

GENETICS OF HEADING TIME IN WHEAT (*TRITICUM AESTIVUM* L.). I. THE INHERITANCE OF PHOTOPERIODIC RESPONSE

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ABSTRACT

The inheritance of photoperiodic response was studied in crosses involving four spring wheats (Sonora 64, Pitic 62, Justin and Thatcher) and three winter wheats (Blackhull, Early Blackhull and Extra Early Blackhull). The parental cultivars were classified into a photoperiod-sensitive group (Justin, Thatcher, Blackhull and Early Blackhull) and a relatively photoperiod-insensitive group (Sonora 64, Pitic 62 and Extra Early Blackhull) based on their heading response when vernalized and grown under different daylength regimes.—F₁ data indicated that daylength insensitivity is not always dominant over daylength sensitivity and that the dominance relationship with respect to photoperiodic response depends on the alleles present in the parents. The heading patterns after vernalization and growth under short days of F₁, F₂, F₃ and backcross generations of a 4-parent diallel cross involving Justin, Sonora 64, Extra Early Blackhull and Blackhull could be satisfactorily explained on the basis of two major loci with three alleles at each locus. The genotype for each parent was suggested in terms of these loci. Genes with minor effects also influenced the photoperiodic response in a quantitative manner.—Diallel cross analysis of the number of days to heading (log scale) indicated significant additive and dominance genetic variances, a high average degree of dominance for earliness (photoperiod insensitivity) and a preponderance of recessive alleles in the parents acting in the direction of lateness (photoperiod sensitivity). Estimation of the genetic components of variation contained in the generation means of individual crosses (untransformed data) showed that, besides additivity and dominance, epistasis was also an important factor in the genetic control of photoperiodic response in wheat.

COMMON wheat (*Triticum aestivum* L.) is grown throughout the world from latitudes ranging between 30°S to more than 60°N. Selection pressures leading to this broad adaptation must have operated to adjust the phasic development of the plant to avoid environmental stresses and to take advantage of seasonal opportunities. Responses to photoperiod and vernalization, two important factors affecting heading time, are undoubtedly two adaptive strategies that have evolved in wheat and in other plant species to cope with challenging environments.

The influence of photoperiod on heading or flowering time in wheat was

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emphasized by several workers (see review by KIRBY 1969). Characterization of varietal differences generally is made on vernalized material by obtaining response curves representing the number of days to ear emergence in relation to daylength. Cultivars showing a steep slope between the short and long day regimes are described as photoperiod-sensitive while those with little or no change are insensitive or day neutral. In other instances the length of pre-initiation and post-initiation phases of flowering as affected by photoperiod were studied independently (GOTT 1961; HALSE and WEIR 1970). Results from these physiological studies indicate that wheat cultivars differ greatly in their response to daylength and the period from germination to flower initiation is more strongly affected by short days than that from flower initiation to head emergence.

In spite of the worldwide importance of wheat as a food crop and the recognized influence of photoperiod on adaptation (BORLAUG *et al.* 1964), little is known about the genetic basis of the observed differences between wheat cultivars in response to daylength. The results obtained by PUGSLEY (1965) have so far indicated that one major gene difference governs the heading behavior under short days of the cultivars Triple Dirk and Selkirk. Two genes, one with major and one with minor effects, differentiated this behavior in crosses between Triple Dirk and Thatcher (PUGSLEY 1966). Cytogenetic studies using the chromosome substitution technique have led to the recognition of several chromosomes involved in photoperiodic response. MORRISON (1960) found that chromosome 6B, and possibly other chromosomes, affected response to photoperiod in crosses of winter wheats with the Chinese Spring monosomes. When each chromosome of the cultivar Hope was individually substituted for its homolog in Chinese Spring, five chromosomes were found to affect heading time in plus (chromosomes 1A, 4B and 6B), or minus (chromosomes 3B and 7D) directions (HALLORAN and BOYDELL 1967). Depending on the magnitude of response obtained in each case, chromosomes with major effects and others with minor effects were recognized. Assuming that the effect of each chromosome was due to the action of a single gene, HALLORAN and BOYDELL regarded the genetic control of photoperiodic response as not being very complex. While this technique offers the advantage of associating genes with particular chromosomes, no attempt has been made to determine how these genes act and interact in determining the photoperiodic phenotype of a given cultivar.

The quantitative nature of photoperiodic response was emphasized by previous workers (YASUDA and SHIMOYAMA 1965; KIRBY 1969), but has not been thoroughly investigated as yet. More knowledge is needed on the importance of various components of gene action and interaction and information is almost completely lacking with respect to the allelic variation at loci governing this response in wheat.

The present study was initiated to obtain information on the qualitative and quantitative inheritance of photoperiodic response in crosses between a selected sample of spring and winter wheat cultivars, and on the allelic variation at major loci governing this attribute. A second paper will report on the inheritance of vernalization response using these same cultivars.

MATERIALS AND METHODS

Development of hybrid populations: Study of the inheritance of photoperiodic response was initiated at Davis, California, with seven wheat (*Triticum aestivum* L.) cultivars (Table 1). A 7-parent diallel cross, not including reciprocals, was completed in May 1970. The 21 F_1 's with their parents were grown in the field from July to December, 1970. Only the spring parents and the F_1 's involving spring \times spring and spring \times winter crosses flowered and matured. Germinating seeds from the remaining F_1 's involving winter \times winter crosses were vernalized at $2 \pm 1^\circ\text{C}$ for six weeks in darkness, and later grown under continuous light in a greenhouse. This treatment allowed these F_1 's to flower and mature in time for the next fall planting. F_2 seed was harvested from individual F_1 plants grown in the field or greenhouse. For each of the 6 crosses of a 4-parent diallel involving Sonora 64, Justin, Blackhull and Extra Early Blackhull, one row of F_1 , one row of each parent and 20 rows of F_2 were space-planted in the field in December 1970. The rows were 5m long, 30 cm apart, and the seeds were spaced 30 cm within the row.

Backcrosses to both parents of each F_1 in this 4-parent diallel were made in April and May 1971. Five early, five intermediate and five late F_2 plants from each of the three crosses, $S \times EE$, $J \times EE$ and $B \times EE$, were harvested at maturity.

