IRRI RESEARCH PAPER SERIES
Number 35 August 1979

GENETIC ANALYSIS OF TRAITS RELATED TO GRAIN CHARACTERISTICS AND QUALITY IN TWO CROSSES OF RICE

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GENETIC ANALYSIS OF TRAITS RELATED TO GRAIN CHARACTERISTICS AND QUALITY IN TWO CROSSES OF RICE[1/]

ABSTRACT

A genetic study was made on the rice crosses IR648-3-1-2-3/Gow Ruang 88 and IR648-3-1-2-3/Khao Pahk Maw 148 to determine the genetic components of five grain characteristics and plant type, and the genotypic relationship between the two groups of characters. The genetic materials in each cross included the two parents and F_1, F_2, F_3, B_{1S}, and B_{2S} populations grown in replicated plots.

Analysis of generation means indicated that the variation in 100-grain weight was predominantly due to additive gene effect. Both additive and dominance effects were major contributors to the variation in grain length and the ratio of grain length to width. Variations in chalkiness score and alkali digestion index in IR648/KPM148 were largely due to additive gene effect; in IR648/GR88 both additive and dominance effects were important. For amylose content, dominance effect appeared more important than additive gene effect.

Analysis of F_2 data indicated that amylose content was controlled by a single dominant gene along with minor genes with modifying effect. In both crosses, among the three types of epistatic gene effect, additive × additive and dominance × dominance gene effects appeared more important than the additive × dominance type. A difference in the signs of dominance and dominance × dominance components was observed in all cases, indicating a duplicate type of epistasis.

The heritability for 100-grain weight ranged from 40 to 60%. Estimates of heritability for grain length, length-width ratio, alkali digestion index, chalkiness, and amylose content ranged from moderately high to high.

In both crosses, grain length exhibited a significant association with the degree of slenderness, low degree of chalkiness, low gelatinization temperature, and high amylose content. The 100-grain weight was significantly and positively correlated with grain length, translucency, and amylose content. High amylose content was strongly correlated with low gelatinization temperature.

The different types of gene effects controlling selected traits and the independence between the yield component characters and grain characteristics found in this study provide directions in formulating useful effective selection procedures for specific traits or the combination of desired traits in a breeding program.

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GENETIC ANALYSIS OF TRAITS RELATED TO GRAIN CHARACTERISTICS AND QUALITY IN TWO CROSSES OF RICE

Although the development of the semidwarf rices has markedly upgraded yield potential in tropical rice production, concurrent progress in incorporating traits related to fine grain quality into the semidwarfs lags behind those for pest resistance and grain yield.

The physical properties of the rice grain are related to its dimensions, weight, and structural features of the starch granules in the endosperm, whereas cooking and eating quality is largely related to the gelatinization temperature and amylose content of the starchy endosperm.

Previous studies on the grain characteristics of rice focused mainly on the simply inherited traits within one ecogeographic race or on mutants (USDA 1963, Chang 1964). Little attention was given to the continuous distribution in F_2 populations of the quality characteristics that a rice breeder frequently encounters in a breeding program. Moreover, investigations that relate the physical properties to the chemical characteristics of the rice grain are few and limited in scope.

The research reported here aimed at determining the mode of inheritance and genotypic correlation on several important grain characteristics that constitute grain quality in crosses involving a semidwarf with the improved plant type and two tall Thai varieties with good grain quality for the export market.

MATERIALS AND METHODS

Parents and hybrid populations

IR648-3-1-2-3 (Sigadis*5/TN1), a semidwarf selection, was used as a common parent in crossing with two fine-grained Thai varieties, Gow Ruang 88 and Khao Pahk Maw 148. The characteristics of the three parents are in Table 1.

The parental varieties along with populations of F_1, F_2, F_3, and self reciprocal backcrosses (denoted as P_1, P_2, P_3, F_1, F_2, F_3, B_{1S}, and B_{2S}, respectively) were grown at the IRRI Farm during the 1972 wet season and 1973 dry season.

Experimental design and layout

During the 1972 wet season, a complete set of populations from each cross was planted in a randomized, complete block design with 2 replications and the 13 populations were planted in 1,110 single-row plots. In the 1973 dry season, 12 populations were planted in 1,060 single-row plots, each row measuring 5 m long. Seedlings were transplanted in single-plant hills 30 cm between rows and 25 cm between plants. Twenty-one plants were planted in each row. The number of single-row plots sampled from each population follows:

Population	Plots sampled (no.)
P_1, P_2, P_3, or F_1	2
F_2	20
F_3	400
B_{1S} or B_{2S}	20

For the F_3 and reciprocal backcross generations, each line was planted in a single-row plot. The F_3 and backcross lines were divided into three groups each, according to height, to minimize mutual shading between short and tall plants.

Traits recorded

The following agronomic characters and grain quality traits were recorded:

Plant type - observed at full heading and scored on a 3-class scale: semidwarf, 1; intermediate, 2; tall, 3.

100-*grain weight* - weight of 100 fully developed grains sampled from an individual plant after drying and cleaning.

Chalkiness - the milled kernels were individually examined and scored on the following scale.

Description of chalky spot on a kernel	Score	Corresponding to SES code[a]
No chalky spot observable	1	0
Minute chalky spot, about 1.0 x 0.5 mm (length x width) or smaller	2	1
Spot enlarged up to 2.0 x 1.0 mm	3	3
Medium chalky spot restricted to 2.5-3.0 x 1.0 mm	4	5
Medium large chalky spot, about 3.0-4.0 x 1.5-2.0 mm (length x width)	5	7
Chalky area extended to 4.0 x 2.0 mm or larger	6	9

[a] See IRRI 1975, Standard evaluation system for rice.

Length and shape of milled rice - length and width (mm) were obtained from the image projected from a photographic enlarger on a calibrated grid.

Gelatinization temperature - the alkali digestion test was performed on duplicate samples of six milled kernels each to estimate the gelatinization temperature of the grains of each plant. Scores were from 1 (low) to 7 (high), representing high to low gelatinization temperatures, respectively (Little et al 1958).

