ANALYSIS OF YIELD AND RELATED TRAITS IN A DIALLEL CROSS OF WINTER WHEAT WITH REFERENCE TO LONG AND SHORT PHOTOPERIOD TREATMENTS

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CHAPTER I

INTRODUCTION

All growth and developmental processes of a plant are considered to be governed by the genotype of the plant. However, these growth and developmental processes are also conditioned and directed by external environmental factors. A striking example of environmental control is the phenomenon known as photoperiodism; the response of plants to the relative length of day and night periods (8, 9, 10).

Wheat (Triticum aestivum L. emend. Thell) is one of many plant species in which floral initiation and development is dependent upon photoperiod. In this regard, wheat is generally classified as a long-day plant (4, 6). In other words, it requires long days for maximum rate of development while exposure to short days delays the flowering process. However, the optimum day length is not the same for all wheat varieties. Some require longer days than others. It is also recognized that some varieties behave the same way under both long and short days. Such types are said to be day-length insensitive. That is, the initiation of the flowering process in these varieties is independent of day length once the threshold photoperiod is reached. Therefore, with regard to photoperiodic response wheat can be considered a quantitative long-day plant (9, 33, 34).

Day-length insensitivity has played an important role in the world wide adaptation of certain spring wheat varieties and may also be important in winter types. One of the main reasons for the wide adaptation of the semi-dwarf spring wheats developed by the International Maize and Wheat Improvement Center in Mexico (CIMMYT) is that they are insensitive to photoperiod (3, 37).

Day length insensitivity also exists in winter wheats (5, 21, 22, 23, 35). However, unlike the spring wheats, very little effort has been made to utilize this trait in breeding programs because other factors such as cold requirement and winter hardiness tend to limit ranges of adaptation of winter types. Otherwise, day length insensitive plants can start spring development earlier in the growing season. This, of course, is advantageous provided that the varieties are cold tolerant and winterhardy (35).

Since photoperiod plays an important role in the control of flowering and subsequent seed production, many scientists believe that it may be an important consideration in increasing yield potential. However, yield increase can be achieved only when important yield related factors are understood better by the plant breeder. Therefore, knowledge of the genetic system of response to photoperiod in winter wheat is essential for the development of improved varieties with wide adaptation. Knowledge of photoperiod response is also important in the development of varieties that would be most suitable to a given set of local environmental conditions.

The purpose of this study was to determine the effects of photoperiod on yield and yield-related traits in a diallel cross of winter wheat and to investigate the genetic system controlling these traits.

CHAPTER II

REVIEW OF LITERATURE

Photoperiodism in Wheat

Since the discovery of the phenomenon of photoperiodism in plants by Garner and Allard (10) in 1920, numerous physiological studies have been conducted to determine the photoperiodic response of bread wheat. Wanser (41) in 1922, noted the importance of photoperiod in the adaptation of wheat. He also proposed that winter wheat required separate and distinct photoperiods for jointing and heading while in spring wheat the "critical" photoperiods tended to overlap.

Cooper (6), Hurd-Karrar (15), and McKinney and Sando (24, 25, 26) reported that long photoperiods hastened heading in spring wheats much more than the winter wheats while short days retarded heading in both types. This latter effect tended to be more pronounced in the case of winter wheat. Foster et al. (9) observed that Australian wheat varieties when grown in England were extremely early while the English varieties grown in Australia were extremely late and tillered excessively. They concluded that the longer day of England was responsible for the early heading of Australian varieties while the shorter day of Australia delayed heading of the English varieties. Kirby (19), in a recent comprehensive review of the effects of day length on wheat, barley, and oats stated that in general, varieties of high latitude origin were strongly sensitive to changes in photoperiod.

Hurd-Karrar (15) reported that exposure to short days followed by long days produced early jointing in 'Turkey' winter wheat. McKinney and Sando (24) and Foster *et al*. (9) also reported that heading in winter wheat was favored by an initial exposure to short days followed by long days. Ormord (29) tested several wheats at photoperiods ranging from 9 to 24 hours and found marked differences in sensitivity as measured by head differentiation and culm elongation.

Recently, Coffman (5) studied the phasic development of several wheat varieties under long and short days. He found that some varieties differed only with respect to elongation rate under short days while others showed differences with respect to preinitiation development. He also observed differences among the varieties with respect to earliness which were unrelated to differences in day length.

Adams, according to McKinney and Sando (26), was the first to point out the importance of temperature in relation to the daily photoperiod in regulating the time of flowering in winter wheat. He claimed that these two factors were interchangeable. McKinney and Sando (24) subjected 'Harvest Queen', a winter wheat, and 'Purple Straw', a spring wheat, to different light and temperature treatments. Harvest Queen headed earlier when given short day treatment in the early stages of growth but produced irregular heads and tillered excessively. Long days favored early heading in Purple Straw. They also observed that heading of winter wheat could be accelerated by subjecting the freshly germinated seeds to temperatures slightly above freezing under short days before growing them under long days. They concluded that early heading in winter wheat is enhanced by short days during early stages of development. In a later report (26), they showed that winter wheats have short-day (9-12 hours) low-temperature optima during the initial growth phases and long-day (15-18 hours) high-temperature optima thereafter. On the other hand, they found that spring wheats would flower at any day length given sufficient time and favorable temperatures, but required high temperatures of 23.8^{o}C or above and long days throughout their life cycle for early heading. They also pointed out that other factors such as light intensity, light quality, and soil fertility could influence heading in wheat.

Studies regarding the importance of vernalization or cold requirement in the initiation of flowering in winter wheat were reviewed recently by Tu (38). Coffman (5), studied the effects of vernalization and day length on several winter and spring wheat varieties and their hybrids. He found that the spring varieties and most of the F_1 hybrids showed a greater response to vernalization under short days than under long days. On the other hand, all of the winter varieties were sensitive to day length relative to the spring insensitive type, 'Sonora 64'. However, the variety 'Besostoya 1' was less sensitive than other winter types tested under the short day regime. This was considered significant in view of the fact that Besostoya 1 is one of the most widely adapted winter wheats in existence. This variety was also very responsive to vernalization, while another winter variety, CI 15069, did not respond to vernalization at all, although it had a strong response to day length. Studies of F_2 populations derived from crosses involving certain winter and spring types indicated that day length insensitivity may be associated with lower vernalization requirement in certain varieties.

Influence of Photoperiod on Yield Components in Wheat

Grain yield in wheat and other cereals is determined by several secondary factors such as number of tillers, number of spikelets, and number of fertile florets which in turn are influenced by certain external environmental factors such as photoperiod (4, 17). In general, photoperiod treatments that shorten the vegetative period of wheat have been found to reduce the number of internodes, leaves and tillers (20, 27). It has also been reported that plants transferred from a controlled long day to a shorter day occassionally developed abnormalities such as branched spikes, compound lower spikelets and sterile pollen, thereby affecting yield of the plant (15, 20).

Nanda and Chinoy (27) studied the effects of photoperiod on three Indian wheats. They reported lower yields of grain and straw under both short days (6 hours light) and long days (18 hours light) than that under normal day lengths (12 hours light) similar to the conditions in India. They attributed the low yields under short days to a "low rate of assimilation" and suggested that higher temperatures during the ripening period were responsible for the low yields under long days. In a later experiment (28), they noted the importance of the relationship between yield and other plant characters and pointed out that various factors affecting the growth of the wheat plant influenced the number of spikes, length of spike, number of spikelets and grain per spike and ultimately grain yield.

Coffman (5), showed that photoperiod and vernalization treatments affected tiller number as well as leaf number in wheat at several stages of development. Number of spikelets, plant height, degree of nodding, and days required for maturity were also affected.

Genetic Studies of Photoperiodism in Wheat

Although the influence of photoperiod on the floral initiation in wheat has been well recognized, only a few studies have been made regarding the genetic basis for the observed differences in the behavior of wheat varieties. The lack of genetic information is especially apparent with regard to photoperiod response in winter wheat.

Several studies have indicated that the inheritance of photoperiod response in wheat is controlled by one or two genes. Borlaug *et al*. (3) observed that the spring wheat varieties 'Selkirk', 'Thatcher', and 'Justin' were sensitive to day length and suggested that the specific adaptation of these varieties to long days was controlled by only a few genes. Later, Pugsley (30, 31) indicated that two genes in Selkirk and one gene in Thatcher controlled day length sensitivity. Borlaug *et al*. (3) pointed out that many of the semi-dwarf varieties developed by the International Wheat and Maize Improvement Center in Mexico (CIMMYT) were insensitive to day length. In one such variety, 'Sonora 64'. according to Keim *et al*. (18), insensitivity to day length was due to the presence of a single dominant gene.

Pugsley (30) also studied the inheritance of photoperiodism between 'Triple Dirk' and Thatcher. He found day length insensitivity to be completely dominant in the F_1. Furthermore, F_2 and backcross ratios indicated a one-gene difference between sensitivity and insensitivity.

Coffman (5) studied the inheritance of day length sensitivity by considering separately the two phases of growth which lead to heading. He observed that some varieties differed only with respect to stem elongation rate under short days while others differed with respect to preinitiation development. His results showed that Sonora 64 (insensitive) and 'Justin' (sensitive) differed by rate of elongation and time required for initiation under short days while Sonora 64 and 'Sensitive Sunset' (sensitive) differed only by rate of elongation. He concluded that at least two genes were responsible for controlling day length insensitivity in addition to differences in earliness which were unrelated to sensitivity reaction. In Coffman's study (5), F_1 and F_2 data indicated that insensitivity was controlled by more than one gene in the Sonora 64 X Justin cross and by one gene in the Sonora X Sensitive Sunset cross. However in neither case were the results conclusive.

Keim _et al_. (18) also studied the inheritance of photoperiod response in two winter wheat varieties, 'Lancer' and 'Warrior', which were sensitive to photoperiod. These were crossed to Sonora 64, an insensitive spring wheat. The parental, F_1 and F_2 populations were then grown in pots in a cold chamber until each seedling had produced several tillers. Then, each plant was divided at the crown into two clones: one clone received a 10 hour photoperiod exposure in a growth chamber while the other clone received a 16 hour photoperiod in another growth chamber. The results indicated a strong dominance system for insensitivity in the F_1 while the F_2 distribution supported by F_3 data showed a segregation ratio of 12 early: 3 late: 1 very late. This suggested a two gene inheritance system with dominant epistasis for insensitivity.

In Yugoslavia, Martinic (22) crossed a spring wheat, NT-1/66, which was sensitive to day length to four low responding (insensitive) wheat lines, of which two, Sp-1/63 and 'Etoile de Choisy', were winter types. He grew vernalized seedlings of the parental, F_1 and F_2 populations in the growth chamber under 11½ hours of light. In three crosses, the ratio between low and high responding plants of the F_2 generation was 10:6. He concluded that the inheritance of photoperiodic response was governed by genes at two loci. Furthermore, he suggested that the loci were on different chromosomes.

CHAPTER III

MATERIALS AND METHODS

Two experiments were involved in the study. The first one, Experiment I, was conducted in the field at the Agronomy Research Station, at Stillwater, Oklahoma, during the growing season of 1971-72. The second, Experiment II, was carried out in the controlled environmental chamber at the campus of the Oklahoma State University, Stillwater, in the winter of 1971 and summer of 1972. In both experiments, the effects of long and short photoperiods on winter wheat were studied.

Six varieties of winter wheat namely, 'Triumph 64', 'Parker', 'Scout 66', 'Sturdy', 'Bezostaia 1', and 'San Pastore', were selected as parents for the study. The first four varieties are, or have been grown commercially in Oklahoma while the remaining two varieties, Bezostaia 1 and San Pastore, have been used exclusively as wheat breeding stocks at the Oklahoma Agricultural Experiment Station in Stillwater. The six varieties were selected because they were judged to represent a wide range in reaction to photoperiod based on reports in literature, preliminary observations under artificial short day conditions at Oklahoma State University, and because they had been developed at stations situated at different latitudes. The pedigree and origin of these varieties are presented below.

Triumph 64 (Danne Beardless - Blackhull X Kanred - Blackhull X

Florence X Kanred - Blackhull X Triumph) was developed by the late Joseph E. Danne at El Reno, Oklahoma.

Parker (Quivira^2 X Kanred-Hard Federation^2 X Prelude - Kanred 4 X Kawvale - Marquillo^3 X Kawvale - Tenmarq) was developed by the Kansas Agricultural Experiment Station.

Scout 66 (Nebred - Hope - Turkey X Cheyenne - Ponca) was developed by the Nebraska Agricultural Experiment Station.

Sturdy (Sinvalocho - Wichita X Hope - Cheyenne - Wichita X Sen Seun 27) was developed and released by the Texas Agricultural Experiment Station.

Bezostaia 1 (Skoraspeyla 2 X Lutescens 17) was developed at Krasnodor, in Southern Russia.

San Pastore (Balilla X Villa Glori) was developed at a research station near Rome, Italy.

In the spring of 1970, the six winter wheat parents were crossed in all 15 possible combinations to comprise a diallel system. Reciprocal crosses were not kept separate. Plants of the 21 genotypes (six parents and 15 F_1 hybrids) were used in all experiments.

