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GENETIC CONTROL OF PHOTOPERIOD RESPONSE IN WHEAT

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SUMMARY

Three studies were conducted in controlled environment chambers. F_2 segregates of the insensitive spring cultivar Sonora 64 x two sensitive winter cultivars, Warrior and Lancer, showed insensitivity to be controlled by two major genes with dominant epistasis. Minor modifiers were present. A second experiment with four spring cultivars of varying sensitivity showed that a minimum of two weeks of plant development was necessary before the sensitivity mechanism became operational. Monosomic analysis of the cross Sonora 64 x Cheyenne showed the two major genes to be located on 2D and 2B. A third major gene difference is suggested between these two cultivars.

Interest has recently been focused on photoperiod-controlled heading response in wheat because of the incorporation of this character in widely adapted cultivars of CIMMYT origin (BORLAUG *et al.*, 1964; SYME, 1968). The general situation is that the photoperiod-sensitive genotypes are delayed in heading by short photoperiods, while insensitive genotypes head in a normal time period regardless of photoperiod. Several variations of this system appear to exist with respect to degree of sensitivity of different cultivars.

PUGSLEY (1965, 1966) found two genes, one major and one minor, governing the inheritance of daylength sensitivity in the cross Triple Dirk/Thatcher, while he proposed one major gene for the cross Triple Dirk/Selkirk. In both cases there was a strong dominance for insensitivity. PINTHUS (1963) studied the inheritance of the length of the two major phases of development, emergence to spike initiation, and initiation to heading. Under short days a dominant gene for earliness was found to govern the time from plant emergence to spike initiation. Days from spike initiation to heading was governed by a single but separate factor. Linkage between these two genes was proposed. TAKAHASHI and YASUDA (1956, 1957) reported that heading-response variations in barley cultivars completely vernalized and grown under continuous illumination were heritable and controlled by polygenes.

This paper serves to summarize previously reported studies (KEIM, WELSH, and McCONNELL, 1973) and recent work conducted at Colorado State University on the genetic control of photoperiod response in wheat.

INHERITANCE OF PHOTOPERIOD RESPONSE IN TWO WINTER WHEATS

In this study conducted in controlled environment chambers, two highly photoperiod-sensitive winter cultivars, Warrior and Lancer, were crossed with a highly insensitive spring cultivar, Sonora 64. Parental, F_1, and F_2 populations were vernalized for 12 weeks at 1°C. One growth chamber was set at 10 hours light - 14 hours dark, and the other at 16-8. Temperatures were maintained at a constant 70°F. Plants were grown in the short photoperiod until about two weeks of age. At that time they were vegetatively divided at the crowns. One half of each plant was grown in the short photoperiod and the other in the long photoperiod. Heading was measured as days from planting to head emergence from the boot. Results are given in Table 1. In the short photoperiod Lancer and Warrior headed about 150-175 days after planting. In the long photoperiod they headed in 70-75 days. Sonora 64 headed in 50-60 days under either photoperiod. The F_1's showed strong dominance for earliness and headed in 58-64 days under either photoperiod. The F_2 populations in the long photoperiod were normally distributed between the insensitive and sensitive parents. In the short photoperiod (Fig. 1, Table 2) they showed a skewed distribution with strong dominance for earliness. From distribution patterns a two-gene system with dominant epistasis for earliness was proposed. The ratio of 12 early : 3 intermediate : 1 very late fits the data with a X^2 probability of 0.50-0.30.

TABLE 1. Days to heading of winter and spring wheat parent plant-halves following vernalization under two photoperiods.

		Photoperiod	
		10-hour	16-hour
Cultivar	n	Plant-half A	Plant-half B
Sonora 64	19	50.1	58.0
Lancer	20	172.1	72.6
Warrior	20	153.6	72.2

Gene symbols are proposed as follows:

Ppd1: dominant epistatic for insensitivity
Ppd2: dominant for partial insensitivity

Sonora 64 represents the homozygous dominant at both loci, while Lancer and Warrior are homozygous recessive at both loci. F_2 genotype and phenotype grouping are as follows:

$$\left.\begin{array}{ll} Ppd1\_\_\_\_ & Ppd2\_\_\_\_ \\ Ppd1\_\_\_\_ & ppd2ppd2 \end{array}\right\} \quad \text{12 early}$$

TABLE 2. Chi-square test of F_2 heading data with a 12:3:1 expected ratio in two crosses involving photoperiod-sensitive and -insensitive parents under a 10-hour photoperiod.

