Cereal Chemistry

Vol. 50 | November-December 1973 | No. 6

Inheritance of Amylose in Two Hybrid Populations of Rice[1]

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ABSTRACT

A suggested explanation for the inheritance of amylose in the two crosses studied is that the parental mean difference of 4.5 to 7.0% amylose in the C.I. 9444 × P.I. 215936 cross was controlled by one pair of genes of major effect and modifying genes of minor effect. The major gene for high amylose was incompletely dominant to its allele. In the Nato × Asahi cross, the parental mean difference of 2.5% was controlled by a few pairs of modifying genes of small and approximately equal effect. Both Nato and Asahi possessed the same or a similar gene of major effect for low amylose. The results of this study indicate that selection for amylose on the basis of single F_2 plant values would be effective in populations derived from crosses in which the parents differed to any practical extent in amylose content. In crosses in which the parental difference was relatively small, selection would be effective, but to a lesser degree.

Amylose content of rice (*Oryza sativa* L.) is considered to be one of the more important compositional indices of rice cooking and processing behavior (1,2). In studies on domestic varieties (2), it was shown that preferred long-grain types known to cook dry and flaky were characterized by a relatively high amylose content (24 to 28%), whereas typical cooking short- and medium-grain varieties had relatively low amylose content (15 to 20%). As a result of these studies, amylose content came into widespread use as a selection technique in practical rice-breeding programs, even though little published information is available regarding its mode of inheritance.

Using the starch-iodine-blue test (3) as an empirical measure of amylose content, Beachell and Halick (4) concluded that the high iodine value of Century Patna 231 was controlled by a single gene in a cross of that variety and Texas Patna. In a cross of Century Patna 231 × C.I. 9359, these same investigators indicated that two or more genetic factors appeared to be governing iodine value. In a study of the F_1, F_2, and F_3 generations of the cross Texas Patna × Toro, Seetharaman (5) concluded that the difference in starch-iodine-blue value between the parents was

[1]Cooperative investigations, Agricultural Research Service, U.S. Department of Agriculture, Southern Region; Texas A&M University Agricultural Research and Extension Center of the Texas Agricultural Experiment Station; and the Texas Rice Improvement Association. Grateful acknowledgment is made to the Louisiana Agricultural Experiment Station for use of data on plants grown at the Louisiana State University Rice Experiment Station, Crowley, La. Presented in part at the 52nd Annual Meeting, Los Angeles, April 1967.

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controlled by one pair of major genes and several modifiers. Using the same test in a study of the F_1 and F_2 generations of a cross of Nira and an unknown variety, Kahlon (6) arrived at the same conclusion. Stansel (7) stated that amylose content appeared to be governed by at least two gene pairs in addition to the waxy gene in a study of crosses of several varieties of different endosperm types.

This study was undertaken to obtain additional information on the mode of inheritance of amylose value of rice, and on relations among this and other measured agronomic characteristics.

MATERIALS AND METHODS

The inheritance of amylose was studied with F_2 plant populations and F_3 lines of the crosses C.I. 9444 X P.I. 215936 and Nato X Asahi. The F_2 populations were grown at Crowley, La., in 1963 and the F_3 lines at Beaumont, Tex., in 1964. It should be noted that amylose is an endosperm character and exhibits xenia. Therefore, F_2 plant values and F_3 line means actually represent bulk F_3 and F_4 endosperm populations, respectively. F_3 lines were randomly selected. All populations and lines were space-planted and each plant was harvested and threshed separately. The seed was air-dried and stored in an air-conditioned room until analyzed. A representative seed sample (8 g.) from each plant was hulled, milled, and polished by micro-milling methods (8). Amylose content of the milled rice was determined according to the colorimetric procedure[3] outlined by Williams et al. (2) using Nutritional Biochemicals[4] amylose to construct the standard curve. Results are expressed as percent amylose of milled kernels on an 11% moisture basis.

RESULTS AND DISCUSSION

C.I. 9444 X P.I. 215936 Cross

In 1963, the mean amylose content of P.I. 215936 was 17.5%. The 39 plants tested ranged from 14 to 21%, the mode was 17%, and the coefficient of variation was 7.84% (Table I). The mean of C.I. 9444 in 1963 was 24.5% for 40 plants, ranging from 23 to 27%. The mode was at 24 to 25% amylose content and the coefficient of variation was 3.0%. The coefficients of variation of the parents are regarded as an estimate of the environmental, or nonheritable, variation under the conditions of this test.

The 267 F_2 plants of the cross C.I. 9444 X P.I. 215936, grown in 1963, ranged in amylose from 13 to 28%. The mean of the F_2 population was 21.5%, which was close to the mean of the two parents, 21.0%, and the coefficient of variation was 13.7%. The coefficient of variation for the F_2 population is a measure of the total variation, i.e., both environmental and genetic variation.

The amylose values for the F_2 population formed essentially a bimodal curve, with maximum frequency classes at 18 and 24% and the minimum frequency class

[3]It is recognized that this procedure gives a relative estimate of percent amylose. To determine the exact amylose content, the iodine absorption of each amylose would have to be determined.