Amylose content - percent amylose was determined by the simplified amylose test using an Autoanalyzer (cf. Juliano 1971 for procedure).

Methods of statistical analysis

The mean values were computed for all traits for measurements on the individual plants (or samples) of each replication in each population of parent 1, parent 2, parent 3, F_1, and F_2. Variance (V_x), variance of the mean ($V_{\bar{x}}$), and the standard error of the mean ($s_{\bar{x}}$) were computed from the respective samples. In the F_3 and backcross populations, the population means (denoted by $\bar{F}_3$, $\bar{B}_{1S}$, and $\bar{B}_{2S}$) and the line means were computed. The variances of these populations were derived as follows:

(1) Variance of line means was calculated from line means in a population, and

(2) Mean variance of all lines were computed from individual measurements within each line and averaged over the population.

The data were analyzed with the following assumptions:

1. Homozygous parents
2. Diploid segregation
3. No multiple allelism
4. No correlated distribution of genes between parents
5. No maternal effect
6. Absence of genotype-environment interaction
7. No lethal genes, no gene mutation, and constant viability for all genotypes
8. No linkage and no trigenic or higher order interaction.

The genetic analysis consisted of:

Table 1. Comparison of agronomic and grain characteristics of parents.

Characters	Parents[a]		
	IR648-3-1	GR88	KPM148
Yield (kg/ha)	3650	2250	2525
100-grain weight (g)	2.5	2.7	3.3
Plant type	semidwarf	tall	tall
Tillering	medium high	low	medium low
Tillers (no.)	15	9	12
Maturity			
1. photoperiod sensitivity	insensitive	weakly sensitive	strongly sensitive
2. days from seeding to flowering (no.)	110	106	122
Milled rice appearance			
1. length (mm)	6.30	7.30	7.60
2. length-width ratio	2.45	3.30	3.30
3. chalkiness	4	1	1
Physicochemical properties of milled rice			
1. amylose content (%)	28.3	24.0	24.6
2. gelatinization temperature	low	intermediate	intermediate

[a] IR648-3-1 (P_1) = Sigadis*5/TN1, GR88 (P_2) = Gow Ruang 88, and KPM148 (P_3) = Khao Pahk Maw 148.

- *Analysis of generation means.* The analysis involved:

  a. Test of the additive-dominance effect. The adequacy of the additive-dominance effect in a generation was detected by the insignificant deviation of observed generation means from their respective expected values in scaling test. The expected means of various generations, deviations, and the standard errors of the deviations were derived from the relationship between the means of generations as explained by Mather and Jinks (1971).

  b. Six-parameter digenic epistasis model. The separation of digenic nonallelic interactions from additive-dominance effect in generation means was adopted when a significant deviation of observed generation means from their expected values was obtained. For the data collected in the wet season, the estimates of the six parameters -- midparent value (m), additive (d), dominance (h), additive × additive (i), additive × dominance (j), and dominance × dominance (l) gene effects -- were calculated from the equations of generation means (Jinks and Jones 1958, Mather and Jinks 1971).

- *Partitioning of variance components.* The analysis followed the simple unweighted procedures and notations given by Mather and Jinks (1971).

- *Estimates of heritability.* Heritability estimates were calculated by three methods:

  a. Broad sense heritability (h_1^2) - computed as the ratio of genotypic variance (V_G) to phenotypic variance (V_P) in the F_2 population (Allard 1960).

  b. Narrow sense heritability (h_{11}^2) - the ratio of additive genetic component to the phenotypic variance in the F_2 population (Warner 1952).

  c. Heritability as estimated from parent-progeny regression (denoted as h_{111}^2) - based on the formula described by Chandraratna and Sakai (1960).

- *Associations among characters.* Phenotypic, genotypic, and environmental correlations between all possible pairs of characters in the F_2 population were calculated from the formulas of Weber and Moorthy (1952).

RESULTS

Analysis of generation means

Mean performance. The observed values of all generation means for the nine traits obtained in the two crop seasons, and their standard errors are in Table 2.

The grain characteristics of F_1 were generally intermediate between the two parental means, except for amylose content in the F_2 population of IR648/KPM148 which was slightly higher than the high parent.

The five grain characteristics of F_2 plants also lay somewhere between the two parental means. The F_2 means were lower than the corresponding F_1 means in most traits.

The grain characteristics of F_3 of both crosses exhibited a similar trend as those of F_2 plants, except that the progeny of IR648/KPM148 showed a lower percentage of amylose content than the low parent.

For the F_2 and F_3 population of IR648/GR88 planted in the dry season, the 100-grain weight was intermediate between the 2 parents. On the other hand, the measurement of grain length from F_1 plants was near to the mean of the long-grained parent whereas the F_2 and F_3 populations gave even larger means. The grain length-grain width ratio in the F_1 and F_3 populations was close to the midparent values; in the F_2 it was slightly larger and closer to the ratio of the high parent. In degree of chalkiness, alkali digestion index, and amylose content, the generation means were closer to the high parent in most instances.

Scaling test and adequacy of the additive-dominance effect. The deviations of the observed generation means from their expected values and the significance tests were based on four scaling tests of the wet season data; only two tests were available for the dry season.[2]

The five grain characteristics in IR648/GR88 produced significant deviations in at least one of the tests (as found in grain length) or in all four tests (in the case of chalkiness). In IR648/KPM148, 100-grain weight and other grain characteristics showed significant deviations from expected values in 2 or 3 tests, except for the degree of chalkiness which gave nonsignificant values in all tests.

The 2 scaling tests for the observed F_2 and F_3 means indicated significant deviations from their expectations in all of the traits except 100-grain weight measured by either 1 or both tests (for the dry season data only).

The significant deviations of the observed generation means from the expected means suggested that either the scale or scales used in the measurements were inadequate or that nonallelic interactions were present, whereas the nonsignificant results indicated an adequacy of the additive-dominance model.

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[2]Full information may be obtained in the first author's Ph D thesis deposited at the Indian Agricultural Research Institute (New Delhi), the International Rice Research Institute (Los Baños), and the Rice Division of Thailand (Bangkhen).

