

Agronomic Characteristics of Rice Recombinant Inbred Lines (RILs) Developed from a Cross of Nonganbyeon and BG 279

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ABSTRACT

A set of rice recombinant inbred lines was developed from a cross between a Tongil type variety, Nonganbyeon, and an *indica* variety, BG276, by the single seed descent method. The number of the lines in the population was 272. All the agronomic characters studied except ADV (alkali-digestion value) showed continuous variation among the RILs, implying that their inheritance mode should be quantitative. The patterns of the variation in the RILs were either normal or skewed distribution. ADVs of RILs were segregated into two groups with 1:1 ratio, indicating that ADVs in this RIL population might be controlled by one major gene. Transgressive variations were also observed in all characters. Heritability values of the characters varied from 0.488 in brown/rough rice ratio to 0.895 in alkali-digestion value. In the analysis of genotypic and phenotypic correlations, the character of yield was positively correlated with 8 different agronomic characters. The number of panicles per hill was negatively correlated with culm length, panicle length, and number of spikelets per panicle. Grain length was positively correlated with grain width, grain thickness, grain length/width ratio, white belly, ADV, and amylose. However, grain length/width ratio was negatively correlated with grain width. White core was also negatively correlated with white belly and ADV.

Key words : rice, recombinant inbred lines, quantitative trait locus, heritability, genotypic correlation coefficient, phenotypic correlation coefficient.

Recombinant inbred lines (RILs) could be developed by successive selfing or sib-mating of the individual F_2 progenies until a certain level of homozygosity is achieved (Evola et al., 1986). Since each RI line is fixed for different combinations of linked blocks of parental alleles, RILs are preferable in many aspects including genetic mapping. Another advantage of RILs compared to other segregating populations such as F_2 or back crossed populations is that the linked genes have a greater probability of recombination due to the multiple rounds of meiosis to be a state of recombinant inbred lines (Taylor, 1978; Burr & Burr, 1991).

Since most of the loci in the RILs are fixed, the lines can be distributed and replicated for different laboratories and environments. This characteristic is particularly useful for the analyses of quantitative traits because it allows

for a reduction of the environmental component of total phenotypic variation. In many mapping studies of quantitative trait loci (QTL) one or more limited environments have been used for the evaluation of the phenotype (Nienhuis et al., 1987; Paterson et al., 1988; Paterson et al., 1991). This result indicates the need for RILs as a mapping population that can be replicated and evaluated in multiple environments. QTL-mapping with RILs is more efficient than with F_2 populations because fewer individuals are needed to detect linkage of the same magnitude between markers and QTL (Simpson, 1989) due to a greater chance of recombination events in RILs than in the F_2 population (Taylor, 1978).

Genetic variation in a population could be either continuous or discontinuous. The discontinuous or discrete variation should be derived from macromutations so that their inheritance follows simple Mendelian manners. However, these macromutations are rare in nature since most of them are deleterious to the individuals and would be weeded out of the population by natural selection (Tanksley, 1993). The continuous variation is mainly determined by segregating multiple genetic loci with relatively small genetic effects. The influence of the allelic differences can be sometimes smaller than the environmental influence so that the partitioning of these continuous variations is not as simple as discrete Mendelian genetics.

We produced a set of recombinant inbred lines derived from a cross between Tongil type variety, Nonganbyeon and *indica* variety, BG276. These RILs were F_7 and consisted of 272 lines. This paper describes the production and phenotypic variations among the RILs for some quantitative trait loci.

MATERIALS AND METHODS

Production of recombinant inbred lines

Twenty-five F_1 hybrid seeds were obtained from a cross between Nonganbyeon and BG276 in the winter of '93/'94 (Fig. 1). These F_1 seeds were germinated and grown in the summer of 1994 to produce 1,500 F_2 plants which were proceeded to F_6 by the single seed descent method

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in the greenhouse during the winter season and field during the summer season. Among the 1,500 F₆ lines, 272 lines were selected randomly and planted in duplicate in the field at the National Crop Experiment Station in Suwon, Korea in 1997. They were seeded in nursery plots on April 20 and transplanted into the field on May 25 by hand 4 plants in each row with a spacing of 30×15 cm. Fertilizer was applied at the rate of 150-90-110 kg/ha (N-P₂O₅-K₂O).

Evaluation of Agronomic Characters among the RILs

Some important characteristics including days to heading, culm length, panicle length, yield, number of panicles per hill, number of spikelets per panicle, percentile of ripened grain, 1,000 grain weight, brown/rough rice ratio, grain length, grain width, grain thickness, grain length/width ratio, white core, and white belly were measured following the standard method of RDA. The alkali digestion value was measured after a 24 hour incubation period in 1.4% KOH solution at room temperature. Amylose content in grains was measured by iodine coloring method.

Statistical analyses

Mean, standard deviation, range, mode and frequencies of each class of the RILs were calculated using the Microsoft Excel software program. Correlation coefficients among the agronomic characters were calculated using SAS statistics software program (SAS, 1988).

