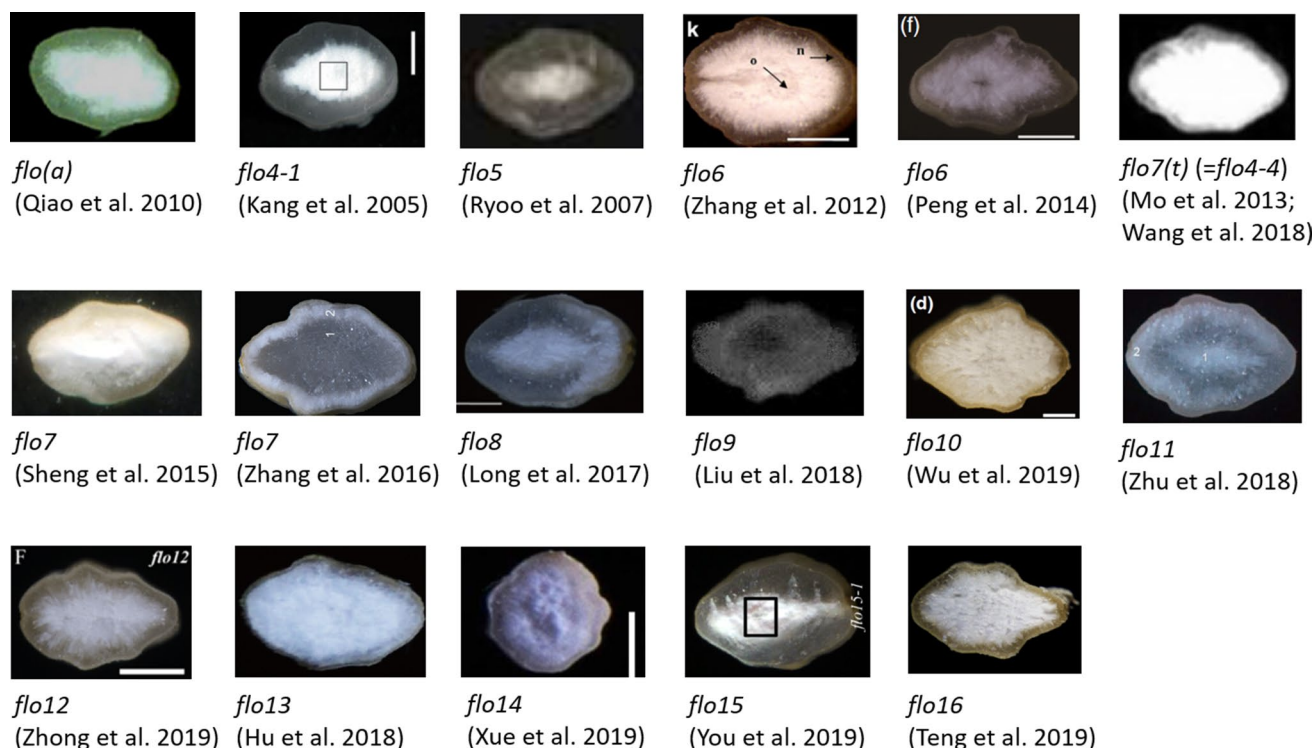
flo(a)
(Qiao et al. 2010)

flo4-1
(Kang et al. 2005)

flo5
(Ryoo et al. 2007)

flo6
(Zhang et al. 2012)

flo6
(Peng et al. 2014)

flo7(t) (=flo4-4)
(Mo et al. 2013;
Wang et al. 2018)

flo7
(Sheng et al. 2015)

flo7
(Zhang et al. 2016)

flo8
(Long et al. 2017)

flo9
(Liu et al. 2018)

flo10
(Wu et al. 2019)

flo11
(Zhu et al. 2018)

flo12
(Zhong et al. 2019)

flo13
(Hu et al. 2018)

flo14
(Xue et al. 2019)

flo15
(You et al. 2019)

flo16
(Teng et al. 2019)