Experiment I

Experimental Design and Procedure

This experiment was conducted during the 1971-72 crop year in a field test at the Agronomy Research Station at Stillwater. The photoperiod treatments consisted of both long and short days. The normal day length at Stillwater during the growing season was used as the long day treatment. On the other hand, the daily light period from March 1 to May 19 was shortened to approximately 9 hours by manipulating a screening structure built over the short day nursery, to provide the short photoperiod treatment. The normal day length while the experiment was under progress varied from 9½ hours on December 1 to 11¼ hours on March 1, to 14 hours on May 19.

Seedlings of the six parents and their 15 F_1 hybrids were started in flats in the greenhouse. On October 5, 1971, when most of the seedlings had attained the four-leaf stage (approximately 2 weeks old), they were transplanted in the field in the respective long day and short day nurseries. In both nurseries, the plots consisted of single rows 150 cm in length. The rows were 30 cm apart. Each plot consisted of eight test plants spaced 15 cm apart within plots plus a guard plant at each end of the plot. In the long day nursery, each entry was replicated 6 times using a randomized complete block design. A replication consisted of 2 ranges of 11 rows each, separated by a 30 cm space. Extra seedlings were transplanted adjacent to the first and last row in each range to minimize competition effects. Due to the problems imposed by artificially controlling the duration of exposure to day light, only one replication was grown in the short day nursery. However since the eight plants in each entry were planted at random within the plot, observations were made on individual plants so that a completely random design statistical analysis could be made on the data obtained.

The occurrence of rain immediately after transplanting ensured the establishment of the seedlings. Both nurseries were irrigated in the spring when evidence of drought stress became apparent.

On March 1, 1972, a rectangular wooden shade structure, 5.30m long, 3.80m wide and 1.20m high was built over the short day nursery to control exposure to natural day light. The east-west sides and the top of the shade structure were detachable. The north-south sides were stationary and each was made of four panels of wood fitted together in such a way that air would circulate freely without the admission of light. Every afternoon, after the plants had received the required 9 hours of day light, the sides and top panels were placed into the frame, and all crevices by which light might enter were covered. Late in the evening, after dark, the panels were removed so that the plants inside the frame would experience the same environmental conditions as those in the long day nursery until the 9 hours of daily light requirement was fulfilled the next day. In contrast, plants in the long photoperiod nursery were exposed to full natural day and night environmental conditions all the time. Other than the differences in photoperiod treatments, every possible effort was made to treat the plants in both trials alike.

The wooden frame structure was dismantled from the short day nursery on May 19, 1972, approximately three weeks after the latest entry had headed. Then all entries received full natural day length until maturity.

During the course of the growing season the following observations were recorded in the nurseries:

1. Days to head: This trait was determined as the number of days from germination to complete emergence of the first spike from the boot on each plant. In both nurseries, heading was recorded as the number of days when 75% of the plants in each plot had headed.

2. Days to mature: This trait was determined as the number of days from germination to the time when kernels were in the hard dough stage. In both nurseries, maturity was recorded as the number of days when 75% of the plants in each plot had reached maturity.
3. Plant height: This trait was determined as the distance in centimeters from the base of the stem to the tip of the spike (awns excluded) at maturity. In both nurseries, plant height was expressed as the average of eight plants per plot.
4. Tiller number: This trait was determined as the number of headed tillers at maturity. For the long day trial, tiller number was expressed as the average of eight plants per plot. This trait was expressed on a per plant basis for the short day trial.
5. Spike length: This trait was determined as the distance in centimeters of the spike of the primary tiller of each plant from the basal rachis node to the tip of the spike (awns excluded) at maturity. Spike length was expressed as the average of eight plants per plot in the long day trial. For the short day trial, this trait was expressed on a per plant basis.
6. Spikelet number: This trait was determined by counting the number of spikelets on the spike of the primary tiller of each plant. Spikelet number was expressed as the average of eight spikes per plot in the long day trial. For the short day trial, this trait was expressed

on a per plant basis.

7. Seed number: This trait was determined by counting the number of seeds produced on the spike of the primary tiller of each plant. Seed number was expressed as the average of eight spikes per plot in the long day trial. For the short day trial, this trait was expressed on a per plant basis.

8. Grain yield: This trait was determined by weighing the seeds obtained from each plant in grams. Grain yield was expressed as the average of eight plants per plot in the long day trial. For the short day trial, this trait was expressed on a per plant basis.

Statistical Procedure

For the long day treatment, an analysis of variance was conducted on a plot mean basis for each trait. An analysis of variance for the short day treatment was performed only on those traits for which single plant values were recorded. Correlation coefficients among the traits were also computed for each nursery. The methods described by Steel and Torrie (36) were followed in making the test of significance.

Finally, in order to investigate the genetic system of important characters, with regards to the effects of photoperiod treatments, the data for each character measured in the long day trial were subjected to diallel cross analysis as outlined by Hayman and Jinks (11, 12, 13, 14, 16, 17). For the short day trial, only the data for tiller number, spike length, spikelet number, seed number and yield were subjected to the diallel analysis since individual plant measurements for these characters were recorded. The procedure for the diallel analysis will be described in the results and discussion section. All analyses were conducted by the use of the computer, at the Oklahoma State University Computer Center.

Experiment II

Experimental Design and Procedure

A controlled environmental growth chamber was used for Experiment II. The growth chamber was a walk-in type with automatic temperature and light controls. The light source used was a combination of inflorescent and incandescent bulbs capable of delivering light at an intensity of about 3500 foot candles. Two photoperiod treatments were employed. Conditions of the short-day chamber were 10 hours of daily illumination alternating with 14 hours of darkness. The temperature inside the chamber was maintained at approximately 23.8^{o}C during the light period and 18.3^{o}C during the dark period. The long day chamber had exactly the same conditions except that it provided 16 hours of full light alternating with 8 hours of darkness. The short day trial was conducted first and this was followed by the long day trial. The same growth chamber was used for both trials.

Identical plantings were made for each trial. Seeds of each of the 21 entries (6 parents and 15 F_1 hybrids) were first planted in flats filled with a greenhouse soil mixture, and kept in the greenhouse until the seedlings emerged and attained the 3-leaf stage of development. The flats were then moved to a cold room where they were vernalized by exposure to cold treatment at 7.2^{o}C for six weeks, under

1800 foot candles of continuous light. The plants were watered as necessary to avert moisture stress and also were supplied with dilute nitrient plant food solutions.

After the prescribed period of cold treatment, the seedlings were transplanted to 4-inch clay pots at the rate of one plant per pot. For each day length trial, five plants of each of the 21 genotypes were transplanted and were placed in the greenhouse for two days to allow the plants to recover from the effects of transplanting. Finally the seedlings were transferred to the controlled environment chamber.

In each trial, a randomized complete block design was used. The plants were watered regularly to minimize complications that might arise due to drought. Fertilizer was also supplied in solution form.

During the course of the experiment, the following observations were recorded for each plant in both photoperiod trials:

1. Days to head: This was determined as the number of days from germination to the time at which the first spike had completely emerged from the leaf sheath.
2. Days to mature: This was determined as the number of days from germination to the time the grain of the primary spike was in the hard dough stage.
3. Number of leaves per plant: This was determined by counting the number of leaves on all of the tillers of each plant.
4. Number of leaves of the primary tiller: This was determined by counting the number of leaves of the tiller carrying the first emerged spike of each plant.
5. Number of tillers: This was determined by counting the

number of seed-bearing tillers of each plant at time of heading.

6. Plant height: This was determined by the distance in centimeters of the primary tiller from the soil level to the tip of the spike (excluding the awns) at maturity.
7. Spike length: This was determined by the distance in centimeters of the spike of the primary tiller as measured from the basal rachis node to the tip of the spike (excluding the awns) at maturity.
8. Number of spikelets per spike: This was determined by counting the number of spikelets on the primary tiller spike.
9. Number of seeds per spike: This was determined by counting the number of seeds produced on the primary tiller spike of each plant.

Statistical Procedure

Due to the fact that the data in the growth chamber were incomplete because of the failure of some plants to survive, the genetic analyses as applied in the photoperiod field study (Experiment I) were not conducted on the growth chamber study. However, the procedures used in the evaluation of the effects of the long and short photoperiods on the parents and the F_1 hybrids were the same. Entry means were used in making comparisons between short day response and long day response. The student's t test (36) was employed to determine, on the average, whether or not there was significant difference in effects among genotypes grown under long and short days for a particular trait. The standard deviation between the two mean differences ($s_{\bar{d}}$) as well as t values for each trait were calculated the same way as in Experiment I. The calculated t was compared with the tabulated t.05 and t.01 values for 40 degrees of freedom to determine the significance.

CHAPTER IV

RESULTS AND DISCUSSION

Experiment I

Analysis of Variance

An analysis of variance was conducted on a plot mean basis of the long day field trial for each trait measured. Two separate analyses were conducted. One involved the six parents and the other involved the 15 F_1 hybrids. The results of these analyses are presented in Tables I and II. Highly significant differences were detected among the parents and among the F_1 hybrids for all characters studied, indicating the presence of genetic variability in the population for all characters.

For the short day trial, the analysis of variance was based on individual plant values for each trait. Here again, the parents and F_1 hybrids were analyzed separately (Tables III and IV). As in the long day trial, highly significant differences among the parents and the hybrids were observed for all the traits measured.

Jinks-Hayman Diallel Analysis

The diallel analysis as outlined by Jinks and Hayman (11, 12, 16, 17), provides information about the genetic system controlling quantitative traits among parents entering diallel crosses. The

TABLE I

ANALYSIS OF VARIANCE OF VARIOUS TRAITS OF THE DIALLEL CROSS WINTER WHEAT PARENTS GROWN IN THE LONG DAY FIELD STUDY, 1971-72

		Mean Squares							
Source	df	Days to Head	Days to Mature	Plant Height	Tiller Number	Spike Length	Spikelets/ Spike	Seeds/ Spike	Yield Plant
Replication	5	1.2667	4.8500	118.9111**	4.6667	0.0578	0.2667	3.0667	8.2376
Parents	5	34.9333**	90.1833**	393.9111**	92.6000**	4.1771**	7.4667**	132.0000**	52.9379**
Error	25	1.000	8.5433	12.3378	3.7467	0.0722	0.4933	10.4267	4.5961

*,**Significantly different at the .05 and .01 levels of probability, respectively.

TABLE II

ANALYSIS OF VARIANCE OF VARIOUS TRAITS OF THE DIALLEL CROSS WINTER WHEAT F_1 HYBRIDS GROWN IN THE LONG DAY FIELD STUDY, 1971-72

Source	df	Mean Squares							
		Days to Head	Days to Head	Plant Height	Tiller Number	Spike Length	Spikelets/ Spike	Seeds/ Spike	Yield/ Plant
Replication	5	0.8978	32.2244*	191.1911**	21.1111**	0.0649	0.5711	5.1644	23.1758**
F_1s	14	11.8206**	61.5683**	60.7539**	24.3492**	2.2619**	3.2587**	145.2111**	23.5931**
Error	70	0.5883	11.6768	10.5292	4.0825	0.1058	0.6092	10.9692	3.4061

*,**Significantly different at the .05 and .01 levels of probability, respectively.

TABLE III

ANALYSIS OF VARIANCE OF VARIOUS TRAITS OF THE DIALLEL CROSS WINTER WHEAT PARENTS GROWN IN THE SHORT DAY FIELD STUDY, 1971-72

		Mean Squares				
Source	df[1]	Tiller Number	Spike Length	Spikelets/ Spike	Seeds/ Spike	Yield/ Plant
Parents	5	239.138**	12.952**	14.45**	243.95**	30.604**
Error	42	29.717	0.700	1.399	20.714	4.242

*,**Significantly different at the .05 and .01 levels of probability, respectively.

[1]Total degrees of freedom associated with completely random design was 47.

TABLE IV

ANALYSIS OF VARIANCE OF VARIOUS TRAITS OF THE DIALLEL CROSS WINTER WHEAT F_1 HYBRIDS GROWN IN THE SHORT DAY FIELD STUDY, 1971-72

		Mean Squares				
Source	df[1]	Tiller Number	Spike Length	Spikelets/ Spike	Seeds/ Spike	Yield/ Plant
F_1s	14	104.836**	4.534**	10.319**	207.557**	19.673**
Error	105	28.680	0.419	1.716	23.573	5.397

*,**Significantly different at the .05 and .01 levels of probability, respectively.

[1]Total degrees of freedom associated with completely random design was 119.

correctness of the conclusions obtained from this analysis as summarized by Allard (1) and Crumpacker and Allard (7) is dependent upon the validity of the following assumptions: 1) no genotype by environment interaction (within locations and years), 2) homozygous parents, 3) diploid segregation, 4) no reciprocal differences, 5) no epistasis, 6) no multiple alleles, and 7) uncorrelated gene distribution. Since the analysis is invalidated to some degree by the failure of any of the above assumptions, it is important to test the validity of these assumptions so as to determine the reliability of the results.