Photoperiodic response of parents (Experiment P-1): To study the photoperiodic response of parental material, germinating seeds were vernalized for 9 weeks at $2 \pm 1^\circ\text{C}$ in darkness. This vernalization satisfied the cold requirement of the cultivars and limited the possible influence of interactions between daylength and cold requirement on time to heading. Vernalized seedlings were transplanted to flats ($50 \times 35 \times 10$ cm) containing U.C. soil mixture (BAKER 1957) in December 1969 and grown in photoperiod-controlled cabinets with 8-, 11-, 14-, 17- and 24-hr photoperiods. All cultivars in all treatments received a basic 8-hr period of natural daylight. For the treatments receiving more than 8 hr, the light period was extended equally before and after the natural daylight using fluorescent and incandescent lights providing approximately 200 ft-c at the top of the plants. A split-plot randomized design with 3 replicates was used with the photoperiod as main treatment. Within each photoperiod the cultivars were allocated at random in each of 3 flats and 3 plants were used per replication for each cultivar in each treatment. The number of days from transplantation to heading was recorded for each plant and heading was considered as the stage when the spike of the main tiller was fully exerted from the flag leaf sheath.

Inheritance of photoperiodic response in F_1 diallel cross (Experiment P-2): Germinating seeds from the 21 F_1 's and their parents were vernalized for 8 weeks at $2 \pm 1^\circ\text{C}$ in darkness. Six vernalized seedlings from each entry were transplanted to flats and grown in U.C. soil mixture in October 1970. Seedlings of each entry were planted in one row and each flat contained 24 seedlings (4 rows of 6 plants each). The entries were allocated at random in 7 flats and grown under short days (10 hr) in photoperiod-controlled cabinets. The material received a basic 8-hr period of natural daylight and the supplemental artificial light of 200 ft-c was provided equally before and after the natural daylight. The number of days from transplantation to heading was recorded on an individual plant basis.

Inheritance of photoperiodic response in segregating generations (Experiment P-3): Material in this experiment included the four parental cultivars (S, J, B and EE), their 6 F_1 's, 6 F_2 's, 12 first backcrosses and the 15 F_3 families from the 5 early, 5 intermediate and 5 late F_2 plants in each of the crosses, $S \times EE$, $J \times EE$ and $B \times EE$.

Germinating seeds from all generations were vernalized as in Experiment P-2 and transplanted to the greenhouse on September 30, 1971. At this time of the year the daylength in Davis (Lat. $38^\circ 32'N$, Long. $121^\circ 45'W$) was approximately 12 hr and decreasing so that flower initiation and later growth of this material occurred under short days. The material was arranged in six independent studies, each including the parents (P_1 and P_2), F_1 , F_2 , $B_1 = (F_1 \times P_1)$ and $B_2 = (F_2 \times P_2)$ of a given cross. Each study was conducted in a randomized block design with 2 replications using 16 plants for each parent and F_1 , 240 plants for F_2 and 48 plants for each backcross population. Each F_3 family of 24 plants was transplanted to one flat and the flats were distributed randomly in the greenhouse. As for the previous experiments, number of days to heading was recorded for all generations on an individual plant basis.

TABLE 1
Cultivars used in the study

Cultivar	Abbreviation	Growth habit	Parentage	Origin
Sonora 64	S	Spring	[Yaktana 54 × (Norin 10 × Brevor)] × Yaqui 54	Mexico
Pitic 62	P	Spring	Yaktana 54 × (Norin 10 × Brevor)	Mexico
Justin	J	Spring	[(Thatcher × Kenya Farmer) × (Lee × Mida)] × Conley	U.S.
Thatcher	T	Spring	(Marquis × Iumillo) × (Marquis × Kanred)	Canada
Blackhull*	B	Winter	Selection from Turkey wheat (1912)	Russia
Early Blackhull*	E	Winter	Developed from an early plant in a field of Blackhull (1928)	U.S.
Extra Early Blackhull*	EE	Winter	Developed from an early plant in a field of Early Blackhull (1951)	U.S.

* From ATKINS *et al.* (1962).

