

INHERITANCE OF EARLINESS IN A CROSS INVOLVING
TWO HARD RED WINTER WHEATS

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INVOLVING TWO HARD RED
WINTER WHEATS

By

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INHERITANCE OF EARLINESS IN A CROSS INVOLVING
TWO HARD RED WINTER WHEATS

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INTRODUCTION

The importance of early maturity in winter wheat varieties for the Southern Great Plains cannot be overemphasized. For example, the early variety, Triumph has become the most widely grown variety of wheat in Oklahoma. Pawnee, only slightly later than Triumph, is the most widely grown variety of hard red winter wheat in the United States.

Numerous workers have mentioned the importance of early maturity in wheat varieties. Salmon (22)¹ stated that there is abundant evidence to show the superiority of early maturing wheat varieties for the Southern Great Plains. Salmon and Laude (23) pointed out that yielding ability is sometimes of lesser importance than earliness in certain areas of Kansas. They stated that late maturing varieties were frequently injured by heavy rains and hail at harvest time. In a later study, Reitz and Heyne (21) found that late heading and maturity were seldom associated with high yields. Early heading and maturity alone, however, did not insure high productivity. Rather a combination of adaptation, early maturity and disease and insect resistance, such as found in the variety Pawnee, was desirable.

Very early maturing varieties are not always desirable from the standpoint of yield, quality and winterhardiness. In addition, they are frequently injured during blossoming by temperatures of freezing or below. The object of most wheat breeders in the Southern Great Plains is to produce wheat varieties of medium-early maturity.

¹ Figures in parentheses refer to "Literature Cited", page 36.

At the initiation of this research, no genetic studies had been made on the inheritance of earliness in hard red winter wheat despite the importance of this character in breeding programs throughout the hard red winter wheat area. The objectives, then, of this research were as follows: (1) to determine the mode of inheritance of earliness in a cross involving the wheat variety Triumph; (2) to determine the association between height and date of heading in the above cross; and (3) to obtain true breeding segregates of different maturity classes for use in quality determinations.

These studies were made in the field on the Agronomy Farm at Stillwater, Oklahoma during the 1952 and 1953 crop years.

REVIEW OF LITERATURE

Maturity Indices in Cereal Crops

The accurate classification of hybrids in a genetic study of maturity is oftentimes difficult. Consideration must first be given to the various indices which have been used to enable the plant breeder to separate different maturity classes in crosses between varieties.

Various maturity indices have been used in genetic studies. Harlan (13) and Harlan and Martini (14) believed that for barley, date of emergence of the awns was the best method of classification. Harlan stated that the first emergence of the awn is a character possessing heritability equal to that of most plant characters.

Several investigators (10, 11, 12, 25), working with wheat crosses, used the date of emergence of the tip of the first spike as an index. According to Florell (10), the greatest varietal differences can be detected at this stage.

Numerous workers (5, 7, 17, 24, 26), have used date of heading as an index. According to Clark (8), date of heading is usually less affected by environmental conditions than the ripening period. He further stated that heading date was considered by most workers to be the best method of classification. This method was used in the study reported here.

The ripening date of the early wheat parent was used by Biffen (4), one of the earlier investigators. He used three classes; namely, ripe, half ripe, and unripe. Plants were considered ripe when the straw and glumes were yellow and the grain was hard. Plants with yellow awns, other parts yellowish-green and soft grain were considered half ripe.

Unripe denoted all parts of the plant as being green. Caporn (6), working with oats, used "ripe" to indicate all traces of green had vanished from the tips of the palea.

Inheritance of Earliness in Wheat

In the spring wheat cross Sunset x Marquis, Florell (10), found that the F_2 generation segregated in the proportion of 3.07 early to 0.93 late. The recessive late group of the F_2 generation also headed late in the F_3 generation which tended to verify the 1 factor hypothesis. In a later study (11), he reported 3 or more factors responsible for differences in earliness from crosses of Quality x Jenkin and Quality x Little Club. Backcrosses of the F_1 to the parents indicated that each parent contributed dominant factors for earliness. When backcrossed to the early parent (Quality), the progeny headed near the mean of the early parent while the backcrosses to the late parents resulted in progeny that were intermediate with respect to heading.

Earliness of heading in the spring wheat cross Kota x Hard Federation was studied by Clark (7). The material was grown at 3 locations in order to observe differences due to environment. At all locations earliness of heading was dominant to lateness although not expressed to the same degree. He concluded that date of seeding and location were important factors influencing the expression of this character. In a later study, Clark and Hooker (9) grew F_2 and F_3 plants of the spring wheat cross Marquis x Hard Federation at 3 locations in Montana. Significant positive correlations for date of heading were obtained between F_2 and F_3 plants grown at 2 of the 3 locations.

They found earliness of heading to be partially dominant and due to 1 or 2 genes.

Although earliness did not appear to be completely dominant, Stephens (25) found the means of the F_1 and F_2 generations to be nearer the mean of the early parent in crosses involving 6 varieties of spring wheat. The F_2 generation appeared to be more variable than either parent, although slight differences were observed between certain crosses. Stephens concluded that earliness was due to a number of independent, multiple factors having a cumulative effect. These findings agree rather closely with those of Gfeller (12) who concluded that earliness of heading was very complex and involved many factors. In crosses between Garnett and Red Fife, he was unable to recover the earliness of Garnett. A similar response was obtained both in the field and greenhouse from F_1 and F_2 generations. Newman (16), in reviewing the inheritance of earliness in wheat, also pointed out the complexity of this character. He stated that in most cases the F_1 and F_2 generations were intermediate and that few hybrids had been developed that were as early as the early parent.

Inheritance of earliness in winter x spring wheats appears to be at least as complicated as in spring x spring wheat crosses. According to Quisenberry (20), inheritance of early maturity and winterhardiness appeared to be rather complex in the Minhardi x H44 wheat cross. Mode and mean dates of heading in the F_3 lines were earlier than the Minhardi parent. No explanation as to the mode of inheritance was presented. However, he felt that early, winterhardy segregates could be obtained from winter x spring crosses, although with difficulty.

