JANUARY, 1949 RESEARCH BULLETIN 430

UNIVERSITY OF MISSOURI COLLEGE OF AGRICULTURE
AGRICULTURAL EXPERIMENT STATION
J. H. LONGWELL, *Director*

Inheritance of Earliness in Crosses Between Early Premium and Kawvale Varieties of Common Wheat

J. M. POEHLMAN

Publication authorized January 20, 1949
COLUMBIA, MISSOURI

TABLE OF CONTENTS

Inheritance of Earliness in Crosses Between Early Premium and Kawvale Varieties of Common Wheat

J. M. Poehlman

INTRODUCTION

Knowledge of the factors controlling inheritance of early maturity is important in any breeding program where earliness is a primary objective. Since nothing was known about the inheritance of earliness in Early Premium, a variety of common wheat used in crosses at the Missouri Agriculture Experiment Station as a source of earliness, a study was undertaken in a cross of this variety with Kawvale.

REVIEW OF LITERATURE

The inheritance of date of heading, awn emergence, or maturity of wheat has been studied and reported by several investigators. With one exception, these were studies of crosses between early x late spring varieties or spring x winter varieties. In one study, Shen et al. (18)*, the authors do not state whether spring or winter forms were used but the dates of planting (October) and dates of heading (April) would indicate the varieties to be winter types. A summary of the literature reviewed follows:

SUMMARY OF LITERATURE REVIEWED

Investigator	Character of Plants in		No. factors in inheritance of earliness	Index of earliness
	F_1	F_2		
	Early Spring x Late Spring Crosses			
Biffen (3)	intermediate	early, intermediate and late	one	date of ripening
Thompson (21,22, & 23)	late	range of parents	multiple	date of ripening
Freeman (10)		plants earlier and later than parents with mean near the late parent	three or more	date of heading
Clark (5)		mean of plants approached the maturity of early parent		date of heading

*Refers to Literature Cited, see page 27.

Investigator	Character of Plants in		No. factors in inheritance of earliness	Index of earliness
	F_1	F_2		
Florell (8)	intermediate	3 early to 1 late	one (major)	date of heading
Clark & Hooker (6)		mean near mean of early parent	multiple	date of heading
		intermediate	multiple	date of ripening
Florell (9)	intermediate	progeny from back-cross of F_1 x recessive (late) parent intermediate	three or more	date of heading
Stephens (19)	intermediate	range of parents	multiple	date of heading
Crescini[1]	late	3 late to 1 early	one	date of heading
Newman (13)	intermediate	range of parents	multiple	date of maturity
Gfeller (11)	intermediate	range of parents (none as early as early parent)	multiple	date of heading
	Spring x Winter Crosses			
Bryan & Pressley (4)	intermediate	range of parents	multiple	date of heading
Aamodt (1)		earliness dominant	two or more (in addition to factors for growth habit)	date of heading
Quisenberry (15)		F_3 lines from hardy F_2 plants ranged on either side of winter parents with mode earlier	multiple	date of heading
Powers (14)			three (growth habit and earliness)	date of ripening
Kakizaki & Suzuki (12)	intermediate			date of heading
	Early Winter x Late Winter Cross			
Shen, Tai, & Chang (18)	intermediate (mean near early parent)	range of parents (a few plants earlier than early parent)	multiple	date of heading

1. Crescini, F. Sul comportamento del carattere precocita in F_2 da incroci di Tr. vulgare (Vill.) on the behaviour of the characters "earliness" in the F_2 of crosses of T. vulgare (Vill.). Riv. di Biol., 12:193-206, 1930. After Bell (2).

Diversity in the inheritance of earliness or lateness in wheat is noted in these reports. These results show:

(1) In crosses between spring wheat varieties the F_1 was usually intermediate, with the F_2 covering the range of the parents indicating a multiple factor inheritance between the early and late parents with earliness at least partially dominant. There are exceptions as Thompson (23) and Crescini[1] reported late F_1 progenies, and Biffen (3), Florell (9) and Crescini[1] reported distinct segregation in the F_2 with single factor inheritance.

(2) In crosses between spring x winter varieties of wheat no simple inheritance is indicated, but it is evident that the spring and winter varieties contain factors for earliness which are inherited separately, and in addition to factors for growth habit.

(3) In the cross between winter varieties, multiple factor inheritance was indicated with earliness at least partially dominant.

The results emphasize the need for specific studies of the inheritance of earliness with each variety used as a source of early maturity in a breeding program.

EXPERIMENTAL WORK

Previous Observations at the Missouri Station

Crosses were made at the Missouri Agricultural Experiment Station in 1931 between the Early Premium variety of soft red winter wheat and the varieties Kawvale, Michigan Wonder, Fulcaster, Harvest Queen, and Poole. Selections were made of early plants from the bulk progenies of these crosses in the fifth and sixth generations. Many of these selections were observed to be earlier than the Early Premium parent and in none of the early lines did segregation of later maturing plants occur. This suggested multiple factors with transgressive segregation in the inheritance of date of heading in these crosses with earliness recessive. Results reported here bear out this supposition.

Materials and Methods

A cross of Kawvale x Early Premium was made in the greenhouse in the winter of 1936-1937. The F_1 generation was grown in the field in 1937-1938, and backcrosses were made to each of the parents. In 1938-1939 the F_2 seed was space-planted in the field, along with the seed from the backcrosses to the Early Premium and Kawvale parents. Some of these spaced plants were lost as a result of winter injury, but heading notes were obtained on 524 F_2 plants, 114 plants from the backcross to Early Premium, and 142 plants from the backcross to Kawvale. Seed harvested from each F_2 and B_1 plant was sown in an eight-foot row in the fall of 1939-40 at a normal rate of seeding. From ten to twenty individual plants were selected at random from each F_3 and B_2 family and marked for date of heading. Head selections from selected F_3 and B_2 families were sown in head rows in the fall of 1940. Results presented here are based on the date of heading of F_2 and B_1 plants in 1939, the plants selected at random from the F_3 and B_2 families in 1940, and the heading of F_4 rows in 1941.