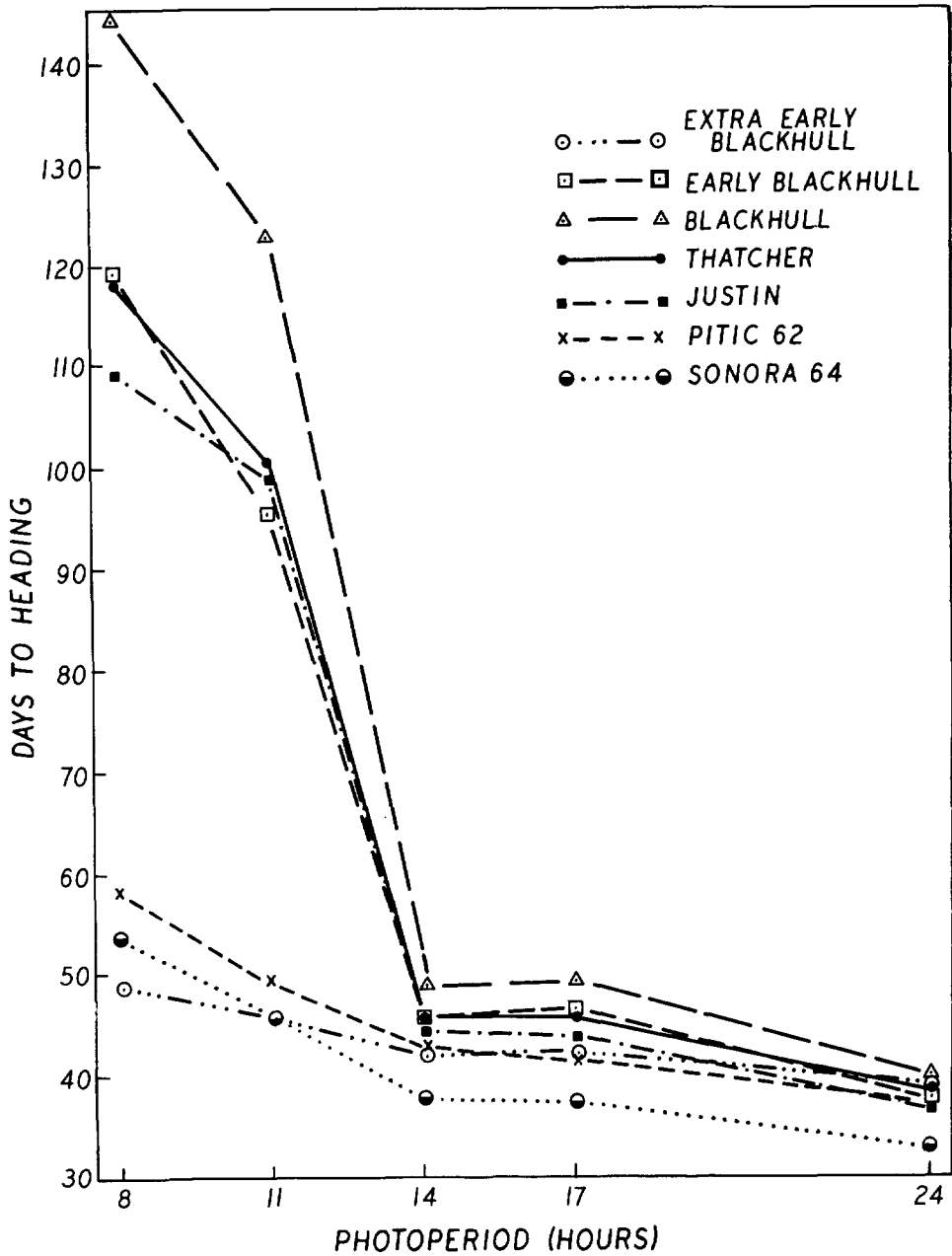


FIGURE 1.—Response of parental cultivars to photoperiod (Exp. P-1). LSR(.05) for photo-period treatments within cultivars = 8.53 days.

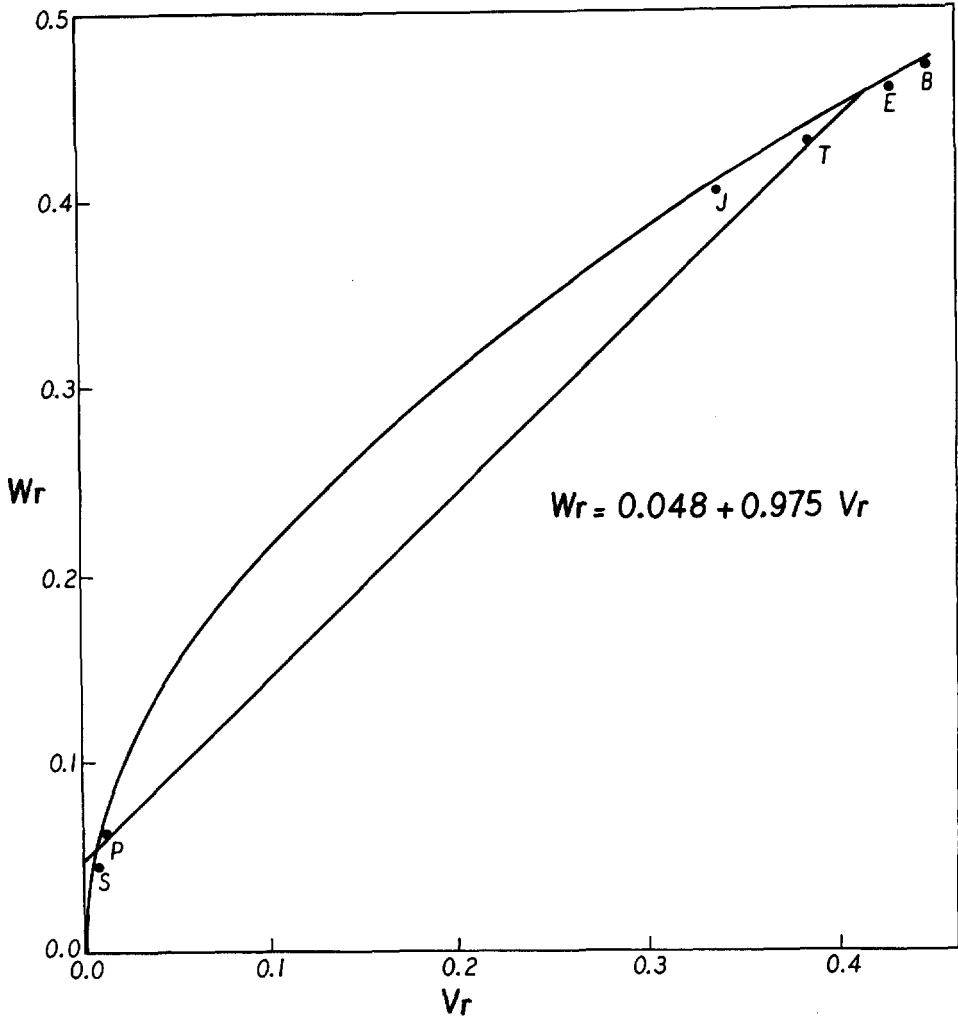


FIGURE 2.—Regression of W_r on V_r for days to heading (log scale) in a 6-parent diallel (Exp. P-2).

tion of no interallelic interactions, the analysis was then performed on a sub-diallel obtained by the elimination of the parent EE.

Figure 2 presents the (W_r, V_r) graph and the limiting parabola $W_r^2 = V_{OLO} V_r$ for the 6-parent diallel lacking EE. The regression of W_r on V_r was not significantly different from unity ($b = 0.975, s_b = 0.035, P > 0.50$) and the $W_r - V_r$ values are homogeneous ($t = 0.568, P > 0.60$) so that the assumptions in this diallel (HAYMAN 1954) are satisfied.

