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Genetic effects for heading date in *indica-japonica* crosses of rice (*Oryza sativa* L.)

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Abstract

The longer growth period of hybrid is one of the limitations for the utilization of intersubspecific *indica-japonica* heterosis in rice. In this study, three *indica* cytoplasmic male sterile lines and four *japonica* restorer lines with wide compatibility were used as parents to make crosses. The additive and nonadditive genetic effects on heading date were analyzed using an additive-dominance-epistatic model. The results showed that the genetic variation of heading date could be attributed to additive, dominance and additive × additive epistatic effects, with dominance genetic effects being predominant, followed by additive × additive epistatic effects. Analysis of genetic effects showed that the additive genetic effect from R 348 increases heading time, while the additive × additive epistatic effects from Zhensan 97A, R 456 and R 496 reduce heading time. In the progenies of crosses heading time was reduced by dominance genetic effects, whereas it was increased by additive × additive epistatic effects.

Key words: Rice; *indica-japonica* cross, heading date, genetic effect

Introduction

In the field of rice heterosis breeding, many rice researchers have attempted to explore new technological approaches for increasing the yield potential of rice. The most successful attempt to date has been the development of intersubspecific (*indica-japonica*) hybrids [1]. Intersubspecific hybrids exhibit obvious heterosis, but there are certain limitations. One of these limitations is the longer growth period of hybrid. The understanding of the inheritance of growth duration of intersubspecific hybrid is important for the selection of parental lines and for the efficient utilization of intersubspecific heterosis.

The growth duration of rice is composed of three stages, the vegetative growth phase, the reproductive growth stage, and the maturity phase. The reproductive growth stage and maturity phase are relatively stable in different varieties, therefore the growth duration of a rice variety is commonly characterized by heading date, namely, the number of days from sowing to heading [2-7]. But a majority of the reported researches have been limited to intrasubspecific hybrids. Less research has been conducted on the genetic effects of heading date of intersubspecific hybrid rice. Yuan *et al.* [8] studied the combining ability and heritability of heading date in F_1 generation deriving from six *japonica* rice varieties and six *indica* rice varieties. Shen *et al.* [9] examined the performance of heading date for *indica-japonica* F_1 hybrids of five mating types. Zhou *et al.* [10] described the significant super-parent phenomena of heading date in F_1 of intersubspecific hybrids. Further research is needed to elucidate the intricate nature of genetic effects for heading date in *indica-japonica* hybrids.

The present study investigated the inheritance of heading date in *indica-japonica* crosses of rice, using the additive-dominant-epistasis genetic model developed by Zhu [11-12]. The objective was to estimate genetic variances and heritability, and determine the relative importance of additive genetic effect, dominant genetic effect and epistatic effect in the genetic variations of this trait.

Materials and methods

Plant materials and field experiments: Seven rice genotypes, including three *indica* cytoplasmic male sterile lines (Jin 23A, ChangfeiA, Zhengsan 97A) and four *japonica* restorer lines with wide-compatibility (R 348, R 456, R 496, R 525) developed by the Laboratory of Genetics of Hubei University in China were selected for this study. Crosses were made during 2003 at Hubei University. The F_1 generations were grown in the winter nursery at Ninshui county, Hainan province, to produce F_2 seeds. Seeds of F_1s, F_2s and the seven parents were grown at the Plant Genetics Research Institute, Hubei University. Seeds were sown in a randomized block design with three replications.

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Standard cultural practices were followed during the growing season.

Heading date was taken as the number of days after planting to when the head of the main tiller for a plant emerged 2cm from the flag leaf sheath. Data on heading date were collected from 20 sample plants selected randomly from each parent and F_1 hybrid, and from 100 sample plants selected randomly from each F_2 hybrid.

Statistical analysis: The additive-dominance-additive × additive (ADAA) genetic model for quantitative traits developed by Zhu [11-12] was used for the analysis. The genetic model for genetic entry of the *k*th type of generation derived from parents *i* and *j* in the *l*th block is

$$Y_{ijkl} = \mu + G_{ijk} + B_l + e_{ijkl}$$

where Y_{ijkl} = 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; μ = population mean; G_{ijk} = the total genetic effect; B_l = the effect of *l*th block; e_{ijkl} = the residual error.

