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Genetic analysis of endosperm mutants in rice *Oryza sativa* L.

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Summary. Sugary, shrunken, floury, white core, amylose extender and dull mutants induced in japonica varieties were used in this study. The results of an allelic analysis conducted in japonica background indicated that the two sugary mutants 82GF and EM5 are allelic. The two amylose extender mutants 2064 and EM16 are also allelic. The opaque mutant ESD7-3(0) and floury mutants 2047, EM17 and EM28 are allelic as well and have the *flo-1* gene. The three white core mutants EM3, EM24 and EM66 were found to be non-allelic. Eleven dull mutants were investigated. Dull mutants 2057, 2083, 2091 and EM15 were found to be allelic to each other. Similarly, dull mutants 2077, 2078 and 2120 have allelic genes. Dull mutants 2035, EM12, EM47, and EM98 are non-allelic to the above loci. Dull genes in EM12, EM15, and EM98 were designated earlier as *du-1, du-2* and *du-4,* respectively.

The mutant genes were transferred to indica background by two backcrosses to IR36. Some of the mutant genes were located to respective chromosomes through trisomic analysis using primary trisomics of IR36. In this way the amylose extender gene *ae* was located to chromosome 2, the *flo-1* was located to chromosome 5 and the *flo-2* to chromosome 4. Dull genes of EM47, 2120, and 2035 were assigned to chromosomes 6, 9, and 6, respectively.

Key words: *Oryza sativa* – Endosperm mutants – Trisomics – Chromosomal location – Allelic relationships

Introduction

The endosperm, which forms the deposition site of large quantities of starch during grain filling, nourishes the embryo during its early stages of development. Endosperm starch consists of a linear fraction amylose and a branched fraction amylopectin. A number of loci at which mutations affect the quality and quantity of the starch synthesized are known in maize. These loci are amylose extender (*ae*), brittle-1 (*bt-1*) and brittle-2 (*bt-2*), shrunken-1 (*sh-1*) and shrunken-2 (*sh-2*), sugary-1 (*su-1*) and sugary-2 (*su-2*), dull (*du*), and waxy (*wx*) (Creech 1965, Shannon and Creech 1973; Boyer and Shannon 1983). Recently, similar endosperm mutants have been induced in different *japonica* varieties using chemical mutagens and radiations (Okuno 1976, Okuno et al. 1983; Satoh and Omura 1981; Yano et al. 1985).

For practical utilization of these mutants, a sound knowledge of their genetic behavior is desirable. This study was undertaken to investigate the mode of inheritance and allelic relationships of the mutants and to locate the non-allelic genes to respective chromosomes by trisomic analysis.

Materials and methods

Endosperm mutants induced in japonica var 'Kinmaze', 'Sasanishiki' and 'Norin 8' (provided by Drs. K. Okuno and H. Satoh of Japan) were used in this study. One opaque mutant in var 'ESD7-3' was a gift from Dr. J. N. Rutger of the USA. Various mutants and the varieties in which they were induced as well as the mutagen used are shown in Table 1.

The sugary mutants are characterized by wrinkled but translucent endosperm, and the shrunken mutants have wrinkled and floury white endosperm. Floury mutants have soft white endosperm that breaks easily into a fine powder. The endosperm appearance of amylose extender mutants ranges from completely vitreous grains to floury white grains. The white-core mutants have a central white portion that consists mainly of loosely packed starch. The endosperm appearance of dull mutants is in between waxy and translucent. Unlike the floury character, the dull character is expressed only when the grains are completely dry.

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Table 1. Description of endosperm mutants used in the study