Genotypes giving a continuous range for earliness and lateness in crosses between Hybrid 128 winter and Velvet Node spring wheat were obtained by Powers (18). He concluded that 3 major factors were responsible for earliness and habit of growth with additional modifying factors affecting earliness. These findings are in fairly close agreement with those of Aamodt (1) who studied crosses between Kanred winter and Kota spring wheat. He stated that there were at least 2 factors responsible for earliness of heading, in addition to 2 factors for habit of growth.

From the wheat cross Turkey x Sonora, Bryan and Pressley (5) were able to recover F_2 plants as early as the early parent, although the majority of plants were intermediate. In this cross approximately one-third of the total F_2 population headed within the range of Turkey, the late parent.

From a cross between the soft red winter wheats, Kawvale and Early Premium, Poehlman (17) grew F_1 , F_2 , F_3 , F_4 , B_1 and B_2 generations. The F_1 generation headed 4 to 5 days later than Kawvale, the late parent. Very early and very late types in the F_2 generation indicated transgressive segregation. When grown in subsequent generations, many of these new types were true breeding. A very good fit to a 3 factor hypothesis was obtained from the different generations grown. Earliness of heading therefore, appeared to be due to 3 complementary factors, inherited independently with earliness recessive in each.

Inheritance of Earliness in Other Crops

In the oats cross Clinton x Santa Fe, Litzenberger (15) reported earliness of heading to be dominant and due to one factor. Probability values for goodness of fit to a 3:1 ratio ranged from 0.10 to 0.80

depending on whether the material was grown in the field or greenhouse. The highest probability values were obtained from field tests. Caporn (6) reported that three factors, cumulative in effect, appeared responsible for differences in maturity observed in the oats cross Mesdag x Hopetown. From classification of material in the F_3 generation, he concluded that the factor for early ripening was recessive.

Earliness appeared to be only partially dominant in 2 different oat crosses reported by Torrie (26). In the cross Victoria x Richland, 2 factors appeared to be responsible for earliness of heading while in the Iowa No. 44 x Bond cross multiple factors were believed to be present. Sappenfield (24) reported earliness of heading to be incompletely dominant from a study of all possible cross combinations in 6 varieties of common cultivated oats. Gene interaction and heterosis were believed to be responsible for earliness appearing to be completely dominant in certain crosses. The number of gene differences became progressively greater as the difference in date of heading between varieties increased.

In barley, Bell (3) was able to affect the heading dates of F_1 and F_2 hybrids originating from crosses of 2 widely different types by sowing a portion of the seed at 2 different dates. He emphasized the need of understanding the physiological nature of earliness before genetic analyses were undertaken. An involved length-of-day factor, similar to that suggested by Bell was reported by Harlan and Martini (14) from a study of date of awn emergence of F_1 barley hybrids. In some instances, the hybrids headed from 2 weeks before to 2 weeks after the parental limits. Although no data were included to support their contention, they believed that had the experiment been grown at a different geographic location, dissimilar results would have been obtained.

In crosses between varieties of milo, Quinby and Karper (19) reported that genes for earliness were essentially adaptation genes. They explained this on the basis that these genes determine the range of latitude, longitude and rainfall belt in which a variety of milo can be successfully grown as a crop. There appeared to be 3 genes responsible for date of maturity with earliness recessive.

In Bateson's (2) translation of Mendel's work with peas, it was noted that the hybrids were intermediate to the parents with respect to flowering time. Mendel believed this character to be subject to the other laws of inheritance. He stated that the parents of a cross should differ by at least 20 days in flowering time in order to detect different classes of hybrids.

MATERIALS AND METHODS

The 2 hard red winter wheat varieties, Triumph C.I. 12132¹² and Blackhull-Oro X Pawnee C.I. 12516 were used in this study. Triumph was selected as one parent because of earliness, good yields and wide-spread acreage throughout Oklahoma. The parentage of Triumph is unknown. It was developed by Mr. Joseph Danne, a private plant breeder at El Reno, Oklahoma. In 1948, it was placed on the recommended list of wheat varieties for this state. Triumph is fully awned and is considered short when compared with other varieties grown in Oklahoma. It has white glumes, short beaks, is resistant to loose smut, but susceptible to all the predominant races of leaf rust in Oklahoma.

The variety C.I. 12516¹³ was selected as the other parent because of high yield, medium maturity, and good test weight. The cross and subsequent selection was made at the Southern Great Plains Field Station, Woodward, Oklahoma. This variety has not been released for commercial production. It is fully awned, has white chaff, medium length beaks, and is of medium height. C.I. 12516 is resistant to some races of leaf rust. Its loose smut resistance has not been completely determined, although it appears to be less resistant than Triumph.

The average date of heading and the height of these 2 varieties grown in tests at Stillwater and Perkins, Oklahoma, during the period 1949 to 1953 is presented in Table 1. It can be noted that Triumph averaged 6 days earlier and was 4 inches shorter than C.I. 12516.

¹² Refers to accession number assigned by the Division of Cereal Crops and Diseases.

¹³ Hereafter this variety will be referred to by its C.I. number.

Table 1.—Date of heading and average height of Triumph and C.I. 12516 grown in test plots at the Stillwater and Perkins Agronomy Farms, 1949-1953.

Year	Triumph		C.I. 12516	
	Date Headed	Ht./Ins.	Date Headed	Ht./Ins.
1949 ¹	4-30	31	5-7	34
1950 ¹	4-25	25	4-30	29
1951 ¹	4-30	26	5-6	33
1951 ²	4-30	26	5-6	29
1952 ²	5-2	35	5-7	35
1953 ²	<u>4-25</u>	<u>40</u>	<u>5-6</u>	<u>42</u>
Average	4-29	30	5-5	34

¹ Data taken from the Uniform Hard Red Winter Wheat Yield Nursery grown at Stillwater, Oklahoma.

² Data taken from the Field Plot Variety Test grown on the Perkins Agronomy Farm near Perkins, Oklahoma.

The F_1 and F_2 generations of the cross Triumph X C.I. 12516 were grown in 1952 and B_1 , F_2 , and F_3 generations were grown in 1953. The space-planted material is listed in Table 2 according to generation and number of seeds planted.