Fig. 1 Transverse sections of the rice mutants with floury endosperm. Each figure was imported from the relevant reference with minor modification (i.e. cropping and rotation). The permission to reuse the images of *flo4-1*, *flo5*, *flo6* (both Zhang et al. 2012 and Peng et al. 2014), *flo8*, *flo10*, *flo11*, *flo12*, *flo13*, and *flo15* were obtained through Copyright Clearance Center (http://www.copyright.com/publishers/rightslink/). The images of *flo7(t)*, *flo7* (both Sheng et al. 2015 and Zhang et al. 2016), *flo14*, and *flo16* were imported from the open access articles distributed under the terms of the Creative Commons Attribution License (https://creativecommons.org/licenses/). The permission to reuse the images of *flo(a)* and *flo9* were obtained directly from the publisher (Korean Society for Molecular and Cellular Biology) and the corresponding author (Dr. Yihua Wang), respectively

by researchers and consumers reported no quality difference between the products made from dry-milled and wet-milled Suweon542 flour, demonstrating that Suweon542 would provide a promising genetic source to breed rice cultivars suitable for dry milling (KIPRIS 2012).

To identify the causal mutation responsible for Suweon542's floury endosperm, genetic analysis was conducted using an F_2 population derived from the cross between Suweon542 and Milyang23 (Mo et al. 2013). The causal gene was initially mapped at the 19.3–20.1 Mb region on chromosome 5 and temporarily designated *flo7(t)*. Fine-mapping with the segregating $F_{3:4}$ progenies further delimited the *flo7(t)* locus within the 33 kb interval containing four candidate genes (Wang et al. 2018). Sequencing of the candidate genes revealed a G-to-A SNP (Gly-to-Asp) in exon 8 of cy*OsPPDK* (*Os05g0405000*) which encodes a cytosolic pyruvate orthophosphate dikinase protein. As the three mutated alleles of cy*OsPPDK* (*flo4-1*, *flo4-2* and *flo4-3*) had been reported previously (Kang et al. 2005), the novel allele from Suweon542 was named *flo4-4* (Wang et al. 2018). To facilitate molecular breeding, PCR-based allele specific markers were developed for *flo4-4* (KIPRIS 2019a).

Molecular breeding to improve rice cultivars for dry milling

Despite the novel starch properties suitable for dry milling, Suweon542 has two major drawbacks—the high susceptibility to bacterial blight, stripe virus and blast that are rampant in the Southern plain area of Korea, and the frequent occurrence of pre-harvest sprouting under the wet weather during grain filling. To overcome these limitations, we crossed Suweon542 with "Jopyeong", an early-maturing Korean *japonica* rice cultivar carrying the *Xa3* gene for bacterial blight resistance and the *Stv-b^i* gene for stripe virus resistance (Nam et al. 2013). While the blast resistance gene carried by Jopyeong is unclear, pedigree information suggests that Jopyeong has a blast resistant allele at the *Piz* locus from a Korean rice cultivar "Jinbubyeo" (Jeung et al. 2007).