[4]Trade names are used in this publication solely for the purpose of providing specific information. Nutritional Biochemicals is a trademark name of Nutritional Biochemicals Company, Cleveland, Ohio. Mention of a trade name does not constitute a guarantee or warranty of the product by the U.S. Department of Agriculture or an endorsement by the Department over other products that are also available.

TABLE I. FREQUENCY DISTRIBUTION OF AMYLOSE (IN PERCENT OF MILLED RICE) FOR THE PARENTS AND F_2 PLANTS OF THE CROSS C.I. 9444 X P.I. 215936

Population	Percent Amylose Classes																	
	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	Mean	C.V. %
C.I. 9444											2	17	17	3	1		24.485	3.10
P.I. 215936		1		2	18	12	6		1								17.525	7.84
F_2	1	4	4	9	14	20	15	12	31	40	32	50	19	11	3	2	21.525	14.35

at 20%. The distribution of the F_2 plants into two distinct amylose groups, i.e., a relatively low and a relatively high group, with approximately one-fourth of the plants falling into the low group and three-fourths in the high, indicates segregation for one major pair of genes, with high amylose incompletely dominant. Further evidence of this is the fact that about one-fourth of the F_2 plants had essentially the same phenotypic expression for amylose value as the recessive parent, P.I. 215936.

Data from the F_3 lines also indicate segregation for one pair of major genes, with high amylose dominant (Table II). However, there was strong evidence of transgressive segregation in the F_3 generation. A relatively large number of F_3 lines had means either lower than the mean of the low-amylose parent or higher than that of the high-amylose parent. The presence of transgressive segregation would indicate that P.I. 215936 possesses, in addition to a pair of genes of major effect for low amylose, one or more pairs of lesser effect for high amylose, and that C.I. 9444 possesses a gene pair of major effect for high amylose and one or more gene pairs of lesser effect for low amylose.

The correlation coefficient between percent amylose of F_2 plants and the means of F_3 lines derived from them was 0.73, and the regression of F_3 line means on F_2 plant values was 0.63. The sizes of these values suggest that selection for high-amylose types on the basis of single F_2 plant values would be effective.

Nato X Asahi Cross

When grown with the F_2 population, 1963, the mean amylose content of 80 Nato plants was 14.5% (Table III). The plants ranged from 12 to 16% amylose, and the coefficient of variation was 6.4%. The 80 Asahi plants had a mean of 17.0%, ranging from 14 to 19% amylose, and had a coefficient of variation of 5.4%. The difference in the parent means of 2.5% is relatively small and, from a practical breeding standpoint, the two varieties are considered to have similar amylose contents.

A total of 389 F_2 plants were tested for amylose value, and they ranged from 11 to 20%, with a coefficient of variation of 9.0%. The mean of the F_2 population, 16.1%, was slightly above the mean of the parents, 15.8%. The mode of the F_2 was at 16%, which was closer to that of Asahi, 17%, than that of Nato, 14%, suggesting a slight degree of partial dominance for high amylose.

The F_2 plant values for amylose content formed a relatively symmetrical unimodal curve. The range of the F_2 population exceeded the combined ranges of the parents. However, the number of F_2 plants that had amylose values below that of the low-amylose parent or above that of the high-amylose parent were so few, only 5 out of 389, that chance rather than transgressive segregation is indicated.

TABLE II. FREQUENCY DISTRIBUTION OF AMYLOSE (IN PERCENT OF MILLED RICE) FOR THE PARENTS AND F_3 LINES OF THE CROSS C.I. 9444 X P.I. 215936

	Percent Amylose Classes																			
Population	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	F_3 Line Mean	F_2 Plant Value	C.V. %
C.I. 9444										3	8	5	3		1			22.570		5.26
P.I. 215936					1	5	7	2	5									18.130		6.69
94002-29	1		2	3	3															
-10			1	3	2	3	1						1					15.7	16.0	
-25				4		5	1											16.0	21.8	
- 3			1		2	4	1	1										16.3	16.8	
-19					1	4	2	3			1							17.1	17.4	
-52				2		1	2	3	1									17.7	20.2	
-23		1	1	1			1		3	2		1						18.3	14.6	
-48						3	3		3	1	1							18.4	21.8	
-24				1	2			1	3	2								18.5	16.2	
-27							2	3		5	1							19.1	23.6	
- 7					1	1	1	1	2									19.8	20.0	
-21						2	1	2		3	1	2						19.9	22.0	
-13							3	1	1	2			2					20.2	23.6	
- 5						1	2			2	1	1	1					20.5	21.8	
-11					1	1	2				2	2	1					20.8	22.0	
- 2					1		1	1		1	3	1		1	1			20.9	21.8	
-26					1			1		1	2	3	1					21.2	23.6	
-22							1	2			1	4		1				21.6	24.2	
- 8						1				3	2	4			1			21.7	22.2	
-15			1								3		2	1				22.0	23.0	
- 1							1	1		2	3	3	3					22.1	24.8	
- 6						1			1	2			6					22.1	24.2	
- 9							1			2	1	1		4				22.3	23.0	
-16										1	1	1	2	2			1	23.0	25.6	
-20										1	4	1	2	1	1			23.0	23.6	
-14											1	5	2	1				23.0	23.0	
-36											2	3	2	2	1			23.5	24.2	
-17											1	3	3	2	1			23.9	24.8	
-18											1		5	2	2			24.2	23.0	
-55												1	4	5				24.3	27.8	
											1		1	4	2	2		25.2	21.8	
																	Mean	20.7	21.9	