The mean values of each repeat in duplicate plots of RILs were calculated to get the genetic variance (σ^2_g) and phenotypic variance (σ^2_p). The heritability (h^2) was calculated using the equation of $h^2 = \sigma^2_g / \sigma^2_{total}$. Phenotypic correlation coefficient (rPh) and genotypic correlation coefficient (rG) were calculated from the covariance method, $rPh = Cov.XY / \sqrt{\sigma^2_X \cdot \sigma^2_Y}$, $rG = Cov.XY_G / \sqrt{\sigma^2_{XY_G} \cdot \sigma^2_{XY_G}}$, respectively. Here, the Cov.XY and Cov.XY_G were the phenotypic and genotypic covariances between characters X and Y, and $\sigma^2_{XY_G}$ was genotypic variance between characters X and Y, respectively.

RESULTS AND DISCUSSION

Variations in days to heading, culm length, and panicle length among the RILs

Table 1 and Fig. 2 show the variations for days to heading, culm length, and panicle length among the RILs. The female parent Nonganbyeon headed at 111 days and the male parent BG276 headed at 104 days after planting, respectively. The RILs derived from both parents headed from 91 to 124 days after planting with the mean of 104±5.9 days. The frequency distribution of the heading days showed normal distribution which might suggest the effect of polygenes on heading. Four

major QTLs for heading date had been identified on the chromosomes of 1, 8, and 10 in a recent study using a doubled haploid population by Lu et al. (1997). However, these four QTLs were not always significant in the four different sites in China using the same population, which indicated that the heading date was heavily dependent on the altitude of the cultivation for each ecotype (MacKill et al., 1993; Li et al., 1995; Kang 1996; Yano et al., 1997).

In spite of insignificant differences from their parents, the RILs showed normal distribution for culm length with a range of 59 to 110 cm (Table 1 and Fig. 2). From the diallelic crosses between *indica* and *japonica* varieties, Chang et al. (1978) reported that the culm length was controlled by a gene in a manner of incomplete dominance. On the other hand, continuous variation among the RILs derived from a cross of a *indica* variety, Milyang 23 and a *japonica* variety, Kihobyeon was reported by Kang (1996).

Panicle length of the parents was the same (26 cm) and was insignificantly different from the mean of the RILs (26.5±2.9 cm). The mode of the RILs was 26 cm and normal distribution with a range of 18 to 35 cm. The transgressive phenotypic distribution for this character was similar to that of culm length, which was also reported by others (Chang et al., 1978; Xiao et al., 1996; Kang et al., 1998). While Chang et al. (1978) reported that the long panicle length was dominant to short panicle with additive effect, partial or over dominance of the long panicle were also reported by others (Chang et al., 1978; Jun et al., 1985).

Variations of yield and yield component characters among the RILs

Table 2 and Fig. 3 show the variations of yield and yield component characters among the RILs. Normal distribution was observed for the number of panicles per hill, number of spikelets per panicle, and 1,000 grain weight, but skewed distribution for the traits of percent of ripened grains, milled rice yield, and brown/rough rice ratio. These patterns of distribution were similar to the report by Kang (1996).

Although the parents had 9 and 14 panicles per hill, respectively, the RILs showed normal distribution with transgressive variation ranging from 6 to 18. Jun et al. (1985) reported that high tillering was incompletely dominant to low tillering from the F₂ analysis of *indica/japonica* cross. The number of spikelets per panicle among the RILs ranged from 78 to 215 with the mean of 154±44.3. Normal distribution was observed for the number of spikelets per panicle in this study, which was not similar to the report of Xiao et al. (1996). In spite of no significant difference between the parental mean and the mean value of the RILs for the proportion of ripened grain, RILs had the range of 60.5~96% at the mode of 78%. Although a low ratio of ripened grains due to high sterility was frequently observed in the crosses between

Table 1. Variation of some characters in RILs derived from the cross between Nonganbyeo and BG276.

Character	Nonganbyeo (Female)	BG276 (Male)	RILs		
	M ± SD	M ± SD	M ± SD	Range	Mode
Days to heading (days)	111 ± 1.8	104 ± 1.5	104.1 ± 5.9	91 ~ 124	98
Culm length (cm)	79 ± 2.8	81 ± 3.1	82.4 ± 9.4	59 ~ 110	80
Panicle length (cm)	26 ± 0.9	28 ± 1.6	26.5 ± 2.9	18 ~ 35	26

Table 2. Variation of yield and yield components in RILs derived from the cross between Nonganbyeo and BG276.