For parent P_i ($k = 0$):

$$G_{ii0} = 2A_i + D_{ii} + 2AA_{ii}$$

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

$$G_{ij1} = A_i + A_j + D_{ij} + AA_{ii} + AA_{jj} + 2AA_{ij}$$

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

$$G_{ij2} = A_i + A_j + 0.25\ D_{ii} + 0.25\ D_{jj} + 0.5\ D_{ij} + AA_{ii} + AA_{jj} + 2AA_{ij}$$

where A = additive effect, D = dominance effect, AA = additive × additive epistatic effect. These are random effects, with variances σ_A^2, σ_D^2, σ_{AA}^2, respectively.

The phenotypic mean of the genetic model can be expressed by a mixed linear model as

$$y = Xb + U_A e_A + U_D e_D + U_{AA} e_{AA} + e_e = Xb + \sum_{u=1}^{4} U_u e_u$$

with variance-covariance matrix

$$\text{var}(y) = \sigma_A^2 U_A U_A^T + \sigma_D^2 U_D U_D^T + \sigma_{AA}^2 U_{AA} U_{AA}^T + \sigma_e^2 I = \sum_{u=1}^{4} \sigma_u^2 U_u U_u^T.$$

Unbiased estimation of variances were obtained by MINQUE(I) approach [13]. When experimental variances $\left(\sigma_u^2\right)$ are estimated, genetic variance components can be obtained by $V_A = 2\sigma_A^2$, $V_D = \sigma_D^2$, $V_{AA} = 4\sigma_{AA}^2$, $V_e = \sigma_e^2$. The total phenotypic variance is $V_P = V_A + V_D + V_{AA} + V_e$, where V_A is the additive variance, V_D is the dominance variance, V_{AA} is the additive × additive epistatic variance, and V_e is the residual variance. Heritabilities were estimated by the following method [11]:

$$h_B^2 = (V_A + V_D + V_{AA})/V_P,\ h_N^2 = (V_A + V_{AA})/V_P$$

where h_B^2 is the broad sense heritability, h_N^2 is the narrow sense heritability.

Genetic effects were predicted by the adjusted unbiased prediction (AUP) method [14]. The potential value of parental lines was then evaluated. Standard errors of the statistics were obtained by the jackknife procedures [13, 15], and *t*-tests were performed for testing null hypothesis of zero parameters. All the analyses were performed using the software QGA Station 1.0 developed by Chen and Zhu (http://ibi.zju.edu.cn/software/qga/index.htm).

Results and discussion

Mean performance of parents and hybrids for heading date: Mean heading dates for parents and their F_1s and F_2s are presented in Table 1. The mean heading date of the seven parents ranged from 80.3 to 85.6 days. The performance of the F_1S and F_2s differed over crosses. The F_1 and F_2 means for Jin 23A × R 348 and ChangfeiA × R 525 were intermediate between their parents. Positive super-parent heterosis were observed in the F_1 and F_2 of Zhengsan 97A × R 348 and ChangfeiA × R 348, and negative super-parent heterosis were observed in the F_1 and F_2 of Jin 23A × R 456 and Zhengsan 97A × R 525.

Genetic variance components and heritability: Heading date of rice is primarily determined by photosensitivity, thermosensitivity and basic vegetative growth character of a variety, and these characteristics are controlled by various genes. Therefore, the genetic effects of heading date are complicated. Estimates of genetic variance components are presented in Table 2. In the present study, significant additive effects, dominance effects and additive × additive epistasis for heading date were observed in *indica-japonica* crosses of rice. Dominance variance (C_D) was greater than additive variance (V_A) and additive × additive epistatic variance (V_{AA}). Heritability estimates are also presented in Table 2. The estimate of the narrow sense heritability

Table 1. Mean heading date in parents, F_1s and F_2s

Combinations	P_1	P_2	F_1	F_2
Jin 23A × R 348	81.9	85.6	84.9	85.5
Jin 23A × R 456	81.9	82.5	79.5	81.0
Jin 23A × R 496	81.9	82.5	79.6	81.8
Jin 23A × R 525	81.9	85.1	80.5	82.7
Zhengsan 97A × R 348	84.3	85.6	92.8	98.0
Zhengsan 97A × R 456	84.3	82.5	79.2	83.2
Zhengsan 97A × R 496	84.3	82.5	80.8	85.5
Zhengsan 97A × R 525	84.3	85.1	81.6	85.4
ChangfeiA × R 348	80.3	85.6	86.3	89.9
ChangfeiA × R 456	80.3	82.5	80.2	86.3
ChangfeiA × R 496	80.3	82.5	78.7	87.7
ChangfeiA × R 525	80.3	85.1	81.3	84.1

