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A DIALLEL CROSS ANALYSIS OF HEADING DATE IN WHEAT

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A complete diallel cross of 10 selected wheat varieties was grown for three years (1957–1959) at Davis, California, to determine whether genetic information useful in the breeding of self-pollinated plants could be obtained from parental and F_1 data. The character studied was heading date. Analysis of the data indicated that a few major genes with dominance effects were the most important feature of the genetic system. A system of minor genes displaying little or no dominance was also discovered. There was no evidence for any important epistatic effects. The various genotypes were found to behave fairly similarly over the three-year period. Variances and frequency distributions observed in 7 F_2 test populations and certain other segregating generations grown in 1958 corresponded closely in most cases to those predicted on the basis of the 1957 diallel cross analysis.

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H I L G A R D I A

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A DIALLEL CROSS ANALYSIS OF HEADING DATE IN WHEAT[1]

DAVID W. CRUMPACKER[2] and R. W. ALLARD[3]

THE THEORY OF DIALLEL CROSSES and the usefulness of diallel cross techniques in genetic analysis of populations have received considerable attention in recent years. Several diallel cross techniques have been proposed and applied to diverse problems. Thus, for example, Sprague and Tatum (1942), Henderson (1948, 1952), Griffing (1950, 1956*a*, 1956*b*), and Matzinger, Sprague, and Cockerham (1959) have considered the utility of diallel crosses in investigation of the notions of general and specific combining ability in plant and animal materials. Another application to a practical problem—the early generation evaluation of parental materials in breeding programs—has been discussed by Jinks (1955), Allard (1956*b*, 1956*c*), and Whitehouse, Thompson, and Valle Ribeiro (1958). The application to still another problem—the investigation of genotypic-environmental interactions—has been considered by Rojas and Sprague (1952), Matzinger and Kempthorne (1956), Allard (1956*a*), and Matzinger, Sprague, and Cockerham (1959). The theory of diallel crosses, and procedures for estimating certain genetic parameters in terms of gene models in varying degrees of complexity, have been discussed by Hull (1952), Griffing (1950, 1956*a*, 1956*b*), Hayman (1954*a*, 1954*b*, 1957, 1958, 1960), Jinks (1954, 1956), Dickinson and Jinks (1956) and Kempthorne (1956).

A diallel crossing system can be defined as one in which p genotypes are chosen and intercrossed. The parental genotypes are usually inbred lines, but they can also be individuals, clones, open-pollinated varieties, or other genetic entities. If all possible crosses are made among the p parents, leading to p^2 matings, the cross is called a complete diallel cross. These p^2 combinations are conveniently divided into three groups: (1) the p parental combinations $p_1 \times p_1$, $p_2 \times p_2 \ldots p_n \times p_n$; (2) one set of $\frac{1}{2}p(p-1)$ F_1 combinations; and (3) the set of $\frac{1}{2}p(p-1)$ reciprocal F_1 combinations.

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Diallel crossing techniques vary with inclusion or absence of parental inbreds and/or reciprocal F_1's, and with sampling assumptions. Following the classification of Griffing (1956*b*) there are four possible diallel crossing techniques: (1) parents, one set of F_1's, and reciprocal F_1's are included (p^2 combinations); (2) parents and one set of F_1's are included, $\frac{1}{2}p(p + 1)$ combinations; (3) reciprocal F_1's are included but not the parents, $p(p - 1)$ combinations; and (4) one set of F_1's only is included, $\frac{1}{2}p(p - 1)$ combinations. There are two alternative sampling assumptions: (1) parental genotypes are assumed to be a random sample from some population about which inferences are to be made, and (2) the parental genotypes are deliberately chosen and cannot be regarded as a random sample from any population, that is, the experimental material constitutes the entire population about which inferences are to be made. These four different diallel crossing procedures and the two sampling assumptions give rise to eight different situations, each requiring different analysis.

In the breeding of self-pollinated crops, such as wheat, the breeder usually has available a multiplicity of pure lines, any one of which may be capable of producing desirable progeny in particular hybrid combinations. Accumulated experience indicates that the best progeny are usually produced by parents which possess many desirable characteristics between them. Still, the breeder is likely to have so many desirable parents at his disposal that it is difficult to choose among many crosses that seem equally likely to produce outstanding offspring. The only certain way to determine which hybrids produce many superior offspring and which do not has been to grow segregating generations from each hybrid. This is expensive and time consuming. Methods that permit identification in early generations of the hybrids promising the greatest advance would clearly be advantageous, but progress toward such methods has been slow.

In 1950 Griffing noted that parental and F_1 data have distinct advantages over data from segregating generations in studying quantitative genetic systems because, being unaffected by genetic segregation and linkage, the former data require relatively few individuals for efficient estimation of certain relevant genetic parameters. Therefore more parents can be included and a wider range of germ plasm can be sampled in diallel crosses. A method of analysis of parental and F_1 generations from a set of diallel crosses presented by Jinks and Hayman (1953) appeared to provide a rapid evaluation of the genetic relationships among a number of parents. The method thus seemed to offer promise in identifying parents whose hybrids are most likely to respond to selection. Since the parents of interest to breeders of self-pollinated crops will almost always be a selected sample, the appropriate sampling assumption is that the experimental material itself constitutes the entire population about which inferences are to be made. The analysis proposed by Jinks and Hayman includes parents and one or both sets of F_1 crosses. Hence, with respect to Griffing's classification of diallel crossing techniques, it is applicable to both experimental methods 1 and 2.

Kempthorne (1956) criticized the Jinks-Hayman analysis on the basis that "the diallel cross must be interpreted in terms of some population which has given rise to the homozygous parents in inbreeding. If such a population does not exist then the whole analysis . . . is likely to lead nowhere. From quite another viewpoint one may question the value of estimating additive variance, dominance variance and so on . . . unless the estimated quantities are measures of the characteristics of a definite population." Since the parents of primary interest to breeders of self-pollinated crops will usually not have been derived by inbreeding from some definite population, Kempthorne evidently considers that the Jinks-Hayman type of analysis of diallel crosses has little practical value as an aid in the improvement of self-pollinated crops. Hayman (1957, 1958, 1960) has considered these criticisms and has discussed some additional aspects of the theory and analysis of diallel crosses. Gilbert (1958) has also criticized the assumptions on which the Jinks-Hayman analysis is based (see p. 279), concluding that the method is not directly relevant to plant breeding.

This paper reports on an investigation to determine the usefulness of the Jinks-Hayman type of analysis in the breeding of self-pollinated crops. "Heading date" in wheat is used as the test character. The problem is considered in four parts: (1) determination of whether the assumptions upon which the diallel analysis is based are valid for the particular character, heading date; (2) analysis of the experimental data for the information they contain about the genetic system governing heading date; (3) assessment of the importance of genotypic-environmental interactions in the genetic system, and (4) consideration of the accuracy with which the genetic system deduced from the parental and F_1 diallel cross data can be used to predict segregation in later generations.

MATERIALS AND DESIGN

The parents chosen for the study were 10 varieties of wheat that are, or have been, grown commercially in California: Baart 46 (BA), Ramona (RA), White Federation (WF), Hard Federation (HF), Bunyip (BU), Big Club (BC), Poso (PO), Galgalos (GA), Sonora (SO), and Onas (ON). Detailed descriptions and genealogies of these varieties may be found in publications by Clark and Bayles (1942) and Bayles and Clark (1954). White Federation, Hard Federation, Bunyip and Onas, developed in Australia, are related in varying degrees. Ramona originated at Davis, California, from a cross between Hard Federation and Bunyip. The degree of relationship between Big Club and Poso is uncertain. Baart 46, Galgalos and Sonora are old varieties that apparently are not related to one another or to any of the other parents. These 10 varieties clearly do not constitute a random sample from any population. Rather they are a selected sample and constitute the entire population about which inferences can be made.

The 10 parents were crossed in all possible combinations to produce 100 matings (parents are treated as F_1's for purposes of analysis). This 10×10

diallel cross nursery was repeated over a three-year period (1957–1959) at Davis, California. Duplicate sets of parents were included, so that each nursery contained a total of 110 parental and F_1 families. Four randomized complete blocks were used in 1957 and 1958, and two in 1959. Thus, the 1957 and 1958 nurseries contained 440 plots, and the 1959 nursery contained 220. The plots were unguarded, and consisted of single rows, 1 foot apart. The planting rates within a row were: 1957, six kernels, 1 foot apart; 1958, five kernels, 1 foot apart; 1959, ten or eleven kernels, 1 foot apart. These planting rates yielded an average of 4.3 plants per plot in 1957, 3.8 in 1958, and 9.3 in 1959.

TABLE 1

HEADING DATE OF PARENTS.
AVERAGED OVER FOUR BLOCKS IN 1957 AND 1958,
AND OVER TWO BLOCKS IN 1959

Parent*	1957	1958	1959	Mean
BA	27.1	36.3	21.0	29.6
RA	10.1	18.6	9.8	13.4
WF	24.8	30.8	16.8	25.6
HF	27.1	33.6	19.0	28.0
BU	16.4	24.7	14.8	19.4
BC	34.9	41.4	29.0	36.4
PO	19.7	26.4	14.8	21.4
GA	34.4	44.9	31.6	38.0
SO	29.4	34.5	24.5	30.4
ON	28.8	37.4	23.0	31.1
Mean	25.3	32.8	20.4	

* For parental means in 1957 or in 1958: $LSD_{0.05} = 1.33$; $LSD_{0.01} = 1.77$. For parental means in 1959: $LSD_{0.05} = 1.89$; $LSD_{0.01} = 2.51$.

Summing over reciprocals or duplicates, and over blocks, the F_1 and parental families therefore contained, on an average, 34.4 plants in 1957, 30.4 in 1958, and 37.2 in 1959.

The heading date for each plant was determined as the number of days from an arbitrary date, March 31, to the time at which the first spike had completely emerged from the leaf sheath. Mean heading dates for the parents are given in table 1.

An F_2 nursery was grown in the same field as the 1958 diallel cross nursery, but separated from it by about 120 feet. This included 10 F_2 generations, derived from certain F_1 combinations in the 1957 diallel cross nursery, as well as the 10 original parental lines. These 10 F_2's were so chosen as to provide tests of the usefulness of the diallel cross analysis.

In the 1957 and the 1958 diallel cross nurseries, and in parts of the F_2 nursery, individual plants were scored for kernel weight, rachis internode length, height, awn type, glume color, and glume pubescence. This information was used to check on the success of the original hand pollinations.

VALIDITY OF ASSUMPTIONS

The diallel cross analysis as developed by Jinks and Hayman (Jinks and Hayman, 1953; Jinks, 1954; Hayman, 1954*a*, 1954*b*) assumes:

(1) no genotype-environment interaction within locations and years (except within certain prescribed limits)
(2) homozygous parents
(3) diploid segregation
(4) no reciprocal differences
(5) no epistasis (that is, no nonallelic gene interaction)
(6) no multiple alleles
(7) uncorrelated gene distributions

When these assumptions are valid, the contribution of a locus A,a, to the family means in a p^2 diallel cross may be described in terms of the parameters u_a (proportion of parents that are AA), v_a (proportion of parents that are aa), d_a (additive phenotypic increment of the gene A,a), and h_a (dominance phenotypic increment of the gene A,a). The notation used is that of Mather (1949). A number of first- and second-degree statistics can be calculated from the family means. The genetic content of certain of these statistics in terms of the above parameters can be shown to be as follows:

Variance of parents = $V_{0L0} = 4\Sigma uvd^2$

Mean variance of arrays = $V_{1L1} = \Sigma[uv(d^2 - 2\{u - v\}dh + h^2)]$

Variance of array means = $V_{0L1} = \Sigma[uv(d - \{u - v\}h)^2]$

Mean covariance of arrays = $W_{0L01} = 2\Sigma[uvd(d - \{u - v\}h)]$, in which the subscript L refers to the diallel cross-mating system, and the subsequent number(s), beginning with zero for the parents, refer to the generations under consideration. In variances of individual measurements, the number preceding L is the same as that following, whereas in variances of means and in covariances, the number(s) preceding L refers to the generation(s) of the common parent(s).

If the diallel cross components of variance are defined as

$$D = 4\Sigma uvd^2$$

$$H_1 = 4\Sigma uvh^2$$

$$H_2 = 16\Sigma u^2v^2h^2$$

$$F = 8\Sigma[uv(u - v)dh],$$

then

$$V_{0L0} = D + E$$

$$V_{1L1} = \tfrac{1}{4}D + \tfrac{1}{4}H_1 - \tfrac{1}{4}F + E$$

$$V_{0L1} = \tfrac{1}{4}D + \tfrac{1}{4}H_1 - \tfrac{1}{4}H_2 - \tfrac{1}{4}F + \frac{(n - 1)E}{n^2}$$

$$W_{0L01} = \tfrac{1}{2}D - \tfrac{1}{4}F + E/n,$$

in which the additional term E = environmental variance of diallel cross family means, and n = number of parents or number of arrays. These equations differ slightly from those given by Hayman (1954*b*), in that the coefficients of the E terms are unweighted, and, also, parental and F_1 variances are considered to be homogeneous. Weighting is not necessary in the present analysis, since each parental mean is an average of duplicate plots and therefore is comparable to an F_1 mean averaged over reciprocal plots. An estimate of E is readily obtained from a replicated experiment. Once this estimate has been made and substituted in the above equations, there remain four equations in four unknowns, which can be solved for the components D, H_1, H_2 and F.

Failure of any of the seven assumptions invalidates the analysis in some degree, so it is important to test the validity of these assumptions before proceeding with the genetic analysis. The validity of certain of the assumptions can be ascertained from inferences based on knowledge of the wheat species and the particular parents entering this diallel cross. Judgments concerning other of the assumptions must be based on detailed statistical tests too lengthy to be reported here.[4] Consequently, only a summary of the conclusions regarding validity of the assumptions will be presented.

Summary: Validity of Assumptions

Validity of the assumptions of parental homozygosity and diploid segregation is assured from the history of self-pollination of the parents, and from numerous reports in the literature not only that wheat regularly forms 21 bivalents at meiosis but also that inheritance in this species is uniformly disomic.

The absence of reciprocal differences was established from the data by the observation that the value of an F_1 does not depend on the direction of the cross.

The data indicated that the assumption of absence of genotypic-environmental interaction within locations and years was not always valid, particularly when the basis of comparisons was individual plants rather than block means. Even so, differences in performance of certain genotypes in different parts of the nursery were small compared with genetic differences among parents and F_1 hybrids, and such differences appeared unlikely to introduce more than a trivial bias into the genetic analysis.

