



Genetic effects and genotype \times environment interactions for cooking quality traits in *Indica-japonica* crosses of rice (*Oryza sativa* L.)

Jianguo Chen¹ & Jun Zhu²

¹Faculty of Life Science, Hubei University, Wuhan, Hubei, China; ²Department of Agronomy, Zhejiang Agricultural University, Hangzhou, Zhejiang, China

Received 23 June 1998; accepted 4 February 1999

Key words: cooking quality traits, genetic effect, genotype \times environment interaction, *Indica-japonica* hybridization, rice (*Oryza sativa* L.)

Summary

Indica-japonica hybridization is an important approach for developing superior performing hybrids in rice (*Oryza sativa* L.). In view of the scanty information available on cooking quality characters in *indica-japonica* crosses, an investigation was undertaken to estimate genetic and genotype \times environment variance and covariance components of amylose content, gel consistency and alkali digestion value, and to determine the relative importance of direct genetic effects, maternal genetic effects and cytoplasmic effects in the genetic variations of the three quality characters. Two *indica* photo-sensitive genic male sterile (PGMS) lines and four *japonica* varieties were used as parents to make crosses. Genetic model with genotype \times environment interactions for triploid endosperm was used for genetic studies of the three cooking quality characters. Variance component analysis revealed that genetic variations of the three characters were mainly attributable to direct additive and maternal additive effects, and the three traits had significant direct and maternal heritabilities. Genotype \times environment interactions were mainly dominance \times environment (including direct dominance \times environment and maternal dominance \times environment) and cytoplasm \times environment interactions. Environment factors could only affect the expression extent of dominant genes, without changing their directions. Predicted values of genetic effects indicated that the parental lines, 'V1-70' and 'H9304-1', appeared to be best for amylose content, 'T 1950' and 'Suxuan' appeared to be best for gel consistency and alkali digestion value.

Introduction

The emphasis on breeding for quality rice has assumed great significance in recent years. Consumer's acceptance of a variety depends primarily on its cooking quality (Kumer & Khush, 1986). Amylose content, gelatinization temperature and gel consistency are the major cooking quality components of milled rice. Although different regions of the world prefer rice varieties with different cooking characteristics, varieties with intermediate amylose content, intermediate gelatinization temperature and softer gel consistency are preferred in most of the rice-growing areas (Khush et al., 1979). In the breeding program, gelatinization temperature is estimated with the alkali digestion value.

Several investigators have reported on the inheritance of amylose content and gelatinization temperature. Some reports indicated that high amylose content seemed to be incompletely dominant to low amylose content and controlled by one major gene with several modifiers (Chang & Li, 1981; McKenzie & Rutger, 1983; Kumar & Khush, 1986, 1987). The role of two complementary genes was also indicated (McKenzie & Rutger, 1983; Heda & Reddy, 1986). Other reports supported the rationale of complex nature of inheritance of amylose content (Bollich & Webb, 1973; Singh & Singh, 1977; Pooni et al., 1993). Earlier genetic studies reported that gelatinization temperature, as measured by alkali digestion value, seemed to be simply inherited (Stansel, 1966; McKenzie & Rutger, 1983), while the more recent studies tended to offer

complex nature (Singh & Singh, 1977; Heda & Reddy, 1986). Only a few reports covered the inheritance of gel consistency. The monogenic control and modifiers affection for the expression of gel consistency were reported by Chang & Li (1981) and Tang et al. (1989), and the multigenic control of additive effects was suggested by Zaman et al. (1985).