According to the diallel cross theory, the dominance order of the parents is indicated by the relative position of the array points along the regression line of W_r on V_r . Parents with mostly dominant alleles lie closer to the origin because of low W_r and V_r values, those with mostly recessive alleles lie towards the opposite

TABLE 3

*Estimates of genetic variances and their standard errors (log scale)
in a 6-parent diallel (Experiment P-2)*

Estimate	Genetic variance*				
	\hat{D}	\hat{F}	\hat{H}_1	\hat{H}_2	\hat{h}^2
Estimate	0.494	-0.260	0.329	0.288	0.128
S.E.	0.012	0.029	0.034	0.029	0.018

* Genetic variances \hat{D} , \hat{F} , \hat{H}_1 , \hat{H}_2 and \hat{h}^2 are as described by HAYMAN (1954).

end because of high W_r and V_r values, while those with alleles of intermediate dominance occupy an intermediate position along this regression line. It can be seen that the parents fall into two distinct groups with S and P possessing mostly dominant alleles and J, T, B and E possessing mostly recessive alleles. The dominance order of the parents as determined from their respective $W_r + V_r$ statistics is S, P, J, T, E and B, which is in complete agreement with the order of heading time obtained in greenhouse (Table 2). This result, together with the position of the regression line above the origin, indicates that early heading (photoperiod insensitivity) is partially dominant over late heading (photoperiod sensitivity) in the present material.

The correlation between γ_r (parental mean) and $W_r + V_r$ is nearly unity ($r = 0.997$). This provides supporting evidence that most of the recessive alleles act in the direction of lateness.

Estimates of the genetic variances with their standard errors are presented in Table 3. All genetic variances are significant and $0 < H_1 < D$ confirms the incomplete dominance suggested by the (W_r, V_r) graph. The weighted average degree of dominance over all loci is $\sqrt{H_1/D} = 0.817$.

An estimate of the average value of uv (product of the frequencies of plus and minus alleles) is $H_2/4H_1 = 0.218$. Its maximum value is 0.25 when $u = v = 0.5$ but this product is not sensitive to small changes in allelic frequencies (CHAI 1971). The ratio of dominant to recessive alleles is given by $(\sqrt{4DH_1} + F)/(\sqrt{4DH_1} - F) = 0.512$. There seems to be a preponderance of recessive alleles in the parents corroborating the previous result that $u \neq v$ and the fact that the estimate of F is negative (Table 3).

Inheritance of photoperiodic response in segregating generations (Experiment P-3): Table 4 contains the heading time distributions of the parental F_1 , F_2 , B_1 and B_2 generations of the six crosses in Experiment P-3). It is apparent from the distributions in nonsegregating generations (parents and F_1 's) that the environmental variance of the light-insensitive (early) material is very small compared to that of the light-sensitive (late) material. Indeed, the range of heading time does not exceed 5 to 7 days in the former but extends to approximately 35 to 40 days in the latter.

Photoperiod insensitivity is not always dominant over photoperiod sensitivity

TABLE 4
Heading distributions (number of plants) of parental, F₁, F₂, B₁, and B₂ generations (Experiment P-3)

Cross and generation*	Upper class limit, days to heading																				Total							
	36	41	46	51	56	61	66	71	76	81	86	91	96	101	106	111	116	121	126	131		136	141	146	151	156	161	166
<i>S × J</i>																												
S	12	4	1	2	..	3	2	3	2	2	1	16
J	16
F ₁	2	13	1	16
F ₂	42	86	42	14	10	5	2	1	1	..	1	..	1	2	2	1	211	
B ₁	31	16	47	
B ₂	..	12	13	1	2	3	2	3	1	..	1	4	2	1	1	46	
<i>S × B</i>																												
S	12	3	1	2	1	1	3	1	3	5	16	
B	16
F ₁	..	16	16
F ₂	33	74	42	8	13	10	11	3	3	1	..	1	..	1	1	1	1	..	3	1	206	
B ₁	36	11	1	48	
B ₂	2	13	6	..	1	2	6	2	2	3	2	2	..	2	1	2	2	48	
<i>S × EE</i>																												
S	12	4	16	
EE	1	15	16	
F ₁	11	5	16	
F ₂	1	46	80	45	8	5	4	2	2	1	..	1	..	1	..	1	2	2	1	202	
B ₁	38	10	48	
B ₂	3	9	11	10	4	5	2	3	1	48	
<i>J × B</i>																												
J	2	4	3	2	1	2	14	
B	1	2	3	4	2	14	
F ₁	2	5	..	2	3	12	
F ₂	3	5	5	7	6	7	8	17	26	19	17	16	15	7	7	181	
B ₁	1	4	2	2	3	4	7	4	8	2	5	4	1	47	
B ₂	2	5	3	2	7	9	1	29	

TABLE 4—Continued

Cross and generation*	Upper class limit, days to heading																	Total											
	36	41	46	51	56	61	66	71	76	81	86	91	96	101	106	111	116		121	126	131	136	141	146	151	156	161	166	
<i>J</i> × <i>EE</i>
<i>J</i>
<i>EE</i>	15	1
<i>F</i> ₁
<i>F</i> ₂	7	1	..	3	5	12	5	6	8	8	2	10	11	9	8	10	25	17	22	21	9	9	3	5
<i>B</i> ₁	1	1	3	5	9	6	4	8	3	2
<i>B</i> ₂	4	3	1	..	3	4	3	1	1	1	1	1	2	1	2	3	1	2	2	2	2	2	2	2
<i>B</i> × <i>EE</i> †
<i>B</i>
<i>EE</i>	12	3
<i>F</i> ₁	1	1	3	3	5	2
<i>F</i> ₂	2	3	2	2	3	2	5	4	4	5	4	11	11	5	8	23	19	21	18	15	10	4
<i>B</i> ₁	1	2	5	3	7	12	5	5	6
<i>B</i> ₂	2	10	2	1	1	3	2	2	..	2	3	4	3	4	3	4	2

* *B*₁ and *B*₂ are backcrosses of the *F*₁ to the first and second parent as they appear in the cross, respectively.
 † The intermediate group in this cross covers the interval 66–106 days.