Character	Nonganbyeo (Female)	BG276 (Male)	RILs		
	M ± SD	M ± SD	M ± SD	Range	Mode
Number of panicles /hill	9 ± 1.1	14 ± 1.3	11.4 ± 2.1	6 ~ 18	11
Number of spikelets /panicle	125 ± 10.2	178 ± 13.8	154.7 ± 44.3	78 ~ 215	131
% of ripened grain	83 ± 2.9	70 ± 4.7	79.5 ± 7.7	60.5 ~ 96.0	78
1,000 grain weight (g)	7.8 ± 0.4	23.5 ± 0.6	19.8 ± 2.61	13.9 ~ 27.1	21
Brown /rough rice ratio	79.9 ± 1.0	74.0 ± 0.8	77.6 ± 2.20	71.3 ~ 82.4	76.9
Milled rice yield (ton/1ha)	5.10 ± 0.09	6.92 ± 0.12	5.85 ± 1.33	1.46 ~ 8.52	5.47

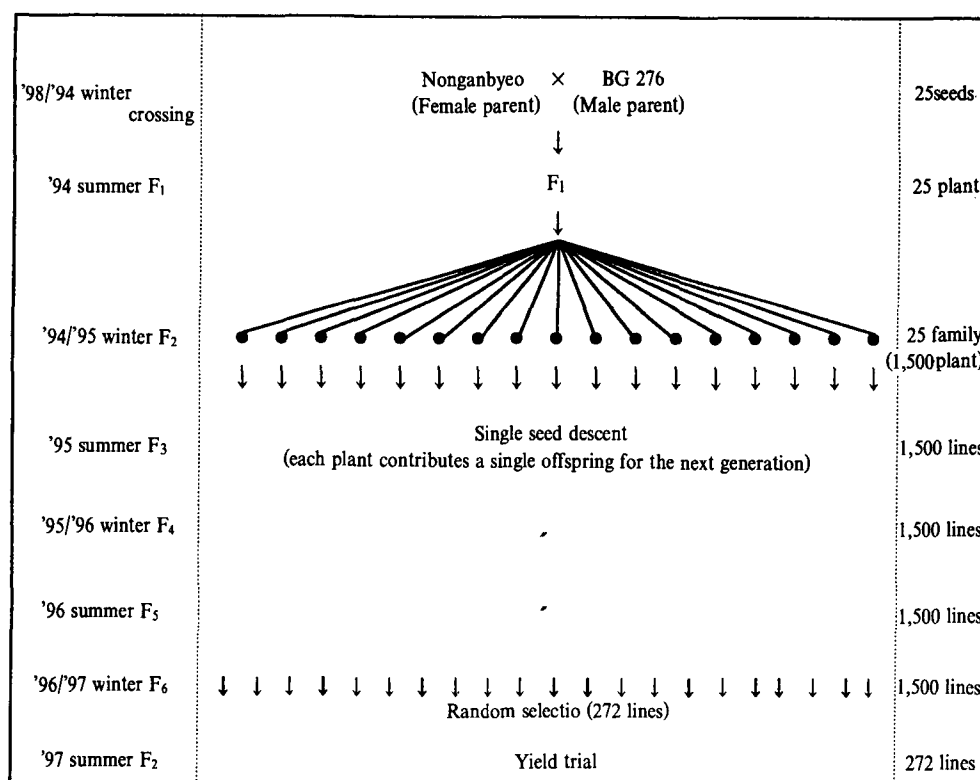


Fig. 1. Development of recombinant inbred lines.

genetically distant plants such as *indica* and *japonica* rice varieties our results did not show this problem since the Tongil type female parent was crossed with an male parent.

Though the parents were not quite different from each other for 1,000 grain weight, the frequency distribution in the RILs was normal at the mode of 21 g with a range of 13.9~ 27.1 g. Saito et al. (1991) reported that the grain

weight in rice was controlled by the interaction between one recessive major gene and a dominant gene with low environmental effect. The distribution of brown/rough rice ratio was skewed to male parent BG276 from the mode value of 76.9% and had a range from 71.3 to 82.4%. The mean yield of milled rice among the RILs (5.85 ± 1.33 ton) was different from that of the parents, 5.10 ton in female and 6.92 ton in male parents. Milled rice yield among the RILs ranged from 1.46 to 8.52 ton with the mode of 5.47 ton. Slightly skewed distribution to the male parent was also observed. A wide range of yield among the RILs might be due to non-selection during RIL development.

The variations in the characters related to seed shape and grain quality among the RILs

Table 3, Fig. 4, and Fig. 5 show variations of the characters related to seed shape and grain quality among the parents and RILs. Symmetrical normal distribution was observed for grain length, grain width, and white belly, but skewed frequency distribution for grain thickness, grain length/width ratio, and amylose content among the RILs. Chang (1974) and Lin & Chang (1981) said that genes had various genetic effects on the phenotypic expression depending on different cross combinations. Somrith et al. (1979) reported that grain length was controlled by additive genetic effects and dominant effects, but grain width was not related to any genetic

effects. However, Ramiah & Parthasarothi (1982) reported that the inheritance of grain length was controlled by multiple genes and there was a relationship between the genes for grain length and grain width.