[1]Crescini, after Bell (2).

Parent Varieties and Their Relative Maturity

Early Premium is an early variety developed as a pure line selection from Early May. Kawvale averages five to six days later in heading than Early Premium, when planted in the field at a normal rate of seeding at Columbia, Missouri (Table 1).

Table 1.--Date of Heading of Early Premium and Kawvale Varieties of Wheat in Field Plots

Year	Early Premium	Kawvale	Difference
1936	May 14	May 19	5 days
1937	May 24	May 30	6 days
1938	May 6	May 18	12 days
1939	May 16	May 18	2 days
1940	May 20	May 24	4 days
1941	May 15	May 19	4 days
		Average	5.5 days

Heading in the F_1

The F_1 generation, consisting of 30-40 plants, was grown in the field during the winter of 1937-38, and was observed to head uniformly four to five days later than the Kawvale parent variety.

Table 2.--Dates of Heading of F_2 Plants from Cross Kawvale x Early Premium and of Parent Varieties (1939)

Date of Heading (1939)	No. F_2 plants headed on each date	Per cent F_2 plants headed on each date	No. plants Early Premium headed on each date	No. plants Kawvale headed on each date
May 18	2	0.38		
19	5	0.95		
20	1	0.19		
21	2	0.38	1	
22	5	0.95	3	
23	4	0.76		1
24	5	0.95	1	
25	33	6.30		
26	46	8.78	2	1
27	78	14.89		4
28	95	18.13		1
29	51	9.73		1
30	47	8.97		
31	40	7.63		
June 1	24	4.58		
2	32	6.11		
3	15	2.86		
4	11	2.10		
5	8	1.53		
6	5	0.95		
7	12	2.29		
8	2	0.38		
9	0			
10	1	0.19		
Total	524	99.98	7	8

Heading in the F_2 Generation

The dates of heading of 524 spaced F_2 plants and comparably spaced parent plants are recorded in Table 2. The F_2 plants started heading before the Early Premium parent and continued heading later than the Kawvale parent. Although the heading period of the F_2 extended over a period of 24 days, most of the plants headed during a nine-day period from May 25 to June 2. This corresponds to the heading period of the Kawvale variety and a short period following. Individual F_2 plants continued to head until June 10, but these were mostly weak plants and probably headed late because of their lack of vigor (Table 10).

Heading in the F_3 Generation

As winter killing from heaving is severe in spaced plantings of fall seeded small grains planted at Columbia, Missouri, it was not considered feasible to space plant the F_3. It also appeared desirable to discard at this stage a number of the weaker lines and these were eliminated on the basis of the height, number of heads and general vigor of the F_2 plant. To record dates of heading in the thickly seeded F_3 rows, individual plants were tagged. The first plants to head in each F_3 family were tagged on the day they headed (or the day following, as tagging was done mostly on alternate days) and other plants

Table 3.--Range of Heading Dates of F_3 Plants and of Parent Varieties

Dates of Heading of F_3 (1940)	No. of plants recorded on each date	No. of families heading on each date	Per cent of families heading on each date	Parent Varieties (No. of plants headed on each date)	
				Early Premium	Kawvale
May 12	11	4	1.09		
13	53	28	7.61		
14	211	51	22.01		
15					
16	164	111	30.16		
17					
18	318	139	37.77		
19				2	
20	298	167	45.38	3	
21	51			4	
22	436	213	57.88	8	
23				2	2
24	438	274	74.46	1	4
25	430	261	70.92		7
26					5
27	306	241	65.49		2
28					
29	484	137	37.23		
30					
31	63	37	10.05		
June 1	4	12	3.26		

Total number of F_3 plants - 3267
Total number of F_3 families - 368
Average date of heading of parents: Early Premium - May 21
Kawvale - May 25

tagged on successive or alternate days as long as they continued to head within each specific family. This method gave the range of heading within each family, not an accurate record of the proportion of segregates heading on any date. A total of 3,267 F_3 plants from 368 families were checked for heading date with a range in heading from May 12 to June 1 (Table 3).

Heading in B_1 (Backcross) Generation

The F_1 generation was backcrossed to each of the parent varieties. The first generation of these backcrosses was grown in the field in 1939 in space plantings along with the spaced F_2 plants. Dates of heading of each plant, height and other agronomic data were recorded. The number of plants headed on each date in comparison with the heading dates of the parent varieties is listed in Table 4.

Seed harvested from the B_1 plants was planted to grow the B_2 generation in 1939-40. Plants from each row were tagged to show the range of heading within each B_2 family (Tables 8 and 9), as was done in the F_3 families.

Table 4.--Date of heading of B_1

	F_1 x Early Premium		F_1 x Kawvale			
Date of Heading	No. plants headed on each date	Per cent of plants headed on each date	No. plants headed on each date	Per cent of plants headed on each date	Early Premium	Kawvale
May 17	1	0.88				
May 18	7	6.14				
May 19	3	2.63				
May 20						
May 21	1	0.88			1	
May 22			1	0.70	3	
May 23	3	2.63	3	2.11		1
May 24	5	4.38	13	9.15	1	
May 25	11	9.65	26	18.31		
May 26	6	5.26	28	19.72	2	1
May 27	15	13.16	20	14.08		4
May 28	19	16.67	16	11.27		1
May 29	13	11.40	14	9.86		1
May 30	14	12.28	5	3.52		
May 31	10	8.77	7	4.93		
June 1	3	2.63	1	0.70		
June 2			6	4.23		
June 3			1	0.70		
June 4						
June 5	1	0.88	1	0.70		
June 6						
June 7	1	0.88				
June 8	1	0.88				
Total	114	100.00	142	99.98	7	8

Factorial Explanation for Inheritance of Earliness

The formulation of a factorial basis to explain the inheritance of date of heading in this cross needs to satisfy the following observations: (1) The F_1 generation headed later than the late parent, indicating dominance of lateness; (2) the range of heading in the F_2 exceeded the range of the parent varieties,

indicating transgressive segregation; and (3) early-heading plants in the F_2 and F_3 produced early progenies in advanced generations, while late-heading plants either produced late progenies or progenies containing both late and early plants.