TABLE 5

Number of segregates in each photoperiodic class, and tests of the segregation ratios for F₂ and backcross generations with the expected ratios for 2-gene segregation (Experiment P-3)

Cross	Photoperiodic class			Total	Expected ratio	P
	Insensitive	Intermediate*	Sensitive			
S × J, F ₂	170	31 (—)	10	211	12:3:1	>0.10
(S × J) × S	47	0	0	47	1:0:0	1.00
(S × J) × J	25	8 (—)	13	46	2:1:1	>0.40
S × B, F ₂	149	45 (—)	12	206	12:3:1	>0.50
(S × B) × S	48	0	0	48	1:0:0	1.00
(S × B) × B	21	13 (—)	14	48	2:1:1	>0.60
S × EE, F ₂	172	19 (—)	11	202	13:2:1	>0.30
(S × EE) × S	48	0	0	48	1:0:0	1.00
(S × EE) × EE	33	15 (—)	0	48	3:1:0	>0.60
J × B, F ₂	0	0	181	181	0:0:1	1.00
(J × B) × J	0	0	47	47	0:0:1	1.00
(J × B) × B	0	0	44	44	0:0:1	1.00
J × EE, F ₂	8	47 (+)	161	216	1:3:12	>0.10
(J × EE) × J	0	0	42	42	0:0:1	1.00
(J × EE) × EE	8	14 (+)	22	44	1:1:2	>0.40
B × EE, F ₂	7	29 (+)	145	181	1:3:12	>0.20
(B × EE) × B	0	0	46	46	0:0:1	1.00
(B × EE) × EE	14	7 (+)	27	48	1:1:2	>0.20

* (—) and (+) signs indicate earlier and later heading, respectively, within the intermediate class.

as indicated by the F₁ data of the crosses involving S and EE parents. Although all crosses with S show more or less complete dominance of insensitivity, those crosses involving EE, the most day-neutral genotype in the parental group, show almost complete recessiveness of this character (Table 4).

Except for the J × B cross, all others show clear discontinuities in heading distributions of their F₂ and/or B₂ generations, suggesting the presence of major genes controlling photoperiodic response in this material. The crosses S × J, S × B and S × EE gave approximately 1/16 sensitive segregates, while J × EE and B × EE yielded about 1/16 insensitive segregates in their F₂ generation. Additionally, the trimodal distributions of F₂ or B₂ populations apparent in most crosses strongly suggest the operation of at least two major genes.

The distributions in Table 4 were condensed for F₂ and backcross F₁ generations to provide clearer evidence for this hypothesis (Table 5). In this grouping, plants heading in the intervals 36 to 51, 52 to 86 and 87 to 166 days after transplantation were classified as photoperiod-insensitive, intermediate and photoperiod-sensitive, respectively. Moreover, a (+) or (—) sign following the intermediate group indicates whether heading within this group was skewed towards the upper or lower end of the corresponding interval. A wider interval was

adopted for the photoperiod-sensitive group because of its large environmental effect as indicated by the variation in heading time of the homozygous-sensitive parental genotypes.

Table 5 shows that all crosses, with the exception of $J \times B$, segregate in ratios suggesting two major gene differences between any two parents. The cultivars J and B appear to possess the same alleles with respect to these major genes as indicated by the absence of clear segregations in all generations of the cross $J \times B$, and by the similarity in heading distributions of all crosses of these cultivars to a common parent ($S \times J$ and $S \times B$, on the one hand, and $J \times EE$ and $B \times EE$, on the other). The problem of assigning a genotype for each parent is therefore reduced to designating three genotypes differing at two loci in all combinations such that the expected frequencies of their phenotypic classes in a diallel cross agree with the results obtained in Table 5.

If two multiple-allelic loci are considered, a genotype for each parent may be given as follows:

<i>Parent</i>	<i>Genotype</i>
S	$A_1A_1B_1B_1$
J and B	$A_2A_2B_2B_2$
EE	$A_3A_3B_3B_3$

It is assumed that A_1 and B_3 are strong alleles determining photoperiod insensitivity, A_3 and B_1 are intermediate in their effects but interacting for sensitivity when both are homozygous and A_2 and B_2 have unequal effects ($A_2 > B_2$) determining photoperiod-sensitivity. Moreover, it is assumed that A_1 is dominant to A_2 , A_2 to A_3 and A_1 to A_3 . And B_1 is dominant to B_2 , B_2 to B_3 , but B_1 and B_3 are codominant.

Under these assumptions the expected genotypic and phenotypic frequencies in F_2 and backcross generations of each segregating cross can be written as in Table 6. In all cases, the chi-square probabilities show agreement between the observed ratios and those expected with this model (Table 5).

F_3 families also provide supporting evidence for the proposed genotypes and mode of gene action. It will be recalled that five F_3 families representing each of the early, intermediate and late F_2 plants were grown for each of $S \times EE$, $J \times EE$ and $B \times EE$ crosses. However, due to the small number of plants per family (20 to 24), within-family segregates were classified here as photoperiod-sensitive or insensitive only, pooling the intermediate (+) and intermediate (-) classes with the sensitive and insensitive groups, respectively. With this simplification in mind, a random sample of F_2 plants from the cross $S \times EE$ would be expected to yield homozygous insensitive, homozygous sensitive and segregating F_3 families in the ratio 7:1:8, respectively. Moreover, within the segregating group, one half should show 15:1 and the other 3:1 insensitive to sensitive segregates. For the crosses $J \times EE$ and $B \times EE$ the expected ratios are the same as for $S \times EE$, except that insensitive and sensitive groups are now interchanged due to reversal of dominance.