The complex inheritance of quality characters of rice lies in the fact that they may be contributed by several genetic systems (e.g., nuclear genes of maternal plants, nuclear genes of endosperms, and cytoplasmic genes), because the grain of rice is composed of diploid maternal tissues (pericarp and testa), diploid hybrid tissues (embryo), and triploid hybrid tissues (endosperm). Most of the above reports did not take these different genetic systems into account simultaneously for shortage of analysis methods. Foolad & Jones (1992) and Pooni et al. (1992) developed genetic models for the estimation of genetic effects of endosperm characters. But these models cannot yield unbiased estimates of the different effects, because linear correlation exists among the genetic parameters. And these methods cannot estimate the genetic variance and covariance components. Therefore, further information on other genetic properties of quality traits, such as heritability, genetic correlation and selection response cannot be obtained. Furthermore, the above models cannot analyze genotype \times environment interactions in quality traits. Zhu & Weir (1994b) and Zhu (1996) recently proposed a series of models for quantitative traits controlled by triploid endosperm nuclear genes, maternal plant nuclear genes and cytoplasmic genes. These models can be used for the estimation of variance and covariance components and genotype \times environment interaction effects of different genetic systems.

This study investigated the inheritance of amylose content, alkali digestion value and gel consistency in *indica-japonica* crosses of rice, using genetic model with genotype \times environment interactions for triploid endosperm developed by Zhu (1996). The objectives were to (1) estimate genetic and genotype \times environment variances and covariances for deriving statistics, such as heritability, and (2) determine the relative importance of direct genetic effects, maternal genetic effects and cytoplasmic effects in the genetic variations of the three quality characters.

Table 1. Parental varieties and mean values for quality characters

Parental varieties	Amylose content (%)	Gel consistency (mm)	Alkali digestion value
Peiai64s [‡]	22.8	28.4	2.3
3168s [‡]	24.5	51.3	2.8
T1950	18.6	69.0	6.1
V1-70	15.4	68.5	5.6
Suxuan	19.6	74.0	6.5
H9304-1	13.7	79.8	4.2

[‡] Photo-sensitive genic male sterile (PGMS) lines.

Materials and methods

Plant material

Two *indica* photo-sensitive genic male sterile (PGMS) lines (Peiai64s, 3168s) were used as maternal parents and four *japonica* varieties (T1950, V1-70, Suxuan and H9304-1) were used as paternal parents in crossing. The grain quality characteristics of the parents are presented in Table 1. Crossed (F₁) and selfed-seeds were obtained from the same plants. Individuals of these F₁s and selfed parents were grown at two locations (Lianyungang city in Jiangsu province and Linsui county in Hainan province) during 1994 and 1995. Seeds of parents, F₁'s and F₂'s were obtained by self/cross-pollination from entries in two replicates with randomized complete block design.

Trait evaluation

The seeds obtained were evaluated for amylose content, alkali digestion value and gel consistency. Amylose content was estimated using the methods developed by Juliano (1971). The analysis was repeated two times. Alkali digestion value was estimated by use of the alkali digestion test and spreading scores of Little et al. (1958). There were two samples for each replicate. Test was conducted based on 30 grains per sample. Gel consistency determinations were made in duplicate using the procedure outlined by Cagampang et al. (1973).

Statistical analysis

The genetic model for quantitative traits of triploid endosperm developed by Zhu (1996) was used for the

analysis of inheritance. The model used for the analysis is

$$Y_{hijkl} = \mu + E_h + G_{ijk} + GE_{hijk} + B_{l(h)} + e_{hijkl}$$

where Y_{hijkl} = the phenotypic mean of the k th mating type of the cross of maternal parent i and paternal parent j in the l th block within the h th location; μ = population mean; E_h = the environment effect at location h ; G_{ijk} = the total genetic effect; GE_{hijk} = the total genotype \times environment effect; $B_{l(h)}$ = the effect of l th block within location h ; e_{hijkl} = the residual error.

The partitioning of genetic effect G_{ijk} and genotype \times environment interaction effect GE_{hijk} depends on specific genetic entry. In this study, seed materials of three generations were used, hence the components of the genetic and genotype \times environment effects are as follows:

For parent P_i ($k = 0$):

$$\begin{aligned} G_{ii0} &= 3A_i + 3D_{ii} + C_i + 2Am_i \\ &\quad + Dm_{ii} \\ GE_{hii0} &= 3AE_{hi} + 3DE_{hii} + CE_{hi} + 2AmE_{hi} \\ &\quad + DmE_{hii} \end{aligned}$$