These facts may be explained by the following hypothesis: that the Kawvale variety carries two pairs of factors, $E_1E_1E_2E_2$ dominant for lateness; that the Early Premium variety carries a third pair of factors E_3E_3 also dominant for lateness; that these three pairs of factors are of equal importance in determining date of heading; and that they are independent in inheritance and complementary in effect.

On this basis, the genetic constitution of the F_1 and F_2 generations, with respect to earliness, would be as follows:

P_1	Kawvale	X	Early Premium
	$E_1E_1E_2E_2e_3e_3$		$e_1e_1e_2e_2E_3E_3$
F_1		$E_1e_1E_2e_2E_3e_3$	
F_2	Phenotypes		Character of Phenotype
1	$e_1e_2e_3$		1 very early (heading earlier than Early Premium)
3	$E_1e_2e_3$		9 early (similar in heading to Early Premium)
3	$e_1E_2e_3$		
3	$e_1e_2E_3$		
9	$E_1E_2e_3$		27 late (similar in heading to Kawvale)
9	$E_1e_2E_3$		
9	$e_1E_2E_3$		
27	$E_1E_2E_3$		27 very late (heading later than Kawvale)

Plants in which all of the factors are recessive would head earlier than Early Premium; plants in which only one factor is dominant would head similarly to Early Premium; plants in which two factors are dominant would head similarly to Kawvale; plants in which three factors are dominant would head later than Kawvale. This results in four heading groups which, for convenience, shall be referred to as *very early*, *early*, *late* and *very late*.

This basis of explaining the difference in date of heading of the parent varieties and the heading of the F_1 and F_2 generation, appears to satisfy the conditions outlined earlier. For, if the hypothesis is correct, we would expect an F_1 later than Kawvale as a result of the dominance of lateness and the complementary effect of three dominant factors. In the F_2 we would expect

a relatively few multiple recessive (*very early*) plants that would head earlier than Early Premium and relatively large proportions that would head with Kawvale or later (*late* and *very late*). Plants homozygous for the three pairs of factors in question would produce progeny with similar heading dates, while those heterozygous for one or more pairs would segregate earlier maturing plants. The possibility of minor or modifying factors should not be overlooked. Also, environmental conditions may alter heading dates. But as will be shown, a reasonable explanation of the data can be made with this hypothesis.

Inheritance of Heading in F_2

In Table 2, it was noted that the heading range of 524 F_2 plants was May 18 to June 10. This range represents plants heading three days earlier than Early Premium to twelve days later than Kawvale. According to the factorial basis suggested we should expect 8 of these plants to classify as *very early*, 74 as *early*, 221 as *late*, and 221 as *very late*. The F_2 plants, on the basis of their date of heading, fit into this pattern if, for example, we consider those plants heading before the Early Premium parent as *very early*, those heading with Early Premium as *early*, those heading with Kawvale as *late*, and those heading after Kawvale as *very late*. However, classification of specific plants into heading groups on date of heading in F_2 only, may lead to an inaccurate classification because (1) variation in spacing resulting from missing plants may alter the normal heading date, (2) the mean dates of heading of the parents are never greatly different (in this particular season the difference was less than four days with some overlapping), and (3) many of the extremely late F_2 plants were probably late because of inherent weakness rather than inherent lateness (Table 10). With the narrow class limits of the four heading groups, overlapping in the heading dates of F_2 plants that should properly be classified into each class may be expected. Thus a more accurate grouping of the F_2 plants could be made from the segregation of their progenies in the F_3 generation.

Inheritance of Date of Heading from the Range of Segregation within F_3 Families

Using the factorial explanation suggested, it is possible to predict from the genotype of an F_2 plant the segregation within the F_3 family. By classifying the F_2 genotypes into groups that will segregate in a similar manner, it is also possible to predict the number of the 368 F_3 families that would be expected in each of these segregation groups. From the range of segregation of heading within an F_3 family, it is then possible to classify each family into a specific segregation group. The F_2 genotypes, grouped according to this segregation in the F_3, the number of the 368 F_3 families expected in each, and the probable range in heading of each segregation group are listed here.