The assumptions of no epistasis, no multiple alleles, and uncorrelated gene distributions are difficult to evaluate independently of each other. Analysis of the data indicated that one or more of these assumptions, including that of "no epistasis," were not strictly valid, but the fact that the (V_r, W_r) graphs were not distorted indicates that these factors were unlikely to be a significant source of bias. (V_r and W_r are the variance and covariance, respectively, of an individual array; if all assumptions are valid, the regression of W_r upon V_r over all arrays is expected to be a straight line of unit slope.)

In sum, the effects of partial failure of certain of the assumptions seemed unlikely to be large enough to disturb a genetic analysis of the data.

[4] Sections deleted from the original manuscript, including details of the statistical tests, are available on microfilm (see inside front cover for details). For information deleted from this section, see Section I, pp. 1–11, of the microfilmed copy.

DIALLEL CROSS ANALYSIS

The diallel cross analysis was carried out by the methods of Jinks (1954) and Hayman (1954*b*). In this type of analysis two approaches are possible. Equations of estimation can be set up and solved to obtain estimates of the parameters D, H_1, H_2 and F, whose genetic content is interpretable on the basis of diallel theory. Alternatively, the data can be used to construct graphs that can be interpreted in terms of the genetic control of the character under investigation.

Analysis of the Genetic System in Terms of Diallel Cross Parameters

The equations on page 279 were used to estimate the diallel cross parameters in 1957 and 1959. To compensate for an inequality of parental and F_1 variances in 1958, the following equations of estimation were used in that year:

$$V_{0L0} = D + E$$

$$V_{1L1} = \tfrac{1}{4}D + \tfrac{1}{4}H_1 - \tfrac{1}{4}F + \frac{E + (n-1)E'}{n}$$

$$V_{0L1} = \tfrac{1}{4}D + \tfrac{1}{4}H_1 - \tfrac{1}{4}H_2 - \tfrac{1}{4}F + \frac{E + (n-2)E'}{n^2}$$

$$W_{0L01} = \tfrac{1}{2}D - \tfrac{1}{4}F + \frac{E}{n},$$

where E and E', respectively, represent the environmental variances of parental and F_1 families. These equations can be solved by a method (Mather, 1949; Hayman, 1954*b*) similar to that of classical least squares (Aitken, 1944). The normal equations of D, H_1, H_2, and F are obtained and their coefficients set in a square matrix that is symmetrical about the main diagonal. This matrix is then inverted to obtain the covariance matrix or, as it is sometimes called, matrix of Gauss multipliers. The Gauss multipliers are used to provide estimates of D, H_1, H_2, and F. This method has two advantages: (1) the same covariance matrix can be used to estimate D, H_1, H_2, and F from any number of similar experiments; (2) the Gauss multipliers on the main diagonal can be multiplied by the mean square for residuals to obtain direct estimates of the variances of D, H_1, H_2, and F. The mean square for residuals is obtained from the sum of squares of deviations of observed from expected values of the diallel cross statistics. This method also has certain disadvantages which have been discussed by Nelder (1953). In classical least squares analysis it is assumed that the variances of the residuals are homogeneous and uncorrelated. Dependent variables such as V_{0L0}, V_{1L1}, V_{0L1}, and W_{0L01} are, however, estimated with varying accuracy; hence their errors are not expected to be homogeneous. In addition, V_{0L0}, V_{1L1}, and W_{0L01} are correlated to a degree. Finally, V_{0L0}, V_{1L1}, V_{0L1}, and W_{0L01} are second-degree statistics and may not necessarily be normally distributed.

TABLE 2*

MEANS, STANDARD ERRORS, AND 95 PER CENT CONFIDENCE LIMITS OF DIALLEL CROSS PARAMETERS

Method† and year	Parameter	Mean	Standard error	95 per cent confidence limits
2 1957	D	59.8	3.8	47.7–71.9
	H_1	18.2	2.8	9.3–27.1
	H_2	12.1	2.4	4.5–19.7
	F	−28.2	2.1	(−34.9)–(−21.5)
3 1958	D	62.9	3.0	53.4–72.4
	H_1	14.6	2.1	7.9–21.3
	H_2	9.3	1.5	4.5–14.1
	F	−13.4	3.8	(−25.5)–(−1.3)
3 1959	D	45.9	2.1	19.2–72.6
	H_1	10.5	0.1	9.2–11.8
	H_2	6.6	0.2	4.1–9.1
	F	− 4.0	0.8	(−14.2)–6.2

* Additional information on table 2 is given in table 7 of the microfilmed sections (see footnote 4).

† See text, p. 283, for explanation.

TABLE 3

MEANS, STANDARD ERRORS, AND 95 PER CENT CONFIDENCE LIMITS OF DIALLEL CROSS ESTIMATORS

Method* and year	Estimator	Mean	Standard error	95 per cent confidence limits
2 1957	H_1/D	0.30	0.05	0.13–0.47
	$V_{1L1} - E/W_{0L01} - E/n$	0.72	0.02	0.66–0.78
	$\overline{F}_1 - \overline{P}$	−1.70	0.34	(−2.39)–(−1.01)
	$\frac{1}{4}\, H_2/H_1$	0.16	0.02	0.08–0.24
	K	0.65	0.11	0.30–1.00
3 1958	H_1/D	0.24	0.09	(−0.03)–0.51
	$V_{1L1} - \frac{E + (n-1)E'}{n} \Big/ W_{0L01} - E/n$	0.66	0.04	0.53–0.79
	$\overline{F}_1 - \overline{P}$	−1.60	0.29	(−2.18)–(−1.02)
	$\frac{1}{4}\, H_2/H_1$	0.16	0.03	0.06–0.26
	K	0.78	0.19	0.18–1.38
3 1959	H_1/D	0.23	0.01	0.10–0.36
	$V_{1L1} - E/W_{0L01} - E/n$	0.63	0.004	0.59–0.67
	$\overline{F}_1 - \overline{P}$	−1.32	0.30	(−1.93)–(−0.71)
	$\frac{1}{4}\, H_2/H_1$	0.16	0.01	0.03–0.29
	K	0.68	0.15	(−1.23)–2.59

* See text, p. 283, for explanation.

To avoid any assumptions about the variance matrix of such second-degree statistics, Nelder suggested that each replication be treated as a separate experiment with its own environmental component of variance. It is then necessary only to assume that the estimates of D, H_1, H_2, and F from each block are samples from normal populations. The standard error of the mean of each of these parameters can then be estimated from the variation of the block values around the over-all mean. This also appears to be a desirable procedure on the grounds that the distribution of a sample mean tends toward normality with increasing size of sample, even though the individual variates may not be normally distributed.

The estimates of the diallel cross parameters and their standard errors were obtained from the 1957 data by three methods:

(1) covariance matrix or "quasi least squares"
(2) Nelder's method with separate estimates of E for each block
(3) Nelder's method with a uniform estimate of E applied to each block

Method 2 was considered preferable to method 1 for reasons stated previously, and also because the standard errors it provided were considerably lower except in the case of D. Whenever E is relatively small, as in the present analysis, method 3 should give results comparable to method 2, with much less labor. This was actually found to be the case. Table 2 lists the estimates of the means, standard errors and 95 per cent confidence limits of the diallel cross parameters. These were obtained by method 2 in 1957, and by method 3 in 1958 and 1959.[5]

Some of the important estimators (Jinks, 1954) that may be derived from the diallel cross parameters are listed in table 3, together with their means, standard errors, and 95 per cent confidence limits. Most of these estimators are ratios, and the question of their accuracy immediately arises. This problem, reviewed by Craig (1942), is not a simple one. Probability functions have been determined for a few important ratios, such as Snedecor's F, which possesses a finite number of moments, and tables are available. Nevertheless, the problem is a troublesome one, even when the variables that form a ratio are normally and independently distributed. In the present case an attempt was made to determine only the approximate standard errors and confidence limits of these ratios as estimated by methods 2 and 3, discussed previously. For example, the ratio H_1/D was determined for each block, and the block values were then used to estimate the mean, standard error of the mean, and confidence limits for H_1/D.

H_1/D is an estimator of the average degree of dominance, since

$$\frac{H_1}{D} = \frac{\Sigma uwh^2}{\Sigma uvd^2}.$$

[5] A more complete discussion of methods 1 to 3, with comparative data on standard errors, is given on pp. 11–12 of the microfilmed sections (see inside front cover).

It is weighted in favor of genes which have both alleles represented equally in the parents, that is, $u_a = v_a = \frac{1}{2}$. In this analysis, with respect to a particular gene A,a, u_a will represent the frequency of the negative or early allele A in the parents, and v_a will represent the frequency of the positive or late allele a. H_1/D is also weighted in favor of genes, or closely linked blocks of genes, with large effects. With average partial dominance, H_1/D is expected to fall within the range 0–1. The values of H_1/D in table 3 provide evidence for average partial dominance in the experimental materials. The quantity $\sqrt{H_1/D}$ is a weighted measure of the average degree of dominance at each locus. Since $\sqrt{H_1/D}$ or $\bar{h}/\bar{d}$ approximates 0.5 in each year, the average degree of partial dominance at any locus is intermediate.

Another estimate of average dominance may be obtained from the ratio

$$\frac{V_{1L1} - E}{W_{0L01} - E/n} = \frac{\Sigma[uv(d^2 + h^2 + 2\{v - u\}dh)]}{\Sigma[uv(2d^2 + 2\{v - u\}dh)]},$$

which also falls in the range 0–1 with partial dominance. This is a weighted estimator in the same sense as H_1/D. Again there is evidence for average partial dominance in the experimental materials. If $u = v = \frac{1}{2}$ for all alleles, H_1/D and

$$\frac{V_{1L1} - E}{W_{0L01} - E/n}$$

can be converted to the same scale of measurement (Jinks, 1954).

If many of the u's and v's are equal, rescaling of

$$\frac{V_{1L1} - E}{W_{0L01} - E/n}$$

should bring its value much closer to that of H_1/D. Rescaling was performed, and values obtained in 1957, 1958 and 1959, respectively, were 0.44, 0.32 and 0.26. These values agree much more closely with those of H_1/D. It appears that many of the positive and negative alleles are present in the parents in approximately equal numbers.

Since $\bar{F}_1$ and $\bar{P}$ are the over-all F_1 and parental means, the sign of $\bar{F}_1 - \bar{P}$ is an indicator of the average direction of dominance. The variation of the individual deviations, $F_1 - P$, around $\bar{F}_1 - \bar{P}$ was used to estimate a standard error for $\bar{F}_1 - \bar{P}$. The data indicate average partial dominance for earliness in each year.

The quantity $\frac{1}{4} H_2/H_1$ is an estimator of the average frequency of negative versus positive alleles in the parents. Since

$$\tfrac{1}{4}\frac{H_2}{H_1} = \frac{\Sigma u^2 v^2 h^2}{\Sigma w h^2} = \bar{u}\bar{v},$$

it has a maximum value of $\frac{1}{4}$ when $\bar{u} = \bar{v} = \frac{1}{2}$. If the negative and positive alleles are not distributed equally among the parents, $\bar{u}\bar{v} < \frac{1}{4}$. The estimator

$\frac{1}{4} H_2/H_1$ or $\bar{u}\bar{v}$ is weighted. If the h effects of genes, or closely linked blocks of genes, are unequal, the genes with large h effects will be favored. Genes with both alleles represented equally in the parents will also receive more weight. It is important to note that no information is provided about genes that have no dominance effect. In each year the value of $\frac{1}{4} H_2/H_1$ was 0.16. The negative and positive alleles of genes that exhibit dominance, therefore, do not appear to be distributed equally among the parents. Since evidence has already been presented for the equal distribution of many of the negative and positive alleles in the system, it follows that many of the genes in the system have little or no dominance effects.

The parameter $F = 8\Sigma[uv(u - v)dh]$. Its sign depends on the sign of $(u - v)h$. If no genes exhibit dominance effects, or if the dominant and recessive alleles of each gene are distributed equally among the parents, $F = 0$. If there is an excess of dominant alleles (or of dominant genic effects) F will be positive. An excess of recessive alleles (or effects) will cause F to be negative. Thus, the sign of F is an indicator of the relative frequencies of dominant and recessive alleles in the parents. When the h effects of different genes are unequal, the sign of F will be weighted in favor of genes with large h effects. There appears to be an excess of recessive alleles, or of recessive genic effects, in each year, although this excess is considerably smaller in the last two years, particularly in 1959 (table 2, p. 282).

An effective factor has been described by Mather as the smallest unit of hereditary material that is capable of being recognized by the methods of biometrical genetics (Mather, 1949). It may be a group of closely linked genes, or, at the lower limit, a single gene. In a diallel cross,

$$K = \frac{(\text{over-all progeny mean} - \text{parental mean})^2}{\frac{1}{4}H_2} = \frac{(\Sigma uvh)^2}{\Sigma u^2v^2h^2},$$

where K = number of effective factors. The value of K will be underestimated unless the h effects of all the genes are equal in sign and size, and the distribution of the genes is uncorrelated (Mather, 1949; Jinks, 1954). Again the analysis gives no information about genes that have no dominance effects. The values of K in table 3 (p. 282) approximate one effective factor in each year. These values are quite low, which suggests that there are among the genes governing heading date, one or two whose high dominance leads to disproportionate effect on the estimate of K.

The means of individual diallel cross families (table 4) were inspected to determine the degree and direction of dominance in specific F_1 combinations.

In each of the three years, two types of comparisons were tested:

(1) For partial dominance:

$$\overline{X}_{12} - \frac{\overline{X}_{11} + \overline{X}_{22}}{2},$$

where $\overline{X}_{11}$ and $\overline{X}_{22}$ are the early and late parental means, respectively, in a particular cross, and $\overline{X}_{12}$ is the F_1 mean.