In all instances, a uniform piece of ground was selected with the overall design of the experiment approximating a square. Seeding was accomplished on October 16 in 1952, but not until December 8 in 1953. October is the optimum seeding date for winter wheat in Oklahoma. Sufficient moisture was available at optimum seeding time in 1952; but in 1953 severe drought conditions caused a delay in planting. In 1953, continued drought, in addition to low temperatures prevented emergence until February 8.

The method of seeding consisted of opening a furrow with a garden plow. A heavy wheel having a bolt head projecting every 3 inches was used to mark depressions in the furrow. Twenty seeds were then planted 6 inches apart in each row. A Columbia drill with a cover attachment was used to cover the seed. Special care was taken to insure a uniform depth of seeding.

In 1952, seeds of Concho C.I. 12517, which could be distinguished from the parents and hybrids by its bronze-colored glumes at maturity, were planted at the ends of each row to reduce border effect. In addition, approximately 200 seeds of this variety were planted in individual cardboard containers nearby. These seedlings were transplanted wherever a hybrid or parent failed to germinate or died soon after emergence. Transplants were not used in 1953 due to late emergence.

Table 2.--Total number of space-planted parent and hybrid seeds used in a field planting for an inheritance of earliness study conducted on the Agronomy Farm, Stillwater, Oklahoma during the crop years 1952 and 1953.

Variety or Cross	C.I. or Cross No.	No. Seeds Planted	
		1952	1953
Triumph (P)	12132	160	220
Blackhull-Oro X Pawnee (P)	12516	160	220
Triumph X (Bkhl-Oro X Paw.) F ₁	'48 X 1	14	---
do.	'51 X 17 & 18	36	---
(Triumph X C.I. 12516 F ₁) X C.I. 12516 B ₁	'52 X 8 & 9	---	54
(Triumph X C.I. 12516 F ₁) X Triumph B ₁	'52 X 6 & 7	---	72
Triumph X C.I. 12516 F ₂	'48 X 1 & 10	600	---
do.	'51 X 17 & 18	---	600

Plant counts of the space-planted material were taken soon after emergence in order to determine germination percent. During April, 1952, the material was sprayed with Metacide at the recommended rate to control a rather heavy infestation of greenbugs. A satisfactory kill was obtained before the plants were damaged materially.

Date of heading was used as the maturity index. It was felt that this would be the most accurate method for classifying plants under Oklahoma conditions, since high temperatures are usually present at ripening time, tending to decrease differences due to maturity.

During 1952, a small white tag was attached to the culm of the plant with the plot number and date as soon as the first head had completely emerged from the leaf sheath. Heading notes were recorded daily except near the end of the heading period when notes were taken on alternate days due to the late heading of a few weak plants. In 1953, plant numbers were stamped on small pot labels and these were placed immediately in front of each plant. This method proved to be much more satisfactory for the purposes of this study since several tags were lost in 1952 due to strong winds.

Height notes were recorded for each plant at maturity. Measurements were based on the number of inches from the ground level to the apex of the spike of the first tiller to head. After height measurements were recorded, heads from individual plants were harvested and placed in side-opening envelopes. The number of fertile tillers produced by each plant was noted in the laboratory. Each plant was then threshed separately and the weight of seed recorded.

From the F_2 generation grown in 1952, 215 lines were selected for growing F_3 families. The F_2 plants could not be selected entirely at random since 4 grams of seed were needed for growing the F_3 families. Thirty plants representing each parent also were selected for use as checks.

Threshed seed of each selected plant was divided into 2 lots of 2 grams each for planting in duplicate plots of a randomized block design. The parents and families were planted in rows 1 foot apart and four-and-one-half feet in length. Seeding was delayed until December 8, 1952 because of extremely dry soil conditions. Due to continued dry, cold weather, emergence was not completed until February 8, 1953. Generally, poor emergence resulted. Several families as well as parents failed to emerge, and others contained a low number of plants. However, good to excellent stands were obtained in some lines.

Stand notes were recorded for each family on March 10, 1953 to determine, if possible, the relationship between date of heading and percent germination. Lines which were outstanding for seedling vigor and general appearance were noted also.

Heading notes were recorded daily during the heading period. A line was regarded as headed when 75% of the tillers had completely emerged from the leaf sheath. Each row was carefully examined for evidence of segregation before classifying it in one of the following ways: (1) True breeding for earliness of heading; (2) segregating, majority of the plants heading early; (3) segregating, majority of the plants heading late; and (4) true breeding for lateness of heading. It was felt that a fairly accurate classification could be obtained in this way, although individual plants within a row could not be examined.

Height notes were recorded for each line after ripening was completed. It was believed that height measurements in inches would not be as accurate as taking comparative notes of the hybrids in relation to the parents. Determinations were made by comparing each line with the parents growing nearest to it. For this study, Triumph was considered short and C.I. 12516 tall. Each family was classified in one of the following ways: (1) True breeding, short plants; (2) segregating, majority of plants short; (3) segregating, majority of plants tall; and (4) true breeding, tall plants.

On the basis of stand and appearance approximately 60 lines were harvested for further study.

EXPERIMENTAL RESULTS

Heading of Parent Varieties

The heading dates of the parents when grown in field plots and yield nurseries near Stillwater, showed an average difference of 6 days between Triumph and C.I. 12516.

The effect of rate of seeding on heading date could not be measured in 1952 since both parents were space-planted in order to make direct comparisons with the hybrids. The mean date of heading for Triumph was May 7 with the range from May 3 to May 13. C.I. 12516 headed within a period of 17 days, namely, May 8 to May 25 with May 17 being the average.

Parents were grown under comparable conditions in both space-planted and thickly-seeded rows in 1953. The effect of rate of planting on heading date is shown in Table 3. It can be noted that parents in the thickly-seeded rows averaged from 3 to 4 days earlier in heading than the space-planted parents. However, the mean difference in heading dates of the 2 parents was about the same regardless of seeding rate. As stated previously, the heading date of individual plants could not be determined in the thickly-seeded rows. Consequently, there may be a certain amount of error involved in comparing the heading dates of the two rates of planting.