Table 7 contains the results obtained with F_3 families. Since these were not

TABLE 6
Expected genotypes and phenotypes for photoperiodic response in a 4-parent diallel (Experiment P-3)

Cross	Genotype	Phenotype	Cross	Genotype	Phenotype	Cross	Genotype	Phenotype	Frequency		
S × J (F ₂) or S × B (F ₂)	A ₁ A ₁ B ₁ B ₁	Insensitive	S × EE (F ₂)	<i>A. F₂ generation*</i>					A ₂ A ₂ B ₂ B ₂	Sensitive	1/16
	A ₁ A ₁ B ₁ B ₂	Insensitive		A ₁ A ₁ B ₁ B ₁	Insensitive	A ₂ A ₂ B ₂ B ₂	Sensitive	2/16			
	A ₁ A ₁ B ₂ B ₂	Insensitive		A ₁ A ₁ B ₁ B ₃	Insensitive	B × EE (F ₂)	A ₂ A ₂ B ₂ B ₃	Sensitive	1/16		
	A ₁ A ₃ B ₁ B ₁	Insensitive		A ₁ A ₁ B ₂ B ₃	Insensitive		A ₂ A ₃ B ₃ B ₃	Sensitive	2/16		
	A ₁ A ₂ B ₁ B ₂	Insensitive		A ₁ A ₃ B ₁ B ₁	Insensitive		A ₂ A ₃ B ₂ B ₂	Sensitive	4/16		
	A ₁ A ₂ B ₂ B ₂	Insensitive		A ₁ A ₃ B ₁ B ₃	Insensitive		A ₂ A ₃ B ₂ B ₃	Sensitive	2/16		
	A ₂ A ₃ B ₁ B ₁	Intermediate		A ₁ A ₃ B ₂ B ₃	Insensitive		A ₃ A ₃ B ₂ B ₂	Intermediate	1/16		
	A ₂ A ₃ B ₁ B ₂	Intermediate		A ₃ A ₃ B ₁ B ₁	Sensitive		A ₃ A ₃ B ₂ B ₂	Intermediate	2/16		
	A ₂ A ₂ B ₁ B ₂	Sensitive		A ₃ A ₃ B ₁ B ₃	Intermediate		A ₃ A ₃ B ₂ B ₃	Intermediate	1/16		
				A ₃ A ₃ B ₂ B ₃	Insensitive				1/16		
(S × J) × S or (S × B) × S	A ₁ A ₁ B ₁ B ₁	Insensitive	<i>B. Backcross generations*</i>					A ₂ A ₂ B ₂ B ₂	Sensitive	1/4	
	A ₁ A ₁ B ₁ B ₂	Insensitive	(S × EE) × S	A ₁ A ₁ B ₁ B ₁	Insensitive		A ₂ A ₂ B ₂ B ₃	Sensitive	1/4		
(S × J) × J or (S × B) × B	A ₁ A ₂ B ₁ B ₂	Insensitive	(S × EE) × EE	A ₁ A ₁ B ₁ B ₃	Insensitive	(J × EE) × J or (B × EE) × E	A ₂ A ₂ B ₂ B ₃	Sensitive	1/4		
	A ₁ A ₂ B ₂ B ₂	Intermediate		A ₁ A ₃ B ₁ B ₁	Insensitive		A ₂ A ₃ B ₂ B ₂	Sensitive	1/4		
	A ₂ A ₂ B ₁ B ₂	Sensitive		A ₁ A ₃ B ₁ B ₃	Insensitive		A ₂ A ₃ B ₂ B ₃	Sensitive	1/4		

* All genotypes of the cross J × B and the backcrosses (J × B) × J and (J × B) × B are photoperiod sensitive.

TABLE 7

Number of F₃ families in homozygous and segregating classes (Experiment P-3)

Cross	F ₂ plant phenotype	Homozygous		Segregating*			
		Insensitive	Sensitive	15:1	3:1	1:15	1:3
S×EE	Early	4	0	1	0	0	0
	Intermediate	2	0	2	1	0	0
	Late	0	2	1	2	0	0
J×EE	Early	3	0	0	0	2	0
	Intermediate	0	2	0	0	2	1
	Late	0	4	0	0	0	1
B×EE	Early	5	0	0	0	0	0
	Intermediate	0	3	0	0	2	0
	Late	0	4	0	0	0	1

* Segregation ratios refer to insensitive and sensitive classes, respectively.

taken at random but were selected on the basis of the heading response of the F₂ plant as described earlier, no test of goodness of fit was made between the observed and expected number of families in each class. However, the results do show that in all crosses, the F₃ families follow the pattern of homozygosity and segregation expected according to this multiple-allelic, two-locus model.

So far the attempt has been made to simplify the genetic system in terms of major genes suggested by gaps in the frequency distributions. The model developed in terms of these genes seems to explain satisfactorily the results obtained in various generations. However, the likelihood that other minor genes may also be involved in photoperiodic response is strongly suggested by shifts in the modal classes when two or more crosses are compared. In all crosses involving S, for example, the intermediate and photoperiod-sensitive groups were earlier than the corresponding groups in the remaining crosses. Also, the cultivars J and B, assumed to be homologous in terms of major genes, did show some transgression within the sensitive range when crossed to each other, indicating that other modifiers are also involved in the expression of sensitivity in this cross.

A more realistic approach would therefore be to consider the photoperiodic response as a quantitative process influenced by many genes and to attempt to determine the mode of gene action involved in this process.

Table 8 contains the generation means and Table 9 the weighted least square estimates of the genetic components of variation for each cross in Experiment P-3. None of the crosses fits a three-parameter model indicating the presence of significant non-allelic interactions. Estimates of the main effects in this model are unique and show that the additive and dominance parameters are significant and comparable in sign and magnitude within each cross. In the presence of significant interactions, however, these estimates are not epistasis-free and, consequently, are not amenable to a completely reliable interpretation.