Genotype of F_2 Plant	Per cent of F_2 population	Segregation in F_3	Expected number of F_3 families (1)
Plants classified as very early in F_2:			
$e_1e_1e_2e_2e_3e_3$	1.5625	all very early	6
Plants classified as early in F_2:			
$E_1E_1e_2e_2e_3e_3$ $e_1e_1E_2E_2e_3e_3$ $e_1e_1e_2e_2E_3E_3$	4.6875	all early	17
$E_1e_1e_2e_2e_3e_3$ $e_1e_1E_2e_2e_3e_3$ $e_1e_1e_2e_2E_3e_3$	9.3750	1 very early 3 early	35
Plants classified as late in F_2:			
$E_1E_1E_2E_2e_3e_3$ $E_1E_1e_2e_2E_3E_3$ $e_1e_1E_2E_2E_3E_3$	4.6875	all late	17
$E_1E_1E_2e_2e_3e_3$ $E_1E_1e_2e_2E_3e_3$ $E_1e_1E_2E_2e_3e_3$ $E_1e_1e_2e_2E_3E_3$ $e_1e_1E_2e_2E_3E_3$ $e_1e_1E_2E_2E_3e_3$	18.750	1 early 3 late	69
$E_1e_1E_2e_2e_3e_3$ $E_1e_1e_2e_2E_3e_3$ $e_1e_1E_2e_2E_3e_3$	18.750	9 late 6 early 1 very early	69
Plants classified as very late in F_2:			
$E_1E_1E_2E_2E_3E_3$	1.5625	all very late	6
$E_1E_1E_2E_2E_3e_3$ $E_1E_1E_2e_2E_3E_3$ $E_1e_1E_2E_2E_3E_3$	9.375	3 very late 1 late	34
$E_1E_1E_2e_2E_3e_3$ $E_1e_1E_2e_2E_3E_3$ $E_1e_1E_2E_2E_3e_3$	18.750	9 very late 6 late 1 early	69
$E_1e_1E_2e_2E_3e_3$	12.500	27 very late 27 late 9 early 1 very early	47

(1) 368 F_3 families studied.

Inasmuch as the tagging of the F_3 plants as they headed gives us the range of actual heading within each F_3 family, we can, from this information, classify each F_3 family into one of the segregation groups listed above, and thereby identify the genotype of the F_2 plant (within the limits of each segregation group). Table 5 shows the number of F_3 families classified in this manner

Table 5.--Classification of 368 F_3 Families into Segregation Groups on the Basis of the Range of Heading Within Each Family

Heading date of F_2 plant from which the F_3 family originated	Number of F_3 families classified into each segregation group									
	ve	e	3 e 1 ve	l	3 l 1 e	9 l 6 e 1 ve	vl	3 vl 1 l	9 vl 6 l 1 e	27 vl 27 l 9 e 1 ve
May 18	1		1							
19	4	1								
20	1									
21			2							
22		2	3							
23		1	1	2						
24		2	2	1						
25		9	8	5	7	2				
26		5	13	6	11	10				
27		1	6	4	29	25	1	2	1	
28				3	30	25	1	7	11	1
29					1	7		6	20	8
30						1	3	7	10	6
31							2	5	8	8
June 1								4	5	2
2							1	1	4	4
3										1
4							2		1	1
5									2	
6										
7									1	
Total	6	21	36	21	78	70	10	32	63	31
Expected	6	17	35	17	69	69	6	34	69	46

$X^2 = 11.297$ (P = .20 to .30)

ve = very early
e = early
l = late
vl = very late

into each segregation group in relation to the heading dates of the F_2 plants.

From this table it may be observed: (1) that plants *very early* in the F_2 (with two exceptions) produced F_3 progenies that were uniformly *very early*, (2) that *very late* F_2 plants all produced *very late* plants in the F_3 although specific families also segregated *late*, *early*, and *very early* plants, and (3) that there was an overlapping of the heading dates of F_2 plants that could be classified into the *very early* or *early*, *early* or *late*, and *late* or *very late* classes. This overlapping of the classes may be expected since there was an overlapping of the dates of heading of individual plants of the Early Premium and Kawvale parents and substantiates the suggestion that no accurate classification of the

F_2 could be made from the heading dates of spaced plants only. Chi-square for "goodness of fit" of the actual classification to the expected equaled 11.297 with a P value of .20 to .30. The greatest deviation of the actual to the expected classification of families was in the group descendent from very late F_2 plants. This deviation may have been due to failure to recognize *very late* plants, with the result that some plants were classified into the earlier maturing groups, or may have resulted from the discarding of the very weak late-heading plants in the F_2. In general the segregation in the F_3 appears to be as expected, and the inheritance of date of heading in this cross to be explained reasonably well on the three-factor basis outlined.

Table 6.--Range of Heading in Selected F_3 Families

Classification of F_2 Plant	Segregation within F_3 family	Number of F_3 family	Number of plants heading on each date (May 12 - June 1)																				
			12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	1
very early	very early	1			3		6		2		1												
		453	8	2	1		2		1		3												
	early	201									9	5	2		2								
		341									7		9		6								
early																							
	3 early	323			2		2		3		6		4										
	1 very early	342			2		4		1		3		9		1								
	late	36													2	6		3					
		378													5	3		2					
	3 late	206									1		4		5	1		2					
late	1 early	214								1	1		1		2	2		4					
	9 late	97			1		1		2		2	1			5	2		1					
	6 early	217			1		3		2		2		3		4	2							
	1 very early																						
	very late	149																		8		3	2
		516																		2		5	1
	3 very late	37													1	2		1		4		3	
	1 late	210													1	2		5		5		2	1
very late																							
	9 very late	100										1	2		1	4		2		4		4	
	6 late	144									1	1	2		2	2		1		4		2	
	1 early																						
	27 very late	142	1				1			2			1		2	2		1		5		2	
	27 late	155					1		1		1	2			3			4		3		1	1
	9 early																						
	1 very early																						
Early Premium parent (early)										2	3	4	8	2	1								
Kawvale parent (late)														2	4	7	5	2					

The range of heading of selected F_3 families is recorded in Table 6. This table illustrates how families were classified into the various segregation groups on the basis of the range of heading of individual plants within each.

