Plant Breeding

Vol. 118 (6), 465–584 December 1999

Contents

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Blackwell Science

Plant Breeding **118**, 574– 576 (1999)

ISSN 0179-9541

Short Communication

Analysis of embryo, endosperm, cytoplasmic and maternal effects for heterosis of protein and lysine content in *indica* hybrid rice

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Received March 10, 1999/Accepted July 2, 1999
Communicated by W. E. Weber

Abstract

The heterosis controlled by genetic main effects and genotype × environment (GE) interaction effects for protein content and lysine content traits of *indica* hybrid rice, *Oryza sativa* L., was studied by using a genetic model for quantitative traits of triploid endosperm. The experiment was conducted over 2 years in a factorial design that included nine cytoplasmic male-sterile lines as females and five restorer lines as males. It was revealed that heterosis of protein content and lysine content were simultaneously controlled by genetic main effects and GE interaction effects. Maternal general heterosis and maternal interaction heterosis were observed. Embryo heterosis or cytoplasm heterosis for lysine content and endosperm heterosis for protein content were more important in general heterosis. Embryo interaction heterosis and cytoplasm interaction heterosis were more important for protein content, but endosperm heterosis was only important for lysine content in GE interaction heterosis. It was shown that some *indica* hybrid crosses had significant positive heterosis for protein content. Negative heterosis for lysine content was observed in most hybrid crosses.

Key words: *Oryza sativa* — hybrid rice — genetic main effects genotype × environment interaction effects — heterosis — nutrient quality traits

Physicochemical characteristics and nutrient composition are the important factors which determine rice quality, its acceptability to rice-consuming people. After analysing the heterosis of protein content by using 21 crosses, Singh et al. (1977) found that the average heterosis was −3.38% (−24.25–26.33%). Liu et al. (1990) observed that five crosses had positive heterosis for the protein content among 17 *indica* hybrid crosses. Kaw and Dela Cruz (1991) found that the average heterosis over the midparent for 102 F_1 hybrids was 5.2% for amylose content, −1.1% for gelatinization temperature and −23.0% for gel consistency in the *indica* × *indica* crosses, respectively. Heterosis of rice nutrient quality traits can be simultaneously affected by endospermic, cytoplasmic and maternal effects (Shi et al. 1996a, b). Since the variation for gene expression will be observed in different environments, the performance of heterosis for quantitative traits is also affected by genotype × environment (GE) interaction effects. Chauhan et al. (1992) observed that traits such as amylose content, milling recovery, water uptake and kernel elongation of rice behaved differently across environments. Shi et al. (1997) also observed that heterosis of amylose content in *indica* hybrid rice was affected by endospermic, cytoplasmic and maternal genetic effects, as well as GE interaction effects. Genetic main effects and GE interaction effects due to diploid embryo genes could also affect the performance of nutrient traits of rice (Shi et al. 1999a, b).

The objective of this study was to evaluate the genetic main effects of embryo, endosperm, cytoplasm and maternal plant, as well as their GE interaction effects, on the heterosis of nutrient quality traits of *indica* hybrid rice.

The experiment was conducted in a factorial design with 14 lines of *Oryza sativa* L. Nine cytoplasmic male-sterile (A) lines and their maintainer lines (B) and five restorer lines (R) were used. Crosses of F_1 (A × R) and reciprocal RF_1 (R × B) were obtained in 1994. Seedlings of parents, F_1 and RF_1 were planted in the field of the experimental farm at Zhejiang Agricultural University, China, in 1995 and 1996. Seed samples of parents, F_2 from F_1 (A × R) plants and RF_2 from RF_1 (R × B) plants were harvested at maturity. The F_1 (A × R) and BC_1 (A × F_1) seeds were obtained by crossing. Quantitative traits analysed were protein content (%) determined by Kjeldahl extraction methods (South-west Agric. University and China South Agric. University 1992) and lysine content (%) determined by colorimetric method (Shandong Agric. University and North-west Agric. University 1980), and measured with three replications for each sample of parents, F_1, F_2, RF_2 and BC_1.

Analysis of the genetic main effects and their GE interaction effects of embryo, endosperm, cytoplasm and maternal plant was undertaken by using the genetic model for quantitative traits of seed in cereal crops (Zhu 1997). This model is derived by combining embryo effects in a diploid seed model (Zhu and Weir 1994a) with other genetic effects in a triploid endosperm model (Zhu and Weir 1994b) with extension including GE interaction effects (Zhu 1996). The adjusted unbiased prediction method (AUP method) (Zhu 1993, Zhu and Weir 1996) was used to predict genetic main effects and GE interaction effects, from which heterosis over the mean of the parents was calculated for the seed of F_2. The partitioning of total heterosis is as follows:

$$H = H_G + H_{GE} = (H_{Go} + H_{Ge} + H_c + H_{Gm}) + (H_{GoE} + H_{GeE} + H_{CE} + H_{GmE})$$