Mutant	Parent variety	Mutagen treatment[a]	Gene symbol	Amylose content (%)[b]
Sugary				
82GF	Norin 8	^{32}P B-rays	–	0.0
EM5	Kinmaze	MNU	*sug*	6.0
Shrunken				
EM20	Kinmaze	MNU	*shr-1*	9.3
Amylose-extender				
EM16	Kinmaze	MNU	*ae*	26.2
2064	Sasanishiki	EMS	–	31.3
Fluory				
EM17	Kinmaze	MNU	*flo-1*	11.6
EM28	Kinmaze	MNU	–	10.4
EM36	Kinmaze	MNU	*flo-2*	5.6
2047	Sasanishiki	EMS	–	12.1
Opaque				
ESD7-3(o)	ESD7-3	–	*o*	7.1
White-core				
EM3	Kinmaze	MNU	–	12.2
EM24	Kinmaze	MNU	–	11.3
EM66	Kinmaze	MNU	–	10.6
Dull				
2035	Sasanishiki	EMS	–	4.6
2057	Sasanishiki	EMS	–	2.3
2077	Sasanishiki	EMS	–	5.9
2078	Sasanishiki	EMS	–	6.1
2083	Sasanishiki	EMS	–	2.8
2091	Sasanishiki	EMS	–	2.7
2120	Sasanishiki	EMS	–	4.9
EM12	Kinmaze	MNU	*du-1*	2.6
EM15	Kinmaze	MNU	*du-2*	1.1
EM47	Kinmaze	MNU	–	1.9
EM98	Kinmaze	MNU	*du-4*	1.5

[a] EMS, Ethyl methane sulphonate; *MNU*, *N*-methyl *N*-nitrosourea

[b] Amylose content of parent varieties is 13–15%

The japonica var 'Kinmaze,' 'Sasanishiki' and 'Norin 8' have a low amylose content (13–15%). Sugary mutants 82GF and EM5 have either no amylose at all (82GF) or only very low amount as of it (5–6%) (EM5). The amylose content of the shrunken mutant as well as that of the floury mutants was reduced to about 8–10%; the amylose content of floury mutant EM36 is even lower (5–6%). There was a slight reduction in the amylose content of white-core mutants. However, the amylose content of all of the dull mutants was reduced considerably. Conversely, the amylose extender mutants contain more amylose than the parental varieties (Table 1; Kaushik and Khush 1991).

Similar mutants in the original background of japonica varieties were crossed with each other in a diallel fashion without reciprocals during the 1986 wet season (WS) and the 1987 dry season (DS). The mutants were also crossed to the respective parent varieties. The F_1 hybrids of the following crosses along with the parents were grown in the 1987 DS and WS at the International Rice Research Institute (IRRI) Los Banos: 3 crosses among sugary and shrunken mutants; 1 among two amylose extender mutants; 10 crosses among four floury and an opaque mutant; 3 crosses among three white-core mutants, 55 crosses among the 11 dull mutants. The F_2 seeds borne on F_1 plants were harvested.

The dehulled F_1 and F_2 grains along with those of the parents were milled in a test-tube mill. The F_2 grains of all crosses were classified for endosperm appearance. The analysis for amylose content of F_1 and F_2 grains was carried out in 7 crosses of mutants (one amylose extender and six dull) with parents; 1 cross of the two amylose extender mutants; 15 crosses involving six non-allelic dull mutants. Single grains were used for amylose analysis. Embryos were removed from each milled grain with a blade, and the individual grains were ground in a Wig-L-Bug. Single grain analysis for amylose content was carried out by using 20 seeds of each parent, 5–10 F_1 hybrid seeds and about 100–200 F_2 seeds of each cross. The amylose analysis was done on a Technicon Autoanalyzer according to the procedure of Juliano (1971).

Six non-allelic mutant genes in an IR36 background namely, 2064 (*ae*), *ESD7-3(o)* (*flo-1*), EM36 (*flo-2*), 2035 (*du*), 2077 (*du*) and EM47 (*du*), were crossed to the primary trisomics of IR36 (Khush et al. 1984) during the 1987 WS and the 1987 DS. The trisomic F_1 progenies were grown during the 1988 DS. Trisomic F_1 plants of triplo 1 and triplo 2 were backcrossed to the respective mutants. The F_2 seed produced on trisomic F_1 and disomic plants of each cross were dehulled, milled wherever necessary, and classified for endosperm appearance. In the crosses of the amylose extender mutant we analyzed about 100 F_2 seeds of each trisomic and of one disomic plant to check segregation for amylose content.