TABLE 4

MEAN HEADING DATES OF DIALLEL CROSS FAMILIES.
EACH MEAN AVERAGED OVER RECIPROCALS (DUPLICATES) AND BLOCKS

Parent*	BA	RA	WF	HF	BU	BC	PO	GA	SO	ON
					1957					
BA	27.1	14.3	26.0	26.6	16.4	30.6	25.7	29.6	27.7	28.8
RA	..	10.3	13.1	14.3	12.3	14.8	12.4	14.8	12.7	15.4
WF	..	..	24.7	25.4	15.8	29.9	22.3	28.3	27.1	26.3
HF	..	..	..	27.2	19.2	30.4	24.5	30.2	28.1	28.1
BU	..	..	..	..	16.4	20.2	15.3	18.7	18.0	19.7
BC	..	..	..	..	..	35.1	28.0	33.6	31.9	32.1
PO	..	..	..	..	..	..	19.5	28.4	22.7	27.0
GA	..	..	..	..	..	..	..	34.3	31.6	32.3
SO	..	..	..	..	..	..	..	..	29.4	30.5
ON	..	..	..	..	..	..	..	..	..	28.8
					1958					
BA	36.2	23.4	33.8	35.8	27.7	38.6	33.4	38.2	34.1	36.7
RA	..	18.6	25.6	22.6	20.6	23.7	20.8	25.5	20.5	22.7
WF	..	..	30.8	33.1	23.1	36.6	30.4	37.1	32.7	33.5
HF	..	..	..	33.5	26.4	38.0	31.7	38.1	33.5	33.3
BU	..	..	..	..	24.4	28.7	22.9	30.4	23.3	25.8
BC	..	..	..	..	..	41.5	33.8	43.5	37.2	39.5
PO	..	..	..	..	..	..	26.4	35.4	29.3	31.5
GA	..	..	..	..	..	..	..	44.9	37.3	39.0
SO	..	..	..	..	..	..	..	..	34.5	35.1
ON	..	..	..	..	..	..	..	..	..	37.2
					1959					
BA	21.2	11.9	18.5	20.5	16.2	23.5	19.2	23.7	21.5	22.6
RA	..	9.8	10.7	12.3	11.5	12.1	10.4	16.3	11.9	13.1
WF	..	..	16.8	17.5	13.1	23.1	16.7	24.2	21.0	19.5
HF	..	..	..	19.0	15.9	24.4	19.8	25.3	23.5	21.2
BU	..	..	..	..	14.9	17.8	13.7	18.8	15.5	17.9
BC	..	..	..	..	..	29.0	19.9	29.3	23.9	25.8
PO	..	..	..	..	..	..	14.8	23.2	18.0	19.3
GA	..	..	..	..	..	..	..	31.6	26.6	27.6
SO	..	..	..	..	..	..	..	..	24.5	23.4
ON	..	..	..	..	..	..	..	..	..	23.1

* Parental means (along diagonal) are averages of combined data from duplicates and blocks. They will differ by errors of rounding off from the means in table 1, which are averages of block means (data from duplicates having been combined within blocks).

(2) For overdominance: $\overline{X}_{12} < \overline{X}_{11}$ or $\overline{X}_{12} > \overline{X}_{22}$; that is, $\overline{X}_{11} - \overline{X}_{12}$ or $\overline{X}_{12} - \overline{X}_{22}$.

There were 45 possible comparisons of type (1) in each year. Tests of significance were actually performed only on those which fell within the range of partial dominance. Ninety comparisons of type (2) were possible in each year, but tests were performed only on those which fell within the range of overdominance.

Tests of significance were based on error mean squares obtained from analyses of variance of the diallel cross family means in each of the three years. The *F* values based on these analyses were very large and highly significant.

The results of the tests of significance, using the *LSD* method with the correction suggested by Federer (1955), are presented in table 5.[6]

TABLE 5

DEGREE AND DIRECTION OF DOMINANCE IN INDIVIDUAL DIALLEL CROSS F_1 FAMILIES

Degree	Direction	Number of F_1 combinations showing significance					
		1957		1958		1959	
		$P =$ 0.05–0.01	$P =$ < 0.01	$P =$ 0.05–0.01	$P =$ < 0.01	$P =$ 0.05–0.01	$P =$ < 0.01
Partial dominance	Earliness	0	13	0	13	2	14
	Lateness	0	2	1	0	0	0
Overdominance	Earliness	0	0	0	0	0	0
	Lateness	0	0	0	0	0	0

There were no cases of significant overdominance. In 1957, 29 per cent of the F_1's exhibited significant partial dominance for earliness; in 1958 and 1959, 29 per cent and 36 per cent, respectively, showed significance. There was also a general tendency toward partial dominance for earliness, since approximately 60 per cent of the F_1 means in each of the three years fell within the range of partial dominance for earliness. Of the crosses showing significant partial dominance for earliness, either Ramona or Bunyip was a parent in 13 out of 13 in 1957, 11 out of 13 in 1958, and in 12 out of 16 in 1959. The remaining crosses that showed significant partial dominance for earliness were: 1958, BA × GA, GA × SO; 1959, BA × BC, BA × GA, BC × PO, PO × SO.

The cross RA × BU did not exhibit significant partial dominance in any year.

Of the crosses tested, 4 per cent in 1957, 2 per cent in 1958, and 0 per cent in 1959 showed significant partial dominance for lateness. These were: 1957, BA × PO, PO × ON; 1958, BA × PO. The evidence for partial dominance for lateness in 1958 could easily have resulted from sampling variation. The

[6] A more complete discussion of the tests of significance is given on pp. 12–14 of the microfilmed sections (see inside front cover).

two cases observed in 1957, however, were significant at the 1 per cent level. Furthermore, it is unlikely that all three of the cases of partial dominance for lateness observed over the three-year period would involve the parent PO by chance. Crosses that approached significant partial dominance for lateness were: 1957, HF × PO, PO × GA; 1958, HF × PO, WF × PO; 1959, BA × PO, WF × PO, HF × SO. Since PO is earlier than any other parent in the crosses that show significant or almost significant partial dominance for lateness, it may contain one or more recessive alleles of a gene or genes that show partial dominance for lateness. Epistatic gene action may also contribute to this apparent partial dominance for lateness, since epistasis was detected by scaling tests in the cross BA × PO in 1958.[7]

This inspection of diallel cross F_1 families indicates that there is in the individual crosses a general tendency toward partial dominance for earliness that is especially pronounced in the crosses involving RA or BU. Sporadic cases do occur of apparent partial dominance for lateness, and nearly all of these involve crosses with PO. Evidently the genes which exhibit dominance are more important contributors to the total variability among the F_1 crosses than are the genes with little or no dominance effects.

Genetic Analysis by Means of Diallel Cross Graphs

The quantity $W_r - V_r$ is equal to $\frac{1}{4}(D - H_1)$ and is expected to be constant over all arrays if the basic assumptions of the diallel cross analysis are valid and environmental effects are zero. Since $\frac{1}{4}(D - H_1)$ does not vary with arrays under these conditions, W_r = constant + V_r, and the regression of W_r upon V_r is a straight line of unit slope. When $V_r = 0$, $W_r = \frac{1}{4}(D - H_1)$. Thus, on the (V_r, W_r) graph, the W_r intercept is an indicator of the average degree of dominance in the experimental materials. With partial dominance, $H_1 < D$, and the W_r intercept is positive. With overdominance, $H_1 > D$, and the W_r intercept is negative. If there is no dominance, $H_1 = 4\Sigma uvh^2 = 0$ and $F_r = \pm 8\Sigma uvdh = 0$, so that

$$V_r = \tfrac{1}{4}D + \tfrac{1}{4}H_1 - \tfrac{1}{4}F_r = \tfrac{1}{4}D$$
$$W_r = \tfrac{1}{2}D - \tfrac{1}{4}F_r = \tfrac{1}{2}D$$

or

$$V_r = \Sigma uv(d \pm h)^2 = \Sigma uvd^2$$
$$W_r = 2\Sigma uvd(d \pm h) = 2\Sigma uvd^2$$

In this case all points on the (V_r, W_r) graph are estimates of the single point $W_r = 2V_r$, and there is no regression. Therefore the (V_r, W_r) graph provides tests of significance for the presence of dominance ($b \neq 0$) and the average degree of dominance (sign of a), in which b is the slope of the regression line and a is the W_r intercept.

Since V_r and W_r each contain environmental components, Allard (1956*b*) suggested that analyses of variance be performed to determine the effects of

[7] A discussion of the scaling tests used to detect epistasis is given on page 9 of the microfilmed sections (see inside front cover).

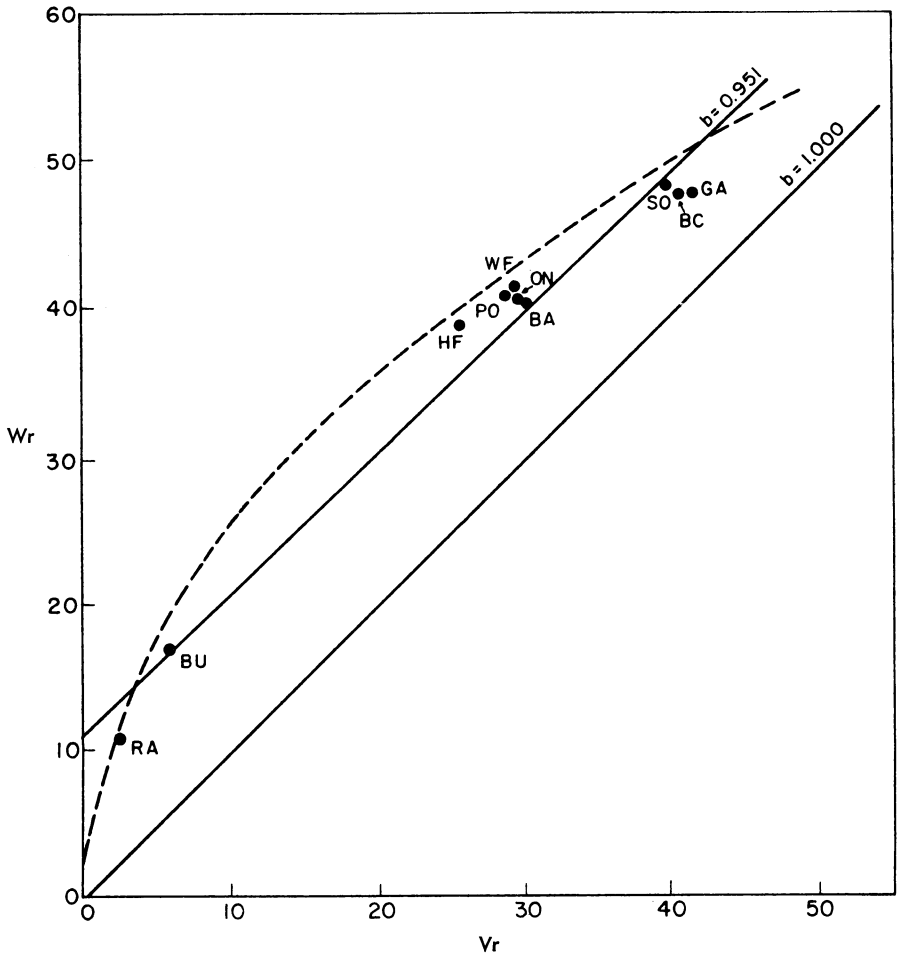

Fig. 1. (V_r, W_r) graph for 1957. The dots represent parental arrays. The solid lines are the line of best fit to the parental arrays and a reference line of unit slope through the origin. The broken line is the theoretical, limiting parabola within which all array points must lie. 95 per cent confidence limits of slope: $\beta = 0.824 - 1.078$.

environment upon V_r and W_r before proceeding with the graphical analysis. In the case of V_r, the variance ratio for arrays was highly significant in each year, whereas that for blocks was significant at the 5 per cent level in 1957 and nonsignificant in 1958 and 1959. For W_r, the variance ratios for both arrays and blocks were highly significant in each year; however, the magnitude of the variance ratio for arrays was 3 to 4 times that for blocks. Fluctuations in W_r resulting from block effects, though greater than fluctuations in V_r, are still small in comparison to those resulting from array (genotypic) effects.

It has already been mentioned that the slope of the regression line, b, was not significantly different from unity in any year (p. 280), and that a signifi-

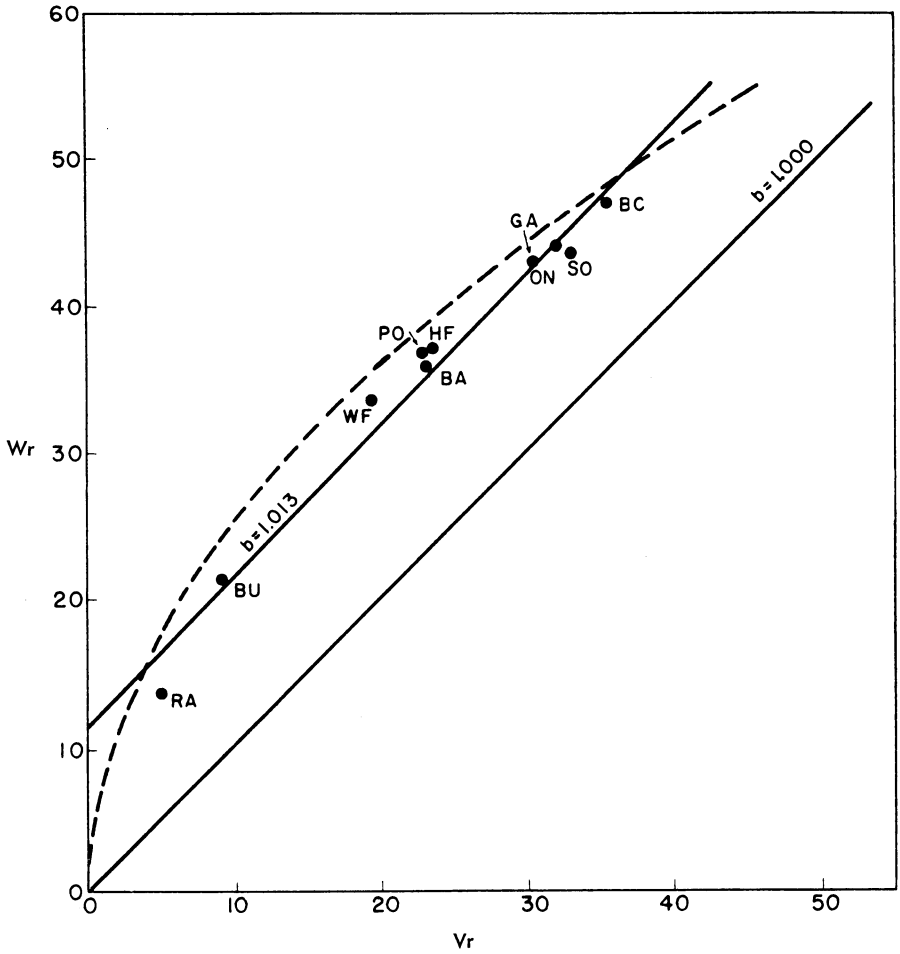

Fig. 2. (V_r, W_r) graph for 1958. 95 per cent confidence limits: β = 0.888 – 1.138.

cant regression exists, indicating the presence of dominance. The values of the W_r intercept, a, were respectively 11.15, 11.50 and 8.91 in 1957, 1958 and 1959 (figs. 1 to 3). Each of these values is significantly greater than zero ($P < 0.001$). Thus, the (V_r, W_r) graph also indicates that there is average partial dominance in the experimental materials.