The parents showed 0~3 in the white core character. However, the RILs varied from 0 to 8 with skewed distribution. For the alkali digestion, the same trends were observed: The RILs showed more variations than parents in their alkali digestion value. The bimodal distribution for alkali digestion in our study might indicate that this character was controlled by one major quantitative trait locus. This was in contrast to an observation by Kang (1996) who reported a skewed distribution in a RIL population and detected QTL on chromosomes 3, 7, and 8. The RILs varied from 12 to 25.9 % and their distribution was skewed to the lower content with the mode value of 15.9%. From the above studies, we had two conclusions concerning the inheritance of several agronomic characters. First, normal distribution was observed for the major agronomic characters except ADV. The other patterns of distribution were either symmetry to the mode or skewed distribution. The continuous variation was mainly derived from the action of polygenes. These phenotypic variations in our study were also reported by other QTL studies (Li et al., 1995; Paran et al., 1995). Second, transgressive variation was observed in most of the characters. This pattern of phenotypic distribution was reported in other studies (Tanksley 1993; Xiao et al., 1996; Kang et al., 1998). Tanksley (1993)

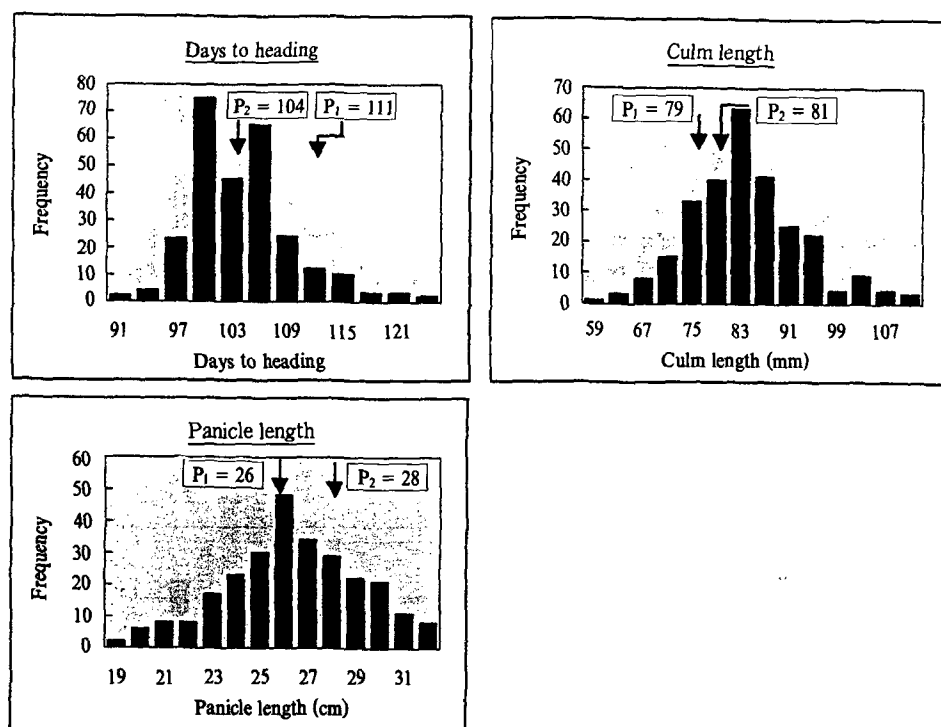


Fig. 2. Frequency distribution of the plant growth-related characters of 272 RILs and their parents, Nonganbyeo(P₁) and BG276(P₂).