To determine whether the assumptions of the anlaysis were fulfilled by the trait as a whole, the following three broad, general tests, as outlined by Verhalen and Murray (39, 40) were carried out: 1) analysis of variance of the quantity (W_r-V_r), 2) analysis of the (W_r,W'_r) regression, and 3) analysis of the (V_r,W_r) regression.

V_r is the variance of all of the offspring of each parental array; W_r is the covariance of the offspring of each array with the nonrecurrent parents; and W'_r is the covariance of the offspring of each array with the array means. An array includes a parent as well as all crosses derived from it.

The above three general tests of the assumptions were conducted for all traits for both the long day trial and short day trial. The results of these tests indicated that only yield per plant in the long day trial seemed to have satisfied all the requirements of the assumptions, while the other traits in this trial as well as those in the short day trial indicated partial failure of the assumptions (Appendix Tables XXXIX through XLIV).

Estimates of Diallel Cross Parameters

Although partial failure of the assumptions were indicated for most of the traits, estimates of the population parameters could still be made (2, 39, 40). However, the estimates concerning genetic systems might not be as accurate as the case if all the assumptions had been fulfilled.

The parameters estimated were E_o, E_1, D, H_1, H_2 and F. The parameter E_o, is an estimate of the parental environment variation, while E_1 is the estimate of the F_1 environmental variation. The error mean squares of the analyses of variance of the parental entries and F_1 entries were used as estimators of E_o and E_1, respectively, for each of the traits studied.

D is an estimate of additive genetic variance while H_1 and H_2 are different estimates of dominance genetic variance. D may include additive by additive epistatic effects while H_1 and H_2 may include additive by additive, additive by dominance, and dominance by dominance epistatic effects. Since they are variances, D_1, H_1, and H_2 are expected to be positive.

F serves as an indicator of the relative frequency of dominant and recessive alleles in the parents. A positive F value indicates an excess of dominant alleles while a negative F value indicates an excess of recessive alleles in the parents. On the other hand, an F value of zero indicates that the dominant and recessive alleles are equally distributed among the parents.

In estimating the parameters D, H_1, H_2 and F for each trait, Nedler's suggestion of analyzing each replication separately as outlined by Verhalen and Murray (39, 40) was followed. In the long day trail, each parameter was estimated in each replication independently and the variation of the block means around the overall mean was used to calculate the standard error of the mean in order to make tests of significance. In the short day trial, however, each parameter was estimated on individual plant basis. Standard errors were also calculated on this basis for tests of significance.

The following equations (7, 11, 39, 40) were used in the estimation of the diallel cross parameters in the parental and F_1 data, in both long day and short day trials.

1. Variance of the parents = $V_{0L01} = D+E_0$
2. Mean covariance of arrays = $W_{0L01} = \frac{1}{2}D-\frac{1}{4}F+E_o/n$
3. Mean variance of arrays = $V_{1L1} = \frac{1}{4}D+\frac{1}{4}H_1-\frac{1}{4}F+E_o+(n-1)E_1/n$
4. Variance of array means = $V_{0L1} = \frac{1}{4}D+\frac{1}{4}H_1-\frac{1}{4}H_2-\frac{1}{4}F+E_o+(n-2)E_1/n^2$

The estimates of V_{0L0}, W_{0L01}, V_{1L1}, and V_{0L1} were obtained from the diallel table and n equals the number of parents involved in the cross. The diallel cross parameter estimates for the traits in the long day and short day trials are presented in Tables V and VI, respectively.

Long Day Trial

In this trial (Table V), the estimates of additive effects (D) for all eight trials were significantly different from zero. Estimates of dominance effects (H_1 or H_2) for days to head, spike length, and yield per plant were statistically significant. The observed pattern of the parameter estimates indicated that in general additive effects were more important than dominance effects for the traits measured in the long day trial. The negative H_1 value for spikelet number could be due to error variation (16).

TABLE V

MEAN PARAMETER ESTIMATES OF GENETIC AND ENVIRONMENTAL VARIANCE COMPONENTS OF VARIOUS TRAITS FROM A DIALLEL CROSS ANALYSIS OF WINTER WHEAT GROWN IN THE LONG DAY FIELD STUDY, 1971-72

	Trait							
Parameter	Days to Head	Days to Head	Plant Height	Tiller Number/ Plant	Spike Length	Spikelets/ Spike	Seeds/ Spike	Yield/ Plant
D	5.66**	13.6**	63.59**	14.81*	0.68**	1.16*	20.26*	8.06**
H_1	3.23**	16.48	20.39	1.36	0.21**	-0.11	15.77	3.79
H_2	3.16**	14.84	13.28	1.21	0.18*	0.01	8.79	3.72**
F	1.16	1.74	38.37	4.37	-0.12	-0.17	-16.18	1.42
E_o	1.00	8.54	12.38	3.75	0.07	0.49	10.43	4.59
E_1	0.59	11.68	10.53	4.08	0.11	0.61	10.97	3.41

*,** Significantly different from zero at the .05 and .01 levels of probability, respectively.

None of the estimates of F were significantly different from zero. However, based on the fact that the dominance effects (H_1 and H_2) for days to head and yield per plant were significantly different from zero, the positive F values for these two traits would indicate an excess dominant alleles in the parents. On the other hand, the negative F value for spike length suggested an excess of recessive alleles in the parents. Since D was the only parameter that was significantly different from zero for the other traits, positive or negative F values would probably suggest an incomplete dominance system and that additive effects of these genes were primarily responsible in controlling these traits.

No test of significance for E_o and E_1 were made since they were error mean squares of the analysis of variance of the parental entries and F_1 entires, respectively.

Short Day Trial

In the short day trial the estimate of additive effects (D) for tiller number, spike length, and spikelets per spike were significantly different from zero as were the estimates of dominance effects (H_1 or H_2) for spike length, spikelets per spike and seeds per spike (Table VI). The observed parameter estimates indicated that both additive and dominance effects were important for spike length and spikelets per spike, while additive effects were more important than dominance effects for tiller number. Dominance effects appeared to be more important than additive effects for seeds per spike. Neither additive nor dominance estimates were statistically significant for yield per plant.

TABLE VI

MEAN PARAMETER ESTIMATES OF GENETIC AND ENVIRONMENTAL VARIANCE COMPONENTS OF VARIOUS TRAITS FROM A DIALLEL CROSS ANALYSIS OF WINTER WHEAT GROWN IN THE SHORT DAY FIELD STUDY, 1971-72

	Trait				
Parameter	Tiller Number	Spike Length	Spikelets/ Spike	Seeds/ Spike	Yield/ Plant
D	27.86*	1.58**	1.60*	45.16	3.28
H_1	48.99	1.28*	1.94	116.42*	3.24
H_2	24.87	0.91*	1.80*	86.91*	4.18
F	-11.31	0.85	-0.22	54.37	-0.64
E^o	29.72	0.70	1.40	20.71	4.24
E_1	28.68	0.42	1.72	23.57	5.40

*,** Significantly different from zero at the .05 and .01 levels of probability, respectively.

All estimates of F were nonsignificant. However, the positive F values for spike length and number of seeds per spike might suggest an excess of dominant alleles in the parents while excess recessive alleles could be the case in number of spikelets per spike as indicated by the negative F value.

When parameter estimates from both long and short days are considered, additive gene effects appeared to be more important than dominance gene effects for tiller number. Estimates from both trials also showed that for spike length both additive and dominance gene effects were important. On the other hand, the estimates of the relative importance of additive and dominance effects for spikelets per spike, seeds per spike and yield per plant were inconsistent in long versus short day comparisons. The possibility exists that these inconsistencies are the result of interaction between the genetic system and the day length treatments.

Investigation of Genetic System in Terms of Diallel Cross Estimators

After the parameters D, H_1, H_2 and F were estimated, various ratios were calculated to obtain further information about the genetic systems controlling each trait. Standard errors and confidence limits of these ratios were also determined (7, 39, 40).

Degree of Dominance

The ratios H_1/D, $(H_1/D)^{1/2}$, and $(V_{1L1}-E)/(W_{0L01}-E/n)$ are weighted measures of the average degree of dominance at each locus (7, 39, 40). With no dominance, the estimates are zero. With partial dominance, they are expected to fall within the range of zero to one. In the case of complete dominance, the estimates are equal to one. Values greater than one indicate overdominance (7, 39, 40).

Direction of Dominance

The quantity $(\bar{F}_1 - \bar{P})$ is an indicator of the average direction of dominance. If no dominance exists, the estimate is zero. If the value is greater than zero, the direction of dominance is in favor of the parent with the higher value for the trait in question. If the value is lower than zero the direction of dominance is in favor of the parent with the lower value.

Distribution of Alleles

The quantity $(\frac{1}{4}H_2/H_1)$ is an estimator of the average frequency of the negative versus the positive alleles in the parents exhibiting some degree of dominance. The ratio is expected to be ¼ when the distribution is equal and to be less than ¼ when the distribution is unequal (7, 16, 39, 40).

Number of Effective Factors

The number of effective factors, K, is defined as the smallest unit of hereditary material that is capable of being recognized by the methods of biometrical genetics (7, 16). It may be a group of closely linked genes or at the lower limit, a single gene, which control the trait and exhibits dominance to some degree. For each trait, K was estimated using the following formula:

$$K = (\text{Overall progeny mean} - \text{Parental mean})^2 / \tfrac{1}{4}H_2$$

The value of K will be underestimated if the dominance effects of all the genes concerned are not equal in sign and size, and if the distribution of the genes is correlated or both (7, 16, 39, 40).

Narrow-Sense Heritability

The ratio $\frac{1}{4}D/\frac{1}{4}D+\frac{1}{4}H_1-\frac{1}{4}F+E$ estimates narrow-sense heritability (7, 39, 40). In the present study, these estimates were calculated on a plot mean basis in the long day trial and on single plant values in the short day trial.

Long Day Trial

Days to Head

Two of three estimates of degree of dominance (Table VII) were significantly different from zero but not from one, indicating that partial dominance was involved in the control of days to head. The negative value observed for the quantity $\bar{F}_1-\bar{P}$ indicated that earliness was partially dominant to lateness (7). The estimate of $\frac{1}{4}H_2/H_1$ indicated equal distribution of positive and negative alleles in the parents. The estimate of K was fairly high (4.47) but was not significantly different from zero. This was probably due to the large standard error of means used for making the test of significance. The heritability estimate of 0.48 was significantly different from zero. However, this value seemed very low for heading date.

Days to Mature

All three estimates of degree of dominance (Table VIII) had values greater than one, suggesting overdominance, however, none of these

TABLE VII

MEAN RATIOS ESTIMATING GENETIC CHARACTERISTICS OF DAYS TO HEADING OF THE DIALLEL CROSS OF WINTER WHEAT PARENTS AND F_1 HYBRIDS GROWN IN THE LONG DAY FIELD STUDY, 1971-72

Estimator	Mean	Standard Error	95% confidence Limits
H_1/D	0.59	0.11	0.31 - 0.87
$(H_1/D)^{½}$	0.77	0.33	(-0.07) - 1.66
$(V_{1L1}-E)/(W_{0L01}-E/n)$	0.63	0.05	0.50 - 0.76
$\bar{F}_1-\bar{P}$	-1.61	0.23	(-2.20) - (-1.02)
$¼H_2/H_1$	0.25	0.02	0.20 - 0.30
K	4.47	3.91	(-5.58) -14.52
$¼D/(¼D+¼H_1-¼F+E)$	0.48	0.03	0.40 - 0.56

TABLE VIII

MEAN RATIOS ESTIMATING GENETIC CHARACTERISTICS OF DAYS TO MATURITY OF THE DIALLEL CROSS OF WINTER WHEAT PARENTS AND F_1 HYBRIDS GROWN IN THE LONG DAY FIELD STUDY, 1971-72

Estimator	Mean	Standard Error	95% confidence Limits
H_1/D	1.45	0.82	(-0.66) - 3.56
$(H_1D)^{½}$	1.20	0.91	(-1.13) - 3.55
$V_{1L1}-E/(W_{0L01}-E/n)$	1.71	0.39	0.71 - 2.71
$\bar{F}_1-\bar{P}$	-1.18	0.55	(-2.59) - 0.23
$¼H_2/H_1$	0.19	0.04	0.08 - 0.29
K	2.33	1.86	(-2.45) - 7.11
$¼D/(¼D+¼H_1-¼F+E)$	0.22	0.04	0.12 - 0.32

estimates were significantly different from zero as a result of large standard errors. Therefore, dominance to overdominance gene action could be suggested for the control of days to mature in this trial. The ratio $\frac{1}{4}H_2/H_1$ showed that positive and negative alleles were not distributed equally in the parents. The heritability estimate of 0.22 for this trait was significant but much lower than expected.

Plant Height

Two of three estimates of degree of dominance (Table IX) were not significantly different from zero, while the third estimate was significant and indicated partial dominance gene action. The estimate for direction of dominance ($\bar{F}_1-\bar{P}$) indicated dominance in the direction of taller stature. The estimate of $\frac{1}{4}H_2/H_1$ was smaller than 0.25, indicating unequal distribution of positive and negative alles in the parents. The heritability estimate of 0.67 was significant and indicated a rather high genetic control for this trait.

