THE DETECTION AND MEASUREMENT OF THE EFFECTS OF INDIVIDUAL GENES INVOLVED IN THE INHERITANCE OF A QUANTITATIVE CHARACTER IN WHEAT[1]

CONRAD WEHRHAHN[2] AND R. W. ALLARD

Departments of Genetics and Agronomy, University of California, Davis

Received August 26, 1964

IN the study of quantitative inheritance it has been customary, since the first formulation of the necessary statistical procedures by FISHER in 1918, to base genetic analyses on covariances between relatives. The characterizations of the inheritance of continuously varying characters provided by these statistical analyses are in terms of the action of systems of genes, and although these characterizations have been highly informative, they do not suffice to answer many questions concerning the nature of polygenes. THODAY (1961) has emphasized that the isolation of individual genes affecting quantitative characters is a prerequisite to answering questions about the randomness of distribution of polygenes in chromosomes, about the relationship of polygenes to major genes and to heterochromatin and about the homogeneity of polygenes as a class of genes. This paper describes a technique based on common breeding procedures which appears to be useful in identifying some of the major genes (effective factors) in the presumably complex genetic systems responsible for the heritable differences in quantitative characters between pure lines. It also describes the results of an application of this technique to the determination of genetic differences between two varieties of wheat (*Triticum aestivum* L.).

MATERIALS AND METHODS

Theory and design of the technique: The breeding procedure consists of the following steps: (1) two pure line parents are crossed to produce an F_1; (2) the F_1 is backcrossed to one of the parents: (3) a large number of the resultant plants are backcrossed to the parent successively until plants are obtained which have k backcrosses in their pedigrees; (4) these backcross plants and their descendents are selfed until a state of almost complete homozygosity is attained; (5) the "inbred backcross' lines are propagated until sufficient seed is available to permit the inclusion of the lines in large replicated field trials. The probability is $(\frac{1}{2})^{k+1}$ that a specific gene from a donor parent will be incorporated into any one of the resultant lines .The probability is $(\frac{1}{2})^{2k+2}$ that two specific but unlinked genes will be incorporated into a line. This probability is 1/64 when $k = 2$. 1/256 when $k = 3$, and 1/1024 when $k = 4$. It is assumed that plants are chosen at random in each generation and that all genotypes are equally viable.

In general, if N genes are involved in the inheritance of a character, the probability that R genes from the donor parent will be found in a line is

$$N^{C}R \times (P_k)^R \times (1 - P_k)^{N-R}, \text{ where } P_k = (\tfrac{1}{2})^{k+1}.$$

[1] The investigation was supported in part by a grant from the National Science Foundation, G14991.

[2] Present address: University of Saskatchewan, Saskatoon, Canada.

TABLE 1

The proportion, $P(R = 1/P(R = 1, 2, \ldots, N)$, *of nonparental lines which are single gene deviates from the recurrent parent, and the probabilities involved in the calculation of* $P(R = 1)/P(R = 1, 2, \ldots, R)$

N	k	P_k	$P(R=0)$	$P(R=1)$	$P(R=1)/P(R=1, 2, \ldots, N)$
4	2	1/8	0.586	0.335	0.809
	3	1/16	0.773	0.206	0.905
	4	1/32	0.881	0.114	0.953
10	2	1/8	0.263	0.376	0.510
	3	1/16	0.525	0.350	0.735
	4	1/32	0.728	0.235	0.863

The proportion of nonparental lines which are single-gene deviates from the recurrent parent is given in the last column of Table 1 for $N = 4$ and $N = 10$.

It appears that a set of "inbred backcross" lines should consist largely of lines genotypically identical to the recurrent parent, and of single-gene deviates from the recurrent parent, even if the number of genes involved is as great as ten and the number of backcrosses is as few as three.