Marker assisted selection (MAS) was carried out from the F_2 generation using the *flo4-4* marker (KIPRIS 2019a) for floury endosperm, the 9643.T4 marker (Park et al. 2013) for *Xa3*, the InDel7 marker (KIPRIS 2013) for *Stv-b^i*, and the 9871.T7E marker (Jeung et al. 2007) for the resistant allele at the *Piz* locus (Fig. 3). This enabled us an efficient
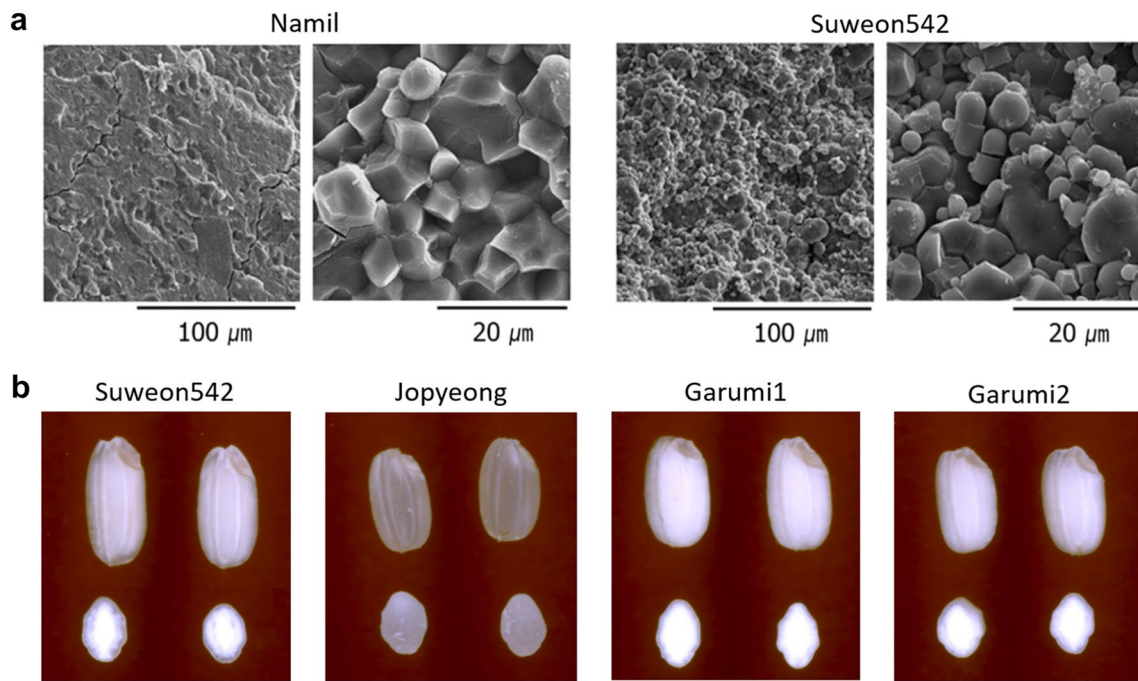
Fig. 2 Electron microscopy visualization of endosperm and brown rice appearance in floury endosperm rice cultivars. **a** Electron microscopy observation of endosperm in non-mutagenized Namil and its floury mutant line Suweon542. The pictures were imported from Mo et al. (2013) with minor modification under the terms of the Crea- tive Commons Attribution License (https://creativecommons.org/ licenses). **b** Brown rice and its transverse section of Suweon542, Jopyeong, and the two floury rice cultivars Garumi1 and Garumi2 derived from the cross between Suweon542 and Jopyeong

breeding scheme as all the breeding lines evaluated in the field at F_6 generation were fixed with the favorable alleles for floury endosperm and resistance to bacterial blight, stripe virus and blast. As MAS was not feasible for pre-harvest sprouting, phenotype selection was conducted by visually screening brown rice at F_2–F_4 generations and evaluating panicles for vivipary under saturated humidity at F_5 generation. Two promising lines, "SR34136-B < fl-19-7-2-5" and "SR34136-B < fl-19-7-8-6", showed pre-harvest sprouting resistance and were further evaluated in yield trials, demonstrating higher yield compared to Suweon542 under the late planting conditions (transplanting in late June–early July in Korea). These lines were subsequently registered as the new cultivars "Garumi1" and "Garumi2" (KIPRIS 2019b).