Tiller Number per Plant

One of three estimates of degree of dominance for tiller number (Table X) appeared to be a reasonable estimate as evidenced by its standard error and indicated that this trait was controlled by partially dominance gene action. The distribution of the positive and negative alleles in the parents was unequal as indicated by the ratio of $\frac{1}{4}H_2/H_1$. A heritability estimate of 0.56 was observed. This estimate was accompanied by an acceptable standard error.

TABLE IX

MEAN RATIOS ESTIMATING GENETIC CHARACTERISTICS OF PLANT HEIGHT OF THE DIALLEL CROSS OF WINTER WHEAT PARENTS AND F_1 HYBRIDS GROWN IN THE LONG DAY FIELD STUDY, 1971-72

Estimator	Mean	Standard Error	95% confidence Limits
H_1/D	0.19	0.23	(-0.40) - 0.78
$(H_1/D)^{\frac{1}{2}}$	0.44	0.48	(-0.79) - 1.67
$(V_{1L1}-E)/(W_{0L01}-E/n)$	0.43	0.11	0.15 - 0.71
$\bar{F}_1-\bar{P}$	2.39	0.76	0.44 - 4.34
$\frac{1}{4}H_2/H_1$	0.16	0.01	0.13 - 0.19
K	3.69	2.62	(-3.05) -10.43
$\frac{1}{4}D/(\frac{1}{4}D+\frac{1}{4}H_1-\frac{1}{4}F+E)$	0.67	0.05	0.54 - 0.80

TABLE X

MEAN RATIOS ESTIMATING GENETIC CHARACTERISTICS OF TILLER NUMBER PER PLANT OF THE DIALLEL CROSS OF WINTER WHEAT PARENTS AND F_1 HYBRIDS GROWN IN THE LONG DAY FIELD STUDY, 1971-72

Estimator	Mean	Standard Error	95% confidence Limits
H_1/D	0.26	0.31	(-0.54) - 1.06
$(H_1/D)^{1/2}$	0.51	0.56	(-0.93) - 1.95
$(V_{1L1}-E)/(W_{0L01}-E/n)$	0.64	0.19	0.15 - 1.13
$\bar{F}_1-\bar{P}$	0.85	0.23	0.16 - 1.54
$\frac{1}{4}H_2/H_1$	0.17	0.05	0.04 - 0.29
K	0.45	0.48	(-0.78) - 1.68
$\frac{1}{4}D/(\frac{1}{4}D+\frac{1}{4}H_1-\frac{1}{4}F+E)$	0.56	0.12	0.25 - 0.87

Spike Length

Two of three estimates (Table XI) of degree of dominance indicated partial dominance with acceptable confidence limits. The ratio of $\frac{1}{4}H_2/H_1$ indicated that the distributions of the positive and negative alleles in the parents were nearly equal. The heritability estimate of 0.54 showed that the trait was moderately heritable.

Spikelet Number per Spike

Two of three estimates of degree of dominance (Table XII) were non-significant and negative. The negative values could only arise by an excessively large error variation (16). The third estimate showed partial dominance gene action however, the value was not significantly different from zero. Further, it was indicated that the positive and negative alleles were nearly equally distributed in the parents. The heritability estimate of 0.40 showed that the trait was slightly less heritable than spike length.

Seed Number per Spike

For probably the same reason as in spikelet number, two of the estimates of degree of dominance (Table XIII) were negative and non-significant. However, on the basis of the third estimate, a rather high degree of dominance gene action could be involved in the control of seed number. The estimate of $\frac{1}{4}H_2/H_1$ suggested that the positive and negative alleles were almost equally distributed in the parents. This could be one of the reasons for the nonsignificance of H_1 and or H_2 for this trait in Table V. The estimate of K was significant but low (0.17). As a result, the validity of the estimate is doubtful. The

TABLE XI

MEAN RATIOS ESTIMATING GENETIC CHARACTERISTICS OF SPIKE LENGTH IN THE DIALLEL CROSS OF WINTER WHEAT PARENTS AND F_1 HYBRIDS GROWN IN THE LONG DAY FIELD STUDY, 1971-72

Estimator	Mean	Standard Error	95% confidence Limits
H_1/D	0.33	0.08	0.12 - 0.54
$(H_1/D)^{\frac{1}{2}}$	0.57	0.28	(-0.14)-(1.29)
$(V_{1L1}-E)/(W_{0L01}-E/n)$	0.76	0.05	0.63 - 0.89
$\bar{F}_1-\bar{P}$	0.31	0.03	0.23 - 0.39
$\frac{1}{4}H_2/H_1$	0.21	0.03	0.13 - 0.29
K	3.62	1.43	(-0.06)- 7.29
$\frac{1}{4}D/(\frac{1}{4}D+\frac{1}{4}H_1-\frac{1}{4}F+E)$	0.54	0.07	0.36 - 0.72

TABLE XII

MEAN RATIOS ESTIMATING GENETIC CHARACTERISTICS OF SPIKELET NUMBER PER SPIKE IN THE DIALLEL CROSS OF WINTER WHEAT PARENTS AND F_1 HYBRIDS GROWN IN THE LONG DAY FIELD STUDY, 1971-72

Estimator	Mean	Standard Error	95% confidence Limits
H_1/D	-0.43	0.41	(-1.48) - 0.62
$(H_1/D)^{\frac{1}{2}}$	-0.43	0.64	(-1.97) - 1.31
$(V_{1L1}-E)/(W_{0L01}-E/n)$	0.60	0.24	(-0.02) - 1.22
$\bar{F}_1-\bar{P}$	0.32	0.06	0.17 - 0.47
$\frac{1}{4}H_2/H_1$	0.26	0.03	0.18 - 0.33
K	-1.33	1.02	(-3.95) - 1.29
$\frac{1}{4}D/(\frac{1}{4}D+\frac{1}{4}H_1-\frac{1}{4}F+E)$	0.40	0.13	0.07 - 0.73

TABLE XIII

MEAN RATIOS ESTIMATING GENETIC CHARACTERISTICS OF SEED NUMBER PER SPIKE IN THE DIALLEL CROSS OF WINTER WHEAT PARENTS AND F_1 HYBRIDS GROWN IN THE LONG DAY FIELD STUDY, 1971-72

Estimator	Mean	Standard Error	95% confidence Limits
H_1/D	-1.35	1.89	(-6.21) - 3.51
$(H_1/D)^{\frac{1}{2}}$	-1.35	1.38	(-4.89) - 2.19
$(V_{1L1}-E)/W_{0L01}-E/n)$	1.11	0.26	0.44 - 1.78
$\bar{F}_1-\bar{P}$	0.09	0.23	(-0.50) - 0.68
$\frac{1}{4}H_2/H_1$	0.21	0.05	0.08 - 0.34
K	0.17	0.06	0.02 - 0.32
$\frac{1}{4}D/(\frac{1}{4}D+\frac{1}{4}H_1-\frac{1}{4}F+D)$	0.22	0.06	0.07 - 0.37

heritability estimate of 0.22 was rather low, indicating that seed number was greatly influenced by environment.

Yield per Plant

The estimates of degree of dominance for yield (Table XIV) ranged from partial dominance to overdominance. However, none of the three estimates were significant. Nonetheless, there was an indication of some dominance gene action for this trait as evidenced from the significant estimate of H_2 (Table V). Therefore, at least partial dominance gene action would be suggested as a genetic system controlling yield. The estimate of $\frac{1}{4}H_2/H_1$ indicated that the positive and negative alleles were unequally distributed in the parents. The estimate of the number of effective factors, K was significant and higher than that of the estimate of K for seed number. On the other hand, the heritability estimate of 0.26 was lower than most other traits, which is to be expected since yield is known to be greatly influenced by environment.

Short Day Trial

Tiller Number per Plant

None of the three estimates of degree of dominance for tiller number (Table XV) were within acceptable confidence limits. Also, since neither H_1 nor H_2 were significant for tiller number (Table VI), no valid inference regarding the degree of dominance gene action could be made. The heritability estimate of 0.12 was rather low for the trait, indicating that environment had a rather great effect on it.

TABLE XIV

MEAN RATIOS ESTIMATING GENETIC CHARACTERISTICS OF YIELD PER PLANT IN THE DIALLEL CROSS OF WINTER WHEAT PARENTS AND F_1 HYBRIDS GROWN IN THE LONG DAY FIELD STUDY, 1971-72

Estimator	Mean	Standard Error	95% confidence Limits
H_1/D	3.17	2.66	(-3.67) - 10.01
$(H_1/D)^{\frac{1}{2}}$	1.78	1.63	(-2.41) - 5.97
$(V_{1L1}-E)/(W_{0L01}-E/n)$	0.29	0.25	(-0.35) - 0.93
$\bar{F}_1-\bar{P}$	3.69	2.62	(-3.05) - 10.43
$\frac{1}{4}H_2/H_1$	0.20	0.03	0.12 - 0.28
K	2.39	0.76	0.44 - 4.34
$\frac{1}{4}D/(\frac{1}{4}D+\frac{1}{4}H_1-\frac{1}{4}F+E)$	0.26	0.06	0.11 - 0.41

TABLE XV

MEAN RATIOS ESTIMATING GENETIC CHARACTERISTICS OF TILLER NUMBER PER PLANT IN THE DIALLEL CROSS OF WINTER WHEAT PARENTS AND F_1 HYBRIDS GROWN IN THE SHORT DAY FIELD STUDY, 1971-72

Estimator	Mean	Standard Error	95% confidence Limits
H_1/D	2.89	6.25	(-11.89) - 17.67
$(H_1/D)^{\frac{1}{2}}$	1.71	2.50	(-4.20) - 7.62
$(V_{1L1}-E)/(W_{0L01}-E/n)$	-1.42	2.05	(-6.16) - 3.32
$\bar{F}_1-\bar{P}$	-1.81	0.64	(-3.32) - 0.30
$\frac{1}{4}H_2/H_1$	0.17	0.03	0.10 - 0.24
K	1.68	0.99	(-0.66) - 4.02
$\frac{1}{4}D/(\frac{1}{4}D+\frac{1}{4}H_1-\frac{1}{4}F+E)$	0.12	0.03	0.05 - 0.19

Spike Length

Due to the large standard error of means used in setting the confidence intervals, two of three estimates of degree of dominance (Table XVI) showed nonsignificance. However, the third estimate suggested a high degree of dominance. The estimate of $\frac{1}{4}H_2/H_1$ indicated unequal distribution of positive and negative alleles in the parents. The heritability estimate of 0.33 showed that the trait was more heritable than tiller number.

Spikelet Number per Spike

The three estimates of degree of dominance (Table XVII) were in the overdominance range, however each was accompanied by unacceptable confidence intervals. Consequently, no valid estimate of degree of dominance for this trait could be made. Based on the significance of H_1 and/or H_2 for spikelet number (Table VI) a high degree of dominance was probably involved in the control of this trait. The heritability estimate of 0.19 was rather low indicating that this trait was greatly influenced by environment.

Seed Number per Spike

All three estimates of degree of dominance (Table XVIII) were in the overdominance range but were nonsignificant statistically. Nonetheless, on the basis of significance of H_1 and/or H_2 for this trait (Table VI), at least partial dominance could be suggested. The negative $\bar{F}_1-\bar{P}$ value was also in agreement with this gene action (7). The estimate of $\frac{1}{4}H_2/H_1$ indicated that positive and negative alleles in the parents were not distributed equally. The estimate of K was

TABLE XVI

MEAN RATIOS ESTIMATING GENETIC CHARACTERISTICS OF SPIKE LENGTH IN THE DIALLEL CROSS OF WINTER WHEAT PARENTS AND F_1 HYBRIDS GROWN IN THE SHORT DAY FIELD STUDY, 1971-72

Estimator	Mean	Standard Error	95% confidence Limits
H_1/D	0.84	0.31	0.11 - 1.57
$(H_1/D)^{\frac{1}{2}}$	0.91	0.56	(-0.41)- 2.23
$(V_{1L1}-E)/W_{0L01}-E/n)$	-5.88	6.41	(-21.04)- 9.28
$\bar{F}_1-\bar{P}$	-0.01	0.15	(-0.36)- 0.34
$\frac{1}{4}H_2/H_1$	0.18	0.03	0.11 - 0.25
K	2.78	2.33	(-2.73)- 8.29
$\frac{1}{4}D/(\frac{1}{4}D+\frac{1}{4}H_1-\frac{1}{4}F+E)$	0.33	0.06	0.19 - 0.47

TABLE XVII

MEAN RATIOS ESTIMATING GENETIC CHARACTERISTICS OF SPIKELET NUMBER PER SPIKE IN THE DIALLEL CROSS OF WINTER WHEAT PARENTS AND F_1 HYBRIDS GROWN IN THE SHORT DAY FIELD STUDY, 1971-72

Estimator	Mean	Standard Error	95% confidence Limits
H_1/D	9.93	12.13	(-18.76) - 38.62
$(H_1/D)^{\frac{1}{2}}$	3.14	3.46	(-5.04) - 11.32
$(V_{1L1}-E)/(W_{0L01}-E/n)$	1.82	0.56	0.49 - 3.14
$\bar{F}_1-\bar{P}$	0.96	0.24	0.39 - 1.53
$\frac{1}{4}H_2/H_1$	0.23	0.02	0.18 - 0.28
K	2,68	2.66	(-3.61) - 8.97
$\frac{1}{4}D/(\frac{1}{4}D+\frac{1}{4}H_1-\frac{1}{4}F+E)$	0.19	0.06	0.05 - 0.33

TABLE XVIII

MEAN RATIOS ESTIMATING GENETIC CHARACTERISTICS OF SEED NUMBER PER SPIKE IN THE DIALLEL CROSS OF WINTER WHEAT PARENTS AND F_1 HYBRIDS GROWN IN THE SHORT DAY FIELD STUDY, 1971-72

Estimator	Mean	Standard Error	95% confidence Limits
H_1/D	1.88	3.06	(-5.36) - 9.12
$(H_1/D)^{½}$	1.37	1.75	(-2.77) - 5.50
$(V_{1L1}-E)/(W_{0L01}0E/n)$	3.09	1.47	(-0.38) - 6.56
$\bar{F}_1-\bar{P}$	-2.71	0.88	(-4.79) - 0.63
$¼H_2/H_1$	0.21	0.02	0.16 - 0.25
K	0.70	0.22	0.18 - 1.22
$¼D/(¼D+¼H_1-¼F+E)$	0.21	0.08	0.02 - 0.40

significant but low (0.70), therefore, the validity of the estimate is doubtful. The heritability estimate of 0.21 was higher than for spikelet number.

