

Diallel Analysis of Heading Date in Rice (*Oryza sativa* L.)

S.L. Dwivedi, K.N. Rai and R.B. Singh

Department of Genetics and Plant Breeding, Banaras Hindu University, Varanasi (India)

Summary The genetics of heading date was investigated in an 8×8 diallel set of crosses involving diverse rice cultivars. W_r , V_r graph analysis revealed the presence of a complementary type of non-allelic interaction which apparently affected the position and slope of the regression line such as if there were overdominance. Omission of two interacting parents resulted in a 6×6 subset of diallel crosses from which, as observed in the W_r , V_r graph, the non-allelic interaction had disappeared and the regression line exhibited partial dominance. Estimates of the genetic components of variation were in close conformity with the results obtained from the W_r , V_r graph: the average degree of dominance, as measured by $(H_1/D)^{1/2}$, was in overdominance range in the interacting 8×8 set of diallel crosses whereas it was reduced to partial dominance in the non-interacting 6×6 set of crosses. Further analysis by a standardized deviations graph indicated that earliness was controlled, on the average, by an excess of dominant alleles.

Key words: *Oryza sativa* – Heading date – Diallel – Complementary interaction – Overdominance

Introduction

Breeding for earliness still remains one of the major objectives in rice breeding programmes. Such varieties fit well into multiple cropping systems, and have a natural advantage of drought avoidance in the later part of the crop cycle, particularly in the areas where it is grown under rainfed cultivation. An understanding of the nature and the magnitude of genetic variability for earliness, therefore, becomes an important first step in evolving an effective breeding strategy and in predicting the genetic gain that could be expected for a given set of materials. Diallel cross analysis has been extensively used in the genetic analysis of quantitative characters, particularly in self-pol-

inated crops, for more than two decades. Experimentally, it is a systematic approach, and analytically it offers an overall genetic evaluation of the materials under investigation that would permit the identification, in an early generation, of the crosses of best selection potential (Johnson 1963).

Very limited and conflicting information is available on the inheritance of heading date in rice (Wu 1968; Ranganathan, Menon and Rangasamy 1973; Nancharuiah, Nanda and Chaudhary 1974; Khaleque and Eunus 1975; Ganashan and Whittington 1976). The present investigation was undertaken to characterize the nature and magnitude of genetic variability for earliness in eight diverse rice cultivars.

Materials and Methods

Eight diverse and elite rice cultivars, viz., 'TKM6', 'IR8', 'Sabarmati', 'T(N)1', 'Jaya', 'IET 2923', 'IET 1991' and 'N22', having a wide range of heading dates, were crossed in all possible combinations, excluding reciprocals. The resulting twenty eight F_1 hybrids, along with the corresponding eight parents, were grown in a randomized block design with two replications at the Agricultural Research Farm, Banaras Hindu University, Varanasi, India. A single row of ten plants each constituted the experimental plot. The between row spacing was 30 cm and plant to plant spacing within the row was 15 cm. Observations on heading date were recorded on five random plants, excluding the border plants. The date on which the top of the uppermost spikelet of the main panicle emerged beyond the auricle of the flagleaf was recorded as the heading date.

Plot means were used for statistical and graphical analyses. The data were subjected to W_r , V_r graph analysis and to the estimation of genetic parameters following Hayman (1954, 1957) and Jinks and Hayman (1953). Analysis of Y_r , ($W_r + V_r$) standardized deviations graph was done following Johnson and Aksel (1959), where Y_r is the parental measurement and ($W_r + V_r$) is an index of the parental order of dominance. In addition to a t^2 test, which tests for the overall assumptions of diallel analysis, ($W_r + V_r$) and ($W_r - V_r$) heterogeneity tests were carried out following Allard (1956) to determine the adequacy of the model with respect to non-allelic interactions.

Results

The analysis of variance of plot means showed highly significant differences among parents and their crosses (Table 1). The t^2 test showed that the assumptions underlying diallel analysis are fulfilled ($t^2 = 0.028$) and the additive-dominance model is the adequate description of the data. The regression of covariance (W_r) on variance (V_r), however, was significantly different from unit slope, indicating the presence of non-allelic interaction, and hence the inadequacy of the additive-dominance model (Fig. 1a). The pattern of distribution of the array points in W_r, V_r plane is indicative of a complementary type of non-allelic interaction rather than true overdominance as expressed in the interception of W_r axis by the regression line below the origin. Furthermore, the distribution of array points indicates that 'T(N)1' and 'N22' possess an excess of dominant alleles; 'TKM6', 'Sabarmati' and 'IET 2923' possess an excess of recessive alleles; and the remaining parents possess more or less equal proportions of dominant and recessive alleles.