A hypothetical breeding procedure with $k = 3$ and the corresponding genetic expectations for one locus are outlined in Table 2. The 256 "backcross pure lines" produced could be tested as extensively as desired and data of any necessary degree of accuracy could, in theory, be obtained. The number of lines expected (with 95 percent confidence) to carry a specific gene from their donor parent is approximately $16 \pm 2 \times (256 \times 1/16 \times 15/16)^{1/2} = 16 \pm 7.76$. The number of lines expected to carry two specific unlinked genes is $1/256 \times 256 = 1$. Thus, so long as the number of genes with appreciable effects on a character is not too large, the distribution of the "backcross pure lines" should be discontinuous and consist of a number of distinct groups. Groups including eight to 24 lines should be due to one gene from the donor parent. The magnitude of effect of a gene is expected to be equal to the distance of the group from the class in which the recurrent parent falls. If two genes have the same effect, a group containing approximately $32 \pm 2 \times (30)^{1/2}$, or 21 to 43 lines, should be present. This technique is similar in principle to a monosomic substitution technique which has been used by WEHRHAHN (1961) to analyze quantitative genetic systems.

TABLE 2

A hypothetical breeding precedure with $k = 3$ *and the corresponding genetic expectations for one locus*

Generation	Breeding procedure	Genetic expectation
1	$P_1 \times P_2$	$aa \times AA$
	/	
2	$F_1 \times P_1$	$Aa \times aa$
	/	
3	$256\ B_1 \times P_1$	$(128\ Aa{:}\ 128\ aa) \times aa$
	/	
4	$256\ B_{11} \times P_1$	$(64\ Aa{:}\ 192\ aa) \times aa$
	/	
5–10	$256\ B_{111}$ selfed 5 generations	$(32\ Aa{:}\ 224\ aa)$
11	$256\ B_{11100000}$ "Pure Lines" tested in replicated field trials	$(16\ AA{:}\ 240\ aa) =$ $1/16\ AA{:}\ 15/16\ aa$

Experimental methods: The parent varieties used in the study were Baart 46 and Ramona. These parents were chosen because much is already known about genetic systems involving Baart 46 and Ramona (see ALLARD and HARDING 1963). We let P_1 denote Baart 46 and P_2 denote Ramona; then B_{11000} denotes a line that has in its pedigree two successive backcrosses to P_1 (Baart 46) followed by three generations of selfing. When the 1's are replaced by 2's in this notation, backcrosses to P_2 (Ramona) are indicated.

The experiment consisting of a set of B_{22000} and a set of B_{220000} lines is labelled Experiment 1. The experiment consisting of B_{11000} and B_{110000} lines is labelled Experiment 2. The numbers of lines which were field tested in the two experiments are given in Table 4. The field arrangement followed a randomized complete block design in which each "inbred backcross" line was included only once in each of the two replications. Each plot consisted of one row ten feet long separated by one foot from adjacent rows. Seeds were sown at one foot intervals within each row.

Date of heading was recorded on an individual plant basis and time to heading was expressed as the number of days after an arbitrary date (April 16, 1963) required for the first spike to emerge completely from the boot.

EXPERIMENTAL RESULTS

An analysis of variance for heading date was conducted on each of the sets of lines in Experiments 1 and 2. Parents and F_2's, as well as inbred backcross lines, were included in these analyses. The results indicate that genetic differences significant at the 1 percent level occurred in all sets of lines (Table 3).

The phenotypic, environmental and genetic variances for each of the four sets of inbred backcross lines are given in Table 4. The environmental variance was very small relative to genetic variance indicating that heading time is a highly heritable character.

TABLE 3

Summaries of analyses of variance for heading date

	Set	Variation	Degrees of freedom	Mean squares	F
Experiment 1	B_{22000}	Family	74	60.674	23.33
		Error	74	2.601	
	B_{220000}	Family	58	63.869	20.68
		Error	58	3.089	
Experiments 2	B_{11000}	Family	81	42.211	28.25
		Error	81	1.494	
	B_{110000}	Family	84	39.028	20.58
		Error	84	1.906	

TABLE 4

Phenotypic, environmental and genetic variances of "inbred backcross" line means

Designation	Number	Variance		
		Phenotypic	Environmental	Genetic
B_{22000}	69	32.38	1.301	31.08
B_{220000}	52	32.43	1.544	30.89
B_{11000}	75	17.59	0.747	16.84
B_{110000}	76	15.88	0.953	14.93