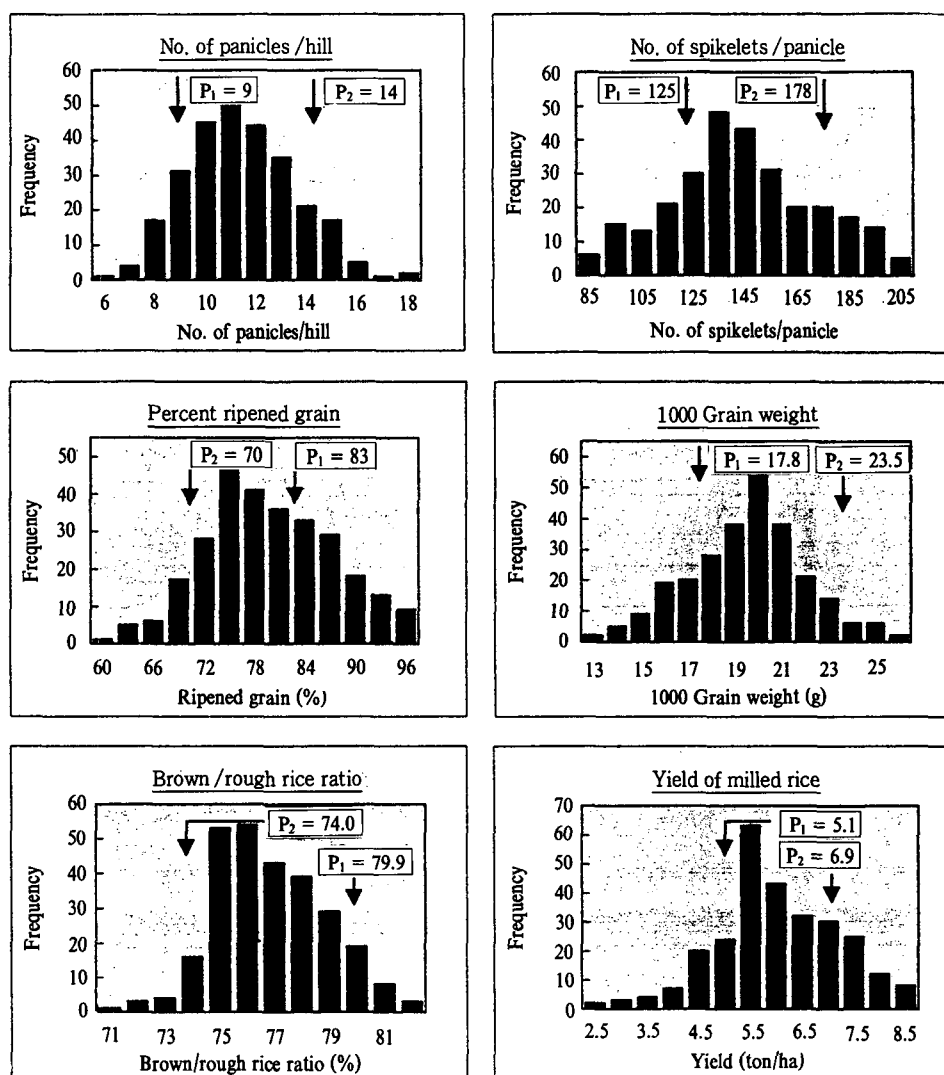


Fig. 3. Frequency distribution of the yield-related characters of 272 RILs and their parents, Nonganbyeo (P_1) and BG276 (P_2)

Table 3. Variation of some grain characters, ADV, and amylose in RILs derived from the cross between Nonganbyeo and BG276.

Character	Nonganbyeo (Female)	BG276 (Male)	RILs		
	M \pm SD	M \pm SD	M \pm SD	Range	Mode
Grain length (mm)	5.5 \pm 0.2	6.5 \pm 0.3	5.8 \pm 0.58	4.3~7.4	6
Grain width (mm)	2.4	2.5	2.5 \pm 0.15	2.0~2.9	2.5
Grain thickness (mm)	1.7	1.85 \pm 0.05	1.8 \pm 0.11	1.4~2.1	1.8
Grain length /width ratio	2.2 \pm 0.01	2.60 \pm 0.02	2.3 \pm 0.25	1.7~3.1	2.4
White core (0-9)	0	3	1.8 \pm 1.51	0 ~8	1
White belly (0-9)	1	5	3.4 \pm 1.74	0 ~9	3
Alkali digestion value (1-7)	6.1	2.0	4.2 \pm 1.99	2.0~6.9	2
Amylose (%)	15.8 \pm 0.9	24.5 \pm 1.11	17 \pm 2.77	12~25.9	15.9

explained that transgressive variation among the RILs might be due to the accumulation of complementary alleles inherited from the parents at multiple loci in certain progeny. No selection effect was observed among the RILs with the PCA analysis (data not shown).

Heritabilities of the agronomic characters in the RILs

Heritability values (h^2) of the studied characters are shown in Table 4. If the heritability value is close to 1, it means that most of the measured variation was derived from genotypic variation. The h^2 values of the characters such as days to heading, culm length, 1000 grain weight,

grain length, grain width, grain length/width ratio, alkali digestion value, and amylose content were above 0.8 which means that the environmental effect on these characters was low. However, the h^2 values of brown/rough rice ratio, white core, and white belly were lower than 0.5. For number of panicles/hill, percent of ripened grain, yield, and grain thickness, the h^2 values were around 0.5. The heritability values for the panicle length and number of panicles per hill in our study were lower than those of Chang et al., (1997). Among the 17 quantitative characters in our study, ten characters were also tested in the RIL population from a cross between Milyang 23 and Kihobyoe (Kang 1996). Kang's studies