TABLE III. FREQUENCY DISTRIBUTION OF AMYLOSE (IN PERCENT OF MILLED RICE) FOR THE PARENTS AND F_2 PLANTS OF THE CROSS NATO X ASAHI

Population	Percent Amylose Classes														Mean	C.V. %
	10	11	12	13	14	15	16	17	18	19	20	21	22	23		
Nato			2	5	36	27	10								14.530	6.38
Asahi					1	6	19	35	16	3					16.995	5.423
F_2	1	3	1	6	50	72	114	83	44	13	1			1	16.135	9.359

Although the relatively symmetrical, unimodal form of the F_2 curve is typical of quantitative inheritance, which usually involves numerous genes of small and equal effect, the evidence in this cross is that the number of genes for amylose by which the parents differ is small. Primary evidence of a small number of genes differentiating the parents for amylose is the fact that so many parent phenotypes were recovered in an F_2 population of only 389 plants. Sixty-one F_2 plants were recovered that had a mean amylose percent as low as the low-amylose parent, Nato, indicating the action of one or two genes only.

TABLE IV. FREQUENCY DISTRIBUTION OF AMYLOSE (IN PERCENT OF MILLED RICE) FOR THE PARENTS AND F_3 LINES OF THE CROSS NATO X ASAHI

Population	Percent Amylose Classes										F_3 Line Mean	F_2 Plant Value	C.V. %
	12	13	14	15	16	17	18	19	20	21			
Nato			12	7		7					14.480		5.23
Asahi				1	5	8	4	2			17.000		5.76
94001- 8	2	1	4	1	2						14.0	10.6	
- 9		3	2	3	1	1					14.5	12.2	
-20		1	5	2	2						14.5	16.0	
-17			5	4							14.5	14.8	
- 4			3	6		1					14.9	13.6	
-19		1	3	1	3	2					15.2	14.4	
-14		1	1	3	2	3					15.4	14.0	
-12			2	4		1	1				15.4	14.4	
-24		1	1	3	2	2	1				15.6	17.4	
-26				6	2	1	1				15.8	16.8	
- 7			2	2	4		2				16.0	13.0	
-18			1	4	1	4					16.0	13.6	
-13			1	3	2	3	1				16.1	15.4	
- 6				2	4	4					16.2	16.8	
-15			2	1	2	3		2			16.4	16.4	
-22			1	1	4	3			1		16.6	18.2	
-11				1	2	5	2				16.7	16.8	
-21				1	2	3	4				16.9	16.4	
- 3		1			2	4	2			1	17.0	16.0	
- 5			1		1	4	3	1			17.1	13.0	
- 2				1	1	5	2	1			17.1	14.4	
-23				1	1	2	4	2			17.5	17.4	
-16				1	1	3	3	1	1		17.5	14.8	
- 1						4	4	2			17.7	14.8	
-25					1	4	1	4			17.9	17.4	
									Mean		16.1	15.1	

Of the 247 F_3 plants tested, 11 had an amylose content below the range of Nato and 3 were above the range of Asahi (Table IV). These few plants with amylose values beyond the ranges of the parents can probably be explained on the basis of chance rather than transgressive segregation. If one assumes the absence of transgressive segregation, there is nothing to contradict the estimate that one or two gene pairs differentiate the parents for amylose content, based on F_2 results. On the other hand, if one assumes the presence of transgressive segregation, the parents must differ by a minimum of three gene pairs, unless it is further assumed that the genes were not of equal effect, in which case the parents might differ by only two pairs of genes.

The correlation coefficient between percent amylose of the F_2 plants and the means of F_3 lines derived from them was 0.48, and the regression of F_3 line means on F_2 plant values was 0.29. These values are lower than the corresponding values obtained in the C.I. 9444 × P.I. 215936 cross, which is not unexpected, since the difference in amylose content between Nato and Asahi was less than that between C.I. 9444 and P.I. 215936. In general, the narrower the difference between parents of a cross, the greater will be the amount of environmental variation relative to genetic variation in the segregating generations and the lower the heritability.

These results suggest that selection for amylose content on the basis of single F_2 plant values would not be as effective in the Nato × Asahi as in the C.I. 9444 × P.I. 215936 cross, although one could select for extreme amylose value. However, from a practical breeding standpoint, Nato and Asahi are considered to have essentially the same amylose content, and such a narrow cross would not be utilized in a breeding program to increase amylose content.

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[Received February 22, 1972. Accepted December 19, 1972]