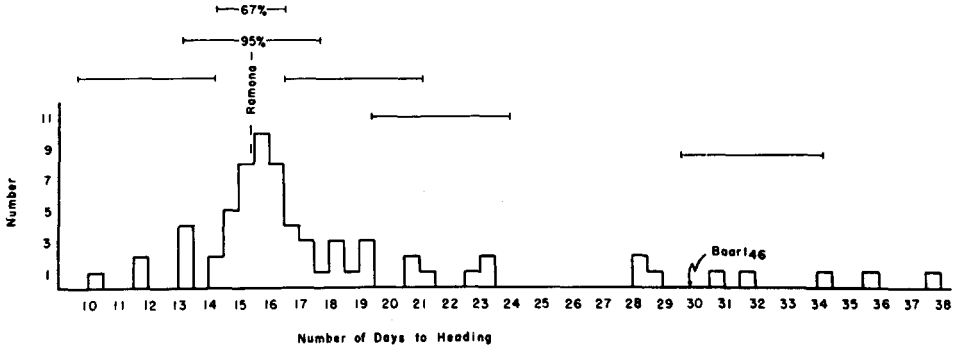

FIGURE 1.—Distribution for heading date of 69 B_{22000} lines.

Experiment 1: The distribution of 69 B_{22000} backcross lines is given in Figure 1. On the simplifying assumption that all lines are homozygous for relevant genes, the number of lines expected to carry any specific gene from their Baart 46 ancestor is approximately $1/8 \times 69 \pm (69 \times 1/8 \times 7/8)^{1/2} = 8.6 \pm 2.75$.

The expected distribution of the parental class has been indicated in Figure 1 by constructing 67 percent and 95 percent "probability intervals" about the mean (15.4) of six Ramona families which were included in the field planting. The estimate of error variance (1.301) used in the calculation of the intervals is given in Table 4.

A distinctly late group of eight lines is apparent with a mean of about 32 days to heading. This group of lines almost certainly carries the late allele of the major gene for earliness described by ALLARD and HARDING (1963). The locus involved is designated locus 1 in Table 5. In addition to the eight very late lines, 14 other lines lie to the right of the parental 95 percent probability interval. Since a single gene is expected to give rise to a group of only six to 11 lines, it is probable that two genes are responsible for the lateness of these 14 lines.

Between three and seven lines lie to the extreme left of the distribution; these lines appear to be too early to be chance deviates from the parental class, indicating that Baart 46, the late parent, carries a gene for earliness.

Many of the above backcross B_{22000} lines have descendents in the set of B_{220000} lines. In cases where B_{22000} lines are homozygous for genes of large effect, their B_{220000} descendents should be homozygous and of the same genotype. It follows that lines which belong to any group should tend to have descendents which fall into the same group.

The distribution of B_{220000} lines versus the means of their B_{22000} ancestral lines is shown in Figure 2. To avoid confusion, the lines in the latest group are omitted. Approximate 50 percent and 90 percent "probability ellipses" about the mean of the Ramona parent are shown. These ellipses are sets of minimum area which, respectively, should contain 50 percent and 90 percent of all lines on the hypothesis that there is no genetic variation. The derivation of the ellipses is given by WEHRHAHN (1964). Six Ramona lines included with the B_{220000} and B_{22000} sets of lines had means of 14.8 and 15.4 respectively. Therefore, the point (15.4, 14.8)