Heading in the F₁ Generation

Fifty F₁ seeds were planted. Fourteen of these were 3 years old and failed to germinate. The remainder of the seed was less than one year old and produced 21 plants from which heading dates were obtained.

Table 3.—Comparison of date of heading of Triumph and C.I. 12516 space-planted and grown in thickly-seeded rows on the Agronomy Farm at Stillwater, Oklahoma, 1952-53.

Space-Planted ¹			Thickly-Seeded ²		
Date Headed	No. of Plants	% of Plants	Date Headed	No. of Rows	% of Rows
May			May		
		TRIUMPH			
9	8	25.8	9	9	69.2
11	3	9.7	11	1	7.7
13	2	6.5	13	3	24.1
15	13	41.9			
17	3	9.7			
<u>19</u>	2	6.5	—		
Av. 14			11		
		C.I. 12516			
21	9	15.3	19	7	53.9
23	13	22.0	21	6	46.1
25	20	33.9			
27	8	13.6			
29	7	11.9			
<u>31</u>	2	3.4	—		
Av. 25			21		

¹ Seeds were spaced 6 inches apart. Heading dates are based on individual plants.

² Date of heading was recorded when approximately 75% of the tillers in a single row were headed.

As shown in Table 4 and Figure 1, a majority of the hybrids headed within a period of 6 days. Both the mode and mean of the F_1 are similar to Triumph which would indicate that earliness is dominant. It can also be noted in Table 4 that the standard deviation of the F_1 and Triumph are nearly the same. It must be remembered in the evaluation of this comparison that only 21 F_1 plants were produced as compared to 96 plants of Triumph. However, performance of the F_2 generation in 1952 supports the conclusion drawn here.

The appearance of the distribution curves for the heading classes of C.I. 12516 shown in Figures 1 and 2 might lead to the conclusion that this variety was not genetically pure for maturity. However, daytime maximum temperatures fluctuated considerably during the period in which it headed. The maximum temperatures for May 11 and 17 were 72 and 58 degrees F. respectively, whereas, the maximum temperatures most of the other days was in the upper 80's and lower 90's. Cool temperatures, such as these, can effect a sudden decrease in the rate of head exertion. The uniformly high temperatures which prevailed during the heading period of Triumph were undoubtedly responsible for its more uniform appearance.

Heading in the F_2 Generation

Six-hundred F_2 seeds were planted in 1952 and from those, 298 plants were produced that were used in this study. Seed used in 1952 was 2 years old and may have contributed to poor germination and some weak seedlings. These obviously weak plants were eliminated from this study.

Distribution of the parents and hybrids by maturity classes is shown in Figure 2. It can be noted that the hybrids extended the range of both parents, but otherwise the distribution of the hybrids followed that of the parents very closely. Considering that part of the population from

Table 4.—Heading dates of parents and of the F₁, F₂, F₃ and B₁ hybrid generations of the cross Triumph X C.I. 12516 expressed at 2-day class intervals when grown at Stillwater, Oklahoma, in 1952 and 1953.

Variety or Cross	Year	Heading Class																	Total	Mean
		Apr. 29	1	3	5	7	9	11	13	15	17	19	21	23	25	27	29	31		
Triumph <u>SP</u> ¹	1952		2	16	30	41	14	4	3										110	6.9+2.36
C.I. 12516 <u>SP</u>	1952					1	12	6	17	13	2	36	17	-	5				109	16.8+4.26
Triumph X C.I. 12516 F ₁ <u>SP</u>	1952			2	1	11	5	1	1										21	8.0+2.33
Triumph X C.I. 12516 F ₂ <u>SP</u>	1952	3	2	25	52	63	58	16	44	12	-	20	2	-	1				298	9.5+4.39
Triumph <u>R</u> ²	1953						9	1	3										13	10.7+1.55
C.I. 12516 <u>R</u>	1953											7	6						13	20.6+1.26
Triumph X C.I. 12516 F ₃ <u>R</u>	1953					1	13	15	19	8	8	16	10						90	15.0+2.94
Triumph <u>SP</u>	1953						8	3	2	13	3	2							31	13.8+3.23
C.I. 12516 <u>SP</u>	1953												9	13	20	8	7	2	59	25.4+2.62
Triumph X C.I. 12516 F ₂ <u>SP</u>	1953					1	10	4	11	23	52	46	53	28	20	6	6		260	19.9+4.27
(Triumph X C.I. 12516 F ₁) X Triumph F ₁ <u>SP</u>	1953						1	3	7	10	22	4	4	3					54	16.7+3.01
(Triumph X C.I. 12516 F ₁) X C.I. 12516 F ₁ <u>SP</u>	1953						1	-	3	5	7	12	6	11	1				46	19.5+3.50

¹ SP = Space planted.

² R = Thickly seeded rows.