In the presence of non-allelic interactions, the deductions from the W_r, V_r graph are likely to be erroneous. To test this, the interacting arrays 1 and 6 were eliminated, and the resulting 6×6 diallel set of crosses was reanalyzed by an analysis of variance and a W_r, V_r graph analysis. The W_r, V_r graph (Fig. 1b) reveals the following points: (1) the regression of W_r on V_r does not differ significantly from unity, indicating the absence of non-allelic interactions, (2) the regression line intercepts the W_r axis above the origin, indicating partial dominance, and (3) the parental order of dominance remains more or less unaltered from the original 8×8 diallel analysis. Moreover, three well-defined and undiffused groups emerged; 'T(N)1' and 'N22' belonging to lowest W_r, V_r group and hence possessing the greatest excess of dominant alleles; 'Sabarmati' and 'Jaya' belonging to highest W_r, V_r group

and hence possessing the greatest excess of recessive alleles; and 'IR8' and 'IET 1991' belonging to an intermediate W_r, V_r group and hence possessing dominant and recessive alleles in more or less equal proportions.

An examination of the standardized deviation graph of parental measurement, Y_r , and the parental order of dominance ($W_r + V_r$), (Fig. 1c), indicates a significantly positive association ($r = 0.8467b$) between Y_r and ($W_r + V_r$). This graph confirms the results of W_r, V_r graph analysis regarding the distribution of dominant and recessive genes among the parents. Additionally, it also shows that the earliness in 'T(N)1' and 'N22' is governed by dominant alleles and the lateness in 'Sabarmati' and 'Jaya' is governed by recessive alleles.

Estimates of the genetic components of variation are given in Table 2. In the interacting 8×8 set of diallel crosses, $(H_1/D)^{1/2}$, a measure of the average degree of dominance, indicates overdominance which is in conformity with the results of W_r, V_r graph analysis. Inequality of the estimates of H_1 and H_2 indicates that the positive and negative alleles at most of the loci exhibiting dominance are unequal. Estimates of other parameters, viz. h^2 and F , are unreliable because of their high standard errors.

In the non-interacting 6×6 diallel set of crosses, the standard errors of all the estimates are reduced (Table 2). The most revealing results are: (1) the reduction in the level of dominance, from overdominance to partial domi-

Table 1. Analysis of variance for heading date in rice

Source of variation	8 × 8 diallel			6 × 6 diallel		
	d.f.	M.S.	F. value	d.f.	M.S.	F. Value
Treatment	35	125.467	88.86 ^a	20	73.442	46.29 ^a
Error	35	1.412	—	20	1.586	—

^a Significant at 0.01 probability level

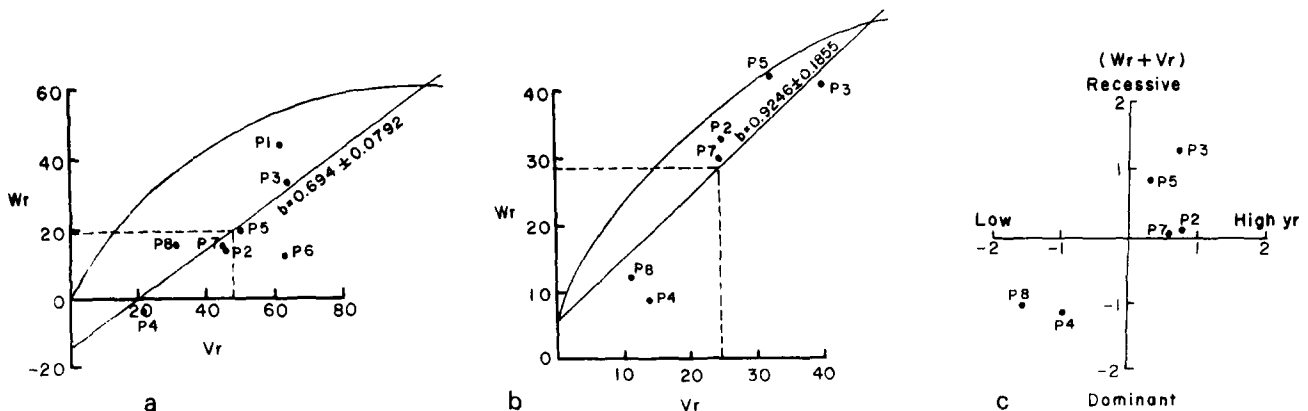


Fig. 1a-c. (W_r, V_r) graph and standardized deviations ($Y_r, W_r + V_r$) graph for heading date in rice, P1 = TKM6; P2 = IR8; P3 = Sabarmati; P4 = T(N)1; P5 = Jaya; P6 = IET 2923; P7 = IET 1991; P8 = N22. a (W_r, V_r) graph for an 8×8 diallel; b (W_r, V_r) graph for a 6×6 diallel, excluding two interacting arrays 1 and 6; c Standardized deviations ($Y_r, W_r + V_r$) graph for a 6×6 diallel

Table 2. Estimates of genetic parameters for heading date in rice.