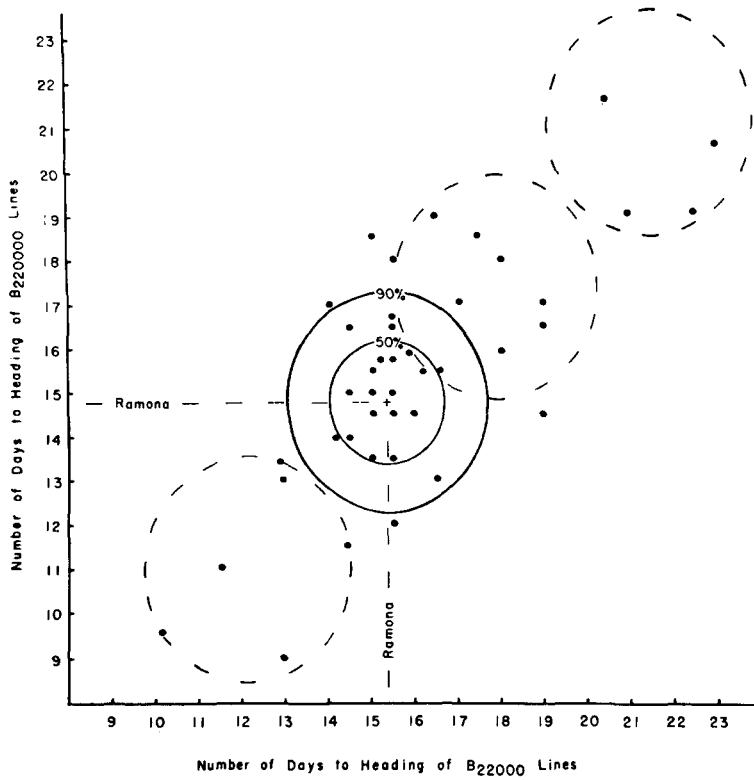

FIGURE 2.—Distribution for heading date of B_{220000} lines versus their B_{22000} ancestral lines.

was chosen as the center of ellipses. This information together with that on environmental variances in Table 4 is sufficient to permit the calculation of probability ellipses. It must be stressed that the true probability ellipses may differ slightly from those pictured in Figure 2 because the estimated center and error variances are subject to estimation error. Tentative 90 percent probability ellipses about postulated nonparental groups are also indicated.

In Figure 2, 14 lines are seen to be significantly later than Ramona. The number of lines expected to carry any single gene from their Baart ancestor is approximately $1/8 \times 42 \pm (42 \times 1/8 \times 7/8)^{1/2} = 5.25 \pm 2.14$, i.e. between 3.11 and 7.39. These expected numbers are much smaller than the observed number of 14 lines, which suggests that two genes must be involved. The fact that two 90 percent probability ellipses are needed to cover the lines satisfactorily provides more convincing evidence that two loci are involved. The locus responsible for the later heading of the two groups is designated locus 2 in Table 5. It has an effect of about 6.0 days on heading time. The locus responsible for the earlier group is designated locus 3. It has an effect of about 2.7 days on heading time.

Six lines lie below and to the left of the parental class. These lines can be satisfactorily covered by a single 90 percent probability ellipse. Thus, one locus, designated locus 4 in Table 6, appears to be responsible for this group. Two genes

differentiate fully awned plants from awnless plants and homozygotes which have only one of the awn inducing genes are tip-awned. The Ramona parent is awnless and most of the lines in Experiment 1 are awnless. However, all six of the lines thought to have the early allele of locus 4 were tip-awned. The probability that this is a chance association is $[1 - (7/8)^2]^6 = 0.000166$. Thus we conclude that locus 4 either has pleiotropic effects or is very closely linked to an awn inducing gene.

A summary of the loci which Experiment 1 indicates are involved in the genetic differentiation of Ramona and Baart 46 is presented in Table 5. The approximate effect on heading time, MATHER's "*d*" (MATHER 1949), and the contribution to the total additive genetic variance of each locus are also given in this table.

Experiment 2: The distribution of 76 B_{110000} lines is given in Figure 3, together with 67 percent and 95 percent probability intervals to indicate the expected distribution about the mean (29.6) of the Baart 46 parental class. The error variance used in the calculations is 0.953 (Table 4).

An obvious feature of the distribution is a distinctly early group of seven lines with a mean heading time of 17.8 days. This group is almost certainly attributable to the major locus in Experiment 1 and is designated locus 1 in Table 6.