The positions of the array points along the line of regression of W_r on V_r depend on the relative proportion of dominant and recessive alleles present in the common parent of each array (Jinks, 1954; Hayman, 1954*b*). Parents with a preponderance of dominant alleles will have a low array variance and covariance, and will lie near the origin. Highly recessive parents will have a large array variance and covariance, and will lie at the opposite end of the regression line. If the dominance effects of the genes are unequal, the position

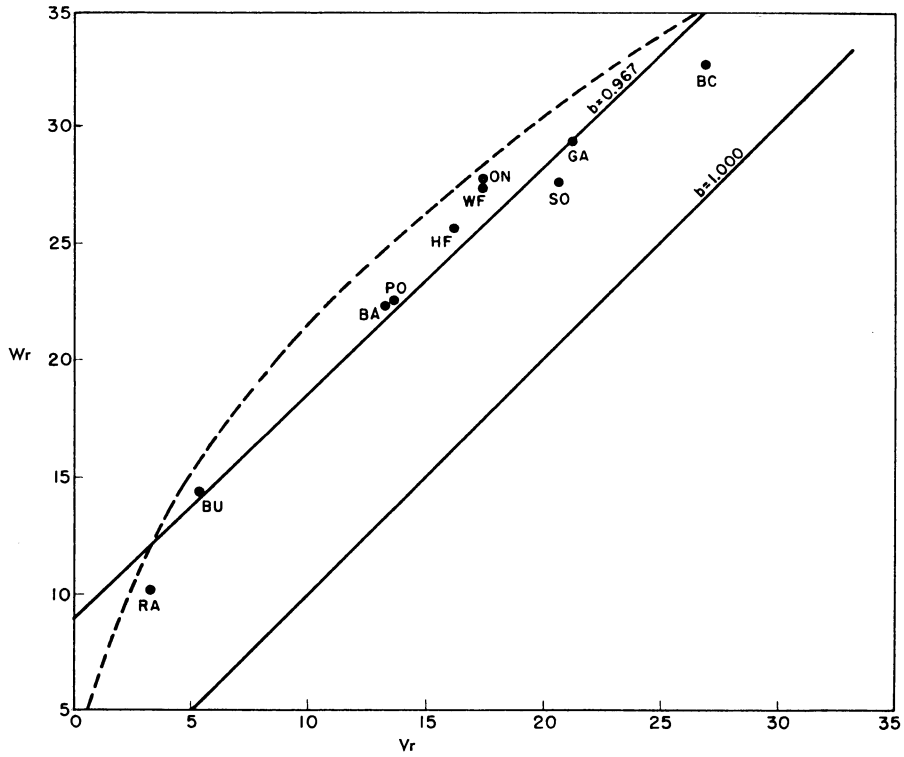

Fig. 3. (V_r, W_r) graph for 1959. 95 per cent confidence limits: β = 0.801 – 1.133.

of an array point will be weighted in favor of genes with large dominance effects. Figures 1 to 3 indicate that the parents with relatively high, low and intermediate levels of dominance maintained their positions on the graph reasonably well over the three-year period.

An idea of the limits of selection for genes with dominance effects can be obtained from the (V_r, W_r) graph (Hayman, 1954*b*).

The correlation coefficients of y_r (parental mean) and $W_r + V_r$ were found to be 0.907 (P = < 0.001) in 1957, 0.836 (P = 0.01–0.001) in 1958, and 0.848 (P = < 0.001) in 1959. Thus correlation was positive and high in each year. This provides evidence that most of the recessive alleles in the parents are acting in the direction of lateness and the dominant alleles in the direction of earliness, and agrees with the results presented in table 5 (p. 287).[8] Since an excess of recessive alleles (or gene effects in a weighted sense) among the parents was indicated by the negative values of F in each year (table 2, p. 282), there is probably an excess of positive (late) alleles as well. Thus a majority of the points on the (V_r, W_r) graphs (figs. 1 to 3) lie closer to the recessive end, particularly in 1957, when F had its largest negative value. These points

[8] A more complete discussion of this section is given on pp. 14–15 of the microfilmed sections (see inside front cover).

also represent the parents with later heading dates. After the values of $W_D + V_D$ and $W_R + V_R$ (array covariance and variance of the theoretically top dominant and bottom recessive parents) were obtained from the (V_r, W_r) graphs and substituted in the regression equation of y_r on $W_r + V_r$, the estimated means of the theoretically top dominant and bottom recessive parents were obtained (table 6). In each case the observed mean of the earliest parent was slightly earlier than the estimated mean for the theoretically top dominant parent, whereas the observed mean of the latest parent was later than the estimated mean for the theoretically bottom recessive

TABLE 6

COMPARISON OF EXTREME PARENTAL MEANS WITH THOSE OF THE THEORETICALLY TOP DOMINANT (y_D) AND BOTTOM RECESSIVE (y_R) PARENTS

Year	Parent	Observed mean	Estimated mean	95 per cent confidence limits*
1957	RA	10.3	11.4	5.6–17.2
	y_D	....	12.5	.....
	BC	35.1	31.5	28.0–35.0
	y_R	....	33.0	.....
1958	RA	18.6	18.9	12.6–25.2
	y_D	....	21.0	.....
	GA	44.9	39.0	35.3–42.7
	y_R	....	43.5	.....
1959	RA	9.8	9.8	3.6–16.0
	y_D	....	10.2	.....
	GA	31.6	24.9	21.3–28.5
	y_R	....	29.9	.....

* Confidence limits refer to the estimated means.

parent. Perhaps this should be expected, since the correlation between y_r and $W_r + V_r$ is not perfect, and there is evidence for some partial dominance in the direction of lateness. Thus the top dominant or bottom recessive genotype in the system would not be expected to have the earliest or latest phenotype, respectively. For genes with dominance effects, however, it appears that the limits of selection for earliness and lateness in the experimental materials have already been approached by the parental genotypes. It should be mentioned that no information has been obtained about the limits of selection for genes tightly linked in repulsion phase, except that they might be expected to produce apparent overdominance in certain F_1 combinations.

The (W_r, W'_r) graph can also be interpreted genetically (Allard, 1956*b*, 1956*c*). Whereas W_r is the covariance of array members with their nonrecurrent parents, W'_r is the covariance of array members with the array means of their nonrecurrent parents. Since W'_r tends toward lower values for dominant parents and higher values for recessive parents, the regression of W'_r on W_r may be used in the same way as that of W_r on V_r to detect the order of dominance in the parents. The (W_r, W'_r) graph does differ, however, from the

(V_r, W_r) graph in several ways. With certain conditions of overdominance some of the points may fall in the third quadrant. This is not possible on the (V_r, W_r) graph, since the values of V_r will, within the limits of sampling error, always be positive. The W'_r intercept is not an indicator of average dominance, since it will always be zero (that is, when $W_r = 0$, $W'_r = 0$). The (W_r, W'_r) graph also differs from the (V_r, W_r) graph in that it is affected by asymmetry of gene distribution. According to Hayman (1958), $W_r - 2W'_r = 1/8\ H_{r_2} +$ a constant, in which H_{r_2} is a quantity that varies over arrays only when there is an unequal distribution of positive and negative alleles (with respect to genes with dominance effects) among the parents. With gene symmetry ($u = v$ for all genes with dominance effects) W'_r = constant + $\frac{1}{2}W_r$, and the regression of W'_r on W_r is a straight line of slope one half. When there is asymmetry of gene distribution, parents with common genotypes will have relatively small values of H_{r_2}, and will fall above the line of slope one half. Parents with different or relatively rare genotypes will have larger H_{r_2} values and a position below the line of slope one half.

The (W_r, W'_r) graphs are found in figures 4 to 6. The distribution of parental array points is virtually identical to that found on the (V_r, W_r) graphs. This substantiates the conclusions about dominance order of the parents that were

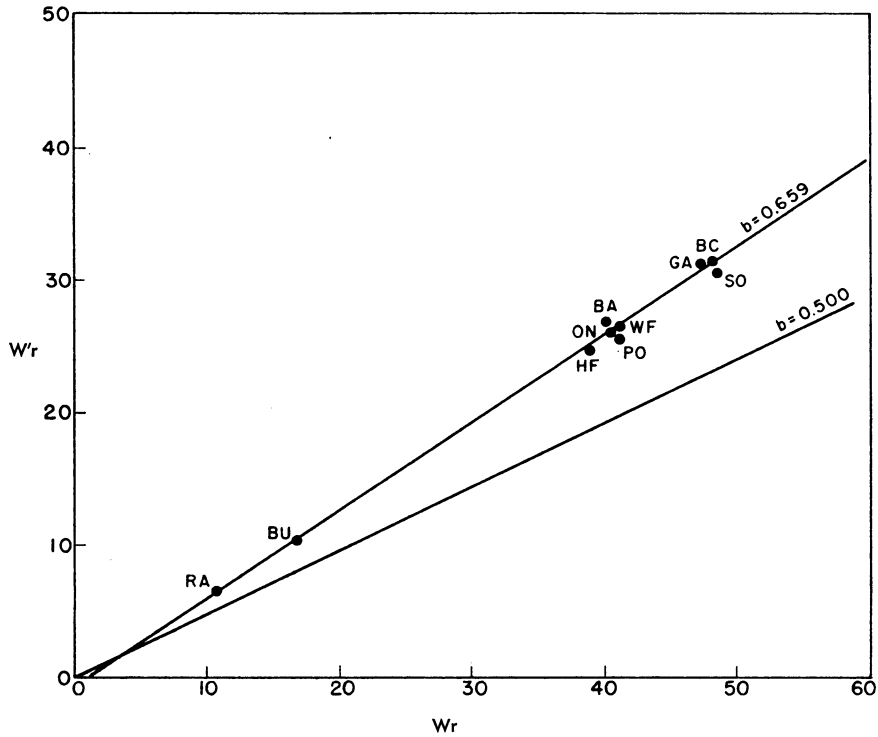

Fig. 4. (W_r, W'_r) graph for 1957. The dots represent parental arrays. The solid lines are the line of best fit to the parental arrays and a reference line of slope one half through the origin. 95 per cent confidence limits of slope: β = 0.631 – 0.687.

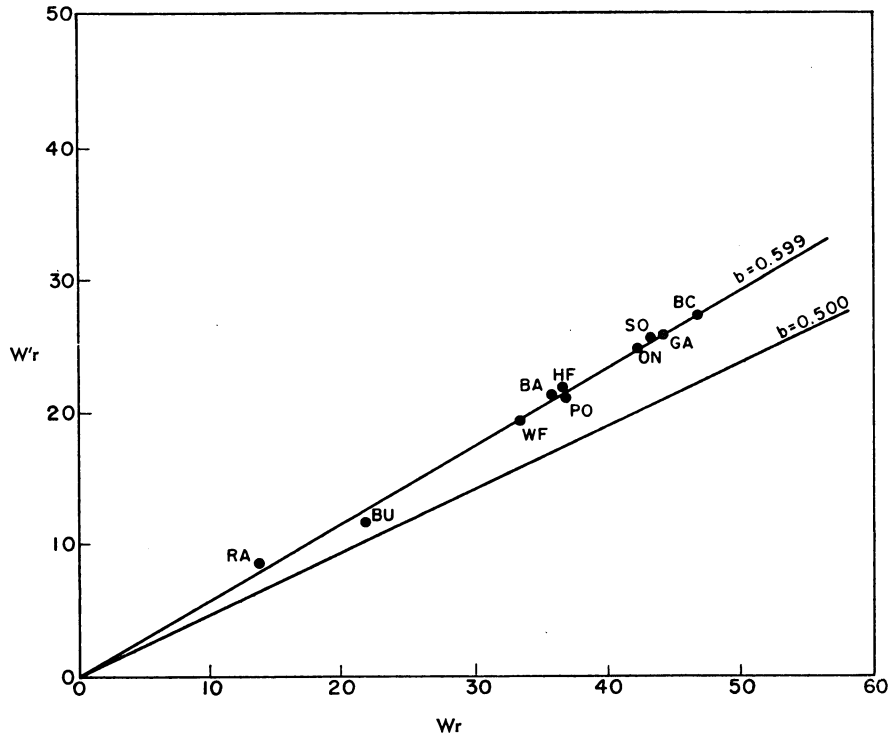

Fig. 5. (W_r, W'_r) graph for 1958. 95 per cent confidence limits: $\beta = 0.560 - 0.638$.

obtained from the regression of W_r or V_r. The slope of the regression line of W'_r on W_r is significantly greater than one half in each year ($P < 0.001$, 1957 and 1958; $P = 0.01$–0.001, 1959). Asymmetry of gene distribution, which was suggested earlier by the observation that $\bar{u} \neq \bar{v}$, is a reasonable explanation for this deviation from a slope of one half. The points representing RA and BU are widely separated from those of the other parents. The high degree of dominance in these 2 parents suggests that their genotypes are different from and rarer than the others. Their points would then be expected to fall below the line of slope one half. The remaining parents, with the more common genotypes, are expected to fall above the line of slope one half, and since they are located toward the distal end of the graph, the combination of these effects could cause the increase in slope.

Summary: The Genetic System

It can be deduced from the analysis in terms of genetic parameters that the genetic system differentiating the 10 parents has the following features:

(1) Heritability is relatively high, that is, a major part of the total phenotypic variability in this diallel cross is genetic. The additive and/or additive ×

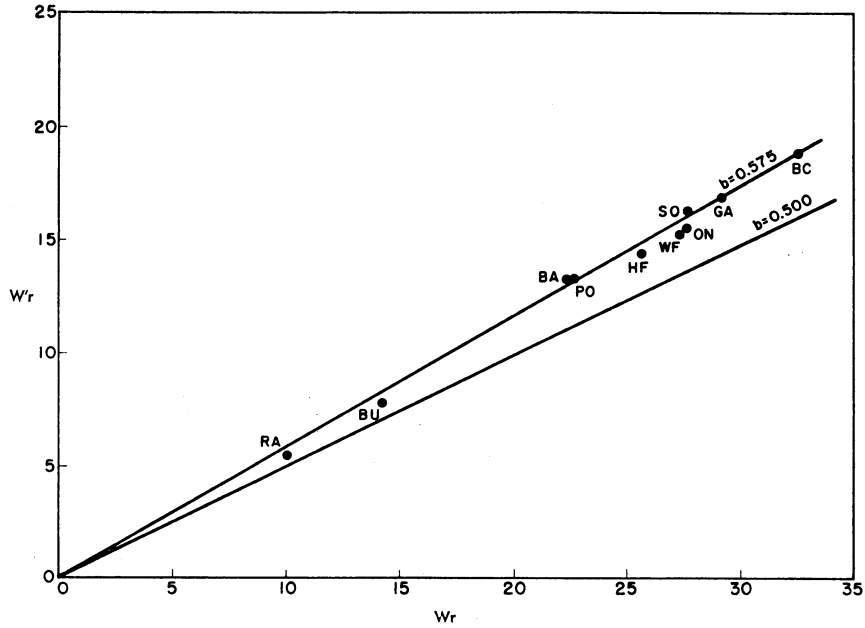

Fig. 6. (W_r, W'_r) graph for 1959. 95 per cent confidence limits: $\beta = 0.538 - 0.612$.

additive portion of the mean variance of arrays,

$$\frac{\frac{1}{4}D}{\frac{1}{4}D + \frac{1}{4}H_1 - \frac{1}{4}F + E},$$

was 55 per cent in 1957, 67 per cent in 1958 and 74 per cent in 1959.