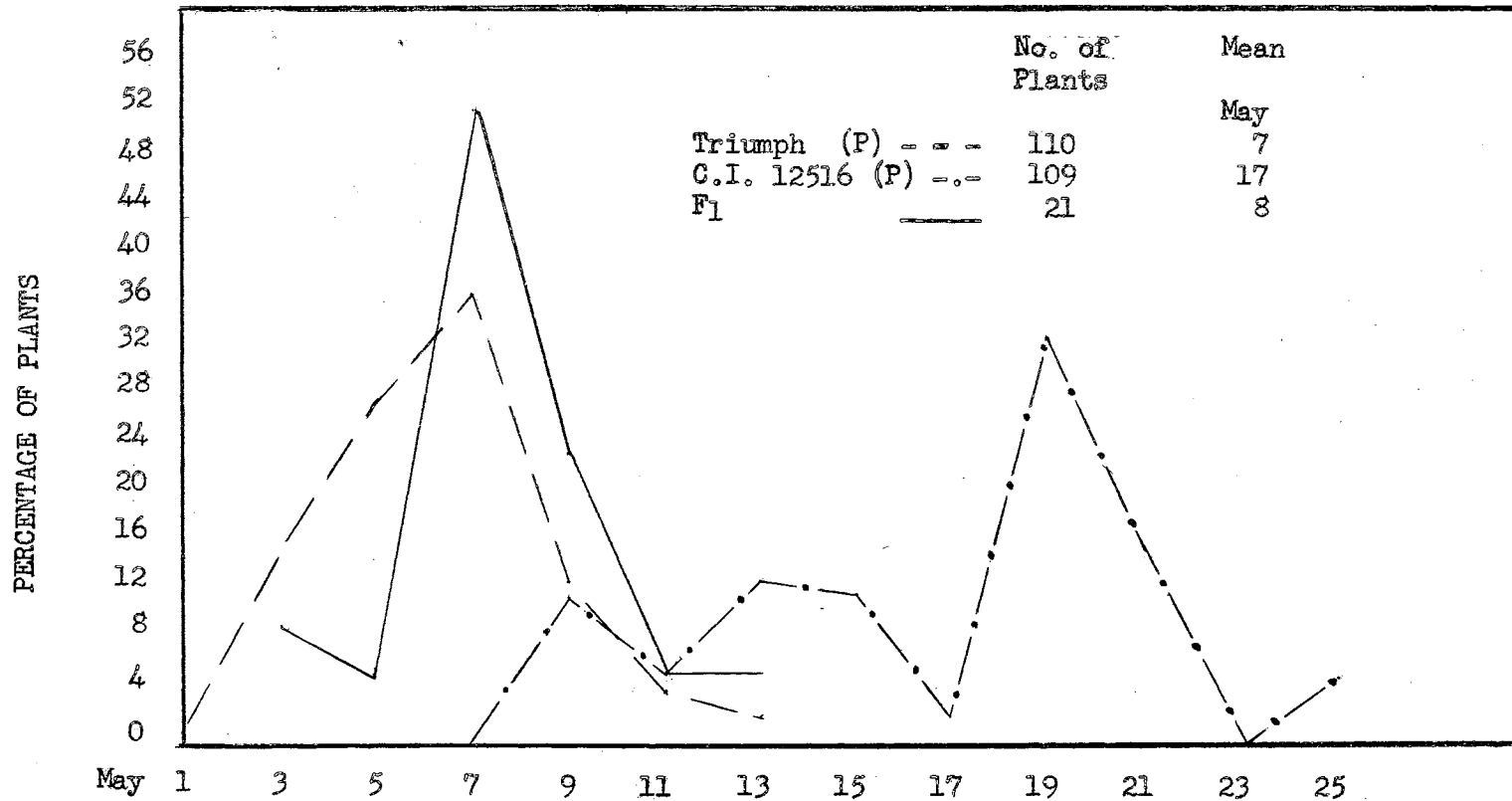


Fig. 1.—Distribution of parent and F₁ plants of Triumph x X.I. 12516 by heading classes when grown on the Agronomy Farm, Stillwater, Oklahoma, in the 1952 crop year.

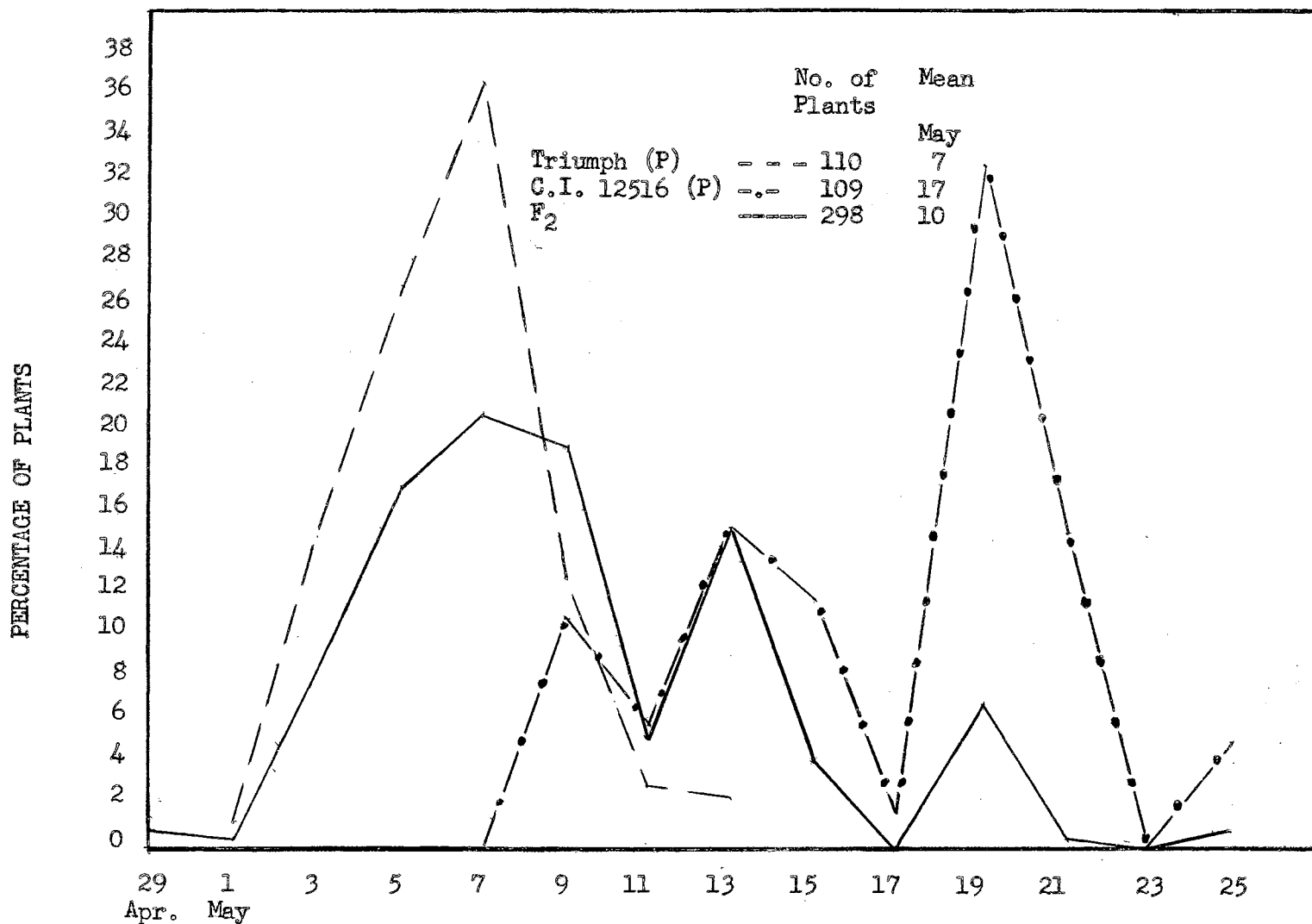


Fig. 2.—Distribution of parent and F₂ plants of Triumph x C.I. 12516 by heading classes when grown on the Agronomy Farm, Stillwater, Oklahoma, in the 1952 crop year.