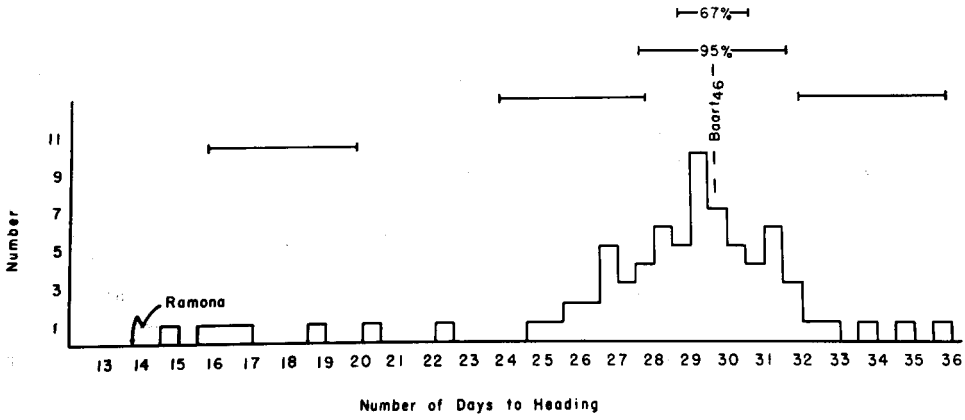

FIGURE 3.—Distribution for heading date of 76 B_{110000} lines.

TABLE 5

Effect (in days), Mather's "d", *and the additive variance* (d^2) *of each locus found in Experiment 1 to control the heading date difference between Ramona and Baart 46. Qualitative effects, when present, are indicated*

Locus	Effect	*d*	d^2	Qualitative effect
1	16.5	8.25	68.06	
2	6.0	3.00	9.00	
3	2.7	1.35	1.82	
4	—3.5	1.75	3.06	Awn development
Absolute total	28.7	14.35	81.94	

TABLE 6

Effect (in days), Mather's "d", *and the additive variance* (d^2) *of each locus found in Experiment 2 to control the heading date difference between Ramona and Baart 46. Qualitative effects, when present, are indicated*

Locus	Effect	d	d^2	Qualitative effect
1	—11.8	5.90	34.81	
2	— 3.0	1.50	2.25	
3	— 3.0	1.50	2.25	
4	4.7	2.35	5.52	Awn inhibition
Absolute total	22.5	11.25	44.83	

Even after the elimination of the lines carrying the early allele of locus 1, considerable genetic variation is obvious in Figure 3. The fact that about seven lines are significantly later and 14 lines are significantly earlier than the parental class suggests that at least two genes for earliness and one for lateness are involved.

The joint distributions of B_{110000} lines and their B_{11000} ancestral lines are shown in Figure 4. Lines belonging to the very early class are omitted from this figure. Approximate 67 percent and 95 percent probability ellipses about the mean (29.6, 29.6) of Baart 46 and tentative 95 percent probability ellipses about the non-parental groups are indicated.

Approximately $\frac{1}{8} \times 54 \pm (1.8 \times \frac{7}{8} \times 54)^{\frac{1}{2}} = 6.75 \pm 2.43$, or 4.32 to 9.18 lines, are expected to carry a given gene from the donor parent. The early class in Figure 4 contains 13 lines. This is approximately the number expected if two genes with similar effect are responsible for the group. These loci are assumed to have equal effects and are designated locus 2 and locus 3 in Table 6. A late group of three lines is also present in Figure 4. The locus responsible for this group is designated locus 4 in Table 6. It is significant that not one of these three lines is awned even though Baart 46 is fully awned and most of the backcross lines in the experiment are also fully awned. This is expected if the locus involved is the one labelled locus 4 in experiment 1. Because two genes are involved in awn inheritance, the probability that not even one of three random lines be fully awned is $(1 - 49/64)^3 = 0.013$, if linkage is absent. Thus, locus 4 of Experiment 2 is almost certainly the same as locus 4 of Experiment 1. This information, together with that on locus 1, suggests that considerable confidence can be had in the conclusion that the same four loci were detected in the two "inbred backcross" experiments and that the loci are correctly labelled in Tables 5 and 6.