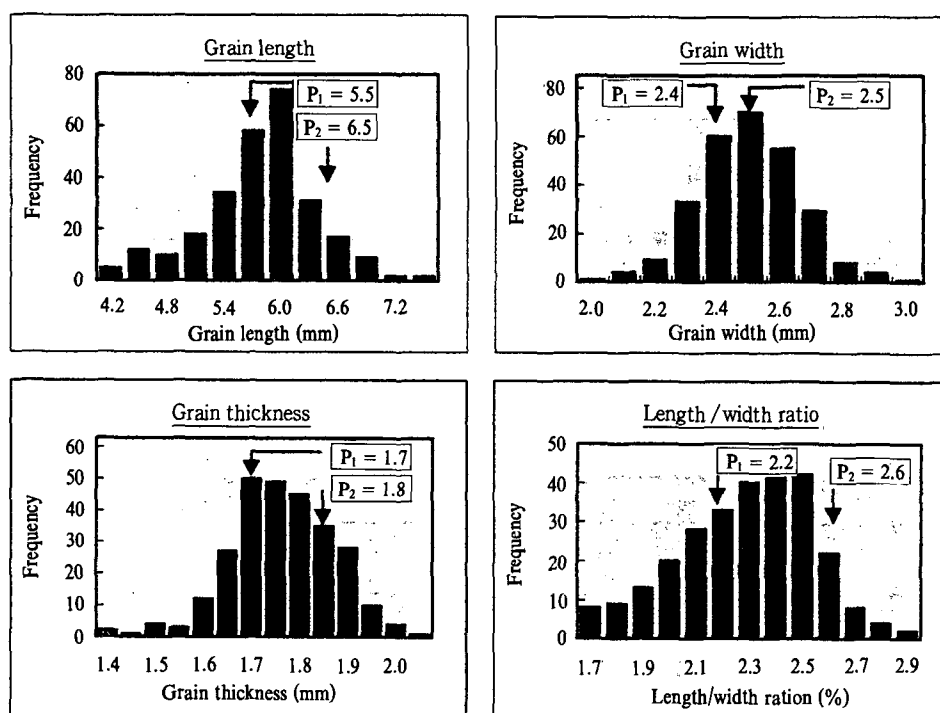


Fig. 4. Frequency distribution of the grain size-related characters of 272 RILs and their parents, Nonganbyeo(P_1) and BG276(P_2).

Table 4. Heritability estimates of some agronomic characters in RILs derived from the cross between Nonganbyeo and BG276.

Characters	Heritability (h^2)	Characters	Heritability (h^2)
Days to heading	0.894	Grain length	0.886
Culm length	0.823	Grain width	0.802
Panicle length	0.690	Grain thickness	0.615
Number of panicle /hill	0.510	Grain length /width ratio	0.861
Number of spikelet /panicle	0.707	White core	0.467
% of ripened grain	0.551	White belly	0.463
1,000 grain weight	0.847	Alkali digestion value	0.895
Brown /rough rice ratio	0.488	Amylose	0.891
Yield	0.576		

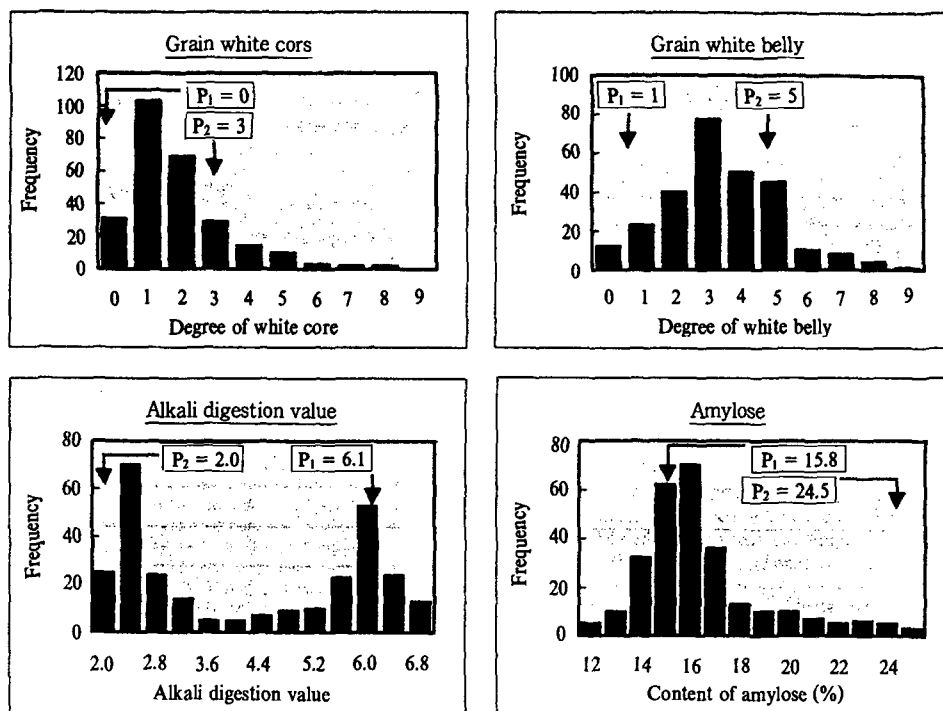


Fig. 5. Frequency distribution of the grain quality-related characters of 272 RILs and their parents, Nonganbyeo(P_1) and BG276(P_2).

(1996) demonstrated that the characters with high heritability showed good high variation in the QTL analysis.

With the aid of a computer simulation analysis for marker assisted selection (MAS), Van Berloo & Stam (1998) reported that phenotypic selection response after MAS was greater as trait heritability approached 1.0. However, the response of MAS was greater than that of phenotypic selection when heritability was between 0.1 and 0.3. However the advantage of MAS over phenotypic selection was insignificant when heritability was 0.5.