Inheritance in the F_4

Plant selections from the F_3 families with the best agronomic characteristics were planted in individual rows in the F_4. During the winter of 1940-41,

winter injury was severe and only rows appearing to have good hardiness were harvested. Heading notes were taken on the rows that were to be harvested by classifying the rows on the basis of their heading dates as follows: May 12 or earlier, *very early;* May 13-20, *early* (corresponding to the heading period of Early Premium); May 21-25, *late* (corresponding to the heading period of

Table 7.--Classification of Selected F_4 Rows Grown from Individual F_3 Head Selections

Number of F_3 family	Segregation within F_3 family	Date of heading of selected plants in F_3	Classification of F_4 plant row
1	very early	May 14	very early
		May 16	very early
		May 18	very early
		May 20	very early
342	3 early	May 14	very early
	1 very early	May 20	early
		May 22	early
36	late	May 24	late
		May 25	late
		May 25	late
206	3 late	May 20	early
	1 early	May 24 segregating	late and early
		May 25	late
217	9 late	May 16	very early
	6 early	May 20	early
	1 very early	May 25	late
		May 25 segregating	late, early and very early
100	9 very late	May 21	early
	3 late	May 25	late
	1 early	May 25 segregating	late, and early
		May 27	very late
142	27 very late	May 13	very early
	27 late	May 21	early
	9 early	May 25	late
	1 very early	May 29	very late
		May 29 segregating	very late, late, early

Kawvale); and May 26 or later, *very late.* Rows that were segregating were so noted. The classification of a few selected F_4 rows are reported in Table 7. It may be observed from this table that classification of these F_4 rows follow the general pattern that would be expected from the three-factor explanation postulated heretofore for the inheritance of earliness in this cross.

Inheritance in the Backcross to Early Premium

If the Kawvale parent contains two dominant factors for lateness, $E_1E_1E_2E_2$, and the Early Premium parent a third dominant factor for lateness, E_3E_3 as has been suggested, then F_1 plants backcrossed to Early Premium would give

three phenotypes (*early*, *late*, and *very late*) in the B_1. The B_1 genotypes, their segregation in the B_2, and the expected number of B_2 families in each segregation group are listed below:

F_1 $E_1e_1E_2e_2E_3e_3$		X	Early Premium $e_1e_1e_2e_2E_3E_3$	
Genotype of B_1 plant	Per cent of B_1 population		Segregation in B_2	Expected number of B_2 families (1)
Plants classified as early in B_1:				
$e_1e_1e_2e_2E_3E_3$	12.5		all early	11
$e_1e_1e_2e_2E_3e_3$	12.5		3 early 1 very early	11
Plants classified as late in B_1:				
$E_1e_1e_2e_2E_3E_3$ $e_1e_1E_2e_2E_3E_3$	25.0		3 late 1 early	23
$E_1e_1e_2e_2E_3e_3$ $e_1e_1E_2e_2E_3e_3$	25.0		9 late 6 early 1 very early	23
Plants classified as very late in B_1:				
$E_1e_1E_2e_2E_3E_3$	12.5		9 very late 6 late 1 early	11
$E_1e_1E_2e_2E_3e_3$	12.5		27 very late 27 late 9 early 1 very early	11

(1) 90 B_2 families studied.

No attempt has been made to classify B_1 plants into the various heading classes for, as has been shown, more accurate classification of F_2 plants was made on the basis of the segregation in the F_3, than from the dates of heading of the spaced F_2 plants.

The classification of the 90 B_2 families grown in 1940-41 into the six possible segregation groups on the basis of the range of heading within each family is recorded in Table 8. Chi-square, calculated to measure the goodness of fit of the actual to the expected distribution, equals 2.071 with a P value of .7 to .8.

Table 8.--Classification of 90 B_2 Families of the Backcross, F_1 x Early Premium, into Segregation Groups on the Basis of the Range of Heading within each Family

Date of Heading of B_1 plant	Number of B_2 families classified into each segregation group					
	early	3 early 1 very early	3 late 1 early	9 late 6 early 1 very early	9 very late 6 late 1 early	27 very late 27 late 9 early 1 very early
May 17		1				
May 18	2	5				
May 19	1	2				
May 20						
May 21	1					
May 22						
May 23	2		1			
May 24	2		1	2		
May 25	2	4	1	3		
May 26			3	2		
May 27			8	7		
May 28			4	7	4	1
May 29			2	1	4	3
May 30					4	3
May 31					2	4
June 1					1	
Total	10	12	20	22	15	11
Expected	11	11	23	23	11	11

$x^2 = 2.071$ (P = .70 to .80)

Inheritance in the Backcross to Kawvale

In the backcross of the F_1 to Kawvale only two phenotypes (*late* and *very late*) would be expected in the B_1. The B_1 genotypes, their segregation in the B_2 and the expected number of B_2 families in each segregation group are listed below:

F_1 $E_1e_1E_2e_2E_3e_3$ X Kawvale $E_1E_1E_2E_2e_3e_3$

Genotype of B_1 plant	Per cent of B_1 population	Segregation in B_2	Expected number of B_2 families (1)
Plants classified as late in B_1:			
$E_1E_1E_2E_2e_3e_3$	12.5	all late	13
$E_1E_1E_2e_2e_3e_3$ $E_1e_1E_2E_2e_3e_3$	25.0	3 late 1 early	28
$E_1e_1E_2e_2e_3e_3$	12.5	9 late 6 early 1 very early	13

Plants classified as very late in B_1:

$E_1E_1E_2E_2E_3e_3$	12.5	3 very late 1 late	13
$E_1E_1E_2e_2E_3e_3$ $E_1e_1E_2E_2E_3e_3$	25.0	9 very late 6 late 1 early	28
$E_1e_1E_2e_2E_3e_3$	12.5	27 very late 27 late 9 early 1 very early	13

(1) 108 B_2 families studied.

On the basis of their segregation, as measured by the range of heading within the B_2 family, each family may be classified into one of the segregation groups listed above.