	Early	Late	Very Late
	48-74 days	75-114 days	>130 days
Observed	222	67	15
Expected	228	57	19

$X^2 = 1.91$

P = 0.50-0.30

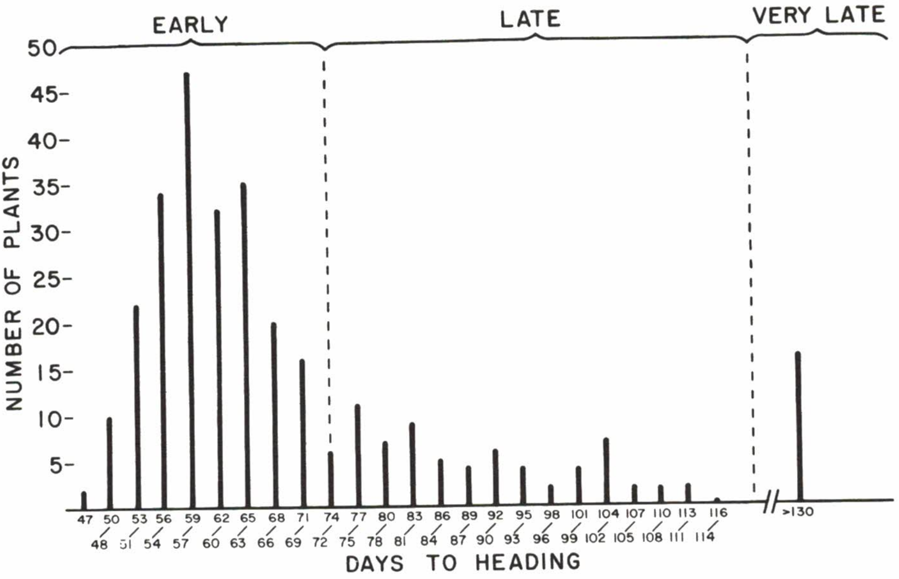

FIGURE 1. Frequency distribution of F_2 individuals from crosses of a photoperiod-insensitive spring wheat cultivar x two sensitive winter cultivars under a 10-hour photoperiod.

ppd1ppd1	*Ppd2*	3 late
ppd1ppd1	*ppd2ppd2*	1 very late

F_2 genotypes were then confirmed with F_3 data. While we were quite confident of two major genes generally controlling the system, we recognized that genotype class intervals were much greater than one would expect from environmental or random variation alone. It was apparent that additional genetic control was modifying the system. This was emphasized by the difference in heading date between Sonora 64 and the winter parents when vernalization was complete and the photoperiod was 16 hours.

RELATING PLANT AGE AND PHOTOPERIOD RESPONSE OF FOUR SPRING WHEATS

This experiment used four spring wheat cultivars, Chris, Selkirk, Era, and Sonora 64, with varying degrees of sensitivity. It was designed to determine the age of the plant at which the sensitivity mechanism became operational, and to determine if the mechanism could be reversed after initiation. Two control-chamber photoperiod environments, 10-14 and 16-8, were utilized. Plantings were made of all four cultivars in each photoperiod. At each two-week interval following emergence, several plants of each cultivar were switched to the alternate environment and held there for the duration of the experiment. Some plants of each cultivar were held under each environment without switching to serve as controls. Results are presented in Table 3. Sonora 64 had approximately the same heading date under all treatments. However, there was a retardation of heading associated with the short photoperiod after the first two weeks of growth. This would indicate that there is a slight photoperiod response in Sonora 64 and this mechanism becomes operational sometime after the first two weeks of growth. Chris was quite insensitive, with only a 16-day delay in heading in the short photoperiod. A slight delay was experienced in the two-week switch from long to short. When Chris plants were switched from short to long at two weeks, they were very similar in response to the long-day check, but additional two-week intervals resulted in heading delays. This again indicated that the mechanism became operational sometime after the second week of growth. Both Selkirk and Era were highly sensitive, and neither had headed under the short photoperiod at the termination of the experiment. The photoperiod mechanism had not been activated in either cultivar at the two-week stage. In Selkirk it was operational at four weeks while in Era it was partially operating at four weeks and fully operating at six weeks. Both cultivars showed the same response patterns in switches from short to long.