April 29 to May 11 as early, and the other group (May 13 to May 25) as late, a ratio of 216 early to 81 late plants was obtained. The Chi-Square test for goodness of fit to a 3:1 ratio gives a value of 0.3624 and a P value of 0.50 to 0.70 which indicates a very good fit. Separation of the early and late class was made at the point where the distribution lines of the 2 parents intersect. There is also a definite break in the F_2 distribution curve at this point.

Six-hundred seeds were planted for growing and additional F_2 population in 1953. Extremely poor germination resulted in fewer plants than in the 1952 population. Low germination was probably due to a combination of delayed emergence and overtreatment with Ceresan. Both parental extremes (Table 4) were recovered and 1 plant headed 2 days earlier than the earliest plant of the early parent. The mean lies almost midway between the 2 parents which would indicate quantitative inheritance. The large early class obtained in 1952 was not evident in this population.

Although these two seed lots were different, it is believed that seed source was not nearly so important as environmental factors in affecting date of heading. A day-length factor, such as that reported by Bell (3), may have been responsible for the apparent lack of dominance of early heading since date of seeding and emergence were very abnormal.

Heading in the F_3 Generation

Only 90 of 215 F_3 families had sufficient stands to justify their use in this report. It was quite apparent that the reduction in stand seriously affected the date of heading both in the parents and hybrids. In general,

as percent stand decreased, date of heading was later. Rows with stands of 60% or over were not so seriously affected; consequently, parents and families with less than 60% stand were omitted from analysis of the data. Early and late heading lines could be distinguished quite easily where good stands were present. For example, in Figure 3, Triumph was completely headed on May 10, whereas the hybrid headed on May 19.

The data are presented in Table 4. Again, both parental extremes were recovered and 1 family headed 1 day earlier than the earliest row of Triumph. The mean of the families lies almost halfway between the mean of the 2 parents. These data do not verify results obtained from the 1952 F_2 generation, since there was a large intermediate class. Although there was a somewhat higher percentage of early lines, no satisfactory ratio can be postulated. It seems possible that late seeding and emergence confounded genetic effects to the extent that the hybrids were unable to exhibit normal character expression.

A highly significant correlation coefficient of 0.704 was obtained between these 90 families and their parent F_2 plants grown the previous year. This would indicate that plants can be selected for the desired maturity class with reasonable success in the F_2 generation.

Heading in the B_1 Generation

Fifty-four plants of the backcross to Triumph and 46 plants of the backcross to C.I. 12516 were studied for date of heading in 1953. Heading dates are presented in Table 4.

It can be noted that heading dates of Triumph and the backcross to it are somewhat similar, although the range and mean of the backcross exceeds Triumph. These data do not support the 1 factor hypothesis



Fig. 3.--Triumph parent (left) fully headed and F_3 family (right) just beginning to head. (May 19, 1953)

which was derived from the 1952 F_2 generation. Further, no other genetic explanation could be determined from this backcross.

The first generation backcross to C.I. 12516 shows a definite break on May 21 when only 6 plants headed. Assuming all plants heading up to and including May 19 were as early as Triumph and that all of those heading later than this were similar to C.I. 12516, a ratio of 28 early to 18 late plants is obtained. No normal backcross ratio is known which will fit these data. It is believed that the environmental factors mentioned earlier were responsible.

Heritability Studies on Date of Heading

Heritability scores were calculated, since the findings of several workers (5, 11, 16, 17, 20, 25) indicated earliness might be controlled by several factors. Table 5 presents heritability estimates obtained by 2 different methods. All of the values obtained are rather high and would indicate that earliness of heading is influenced to a large extent by genetic effects. When dominance deviations were eliminated from the final estimate, as described by Warner (27), a score of 0.83 was obtained. If it is assumed that earliness is controlled by several genes as it appeared to be in the 1953 crop year, then it seems probable that these estimates would have significance. However, the validity of this and other estimates might be questioned since only additive genetic effects are supposedly measured. In 1952, earliness in this cross appeared to be completely dominant and due to 1 factor pair.

Table 5.--Number of individuals, average date of heading, variance and heritability estimates of parents and hybrids of the cross Triumph X C.I. 12516 when grown in the 1952 and 1953 crop years at Stillwater, Oklahoma

Variety or Cross	Number of Individuals	Average Heading Date	Variance
May			
1952 Crop Year			
Triumph	110	6.9	5.5504
C.I. 12516	109	16.8	18.1389
Triumph X C.I. 12516 F ₁	21	8.0	5.4500
Triumph X C.I. 12516 F ₂	298	9.5	19.2727
Heritability = $\frac{\text{Variance } F_2 - \text{Variance } F_1}{\text{Variance } F_2} = 0.71$			
1953 Crop Year			
Triumph	31	13.8	10.4333
C.I. 12516	59	25.4	6.8966
Triumph X C.I. 12516 F ₂	260	19.9	18.2201
Triumph X (Triumph X C.I. 12516)B ₁	54	16.7	9.0755
C.I. 12516 X (Triumph X C.I.12516)B ₂	46	19.5	12.2444
Heritability = $\frac{\text{Variance } F_2 - \text{Av. Variance Triumph and C.I. 12516}}{\text{Variance } F_2} = 0.52$			
Heritability ¹ = $\frac{\text{Variance } 2 (F_2) - \text{Variance } (B_1 + B_2)}{\text{Variance } F_2} = 0.83$			

¹ According to Warner (27).