TABLE 8

Mean number of days to heading and their standard errors in crosses of a 4-parent diallel
(Experiment P-3)

Generation	Cross ($P_1 \times P_2$)					
	S×J	S×B	S×EE	J×B	J×EE	B×EE
P_1	39.81±0.19	41.31±0.31	40.75±0.25	135.16±1.16	136.12±1.88	142.36±0.64
P_2	115.13±0.50	137.75±0.87	38.19±0.19	148.60±0.77	40.00±0.38	40.32±0.82
F_1	43.31±1.06	42.82±0.18	40.63±0.62	133.92±0.51	119.75±1.75	129.84±1.46
F_2	49.46±1.46	52.45±0.54	48.86±0.99	132.80±0.55	106.94±1.04	123.60±1.71
$B_1=F_1 \times P_1$	41.30±1.00	40.73±0.21	40.25±0.17	131.10±0.97	133.91±1.09	142.96±0.78
$B_2=F_1 \times P_2$	65.72±1.71	71.85±1.15	48.84±0.80	146.02±0.48	88.98±1.98	103.38±1.62

The six-parameter model provides unique estimates for the epistatic components but estimates of additivity and dominance are now dependent on the background population. Except for l in $S \times J$ and $S \times EE$, j in $J \times EE$ and i in $B \times EE$, all interaction components in all crosses are significant. The similarity between the cultivars J and B is once more apparent from the similarity of the results obtained in their crosses to a common parent. Except for minor differences, the estimates of genetic components are comparable in sign and magnitude in the crosses $S \times J$ and $S \times B$, on the one hand, and in $J \times EE$ and $B \times EE$, on the other. The signs of d and j depend upon which parent is identified as P_1 or P_2 ; however, the signs of h , i and l are not affected by this labeling. Comparisons of parameters in $S \times J$ and $J \times EE$ and in $S \times B$ and $B \times EE$ (Table 9) show opposite signs for h , j and l . These parameters involve dominance or dominance interaction and emphasize the differences in genetic control of photoperiod insensitivity in S and

TABLE 9

Estimates of genetic parameters and their standard errors in crosses of a 4-parent diallel
(Experiment P-3)

Parameter	Cross					
	S×J	S×B	S×EE	J×B	J×EE	B×EE
(3-P. model)						
m	58.38±0.44	62.82±0.21	40.37±0.15	137.15±0.28	107.14±0.56	116.35±0.51
d	-37.30±0.26	-43.55±0.41	0.88±0.15	-10.70±0.57	49.41±0.79	50.41±0.50
h	-37.43±0.92	-41.75±0.46	1.92±0.42	-6.41±0.84	35.23±1.78	47.35±1.24
χ^2 (3 d.f.)	97.23**	673.84**	232.98**	149.32**	25.08**	133.23**
(6-P. model)						
m	49.42±1.48	52.51±0.54	48.99±1.00	132.59±0.56	107.32±1.05	123.03±1.69
d	-24.45±1.99	-30.86±1.16	-8.51±0.82	-14.87±1.10	45.67±2.25	39.67±1.80
h	-17.55±7.29	-32.03±3.19	-16.79±4.40	16.60±3.36	54.44±6.46	39.24±7.75
i	16.40±7.21	14.69±3.15	-17.97±4.36	24.54±3.25	13.44±6.14	0.37±7.58
j	13.21±2.01	17.37±1.25	-9.79±0.83	-8.14±1.30	-2.48±2.44	-11.34±1.87
l	11.14±10.30	25.13±5.18	0.21±5.38	-27.88±5.39	-39.55±10.68	-49.72±10.17

** $P < 0.01$.

EE. Thus the results of the quantitative analysis are consistent with and complementary to the qualitative (major gene) analysis. The opposite signs of h and l in all crosses suggest epistatic interactions of the duplicate type (MATHER and JINKS 1971), which is not surprising in a species such as hexaploid wheat with three homoeologous genomes.

DISCUSSION

The importance of photoperiod in controlling the time to heading or flowering in wheat has been reported by several workers (GRIES, STEARNS and CALDWELL 1956; DOWNS, PIRINGER and WIEBE 1959; GOTT 1961; YASUDA and SHIMOYAMA 1965; PUGSLEY 1966; SYME 1968; HALSE and WEIR 1970; MARCELLOS and SINGLE 1971). Where comparisons are possible the ranking of the cultivars used in this study in terms of their photoperiodic response supports that obtained by PUGSLEY (1968) for B, E and EE, by SYME (1968) for S and P and by LEVY and PETERSON (1972) for S, P and J. Evidence was presented in our study for the control of photoperiodic response by two major genes with other minor genes affecting the expression of this response in a quantitative manner. The presence of major and minor genes controlling the heading response of wheat was reported by ALLARD and HARDING (1963) and effects of individual genes in the same material were further measured by WEHRHAHN and ALLARD (1965). Since their studies were conducted under field conditions the effects of genes for vernalization and photoperiod responses were not differentiated.

The postulation of three alleles at each of the major loci involved was necessary to interpret the results obtained in the present study. Although no reports seem to be available in wheat on the control of photoperiodic response by multiple allelic loci, QUINBY (1967) reported multiple allelic series at each of four independent loci controlling the time to maturity in sorghum. The presence of multiple alleles in our material was strongly suggested by the reversal of dominance in crosses between cultivars of opposite response to daylength. As mentioned earlier, daylength insensitivity was dominant in the crosses $S \times J$ and $S \times B$ and recessive in $J \times EE$ and $B \times EE$. This, along with the fact that a two-gene difference was found in each of these crosses, indicates that S and EE do not carry the same alleles with respect to the insensitive response, and suggests the presence of at least three alleles at each of the major loci involved.

The finding that the winter cultivars B and EE differ by two genes with respect to their photoperiodic response is compatible with the hypothesis formulated by ATKINS, WEIBEL and GILMORE (1962) that E may have arisen from B and EE from E by successive mutations and that these cultivars may be isogenic for maturity classes. E was selected from an early plant in a field of B, and EE from a still earlier plant in a field of E (Table 1). All three cultivars are morphologically similar. It is possible that a first mutation from A_2 to A_3 in the cultivar B ($= A_2A_2B_2B_2$) gave rise to the earlier and less sensitive strain E ($= A_3A_3B_2B_2$) and that a second mutation from B_2 to B_3 in the cultivar E produced the day-neutral strain EE ($= A_3A_3B_3B_3$). The fact that A_2 and B_2 are dominant to A_3 and B_3 , respectively, is compatible with the genetic finding that most naturally

occurring or induced mutations are recessive. The two-gene difference obtained in the cross $B \times EE$ agrees with this mutational hypothesis but its final assessment can only be made when the two other crosses $B \times E$ and $E \times EE$ have been shown to differ by one gene with respect to their photoperiodic response.