For F_{1ij} ($P_i \times P_j$) ($k = 1$):

$$\begin{aligned} G_{ij1} &= 2A_i + A_j + D_{ii} + 2D_{ij} + C_i \\ &\quad + 2Am_i + Dm_{ii} \\ GE_{hij1} &= 2AE_{hi} + AE_{hj} + DE_{hii} + 2DE_{hij} \\ &\quad + CE_{hi} + 2AmE_{hi} + DmE_{hii} \end{aligned}$$

For F_{2ij} ($k = 2$):

$$\begin{aligned} G_{ij2} &= 1.5A_i + 1.5A_j + D_{ii} + D_{jj} + D_{ij} \\ &\quad + C_i + Am_i + Am_j + Dm_{ij} \\ GE_{hij2} &= 1.5AE_{hi} + 1.5AE_{hj} + DE_{hii} + DE_{hjj} \\ &\quad + DE_{hij} + CE_{hi} + AmE_{hi} + AmE_{hj} \\ &\quad + DmE_{hij} \end{aligned}$$

where, A_i is the direct additive effect of endosperm genes from parent i ; D_{ij} is the direct dominance effect of endosperm genes from parent i and j ; C_i is

the cytoplasm effect of parent i ; Am_i is the maternal additive effect of plant nuclear genes from parent i ; Dm_{ij} is the maternal dominance effect of plant nuclear genes from parent i and j ; AE_{hi} is the $A_i \times E_h$ interaction effect; DE_{hij} is the $D_{ij} \times E_h$ interaction effect; CE_{hi} is the $C_i \times E_h$ interaction effect; AmE_{hi} is the $Am_i \times E_h$ interaction effect; DmE_{hij} is the $Dm_{ij} \times E_h$ interaction effect. These are random effects, with variances σ_A^2 , σ_D^2 , σ_C^2 , σ_{Am}^2 , σ_{Dm}^2 , σ_{AE}^2 , σ_{DE}^2 , σ_{CE}^2 , σ_{AmE}^2 , σ_{DmE}^2 , respectively. As two thirds of the endosperm genes come from the maternal plant, the direct genetic effects are correlated with the maternal genetic effects, with covariance components $Cov(A, Am) = \sigma_{A.Am}$ and $Cov(D, Dm) = \sigma_{D.Dm}$, which are the covariance between the direct and maternal additive effects, and that between the direct and maternal dominance effects, respectively. Similarly, the direct genotype \times environment effects are correlated with the maternal genotype \times environment effects, with covariance components $Cov(AE, AmE) = \sigma_{AE.AmE}$ and $Cov(DE, DmE) = \sigma_{DE.DmE}$.

Variance and covariance components were estimated by MINQUE (0/1) method (Zhu & Weir, 1994a), and then the heritability components were calculated. For the model of seed traits in this study, the phenotypic variance V_P can be partitioned as

$$\begin{aligned} V_P &= (V_A + V_D) + V_C + (V_{Am} + V_{Dm}) \\ &\quad + (V_{AE} + V_{DE}) + V_{CE} + (V_{AmE} + V_{DmE}) \\ &\quad + 2(C_{A.Am} + C_{D.Dm}) + 2(C_{AE.AmE} \\ &\quad + C_{DE.DmE}) + V_e \end{aligned}$$

where, $V_A = 4.5\sigma_A^2$ is the direct additive variance; $V_D = 3\sigma_D^2$ is the direct dominance variance; $V_C = \sigma_C^2$ is the cytoplasm variance; $V_{Am} = 2\sigma_{Am}^2$ is the maternal additive variance; $V_{Dm} = \sigma_{Dm}^2$ is the maternal dominance variance; $V_{AE} = 4.5\sigma_{AE}^2$ is the direct additive \times environment interaction variance; $V_{DE} = 3\sigma_{DE}^2$ is the direct dominance \times environment interaction variance; $V_{CE} = \sigma_{CE}^2$ is the cytoplasm \times environment interaction variance; $V_{AmE} = 2\sigma_{AmE}^2$ is the maternal additive \times environment interaction variance; $V_{DmE} = \sigma_{DmE}^2$ is the maternal dominance \times environment interaction variance; $C_{A.Am} = 3\sigma_{A.Am}$ is the covariance between the direct and maternal additive effects; $C_{D.Dm} = \sigma_{D.Dm}$ is the covariance between the direct and maternal dominance effects; $C_{AE.AmE} = 3\sigma_{AE.AmE}$ is the covariance between the direct and maternal additive \times environment effects; $C_{DE.DmE} =$