Results and discussion

Inheritance and allelic relationship

Two sugary mutants (EM5 and 82GF) showed monogenic recessive inheritance in the F_2 of crosses with the parent var 'Kinmaze' and 'Norin 8' respectively (Table 2). However, the chi square value was highly significant for 3:1 ratio in the F_2 derived from the cross of sugary (82GF) with 'Norin 8.' The grains of 82GF are more wrinkled than those of EM5. The F_1 seed of the cross between the two sugary mutants was wrinkled (sugary), and the F_2 seeds segregated into two types – those typical of EM5 and others typical of 82GF – in a 3:1 ratio. This indicates that the phenotypic expression of sugary genes in 82GF and EM5 is specified by multiple alleles, with the allele in EM5 being dominant. This was confirmed by segregation for amylose content in 50 F_2 grains: the grains of 82GF had absolutely no amylose whereas those of EM5 had 5–6% amylose. Amylose content of the F_1 seeds was similar to that found in EM5 seeds and in the F_2 30 grains had amylose in the range of that of EM5 and 11 grains had no amylose like those of 82GF. This segregation agreed with a 3:1 ratio.

The F_1 seeds of crosses of the two sugary mutants with shrunken (EM20) were normal in appearance. The chi-square value for a 9 normal: 7 mutant ratio expected with digenic segregation in the F_2 was non-significant in the 1986 WS (Table 3) but was highly significant in the 1987 DS. The reason for segregation distortion in the

Table 2. Segregation of F_2 grains in crosses of different endosperm mutants with parent varieties

Cross	Mutant	Segregation of F_2 grains			
		Normal	Mutant	Total	χ^2 (3:1)
82GF/Norin 8	Sugary	350	67	417	17.8***
EM5/Kinmaze	Sugary	233	72	305	0.2
EM20/Kinmaze	Shrunken-1	237	64	301	2.2
ESD-7-3(o)/ESD7-3	Floury-1	492	155	647	0.4
EM36/Kinmaze	Floury-2	68	28	96	0.9
EM3/Kinmaze	White-core	454	182	636	3.9*
EM24/Kinmaze	White-core	216	70	286	0.1
EM66/Kinmaze	White-core	250	85	335	0.1
2035/Sasanishiki	Dull	470	106	576	13.4***
2057/Sasanishiki	Dull	347	113	460	0.1
2077/Sasanishiki	Dull	535	146	681	4.6*
EM12/Kinmaze	Dull	358	112	470	0.3
EM47/Kinmaze	Dull	237	61	298	2.2
EM98	Dull	514	139	653	4.8*

*,*** Significant at 5% and 0.1% level, respectively

Table 3. Segregation of F_2 grains for mutant traits in crosses between similar endosperm mutants

Cross combination	Appearance of F_1 seed	Season	Segregation of F_2 grains			
			Normal	Mutant	Total	χ^2 (9:7)
Sugary and shrunken						
82GF/EM20	Normal	86WS	124	87	211	0.54
		87DS	280	156	436	11.25***
EM5/EM20	Normal	86WS	128	100	228	0.02
		87DS	347	182	529	18.77***
Floury and opaque						
2047/EM36	Normal		822	654	1,476	0.18
EM17/EM36	Normal		254	156	411	5.15*
EM28/EM36	Normal		248	223	471	2.48
ESD7-3(o)/EM36	Normal		331	234	565	1.25
White-core						
EM3/EM24	Normal		342	243	585	1.16
EM3/EM66	Normal		449	289	738	6.30*
EM24/EM66	Normal		475	320	795	3.95*

* Significant at 5% level; *** highly significant at 5% level

1987 DS appears to be the low recovery of double recessive grains sugary and shrunken caused by viviparous germination and highly collapsed endosperm, which is highly influenced by environmental conditions prevailing at the time of grain development. These results confirmed the earlier report of Yano et al. (1984), who reported sugary (EM5) and shrunken (EM20) mutants to be non-allelic. Yano et al. (1984) designated the gene for sugary endosperm as *sug* and located it on chromosome 8. Similarly they designated the gene for shrunken endosperm as *Shr-1*^{S} and located it on chromosome 1.