From Table 4 it may be observed that the earliest B_1 plant of the Kawvale backcross headed on May 22, just one day earlier than the heading of the earliest Kawvale plant, while the B_1 plants continued to head until June 5, seven days after the last Kawvale plant headed. From this distribution it may

Table 9.--Classification of 108 B_2 Families of the Backcross, F_1 x Kawvale, into Segregation Groups on the Basis of the Range of Heading within each Family

Date of Heading of B_1 plant	No. B_2 families classified into each segregation group					
	all late	3 late 1 early	9 late 6 early 1 very early	3 very late 1 late	9 very late 6 late 1 early	27 very late 27 late 9 early 1 very early
May 18						
May 19						
May 20						
May 21						
May 22	1					
May 23	1	2				
May 24	2	7	3			
May 25	3	13	8			
May 26	7	11	1		6	3
May 27	1	3		2	6	3
May 28				5	7	
May 29				3	3	2
May 30				1		
May 31					1	
June 1						
June 2				2		
June 3						1
Total	15	36	12	13	23	9
Expected	13	28	13	13	28	13

$X^2 = 4.795$ (P = .40 to .50)

be assumed that all of these plants were either *late* or *very late*. The classification of the B_2 into the six possible segregation groups on the basis of the range of heading within each is listed in Table 9. Chi-square calculated to show the "goodness of fit" to the expected has a value of 4.795 with a P value of .4 to .5.

Date of Heading in F_2 and B_1 Generations Related to Height and Number of Heads per Plant

It has previously been noted that some F_2 and B_1 plants were discarded on the basis of their lack of vigor. Even though a large proportion of those discarded were later than Kawvale, it is not believed that discarding these weak plants has greatly increased the error of classification of F_3 or B_2 populations into segregation groups, except possibly in the F_3 where the proportion of families in the late segregation groups was below the expected (Table 5). That many of the late plants discarded in the F_2 were inherently very weak instead of inherently very late is shown by data on the average height and number of heads per plant for each heading date as recorded in Table 10. The average height and the average number of heads per plant declines after the heading period corresponding to the Kawvale parent was reached. Inclusion of these weak plants would have resulted in a larger proportion of *late* and *very late*

Table 10.--Average Height and Number of Heads Per Plant of F_2 Plants for Each Heading Date

Date of Heading	No. of plants	Av. height of plants (inches)	No. of plants	Av. number of heads per plant
May 18	2	44.0	2	20
19	5	44.5	5	11
20	1	51.0	1	6
21	2	47.0	2	26
22	5	43.4	5	16
23	4	50.5	4	17
24	5	51.2	5	18
25	33	47.7	31	17
26	46	46.3	46	17
27	77	44.8	78	12
28	95	44.6	95	11
29	50	41.8	48	11
30	45	42.4	46	7
31	38	40.7	39	7
June 1	24	38.4	23	8
2	32	34.9	32	5
3	15	33.0	15	4
4	11	35.6	10	4
5	6	32.7	7	4
6	5	28.3	5	3
7	12	26.2	12	2
8	2	21.5	2	3
9				
10	1	17.0	1	1

plants than would have been expected. Many F_2 plants that headed late had good height and a large number of heads per plant. These more vigorous *late* and *very late* plants were kept and only the short and weak plants discarded, along with weak plants in the other heading groups.

Date of Heading and Height in F_3 and B_2 Generations

Within the families that were carried into the later generations there was a definite increase in height in successive heading groups. To measure this, a large number of the plants that were tagged for date of heading in the F_3 and B_2 generations in 1940 were also measured for height. These plants were selected at random and as many measured as time permitted. They have been classified as to heading group and the average height of the plants within each heading group determined. The results are shown in Table 11 and indicate

Table 11.--Relation of Date of Heading to Height in F_3 and B_2

Heading Classification of F_3 or B_2 plant	Kawvale x Early Premium		F_1 x Early Premium		F_1 x Kawvale	
	No. F_3 plants	Av. height (inches)	No. B_2 plants	Av. height (inches)	No. B_2 plants	Av. height (inches)
very early	13	38.1	47	38.9		
early	218	40.1	278	41.7	5	43.2
late	362	49.1	106	46.1	144	48.0
very late	177	49.5	25	50.3		

that the average height of each successive heading group is progressively increased. This conforms with general knowledge that late maturing varieties are usually taller than early maturing varieties. It also conforms to the comparative heights of the Early Premium and the Kawvale parent varieties. This suggests that the decline in height of the late F_2 plants, as reported in Table 10, resulted from the presence of weak plants, which were eliminated before growing the F_3 and B_2 generations.

Date of Heading and "Time" Tests in F_3 and B_2 Families

After plant selections had been made from F_3 and B_2 families, the remainder of the row was harvested and a "Time" fermentation test[1] made from the seed. The parent varieties, Kawvale and Early Premium, vary widely in gluten quality as measured by the "Time" test. The average "Time" of a large number of Early Premium checks was 39 minutes as compared to 170 minutes for the Kawvale checks. The families were grouped according to the heading classification of the F_2 or B_1 plant and the "Time" of the F_3 or B_2 families descendent from plants within each heading group was averaged and is reported in Table 12. It may be observed from these data that there is no relation

[1]"Time" test refers to method of measuring wheat quality with reference to gluten strength, after method outlined by Cutler and Worzella (7).

Table 12.--Relation of Date of Heading to "Time" in F_3 and B_2 Families

Heading Classification of F_2 or B_1 plant	Kawvale x Early Premium		F_1 x Early Premium		F_1 x Kawvale	
	No. F_3 families	Av. "time" (minutes)	No. B_2 families	Av. "time" (minutes)	No. B_1 families	Av. "time" (minutes)
very early	6	52.7				
early	44	51.2	20	40.3		
late	115	52.2	39	38.3	66	85.5
very late	44	55.5	13	40.1	33	90.0

between gluten quality and date of heading. It should be possible then to select lines similar to or approaching the gluten quality of the Early Premium within any of the heading groups (except possibly the lines from the backcross to Kawvale).