$\sigma_{DE.DmE}$ is the covariance between the direct and maternal dominance \times environment effects; and $V_e = \sigma_e^2$ is the residual variance. Components of the total heritabilities ($h^2 = h_O^2 + h_C^2 + h_M^2 + h_{OE}^2 + h_{CE}^2 + h_{ME}^2$) were estimated by the following method:

$$\begin{aligned} h_O^2 &= (V_A + C_{A.Am})/V_P, h_C^2 = V_C/V_P, h_M^2 = \\ & (V_{Am} + C_{A.Am})/V_P \\ h_{OE}^2 &= (V_{AE} + C_{AE.AmE})/V_P, \\ h_{CE}^2 &= V_{CE}/V_P, \\ h_{ME}^2 &= (V_{AmE} + C_{AE.AmE})/V_P \end{aligned}$$

where, h_O^2 is the direct component of heritability; h_C^2 is the cytoplasm component of heritability; h_M^2 is the maternal component of heritability; h_{OE}^2 is the direct \times environment component of heritability; h_{CE}^2 is the cytoplasmic \times environment component of heritability, h_{ME}^2 is the maternal \times environment component of heritability.

Genetic effects were predicted by the adjusted unbiased prediction (AUP) method (Zhu & Weir, 1996). The potential value of parental lines were then evaluated, and the standardized direction index of dominance effects were calculated as

$$\Delta = - \sum_{i=1}^n D_{ii} / \sqrt{n\sigma_D^2}$$

which can be used for the prediction of heterosis (Zhu & Weir, 1996).

Standard errors of the statistics were obtained by the jackknife procedures (Miller, 1974), and t -tests were performed for testing null hypothesis of zero parameters.

Results

Genetic variance and covariance components analysis

Significant variances were observed for the three characters, indicating the importance of both direct and maternal genetic effects (Table 2). The variance components indicated a preponderance of both the direct and maternal additive effects for amylose content and gel consistency, and the direct additive effects for alkali digestion value. For amylose content and gel

Table 2. Estimates of genetic variances and covariances of cooking quality characters

Parameters	Amylose content	Gel consistency	Alkali digestion value
V_A	56.49**	2297.83**	7.27**
V_D	8.27**	693.32**	0.96**
V_C	0.00	486.89**	0.00
V_{Am}	85.46**	6401.04**	0.00
V_{Dm}	3.78**	434.59**	0.77**
$C_{A.Am}$	-16.45**	1220.32**	0.00
$C_{D.Dm}$	4.39**	-0.08	-0.94**
V_{AE}	0.00	0.00	0.00
V_{DE}	11.52**	538.35**	1.92**
V_{CE}	10.66**	0.00	1.57**
V_{AmE}	0.00	0.00	0.00
V_{DmE}	8.31**	417.80**	0.57**
$C_{AE.AmE}$	0.00	0.00	0.00
$C_{DE.DmE}$	-0.04	-45.52*	1.37**
V_e	0.78	24.30*	0.02

** and * indicate significant at the 0.01 and 0.05 levels, respectively.

consistency, the maternal additive variance (V_{Am}) was larger than the direct additive variance (V_A). Dominance (direct and maternal) variances were significant for the three traits, but cytoplasm variance was only significant for gel consistency. Estimates of $C_{A.Am}$, the covariance between direct and maternal additive effects, were also highly significant for amylose content and gel consistency; and estimates of $C_{D.Dm}$, the covariance of direct and maternal dominance effects were significant for amylose content and alkali digestion value. For the three characters, the variances of additive (direct and maternal) \times environment interaction effects and the covariance of additive \times environment effects were not significant, but the variances of dominance (direct and maternal) \times environment interaction effects were highly significant. The covariance of dominance \times environment effects were significant for gel consistency and alkali digestion value, and the cytoplasm \times environment variances were highly significant for amylose content and alkali digestion value.