where H_G = general heterosis controlled by genetic main effects, H_{GE} = interaction heterosis controlled by GE interaction effects, $H_{Go} = 0.5[Do_{ij} - 0.5(Do_{ii} + Do_{jj})]$ is embryo general heterosis, $H_{Ge} = De_{ij} - 0.5(De_{ii} + De_{jj})$ is endosperm general heterosis, $H_C = 0.5(C_i - C_j)$ is cytoplasm general heterosis, $H_{Gm} = Dm_{ij} - 0.5(Dm_{ii} + Dm_{jj})$ is maternal general heterosis, $H_{GoE} = 0.5[DoE_{hij} - 0.5(DoE_{hii} + DoE_{hjj})]$ is embryo interaction heterosis, $H_{GeE} = DcE_{ij} - 0.5(DeE_{ii} + DeE_{jj})$ is

Table 1: Heterosis[1] for protein content and lysine content of F_2 seed in 45 *indica* hybrid crosses

Parameter	H_G		H_{GE} in 1995		H_{GE} in 1996	
	Mean (range)	NCS[2]	Mean (range)	NCS	Mean (range)	NCS
Protein content						
Total heterosis (H_G or H_{GE})	0.033 (–0.153–0.193)	28	0.120 (–0.312–0.410)	14	–0.092 (–0.413–0.523)	3
Embryo heterosis (H_{Go} or H_{GoE})			0.017 (–0.320–0.335)	16	0.073 (–0.144–0.408)	11
Endosperm heterosis (H_{Ge} or H_{GeE})	0.071 (–0.102 0.229)	39	—	—	—	—
Cytoplasmic heterosis (H_C or H_{CE})	—		0.077 (–0.129–0.268)	7	–0.118 (–0.328–0.111)	4
Maternal heterosis (H_{Gm} or H_{GmE})	–0.038 (–0.157–0.141)	39	0.026 (–0.143–0.180)	15	–0.046 (–0.249–0.279)	12
Lysine content						
Total heterosis (H_G or H_{GE})	–0.238 (–0.700–0.172)	32	0.089 (0.549 0.277)	17	–0.027 (–0.446 0.406)	3
Embryo heterosis (H_{Go} or H_{GoE})	–0.023 (–0.213–0.231)	28		—	—	—
Endosperm heterosis (H_{Ge} or H_{GeE})	—	—	0.000 (0.503 0.329)	7	–0.025 (–0.341–0.362)	7
Cytoplasmic heterosis (H_C or H_{CE})	–0.180 (–0.450 to –0.011)	34		—	—	—
Maternal heterosis (H_{Gm} or H_{GmE})	–0.036 (–0.198–0.111)	13	–0.089 (–0.479–0.192)	16	–0.002 (–0.399–0.463)	14

[1] H_G = Genetic main heterosis, H_{GE} = GE interaction heterosis, H_{Go} = embryo heterosis, H_{Ge} = endosperm heterosis, H_C = cytoplasm heterosis, H_{Gm} = maternal heterosis, H_{GoE} = embryo interaction heterosis, H_{GmE} = endosperm interaction heterosis, H_C = cytoplasmic interaction heterosis, H_{GmE} = maternal interaction heterosis.
[2] NCS = Number of crosses with a significant positive and/or negative value at P = 0.05.

endosperm interaction heterosis, $H_{CE} = 0.5(CE_{hi} - CE_{hj})$ is cytoplasm interaction heterosis and $H_{GmE} = DmE_{hij} - 0.5(DmE_{hi} + DmE_{hjj})$ maternal interaction heterosis.

The Jack-knife technique (Miller 1974, Zhu and Weir 1994a,b) was applied by sampling generation means of entries for estimating the standard errors of predicted heterosis. All data were analysed by programs written in C.

Heterosis for protein content of rice

The results in Table 1 showed that heterosis for protein content of *indica* hybrid rice was affected by embryo, endosperm, cytoplasm and maternal effects, as well as their GE interaction effects. The average of total general heterosis was about 0.033 for 45 hybrids, among which 17 hybrids had significantly positive H_G, with an average of 0.114 (0.033–0.193) and 11 hybrids had significantly negative H_G with an average of −0.077 (−0.153 to −0.012). The components of general heterosis for protein content was mainly contributed by endosperm general heterosis ($H_{Ge} \approx 0.071$) and maternal general heterosis ($H_{Gm} \approx -0.038$). For the components of general heterosis, significantly positive heterosis was detected for H_{Ge} of 35 hybrids ($H_{Ge} \approx 0.094$, range 0.020–0.229), and H_{Gm} of 10 hybrids ($H_{Gm} \approx 0.047$, range 0.009–0.141).