Table 2. Generation means and the standard errors of the means for six characters in IR648/GR88 and IR648/KPM148 crosses, 1972 wet season and 1973 dry season.

Generation	Character					
	100-grain weight	Grain length	Length-width ratio	Chalkiness	Alkali digestion index	Amylose content
			IR648/GR88 in 1972 wet season			
P_1 (IR648)	3.00±0.045	6.62±0.035	2.62±0.015	4.82±0.064	6.99±0.008	28.34±0.15
P_2 (GR88)	2.62±0.041	7.10±0.034	3.15±0.018	2.30±0.151	4.94±0.031	23.58±0.12
F_1	3.12±0.022	7.11±0.022	2.95±0.013	3.64±0.094	6.22±0.058	27.99±0.14
F_2	3.00±0.019	6.94±0.050	2.96±0.016	3.10±0.074	6.01±0.064	27.19±0.14
F_3	2.96±0.013	6.94±0.011	3.00±0.011	3.04±0.068	6.19±0.042	25.90±0.12
B_{1S}	3.13±0.026	6.86±0.027	2.76±0.021	3.15±0.121	6.52±0.060	26.95±0.19
			IR648/GR88 in 1973 dry season			
P_1 (IR648)	3.12±0.046	6.49±0.019	2.52±0.015	5.04±0.465	7.00±0.000	27.68±0.15
P_2 (GR88)	2.81±0.031	6.86±0.028	3.00±0.019	1.63±0.114	4.14±0.064	21.[illegible]6±0.31
F_1	3.12±0.039	6.85±0.317	2.81±0.018	3.62±0.083	6.11±0.070	26.44±0.21
F_2	2.99±0.021	6.95±0.016	2.96±0.013	3.11±0.086	6.05±0.058	27.14±0.14
F_3	2.90±0.013	6.70±0.013	2.83±0.010	3.97±0.071	5.81±0.062	25.52±0.16
			IR648/KPM148 in 1972 wet season			
P_1 (IR648)	3.00±0.045	6.62±0.035	2.62±0.015	4.82±0.064	6.99±0.008	28.34±0.15
P_2 (KPM148)	3.39±0.053	7.45±0.024	3.26±0.019	1.58±0.122	4.98±0.011	25.53±0.21
F_1	3.34±0.046	7.18±0.026	2.93±0.019	2.60±0.082	6.31±0.050	29.00±0.15
F_2	3.36±0.020	7.09±0.019	2.94±0.014	2.86±0.083	6.04±0.056	27.96±0.13
F_3	3.40±0.014	6.92±0.012	2.86±0.011	3.16±0.076	6.14±0.034	25.02±0.09
B_{1S}	3.24±0.022	6.62±0.023	2.70±0.020	4.12±0.444	6.66±0.128	26.66±0.19
B_{2S}	3.41±0.023	7.24±0.021	3.04±0.017	2.24±0.114	5.82±0.062	24.47±0.18

Separation of digenic epistasis from additive-dominance effect in generation mean. The estimates of six gene effects (m, d, h, i, j, and l) from the analysis of populations for six traits of the two crosses grown in the wet season are in Table 3.

a. *Additive effect* (d). The 100-grain weight and other grain characteristics of both crosses also indicated a highly significant additive effect, although the estimates were relatively small.

The sign of parameter d appeared to depend on the maternal parent -- when the high parent was considered as P_2 the sign of d became negative. In IR648/GR88, for example, the d estimate for grain length was negative when GR88, a long-grained parent, was considered as P_2.

b. *Dominance effect* (h). The dominance effect was apparently a major component in the genetic variation of all grain characteristics in IR648/GR88. In IR648/KPM148, it was highly significant for grain length, length-width ratio, and amylose content.

In both crosses, the magnitude of h for amylose content exceeded the estimated values of other components. The dominance effect was generally positive, except those for the grain length-width ratio and for alkali digestion index in IR648/GR88.

c. *Epistatic gene effects* (i, j, and l). Among the three types of epistatic gene effects, i

Table 3. Weighted least square estimates of gene effects in a 6-parameter model, for 6 characters of the IR648/GR88 and IR648/KPM148 crosses.

Character	Gene effect					
	m (mp)	*d* (add.)	*h* (dom.)	*i* (add.× add.)	*j* (add.× dom.)	*l* (dom.× dom.)
			IR648/GR88			
100-grain weight	2.88±0.05**	0.17±0.03**	0.43±0.21*	-0.03±0.05	-0.19±0.17	-0.20±0.16
Grain length	6.76±0.070**	-0.24±0.02**	0.86±0.32**	0.11±0.07	-0.23±0.16	-0.52±0.26*
Length-width ratio	3.09±0.04**	-0.26±0.01**	-0.44±0.17*	-0.20±0.04**	-0.17±0.11	0.30±0.14*
Chalkiness	1.30±0.23**	0.35±0.08**	6.33±0.91**	2.12±0.25**	-0.69±0.67	-4.22±0.71**
Alkali digestion index	6.48±0.16**	1.02±0.02**	[illegible]36±0.68*	-0.51±0.16**	-1.01±0.38**	1.10±0.53*
Amylose content	24.05±0.42**	2.40±0.19**	8.[illegible]8±1.68**	1.88±0.45**	-4.31±1.35**	-4.52±1.30
			IR648 KPM148			
100-grain weight	3.48±0.06**	-0.18±0.03**	-0.32±0.23	-0.27±0.06**	0.10±0.19	0.17±0.20
Grain length	6.77±0.05**	-0.46±0.02**	0.83±0.21**	0.29±0.05**	-0.71±0.15**	-0.44±0.17**
Length-width ratio	2.74±0.04**	-0.32±0.01**	0.53±0.16**	0.20±0.04**	-0.04±0.11	-0.33±0.13*
Chalkiness	3.57±0.26**	1.62±0.07**	-1.84±1.04	-0.37±0.27	0.29±1.01	0.87±0.81
Alkali digestion index	6.32±0.14**	1.00±0.01**	-0.89±0.61	-0.34±0.14*	-1.50±0.47**	0.87±0.48
Amylose content	21.10±0.35**	1.49±0.13**	17.43±1.43**	5.59±0.36**	0.52±0.96	-9.40±1.14**

*Significant at the 5% level, **significant at the 1% level.