The quantitative analysis of the diallel cross with parent EE excluded indicated a high average degree of dominance for earliness in spite of the excess of recessive alleles acting in the direction of lateness. This result is compatible with the model proposed where, except for EE , major genes for insensitivity are dominant over their alleles for sensitivity and modifier genes only alter the expression of this response. It should be mentioned, however, that if the mutational hypothesis concerning the Blackhull cultivars is accepted, at least one of the major genes still present will be triallelic and this would violate the assumption of no multiple allelism. In non-segregating generations, however, a triallelic locus may be assimilated to a digenic situation with some interaction (HAYMAN 1954), and it is possible that the disturbances which may have been caused by this multiple allelism at one locus were compensated for by the logarithmic transformation of the data before analysis.

The generation mean analysis, as applied, differs from the diallel cross analysis in that the components of variation in the former were estimated for each cross independently. Also, the absence of interallelic interactions in the diallel is a prerequisite for a meaningful interpretation of the estimated parameters. In the generation mean analysis such an assumption is not made and the components of interaction were themselves estimated in the cases where the additive-dominance model was not adequate. From the results obtained the conclusion may be reached that, beside additivity and dominance, gene interaction constitutes an important factor in the genetic control of photoperiodic response in wheat. This interaction is indicated by the significance of most epistatic components in each cross, by the nature of the segregation ratios in the major gene model proposed, and because a logarithmic transformation of the data was necessary to satisfy the assumptions in the diallel cross analysis. Failure of these assumptions may be due to other causes such as correlated gene distribution in the parents, multiple allelism or linkage.

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 Sci.* **3**: 454-456.
- ATKINS, I. M., D. E. WEIBEL and E. C. GILMORE, 1962 Extra Early Blackhull, an unusual new strain of the "Blackhull" group of wheats. *Crop Sci.* **2**: 357-359.
- BAKER, K. F., editor, 1957 The U.C. system for producing healthy container-grown plants. *Man.* 23. Univ. Calif. Agric. Expt. Ext. Service.
- BORLAUG, N. E., J. ORTEGA C., I. NARVAEZ M., A. GARCIA S. and R. RODRIGUEZ R., 1964 Hybrid wheat in perspective. pp. 1-19. Hybrid Wheat Seminar Report. Crop Quality Council. Minneapolis, Minn.
- CAVALLI, L. L., 1952 An analysis of linkage in quantitative inheritance. In: *Quantitative Inheritance*. pp. 135-144. H.M.S.O. London.

- CHAI, C. K., 1971 Analysis of the quantitative inheritance of body size in mice. VI. Diallel crosses between lines differing at a small number of loci. *Genetics* **68**: 299-311.
- CRUMPACKER, D. W. and R. W. ALLARD, 1962 A diallel cross analysis of heading date in wheat. *Hilgardia* **32**: 275-318.
- DOWNES, R. J., A. A. PIRINGER and G. A. WIEBE, 1959 Effects of photoperiod and kind of supplemental light on growth and reproduction of several varieties of wheat and barley. *Bot. Gaz.* **120**: 170-177.
- GOTT, M. B., 1961 Flowering of Australian wheats and its relation to frost injury. *Aust. J. Agric. Res.* **12**: 547-565.
- GRIES, G. A., F. W. STEARNS and R. M. CALDWELL, 1956 Responses of spring wheat varieties to day-length at different temperatures. *Agron. J.* **48**: 29-32.
- HALLORAN, G. M. and C. W. BOYDELL, 1967 Wheat chromosomes with genes for photoperiodic response. *Can. J. Genet. Cytol.* **9**: 394-398.
- HALSE, N. J. and R. N. WEIR, 1970 Effects of vernalization, photoperiod, and temperature on phenological development and spikelet number of Australian wheat. *Aust. J. Agric. Res.* **21**: 383-393.
- HAYMAN, B. I., 1954 The theory and analysis of diallel crosses. *Genetics* **39**: 789-809. —, 1958 The separation of epistatic from additive and dominance variation in generation means. *Heredity* **12**: 371-390. —, 1960 The separation of epistatic from additive and dominance variation in generation means. II. *Genetica* **31**: 133-146.
- JINKS, J. L., 1954 The analysis of continuous variation in diallel cross of *Nicotiana rustica* varieties. *Genetics* **39**: 767-788.
- KIRBY, E. J. M., 1969 The effects of daylength upon the development and growth of wheat, barley, and oats. *Field Crop Abs.* **22**: 1-7.
- LEVY, J. and M. L. PETERSON, 1972 Responses of spring wheats to vernalization and photoperiod. *Crop Sci.* **12**: 487-490.
- MARCELLOS, H. and W. V. SINGLE, 1971 Quantitative responses of wheat to photoperiod and temperature in the field. *Aust. J. Agric. Res.* **22**: 343-356.
- MATHER, K. and J. L. JINKS, 1971 *Biometrical Genetics*. Second Edition. Cornell University Press. Ithaca, New York.
- MORRISON, J. W., 1960 The monosomic analysis of growth habit in winter wheat. *Z. Vererb.-Lehre* **91**: 141-151.
- PUGSLEY, A. T., 1965 Inheritance of a correlated day-length response in spring wheat. *Nature* **207**: 108-109. —, 1966 The photoperiodic sensitivity of some spring wheats with special reference to the variety Thatcher. *Aust. J. Agric. Res.* **17**: 591-599. —, 1968 Genetic studies of phasic development and their application to plant breeding. pp. 288-293. In: *Proc. Third Int. Wheat Genet. Symp.* Canberra.
- QUINBY, J. R., 1967 The maturity genes of sorghum. *Adv. Agron.* **19**: 267-305.
- SYME, J. R., 1968 Ear emergence of Australian, Mexican, and European wheats in relation to time of sowing and their response to vernalization and daylength. *Aust. J. Exp. Agric. Anim. Husb.* **8**: 578-581.
- WEHRHAHN, C. and R. W. ALLARD, 1965 The detection and measurement of the effects of individual genes involved in the inheritance of a quantitative character in wheat. *Genetics* **51**: 109-119.
- YASUDA, S. and H. SHIMOYAMA, 1965 Analysis of internal factors influencing the heading date of wheat varieties. *Ber. Ohara Inst. Landw. Biol.* **13**: 23-38.