(2) Genotypic-environmental interactions (in terms of interactions between genotypes and blocks within each year) produce a statistically significant but nevertheless trivial part of the total variability. Thus the genetic system can be regarded as generally stable with respect to microenvironmental differences which occur within any single nursery.

(3) Epistasis is not an important feature of the genetic system, that is, most of the genetic variability can be attributed to additive and dominance effects of genes.

(4) Many of the genes in the system show little dominance. The positive (late) and negative (early) alleles of these genes are more or less equally distributed among the parents. In general the genes which exhibit little or no dominance are less important contributors to the total variability in the F_1 crosses than genes which display dominance.

(5) Among genes exhibiting dominance, the dominance effects are unequal in both direction and magnitude. One or two genes with relatively high dominance effects may be present in the system.

(6) Averaged over all genes, the degree of dominance is partial and in the direction of earliness.

(7) The 10 parents fall into three groups according to relative levels of dominance: (a) highly dominant, (b) moderately recessive, and (c) highly recessive. The average dominance rankings of the parents are highly correlated with heading date, as reflected in table 11 (p. 302). The parents with late heading dates tend to have the more recessive genotypes.

(8) Recessive and positive alleles are more frequent among the parents than dominant, negative alleles, that is, the parents with the highest levels of dominance have the rarest and earliest genotypes in the system.

The graphical representations of the data support the above conclusions and permit certain more specific inferences about the genetic differences among the parents.

Phenotypes approaching those expected with the top dominant and bottom recessive genotypes occur among the 10 parents. Thus the extreme types among the parents represent an approach to the limits of selection for those genes which display dominance. The distribution of points on the graphs indicates that the parents Ramona and Bunyip are homozygous for the early allele *A*, of a major gene (or effective factor) that exhibits partial dominance for earliness, while the other 8 parents are genotypically *aa*. On similar evidence these 8 parents can be separated into two groups, one consisting of 5 members (White Federation, Baart 46, Hard Federation, Poso and Onas) carrying the early allele *B* of another gene showing partial dominance for earliness, *B*,*b*, which has somewhat lesser effect on heading date than gene *A*,*a*. Inspection of figures 1 to 3 suggests that the dominance effect of the *B* allele may not have been expressed in the parent Onas in 1958, since it shifted to the highly recessive group in that year. The parents Sonora, Galgalos and Big Club are homozygous for the recessive (late) allele *b* of this gene. The early, recessive allele *c* (of another gene, *C*,*c*, which is partially dominant for lateness) differentiates Poso from the other members of the intermediate maturity group. The estimate of one effective factor in each year (table 3, p. 282) may then have resulted from the fact that the major gene (or effective factor), *A*,*a*, dominates the system, and the genes (or effective factors) *B*,*b* and *C*,*c*, which have dominance effects in opposite directions, cancel each other out in the estimate of *K*. With respect to these three major genes the parental genotypes are postulated to be: Ramona, Bunyip—*AABBCC*; Poso—*aaBBcc;* Baart 46, White Federation, Hard Federation, Onas—*aaBBCC*; Galgalos—*aabbCC*; Big Club, Sonora—*aabbcc*. Thus, regarding the system of major genes, Ramona and Bunyip represent the earliest and Galgalos represents the latest genotype among the parents. The earliest combination of these genes, *AABBcc*, is not represented in any of the parents.

The remaining genetic variability appears to be governed by an indefinitely large number of genes of lesser effect. This polygenic system is in large part obscured by the system of major genes. Hence, the response to selection that the entire system of 10 parents is capable of producing cannot be determined in its entirety from parental and F_1 data alone.

STABILITY OF THE GENETIC SYSTEM IN DIFFERENT ENVIRONMENTS

The genetic model proposed in the previous section was based upon separate analyses of the data for 1957, 1958 and 1959. The similarity of the estimates of the various genetic parameters in the three years, together with the similar patterns in which parental points appeared on the graphs, suggests that genotypic-environmental interactions are not important in these materials. Nevertheless, this is an issue with an important bearing on the value that data obtained under one environment will have for predicting segregation patterns expected in other environments, and more precise analysis is clearly desirable.

A method proposed by Allard (1956*a*) of investigating the interaction of genetic parameters with environment involves an analysis of variance of the parental means and array variances and covariances from a diallel cross over a set of environments. The method permits determination of the stability of three kinds of parameters, namely, additive effects (*d*), dominance effects (*h*), and epistatic effects (*i*). It is assumed that all of the basic diallel cross assumptions are valid except that of "no epistasis." When epistasis occurs, the method is presumably capable of detecting it and assessing its stability in different environments.

The parental means in each year are listed in table 1 (p. 278). Each mean represents an average of four blocks in 1957 and 1958, and of two blocks in 1959. Since the subclass (block) numbers are proportional (4:4:2), the analysis of variance is not disturbed as long as the computations are modified according to the unequal-sized groups (Snedecor, 1946). However, each subclass variate in 1959 is based on the heading dates of approximately twice as many plants as in 1957 and 1958. This might introduce bias into the estimate of the error variance, which includes a composite of the parents × blocks interaction terms for each year. To determine the importance of this possible bias, data from the adjacent blocks 1 and 2, and 3 and 4 in 1957 and 1958 were combined. This restores equality in subclass numbers, and also provides an approximately equal number of plants upon which to base the value of each subclass variate. The results from this analysis were similar enough to those of the original, nonorthogonal analysis that any bias in the original analysis can be regarded as negligible.

The analysis of variance of parental heading dates is presented in table 7. The highly significant variance ratio for parents indicates that the parental genotypes have different additive and/or epistatic effects. In view of the homozygosity of the parents, epistatic effects would be those which result from interactions between homozygous loci, that is, the additive × additive type of interaction (Cockerham, 1954; Hayman and Mather, 1955). The high significance of the variance ratio for years shows that the additive and/or additive × additive effects of the genes, averaged over all parents and blocks, were dissimilar in different years. This is obvious from inspection of the

TABLE 7
ANALYSIS OF VARIANCE OF PARENTAL HEADING DATES

Source of variation	Sum of squares	Degrees of freedom	Mean square	Variance ratio	Probability
Parents	5,194.01	9	577.11	648.44	< 0.01
Years	2,337.31	2	1,168.66	1,313.10	< 0.01
Blocks within years	73.46	7	10.49	11.79	< 0.01
Parents × years	124.43	18	6.91	7.76	< 0.01
Error	55.92	63	0.89	.....	.....
Total	7,785.13	99			

yearly means in table 1. Any of a host of environmental factors that were not the same in the three years could have contributed to these differences. The variance ratio for parents × years was much smaller than that for parents or years, but it was still highly significant. This provides evidence for the interaction of additive and/or additive × additive gene effects with years.

The order in which the parents headed was:

	RA	BU	PO	WF	BA	HF	ON	SO	GA	BC
1957	1	2	3	4	5	5	7	8	9	10
1958	1	2	3	4	7	5	8	6	10	9
1959	1	2	2	4	6	5	7	8	10	9

In an effort to determine which parental genotypes were contributing to the over-all instability, the change in value of each of the 45 parental differences was determined for 1957–1958, 1957–1959 and 1958–1959. Comparisons were of the following type: $(\overline{X}_{1,\,1957} - \overline{X}_{2,\,1957}) - (\overline{X}_{1,\,1958} - \overline{X}_{2,\,1958})$, where $\overline{X}_{1,\,1957}$ is the mean for parent 1 in 1957. This can be rewritten as $(\overline{X}_{1,\,1957} + \overline{X}_{2,\,1958}) - (\overline{X}_{2,\,1957} + \overline{X}_{1,\,1958})$. The standard error for the 1957–1958 comparisons is s and for 1957–1959 and 1958–1959 comparisons, $\sqrt{3/2}\ s$ (because of the smaller number of blocks in 1959), where s is the standard error from the analysis of variance of parental heading dates (table 7). In all, 135 comparisons were made. Tests of significance were based on the *LSD* method, using Federer's suggested correction, as mentioned previously on page 287. Twenty-seven per cent of the 1957–1958, 49 per cent of the 1957–1959 and 36 per cent of the 1958–1959 comparisons showed a significant interaction effect (1 per cent level). The various comparisons which were significant at the 1 per cent level were then ranked in order of decreasing interaction effect (that is, in order of increasing stability). The comparison $(RA_{57} - HF_{57}) - (RA_{59} - HF_{59})$ was found to have the greatest difference or "interaction effect" (numerical value = 7.8 days). From this comparison alone, it is not clear whether the interaction is due to unstable additive and/or additive × additive effects in the Ramona genotype, the Hard Federation genotype or both. However, by observing the number of times that a particular parent occurs throughout the various comparisons, it is possible to obtain

some evidence in this respect. Thus, from a study of table 8 it appears that the Ramona genotype is the most unstable in its additive and/or additive × additive genetic effects, while the genotype of Poso is among the most stable.

To test the constancy of dominance and/or additive × dominance and dominance × dominance effects, an analysis of variance was performed on the array variances and covariances over the three-year period. Since information on the stability of additive and/or additive × additive effects had already been provided by the analysis of variance of parental means, an at-

TABLE 8

RANKING OF PARENTS FOR STABILITY OF ADDITIVE AND/OR ADDITIVE × ADDITIVE EPISTATIC EFFECTS
(from A.O.V. of parental heading dates)

1. In comparisons significant at the 1 per cent level.

Parent	RA	BU	GA	SO	HF	BA	WF	ON	PO	BC
Number of occurrences	14	13	11	11	10	9	8	6	5	5
Rank	1	2	3	3	5	6	7	8	9	9

→ Increasing stability →

2. In comparisons with a numerical difference or "interaction effect" of greater than 5 days (approximately the top ⅓ of those significant at 1 per cent level).

Parent	RA	WF	HF	BA	BU	GA	BC	SO	ON	PO
Number of occurrences	8	4	4	3	3	3	1	1	1	0
Rank	1	2	2	4	4	4	7	7	7	10

→ Increasing stability →

tempt was made to minimize these effects according to Allard's suggestion (1956*a*): prior to analysis, each variance and covariance was divided by the V_{0L0} (variance of parents) value occurring in its respective block. Each transformed variance and covariance was then multiplied by 100 to avoid decimals. Table 9 gives the analysis of variance of the transformed statistics.

The mean square for years is estimated from the sum of $W_r + V_r$ over all blocks and arrays for each year. In the absence of epistasis, it detects variation over years of $W_{0L01} + V_{1L1}$, or $\frac{3}{4}D + \frac{1}{4}H_1 - \frac{1}{2}F$. The variance ratio for years was highly significant. If transformation was effective, this significance probably resulted from a change in mean dominance (H_1) and/or the relative proportion of dominant and recessive genetic effects (F) over years (see table 2, p. 282). Epistatic effects may also have contributed to the variation over years.

The dominance mean square is estimated from the difference between the

TABLE 9

ANALYSIS OF VARIANCE OF ARRAY VARIANCES AND COVARIANCES*

Source of variation	Sum of squares	Degrees of freedom	Mean square	Variance ratio	Probability
Arrays	51,208.8	9	5,689.87	928.20	< 0.01
Years	3,310.1	2	1,655.05	269.99	< 0.01
Dominance	11,689.2	1	11,689.20	1,906.88	< 0.01
Blocks within years	621.9	7	88.84	14.49	< 0.01
Arrays × years	3,338.5	18	185.47	30.26	< 0.01
Dominance × years	90.7	2	45.35	7.40	< 0.01
Dominance × arrays (epistasis)	380.1	9	42.23	6.89	< 0.01
Dominance × arrays × years	126.4	18	7.02	1.15	Not sig.
Arrays × blocks (within years)	6,753.1	63	107.19	17.49	< 0.01
Dominance × blocks (within years)	102.9	7	14.70	2.40	0.05–0.01
Dominance × arrays × blocks (within years)—error	386.1	63	6.13	.....	.....
Total	78,007.8	199			

* Each variance and covariance was transformed prior to analysis through division by the V_{0L0} (variance of parents) value occurring in its respective block, and then multiplied by 100 to avoid decimals.

sum of W_r and the sum of V_r, each sum being taken over all blocks, years and arrays. In the absence of epistasis, it measures the average degree of dominance, that is, $W_{0L01} - V_{1L1}$ or $\frac{1}{4}(D - H_1)$. The magnitude of this difference depends on the degree of dominance, being zero when there is full dominance. The variance ratio for dominance was highly significant. Therefore, on the scale of measurement used, the average degree of dominance is apparently not complete. This is consistent with previous evidence for average partial dominance in the system.

The dominance × years mean square tests the stability of the average degree of dominance and/or epistatic effects over years. The variance ratio was highly significant, indicating that the average degree of dominance changed with years (see table 3, page 282). Epistatic effects may also have contributed to the significance of this variance ratio.

The arrays mean square is estimated from the sums of $W_r + V_r$ for each array, taken over all blocks and years. It tests variation in $W_r + V_r$ from one array to the next. The higher the level of dominance in a parent, the smaller will be its $W_r + V_r$ value and vice versa. Thus $W_r + V_r$ is an indicator of the average level or proportion of dominant and recessive alleles that are present in a particular parent. The $W_r + V_r$ value of a parent determines its rank along the regression line of the (V_r, W_r) and (W_r, W'_r) graphs. If epistatic effects are present, they, too, will contribute to the apparent level of dominance in the different parents. The high significance of the variance ratio for arrays indicates that the different parents have different levels of dominance, and/or possibly different epistatic effects. This supports the evidence presented in the previous section.

The mean square for arrays × years tests the constancy of the average level of dominance and/or epistatic effects for each parent over the three-year

period. The variance ratio was highly significant, indicating that the positions of the parental arrays on the graphs (figs. 1 to 6) did not remain constant in different years. In terms of their average transformed $W_r + V_r$ values, the parents were ranked in order of decreasing level of dominance as follows:

	RA	BU	HF	ON	PO	WF	BA	BC	SO	GA
1957.....	1	2	3	4	5	6	7	8	9	10
1958.....	1	2	6	7	5	3	4	10	8	9
1959.....	1	2	5	6	4	6	3	10	8	9

The contribution of individual parental genotypes to the over-all instability was examined by methods identical to those described on page 298, except that the standard error for 1957–1958 comparisons becomes $\sqrt{\frac{1}{2}}\ s$ and for 1957–1959 and 1958–1959, $\sqrt{\frac{3}{4}}\ s$. The smaller coefficients in the standard error are a result of the fact that two statistics, W_r and V_r, occur in each block, thus doubling the number of individual variates upon which each mean is based. Seventy-six per cent of the 1957–1958, 71 per cent of the 1957–1959 and 33 per cent of the 1958–1959 comparisons showed a significant interaction effect (1 per cent level). The comparison ($RA_{57} - WF_{57}$) − ($RA_{58} - WF_{58}$) was found to have the greatest difference or "interaction effect" (numerical value = 24.5). From a study of table 10 the genotype of White Federation appears to be the most unstable in its dominance and/or epistatic effects, whereas Onas and Poso appear to have two of the more stable genotypes.