Yield per Plant

As with seed number per spike, none of the estimates of degree of dominance (Table XIX) was significant. The negative values for the two estimates could only arise by error variation (16). However, since no dominance gene action was indicated by H_1 and/or H_2 values (Table VI), additive gene action was probably the major genetic system responsible for the control of yield. The estimate of the number of effective factors, K, was significant but unacceptably low (1.02). The heritability estimate of 0.14 was also low which was to be expected.

Comparison of Genetic Estimators for Traits
Evaluated Under both Long and Short Days

The estimates of degree of dominance for tiller number (Tables X andXV) were apparently affected by photoperiod treatment. These estimates changed from partial dominance under long days to over-dominance under short days. The heritability estimate for this trait was also larger under long days than under short days, indicating a rather major influence of day length on heritability. $\bar{F}_1-\bar{P}$ values were positive under long days but negative under short days.

The estimates of the genetic ratios for spike length (Tables XI and XVI) were similar under both photoperiod regimes except for $\bar{F}_1-\bar{P}$ which showed a positive value under long days and a negative value under short days. Also, the heritability estimate obtained from the short day

TABLE XIX

MEAN RATIOS ESTIMATING GENETIC CHARACTERISTICS OF YIELD PER PLANT IN THE DIALLEL CROSS OF WINTER WHEAT PARENTS AND F_1 HYBRIDS GROWN IN THE SHORT DAY FIELD STUDY, 1971-72

Estimator	Mean	Standard Error	95% confidence Limits
H_1/D	-1.87	1.56	(-5.56) - 1.82
$(H_1/D)^{½}$	-1.87	1.25	(-4.83) - 1.09
$(V_{1L1}-E)/(W_{0L01}-E/n)$	4.58	3.36	(-3.37) -12.53
$\bar{F}_1-\bar{P}$	1.21	0.34	0.41 - 2.01
$¼H_2/H_1$	0.29	0.06	0.15 - 0.43
K	1.02	0.35	0.19 - 1.85
$¼D/(¼D+¼H_1-¼F+E)$	0.14	0.08	(-0.05) - 0.33

treatment was lower than that obtained from the long day treatment.

The estimates of degree of dominance for spikelet number were greatly affected by day length (Tables XII and XVII). They changed from partial dominance under long day to complete dominance under short day. A higher heritability estimate was obtained from long day treatment as compared to the short day treatment.

All estimates for seed number except $\bar{F}_1$-$\bar{P}$ were similar for both photoperiod treatments (Tables XIII and XVIII). The $\bar{F}_1$-$\bar{P}$ values were changed from positive under long day to negative under short day.

The estimates of degree of dominance and heritability for yield (Tables XIV and XIX) appeared to be greatly affected by day length. Partial dominance gene action was indicated as the major genetic system for yield under long days while additive gene action was indicated under short days. The heritability estimate of yield was lower under short days.

Correlations Among Yield Components and other Plant Characters

In order to examine the influence of photoperiod on the associations of yield components as well as on other traits, correlation coefficients were determined for all traits measured in the long photoperiod and short photoperiod studies, separately. For each trait, the mean of the 21 genotypes were used. The method described by Steel and Torrie (36) was followed in making the test of significance on the computerized correlation coefficients.

Long Day Trial

Under long days (Table XX) plant height and spike length had significant positive correlation coefficients with yield. None of the other traits was significantly correlated with yield. Days to head was positively correlated with plant height and spike length but was negatively correlated with seeds per spike. Days to mature was not significantly correlated with any of the traits measured. The only other statistically significant correlation was the negative association between seeds per spike and plant height. It was of interest to note that no significant association was observed between tiller number and yield. It is generally accepted that tiller number is closely associated with yield in wheat, at least under normal seeding rates. Apparently this relationship is not valid under the space-planted conditions of this trial.

Short Day Trial

Under short days (Table XXI), none of the three yield components was significantly associated with yield. All of the correlation coefficients were small and the two involving spike length and spikelets per spike were negative. Spike length showed a significant positive correlation with tiller number and was negatively but nonsignificantly correlated with the other traits. All correlations involving seeds per spike were low and nonsignificant.

The Effects of Long and Short Photoperiods

Although one of the most pronounced effects of photoperiod is on floral initiation, other systems of the plant are known to be influenced,

TABLE XX

COEFFICIENTS OF SIMPLE CORRELATIONS AMONG YIELD COMPONENTS AND OTHER TRAITS
OF PARENTS AND HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT
GROWN IN THE LONG DAY FIELD STUDY, 1971-72

	Yield/ Plant	Days to Head	Days to Mature	Plant Height	Tiller Number/ Plant	Spike Length	Spikelets/ Spike
Days to Head	0.093						
Days to Mature	-0.429	0.358					
Plant Height	0.442*	0.641**	-0.096				
Tiller Number/Plant	0.283	0.302	0.139	0.357			
Spike Length	0.469*	0.463*	-0.004	0.410	-0.209		
Spikelets/ Spike	-0.072	0.003	0.151	-0.153	-0.060	0.214	
Seeds/ Spike	0.212	-0.517*	0.126	-0.518*	-0.214	-0.121	0.019

*Significant at the .05 level of probability. The significant value for 19 degrees of freedom is 0.433.

**Significant at the .01 level of probability. The significant value for 19 degrees of freedom is 0.549.

TABLE XXI

COEFFICIENTS OF SIMPLE CORRELATIONS AMONG YIELD COMPONENTS AND OTHER TRAITS OF PARENTS AND HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN THE SHORT DAY FIELD STUDY, 1971-72

	Yield/ Plant	Tiller Number/ Plant	Spike Length	Spikelets Spike
Tiller Number/ Plant	0.257			
Spike Length	-0.059	0.525*		
Spikelets/ Spike	-0.096	-0.408	-0.043	
Seeds/Spike	0.199	-0.109	-0.088	0.270

*Significant at the .05 level of probability. The significant value for 19 degrees of freedom is 0.433.

to a greater or lesser degree, by day length. In order to study some of these influences, comparisons of performance under long day vs short day treatments were made for eight traits of the parents and F_1 hybrids. The short day field trial consisted of one replication with eight plants per entry. The first replication of the long day field nursery grown adjacent to the short day trial was used as a basis of comparison. The results are presented in Tables XXII through XXIX.

Student's t test (36) was used to determine whether or not, on the average, there was a significant difference between the measurements for a particular trait under long and short photoperiods. The standard deviation of the difference between the means of long day and short day nursery was calculated by the formula $s_{\bar{d}} = \sqrt{\frac{2s^2}{n}}$. Then, the t value $\bar{d}/s_{\bar{d}}$ was determined, where $\bar{d}$ is the difference between the long day and short day nursery for a particular trait in question. Finally, the calculated t value was compared with the tabulated value for 40 degrees of freedom ($t_{.05} = 2.021$, $t_{.01} = 2.704$) as a criterion for test of significance.

Days to Head

On the average, there was a highly significant difference among entries for days to head under long day and short day as indicated by the t value (Table XXII). Short days delayed heading of all wheat genotypes, some more than others. San Pastore, Sturdy, and Bezostaia 1 were the least affected by day length and behaved as insensitive types while Scout 66 and Parker were highly sensitive to day length and required longer time to head under short days; Triumph 64 was intermediate in this respect. Of particular interest, however, were the hybrids

TABLE XXII

THE EFFECT OF DAY LENGTH ON DAYS TO HEAD OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN THE FIELD, 1971-72

Designation	Short Day (SD) Mean	Long Day (LD) Mean	Difference SD-LD
San Pastore	195	193	2
Sturdy	197	194	3
Bezostaia 1	202	198	4
Triumph 64	202	196	6
Parker	211	199	12
Scout 66	219	199	20
San Pastore X Triumph 64	194	193	1
San Pastore X Bezostaia 1	197	195	2
San Pastore X Sturdy	197	193	4
San Pastore X Parker	197	193	4
San Pastore X Scout 66	197	193	4
Sturdy X Bezostaia 1	197	195	2
Sturdy X Parker	197	195	2
Sturdy X Triumph 64	198	193	5
Sturdy X Scout 66	200	195	5
Bezostaia 1 X Parker	199	195	4
Bezostaia 1 X Triumph 64	200	196	4
Bezostaia 1 X Scout 66	200	195	5
Triumph 64 X Parker	203	195	8
Triumph 64 X Scout 66	203	195	8
Parker X Scout 66	213	198	15
Treatment Mean	200.86	195.14	5.72 ($\bar{d}$)

$s_{\bar{d}}$	1.44
t (calculated as $\bar{d}/s_{\bar{d}}$)	3.98**
t.05, 40 df	2.02
t.01, 40 df	2.70

**Highly significant difference between the treatment means. The calculated "t" value exceeds the tabulated t.05 and t.01 values for 40 degrees of freedom.

between the sensitive and insensitive parents. All hybrids between insensitive parents (e.g. San Pastore, Sturdy) and strongly sensitive parents (e.g. Parker, Scout 66) were similar to the insensitive parent in days to head, indicating that insensitivity was partially dominant in the F_1.

These findings, in addition to supporting the universality of short days in delaying heading of wheat types that are particularly sensitive to day length, are also in agreement with other workers (5, 18, 30, 31). Coffman (5) found the Bezostaia 1 tended toward day length insensitivity. Coffman (5), Keim _et al._ (18) and Pugsley (30, 31) indicated that insensitivity was more or less dominant in the F_1.

Days to Mature

As in heading, most of the genotypes took significantly longer to mature under short days than under long days (Table XXIII). Again, Parker and Scout 66 were affected the most by day length. In general, the hybrids except San Pastore X Triumph 64, were intermediate between the parents. The maturity date of this hybrid was much less affected by day length.

Plant Height

On the average, no significant difference in plant height was indicated due to day length (Table XXIV). However, Parker, Scout 66, Parker X Scout 66, Parker X San Pastore, and Sturdy X San Pastore were taller under long days. All the other genotypes tended to be taller under short days.

TABLE XXIII

THE EFFECT OF DAY LENGTH ON DAYS TO MATURE OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN THE FIELD, 1971-72

Designation	Short Day (SD) Mean	Long Day (LD) Mean	Difference SD-LD
San Pastore	251	241	10
Bezostaia 1	251	241	10
Sturdy	255	241	14
Triumph 64	255	241	14
Parker	269	251	18
Scout 66	266	241	25
San Pastore X Triumph 64	245	244	1
San Pastore X Bezostaia 1	251	241	10
San Pastore X Sturdy	251	241	10
San Pastore X Scout 66	248	238	10
San Pastore X Parker	251	238	13
Sturdy X Scout 66	251	241	10
Sturdy X Parker	255	244	11
Sturdy X Triumph 64	251	238	13
Sturdy X Bezostaia 1	251	235	16
Bezostaia 1 X Parker	251	248	7
Bezostaia 1 X Triumph 64	251	235	16
Bezostaia 1 X Scout 66	257	241	16
Triumph 64 X Parker	255	238	17
Triumph 64 X Scout 66	255	238	17
Parker X Scout 66	260	245	15
Treatment Mean	253.81	240.81	13 ($\bar{d}$)

$s_{\bar{d}}$	1.45
t (calculated as $\bar{d}/s_{\bar{d}}$)	8.96**
t.05, 40 df	2.02
t.01, 40 df	2.70

**Highly significant difference between the treatments. The calculated "t" value exceeds the tabulated t.05 and t.01 values for 40 degrees of freedom.