The variance of residual error of gel consistency was significant, implying that there might exist other factors (such as epistasis) in the genetic control of this trait.

Table 3. Heritabilities of cooking quality characters in *indica-japonica* crosses

Parameters [†]	Amylose content	Gel consistency	Alkali digestion value
h^2_O	0.25**	0.26**	0.52**
h^2_C	0.00	0.04**	0.00
h^2_M	0.43**	0.56**	0.00
h^2_{OE}	0.00	0.00	0.00
h^2_{CE}	0.07	0.00	0.11**
h^2_{ME}	0.00	0.00	0.00

Table 4. Directions of dominant gene effects for cooking quality characters in *indica-japonica* crosses

Parameters [†]	Amylose content	Gel consistency	Alkali digestion value
Δ_O	-0.14*	0.07	-2.04**
Δ_M	-0.41*	0.78*	-0.48*
Δ_{OE}	-0.78*	0.23*	-0.29*
Δ_{ME}	0.00	0.66**	-0.82**

[†] Δ_O = Direct dominance, Δ_M = Maternal dominance, Δ_{OE} = Direct dominance \times environment, Δ_{ME} = Maternal dominance \times environment.

Heritabilities

Heritability estimates are presented in Table 3. The total heritability consists of the sum of general and interactive heritability component each can be further partitioned in terms of the direct, maternal and cytoplasmic components.

Heritabilities were mainly composed of general components for the three traits, indicating that selections for these traits would be generally effective for various environments. For amylose content and gel consistency, the estimates of the maternal heritability component were more important than those of the direct heritability component, therefore, selection could be effectively performed based on the maternal plant. For alkali digestion value, only the general direct and the interactive cytoplasmic heritability components were significant, indicating that this trait could be selected based on single seed performance and attention should be paid to the influence of cytoplasm in specific environments.

Direction of dominance effects

In amylose content, estimates of all the significant direction indices of dominance effects (Δ_O , Δ_M , and Δ_{OE}) were negative (Table 4). In gel consistency, estimates of all the significant direction indices of dominance effects (Δ_M , Δ_{OE} and Δ_{ME}) were positive. The direction indices of dominance effects for alkali digestion value were negative, indicating that lower alkali digestion value would be dominant over higher alkali digestion value. The preponderance of direct dominance in alkali digestion value indicated that parents with similar alkali digestion value should be used in hybrid rice breeding to avoid severe segregation of this trait in the F_2 seeds caused by direct heterosis.

For the three traits, general dominance effects (including direct and maternal dominance effects) had the same direction as their respective interaction effect (Table 4). For example, Δ_O and Δ_{OE} were both negative for amylose content, Δ_O and Δ_{OE} , as well as Δ_M and Δ_{ME} were positive for gel consistency, but negative for alkali digestion value. This implied that environmental factors would affect the expression of dominant genes without changing their direction.

Evaluation of genetic effects in parents

The two *indica* PGMS lines (Peiai64s, 3168s) had significant positive direct and maternal additive effects for amylose content, negative direct and maternal additive effects for gel consistency, and negative direct additive effects for alkali digestion value (Table 5). Therefore, these two lines were not suitable for a breeding project aimed at improving the cooking quality of *indica-japonica* hybrids. Among the four *japonica* parents, V1-70 and H9304-1 exhibited negative direct and maternal additive effects for amylose content; T1950 and Suxuan exhibited positive direct and maternal additive effects for gel consistency and positive direct additive effects for alkali digestion value. Therefore V1-70 and H9304-1 might be used to lower amylose content; T1950 and Suxuan might be used to get higher alkali digestion value (lower gelatinization temperature) and softer gel consistency.

Discussion

Indica-japonica hybridization is an important approach for developing superior performing hybrids.