TABLE 10

RANKING OF PARENTS FOR STABILITY OF DOMINANCE AND/OR EPISTATIC GENETIC EFFECTS

(from A.O.V. of array variances and covariances)

1. In comparisons significant at the 1 per cent level.

Parent	WF	RA	BC	BU	BA	SO	HF	GA	PO	ON
Number of occurrences	24	18	17	16	15	15	15	13	13	12
Rank	1	2	3	4	5	5	5	8	8	10

→ Increasing stability →

2. In comparisons with a numerical difference or "interaction effect" of greater than 14.0 (the top ⅓ of those significant at the 1 per cent level).

Parent	WF	BU	RA	BA	GA	PO	SO	ON	HF	BC
Number of occurrences	9	9	7	6	6	5	5	5	1	1
Rank	1	1	3	4	4	6	6	6	9	9

→ Increasing stability →

It is interesting to compare the results of the investigation of instability for additive and/or additive × additive epistatic genetic effects with that of dominance and/or epistatic genetic effects. The parent Ramona was the most unstable in its additive and/or additive × additive effects, and was among the most unstable in its dominance and/or epistatic effects. Evidently, the over-all genotype of Ramona is the most unstable in the group. Its average heading date and $W_r + V_r$ values (table 11) were different enough from those of the other parents in the group that this instability did not result in a change of rank of Ramona with respect to heading date or $W_r + V_r$ value from one year to the next. With respect to additive and/or additive × additive epistatic effects, the interaction effects of the parents as a group were larger and more numerous for the periods 1957–1959 and 1958–1959 than for the period 1957–1958. This may have resulted from similar types of instability in 1957 and 1958, but it seems more reasonable to assume that the parental genotypes were most unstable in 1959. Likewise, in the case of dominance and/or epistatic effects, it seems more logical to assume that the parental genotypes, on the whole, were most unstable in 1957. The prevalence of instability for dominance and/or epistatic effects in 1957 was more pronounced than that for additive and/or additive × additive effects in 1959.

It is also interesting to compare the magnitude of the instability of additive and/or additive × additive epistatic effects in the parents with the magnitude of the instability of their dominance and/or epistatic effects. Scheffe's test (Federer, 1955) has a relatively low type I error and a relatively high type II error in comparison to the *LSD* test (see footnote 6, page 287). When Scheffe's test was applied to the data from the analysis of variance of parental heading dates, it was not possible to demonstrate significant differences for individual comparisons, even at the 5 per cent level. However,

TABLE 11

$W_r + V_r$ VALUES AND PARENTAL MEANS (y_r) AVERAGED OVER BLOCKS AND YEARS

Level of dominance	Parent	$W_r + V_r$*	y_r
Highly dominant	RA	15.8	13.4
	BU	22.6	19.4
Moderately recessive	WF	49.0	25.6
	BA	49.8	29.6
	HF	49.8	28.0
	PO	49.8	21.4
	ON	54.9	31.1
Highly recessive	SO	63.0	30.4
	GA	63.9	38.0
	BC	66.7	36.4

* Each $W_r + V_r$ value transformed as follows: $\frac{100}{2}\left(\frac{W_r}{V_{0L0}} + \frac{V_r}{V_{0L0}}\right)$ prior to averaging over blocks and years. V_{0L0} refers to the variance of the parents in a particular block.

when Scheffe's test was applied to the data from the analysis of variance of W_r and V_r, it was possible to demonstrate a large number of significant differences at the 1 per cent level. In fact, the group of individual comparisons which was significant at the 1 per cent level with Scheffe's test coincides very closely with the group that had interaction effects above a value of 14.0 (table 10). Even though the difference required by Scheffe's test for significance was quite large, it was still possible to demonstrate a significant interaction or instability effect for dominance and/or epistatic effects in a number of instances. In other words, the magnitude of the instability for dominance and/or epistatic effects is much greater than that for additive and/or additive × additive epistatic effects. Instability effects of the former type were also much more prevalent among the parents than those of the latter type. This was indicated by the much greater proportion of cases of significant interaction for dominance and/or epistatic effects which appeared when the individual comparisons were tested over the three-year period.

If epistasis is absent, the variance ratio for dominance × arrays should be nonsignificant, since $W_r - V_r$ will be constant over all arrays. With classical types of epistasis $W_r - V_r$ will no longer be constant over arrays (Allard, 1956*a*), but it will still be independent of fluctuations in the additive and dominance effects of the parental genotypes. Thus the high significance of the variance ratio for dominance × arrays provides evidence for the presence of an epistatic system. This agrees with earlier results obtained from scaling tests (see footnote 7, page 288). Nonsignificance of the variance ratio for dominance × arrays × years suggests that the epistatic effects in the system (at least those of an additive × dominance and/or dominance × dominance nature) were relatively stable over the three-year period.

A comparison of the magnitude of the variance ratio for arrays and for dominance × arrays in table 9 (p. 300) shows that most of the variation in rank along the regression line of the (V_r, W_r) and (W_r, W'_r) graphs can be attributed to different levels of dominance in the various parents. A similar comparison of the variance ratios for arrays × years and for dominance × arrays × years indicates that most of the instability in rank along the regression line is a result of fluctuation in the average level of dominance in the various parents from one year to the next.

USE OF PARENTAL AND F_1 DATA TO PREDICT SEGREGATION IN F_2 AND CERTAIN OTHER GENERATIONS

In 1958 an F_2 nursery was grown to check the accuracy with which the diallel cross analysis predicts segregation in specific crosses. In this nursery observations on heading date were made on five hybrids: RA × PO; RA × BC; BA × PO; BA × GA; BC × GA. These hybrids were selected for study in F_2 because they represent various combinations between and within the highly dominant, moderately recessive and highly recessive parental groups (based originally on the 1957 analysis). Data on two additional combinations, RA × BU (Ashcroft, unpublished) and RA × BA (Allard, unpublished), were also available for additional comparisons between prediction and observation.

Two procedures were used in comparing predictions and observations. First, the phenotypic variances of different F_2 populations were calculated from the observations. The F_2 populations were ranked on the basis of magnitude of variance and these rankings were compared with the rankings predicted from the diallel analysis. Second, observed frequency distributions were compared with the frequency distributions predicted from information provided by the diallel analysis on the major genes differentiating the parents.

Comparisons Between Predicted and Observed Variances

The diallel analysis indicated that the genes exhibiting dominance were responsible for a major part of the total genetic variance. Hence, differences in the sum $W_r + V_r$ should provide a measure of the genetic diversity among parents and thus an indication of the magnitude of the variances expected in segregating generations. The average rankings of the parents in level of dominance and heading date appear in table 11, page 302. The observed differences in the sum of $W_r + V_r$ were as follows: BC − RA = 50.9; PO − RA = 34.0; BA − RA = 34.0; GA − BA = 14.1; BU − RA = 6.8; BC − GA = 2.8; PO − BA = 0.

The F_2 of RA × BC is from the cross of the parents having the maximum difference in $W_r + V_r$. This F_2 is therefore expected to have the largest variance. Conversely, the F_2's of BC × GA, RA × BU, and BA × PO are expected to have the smallest variances on the basis of small differences in $W_r + V_r$. It can be predicted that the three remaining combinations, RA × PO, BA × RA, and BA × GA, which represent intergroup crosses, will have generally intermediate variances in F_2 with the variances of BA × RA and RA × PO expected to exceed that of BA × GA. Prediction appears least likely to be reliable for the combination BA × PO because the diallel analysis indicated considerable genetic diversity within the moderately recessive group and also because of the possibility that epistatic gene action occurs within this group. The variety PO in particular appeared to differ from the

other members of the group by virtue of containing partially recessive allele(s) for earliness. Its mean heading date is several days earlier than those of the other members of the moderately recessive group.

The null hypothesis that there are no differences among the F_2 phenotypic variances was tested by means of an analysis of variance. The F_2 nursery was replicated so that individual block estimates of each F_2 variance were available. Each block estimate was based on an average of 112 degrees of freedom. Since the variance in each block is the mean of a sum of squares, and is based on a large number of degrees of freedom, the distribution of the variances should approximate to normality. When the analysis of variance was performed, almost all of the variation in individual-plant F_2 variances was found

TABLE 12
DUNCAN'S NEW MULTIPLE RANGE TEST APPLIED TO INDIVIDUAL-PLANT F_2 VARIANCES, 1958

5 per cent level test				
RA × BC	RA × PO	BA × PO	BA × GA	BC × GA
79.93	21.50	21.37	10.23	8.63

Variances underscored by the same line do not differ significantly.
Variances not underscored by the same line are significantly different.
Average individual-plant variance of the 5 parents = 5.35.

to result from differences among F_2 populations. Duncan's multiple range test (Duncan, 1955) was used to test the ranking of the F_2 variances. The results are presented in table 12. The average individual-plant variance of the 5 parents, 5.35, is a measure of environmental variance. It provides a base of reference for comparing the variances of the F_2 populations, which contain both genetic and environmental variation. It is assumed that the different F_2 populations will exhibit a similar magnitude of environmental variation. This appears to be a reasonable assumption, since the heterogeneity of individual-plant variances of the 5 parents was found by Bartlett's test to be barely significant (P = 0.05–0.02). Except for the cross BA × PO, the variance estimates agree with the ranking that was suggested by differences in $W_r + V_r$ values. Since the average F_2 individual-plant environmental variance is probably 1 or 2 days higher than that of the parents alone ($V_{F_1} > V_P$ in 1958), the F_2 variance of BC × GA must be largely environmental. The magnitude of the F_2 variance of BA × PO is seen to be practically identical to that of RA × PO. This confirms the earlier suggestion that genetic diversity due to genes exhibiting dominance effects might be considerable between parents within the moderately recessive group. The F_2 variance was smaller for BA × GA than the variance for RA × PO. This was expected since the diallel analysis indicates less genetic diversity between the moderately and highly reces-

sive groups than between the highly dominant and moderately recessive groups. Failure to show a significant difference between BA × GA and BC × GA in F_2 variances may have resulted from the confusing effects of nonallelic interactions which the scaling tests also indicated to be a factor in these crosses (see footnote 7, page 288).

F_2 populations of RA × BU and BA × RA were not included in the above analysis because these populations, while grown in the same field, were in separate nurseries from the other 5 F_2 populations. The F_2 variance of RA × BU was 7.84 (158 degrees of freedom). This small variance was expected since the diallel analysis indicated that RA and BU differ by relatively minor additive and/or dominance and epistatic effects. The F_2 variance of BA × RA was 70.62 (547 degrees of freedom). Since this cross tests the span between the highly dominant and moderately recessive groups, it also agrees with the ranking of F_2 variances suggested by the diallel cross analysis.

Prediction of Segregation Patterns in F_2 and Certain Other Generations

The most conspicuous feature of the graphical analysis was the striking discontinuity between the points representing RA and BU and those representing the 8 other parents. Discontinuity was similar but less striking between the points representing BA, WF, HF, PO, and ON on the one hand and SO, GA, and BC, on the other. Interpretation of these discontinuities and of the diversity within the moderately recessive group in terms of three major genes (see page 296) can be tested by comparing predicted and observed frequency distributions in segregating generations. The tests will not consider epistatic effects although they probably account for at least some of the variation that occurs, particularly in crosses between and within the moderately recessive and highly recessive groups.

The frequency distributions of the F_2 populations are given in figures 7 to 16.

The cross RA × BC is expected to segregate for the major gene, *A,a*, as well as for the genes of lesser effect, *B,b* and *C,c*. This should produce a ratio of approximately 3 early to 1 late plant in F_2. Further, the late class should contain three types of plants in the approximate proportions 3 medium late to 10 late to 3 very late. A good approximation of 3 early to 1 late plants was actually obtained, and the late class was trimodal, as expected (fig. 7). Approximately 1/64 or 6 of the F_2 plants should have been *AABBcc* and thus earlier than RA. Only one possible segregate of this type was actually observed.

The cross BA × RA is expected to segregate for only the *A,a* gene, therefore producing a 3:1 distribution of early and late plants in F_2. Expected ratios of early to late plants for the other generations of this cross are 5:3 (F_3), 1:1 (B_1 F_1), 1:0 (B_2 F_1), 3:5 (B_1 F_2), and 7:1 (B_2 F_2). Good approximations to these ratios were obtained in all cases (figs. 8 to 10).

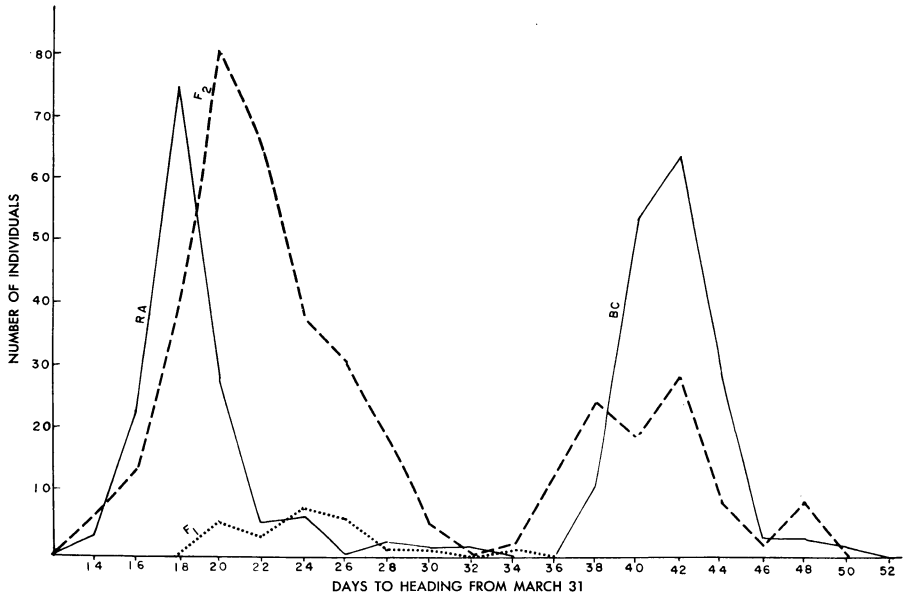

Fig. 7. Frequency distributions from the cross RA × BC.