TABLE XXIV

THE EFFECT OF DAY LENGTH ON PLANT HEIGHT (CMS) OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN THE FIELD, 1971-72

Designation	Short Day (SD) Mean	Long Day (LD) Mean	Difference[1] SD-LD
Bezostaia 1	84	81	3
Sturdy	77	72	5
San Pastore	77	68	9
Triumph 64	94	84	10
Parker	83	85	-2
Scout 66	84	97	-13
San Pastore X Bezostaia 1	80	80	0
San Pastore X Scout 66	87	82	5
San Pastore X Triumph 64	82	70	12
San Pastore X Parker	85	87	-2
San Pastore X Sturdy	82	90	-8
Sturdy X Parker	84	83	1
Sturdy X Bezostaia 1	84	82	2
Sturdy X Triumph 64	84	77	7
Sturdy X Scout 66	94	86	8
Bezostaia 1 X Parker	90	88	2
Bezostaia 1 X Triumph 64	90	84	6
Bezostaia 1 X Scout 66	88	82	6
Triumph 64 X Scout 66	91	84	7
Triumph 64 X Parker	95	88	7
Parker X Scout 66	88	90	-2
Treatment Mean	85.85	82.43	3.43 ($\bar{d}$)

$s_{\bar{d}}$	1.87
t (Calculated as $\bar{d}/s_{\bar{d}}$)	1.83 ns
t.05, 40 df	2.02
t.01, 40 df	2.70

ns No significant difference between the treatment means. The calculated "t" value is less than the tabulated t.05 or t.01 values for 40 degrees of freedom.

Tiller Number

On the average, there was no significant difference among entries for tiller number due to day length (Table XXV). Short days resulted in a higher tiller number in Scout 66 than any other genotype. This is interesting in view of the fact that this variety appears to be strongly sensitive to day length and is also probably more winterhardy than any other parent. On the other hand, the long day regime was more favorable for higher tiller production in Parker which is also sensitive to day length but is not as winterhardy as Scout 66. Long days also favored higher tiller production in the hybrid Parker X Scout 66, and in the insensitive parents, San Pastore and Sturdy. Bezostaia 1 had more tillers under short day treatment.

In a similar study, Coffman (5) also observed that under different photoperiod regimes, tiller production within day length sensitive winter wheat varieties varied with genotype. Coffman noted that nonresponsiveness to vernalization was an additional factor for higher tiller number production of the very sensitive CI 15069 winter wheat variety in his study. On the other hand, the behavior of Bezostaia 1 was the same as in this study.

Spike Length

As indicated by the t value, no difference in spike length occurred, on the average, due to day length (XXVI). Nevertheless, a trend toward longer spikes under short days was exhibited by most genotypes but the long day regime resulted in longer spikes for Bezostaia 1 and the Bezostaia 1 X San Pastore hybrid.

TABLE XXV

THE EFFECT OF DAY LENGTH ON NUMBER OF TILLERS PER PLANT OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN THE FIELD, 1971-72

Designation	Short Day (SD) Mean	Long Day (LD) Mean	Difference SD-LD
Bezostaia 1	16	14	2
Triumph 64	20	18	2
Scout 66	30	19	11
Sturdy	16	17	-1
San Pastore	15	18	-3
Parker	24	27	-3
San Pastore X Triumph 64	18	18	0
San Pastore X Parker	18	18	0
San Pastore X Sturdy	22	17	5
San Pastore X Scout 66	16	18	-2
San Pastore X Bezostaia 1	11	14	-3
Sturdy X Triumph 64	18	16	2
Sturdy X Bezostaia 1	18	15	3
Sturdy X Parker	27	23	4
Sturdy X Scout 66	18	19	-1
Bezostaia 1 X Parker	19	18	1
Bezostaia 1 X Scout 66	19	17	2
Bezostaia 1 X Triumph 64	22	14	8
Triumph 64 X Scout 66	20	20	0
Triumph 64 X Parker	26	20	6
Parker X Scout 66	22	24	-2
Treatment Mean	19.76	18.29	1.47 ($\bar{d}$)

$s_{\bar{d}}$	1.19
t (calculated as $\bar{d}/s_{\bar{d}}$)	1.23 ns
t.05, 40 df	2.02
t.01, 40 df	2.70

ns No significant difference between the treatment means. The calculated "t" value is less than the tabulated t.05 or t.01 values for 40 degrees freedom.

TABLE XXVI

THE EFFECT OF DAY LENGTH ON SPIKE LENGTH (CMS) OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN THE FIELD, 1971-72

Designation	Short Day (SD) Mean	Long Day (LD) Mean	Difference SD-LD
Sturdy	9.8	9.6	0.2
Triumph 64	9.4	9.1	0.3
Parker	9.6	8.8	0.8
San Pastore	8.5	7.4	1.1
Scout 66	10.7	9.5	1.2
Bezostaia 1	10.1	10.4	-0.3
San Pastore X Sturdy	9.2	9.0	0.2
San Pastore X Parker	9.3	8.9	0.4
San Pastore X Scout 66	9.6	8.8	0.8
San Pastore X Triumph 64	8.9	7.9	1.0
San Pastore X Bezostaia 1	8.9	9.5	-0.6
Sturdy X Triumph 64	8.7	8.7	0.0
Sturdy X Scout 66	9.6	9.4	0.2
Sturdy X Bezostaia 1	10.9	10.4	0.5
Sturdy X Parker	10.2	9.5	0.7
Bezostaia 1 X Parker	10.2	9.9	0.3
Bezostaia 1 X Scout 66	11.0	10.4	0.6
Bezostaia 1 X Triumph 64	10.8	9.9	0.9
Triumph 64 X Parker	9.8	9.4	0.4
Triumph 64 X Scout 66	10.3	9.9	0.4
Parker X Scout 66	10.8	9.9	0.9
Treatment Means	9.82	9.35	0.47 ($\bar{d}$)

$s_{\bar{d}}$	0.24
t (calculated as $\bar{d}/s_{\bar{d}}$)	2.01 ns
t.05, 40 df	2.02
t.01, 40 df	2.70

ns No significant difference between the treatment means. The calculated "t" value is less than the tabulated t.05 or t.01 values for 40 degrees of freedom.

Spikelet Number per Spike

On the average, no significant effect due to day length was observed for this trait (Table XXVII).

Seed Number per Spike

Although, there was no significant difference in this trait due to day length treatments, as a whole, most of the wheat genotypes showed an increase in seed number per spike under long days (Table XXVIII). A notable exception was the San Pastore X Sturdy hybrid which had considerably higher seed number under short days. The increase in seed number under long days would suggest that floret sterility was probably encountered under short days. Some research workers (15, 20) have reported sterile pollen to be a factor in certain wheat varieties grown under short days.

Yield per Plant

As indicated by the t test (Table XXIX), there was a highly significant difference among entries for yield due to day length. In all cases, the long day treatment resulted in higher yields than the short day treatment. This was true even for the apparent insensitive types, San Pastore, Sturdy and Bezostaia 1. In general, the hybrids tended to be intermediate to their parents in response to differences in yield due to day length treatment. The consistently low yield by all genotypes under the short day treatment could suggest that short day treatment probably imposed restrictions on photosynthetic activity and altered respiration rates which subsequently resulted in a decrease in yeild.

TABLE XXVII

THE EFFECT OF DAY LENGTH ON NUMBER OF SPIKELETS PER SPIKE OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN THE FIELD, 1971-72

Designation	Short Day (SD) Mean	Long Day (LD) Mean	Difference SD-LD
Sturdy	18	18	0
Triumph 64	19	19	0
Parker	19	19	0
San Pastore	19	18	1
Bezostaia 1	21	22	-1
Scout 66	16	17	-1
San Pastore X Sturdy	19	18	1
San Pastore X Scout 66	19	18	1
San Pastore X Parker	20	18	2
San Pastore X Triumph 64	20	17	3
San Pastore X Bezostaia 1	19	20	-1
Sturdy X Scout 66	18	18	0
Sturdy X Bezostaia 1	21	20	1
Sturdy X Parker	20	19	1
Sturdy X Triumph 64	19	17	2
Bezostaia 1 X Triumph 64	21	21	0
Bezostaia 1 X Parker	21	20	1
Bezostaia 1 X Scout 66	21	19	2
Triumph 64 X Parker	21	18	3
Triumph 64 X Scout 66	19	20	-1
Parker X Scout 66	19	18	1
Treatment Mean	19.48	18.81	0.67 ($\bar{d}$)

$s_{\bar{d}}$	0.42
t (calculated as $\bar{d}/s_{\bar{d}}$)	1.58 ns
t.05, 40 df	2.02
t.01, 40 df	2.70

ns No significant difference between the treatment means. The calculated "t" value is less than the tabulated t.05 or t.01 values for 40 degrees of freedom.

TABLE XXVIII

THE EFFECT OF DAY LENGTH ON NUMBER OF SEEDS PER SPIKE OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN THE FIELD, 1971-72

Designation	Short Day (SD) Mean	Long Day (LD) Mean	Difference SD-LD
Scout 66	34	30	4
Triumph 64	34	39	-5
Parker	26	35	-9
Sturdy	41	50	-9
San Pastore	23	34	-11
Bezostaia 1	31	44	-13
San Pastore X Parker	35	35	0
San Pastore X Sturdy	68	50	18
San Pastore X Triumph 64	29	31	-2
San Pastore X Scout 66	36	38	-2
San Pastore X Bezostaia 1	28	43	-15
Sturdy X Parker	42	39	3
Sturdy X Bezostaia 1	41	48	-7
Sturdy X Triumph 64	31	40	-9
Sturdy X Scout 66	30	39	-9
Bezostaia 1 X Scout 66	31	32	-1
Bezostaia 1 X Triumph 64	33	39	-6
Bezostaia 1 X Parker	33	40	-7
Triumph 64 X Parker	30	37	-7
Triumph 64 X Scout 66	23	35	-12
Parker X Scout 66	26	28	-2
Treatment Mean	33.57	38.38	-4.81 ($\bar{d}$)
$s_{\bar{d}}$	2.46		
t (calculated as $\bar{d}/s_{\bar{d}}$)	-1.99 ns		
t.05, 40 df	2.02		
t.01, 40 df	2.70		

ns No significant difference between the treatment means. The calculated "t" value is less than the tabulated t.05 or t.01 values for 40 degrees of freedom.

TABLE XXIX

THE EFFECT OF DAY LENGTH ON YIELD (GMS) PER PLANT OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN THE FIELD, 1971-72

Designation	Short Day (SD) Mean	Long Day (LD) Mean	Difference SD-LD
San Pastore	3.50	4.13	-0.63
Bezostaia 1	5.00	8.26	-3.26
Sturdy	8.50	13.75	-5.25
Triumph 64	6.00	13.38	-7.38
Scout 66	4.00	12.13	-8.13
Parker	3.40	11.88	-8.48
San Pastore X Triumph 64	6.10	8.25	-2.15
San Pastore X Sturdy	8.60	12.25	-3.65
San Pastore X Parker	5.60	10.00	-4.40
San Pastore X Bezostaia 1	3.60	8.50	-4.90
San Pastore X Scout 66	5.30	12.00	-6.70
Sturdy X Triumph 64	8.00	12.50	-4.50
Sturdy X Scout 66	8.30	15.88	-7.58
Sturdy X Parker	8.30	16.88	-8.58
Sturdy X Bezostaia 1	5.00	14.00	-9.00
Bezostaia 1 X Triumph 64	7.50	12.13	-4.63
Bezostaia 1 X Parker	5.30	12.13	-6.83
Bezostaia 1 X Scout 66	6.70	13.55	-6.85
Triumph 64 X Scout 66	5.70	11.38	-5.68
Triumph 64 X Parker	6.00	13.13	-7.13
Parker X Scout 66	4.00	12.13	-8.13
Treatment Mean	5.93	11.62	-5.69 ($\bar{d}$)
$s_{\bar{d}}$	0.74		
t (calculated as $\bar{d}/s_{\bar{d}}$)	-7.62**		
t.05, 40 df	2.02		
t.01, 40 df	2.70		

**Highly significant difference between the treatment means. The calculated "t" value exceeds the tabulated t.05 and t.01 values for 40 degrees of freedom.

Experiment II

Results and Discussion

The effects of photoperiod on the nine traits of the diallel cross parents and F_1 hybrids measured in the growth chamber study (Experiment II) are presented in Tables XXX thorugh XXXVIII.

Days to Head

There was an overall highly significant difference for days to heading due to day length treatments as indicated by the t test (Table XXX). In all genotypes, heading date was prolonged under short day treatment. Of the parents, Parker and Scout 66 were the most affected by day length. These two varieties behaved as strongly sensitive types and respectively took 90 days and 96 days more to head under short days than under long days. On the other hand, San Pastore, Bezostaia 1 and Sturdy behaved as insensitive types, requiring respectively only 17, 20 and 26 extra days to head under short days, as compared to long days. Triumph 64 was intermediate; the difference in days to head due to photoperiod treatment was 34 days. The hybrids were intermediate to their parents in response to day length but generally inclined more toward the earlier parent. However, the hybrid, San Pastore X Sturdy headed earlier than the early parent while Parker X Scout 66 headed later than the late parent.