The total GE interaction heterosis (H_{GE}) was 0.120 in 1995 but −0.092 in 1996. Embryo interaction heterosis (H_{GoE}), cytoplasm interaction heterosis (H_{CE}) and maternal interaction heterosis (H_{GmE}) were the major components for the total GE interaction heterosis observed. Although H_{GoE} was found, on average, to be positive in both years (0.017 in 1995 and 0.073 in 1996), H_{CE} and H_{GmE} tended to be positive in 1995 ($H_{CE} \approx 0.077$ and $H_{GmE} \approx 0.026$), but negative in 1996 ($H_{CE} \approx -0.118$ and $H_{GmE} \approx -0.046$). Significantly positive GE interaction heterosis was observed in 1995 for H_{GE} of nine hybrids ($H_{GE} \approx 0.199$, range 0.161–0.249), H_{GoE} of 10 hybrids ($H_{GoE} \approx 0.081$, range 0.002–0.185), H_{CE} of three hybrids ($H_{CE} \approx 0.042$, range 0.007–0.075), and H_{GmE} of 10 hybrids ($H_{GmE} \approx 0.069$, range 0.013–0.138).

Since the total heterosis in one environment was contributed by $H_G + H_{GE}$, the heterosis of most hybrids in 1995 could increase protein content and was better than that of 1996.

Heterosis for lysine content of rice

It was suggested, by the negative general heterosis ($H_G \approx -0.238$) and interaction heterosis ($H_{GE} \approx -0.089$ in 1995 and −0.027 in 1996), that hybrids tended to have lower lysine content than their parents in *indica* rice (Table 1).

Thirty-one hybrids were significantly negative in general heterosis $H_G \approx -0.326$ (−0.700 to −0.060). The embryo general heterosis of 45 hybrids was, on average, negative ($H_{Go} \approx -0.023$), among which 15 hybrids had negative heterosis ($H_{Go} \approx -0.118$, range −0.213 to −0.029) and 13 hybrids had positive heterosis ($H_{Go} \approx 0.105$, range 0.019–0.231). However, significant negative cytoplasm general heterosis (H_C) was observed only for 34 hybrids studied, with a mean of −0.226 and range −0.450 to −0.088. The maternal general heterosis (H_{Gm}) of 45 hybrids was, on average, negative ($H_{Gm} \approx -0.036$), among which seven hybrids had negative heterosis ($H_{Gm} \approx -0.070$, range −0.174 to −0.018) and six hybrids had positive heterosis ($H_{Gm} \approx 0.048$, range 0.015–0.084).

There was no embryo or cytoplasmic interaction heterosis for lysine content of rice, since there was no embryo dominant interaction effect or cytoplasmic interaction effect in this experiment. Heterosis relating to the endosperm genes was mainly controlled by GE interaction effects for lysine content. The endosperm interaction heterosis was lower in 1996 ($H_{GeE} \approx$

-0.025) than in 1995 ($H_{GmE} \approx 0.000$). The maternal interaction heterosis tended to be negative for lysine content ($H_{GmE} \approx -0.089$ in 1995 and $H_{GmE} \approx -0.002$ in 1996).

Higher protein content and a better balance among the various amino acids in the protein of rice, especially for some essential amino acids such as lysine content, are preferred when improving the nutrient quality of hybrid rice. Since the performance of some nutrient traits in F_2 seeds from F_1 plants could be affected by genetic effects of embryo, endosperm, cytoplasm and maternal plant, as well as their GE interaction effects (Shi et al. 1999a, b), the heterosis for these quality traits could also be partitioned into components of general heterosis arising from genetic main effects, and GE interaction heterosis arising from GE interaction effects. General heterosis is the performance of heterosis expected across different environments, whereas interaction heterosis is the deviation from general heterosis in a specific environment. Heterosis in a specific environment consists of general heterosis and interaction heterosis in that environment.

In general, if general heterosis is the major component and/or interaction heterosis has the same direction as H_G, the total heterosis is expected to be suitable for different environments for improving quality traits. Therefore, when the general heterosis and interaction heterosis are really important for the quantitative traits studied, experiments should be conducted in different environments (years or locations) because of the different climatic conditions such as illumination, rainfall and temperature. In this experiment, the temperature in June in 1996 was much higher than in 1995. There was considerable rainfall in 1996 and a significant difference in the rainy days between two years at the flowering and seed-filling stages. There were also differences in water and manure management existed in fields between the two years. Therefore, these climatic conditions or cultivation differences could be the cause of different heterosis for protein and lysine content of *indica* hybrids.

The present results indicate that the heteroses of protein and lysine content of *indica* hybrid rice are controlled by genetic main effects and GE interaction effects, especially for maternal effects. In addition to the endosperm, cytoplasm and maternal heteroses and their GE interaction heteroses, one cannot neglect embryo heterosis and embryo interaction heterosis in total heteroses for nutrient quality traits.

Acknowledgements

This work was supported by The Trans-Century Training Programme Foundation for the Talents of the State Education Commission of China, 151 Program for the Talents of Zhejiang Province and the Committee of Science and Technology of Zhejiang Province.

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