Genetic parameter	Estimate	
	8 × 8 diallel	6 × 6 diallel
D	45.56 ± 8.27 ^a	54.09 ± 4.72 ^a
H ₁	131.56 ± 19.01 ^a	37.46 ± 11.96 ^b
H ₂	98.89 ± 16.54 ^a	40.78 ± 10.69 ^b
h ²	7.19 ± 11.09	18.42 ± 7.10 ^b
F	-13.91 ± 19.15	-5.21 ± 5.76
E	0.71 ± 2.76	0.79 ± 1.78
(H ₁ /D) ₂ ¹	1.70	0.83
(H ₂ /4H ₁)	0.19	0.27
K	-	0.45

^a Significant at 0.01 probability level

^b Significant at 0.05 probability level

nance, which is again in conformity with the Wr, Vr graph analysis and (2) the near-equality of the estimates of H₁ and H₂ which indicates that the positive and negative genes are in equal frequencies at all loci exhibiting dominance. K = h²/H₂ estimates the number of effective factors as defined by Mather (1949), and it measures only those factors showing some degree of dominance. In the 8×8 set of diallel crosses where h² estimate was statistically non-significant, K was not estimated whereas in the 6×6 set of diallel crosses, its value was less than one.

Discussion

Diallel analysis, as proposed by Hayman (1954, 1957), Jinks (1954), and Jinks and Hayman (1953) is based on the assumptions that (1) parents are homozygous, (2) segregation is of a diploid nature, (3) reciprocal crosses do not differ significantly, (4) multiple allelism does not exist, (5) non-allelic interaction is absent, and (6) genes are independently distributed among the parents. The first three assumptions are the usual ones and, in all probability, apply to rice which is diploid in nature and its mating system is that of a predominantly self-pollinating species. Reciprocal differences in crosses for heading date have not been found (Singh 1973). The assumption of independent distribution of genes among the parents and the assumption of no multiple allelism are made to simplify the model. Non-allelic interaction can always be tested as a null hypothesis. One can detect multiple allelism in the absence of epistasis, and in the absence of both, the presence of correlated gene distribution, where the parents with the reinforcing or the balancing combinations of alleles with positive and negative effects are in excess over that expected from independent distribution, can be exposed (Hayman 1957).

Covariance (Wr) and variance (Vr) graph analysis is a

type of scaling test which provides useful information on the nature and degree of non-allelic interactions. Furthermore, it provides information on the degree of dominance, distribution of dominant and recessive alleles among the parents, and genetic diversity among the parents. Significant regression ($b \neq 0$) and non-significant deviation from unit slope is the first test of the adequacy of the additive-dominance model. Analysis of the heading date in the present material indicated that the Wr, Vr regression deviated significantly from unit slope, implying the presence of non-allelic interactions. The assumption of non-allelic interaction has been very difficult to satisfy in most of the studies wherever the diallel analysis has been used (Jana 1975).

Mather (1967) has shown that with complementary interaction ($\Delta Vr - \Delta Wr$) is positive (i.e. change in Vr is less than the change in Wr) resulting in the Wr, Vr array points to lie to the right of the straight line of unit slope. Thus, complementary interaction affects the distribution pattern of array points in a characteristic way, generating the curve which is concave upward. In Figure 1a, the values of (Vr - Wr) are positive over all the array points, hence generating a curve which is concave upward and thus indicates complementary type of non-allelic interaction. However, dispersed gene distribution, where the parents with the balancing combinations of alleles with positive and negative effects are in excess over that expected from the independent distribution, also produce a more or less similar distribution pattern of array points (Coughtrey and Mather 1970). Therefore, it becomes difficult to distinguish between the effect of dispersed gene distribution and complementary interaction on a Wr, Vr graph. In the present set of diallel crosses, the latest F₁ hybrids in each array carried 'TKM 6' as one of their parents, although 'TKM 6' as such was one of the earliest parents after 'N 22' and 'T(N)1'. 'Sabarmati' and 'IET 2923' which were late parents, produced an F₁ which was later by 11 days. The fact that earliness is dominant over lateness, as was also found by Khaleque and Eunos (1975), and Ganashan and Whittington (1976), suggests that the above results are better explained in terms of complementary interaction than in terms of dispersed gene distributions. The apparent overdominance, as revealed in the Wr, Vr graph and in the estimates of genetic components of variation, thus apparently has its basis in a complementary type of non-allelic interaction rather than in dispersed gene distribution or true overdominance.