Height and Number of Heads in Relation to Heading Date

Reaction of parent varieties

The height and average number of heads per plant of the 2 parents for each heading date in the crop years 1952 and 1953 are presented in Table 6.

The variety C.I. 12516 averaged 1 inch taller than Triumph in 1952 but measured the same in 1953. Heading began later in 1953 and high temperatures occurred during the heading period of C.I. 12516. This may explain why it was somewhat shorter.

The adverse effect of high temperatures in 1953 is reflected also in the average number of heads produced by C.I. 12516. From a survey of these data, it can be noted that the early maturing plants of both parents exhibited greater height and a larger number of heads than the late plants.

Reaction of F₂ hybrids

Previous observations have indicated that, generally, late maturing varieties were taller than early maturing varieties. Data are presented in Table 7 for average height and number of heads per plant of F₂ populations grown in 1952 and 1953. Heading dates are included for the purpose of determining the relation of these 2 characters to maturity.

Generally, the late heading hybrids were shorter. Although this is true for both years, it was more marked in 1953. Undoubtedly, some of these late heading plants were weak rather than inherently late since very few tillers were produced in most instances.

Table 6.--Date of heading, average height and number of heads per plant of Triumph and C.I. 12516 grown from space-planting in 1952 and 1953.

Date	Triumph (1952)			C.I. 12516 (1952)			Triumph (1953)			C.I. 12516 (1953)		
	No. of Headed Plants	Av. Ht. Ins.	Av. No. Heads	No. of Plants	Av. Ht. Ins.	Av. No. Heads	No. of Plants	Av. Ht. Ins.	Av. No. Heads	No. of Plants	Av. Ht. Ins.	Av. No. Heads
May												
1	2	30	11									
3	16	30	8									
5	30	29	6									
7	41	27	5	1	34	12						
9	14	25	4	12	30	11	8	28	9			
11	4	26	3	6	30	10	3	29	8			
13	3	<u>24</u>	<u>4</u>	17	29	7	2	25	9			
15	Average	27	5.4	13	29	6	13	27	8			
17				2	33	5	3	30	6			
19				36	28	5	2	<u>24</u>	<u>-</u>			
21				17	26	3	Average	27	8.2	9	31	12
23				-	-	-				13	30	4
25				5	<u>28</u>	<u>3</u>				20	26	4
27				Average	28	5.9				8	25	3
29										7	22	-
31										2	<u>21</u>	<u>-</u>
										Average	27	5.2

Table 7.—Date of heading, average height and number of heads per plant of F₂ hybrids from the cross Triumph X C.I. 12516 grown from space-plantings in 1952 and 1953.

Date Headed	1952			1953		
	No. of Plants	Av. Ht. Ins.	Av. No. Heads	No. of Plants	Av. Ht. Ins.	Av. No. Heads
April						
29	3	28	8			
May						
1	2	27	12			
3	25	28	9			
5	52	28	8			
7	63	27	6	1	30	16
9	58	26	6	10	29	12
11	16	27	7	4	31	14
13	44	26	5	11	31	9
15	12	27	5	23	29	8
17	-	-	-	52	30	7
19	20	27	5	46	29	6
21	2	27	3	53	28	5
23	-	-	-	28	26	5
25	1	22	3	20	24	3
27	Average	<u>26.9</u>	<u>6.4</u>	6	23	2
29				6	23	1
				Average	<u>27.9</u>	<u>6.2</u>

Late heading plants had a smaller number of heads and, again, the trend was more pronounced in 1953. Growth of the late heading plants may have been arrested because of the extremely high temperatures at heading time.

Height of F₃ Families in Relation to Heading Date

As mentioned earlier, height of the F₃ families was recorded in one of the following ways; namely, short; short, segregating; tall; and tall, segregating. The distribution of the families on the basis of height and heading date are shown in Figure 4. Lines that appeared to be segregating were placed either in the tall or short class depending on the height of a majority of the plants in a particular segregating row.

Early heading lines tended to be shorter than the late heading lines, although there were a few early families that were classified as tall. The opposite also was true, for some late heading families appeared to be short.

The F₂ generation showed that early heading plants tended to be taller than the later plants while the opposite was true in the F₃ generation. However, it must be pointed out that the F₂ was space-planted and height measurements of this material may not give a true estimate of the behavior of these lines at normal seeding rates. The F₃ results obtained were the ones expected based on previous experience. No explanation is offered for the lack of correlation between the F₂ and F₃ results.

A Chi-Square test for independence was calculated for height and date of heading of these F₃ families. A Chi-Square value of 13.303 and P value of less than 1 percent were obtained, which strongly indicates