Days to Mature

Highly significant differences occurred for days to mature under long and short day treatments (Table XXXI). Just as in days to heading,

TABLE XXX

THE EFFECT OF DAY LENGTH ON DAYS TO HEAD OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN CONTROLLED ENVIRONMENT CHAMBERS

Designation	Short Day (SD) Mean	Long Day (LD) Mean	Difference SD-LD
San Pastore	102	85	17
Bezostaia 1	134	114	20
Sturdy	125	99	26
Triumph 64	139	100	39
Parker	193 (4)	103	90
Scout 66	200 (4)	104	96
San Pastore X Sturdy	106	97	9
San Pastore X Bezostaia 1	115	100	15
San Pastore X Triumph 64	110	91	19
San Pastore X Parker	130	98	32
San Pastore X Scout 66	122 (3)	90	32
Sturdy X Bezostaia 1	123	106	17
Sturdy X Triumph 64	120	100	20
Sturdy X Parker	129	102	27
Sturdy X Scout 66	130	100	30
Bezostaia 1 X Triumph 64	128	101	27
Bezostaia 1 X Parker	141	111	30
Bezostaia 1 X Scout 66	132	103	29
Triumph 64 X Parker	133	96	37
Triumph 64 X Scout 66	158	97	61
Parker X Scout 66	227 (2)	106	121
Treatment Mean	137.93	100.06	37.87 ($\bar{d}$)
$s_{\bar{d}}$	7.09		
t (calculated as $\bar{d}/s_{\bar{d}}$)	5.34**		
t.05, 40 df	2.02		
t.01, 40 df	2.70		

**Highly significant difference between the treatment means. The calculated "t" value exceeds the tabulated t.05 and t.01 for 40 degrees of freedom.

Number in parenthesis indicates number of replications a particular mean represents. Unless indicated each mean represents 5 replications.

TABLE XXXI

THE EFFECT OF DAY LENGTH ON DAYS TO MATURE OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN CONTROLLED ENVIRONMENT CHAMBERS

Designation	Short Day (SD) Mean	Long Day (LD) Mean	Difference SD-LD
San Pastore	151	117	34
Bezostaia 1	186	150	86
Sturdy	183	145	38
Triumph 64	176	138	38
Parker	257 (4)	139	118
Scout 66	275 (4)	141	134
San Pastore X Bezostaia 1	169	143	26
San Pastore X Sturdy	172	135	37
San Pastore X Triumph 64	167	127	40
San Pastore X Parker	180	140	40
San Pastore X Scout 66	174 (3)	120	54
Sturdy X Bezostaia 1	175	146	29
Sturdy X Triumph 64	177	140	37
Sturdy X Scout 66	183	146	37
Sturdy X Parker	180	139	41
Bezostaia 1 X Parker	191	152	39
Bezostaia 1 X Triumph 64	181	141	40
Bezostaia 1 X Scout 66	186	141	45
Triumph 64 X Parker	188	134	54
Triumph 64 X Scout 66	207	137	70
Parker X Scout 66	290 (2)	149	141
Treatment Mean	192.72	139.04	53.68 ($\bar{d}$)
$s_{\bar{d}}$	8.09		
t (calculated as $\bar{d}/s_{\bar{d}}$)	6.63**		
t.05, 40 df	2.02		
t.01, 40 df	2.70		

**Highly significant difference between the treatment means. The calculated "t" value exceeds the tabulated t.05 and t.01 values for 40 degrees of freedom.

Number in parenthesis indicates number of replications a particular mean represents. Unless indicated each mean represents 5 replications.

all the entries took a longer time to mature under short days. Moreover, the sequence in maturity exhibited by each genotype was similar to its sequence in heading. The hybrid, San Pastore X Bezostaia 1, which was the least affected by day length in response to heading was also the least affected in response to maturity, while Parker X Scout 66 showed the greatest response to day length both for heading and for maturity. This suggests that under controlled environment conditions both days to heading and maturity are controlled through the same photoperiod mechanism.

Plant Height

Differences in plant height were significantly different due to day length treatments (Table XXXII). Most genotypes were taller under short days. Exceptions were Parker X Bezostaia 1 and Parker X Scout 66 hybrids which were taller under long day treatment.

Tiller Number

The number of tillers per plant was also affected by photoperiod (Table XXXIII). In general, plants grown under long days produced more tillers than their counterparts under short days. However, the late heading parents (sensitive types), Parker and Scout 66 had slightly more tillers under short days, while day length showed no influence on tiller production of San Pastore (insensitive type) and Triumph 64 X Scout 66 hybrid.

Leaf Number per Plant

Leaf number per plant at heading tended to increase under long day

TABLE XXXII

THE EFFECT OF DAY LENGTH ON PLANT HEIGHT (CMS) OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN CONTROLLED ENVIRONMENT CHAMBERS

Designation	Short Day (SD) Mean	Long Day (LD) Mean	Difference SD-LD
Parker	65.0 (4)	55.0	10.0
Triumph 64	80.8	69.6	11.2
Bezostaia 1	64.4	53.2	11.2
San Pastore	66.4	53.3	13.1
Sturdy	58.5	44.6	13.9
Scout 66	82.0 (4)	66.4	15.6
San Pastore X Parker	69.8	61.9	7.9
San Pastore X Scout 66	72.4 (3)	60.1	12.3
San Pastore X Triumph 64	70.1	44.9	15.2
San Pastore X Bezostaia 1	66.5	50.1	16.4
San Pastore X Sturdy	67.0	49.9	17.1
Sturdy X Parker	66.0	65.2	0.8
Sturdy X Bezostaia 1	69.4	63.4	6.0
Sturdy X Scout 66	70.7	61.3	9.4
Sturdy X Triumph 64	71.9	54.1	17.8
Bezostaia 1 X Triumph 64	80.6	73.8	6.8
Bezostaia 1 X Scout 66	70.1	62.6	7.5
Bezostaia 1 X Parker	56.0	60.1	-4.1
Triumph 64 X Parker	76.0	65.1	10.9
Triumph 64 X Scout 66	79.3	63.8	15.5
Parker X Scout 66	60.5 (2)	60.8	-0.3
Treatment Mean	69.69	59.49	10.20 ($\bar{d}$)
$s_{\bar{d}}$	2.21		
t (calculated as $\bar{d}/s_{\bar{d}}$)	4.61**		
t.05, 40 df	2.02		
t.01, 40 df	2.70		

**Highly significant difference between the treatment means. The calculated "t" value exceeds the tabulated t.05 and t.01 values for 40 degrees of freedom.

Number in parenthesis indicates number of replications a particular mean represents. Unless indicated each mean represents 5 replications.

TABLE XXXIII

THE EFFECT OF DAY LENGTH ON NUMBER OF TILLERS PER PLANT OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN CONTROLLED ENVIRONMENT CHAMBERS

Designation	Short Day (SD) Mean	Long Day (LD) Mean	Difference SD-LD
San Pastore	4	4	0
Parker	7 (4)	6	1
Scout 66	6 (4)	4	2
Bezostaia 1	3	4	-1
Triumph 64	4	6	-2
Sturdy	4	7	-3
San Pastore X Bezostaia 1	4	5	-1
San Pastore X Sturdy	5	6	-1
San Pastore X Scout 66	7 (3)	8	-1
San Pastore X Triumph 64	3	6	-3
San Pastore X Parker	7	11	-4
Sturdy X Triumph 64	5	7	-2
Sturdy X Parker	7	9	-2
Sturdy X Scout 66	4	6	-2
Sturdy X Bezostaia 1	4	8	-4
Bezostaia 1 X Scout 66	5	6	-1
Bezostaia 1 X Triumph 64	4	10	-6
Bezostaia 1 X Parker	5	13	-8
Triumph 64 X Scout 66	7	7	0
Triumph 64 X Parker	6	7	-1
Parker X Scout 66	8 (2)	11	-3
Treatment Mean	5.06	7.04	-1.98 ($\bar{d}$)
$s_{\bar{d}}$	0.59		
t^a (calculated as $\bar{d}/s_{\bar{d}}$)	-3.38**		
t.05, 40 df	2.02		
t.01, 40 df	2.70		

**Highly significant difference between the treatment means. The calculated "t" value exceeds the tabulated t.05 and t.01 values for 40 degrees of freedom.

Number in parenthesis indicates number of replication a particular mean represents. Unless indicated each mean represents 5 replications.

for most of the entries (Table XXXIV). This was especially apparent for the hybrids. The two strongly sensitive parents, Parker and Scout 66 produced more leaves under short days. Short days also increased the number of leaves in four of the hybrids.

Primary Tiller Leaf Number

On the average, primary tiller leaf number at heading was significantly different under long day and short day treatments (Table XXXV). However, day length had no effect on primary tiller leaf number of San Pastore, Sturdy, Triumph 64 and San Pastore X Triumph 64 hybrid. Long days favored more leaf production on primary tillers of the remaining wheat genotypes including the sensitive parents, Parker and Scout 66.

Spike Length

As indicated by the t value (Table XXXVI), there was a significant difference in spike length among entries due to day length. The two insensitive parents, San Pastore and Bezostaia 1, as well as all hybrids derived from them produced longer spikes under long days. The short day treatment resulted in slightly longer spikes in the sensitive parents, Parker and Scout 66.

Spikelet Number

Highly significant differences among entries for number of spikelets were also observed (Table XXXVII). Most genotypes produced more spikelets under long days. Exceptions were Triumph 64 X San Pastore, Triumph 64 X Parker and Triumph 64 X Scout 66 hybrids which had slightly

TABLE XXXIV

THE EFFECT OF DAY LENGTH ON NUMBER OF LEAVES PER PLANT OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN CONTROLLED ENVIRONMENT CHAMBERS

Designation	Short Day (SD) Mean	Long Day (LD) Mean	Difference SD-LD
San Pastore	11	12	-1
Triumph 64	17	22	-5
Bezostaia 1	13	21	-8
Sturdy	18	17	1
Parker	23 (4)	21	2
Scout 66	24 (4)	22	2
San Pastore X Scout 66	26 (3)	22	4
San Pastore X Sturdy	16	17	-1
San Pastore X Bezostaia 1	14	18	-4
San Pastore X Triumph 64	15	23	-8
San Pastore X Parker	32	41	-9
Sturdy X Triumph 64	22	23	-1
Sturdy X Scout 66	22	25	-3
Sturdy X Bezostaia 1	16	33	-17
Sturdy X Parker	30	50	-20
Bezostaia 1 X Scout 66	21	18	3
Bezostaia 1 X Triumph 64	14	39	-25
Bezostaia 1 X Parker	23	56	-33
Triumph 64 X Scout 66	31	28	3
Triumph 64 X Parker	26	22	4
Parker X Scout 66	26 (2)	27	-1
Treatment Mean	21.02	26.81	-5.79 ($\bar{d}$)
$s_{\bar{d}}$	2.77		
t (calculated as $\bar{d}/s_{\bar{d}}$)	-2.09*		
t.05, 40 df	2.02		
t.01, 40 df	2.70		

*Significant difference between the treatment means at the .05 level of probability. The calculated "t" value exceeds the tabulated t.05 value for 40 degrees of freedom.

Number in parenthesis indicates number of replications a particular mean represents. Unless indicated each mean represents 5 replications.

TABLE XXXV

THE EFFECT OF DAY LENGTH ON NUMBER OF PRIMARY TILLER LEAVES OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN CONTROLLED ENVIRONMENT CHAMBERS

Designation	Short Day (SD) Mean	Long Day (LD) Mean	Difference SD-LD
San Pastore	6	6	0
Sturdy	5	5	0
Triumph 64	5	5	0
Bezostaia 1	5	6	-1
Scout 66	5(4)	6	-1
Parker	4(4)	6	-2
San Pastore X Triumph 64	6	6	0
San Pastore X Sturdy	6	4	2
San Pastore X Bezostaia 1	5	6	-1
San Pastore X Parker	5	6	-1
San Pastore X Scout 66	5(3)	6	-1
Sturdy X Bezostaia 1	6	6	-1
Sturdy X Triumph 64	5	6	-1
Sturdy X Scout 66	5	6	-1
Sturdy X Parker	5	7	-2
Bezostaia 1 X Triumph 64	5	6	-1
Bezostaia 1 X Parker	4	6	-1
Bezostaia 1 X Scout 66	4	6	-1
Triumph 64 X Parker	5	6	-1
Triumph 64 X Scout 66	5	7	-2
Parker X Scout 66	4(2)	5	-1
Treatment Mean	4.99	5.62	-0.63 ($\bar{d}$)
$s_{\bar{d}}$	0.19		
t (calculated as $\bar{d}/s_{\bar{d}}$)	-3.23**		
t.05, 40 df	2.02		
t.01, 40 df	2.70		

**Highly significant difference between the treatment means. The calculated "t" values exceed the tabulated t.05 and t.01 values for 40 degrees of freedom.

Number in parenthesis indicates number of replications of a particular mean represents. Unless indicated each mean represents 5 replications.