When interactions are present, Jinks (1954) suggested the removal of interacting arrays as one of the procedures for obtaining a non-interacting subset of diallel which could be analyzed to derive statistically valid genetic interpretations. In the present case, removal of the interacting parents 'TKM 6' and 'IET 2923' led to a non-interacting 6×6 set of diallel crosses. The Wr, Vr graph analysis of

this diallel subset produced a rectilinear regression line of unit slope ($b = 0.924$). With the improvement in the slope of the regression line to unity, the overdominance disappeared and partial dominance emerged. However, Coughtrey and Mather (1970) have pointed out that with additive \times additive (i) type of interaction alone or with dominance \times dominance (l) type of interaction alone, the array points scatter along a regression line of unit slope when $p = q = \frac{1}{2}$. A line of unit slope, therefore, is not a completely unequivocal indication of the absence of non-allelic interactions.

Allard (1956) used the estimates of W_r , V_r values for each of the replications and partitioned the variation among $(W_r + V_r)$ as well as among $(W_r - V_r)$ into those due to arrays and due to replicate blocks. The presence of significant variation for $(W_r + V_r)$ among arrays implies significant non-additive genetic variation which was quite evident in the present study ($F = 12.67a$). The non-significance of $(W_r - V_r)$ differences among the arrays, on the other hand, indicates a satisfactory fit to an additive-dominance model. Considering both results together, we conclude that there exists significant amounts of non-additive genetic variation in the 6×6 diallel subset of crosses and that this variation can be explained on the basis of additive dominance model (Table 3). 'T(N)1' and 'N 22' were found to be the earliest parents possessing greatest excess of dominant alleles whereas Sabarmati and Jaya were found to be the latest parents possessing greatest excess of recessive alleles. The parental order of dominance remained unchanged in both interacting as well as non-interacting sets of diallel crosses, although the grouping of the parents was well-defined and much undiffused in the latter set.

Elimination of interacting parents and the corresponding arrays from the diallel analysis led to much more precision in the estimation of genetic components of variation, and the spurious overdominance [$(H_1/D)^{\frac{1}{2}} = 1.70$] changed to partial dominance [$(H_1/D)^{\frac{1}{2}} = 0.83$]. Khaleque and Eunos (1975) also achieved more precision in their estimates of variance components by eliminating interacting arrays from the analysis. Although the rectilinearity of regression line to unit slope could be achieved in their studies by removing interacting arrays, and the dominance

level could be reduced by 50 per cent, the dominance level still remained in the over-dominance range [$(H_1/D)^{\frac{1}{2}} = 1.4$]. Partial dominance of earliness over lateness was also observed by Nancharuiah, Nanda and Chaudhary (1974), Singh (1973), and Ganashan and Whittington (1976) in a non-interacting diallel set of crosses in rice. As mentioned earlier, a unit slope of the regression line should not be taken as a very certain criterion that the interaction has been completely eliminated. Some interaction may still persist, which along with the unfulfilment of the other underlying assumptions, may lead to the balanced failure of detection, and hence the restoration of rectilinear regression line to unit slope. Jinks (1955) examined such data as the size of the plant from a variety of species, including maize, and did not encounter apparent overdominance in crosses without finding non-allelic interaction to be present. Furthermore, when the interaction effects were reduced in the data either by eliminating the interacting arrays or by transforming it to satisfactory scales, the apparent overdominance was also reduced. In our case where interaction was removed almost entirely, the apparent overdominance vanished.

A final note regarding the insensitivity of the F_1 W_r/V_r graph to certain interactions is in order. Jinks (1954) demonstrated for flowering time in *Nicotiana rustica* that diallel analysis of parents and F_1 's showed no detectable departure from the rectilinear relationship of unit slope between W_r and V_r . Later, the analysis of F_2 and back-cross generations revealed that duplicate gene interactions played key roles in the inheritance of flowering time (Jinks, 1956). Ganashan and Whittington (1976) also found no detectable departure of rectilinear regression line from unit slope in their F_1 W_r/V_r analysis in rice but further analysis of the F_2 generation of a cross led them to conclude that a complementary type of non-allelic interaction was present. Thus, the results of the present investigation involving only F_1 W_r/V_r analysis must be considered in view of these limitations.

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Table 3. Analysis of variance of (V_r , W_r) estimates in a 6×6 diallel set of crosses for heading date in rice

Source of variation	d.f.	MS	F
$(V_r + W_r)$ array differences	5	1153.63	12.67 ^a
$(V_r + W_r)$ block differences	6	91.03	
$(W_r - V_r)$ array differences	5	50.59	2.17
$(W_r - V_r)$ block differences	6	23.30	

^a Significant at 0.01 probability level

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Dr. S.L. Dwivedi
International Crops Research Institute
for the Semi-Arid Tropics (ICRISAT)
Patanchosu P.O.
Andhra Pradesh 502324 (India)

Dr. K.N. Rai,
International Crops Research Institute
for the Semi-Arid Tropics (ICRISAT)
1-11-256, Begumpet
Hyderabad – 500016 (India)