Floury mutants 2047, EM17, EM28 and ESD7-3(*o*) were found to be allelic as no segregation was observed in the F_2 of intercrosses among them and the phenotype of F_1 seed was also floury (Kaushik and Khush 1987). Floury genes in EM17 and EM36 were designated *flo-1* and *flo-2*, respectively, by Satoh et al. (1984). It is therefore obvious that four mutants, 2047, EM176, EM28, and ESD7-3(*o*), have the same *flo-1* gene and that the opaque gene *o* (Rutger et al. 1985) is allelic to *flo-1*. However, the F_1 seeds of the crosses of the above four floury mutants with floury mutant EM36 had a normal appearance and the F_2 seeds segregated into 9 normal: 7 floury (Table 3). These results confirmed that *flo-1* and *flo-2* are independent of each other. The monogenic recessive nature of *flo-1* and *flo-2* was also confirmed as the F_2 seeds

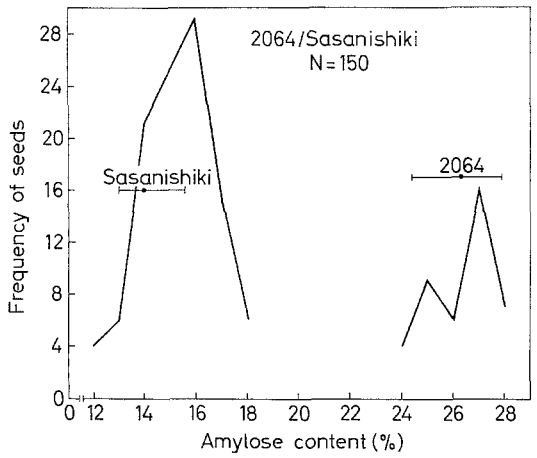

Fig. 1. Distribution of amylose content in F_2 of cross of amylose extender (2064) mutant with parent

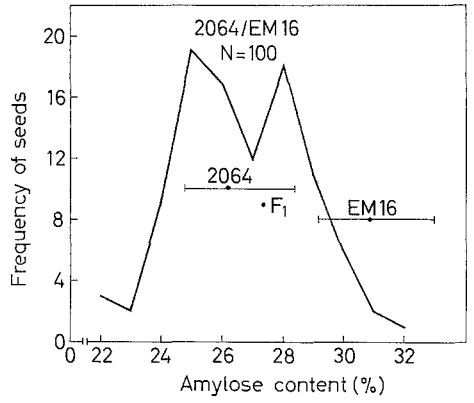

Fig. 2. Distribution of amylose content in F_2 of cross between two amylose extender mutants

of their crosses with parental varieties segregated in a 3 normal: 1 mutant ratio (Table 2).

The amylose extender mutant 2064 (*ae*) was crossed with parental var 'Sasanishiki.' The F_2 grains of this cross segregated into low amylose (107 grains) like those of 'Sasanishiki' and high amylose (43 grains) like those of *ae* (Fig. 1). The segregation agreed with a 3:1 ratio and confirmed the monogenic recessive nature of *ae*. The F_1 grains of the cross between the two *ae* mutants (2064 and EM16) had a high amylose content, and the amylose content of the F_2 grains was within the range of the two parents (Fig. 2). These results show that the two amylose extender mutants have allelic genes.

The three white-core mutants EM3, EM24 and EM66 showed monogenic recessive inheritance when crossed to parent var 'Kinmaze (Table 2). The F_1 grains of the three intercrosses among the three mutants were normal in appearance, and the F_2 grains segregated into 9 normal: 7 white-core (Table 3). However, the chi-square value was significant in crosses involving EM66 as one of the

Table 4. Segregation of F_2 grains for endosperm appearance in the crosses of some dull mutants with parent varieties

Cross	Segregation of F_2 grains for amylose content			
	Normal	Mutant	Total	χ^2 (3:1)
2035/Sasanishiki	124	26	150	4.7*
2057/Sasanishiki	117	33	150	0.7
2077/Sasanishiki	115	35	150	0.2
EM12/Kinmaze	115	35	150	0.2
EM47/Kinmaze	110	40	150	0.2
EM98/Kinmaze	118	32	150	1.1

* Significant at 5% level

parents. The three white-core mutants are thus non-allelic to each other.