Phenotypic and genotypic correlation coefficients between agronomic characters among the RILs

Table 5 represents the correlation coefficients among the nine different agronomic characters in the 272 recombinant inbred lines. At the level of 1%, positively significant correlations with yield in both genotype and phenotype were observed for the characters of days to heading, culm length, number of panicles/hill, number of spikelets/panicle, percent of ripened grain, and brown/rough rice ratio. Panicle length and 1,000 grain weight were highly and positively correlated with the yield when the genotypic variation only was considered. The characters with low heritability showed low genetic correlation coefficients with other characters. The number of spikelets/panicle was also highly positively correlated with such characters as days to heading, culm length, panicle

length, and number of panicles/hill at the level of 1%. Culm length was also correlated with five other characters including panicle length, number of panicles/hill, number of spikelets/panicle, 1,000 grain weight, and yield. The character of 1,000 grain weight showed low phenotypic correlation with yield, but high genotypic correlation with yield. This might be due to the fact that the yield was influenced by multifactors which was also backed by the fact of low heritability. Kang (1996) also reported that not all the yield components were correlated with yield. According to the results of Xiao et al. (1995), the chromosomal locations of the QTL for yield component did not correspond with the QTL for yield. Negative correlations were observed between panicle length and number of panicles/hill at the 1% level. One thousand grain weight was also negatively correlated with the number of panicles/hill and the number of spikelets/panicle at the 5% level.

Phenotypic and genotypic correlation coefficients between grain characters among the RILs

Correlation coefficients among the grain quality related characters are shown (Table 6). Grain length was highly positively correlated with most of the characters except white core. Our data on the correlation coefficient between grain length and grain width was in contrast to the report of Kang (1996) who showed a highly negative cor-

Table 5. Phenotypic (rPh) and genotypic (rG) correlation coefficients among agronomic characters in RILs derived from the cross between Nonganbyeo and BG276.

Characters		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Days to heading	rPh								
(1)	rG								
Culm length	rPh	0.011							
(2)	rG	0.017							
Panicle length	rPh	0.047	0.521**						
(3)	rG	0.083	0.572**						
Number of panicle /hill	rPh	0.101	-0.196**	-0.299**					
(4)	rG	0.129	-0.209**	-0.326**					
Number of spikelet /panicle	rPh	0.157*	0.273**	0.300**	-0.228**				
(5)	rG	0.209**	0.297**	0.311**	-0.245**				
% of ripened grain	rPh	0.093	0.139**	0.041	0.110	-0.038			
(6)	rG	0.091	0.148**	0.047	0.116	-0.042			
1,000 grain weight	rPh	-0.027	0.336**	0.256**	-0.110	-0.112	0.081		
(7)	rG	-0.016	0.399**	0.334**	-0.136*	-0.138*	0.089		
Brown /rough rice ratio	rPh	0.031	0.144*	0.109	0.063	0.001	0.655**	0.180**	
(8)	rG	0.034	0.151*	0.121	0.072	0.010	0.691**	0.206**	
Yield	rPh	0.180**	0.160*	0.115	0.181**	0.258**	0.231**	0.049	0.215**
(9)	rG	0.189**	0.356**	0.178**	0.475**	0.636**	0.648**	0.202**	0.600**

* ** ; significant at the 5% and 1% level, respectively.

Table 6. Phenotypic (rPh) and genotypic (rG) correlation coefficients among some grain character, ADV, and amylose in RILs derived from the cross between Nonganbyeo and BG276.

Characters		(1)	(2)	(3)	(4)	(5)	(6)	(7)
Grain length	rPh							
(1)	rG							
Grain width	rPh	0.190**						
(2)	rG	0.197**						
Grain thickness	rPh	0.134*	0.097					
(3)	rG	0.141*	0.104					
Grain length /width ratio	rPh	0.810**	-0.410**	0.069				
(4)	rG	0.820**	-0.396**	0.080				
White core	rPh	-0.068	-0.094	0.081	0.001			
(5)	rG	-0.081	-0.107	0.089	-0.005			
White belly	rPh	0.144*	0.289**	-0.014	-0.041	-0.173*		
(6)	rG	0.165*	0.324**	-0.022	-0.032	-0.234**		
Alkali digestion value	rPh	0.259**	-0.069	-0.130*	0.273**	-0.158*	0.288**	
(7)	rG	0.261**	-0.071	-0.136*	0.279**	-0.177*	0.317**	
Amylose content	rPh	0.148*	-0.003	-0.003	0.133*	0.202**	0.176*	0.327**
(8)	rG	0.150*	-0.004	-0.001	0.137*	0.228**	0.203**	0.331**

* ** ; significant at the 5% and 1% level, respectively.

relation between these two characters. Negative correlation was observed between grain length and white core as reported in Kang (1996). Amylose content also showed a highly positive correlation with grain length, grain length/width ratio, white core, white belly, and alkali digestion value. However, amylose content showed a negative correlation with grain width and grain thickness. White belly also showed a positive correlation with all

characters except grain thickness and grain width. White core and white belly showed a strongly negative correlation at the level of 1%.

REFERENCES

Burr, B. and F. A. Burr. 1991. Recombinant inbreds for molecular mapping in maize. TIG. vol 7: 55-60.