(additive × additive) and *l* (dominance dominance) were more important than *j* (additive × dominance) for most traits in both crosses.

The sign of parameter *i* was generally positive, indicating its enhancing effect. However, the negative *i*'s, which would indicate a diminishing effect, were obtained from alkali digestion index in both crosses. The *j* and *l* effects had more plus than minus signs. A difference in the signs of *h* and *l* was observed for several traits, indicating the presence of duplicate type of epistasis.

d. *Adequacy of the 6-parameter model.* The X^2 values computed from the deviation of the observed generation means from their expected values provide a test of goodness of fit of the model to the generation means of all traits in this study.

In IR648/GR88, the X^2 test indicated that the 6-parameter model was inadequate for all traits except for amylose content. In IR648/KPM148, the model was appropriate only for the degree of chalkiness.

Inadequacy of the 6-parameter model suggests the presence of higher order interactions or a linkage of interacting genes.

e. *Average degree of dominance in F_1 generation.* The potence ratio was computed to assess the average degree of dominance in the F_1 generation. For grain length, the potence ratios indicated complete dominance of long grains in IR648/GR88 and partial dominance in the IR648/KPM148 cross. No dominance was observed in the case of grain length-width ratio and in the degree of chalkiness. Alkali digestion index showed partial dominance of high values in IR648/GR88 and complete dominance in IR648/KPM 148. High amylose content showed complete dominance in IR648/GR88, whereas overdominance was indicated in the IR648/KPM148 cross.

f. *Analysis of F_2 data.* The F_2 distribution of 100-grain weight in both crosses showed a continuous and unimodal curve (Fig. 1). Transgressive segregation appeared only on the upper end. Variation in population means was largely attributable to additive and dominance effects. Inadequacy of the 6-parameter model indicated higher order gene interactions. In IR648/KPM148, partial dominance was indicated by the F_1 data, although the analysis of components of generation means showed significant additive and additive × additive effects.

The pattern of F_2 distribution in both crosses for grain length was also continuous and unimodal (Fig. 2). Transgressive segregation was indicated for long grains in IR648/GR88. The additive, dominance, and dominance × dominance gene effects were the major contributors in IR648/GR88; in IR648/KPM148 all types of gene effects were significant. The 6-parameter model was inadequate, however, for both crosses.

Continuous and unimodal distribution of plants in the F_2 populations (Fig. 3) was obtained for grain length-width ratio. In IR648/GR88, transgressive segregation occurred on both ends. Few plants in IR648/KPM148 had a ratio beyond the lower parental range. Analysis of population means suggested that the variation could be mainly attributed to additive, dominance, additive × additive, and dominance × dominance effects. Inadequacy of the 6-parameter model indicated the presence of trigenic interactions.

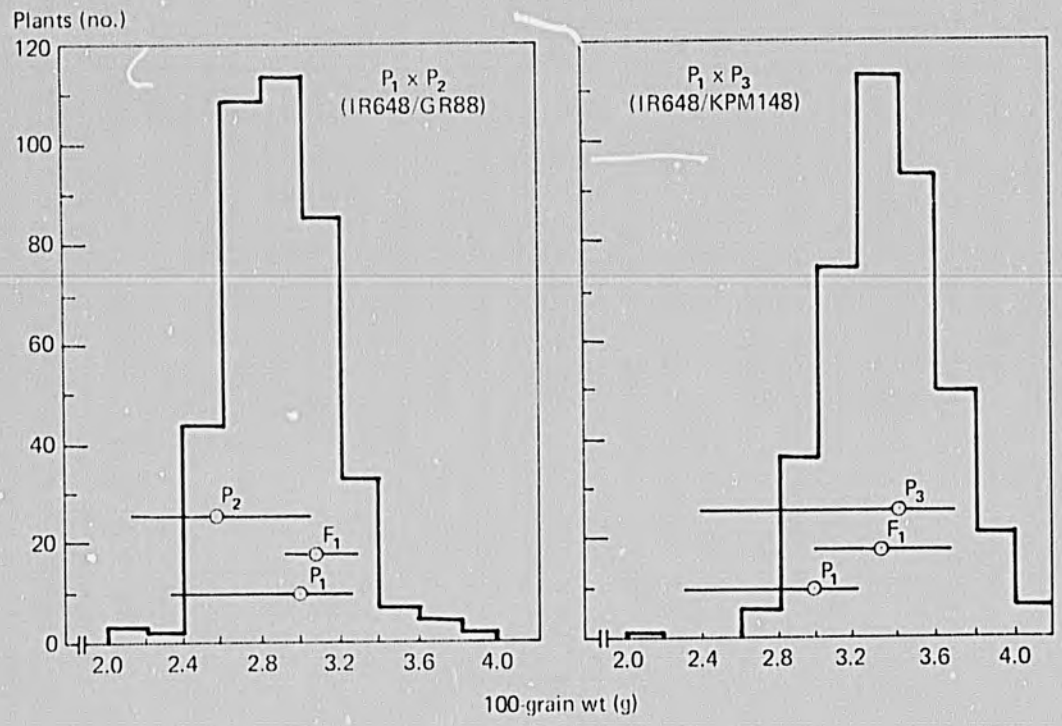

Fig. 1. Distribution and means of parents, F_1 and F_2 plants by 100-grain weight in two crosses, 1972 wet season. Solid horizontal lines show the range of parents and F_1 plants about the means (dotted circles).