Date of Heading and Winter Survival in the F_4

The winter survival of F_4 plant rows, originating from F_3 families apparently homozygous for date of heading, was recorded in 1941 and is reported in Table 13. The number of families represented within each heading group is small, since only families homozygous for date of heading were used.

Table 13.--Winter Survival in F_4

Heading Group	No. F_3 families (1)	No. F_4 head rows	Average Per cent survival 1940-41
very early	7	33	41.1
early	19	112	56.6
late	14	61	69.8
very late	8	39	36.8

(1) F_3 families homozygous for heading classification

Quisenberry and Bayles (16) and Quisenberry and Clark (17) reported that early maturing varieties or selections were less hardy than late maturing varieties or selections. It will be noted here that the average winter survival increased progressively from *very early* to *early*, to *late* families, confirming these reports. The *very late* group had a poorer survival than any of the other three groups but since only eight families were represented this may have resulted from an inadequate sample. These results indicate that fewer of the *early* or *very early* lines than of the *late* may be expected to have satisfactory winter hardiness, but specific lines with good winter hardiness appeared to be present in each of the heading groups.

DISCUSSION

Information is presented here to show that earliness of heading in the cross between Early Premium and Kawvale varieties of wheat is apparently determined by three major complimentary factors of substantially equal value, independently inherited, with earliness recessive in each. From the progeny of this cross various true-breeding lines may be selected that will head earlier than the early parent or later than the late parent, as well as lines that will head on dates corresponding to the heading dates of each of the parents. A large proportion of lines are either as late or later than the late parent, and many of these segregate earlier plants in the following generations.

In an economic breeding program in which the combining of early maturity, high yielding ability and quality is an important objective this information is extremely useful. Its value lies not just in the knowledge that earliness in this cross is inherited by three (or any specific number) major factors, but to the extent it may be useful in the selection of early-maturing lines with good agronomic qualities, and in determining the best procedure for finding these lines in segregating progenies. For example, to obtain from this cross early lines that might combine some of the factors for yield and disease resistance from the Kawvale parent, three methods of procedure are suggested:

(1) Grow the hybrid population in bulk until the F_5 or F_6 generation. Select *very early* or *early* plants in these generations (by comparison with heading date of similarly planted Early Premium check rows). Discard in following year all plant rows still segregating or unsatisfactory from standpoint of agronomic characters, disease resistance, or quality.

(2) Select only *very early* or *early* plants in the F_2. Grow in plant rows in F_3 discarding lines unsuitable from standpoint of agronomic character and quality (determined by "pearling"[1] and/or "Time" tests on seed from F_3 rows). Carry by pedigree method until F_5 or F_6.

(3) Plant seed from all F_2 plants satisfactory from standpoint of agronomic and disease characters. Select and plant seed from *very early* and *early* plants from F_3 rows satisfactory in agronomic characters, disease resistance, and quality. Carry by pedigree method until F_5 or F_6.

The bulk method would enable one to carry a large amount of material in the early segregating generations. But it would be necessary to include a preponderance of unwanted late maturing lines. Experience at the Missouri Experiment Station has indicated that several thousand early selections would probably be needed to find a relatively few early lines combining high quality, yield, winter hardiness, and disease resistance. This would be necessary since a high proportion of early selections from Early Premium crosses appear to be lacking in vigor and productiveness, and a high proportion of selections from Kawvale crosses appear to be undesirable from the quality standpoint.

[1]"Pearling" tests refer to method of measuring kernel hardness after Taylor, Bayles and Fifield (20).

Selection for earliness in the F_2 combined with rigorous selection in the F_3 for agronomic characters, disease resistance, and quality (from seed of F_3 rows) offers the best opportunity of eliminating the large bulk of undesirable material at the earliest generation. But selection in the F_2 would also result in elimination from further consideration many lines heterozygous in earliness that would possibly be satisfactory from an agronomic and quality standpoint, and that would segregate early plants in the F_3 generation. In view of the apparent lack of vigor of many early lines and unsatisfactory quality in many selections from Kawvale crosses, success by major selection for earliness in F_2 could be expected only if an extremely large F_2 population was grown. It has been demonstrated that classification of individual spaced F_2 plants cannot be accurately made, since the heading classes have no well defined limits; thus continued selection in F_3 would be necessary to eliminate late lines inadvertently included. Selection in F_3 for earliness would also be necessary in those lines segregating *early* and *very early* plants.

If the F_2 population was limited in size, then selection for earliness in the F_3 would offer a wider opportunity for finding desirable combinations, as it would permit the sampling of many additional lines that would segregate early plants in the F_3 but which would otherwise be discarded in the F_2. Rigorous selection for agronomic and disease characters could still be made on the F_3 rows and selection for quality by "pearling" and/or "Time" tests on the seed harvested from F_3 rows.

While the discussion here has been limited to progenies of crosses in which Early Premium and Kawvale are the parent varieties, experience at the Missouri Agricultural Experiment Station with crosses of Early Premium and varieties such as Clarkan, Michigan Wonder, Fulcaster, Thorne, Wabash and others indicate that it may be applicable to many crosses in which Early Premium is the early parent variety.

SUMMARY

1. Inheritance of the date of heading in a cross between the Kawvale and Early Premium varieties of wheat is reported.

2. In field plots, the average date of heading of the Early Premium variety at Columbia, Missouri, was 5.5 days earlier than Kawvale for the six-year period from 1936 to 1941.

3. The F_1 generation headed uniformly several days later than Kawvale and the range of heading of the F_2 exceeded the range of heading of the parents with most of the plants heading as late as or later than Kawvale.