Perspectives

With improved resistance to diseases and pre-harvest sprouting, Garumi1 and Garumi2 provide useful materials as specialty cultivars for dry-milled rice flour production. High yield performance of Garumi1 and Garumi2 under the late planting condition is also valuable for promoting diverse double cropping systems in the rice paddies. Different dry milling techniques and conditions are currently being tested in collaboration with processed food manufacturers to optimize the flour characteristics of Garumi1 and Garumi2 for producing various food items such as bakery products, noodles, rice cake and liquor. Further breeding efforts are also underway to develop new floury endosperm cultivars with additional processing qualities such as color and aroma.
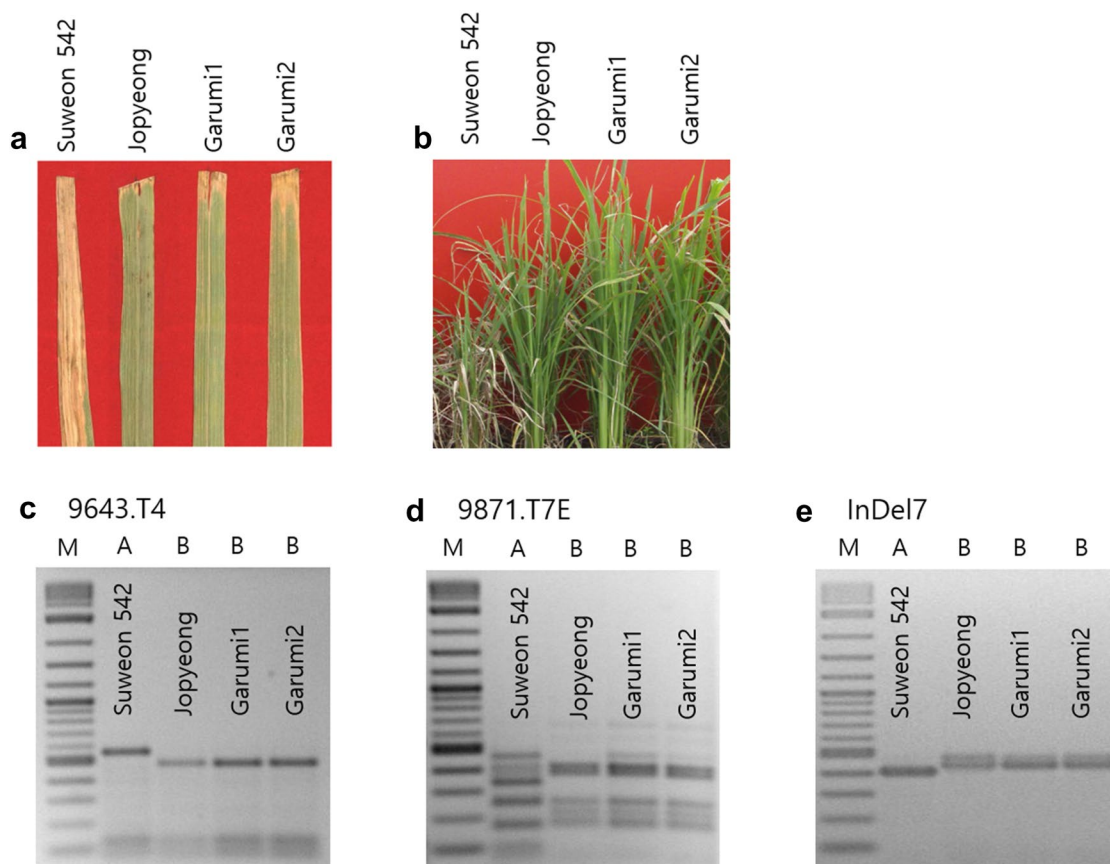
Fig. 3 Enhanced disease resistance of Garumi1 and Garumi2 through molecular breeding. Disease resistance phenotype for bacterial blight (**a**) and blast (**b**). Marker genotypes of 9643.T4 for *Xa3* (**c**), 9871.T7E for *Piz* (**d**) and InDel7 for *Stv-b^i* (**e**). A and B indicate susceptible and resistant alleles, respectively, and M indicates the size marker

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