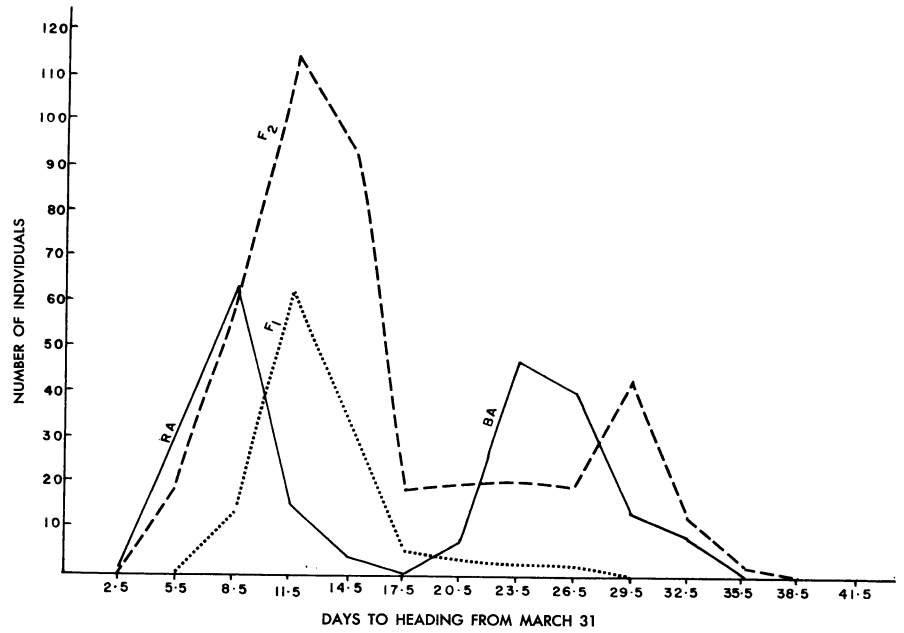

Fig. 8. Frequency distributions from the cross BA × RA.

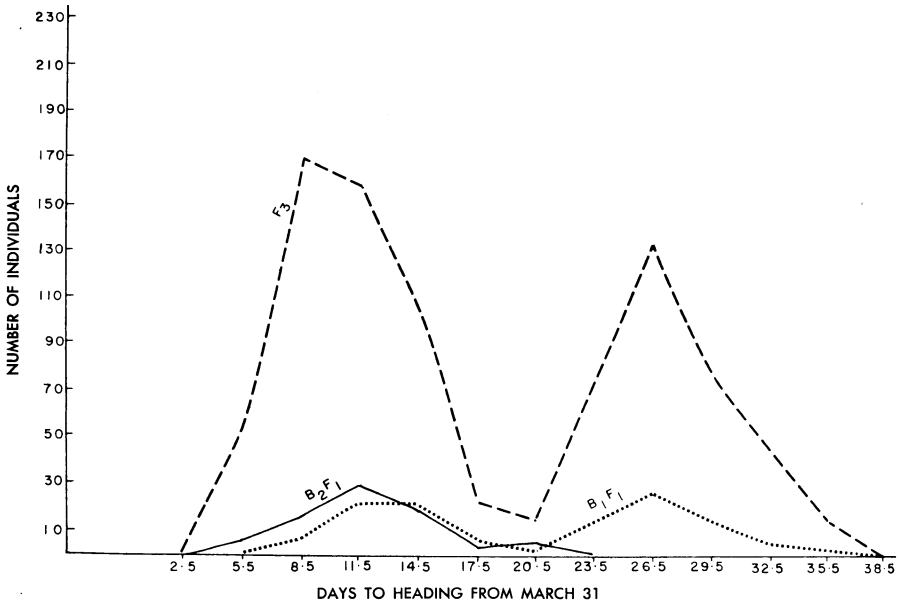

Fig. 9. Frequency distributions from the cross BA (1) × RA (2).

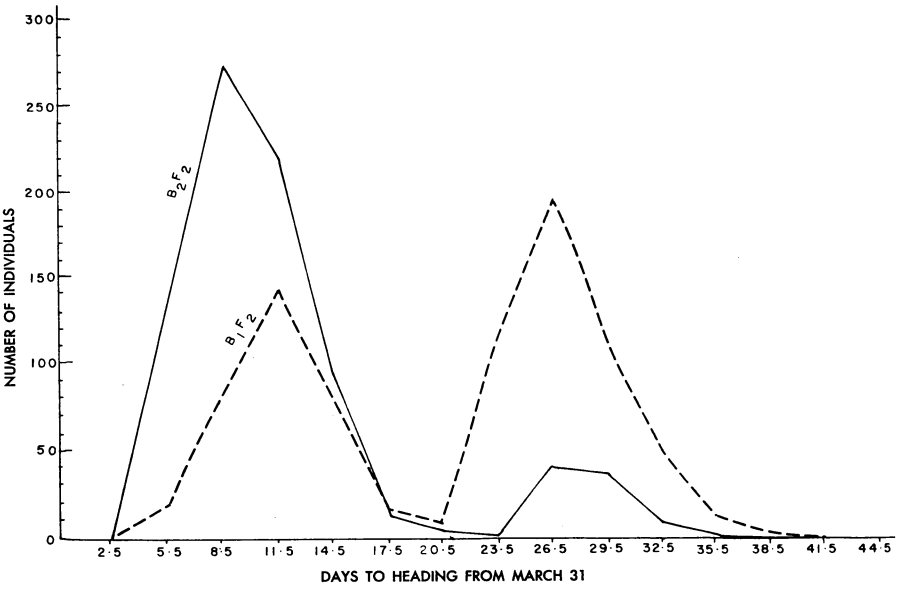

Fig. 10. Frequency distributions from the cross BA (1) × RA (2).

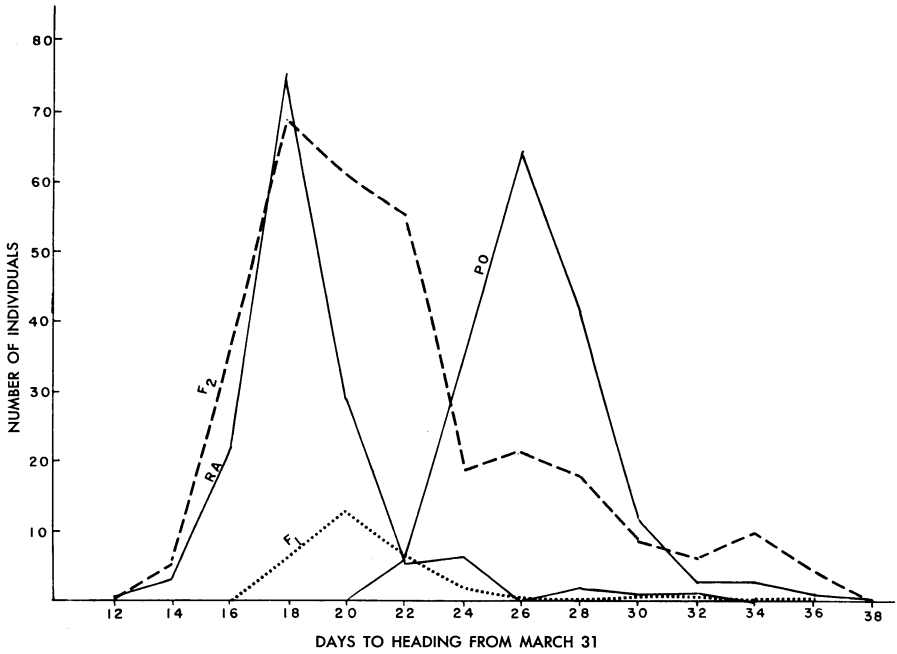

Fig. 11. Frequency distributions from the cross RA × PO.

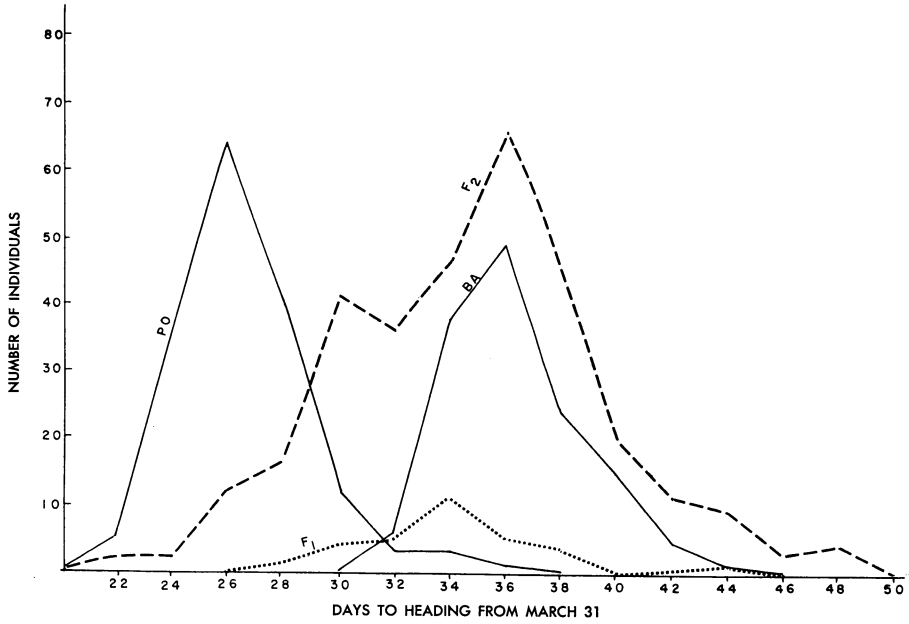

Fig. 12. Frequency distributions from the cross BA × PO.

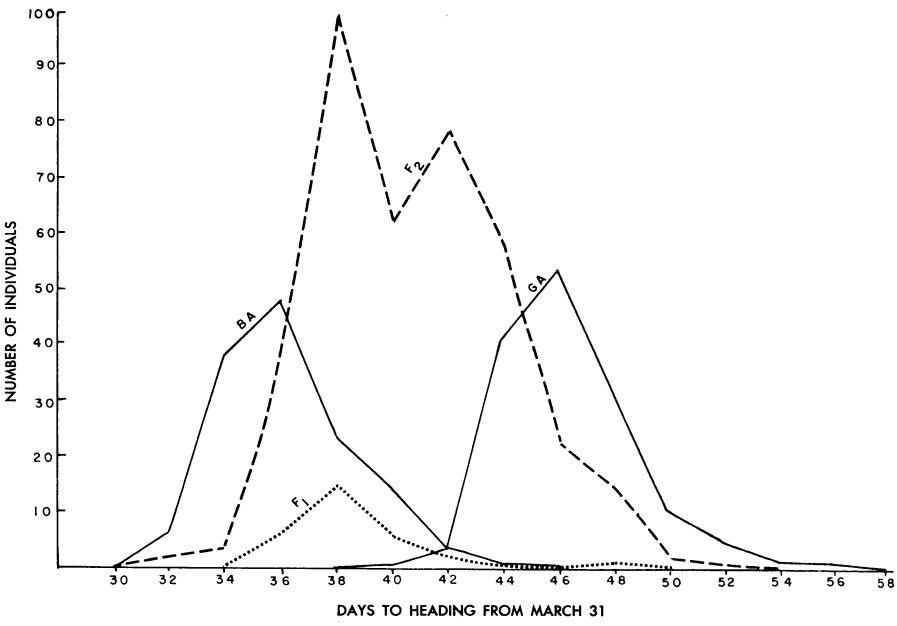

Fig. 13. Frequency distributions from the cross BA × GA.

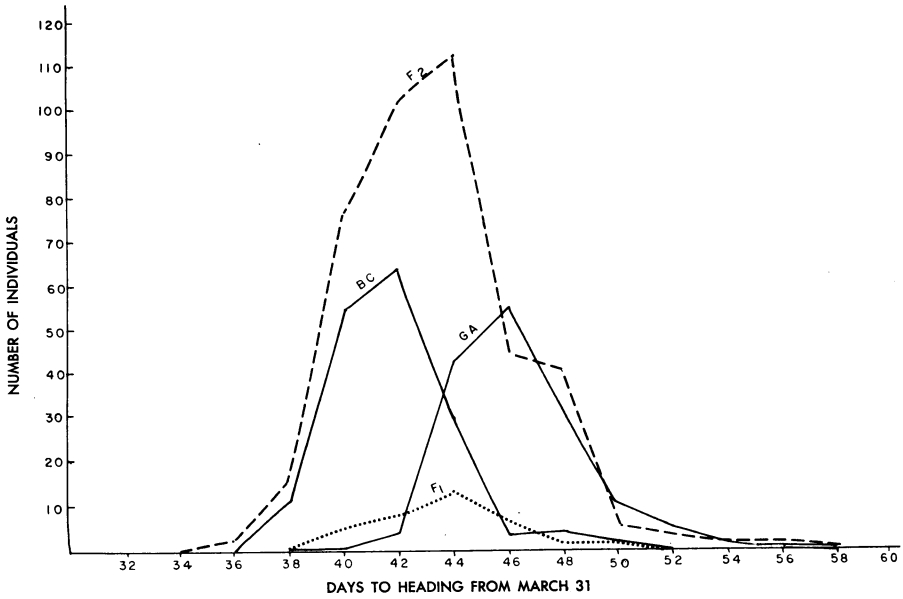

Fig. 14. Frequency distributions from the cross BC × GA.

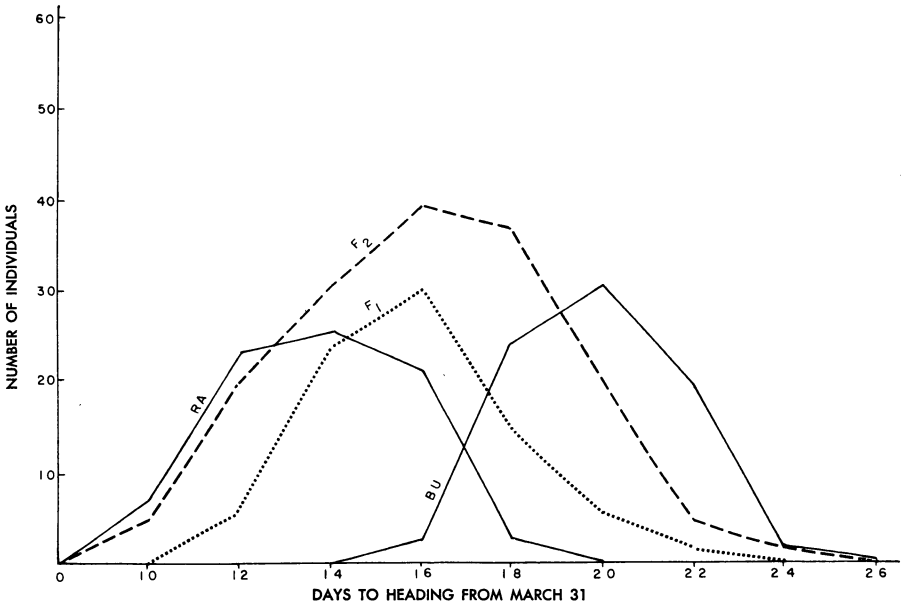

Fig. 15. Frequency distributions from the cross RA × BU.