4. An explanation of inheritance is postulated on the basis of three factors, independently inherited, of equal importance, and with earliness recessive. Two of the three factors (E_1E_2), are assumed to be dominant in the Kawvale variety and the third factor, (E_3), as dominant in the Early Premium variety. With only recessives present, plants are earlier than the Early Premium; pres-

ence of one dominant results in plants maturing with Early Premium; presence of two different dominants results in plants maturing with Kawvale; and presence of three different dominants results in plants later than Kawvale.

5. Inheritance studies in backcrosses to each parent support this hypothesis.

6. The average height of the plants increased progressively in each of the four heading classes, *very early*, *early*, *late*, and *very late*, after the weak lines had been eliminated in early generations.

7. Quality as measured by the "Time" test was not related to date of heading.

8. Average winter survival increased progressively in selections from the *very early* to the *late* heading groups.

9. Methods for selection of early maturing lines from progenies of crosses in which Early Premium is the early parent are discussed.

LITERATURE CITED

1. Aamodt, O. S., *A study of growth habit and rust reaction in crosses between Marquis, Kota, and Kanred Wheats.* Phytopath. 17:573-609. 1927.
2. Bell, G. D. H., *A study on the date of ear emergence in barley.* Jour. Agr. Sci. 29:175-228. 1939.
3. Biffen, R. W., *Mendel's laws of inheritance and wheat breeding.* Jour. Agr. Sci. 1:4-48. 1905.
4. Bryan, W. E., and Pressley, E. H., *Inheritance of earliness in wheat.* Ariz. Agr. Exp. Sta. Ann. Rpt. 32:603-605. 1921.
5. Clark, J., *Segregation and correlated inheritance in crosses between Kota and Hard Federation wheats for rust and drought resistance.* Jour. Agr. Res. 29:1-47. 1924.
6. Clark, J. A., and Hooker, J. R., *Segregation and correlated inheritance in Marquis and Hard Federation crosses, with factors for yield and quality of spring wheat in Montana.* U. S. Dept. of Agr. Bul. 1403:70pp. 1926.
7. Cutler, C. H., and Worzella, W. W., *The wheat meal fermentation time test for measuring quality in wheat.* Purdue Univ. Agr. Exp. Sta. Cir. 218:14pp. 1936.
8. Florell, V. H., *Studies in the inheritance of earliness in wheat.* Jour. Agr. Res. 29:333-347. 1924.
9. Florell, V. H., *A study of certain characters in wheat back crosses.* Jour. Agr. Res. 43:475-498. 1931.
10. Freeman, G. F., *Heredity of quantitative characters in wheat.* Genetics 4:1-93. 1919.
11. Gfeller, F., *Inheritance of earliness of heading and other characters in a Garnet x Red Fife cross.* Sci. Agr. 17:482-491. 1937.
12. Kakizaki, Y., and Suzuki, S., *Earliness as influenced by seasonal growth habit in wheat hybrids.* Japan. Jour. Genetics 16:59-63. 1940.
13. Newman, L. H., *The breeding of early-ripening varieties of spring wheat in Canada.* Emp. Jour. Exp. Agr. 1:1-16. 1933.
14. Powers, L. R., *The nature and interaction of genes differentiating habit of growth in a cross between varieties of* Triticum vulgare. Jour. Agr. Res. 49:573-605. 1934.
15. Quisenberry, K. S., *Inheritance of winter hardiness, growth habit, and stem rust reactions in crosses between Minhardi winter and H-44 spring wheats.* U. S. D. A. Tech. Bul. 218:45pp. 1931.

16. Quisenberry, K. S., and Bayles, B. B., *Growth habit of some winter wheat varieties and its relation to winter hardiness and earliness.* Jour. Amer. Soc. of Agron. 31:785-789. 1939.
17. Quisenberry, K. S., and Clark, J., *Breeding hard red winter wheats for winter hardiness and high yield.* U. S. D. A. Tech. Bul. 136:1-28. 1929.
18. Shen, T. H, Tai, S. E., and Chang, S. C., *The transgressive inheritance of reaction to flag smut, earliness of heading, partial sterility, and stiffness of glumes in a varietal cross of wheat.* Jour. Amer. Soc. Agron. 30:68-79. 1938.
19. Stephens, F. E., *Inheritance of earliness in certain varieties of spring wheat.* Jour. Amer. Soc. Agron. 19:1060-1090. 1927.
20. Taylor, J. W., Bayles, B. B., and Fifield, C. C., *A simple measure of kernel hardness in wheat.* Jour. Amer. Soc. Agron. 31:775-784. 1939.
21. Thompson, W. P., *The inheritance of the length of the flowering and ripening periods in wheat.* Trans. Roy. Soc. Canada (Ser. 3) 12:69-87. 1918.
22. Thompson, W. P., *The inheritance of earliness and lateness in wheat.* Trans. Roy. Soc. Canada (Ser. 3) 13:143-162. 1919.
23. Thompson, W. P., *Earliness in wheat and its inheritance.* Sci. Agr. 1:193-197. 1921.

603018

UNIVERSITY OF MISSOURI - COLUMBIA
VET PER 603018
ISNB 880736 421-435,1948/49
030-000890995

Vet. Lib.

University Libraries
University of Missouri

Digitization Information Page

Local identifier	ResearchBul430

Source information

Format	Book
Content type	Text with images
Source ID	030-000890977
Notes	Copy does not include covers. Bound with other issues.

Capture information

Date captured	April 2019
Scanner manufacturer	Fujitsu
Scanner model	fi-7460
Scanning system software	ScandAll Pro v. 2.1.5 Premium
Optical resolution	600 dpi
Color settings	24 bit color (cover); 8 bit greyscale (text)
File types	tiff

Derivatives - Access copy

Compression	Tiff: LZW compression
Editing software	Adobe Photoshop CC
Resolution	600 dpi
Color	24 bit color (cover); 8 bit greyscale (text)
File types	tiff
Notes	Image cropped, straightened, brightened