This experiment emphasized that a variety of photoperiod responses are possible. In general the photoperiod mechanism in the cultivars tested became operational after the second week of growth and was not reversible once it was initiated.

MONOSOMIC ANALYSIS TO LOCATE PHOTOSENSITIVITY GENES

This study was initiated with the 21 monosomic lines in the photosensitive winter cultivar Cheyenne obtained from Dr. Morris at the University of Nebraska. Sonora 64 was used as the insensitive spring cultivar. Monosomic F_1 plants were identified by PMC analysis, and approximately 90 F_2 progeny in each of the 21 monosomic F_1 lines were vernalized and tested under a 10-hour photoperiod. Normal F_2 segregates and parents were also tested.

While the experiment is not entirely completed and analyzed at the writing of this paper, several observations can be made. We assumed that there should be two linkage groups associated with the two major genes proposed in earlier studies (KEIM *et al.*, 1973). The *Ppd1* gene should be identified in a monosomic analysis of this nature by a lack of late or very late segregates in the F_2. Chromosome 2D had 87 plants in the early group and three in the late class. We have tentatively identified 2D as the carrier of the *Ppd1* locus. *Ppd2* should be identified by a segregation of 3 early : 1 late. No very late plants should be observed. The population of 89 plants in chromosome 2B segregated 71 early : 19 late, which fit the proposed ratio, and 2B has tentatively been identified as the carrier of *Ppd2*.

TABLE 3. Number of days from planting to heading for four spring wheat cultivars under several photoperiod treatments.

	Long to Short		Short to Long	
Cultivar	Weeks	Days to Head	Weeks	Days to Head
Sonora 64	2[1]	44 a[2]	4	49 a
	4	42 ab	Check	48 a
	Check	40 b	2	43 b
Chris	2	54 a	6	66 a
	4	52 b	Check	66 a
	6	52 b	4	61 a
	Check	50 b	2	54 b
Selkirk	2	100+a	Check	100+a
	4	54 b	8	90 b
	8	50 c	6	77 c
	6	49 c	4	63 d
	Check	49 c	2	54 e
Era	2	100+a	Check	100+a
	4	71 b	8	86 b
	6	56 c	6	78 c
	Check	55 c	4	65 d
			2	58 e

[1] Switched from long to short photoperiod at two weeks.

[2] Means followed by different letters are statistically different according to Duncan's multiple range test.

A significant difference between this study and the earlier work has been observed. In the study reported by Keim the segregates headed early, late, or not at all. In the Cheyenne crosses a fourth phenotypic expression was observed. In the new expression the plants differentiated spikes in elongated culms, and the spikes moved up into the boot but emerged very slowly. This was evident in both monosomic and normal F_2 segregates. This suggests a third gene difference between Sonora 64 and Cheyenne, with the gene action associated with the period of elongation following spike differentiation. These observations would agree with those of PINTHUS (1963). Data are insufficiently complete at this time to suggest chromosomal location for this gene. This study agrees with our earlier proposal of two major genes with single dominant epistasis for earliness. However, it suggests the possibility of a third major-gene difference between Sonora 64 and Cheyenne.

DISCUSSION

There are several points that need to be emphasized from these studies:

1. Photoperiod response seems to be under the control of a minimum of two major genes with dominance or dominant epistasis for earliness. Population distributions indicate the presence of modifiers of minor magnitude.

2. Chromosomes 2D and 2B carry the *Ppd1* and *Ppd2* loci, respectively.

3. The photoperiod mechanism is initiated after the first two weeks of growth. It is not reversible, but completion of the process following spike initiation is dependent on a separate genetic system.

4. All studies reported here were conducted at a constant temperature of 70°C and photoperiods of 10-14 or 16-8. Reactions of genotypes under other environments were not investigated.

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