The monogenic recessive nature of six dull mutants was confirmed from the segregation of F_2 grains in the crosses of mutants with parental varieties. On the basis of endosperm appearance all of the mutants showed a segregation ratio of 3 normal to 1 mutant. The analysis of the amylose content of the F_2 grains confirmed the monogenic recessive nature of these mutants (Table 4).

The allelic relationships between dull mutants were investigated from the segregation for endosperm appearance of F_2 grains of crosses between different mutants. The results were confirmed through the analysis of amylose content of 200 F_2 grains of crosses between mutants found to be non-allelic.

The F_2 grains of the crosses amongst dull mutants 2057, 2083, 2091 and EM15 did not show any segregation for grain appearance. The gene for dull endosperm in EM15 was designated *du-2* by Satoh (1985) and Yano et al. (1988). It is therefore obvious that the dull endosperm appearance of these four mutants is conditioned by *du-2*. Similarly, the F_2 grains of the crosses amongst dull mutants 2077, 2078, and 2120 did not show segregation for endosperm appearance. Consequently, the dull appearance of these three mutants is conditioned by the same gene.

A clear segregation for endosperm appearance (normal and dull or normal, intermediate and dull) was observed in other crosses between dull mutants (Table 5). In some crosses segregation ratios agreed with the 9:7 ratio expected for the independent segregation of two non-allelic recessive genes. However, in the crosses involving EM47 and EM98 the segregation ratios did not agree with the 9:7 ratio because these two mutants showed a dosage effect for endosperm appearance. The results suggest that the genes for dull endosperm appearance in mutants 2035, EM12, EM47 and EM98 are non-allelic to each other and to the two dull loci mentioned above. Conclusions about the non-allelic nature of these mutants were confirmed from the analysis for amylose con-

tent of individual F_2 grains. As shown in Fig. 3, a clear segregation for amylose content was observed in all crosses. Thus, it appears that there are at least six non-allelic dull loci. Satoh (1985) and Satoh and Amano (1987) reported five non-allelic dull loci, which they designated *du-1, du-2, du-3, du-4* and *du-5*. The dull endosperm appearance of EM12, EM15 and EM98 is known to be conditioned by *du-1, du-2* and *du-4,* respectively. Therefore, the allelic relationships of mutants 2035 and 2077 on one hand the *du-3* and *du-5* need to be determined.

Table 5. Segregation of F_2 grains for endosperm appearance in crosses among non-allelic dull mutants

Cross	Segregation of F_2 grains for endosperm appearance			
	Normal	Mutant	Total	χ^2 (9:7)
2035/2057	127	73	200	4.3*
2035/2077	129	71	200	5.5*
2035/EM12	126	74	200	3.7
2035/EM47	84	116	200	16.5**
2035/EM98	58	142	200	72.1**
2057/2077	119	81	200	0.1
2057/EM12	116	84	200	0.3
2057/EM47	105	95	200	1.1
2057/EM98	70	130	200	36.6**
2077/EM12	127	73	200	2.3
2077/EM47	68	132	200	40.2**
2077/EM98	60	140	200	56.0**
EM12/EM47	116	84	200	0.3
EM12/EM98	79	121	200	22.7*
EM47/EM98	56	144	200	64.9*

* Significant at 5% level; ** highly significant at 5% level

The tests could not be conducted due to the non-availability of *du-3* and *du-5* seeds.

Chromosomal location of mutant genes

The chromosomal location of the *flo-1, flo-2, ae* and *du* genes of mutants 2035, 2120 and EM47 was determined through trisomic analysis. Crosses were made between mutant stocks in the IR36 background and 11 primary trisomics, and segregation for mutant traits was studied either amongst F_2 or BC_1F_1 seeds. It was not possible to divide the F_2 and BC_1F_1 seeds into disomic and trisomic fractions. Therefore, seeds were classified into normal and mutant classes. The segregation ratios were then tested for fitness to a disomic (3:1) or trisomic (12.5:1) for the F_2 seeds and 1:1 (disomic) and 3.5:1 (trisomic) for the BC_1F_1 seeds. These trisomic ratios are based on 33.3% transmission rates of the extra chromosome in trisomics (Khush 1973).