- Chang, K. Y., B. T. Jun, and Y. H. Kwak. 1978. Genetic studies on some quantitative characters of rice in diallel crosses. II. Distributions of genes of rice for various characters of rice in F₁ and F₂ generations of various characters. *Kor. J. Crop Sci.* 23: 34-39.
- Chang, T. M. 1974. Studies on the inheritance of grain shape. *Taiwan Agri. Res.* 23: 9-15.
- Evola, S. V., F. A. Burr, and B. Burr. 1986. The suitability of restriction fragment length polymorphisms as genetic markers. *Theor. Appl. Genet.* 71: 765-771.
- Jun, B. T., S. Y. Cho, and K. Y. Chang. 1985. Studies on the inheritance of quantitative characters in rice V. Differences of combining ability and degree of dominance for several agronomic characters of rice in F₁ and F₂ generations from diallel cross. *Kor. J. Breed.* 17: 177-182.
- Kang, H. J. 1996. QTL (quantitative trait loci) mapping of genes conferring agronomic traits based on molecular maps in rice. Ph.D. thesis. Seoul National University, Suwon, Korea.
- _____, Y. G. Cho, Y. T. Lee, M. Y. Eun, and J. U. Shim. 1998. QTL mapping of genes conferring days to heading, culm length, and panicle length based on molecular map of rice (*Oryza sativa* L.). *RDA J. Crop Sci.* 40: 55-61.
- Li, Z. K., S. R. M. Pinson, J. W. Stansel, and W. D. Park. 1995. Identification of quantitative trait loci (QTLs) for heading date and plant height in cultivated rice (*Oryza sativa* L.). *Theor. Appl. Genet.* 374-381.
- Lin, M. H. and T. T. Chang. 1981. Inheritance of agronomic traits and character association in crosses between dryland and wetland cultivars of rice. *SABRAO J.* 13: 11-13.
- Lu, C., L. Shen, Z. Tan, Y. Xu, Y. Chen, and L. Zhu. 1997. Comparative mapping of QTLs for agronomic traits of rice across environments by using a doubled-haploid population. *Theor. Appl. Genet.* 94: 145-150.
- MacKill, D. J., M. A. Salam, Z. Y. Wang, and S. D. Tanksley. 1993. A major photoperiod-sensitivity gene tagged with RFLP and isozyme markers in rice. *Theor. Appl. Genet.* 85: 536-540.
- Nienhuis, J., T. Helentjaris, M. Slocum, and B. Ruggero. 1987. Restriction fragment length polymorphism analysis of loci associated with insect resistance in tomato. *Crop Sci.* 27: 793-803.
- Paran, I., I. Goldman, S. D. Tanksley, and D. Zamir. 1995. Recombinant inbred lines for genetic mapping in tomato. *Theor. Appl. Genet.* 90: 542-548.
- Paterson, A. H., E. S. Lander, S. Hewitt, S. Paterson, S. E. Lincoln, and S. D. Tanksley. 1988. Resolution of quantitative traits into Mendelian factors by using a complete linkage map of restriction fragment length polymorphism. *Nature* 335: 721-726.
- _____, S. Damon, J. D. Hewitt, D. Zamir, H. D. Rabinowitch, S. E. Lincoln, E. S. Lander, and S. D. Tanksley. 1991. Mendelian factors underlying quantitative traits in tomato; comparison across species, generations, and environments. *Genetics* 127: 181-197.
- Ramiah, K. and N. Parthasarathy. 1982. *Indian J. Sci.* 3 (5): 808-819.
- Saito, M., Yano, M., N. Kishimoto, and M. Nakagahra. 1991. Linkage map of restriction fragment length polymorphism loci in rice. *Japan. J. Breed.* 41: 665-670.
- SAS Institute. 1988. SAS users guide: SAS Institute, Cary, NC, USA.
- Simpson, S. P. 1989. Detection of linkage between quantitative trait loci and restriction fragment length polymorphism using inbred lines. *Theor. Appl. Genet.* 77: 815-819.
- Somrith, B., T. T. Chang, and B. R. Jackson. 1979. Genetic analysis of rice. *IRRI. Res. paper series No.* 35: 1-14.
- Tanksley, S. D. 1993. Mapping polygenes. *Ann. Rev. Genet.* 27: 205-233.
- Taylor, B. A. 1978. Recombinant inbred strains: use in gene mapping. In 'Origin of inbred mice' Morse H. C. (ed.), Academic Press, New York, pp: 423-438.
- Van Berloo, R. and P. Stam. 1998. Marker-assisted selection in autogamous RIL populations: a simulation study. *Theor. Appl. Genet.* 96: 147-154.
- Xiao, J., J. Li, L. Yuan, and S. D. Tanksley. 1996a. Dominance is the major genetic basis of heterosis in rice as revealed by QTL analysis using molecular markers. *Genetics* 140: 745-754.
- _____, _____, and _____. 1996b. Identification of QTLs affecting traits of agronomic importance in a recombinant inbred population derived from a subspecific rice cross. *Theor. Appl. Genet.* 92: 230-244.
- Yano, M., Y. Harushima, N. Nagamur, Y. Kurata, and Y. Minobe. 1997. Identification of quantitative trait loci controlling heading date data of rice using high density linkage map. *Theor. Appl. Genet.* 95: 1025-1032.