A summary of the loci found to differentiate Ramona from Baart 46 with respect to heading date in Experiment 2 is presented in Table 6. The approximate effect on heading date, MATHER's "*d*" and the contribution to the total additive genetic variance of each locus are also given.

Residual genetic variation: In both Experiments 1 and 2, four genes controlling heading time were detected. However, additional genes with effects too small to be detected by experiments of this type and size may also affect heading time. To determine the amount of genetic variation due to such genes in Experiment 2.

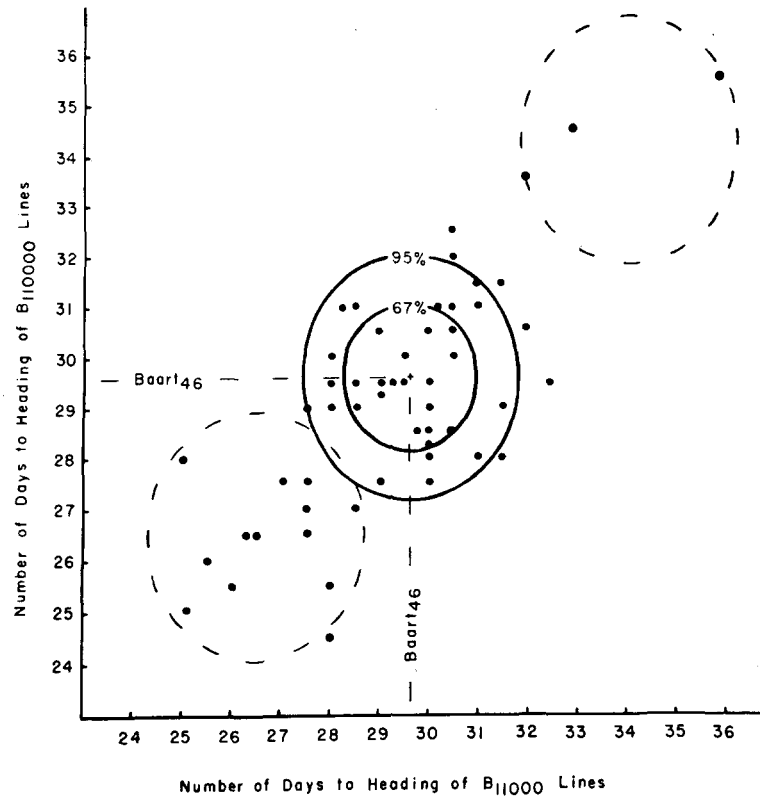

FIGURE 4.—Distribution for heading date of B_{110000} lines versus their B_{11000} ancestral lines.

the variance of the means of the 38 lines in Figure 4 not clearly carrying Ramona genes was computed. The variance is 30.44/37 = 0.823. The expectation of this variance is $V_{R.G.} + V_E = V_{R.G.} + \frac{1}{4}\left(\frac{M.S._e}{2}(B_{11000}) + \frac{M.S._e}{2}(B_{110000})\right)$. Thus, $0.823 = V_{R.G.} + 0.425$ and it follows that the "residual genetic" variance is $V_{R.G.} = 0.398$. The F test for the significance of this variance is (see KENNEY and KEEPING 1951) F = 0.823/0.425 = 1.94, which is significant at the 1 percent level. It is of interest to determine the fraction of the total genetic variance that is due to "residual genetic" variation. Estimates of the total genetic variance, V_G, are given in Table 4. The estimates are $V_G = 16.84$ and $V_G = 14.93$ for the B_{11000} and B_{110000} lines respectively. Thus an estimated (100) (0.398) (2)/(16.84 + 14.93) = 2.51 percent of the total genetic variance in heading date in experiment 2 appears to be due to genes whose individual effects are obscure.

Because of the obvious overlap of the parental class with the locus 3 group in Figure 2, no valid estimate could be made of the "residual genetic" variance in Experiment 1.