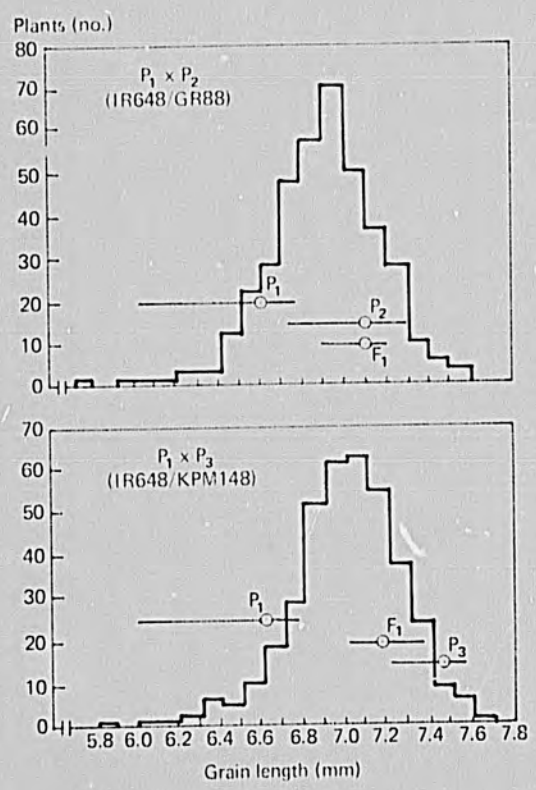

Fig. 2. Distribution and means of parents, F_1 and F_2 plants, by grain length in two crosses, 1972 wet season. Solid horizontal lines show the range of parents and F_1 plants about the means (dotted circles).

The degree of chalkiness showed a continuous variation in the F_2 samples although the distributions were not unimodal (Fig. 4). Very few F_2 plants attained the score of the high parent. Variation in the scores on F_2 plants seemed partly affected by environmental influence which was indicated by the wide range of the scores of the parents and F_1 plants. In IR648/GR88, the variation was attributable to additive, dominance, additive × additive, and dominance × dominance effects as well as to trigenic interactions. In IR648/KPM148 only the additive effect was predominant.

An atypical F_2 distribution was observed for alkali digestion index in both crosses (Fig. 5). Each cross included a large proportion of F_2 plants that have high alkali scores. Analysis of generation means showed the contribution of both additive and dominance effects in IR648/GR88, and the three types of epistatic gene effects. In IR648/KPM148, additive effect was important. Additive × additive and additive × dominance interactions were also present. An inadequacy of the digenic interaction model suggested a presence of higher order interactions in both crosses.

For amylose content, the distribution in either cross was also continuous but it appeared to be bimodal (Fig. 6). Most F_2 plants tended to have high amylose. The segregation in both F_2 populations gave a satisfactory fit to the ratio 3 high:1 intermediate, suggesting that dominant alleles confer high amylose. The analysis of

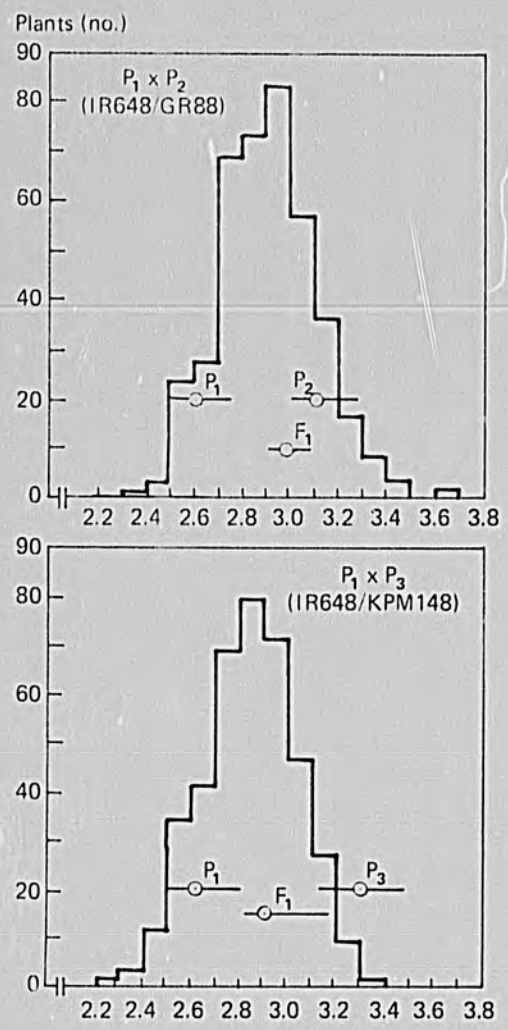

Fig. 3. Distribution and means of parents, F_1 and F_2 plants, by length-width ratio in two crosses, 1972 wet season. Solid horizontal lines show the range of parents and F_1 plants about the means (dotted circles).

generation means showed that all gene effects were significant in IR648/GR88; in IR648/KPM148, only the additive × dominance effect was nonsignificant. The presence of trigenic interactions was indicated in the IR648/KPM148 population.

Estimates of heritability

1. *Broad sense heritability* (h_1^2). Estimates of broad sense heritability for the grain characteristics, based on the percentage of genotypic variance to total F_2 variance, are in Table 4.

   Length-width ratio of grain, chalkiness, alkali digestion index, and amylose content exhibited high heritability estimates ranging from 78 to 97%. Estimate for grain length was moderately high whereas that for 100-grain weight was about 50%.

2. *Heritability estimates by progeny-parent regression* (h_{III}^2). Estimates of heritability by the regressions of F_3 line means on the F_2 individual plant scores and the standard errors of such estimates for the grain characteristics measured from IR648/GR88 are in Table 5. Heritability estimates for grain length, length-width ratio, and 100-grain weight were 50%. Moderately high estimates were obtained for chalkiness and amylose content. The alkali digestion index showed the highest heritability estimate of 80%.

3. *Phenotypic, genotypic, and environmental correlations.* Table 6 presents the phenotypic, genotypic, and environmental correlation coefficients between all possible pairs of 14 characters measured from individual F_2 plants of the 2 crosses grown in the wet season and of 1 cross grown in the dry season. Genotypic correlations were often higher than the corresponding phenotypic correlations. Environmental correlations were larger than either genotypic or phenotypic correlations in certain combinations and smaller in the others. Phenotypic and genotypic correlations between various characteristics in both crosses generally had the same sign.