Table 5. Predicted genetic effects of cooking quality characters in parents

Traits	Effects [†]	Parental varieties [‡]					
		P ₁	P ₂	P ₃	P ₄	P ₅	P ₆
Amylose content	A	6.37**	12.51**	-4.27**	-3.31**	-5.69**	-5.60**
	Am	10.01**	0.72**	12.04**	-19.86*	3.69*	-6.59**
Gel consistency	A	-66.40*	-80.05*	46.89*	-9.48**	41.22*	55.82*
	Am	-26.52**	-33.69**	16.22**	30.73**	14.64**	-19.38**
Alkali digestion value	A	-2.94**	-2.47**	1.89**	2.29**	3.11**	-1.88**

[†] A = direct additive effect, Am = maternal additive effect.

[‡] P₁~P₆ represented Peiai64s, 3168s, T1950, V1-70, Suxuan and H9304-1 respectively.

Whereas information about the inheritance of the quality characters in *indica-japonica* crosses is scanty. Thus, estimates of genetic and genotype \times environment interaction parameters for quality characters are useful to developing selection plans that optimize available resources derived from *indica-japonica* crosses. The result of this study revealed that the genetic control of cooking quality characters in *indica-japonica* hybrids involved the direct genetic effects of endosperm genes, the maternal genetic effects, and the cytoplasm effects. In summary, direct and maternal additive effects contributed much to the genetic variances of the three cooking quality characters. Therefore, selection for these traits would be effective in progenies of *indica-japonica* crosses.

Roach & Wulff (1987) considered three different effects as maternal effects: cytoplasmic genetic, endosperm nuclear and maternal phenotypic effects. This may increase the complexity of the interpretation and design of genetic studies for seed traits. For the cooking quality characters in the present study, maternal effects are defined as the genetic effects on seed traits of the nuclear genes of the maternal plant, which bear the seeds. The dosage effects of the endosperm nuclear genes in Roach & Wulff's (1987) can be regarded as the direct additive genetic effects of the seed. The cooking quality characters either pertain to the major constituents of rice endosperm (e.g., amylose content), or are associated with the physicochemical characteristics of starch in the endosperm (e.g., gel consistency and alkali digestion value). Therefore, it is reasonable that they are under the control of nuclear genes of the endosperm. Whereas, the development of endosperm depends on the sink capacity and the assimilates supplied by maternal plants, and the filling rate is controlled by maternal genotypes. Therefore, it can be expected that maternal genetic effects be also involved in the genetic control of cooking quality characters.

Cytoplasm influences could be useful for plant breeding, even when the effects come from specific nicking of cytoplasm and nuclear genomes. In our study, only 4% of the variation for gel consistency can be attributed to cytoplasmic effect, 7% for amylose content and 11% for alkali digestion value can be attributed to cytoplasm \times environment interaction effects (Tables 2 and 3). This indicated that cytoplasmic effect was not very important for amylose content and alkali digestion value, but might be rather important for gel consistency in certain environments.

The existence of interactions between genotypes and environments has long been recognized. But the observed components of genotype \times environment interactions could not be considered in terms of the parameters of biometrical genetics (Freeman, 1973). The results of this study showed that genetic parameters were influenced by genotype \times environment interactions. The direct additive \times environment variances and the maternal additive \times environment variances were nonsignificant for all the three traits. This indicated that the additive effects were comparatively stable over environments, hence selection for cooking quality traits in *indica-japonica* crosses could be effectively performed in various environments. The genotype \times environment interactions for cooking quality characters were operated mainly via dominance (including direct and maternal dominance) effects. Therefore heterosis of these traits might vary with environments. These results indicated that the partitioning of genotype \times environment interactions of the quality traits into different components in terms of the different genetic effects was significant for the prediction of the usefulness of these traits in a breeding program.

Acknowledgement

This work was supported in part by The Trans-Century Training Program Foundation for Outstanding Individuals in Science and Technology of the State Education Commission of China.