DISCUSSION

In an earlier study of progenies derived from the hybrid between Ramona and

Baart 46, ALLARD and HARDING (1963) observed that heading dates fell into two essentially discrete classes in the F_1, F_2, F_3, and early backcross generations. Observed distributions, and those computed on the assumption that the 15 day difference in heading time between these varieties is governed by a single gene, were in close agreement. Thus early-generation data suggest that most of the variation in heading time in this cross is governed by a single gene-pair, and that selection is likely to result in little more than recovery of the parental genotypes. When the same early-generation data were subjected to a components of variance analysis, the results also led to the prediction that selection was not likely to be rewarding.

How misleading genetic analyses based on early-generation data can be was demonstrated in the same study. ALLARD and HARDING presented data on random F_7 families and on F_6–F_8 families in which selection had been practiced in each generation for earliness or for lateness. An analysis of these data indicated that a minimum of four genes must be involved in the inheritance of heading time. The present experiment gives a still clearer picture of the inheritance of heading time in these materials. Locus 1 (Tables 5 and 6), which has an effect on the phenotype approximately as large as the other three major loci combined, is almost certainly the locus detected by CRUMPACKER and ALLARD (1962) in a diallel cross analysis and the one responsible for the discrete classes observed in early segregating generations by ALLARD and HARDING (1963). The summed effect of the four loci is approximately 25 days, which is slightly less than the total required to account for the range in heading dates observed in the early and late selection experiments. A possible explanation for this discrepancy, suggested by a highly significant "residual genetic" variance, is that it results from unidentified loci which have small individual but considerable cumulative influence on the phenotype.

Since, in biometrical genetics, most inferences and deductions are made in terms of additive genetic variance, it is worthwhile to consider the contributions of the four loci detected to this component of variance. Locus 1 accounts for $(100)(68.06)/81.94 = 83$ percent of the additive genetic variance attributable to known loci in Experiment 1. The comparable value for Experiment 2 is 78 percent. Hence locus 1 would clearly be of major importance in biometrical studies. Locus 3, on the other hand, accounts for 2 percent of the additive variance in Experiment 1 and 5 percent in Experiment 2. These proportions are so small as to be well below the error of estimation of the additive genetic variance in all except the most precise biometrical experiments. Thus, it appears that the units of inheritance which would be of real importance in a components of variance analysis, and some which would contribute little to the variance, were readily detected by inbred backcross line technique.

It has commonly been assumed that continuously varying characters are determined by large numbers of polygenes with small and similar effects. The above results indicate that this generalization does not hold for the genetic system which determines the 15 day difference in heading time between Ramona and Baart 46. Instead the following conception of genetic control emerges. Ramona is

homozygous for an "earliness" allele and Baart 46 is homozygous for a "lateness" allele of a gene which makes a major contribution to the phenotype. The two varieties also differ with respect to three other "major" genes which make somewhat lesser contributions to the phenotype. Ramona is homozygous for earliness alleles of three of these genes and for a lateness allele of the fourth gene. In addition the varieties are differentiated by an indefinite number of genes with presumably very small individual effects. If interest centers on the prediction of the behavior of populations, the value of such information is clear. The distribution and range of phenotypic values of sets of random homozygous families developed by continued self-fertilization in F_2, F_3, . . . F_n generations, as well as the ultimate outcome of selection within and between families in a single selfing series, can be predicted with a great deal of accuracy. The limitations of prediction are also clear. Information about the "major" genes is for the most part restricted to their additive effects in the genetic backgrounds of the recurrent parents. Also little is known of the genes with minor individual effects, and it is conceivable that the cumulative effect of these genes on the phenotype may be great. Finally, since backcrossing and selfing lead rapidly to homozygosity, it is likely that much of the genetic variability detected in the inbred backcross line experiments resulted from the recombination of entire chromosomes or large segments of chromosomes. Thus the information at hand is an uncertain guide for predicting the total progress which might be achieved in breeding programs involving additional cycles of crossing, recombination and selection. However, the genetic understanding gained from a single inbred backcross line experiment provides encouragement that further applications of the same technique to these materials may furnish the information needed for increasingly accurate prediction of responses to selection.