Table 4. Estimates of broad sense heritability (%) for six characters of F_2 populations of IR648/GR88 and IR648/KPM148.

Character	1972 wet season		1973 dry season
	IR648/GR88	IR648/KPM148	IR648/GR88
100-grain weight	60.19	42.18	58.89
Grain length	76.96	78.10	69.98
Length-width ratio	90.59	84.22	81.62
Chalkiness	78.00	87.61	89.03
Alkali digestion index	96.38	97.25	89.89
Amylose content	72.07	82.51	69.42

Table 5. Heritability as estimated by the regression of F_3 line means on F_2 plants for six characters in the IR648/GR88 population.

Character	Heritability (%)
100-grain weight	43.94 ± 15.30
Grain length	52.60 ± 16.85
Length-width ratio	44.16 ± 17.49
Chalkiness	69.96 ± 4.19
Alkali digestion index	80.52 ± 1.82
Amylose content	69.07 ± 7.16

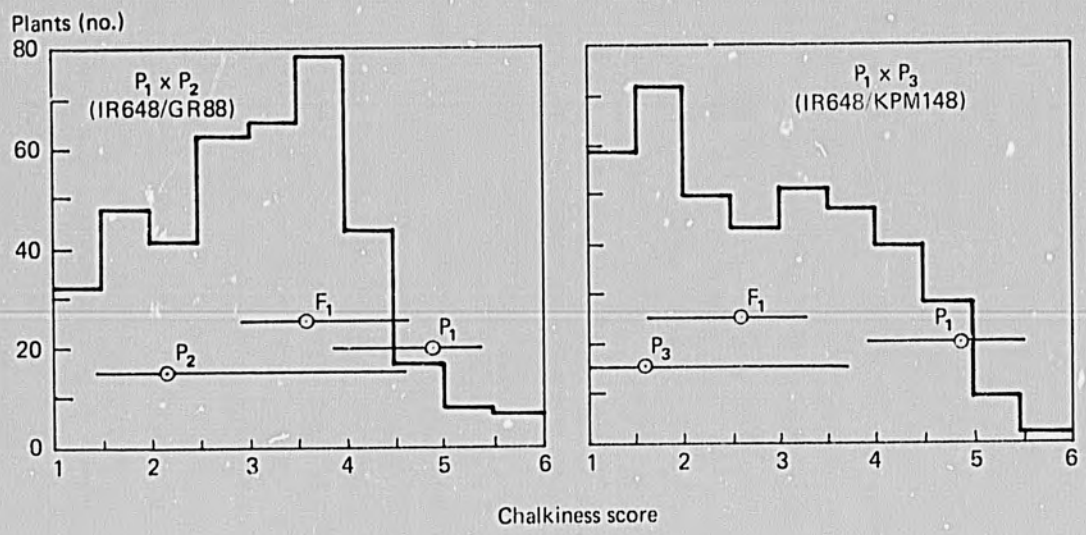

Fig. 4. Distribution and means of parents, F_1 and F_2 plants, by average score of chalkiness in two crosses, 1972 wet season. Solid horizontal lines show the range of parents and F_1 plants about the means (dotted circles).

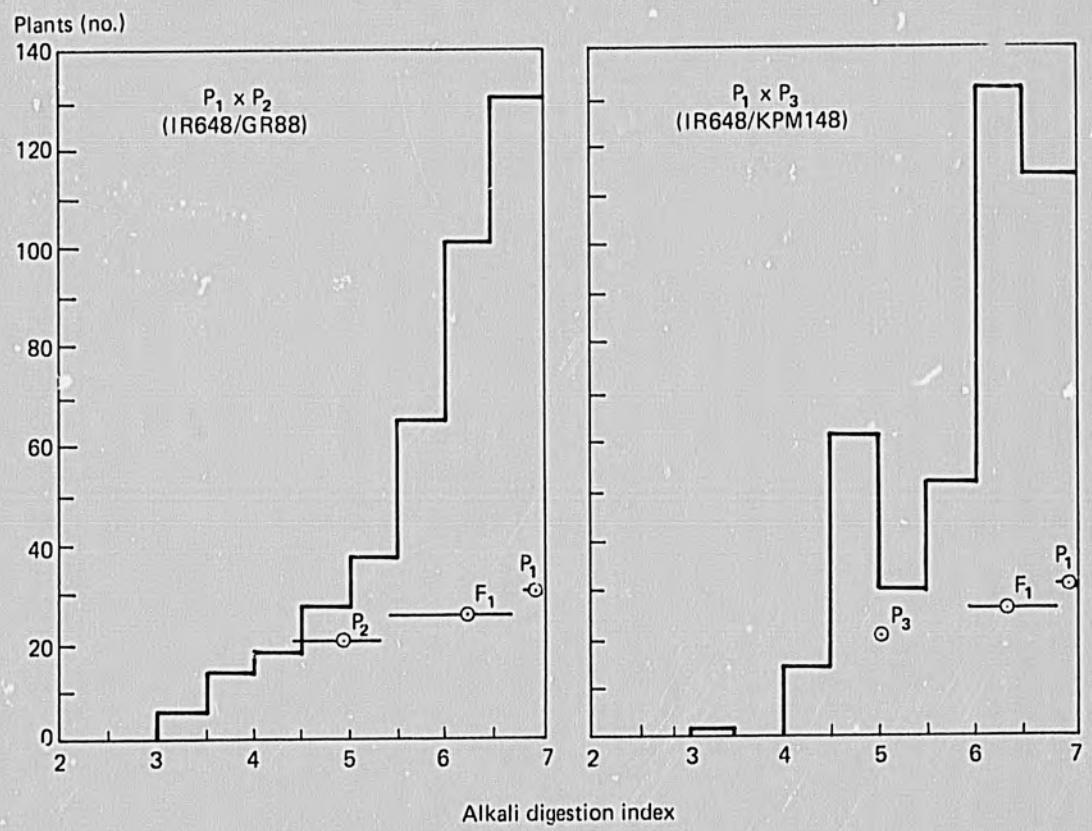

Fig. 5. Distribution and means of parents, F_1 and F_2 plants by the average of alkali digestion index in two crosses, 1972 wet season. Solid horizontal lines show the range of parents and F_1 plants about the means (dotted circles).