As shown in Table 6, segregation for *ae* in the BC_1F_1 seeds of triplo 2 deviated significantly from a 1:1 ratio but agreed with a 3.5:1 ratio. Segregation for *ae* amongst seeds of the remaining trisomics was normal (Table 7). These results show that *ae* is located on chromosome 2.

The floury genes *flo-1* and *flo-2* gave trisomic segregation with triplo 5 and triplo 4, respectively (Table 6), but disomic ratios with ten other trisomics (Table 7). Thus, *flo-1* is located on chromosome 5 and *flo-2* on chromosome 4.

The *du* gene of mutant 2120 gave a trisomic segregation with triplo 9 (Table 6) but disomic segregation with ten other trisomics. Similarly, the *du* genes of mutants

Table 6. Segregation ratios of endosperm mutants in the F_2 or BC of rice trisomics

Trisomic	Gene	F_2 or BC	F_1 plant	Segregation of F_2 grains				
				Normal	Mutant	Total	χ^2	
							3:1	12.5:1 (F_2) 3.5:1 (BC)
Triplo 2	*ae*	F_2	2n	72	28	100	0.4	1.0
		BC	2n+1	70	14	84	37.3**	
Triplo 5	*flo-1*	F_2	2n	507	179	686	0.4	2.1
		F_2	2n+1	797	76	873	123.6**	
Triplo 4	*flo-2*	F_2	2n	477	155	632	0.1	0.4
		F_2	2n+1	709	56	766	125.9**	
Triplo 9	*du* (2120)	F_2	2n	218	54	272	3.8	1.47
		F_2	2n+1	353	35	388	52.8**	
Triplo 6	*du* (2035)	F_2	2n	455	126	581	3.4	0.8
		F_2	2n+1	197	12	209	41.4**	
Triplo 6	*du* (EM47)	F_2	2n	393	104	497	4.4	0.1
		F_2	2n+1	250	21	271	43.0**	