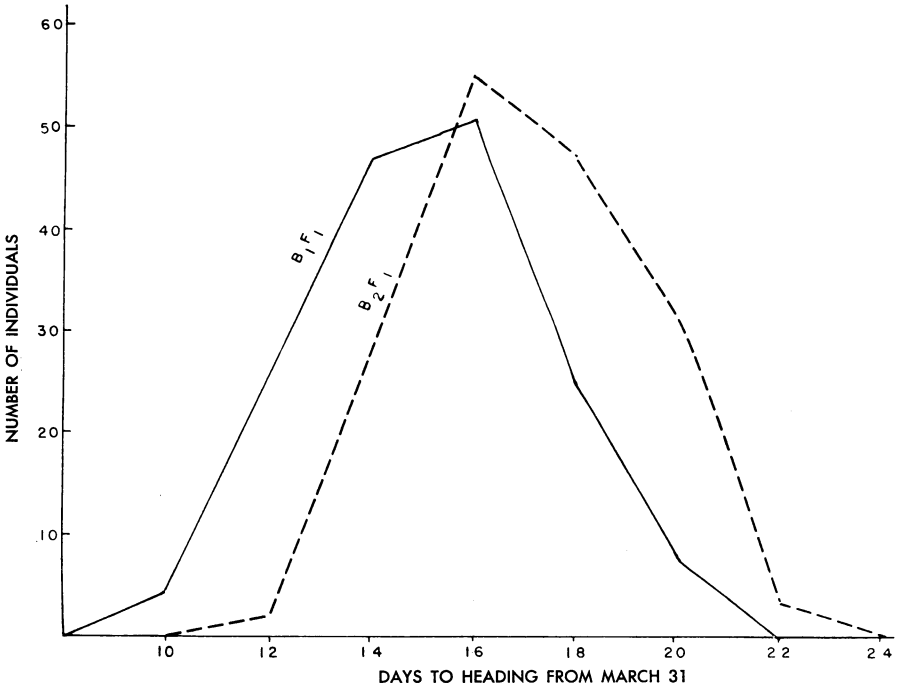

Fig 16. Frequency distributions from the cross RA (1) × BU (2).

The cross RA × PO is expected to segregate for the genes *A,a* and *C,c*. This should result in an F_2 ratio of approximately 3 early to 1 late plants and within the late class 1 medium late to 3 late plants are expected. The actual F_2 distribution was a reasonable approximation of 3:1, and the late class was bimodal, although not clearly in the ratio of 1:3 (fig. 11). However, the means of RA and PO are close enough together so that the partial dominance of heterozygous genotypes may lead to a poor definition of class boundaries. Although approximately 1/16 or 20 of the F_2 plants should have been transgressive segregates of the constitution *AABBcc*, none were observed.

The hybrid BA × PO is expected to segregate only for the gene *C,c* and thus yield in F_2 a bimodal distribution skewed toward lateness. This was found to be the case (fig. 12).

The cross BA × GA should segregate only for the gene *B,b* producing in F_2 a bimodal distribution skewed toward earliness. This type of distribution was actually obtained (fig. 13).

The cross BC × GA should segregate only for the gene *C,c*, producing a bimodal distribution skewed toward lateness in F_2. The actual frequency distribution was unimodal and possibly slightly skewed in the direction of earliness (fig. 14). This case may be complicated by minor epistatic effects postulated for these parents.

The B_1 F_1, B_2 F_1 and F_2 of RA × BU should show evidence of segregation only for genes with very small additive and/or dominance and epistatic effects. The distributions were thus expected to be unimodal and approximately normal, which was the case (figs. 15 and 16).

In summary, the evidence for a partially dominant major gene, *A,a*, which differentiates the highly dominant group from the other two, is very good. The diallel cross analysis was capable of detecting this gene (or effective factor), and of assigning it in one or the other of its allelic forms to each of the 10 parents. The evidence for *B,b*, which supposedly differentiates the moderately recessive from the highly recessive group, is reasonably good, since indications of its presence were obtained from the two crosses (RA × BC and BA × GA) in which it was expected to segregate. The evidence for *C,c* was sporadic and, at best, inconclusive. This gene was included in the simplified genetic hypothesis in order to explain the genetic diversity and apparent partial dominance for lateness which occur within the moderately recessive group. Nonallelic interactions apparently occur in crosses between and within the moderately recessive and highly recessive groups, and these epistatic effects can be expected to complicate the situation.

DISCUSSION

In the breeding of self-pollinated crop plants efficiency depends, first, on accurate identification of the hybrid combinations that have the potential of producing maximum improvement and, second, on identifying, in early segregating generations, superior lines among the progeny of the most promising hybrids. The present investigation was conducted to determine whether diallel analysis of parental and F_1 data can provide information useful for the first of these purposes. The character studied was heading date in a diallel cross among 10 varieties of wheat grown commercially in California in the twentieth century.

Estimates of heritability calculated as the additive and/or additive × additive genetic portion of the mean variance of arrays (V_{1L1}) were respectively 55, 67, and 74 per cent in 1957, 1958, and 1959. These moderate to high heritability estimates indicate that a major part of the total phenotypic variability can be attributed to genetic rather than environmental causes. The diallel cross graphs were quite similar from block to block and from year to year, indicating that genotypic-environmental interactions were small. Supporting evidence for this conclusion was obtained from statistical tests of various genetic parameters. These results are an indication that correspondence between genotype and phenotype is good. It is therefore expected that effective selection should be possible for heading date in segregating generations of hybrids among at least certain of the parents tested.

Tests of the assumptions upon which the diallel cross analysis is based indicated that certain of these assumptions are not strictly valid for these materials (see p. 280). Nevertheless, since these partial failures of assumptions seemed unlikely to introduce gross biases into the genetic analysis, it was concluded that application of the diallel analysis to the data was justified.

On the basis of the diallel analysis it was possible to make several inferences about the genetic portion of the total variability. The most conspicuous feature of this genetic system was the indication that a major part of the genetic variability was probably associated with three major genes (or effective factors). It was postulated that two of these major genes exhibit partial dominance in the direction of earliness, and one exhibits partial dominance in the direction of lateness. The diallel analysis permitted the assigning of genotypic formulas to each of the parents with respect to these major genes. The remainder of the genetic variability was associated with an indefinitely large number of minor genes, many of which display little or no dominance. There were indications of sporadic cases of nonallelic interactions in certain hybrid combinations but epistasis is apparently not an important feature of the genetic system.

This information about the genetic system provided a basis for predicting expected patterns of segregation in specific crosses. Since predicted segregations of genes A,a and B,b [which were postulated to explain the discontin-

uities between the major groupings along the (W_r, V_r) and (W_r, W'_r) graphs] agreed closely with observed segregations in various generations of seven critical hybrids, the diallel analysis evidently was successful in revealing the major features of the genetic system governing heading date in the 10 parents investigated.

The probable outcome of selection in specific crosses can be assessed as follows. The diallel analysis indicated that near-top dominant and near-bottom recessive genotypes were present among the 10 parents. Thus, so far as genes displaying dominance are concerned, the limits of selection have already been reached, or nearly so. Progress under selection must therefore depend largely on a system of numerous minor genes that do not display dominance. The diallel analysis indicated that these nondominant genes control a relatively small part of the total genetic variability. It also indicated that epistasis is a minor feature of the system. It appears likely, therefore, that neither the rate nor total extent of progress under selection will be great. This prediction is supported by the absence or near absence of transgression in the segregating generations of several hybrids.

It is therefore expected that progress under selection is likely to take one of the following forms. In crosses between parents that carry different alleles of the major genes, rapid progress toward homozygous types equaling, or perhaps slightly transgressing, the range of the parents can be expected from selection in a selfing series. Most of this progress is likely to be associated with fixation of the major genes. Considering the high heritability of heading date, a single round of selection in a selfing series should be ample to fix all major genes. Further progress in the desired direction (*i.e.*, toward earliness or lateness) would then be contingent on additional rounds of selection based on intercrosses among either the early or the late types produced by previous rounds of selection. Since the diallel analysis did not provide precise information about the polygenic system, predictions about the rate or extent of the progress to be expected from the hybrid between any two parents must be tenuous. Nevertheless, it seems unlikely that the rate would be rapid or the total progress large.

In crosses between parents carrying the same major genes, progress depends entirely on the polygenic system. Thus the situation in the first round of selection in such crosses would be equivalent to that in the second round of selection in crosses involving parents that carry different major genes. Again it seems unlikely that selection in any one hybrid combination between 2 parents is likely to produce rapid or substantial progress. For example, even though the cross between Ramona and Bunyip can be regarded as the single most promising one from the standpoint of progress in the direction of earliness, this hybrid does not appear capable of producing progeny substantially earlier than Ramona.

Late selections are most likely to be obtained from the cross between Big Club and Galgalos but this cross does not appear to offer outstanding prospects for advance under selection.

The diallel cross analysis gave an indication that polygenes with plus and minus effects are more or less equally distributed among the 10 parents. If that is the case, intercrosses among selected lines derived from different hybrids should provide opportunity for progress beyond that offered by the hybrid between any single pair of parents. The present diallel cross analysis gave little idea of the probable outcome of selection for these polygenes, no doubt in consequence of the dominant role played by the major genes in setting the pattern of genetic variation, thus obscuring the role of the polygenic system. This difficulty could be avoided in a diallel cross among lines selected for homogeneity with respect to the major genes. Assessment of the potential for progress represented by the polygenic system, therefore, appears to require an additional diallel cross based on lines selected from various hybrids. It should be emphasized that a diallel cross among lines derived from the first round of selection would be likely to provide information useful only in predicting the prospects for progress in a second round of selection. It is likely to give a rather superficial assessment compared with complete analysis in terms of the effects of all the genes present in interaction with one another and with the environment. Like the present diallel cross, it would indicate the immediate effects of selection but not the ultimate effects of an appropriate combination of outcrossing, inbreeding and selection, between and within lines. Interactions manifested only in rare combinations of genes may make little or no recognizable contribution at one stage of a recurrent selection program and yet determine genotypes of great value when obtained.

Nevertheless, the present diallel cross provided an assessment of the genetic system that appears to be useful in predicting the immediate outcome of directional selection and this offers hope that subsequent diallel crosses might provide similar useful information in later stages of a selection program for heading date.

SUMMARY

A diallel cross consisting of the p^2 possible combinations [p parents, $\frac{1}{2}p(p-1)$ F_1 hybrids, and $\frac{1}{2}p(p-1)$ reciprocal F_1 hybrids] among 10 selected spring wheat varieties was grown in replicated trials in three years. The objective was to determine whether genetic information useful in predicting probable advance under selection could be obtained from parental and F_1 data. The character studied was heading date, which is a measure of time to maturity.

The genetic model on which analysis of the diallel cross was based assumes: (1) absence of genotypic-environmental interactions within locations and years; (2) homozygosity of the parents; (3) disomic inheritance; (4) no reciprocal differences; (5) no epistasis; (6) no multiple alleles and (7) noncorrelated gene distributions. Evidence was obtained that assumptions 2, 3 and 4 were fulfilled in the present materials. The remaining assumptions were not strictly valid but their partial failure appeared unlikely to introduce significant bias into the analysis.

The genetic analysis indicated that the 10 parents fall into three groups

according to relative level of dominance: (1) highly dominant (Ramona, Bunyip); (2) moderately recessive (White Federation, Baart 46, Hard Federation, Poso, Onas); and (3) highly recessive (Sonora, Big Club, Galgalos). A few genes with major effect appeared to be responsible for most of the differences among the parents. Thus it was postulated that Ramona and Bunyip are homozygous for the early and partially dominant allele *A* of a major gene, *A*,*a*, affecting heading date, whereas the other 8 parents are genotypically *aa*. The 5 members of the moderately recessive group appeared to be homozygous for the early and partially dominant allele *B* of another gene, *B*,*b*, which has somewhat less effect on heading date than *A*,*a*. Another gene, *C*,*c*, which is partially dominant for lateness, may differentiate Poso from the other members of the moderately recessive group. The parental genotypes with respect to these major genes were postulated to be *AABBCC*—Ramona, Bunyip; *aaBBcc*—Poso; *aaBBCC*—Baart 46, White Federation, Hard Federation, Onas; *aabbcc*—Big Club, Sonora; *aabbCC*—Galgalos. Variances and frequency distributions observed in 7 F_2 populations and certain other segregating generations corresponded closely in most cases to those predicted on the basis of this genetic scheme.

Evidence was obtained that the remaining and smaller part of the genetic variability in this diallel cross is governed by a system of minor genes displaying little or no dominance. Some of these minor genes appear to interact with one another and/or with the major genes to produce minor epistatic effects in certain crosses. The diallel analysis was not successful in providing precise information about this polygenic system, probably because of the overwhelming and obscuring role of the major genes in setting the pattern of genetic variability. Possibly this information could be obtained from an additional diallel cross based on intercrosses of selected lines homogeneous for the major genes.

Results from three seasons were moderately to highly consistent, indicating that various genotypes in the system responded fairly similarly in different environments. An analysis of genotypic-environmental interactions indicated that failure of various genotypes to behave entirely consistently in different environments was associated with unstable dominance effects of genes to a greater extent than with unstable additive effects of genes. Heritabilities were respectively 55, 67, and 74 per cent, in 1957, 1958, and 1959.

The diallel cross was thus successful in establishing that: (1) the parents differ substantially from one another genetically; (2) the correspondence between genotype and phenotype is high; (3) the genetic system governing heading date is generally stable in different years; (4) a few major genes are the dominant feature of the genetic system; and (5) a polygenic system is also a feature of the genetic system in this diallel cross.

These results contain implications for predicting the outcome of selection. The present diallel cross was informative in indicating the immediate effects of selection but not the ultimate effects of an appropriate combination of intercrossing, inbreeding and selection.

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APPENDIX

Pacific Bluestem is an old variety, apparently unrelated to the other parents in this study, which was grown extensively at one time in California. It was included in the 1958 and 1959 diallel cross nurseries, and had an average heading date of 43.6 and 30.5 days, respectively. Its genotype was found to be highly recessive. Apparently, this parent is quite similar genetically to Big Club (BC) and Galgalos (GA) with respect to heading date.

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