Table 2. Estimates of genetic variance and heritability of heading date in *indica-japonica* crosses of rice

Parameters	Estimates
Additive variance (V_A)	11.426**
Dominance variance (V_D)	45.954**
Additive × additive epistasis variance (V_{AA})	9.870**
Residual variance (V_e)	10.3025**
Phenotypic variance (V_P)	77.553**
Narrow sense heritability (h_N^2)	0.275**
Broad sense heritability (h_B^2).	0.867**

**Significant at $\alpha = 0.01$.

was relatively lower; therefore, selection for heading date might be inefficient in earlier generations. The high value of broad sense heritability suggests that the phenotypic variation of heading date among *indica-japonica* crosses was largely due to the difference of genotypes, indicating that the screen for hybrid with desirable heading date could be carried out effectively based on the phenotype of this trait. Li *et al.* [16] found that the growth duration of intrasubspecific (*indica-indica*) hybrid rice was regulated jointly by additive effect and dominance effect, with higher heritability. But they did not find any epistatic genetic effect for this trait.

Evaluation of genetic effects in parents and hybrid progenies: Table 3 shows the predicted values of additive effects (A_i) and additive × additive epistatic effects (AA_{ii}) of heading date for the 7 parents P_i (i = 1, 2, ..., 7). P_1 ~ P_7 represent Jin 23A, ChangfeiA, Zhengsan 97A, R 348, R 456, R 496 and R 525, respectively. Among the seven parents, significant additive genetic effect was observed in only one parent (parent 4, R 348) for heading date (Table 3). The additive effect of R 348 was positive, increasing heading date by 1.5 days. Significant additive × additive epistatic effects were observed in three parents (parent 3, 5 and 6), and these additive × additive epistatic effects were all negative in their estimates. These results

Table 3. Predicted values of additive and additive × additive genetic effects of heading date In parents

Additive		Additive × additive	
Parameters	Predicted values	Parameters	Predicted values
A_1	−0.96	AA_{11}	−0.68
A_2	0.78	AA_{22}	−1.09
A_3	0.26	AA_{33}	−2.53*
A_4	1.50*	AA_{44}	−0.44
A_5	−0.60	AA_{55}	−1.15*
A_6	−0.21	AA_{66}	−1.81*
A_7	−0.45	AA_{77}	−0.06

*Significant at $\alpha = 0.05$.

indicated that in the *indica-japonica* crosses of the present study, parents influence the heading date of progenies primarily through additive × additive epistatic effects, which reduce the heading date of hybrids. Therefore, the three lines (parent 3, 5 and 6) were suitable for a breeding project aimed at improving the heading date of *indica-japonica* hybrids. Li *et al.* [16] showed that Zhensan 97A had a relatively short growth duration, and dominance effect which could shorten the growth duration of F_1 hybrid derived from it. The result in the present study showed that the additive × additive epistatic genetic effects of Zhensan 97A (parent 3) might shorten the growth duration of hybrid. These results further suggested that Zhensan 97A is a valuable parental line in early breeding of rice.

Table 4 presents the predicted values of dominance effects (D_{ij}) (i, j = 1, 2, ..., 7) and additive × additive epistatic effects (AA_{ij}) (i, j = 1, 2, ..., 7) of heading date for the 12 hybrid combinations. Negative dominance genetic effects were observed in 11 of the 12 *indica-japonica* hybrid combinations. The predicted values of dominance effects for eight hybrid combinations

Table 4. Predicted values for dominance genetic effects (D_{ij}) and additive × additive genetic effects (AA_{ij}) of heading date in hybrid combinations

Dominance		Additive × additive	
Parameters	Predicted values	Parameters	Predicted values
D_{15}	0.11	AA_{15}	0.45
D_{16}	−2.92*	AA_{16}	−1.34*
D_{17}	−3.63	AA_{17}	−0.94
D_{18}	−4.20*	AA_{18}	−0.93
D_{25}	−4.01*	AA_{25}	6.11**
D_{26}	−5.98*	AA_{26}	−1.03
D_{27}	−5.75*	AA_{27}	0.36
D_{28}	−5.48*	AA_{28}	−0.15
D_{35}	−2.31	AA_{35}	2.63*
D_{36}	−8.00*	AA_{36}	1.34
D_{37}	−12.56**	AA_{37}	1.95*
D_{38}	−2.91	AA_{38}	−0.14