Although information about the additive effects of genes has implications in predicting the behavior of populations, this information in itself is inadequate for the formulation of an integrated view of quantitative genetic systems. Knowledge of the dominance effects of genes and of epistatic interactions are among the items about which additional information is required. The earliness allele of locus 1 (Tables 5 and 6) is known to be nearly fully dominant over the lateness allele (ALLARD and HARDING 1963), but little or nothing is known concerning the dominance relationships of the other three loci which were detected. However, this information can be readily obtained by producing F_1 and F_2 hybrids between a recurrent parent and appropriate single-gene deviates from the parents (Figures 2 and 4). Phenotypic measurements of the recurrent parent, the deviate line, and the F_1 and F_2 provide a basis for estimating the degree of dominance of each "major" gene.

The data in Tables 5 and 6 suggest that the effects of the four detected loci were not precisely the same in the Ramona and Baart 46 genetic backgrounds and hence that epistatic interaction is involved between the loci and the genetic background in which they occur. However, the data are not adequate to establish the magnitude of this sort of interaction other than to suggest that it is relatively unimportant in these particular cases. Another aspect of interaction, that between

different pairs of loci within the Ramona or within the Baart 46 background, can be studied by intercrossing appropriate single-gene deviates following a method described by FASOULAS and ALLARD (1962). This method can be extended to permit the study of higher order interactions, but the costs in terms of time and labor discourage its use for the analysis of systems involving more than three loci at a time.

The availability of techniques which allow single genes affecting heading date to be isolated also permits the investigation of the morphological and developmental effects of these genes, as suggested by THODAY (1961) and demonstrated by SPICKETT (1963). It would be particularly interesting to discover whether different genes affect time to heading in the same or in different ways and whether the different genes have the same or different side effects on morphological and physiological characters. For example, mature height is correlated with time to heading, and it should be possible to determine whether this correlation is associated equally or unequally with the different "major" genes in the genetic system which determines heading time.

SUMMARY

It was demonstrated that among the genes which differentiate the wheat varieties Ramona and Baart 46, there are four which have large enough effects on heading date to be detected by an "inbred backcross line" experiment of modest size. One of these "loci" (effective factors) was responsible for slightly more than 80 percent of the total additive variance expressed in the generations studied and the other three "loci" jointly accounted for about 14 percent of the additive variance. The inbred backcross line technique was sensitive enough to detect a locus which accounted for only 2 percent of the total additive variance. The value and limitations of these results in predicting the behavior of populations are considered and their implications in formulating an integrated view of quantitative genetic systems are discussed.

LITERATURE CITED

ALLARD, R. W., and J. HARDING, 1963 Early generation analysis and prediction of gain under selection in derivatives of a wheat hybrid. Crop Science **3**: 454–456.

CRUMPACKER, D. W., and R. W. ALLARD, 1962 A diallel cross analysis of heading date in wheat. Hilgardia **32**: 275–318.

FASOULAS, A. C., and R. W. ALLARD, 1962 Nonallelic gene interactions in the inheritance of quantitative characters in barley. Genetics **47**: 899–907.

FISHER, R. A., 1918 The correlation between relatives on the supposition of Mendelian inheritance. Trans. Roy. Soc. Edinburgh **52**: 399–433.

KENNEY, J. F., and E. S. KEEPING, 1951 *Mathematics of Statistics*. Part II. Ed. 2. Van Nostrand, New York.

MATHER, K., 1949 *Biometrical Genetics*. Methuen, London.

SPICKETT, S. G., 1963 Genetic and developmental studies on a quantitative character. Nature **199**: 870–873.

THODAY, J. M., 1961 Location of polygenes. Nature **191**: 368–370.

WEHRHAHN, C., 1961 Quantitative genetics of substitution lines involving chromosome 1 of common wheat. Unpublished M.Sc. thesis, University of Alberta. —— 1964 The genetic basis for differences in quantitative characters between two varieties of *Triticum aestivum* L. Unpublished Ph.D. thesis, University of California, Davis.