References

- Bollich, C.N. & B.D. Webb, 1973. Inheritance of amylose in two hybrid populations of rice. *Cereal Chem* 50: 631–636.
- Cagampang, G.B., C.M. Perez & B.O. Juliano, 1973. A gel consistency test for eating quality of rice. *J Sci Food Agr* 24: 1589–1594.
- Chang, W.L. & W.Y. Li, 1981. Inheritance of amylose content and gel consistency in rice. *Bot Bull Of Academia Sinica* 22: 35–47.
- Foolad, M.R. & R.A. Jones, 1992. Models to estimate maternally controlled genetic variation in quantitative seed characters. *Theor Appl Genet* 83: 360–366.
- Freeman, G.H., 1973. Statistical methods for the analysis of genotype-environment interactions. *Heredity* 31(3): 339–354.
- Heda, G.D. & G.M. Reddy, 1986. Studies on the inheritance of amylose content and gelatinization temperature in rice (*Oryza sativa* L.). *Genet Agr* 40: 1–8.
- Juliano, B.O., 1971. A simplified assay for milled rice amylose. *Cereal Sci Today* 16: 334–336, 338, 360.
- Kumar, I. & G.S. Khush, 1986. Genetics of amylose content in rice (*Oryza sativa* L.). *J Genet* 65: 1–11.
- Kumar, I. & G.S. Khush, 1987. Genetic analysis of different amylose levels in rice. *Crop Sci* 27: 1167–1172.
- Khush, G.S., C.M. Paule & N.M. De La Cruz, 1979. Rice grain quality evaluation and improvement at IRRI. In: Proc. of the workshop on chemical aspects of rice grain quality, pp. 21–31. IRRI, Los Banos, Philippines.
- Little, R.R., G.B. Hilder & E.H. Dawson, 1958. Differential effect of dilute alkali on 25 varieties of milled white rice. *Cereal Chem* 35: 111–126.
- McKenzie, K.S. & J.N. Rutger, 1983. Genetic analysis of amylose content, alkali spreading score, and grain dimensions in rice. *Crop Sci* 23: 306–319.
- Miller, R.G., 1974. The jackknife – a review. *Biometrika* 61: 1–15.
- Pooni, H.S., I. Kumar & G.S. Khush, 1992. A comprehensive model for disomically inherited metrical traits expressed in triploid tissues. *Heredity* 69: 166–174.
- Pooni, H.S., I. Kumar & G.S. Khush, 1993. Genetical control of amylose content in selected crosses of *indica* rice. *Heredity* 70: 269–280.
- Roach, D.A. & R.D. Wulff, 1987. Maternal effects in plants. *Ann Rev Ecol Syst* 18: 209–235.
- Singh, N.B. & H.G. Singh, 1977. Heterosis and combining ability for quality components in rice. *Indian J Genet Pl Breed* 37: 347–352.
- Stansel, J.W., 1966. The influence of heredity and environment on endosperm characteristics of rice (*Oryza sativa* L.). *Dissert Abstr* 27: 488.
- Tang, S.X., G.S. Khush & B.O. Juliano, 1989. Diallel analysis of gel consistency in rice (*O. sativa* L.). *SABRAO J* 21: 135–142.
- Zaman, F.U., E.A. Siddiq & A.B. Phasod, 1985. Genetical analysis of gel consistency in rice (*Oryza sativa* L.). *Indian J Genet Plant Breed* 45: 111–118.
- Zhu, J., 1996. Analysis methods for seed models with genotype × environment interactions. *Chinese J Genet* 23: 56–68.
- Zhu, J. & B.S. Weir, 1994a. Analysis of cytoplasmic and maternal effects. I. A genetic model for diploid plant and animals. *Theor Appl Genet* 89: 153–159.
- Zhu, J. & B.S. Weir, 1994b. Analysis of cytoplasmic and maternal effects. II. Genetic models for triploid endosperms. *Theor Appl Genet* 89: 160–166.
- Zhu, J. & B.S. Weir, 1996. Diallel Analysis for Sex-linked and Maternal Effects. *Theor Appl Genet* 92: 1–9.