*,**Significant at α = 0.05 and 0.01 respectively.

were significantly different from zero. Only one combination showed positive predicted value for dominance effect, but it was not significantly different from zero. Therefore it is concluded that, in *indica-japonica* crosses the function of dominance effect is to shorten the growth duration, that is, to decrease heading date. In the 12 *indica-japonica* hybrid combinations, both positive and negative predicted values were obtained for the additive $\times$ additive epistatic genetic effect of heading date, but most of these predicted values were not statistically significant. Only four combinations have significant additive $\times$ additive epistatic effects, three of which gave positive predicted values, one gave negative predicted value. Moreover, the absolute values of the three positive epistatic effects were larger than that of the negative one. These results suggested that in the progenies of the *indica-japonica* crosses, the function of additive $\times$ additive epistatic genetic effect was to delay the heading date, or to increase the growth duration.

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References

1. **Yuan L. P.** 2002. The second generation of hybrid rice in China. Proceedings of the 20th Session of the International Rice Commission: Sustainable rice production for food security, Bangkok, Thailand, July 23-26, pp. 117-119.
2. **Min S., Shen Z. and Xiong Z.** 1996. Rice Breeding. Agriculture Press of China, Beijing, China: 429-430.
3. **Dwivedi S. L., Rai K. N. and Singh R. B.** 1980. Diallel analysis of heading date in rice (*Oryza sativa* L.). Theor. Appl. Genet., **57**: 43-47.
4. **Yano M., Harushima Y., Nagamura Y., Kurata N., Minobe Y. and Sasaki T.** 1997. Identification of quantitative trait loci controlling heading date in rice using a high density linkage map. Theor. Appl. Genet., **95**: 1025-1032.
5. **Maheswaran M., Huang N., Sreerangasamy S. R. and McCouch R. S.** 2000. Mapping quantitative trait loci associated with days to flowering and photoperiod sensitivity in rice (*Oryza sativa* L.). Molecular Breeding, **6**: 145-155.
6. **Takeuchi Y., Lin S. Y., Sasaki T. and Yano M.** 2003. Fine linkage mapping enables dissection of closely linked quantitative trait loci for seed dormancy and heading in rice. Theor. Appl. Genet., **107**: 1174-1180.
7. **Gu X. Y., Foley M. E. and Chen Z. X.** 2004. A set of three genes regulates photoperiodic responses of flowering in rice (*Oryza sativa* L.). Genetica, **122**: 127-140.
8. **Yuan L.** 1989. Studies on the cross breeding between *indica* and *japonica* rice III. Combing ability and heritability of main characteristics in hybridization between *indica* and *japonica* rice. Acta Agronomica Sinica, **2**: 182-188.
9. **Shen S., Zhang N., Yan J. and Xue Q.** 1996. Performance of morphology and growth season characters in five different types of *indica/japonica* hybrids. Seed, **1**: 4-7.
10. **Zhou Q.** 1999. Study on long-duration transgression of rice inter-subspecific F_1. Hubei Agricultural Sciences, **6**: 3-5.
11. **Zhu J.** 1997. Analysis Methods for Genetic Models. Agricultural Publication House of China, Beijing.
12. **Zhu J.** 2003. Diallel analysis for an additive-dominance-epistasis model with genotype-environment interaction effects. *In*: Kang M. S. (Ed.), Handbook of formulas and software for plant geneticists and breeders. The Haworth Reference Press, New York, pp. 51-66.
13. **Zhu J. and Weir B. S.** 1994. Analysis of cytoplasmic and maternal effects. I. A genetic model for diploid plant and animals. Theor. Appl. Genet., **89**: 153-159.
14. **Zhu J. and Weir B. S.** 1996. Diallel Analysis for Sex-linked and Maternal Effects. Theor. Appl. Genet., **92**: 1-9.
15. **Miller R. G.** 1974. The jackknife — a review. Biometrika, **61**: 1-15.
16. **Li Y., Liang K., Wang X. and Chen Z.** 2003. Genetic analysis of the growth stage in three-line *indica* hybrid rice. Journal of Fujian Agriculture and Forestry University, **1**: 10-14.