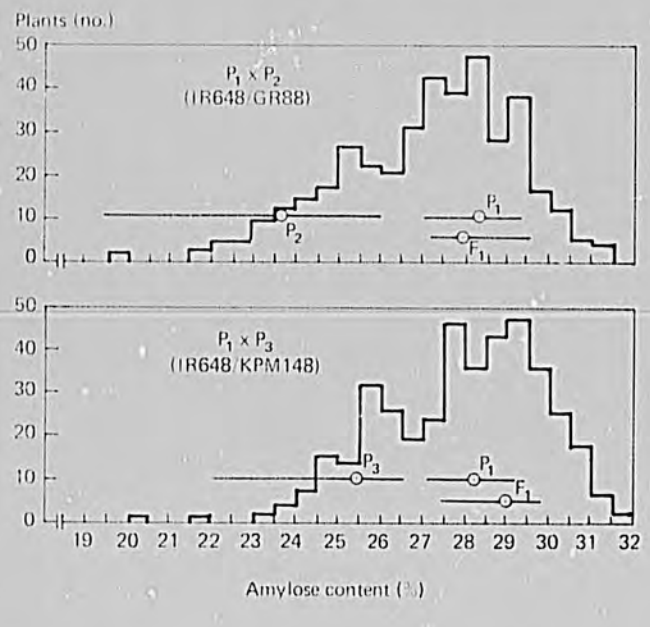

Fig. 6. Distribution and means of parents, F_1 and F_2 plants, by amylose content in two crosses, 1972 wet season. Solid horizontal lines show the range of parents and F_1 plants about the means (dotted circles).

The environmental variation for plant type within each of the parents and F_1 populations was zero, signifying that each population expressed uniformly in plant type. Therefore, only the phenotypic correlation coefficients between plant type and the remaining 13 traits are given.

Associations between grain characteristics and agronomic traits

In both crosses, kernel length showed a positive correlation with grain length-width ratio. Kernel length did not show any obvious correlation with the degree of chalkiness but was positively associated with alkali digestion index and amylose content. Grain length appeared positively correlated with 100-grain weight. Kernel length was positively associated with plant height. Positive phenotypic correlation between grain length and plant type score was observed only in the wet season.

The length-width ratio of the grain was negatively correlated with the degree of chalkiness but it showed a significant and positive association with alkali digestion index and with amylose content. It also gave a negative and significant correlation with 100-grain weight in both crosses although the correlation was not significant in the wet season planting of IR648/GR88. In IR648/KPM148, grain slenderness was observed to be associated with desirable plant type.

Chalkiness was negatively correlated with alkali digestion index and with amylose content in the wet season. A strong and positive association between chalkiness and 100-grain weight was observed in all cases.

Alkali digestion index was significantly and positively correlated with amylose content in both crosses. Table 7 shows a high frequency of the recombinants with high alkali digestibility (low gelatinizing) and high amylose content in the F_2 population of IR648/GR88. Alkali digestion index gave a positive association with 100-grain weight at a significant level in the wet season. Amylose content also indicated a positive correlation with 100-grain weight, plant type score, and plant height in both crosses.

DISCUSSION

Among the grain characteristics, grain length was mainly controlled by both additive and dominance effects. The grain length-width ratio was primarily governed by genes with additive effect in one cross and by genes with both types of effects in the other cross. These two physical features also showed positive correlation. Earlier investigators also reported polygenic inheritance of grain length and grain shape (Mitra 1962, Thullen 1966, Poonai 1966, Murty and Govindaswamy 1967).

Chalkiness score indicated the presence of dominance effect in IR648/GR88, but in IR648/KPM148 the genetic variation was largely due to additive effect. In addition, a substantial portion on the total variation in chalkiness could be attributed to environmental influence. Our findings could not be explained by any of the previous postulates based on one or more recessive mendelian genes (USDA 1963, Seetharaman 1964). On the other hand, the dominant nature of chalkiness has been reported (Nagai 1958).

For alkali digestion index, the F_2 distribution showed an obvious skewness toward the high-index parent, indicating that dominant alleles were operating in IR648/GR88, although significant dominance effect was not detected in IR648/KPM148. The anomalous F_2 segregation of the index could result from digenic and trigenic interactions. Our data could not be interpreted by the postulates of previous workers: (1) a few genes of major effect and several modifiers (Kahlon 1964) or (2) more than three genes were involved (Stansel 1965). Ghosh and Govindaswamy (1972) reported that lack of dominance was observed in F_1 and that the bimodal F_2 distribution did not agree with any conventional genetic ratio.

The analysis of amylose content indicated that the inheritance of this trait was controlled by a single dominant gene along with minor genes with cumulative effect. Our findings agree with the previous findings of Seetharaman (1959), Kahlon (1964), and Ghosh and Govindaswamy (1972).

Heritability estimates obtained by genotypic variance for the grain characteristics and cooking features

Table 6. Phenotypic, genotypic, and environmental correlation coefficients among selected agronomic traits and grain characteristics in the F_2 populations of IR648/GR88 and IR648/KPM148, 1972 wet season data, and of IR648/GR88, 1973 dry season data.