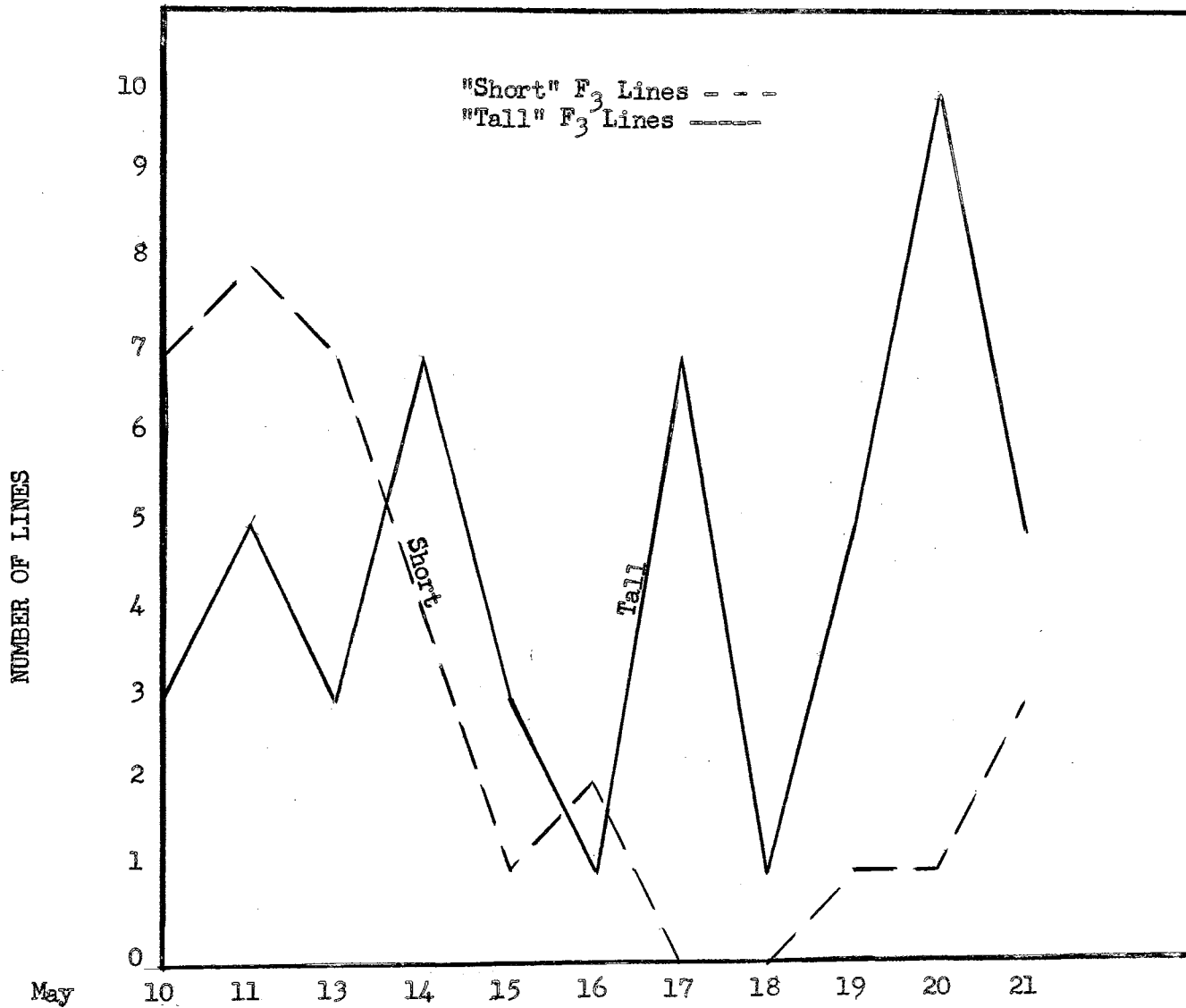


Fig. 4.—Distribution of the "short" (ht. of Triumph) and "tall" (ht. of C.I. 12516) F₃ lines of Triumph x C.I. 12516 by heading dates.

that there was an association between date of heading and height in this cross. This would tend to substantiate previous observations that early maturing varieties usually are shorter than late maturing strains. For purpose of this test, early lines included those which had headed by May 16. Since the parents did not overlap, it was assumed that if a large enough number of parents had been grown, these would have intersected on or near May 16. All lines heading after May 16 were considered late.

SUMMARY

Studies on the inheritance of earliness of heading were conducted during the 1952 and 1953 crop years. In 1952, parents, F_1 and F_2 hybrids were planted in rows 1 foot apart and 10 feet in length. Plants were spaced 6 inches apart to facilitate observations. During 1953, parents, F_2 and B_1 hybrids were planted in a manner similar to that described for 1952. In addition, F_3 families and parents were thickly seeded in duplicate plots of a randomized block design. Each plot consisted of one four and one-half foot row with 12 inches between rows.

Heading notes were recorded daily except near the end of the heading period when these were then taken on alternate days. In the case of space-planted material, date of heading was recorded for each plant the day when the first head was completely exerted from the leaf sheath. In the thickly seeded rows of the F_3 families and parents, heading was recorded when 75 percent of the tillers in a row were headed.

Height measurements and number of heads were recorded on an individual plant basis except in the F_3 families. In these, tiller counts were not taken and each family was classified by observation as being short or tall. Lines which were segregating for height were noted also. Triumph was considered short and C.I. 12516 tall and direct comparisons with the parents determined the classification of each hybrid.

Distribution of heading dates of the 1952 F_1 and F_2 generations indicated earliness of heading was dominant and due to 1 factor pair. Chi Square values for goodness of fit to a 3:1 ratio in the F_2 generation

gave a very good fit ($P = 0.50$ to 0.70). Results obtained by growing F_3 progenies the following year do not entirely bear out this assumption. Comparison of date of heading between F_2 plants and their F_3 progenies grown the following year gave a correlation coefficient of 0.704 which was significant at the 1 percent level of probability. This would indicate that date of heading was highly heritable in this experiment.

Although heading results obtained in 1953 do not entirely agree with those found in 1952, the following points should be mentioned in regard to the 1953 results.

1. None of the 1953 material was seeded until December 8, 1952 and, due to low temperature and moisture conditions, did not emerge until February 8, 1953.
2. Earliness of heading appeared to be at least partially dominant in 1953.
3. Parental extremes were recovered in both the F_2 and F_3 generations with the exception of 2 plants of C.I. 12516 which headed 2 days later than the F_2 hybrids. These 2 plants may have been weak rather than genetically late.
4. The standard deviation of the backcross to Triumph is smaller than that of Triumph although the mean of the backcross is approximately 3 days later.
5. The mean heading date of the backcross to C.I. 12516 was approximately half-way between the mean of the 2 parents. This would be expected based on the hypothesis that Triumph carries the dominant factor for earliness, and C.I. 12516 possesses the recessive factor for lateness of heading.

The 1952 results appear to be more reliable than those obtained in 1953 since date of seeding and emergence were more nearly normal; hence, the mode of inheritance of earliness was based on the 1952 data. Heritability scores obtained from 1953 results indicate that this character was rather simply inherited even though the exact mode of inheritance could not be determined.

Height and number of heads per plant in the space-planted material appeared to be influenced by environment to the extent that genetic differences could not be detected. In both years the late heading plants were shorter and had fewer heads than the early heading plants. This was true for both the parents and the hybrids. It would seem that the high temperatures which occurred during the ripening period in both years arrested the development of late heading plants. A Chi-Square test for independence of heading date and height in the F_3 lines indicated that these characters are associated. It seems probable that the space-planted material was affected by environment to the extent that genetic differences in height were not expressed.

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