** Highly significant at 5% level

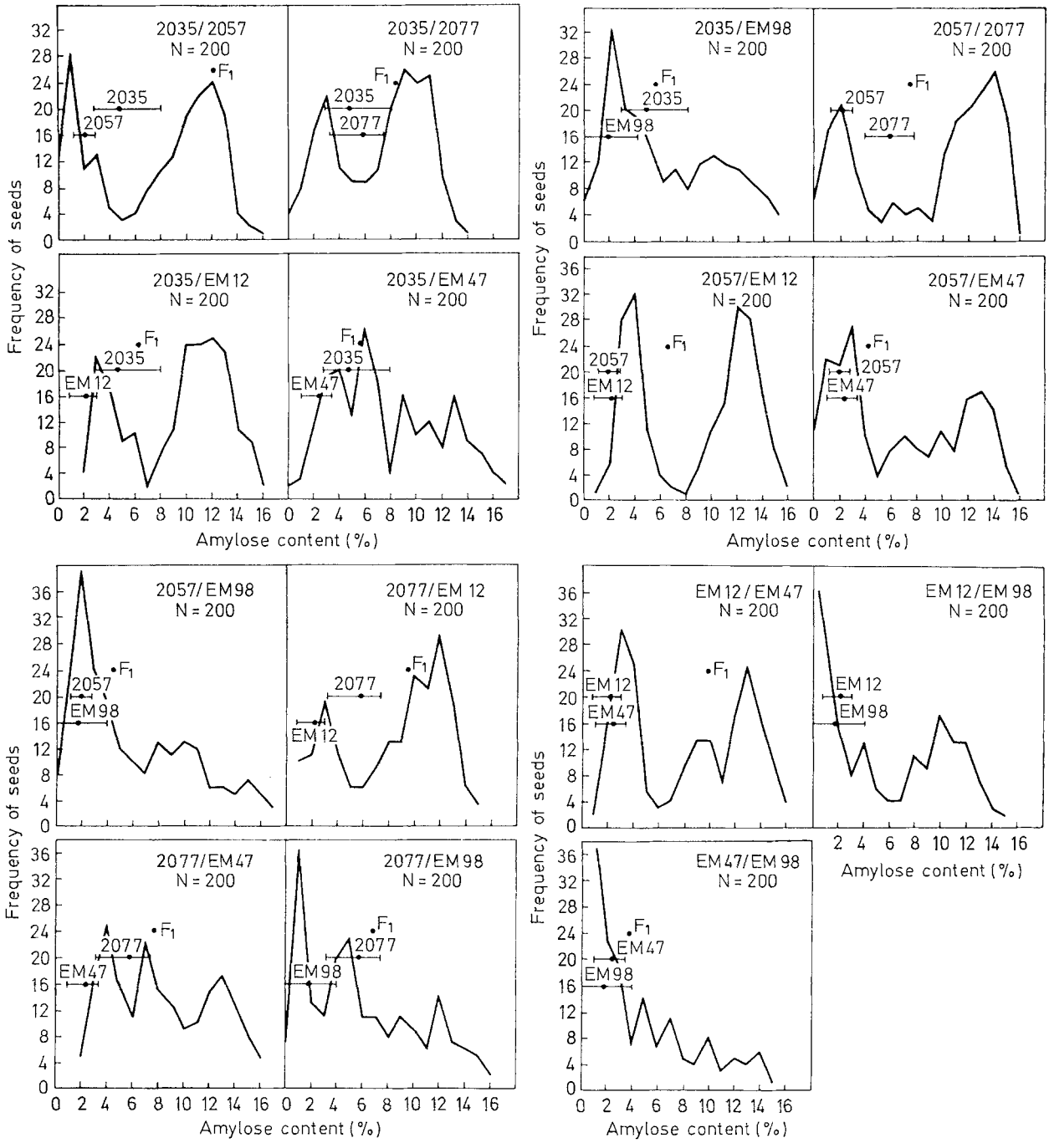

Fig. 3. Distribution of amylose content in F_2 populations of crosses among non-allelic dull mutants

2035 and EM47 gave trisomic segregations with triplo 6 but disomic segregations with ten other trisomics. These results clearly show that the *du* gene of mutant 2120 is located on chromosome 9 while the *du* gene of mutant 2035 and EM47 are both located on chromosome 6. Yano et al. (1988) located *du-1* and *du-4* on chromosomes 10 and 12, respectively. Thus, the chromosomal location of at least five *du* genes is known.

Utility of endosperm mutants

The cooking qualities of the rice grain are dependent on the inherent physical and chemical properties of the endosperm. The amylose content of the endosperm starch is one of the most important traits that influences the cooking and eating qualities of milled rice. Different amylose rices are used for eating in different regions of

Table 7. Summary of trisomic segregation data for endosperm mutant genes

Gene	Trisomic and type of segregation obtained											
	1	2	3	4	5	6	7	8	9	10	11	12
ae	D	T	–	D	D	D	D	D	D	D	D	D
flo-1	D	D	–	D	T	D	D	D	D	D	D	D
flo-2	D	D	–	T	D	D	D	D	D	D	D	D
du (2120)	D	D	–	D	D	D	D	D	T	D	D	D
du (2035)	D	D	–	D	D	T	D	D	D	D	D	D
du (EM47)	D	D	–	D	D	T	D	D	D	D	D	D

the world. In general, low amylose rices are preferred in regions where japonica rices are grown. The mutations which directly influence the starch biosynthesis and alter the relative proportions of amylose to amylopectin have a direct bearing on the cooking quality of a variety. The mutants can serve as useful genetic markers and help breeders in developing high yielding semi-dwarf indica varieties with great diversity for amylose content, thus increasing their acceptability over wider areas. Dull mutations can find direct use in developing very low amylose high yielding semidwarf indica varieties. Varieties with very low amylose or waxy endosperm are the staple food of people in Northern and Northeastern Thailand and Laos. These are also preferred in parts of Burma and Indonesia. The availability of mutants with varying amounts of amylose has opened new vistas for developing improved varieties with great diversity in amylose content and thus a greater range of palatibiltiy. Some of the mutants, such as the amylose extender, may prove useful for industrial purposes. For examples preliminary analysis shows that the high amylose mutant has a total dietary fiber (TDF) of 7.5% as compared to less than 0.5% for milled rice of conventional varieties. The food industry in the USA is exploring the possibilities of developing a natural relatively high fiber rice-based cereal for health and calorie conscious consumers.

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