Character	1972 Wet season						1973 Dry season		
	IR648/GR88			IR648/KPM148			IR648/GR88		
	r_P	r_G	r_E	r_P	r_G	r_E	r_P	r_G	r_E
Grain length and									
Length-width ratio	.521**	.568	.317	.541**	.272	.236	.508**	.165	.381
Chalkiness	.061^{ns}	.087	-.026	-.026^{ns}	-.098	.027	.070^{ns}	.063	.250
Alkali digestion index	.260**	.281	.194	.232**	.493	.068	.262**	.544	-.292
Amylose content	.346**	.361	.376	.310**	b	.468	.238**	b	-.174
100-grain weight	.461**	.486	.432	.409**	.228	.306	.262**	.187	-.096
Plant type	.178*	a	a	.157*	a	a	.099^{ns}	a	a
Plant height	.205**	.196	.293	.160*	.171	.117	.169*	.232	-.050
Length-width ratio and									
Chalkiness	-.409**	-.488	.010	-.515**	b	-.060	-.479**	b	.059
Alkali digestion index	.183**	.197	-.021	.156*	.267	-.145	.161*	.256	-.144
Amylose content	.238**	.310	-.082	.224**	.794	.066	.158*	.518	.040
100-grain weight	-.107^{ns}	-.124	-.076	-.224**	-.091	-.208	-.285**	-.138	-.061
Plant type	.039^{ns}	a	a	.276**	a	a	-.095^{ns}	a	a
Plant height	.048^{ns}	.036	.168	.266**	.315	-.118	-.010^{ns}	.018	-.115
Chalkiness and									
Alkali digestion index	.213**	-.239	-.060	-.225**	b	.115	-.134^{ns}	b	-.131
Amylose content	-.265**	-.232	-.369	-.277**	-.258	-.390	-.066^{ns}	-.004	-.341
100-grain weight	.248**	.500	-.318	.280**	b	-.231	.288**	b	-.322
Plant type	.053^{ns}	a	a	-.137^{ns}	a	a	.197**	a	a
Plant height	-.008^{ns}	.013	-.146	-.199**	-.230	.091	.179*	.210	-.033
Alkali digestion index and									
Amylose content	.544**	.634	.163	.584**	.644	.092	.492**	.615	.035
100-grain weight	.193**	.248	.064	.149*	.327	.024	.134^{ns}	.289	.039
Plant type	-.027^{ns}	a	a	.120^{ns}	a	a	.101^{ns}	a	a
Plant height	.005^{ns}	.009	.062	.127^{ns}	.129	.107	.116^{ns}	.120	.094
Amylose content and									
100-grain weight	.310**	.222	.490	.165*	.128	.440	.205**	.703	.226
Plant type	.262**	a	a	.274**	a	a	.202**	a	a
Plant height	.287**	.295	.310	.335**	.373	.073	.217**	.223	.212
100-grain weight and									
Plant type	.347**	a	a	.061^{ns}	a	a	.246**	a	a
Plant height	.374**	.430	.298	.130^{ns}	.148	.184	.226**	.327	-.024
Plant type and									
Plant height	.835**	a	a	.791**	a	a	.720**	a	a

ns = Not significant. * Significant at the 5% level, ** Significant at the 1% level.
a indicates zero estimate of environmental variance.

were high, ranging from 40 to 97%. Heritability estimates obtained by parent-progeny regression ranged from moderate (about 50%) for 100-grain weight, grain length, and length-width ratio, to moderately high (70-80%) for chalkiness, alkali digestion index, and amylose content. A heritability estimate of 59% for 100-grain weight was reported by Chandraratna and Sakai (1960). Moderate values of heritability were given for chalkiness (Masajo 1971, Nakatat 1972). Grain length and grain shape were found highly heritable traits (Poonai 1966, Nakatat 1972). Seetharaman (1959) reported a high heritability estimate for amylose content. Masajo (1971) obtained a high value for alkali digestion index. Bollich and Webb (1973) reported estimates of 29 and 63% for amylose content in the F_2 and F_3 progenies of different crosses.

The parent-offspring regression coefficient in this study involved the growing of parents and progenies

Table 7. Association between the amylose content and alkali digestion index in the F_2 progeny of IR648/GR88, 1972 wet season.

F_2 plants with a given range of amylose content (no.)	F_2 plants with a given range of alkali digestion index (no.)			
	3.1-4.0	4.1-5.0	5.1-6.0	6.1-7.0
19.1-20.0	1	-	-	-
20.1-21.0	-	-	-	-
21.1-22.0	-	1	1	-
22.1-23.0	3	1	3	1
23.1-24.0	6	8	4	3
24.1-25.0	5	9	8	10
25.1-26.0	3	11	16	20
26.1-27.0	2	6	19	25
27.1-28.0	-	6	26	49
28.1-29.0	-	3	18	54
29.1-30.0	-	-	4	53
30.1-31.0	-	-	2	16
31.1-32.0	-	-	-	3

in different seasons. Heritability values estimated by parent-offspring regression were generally lower than those estimated by genotypic variance because the latter was based on the total genetic variance. On the other hand, Bartley and Weber (1952) pointed out that differences in environmental conditions between seasons would affect the magnitude of the regression coefficients in certain cases.

Correlation values show that long grains tend to be slender in shape. This tendency was also reported in earlier investigations of Ramiah and Rao (1953). Slender grains tended to have low degrees of chalkiness in both crosses. It implies that one can obtain clear and slender grains when selecting for plants with long grains. The long kernels not only tended to be heavy but also showed high amylose content and low gelatinization temperatures (high alkali digestion index) in the two crosses. Our findings indicate a good probability of recovering in the F_2 generation of nonparental combinations with tall plant stature, long and slender grains, high amylose content, and low gelatinization temperature. This type of progeny differs from the traditional Thai rices which have most of the attributes except that they have moderately high amylose.

Traits such as gelatinization temperature and plant height did not show significant correlation with one another, but they were strongly correlated with amylose content. The strong association between high amylose content and low gelatinization temperature has been reported by previous workers (Kahlon 1964, Masajo 1971, Ghosh and Govindaswamy 1972).

In the F_2 populations of this study, the data suggest that the desired levels of amylose content and gelatinization temperature can be selected independently of plant height. But for combinations other than the high amylose-low gelatinizing type, concurrent screening for each of the two traits is necessary in the breeding cycles.

ACKNOWLEDGMENTS

The senior author is indebted to Ms. Sommai Amonsilpa of the Rice Division (Bangkhen) for making the crosses, Mr. Oscar O. Tagumpay of IRRI for providing help on field work, Ms. Carmen Paule of IRRI for her assistance on the quality analysis, Dr. Kwanchai Gomez of IRRI for her help on statistical analysis, and Dr. B. R. Murty of the Indian Agricultural Research Institute (New Delhi) for valuable suggestions.

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