TABLE XXXVI

THE EFFECT OF DAY LENGTH ON SPIKE LENGTH (CMS) OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN CONTROLLED ENVIRONMENT CHAMBERS

Designation	Short Day (SD) Mean	Long Day (LD) Mean	Difference SD-LD
Triumph 64	8.8	8.7	0.1
Parker	8.7 (4)	8.3	0.4
Scout 66	9.9 (4)	9.5	0.4
Bezostaia 1	8.0	8.7	-0.7
San Pastore	5.4	6.9	-1.5
Sturdy	7.3	8.8	-1.5
San Pastore X Scout 66	9.2 (3)	9.1	0.1
San Pastore X Parker	8.3	8.4	-0.1
San Pastore X Triumph 64	6.9	7.7	-0.8
San Pastore X Bezostaia 1	6.9	8.4	-1.5
San Pastore X Sturdy	7.0	8.5	-1.5
Sturdy X Triumph 64	7.0	8.2	-1.2
Sturdy X Scout 66	7.9	9.7	-1.8
Sturdy X Parker	7.6	9.7	-2.1
Sturdy X Bezostaia 1	7.8	10.9	-3.1
Bezostaia 1 X Triumph 64	9.1	10.3	-1.2
Bezostaia 1 X Scout 66	8.4	9.7	-1.3
Bezostaia 1 X Parker	5.9	9.9	-4.0
Triumph 64 X Parker	8.7	8.0	0.7
Triumph 64 X Scout 66	9.5	8.5	1.0
Parker X Scout 66	10.2 (2)	8.7	1.5
Treatment Mean	8.03	8.89	-0.86 ($\bar{d}$)
$s_{\bar{d}}$	0.34		
t (calculated as $\bar{d}/s_{\bar{d}}$)	-2.52*		
t.05, 40 df	2.02		
t.01, 40 df	2.70		

*Significant difference between treatment means at the .05 level of probability. The calculated "t" exceeds the tabulated t.05 value for 40 degrees of freedom.

Number in parenthesis indicates number of replications a particular mean represents. Unless indicated each mean represents 5 replications.

TABLE XXXVII

THE EFFECT OF DAY LENGTH ON SPIKELET NUMBER PER SPIKE OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN CONTROLLED ENVIRONMENT CHAMBERS

Designation	Short Day (SD) Mean	Long Day (LD) Mean	Difference SD-LD
Triumph	16	17	-1
Parker	16	18	-2
San Pastore	13	16	-3
Sturdy	13	17	-4
Bezostaia 1	19	24	-5
Scout 66	12(4)	17	-5
San Pastore X Scout 66	16(3)	16	0
San Pastore X Triumph 64	16	15	1
San Pastore X Parker	17	18	-1
San Pastore X Sturdy	14	17	-3
San Pastore X Bezostaia 1	14	21	-7
Sturdy X Triumph 64	13	16	-3
Sturdy X Parker	15	19	-4
Sturdy X Scout 66	14	18	-4
Sturdy X Bezostaia 1	15	23	-8
Bezostaia 1 X Scout 66	17	18	-1
Bezostaia 1 X Triumph 64	18	20	-2
Bezostaia 1 X Parker	13	21	-8
Triumph 64 X Parker	16	15	1
Triumph 64 X Scout 66	16	15	1
Parker X Scout 66	11(2)	16	-5
Treatment Mean	14.81	17.79	-2.98 ($\bar{d}$)
$s_{\bar{d}}$	0.74		
t (calculated as $\bar{d}/s_{\bar{d}}$)	-4.04**		
t.05, 40 df	2.02		
t.01, 40 df	2.70		

**Highly significant difference between the treatment means. The calculated "t" value exceeds the tabulated t.05 and t.01 values for 40 degrees of freedom.

Number in parenthesis indicates number of replications a particular mean represents. Unless indicated each mean represents 5 replications.

more spikelets under short days, and the hybrid, San Pastore X Scout 66, which was not affected by day length.

Seed Number

Over all, the differences for number of seeds produced under long days and short days were not statistically significant (Table XXXVIII). However, Bezostaia 1 and Sturdy, and the hybrids, San Pastore X Sturdy, San Pastore X Triumph 64, San Pastore X Bezostaia, and Triumph 64 X Sturdy, had more seeds under short days while in fact they had more spikelets under long day, suggesting that more spikelets does not necessarily mean more seeds. This situation could occur when the spikelets under long days have more sterile florets or simply fewer florets per spikelet to start with, or if the spikelets under short days have fertile multiple florets. In this case, sterile florets under long days were unlikely to have caused the low seed number since the above wheat genotypes were more or less insensitive to day length. Therefore, either of the other two alternatives could have accounted for the increase in seed number under short day treatment.

In contrast, San Pastore, Triumph 64, Parker, Scout 66, and Parker X Scout 66 produced more seeds under long days, and also produced more spikelets under long days. However, the hybrids, Triumph 64 X Parker and Triumph 64 X Scout 66 had more seeds under long days although they had more spikelets under short days. The low seed set under short days could have been partially due to sterile florets as evidenced from Parker X Scout 66 hybrid which produced no seed under this photoperiod treatment.

TABLE XXXVIII

THE EFFECT OF DAY LENGTH ON SEED NUMBER PER SPIKE OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN CONTROLLED ENVIRONMENT CHAMBERS

Designation	Short Day (SD) Mean	Long Day (LD) Mean	Difference SD-LD
Bezostaia 1	21	19	2
Sturdy	23	17	6
Triumph 64	25	27	-2
Parker	7 (4)	15	-8
San Pastore	18	29	-11
Scout 66	3	16	-13
San Pastore X Scout 66	20 (3)	12	8
San Pastore X Triumph 64	25	15	10
San Pastore X Sturdy	23	13	10
San Pastore X Bezostaia	24	13	11
San Pastore X Parker	23	25	-2
Sturdy X Triumph 64	22	15	7
Sturdy X Scout 66	19	20	-1
Sturdy X Bezostaia 1	26	37	-11
Sturdy X Parker	12	31	-19
Bezostaia 1 X Scout 66	9	10	-1
Bezostaia 1 X Triumph 64	26	31	-5
Bezostaia 1 X Parker	1	24	-23
Triumph 64 X Parker	17	19	-2
Triumph 64 X Scout 66	2	10	-8
Parker X Scout 66	0 (2)	12	-12
Treatment Mean	16.55	19.59	-3.04 ($\bar{d}$)
$s_{\bar{d}}$	2.63		
t (calculated as $\bar{d}/s_{\bar{d}}$)	-1.15 ns		
t.05, 40 df	2.02		
t.01, 40 df	2.70		

ns No significant difference between the treatment means. The calculated "t" is less than the tabulated t.05 or t.01 values for 40 degrees of freedom.

Number in parenthesis indicates number of replications represented by a particular mean. Unless indicated each mean represents 5 replications.

Comparisons of Photoperiod Effects for Characters Evaluated Under Both Experiment I and Experiment II

The relative response of the wheat parents with respect to photoperiod effects on days to heading was similar both in the field (Experiment I) and in the growth chambers (Experiment II). The response ranking of the parents in the growth chamber study was in complete agreement with that of the field study with the exception of Sturdy and Bezostaia 1 (Tables XXII and XXX). In the field study, Sturdy was rated as being more insensitive than Bezostaia 1, while in the growth chamber study they were switched. An examination of the response of the hybrids in both studies would suggest that on the basis of breeding behavior, Sturdy is more insensitive than Bezostaia 1.

As in all typical photoperiod studies, short days delayed heading of the wheat genotypes. However, the days required for heading under short days in Experiment II were much longer than in Experiment I. This might be ascribed to the uniform environment which the plants encountered in the growth chambers. Although, light and temperature in the growth chambers were different for day and night periods, conditions were uniform during these periods. This, of course, was not the case under field conditions.

The effect of photoperiod on the wheat genotypes for days to maturity in Experiment II was similar to Experiment I (Tables XXIII and XXXI). Just as in days to heading, all entries took a longer time to mature under short days.

No significant difference in plant height due to day length was observed in Experiment I (Table XXIV) while a highly significant difference was shown in Experiment II (Table XXXII). In both experiments, most genotypes tended to grow taller under short days. The Parker X Scout 66 hybrid, a strongly insensitive genotype was an exception in both experiments; it was taller under long days. In general, all plants in the growth chamber study were shorter than those in the field study. This was to be expected since the soil environment of the roots was restricted due to their culture in pots.

The number of tillers produced in Experiment II was affected by photoperiod treatments while no such effect was observed in Experiment I (Tables XXV and XXXIII). In Experiment II, long days were conducive to high tiller production in most genotypes. However, in both experiments, the sensitive genotype Scout 66 produced more tillers under short days.

In Experiment II, there was a significant difference in spike length of the wheat genotypes due to day length (Table XXXVI). In general, long days seemed to favor longer spikes in most genotypes. Exceptions were the insensitive parents which had longer spikes under short days. On the other hand, day length had no significant effect on spike length in Experiment I (Table XXVI), although there was a trend toward longer spikes under short days for most genotypes. In both experiments, the insensitive parents had longer spikes under short days, except for Bezostaia 1 which produced longer spikes under long days.

Day length had a significant effect on spikelet number in Experiment II (Table XXXVII). In general, most genotypes produced higher spikelet number under long days. In Experiment I (Table XXVII), there was a trend of slight increase in spikelet number under short days. However in both experiments, long days favored higher spikelet number in the sensitive parent, Scout 66 and the insensitive parent Bezostaia 1.

Seed number was not significantly affected by day length (Tables XXVIII and XXXVIII). However, most genotypes including those that had higher spikelet number under short days showed a tendency to produce slightly more seeds under long days, indicating that some of the florets were sterile under short days. This was especially evident in the growth chamber study (Experiment II).

In general, comparisons of the results of Experiment I and Experiment II indicated that there was a good relationship between the field study and growth chamber study. However, it should be noted that the photoperiod effects on tiller number, spike length and spikelet numbers were inconsistent, therefore, more photoperiod studies are needed to determine the repeatability of the responses observed in this study.

CHAPTER V

SUMMARY AND CONCLUSIONS

Experiment I

Six winter wheat varieties of diverse origin and differeing in their response to day length were crossed in a diallel mating system to produce the 15 possible F_1 hybrid combinations, excluding the reciprocals. The purpose of the study was to determine the response and mode of inheritance of yield and yield-related traits in a diallel cross of winter wheat with special reference to the effects of long and short photoperiod treatments.

The study was conducted in the field at the Agronomy Research Station, in Stillwater, under long and short photoperiod conditions during the 1971-72 growing season. Plants in the long photoperiod were grown under natural full day length at Stillwater while those in the short photoperiod received only 9 hours of the day light.

During the course of the experiments data were recorded on the various plant characters in each nursery. Finally the data for each trait were analyzed separately to determine the effects of photoperiod and its mode of inheritance in the parental varieties. The genetic analyses were based on the method proposed by Jinks and Hayman. Simple correlation coefficients among yield components and other traits were also calculated.

The analyses of variance of each trait for the parents and hybrids in the long day and short day nursery indicated that there were significant differences among the entries.

The genetic components of variation (D, H_1, H_2 and F) were computed for each trait in the two nurseries. Based on the estimates of these parameters, genetic ratios were calculated so as to determine the genetic system involved in each trait.

Both under long and short days, estimates of additive effect (D) and dominance effects (H_1 and/or H_2) were significant for spike length, indicating that additive and dominance gene effects were important. For tiller number, estimates of additive effects (D) were significant, indicating that additive gene effects were more important than dominance gene effects. For spikelets per spike, seeds per spike and yield per plant, the estimates were inconsistent in long day vs short day comparisons. Days to heading, days to maturity, and plant height were evaluated only under long days. The estimates for days to heading showed that both additive and dominance effects were important while estimates for plant height and days to maturity indicated that additive gene effects were more important than dominance effects.

Based on the above genetic estimators further investigation of the genetic system for each trait under long days and short days were conducted. For tiller number, estimates of degree of dominance changed from partial dominance under long days to estimates of overdominance under short days, indicating that day length had an influence on the degree of dominance in the trait. The heritability estimates were also larger under long days than under short days.

Estimates of degree of dominance for spike length were not affected by day length; however, a lower estimate of heritability was obtained from the short day treatment. On the other hand, estimates of degree of dominance for spikelet number changed from partial dominance under long days to complete dominance under short days while a higher heritability estimates were obtained form long days.

For seed number estimates for degree of dominance and heritability were similar under long and short days while for yield, estimates of degree of dominance changed from partial dominance gene action under long days to no dominance gene action under short days. The estimates of heritability for yield were also lower under short days. Simple correlations among yield components and other traits indicated that in the long day trial, plant height and spike length were positively associated with yield. Days to head was also positively correlated with plant height and spike length but was negatively correlated with seeds per spike. Plant height was also negatively correlated with seeds per spike. Only one association was statistically significant in the short day trial, that being the positive correlation between spike length and tiller number. In general, the study was inconsistent and inconclusive with regards to the associations among yield and yield-related components.

With regards to the effects of photoperiod, short days prolonged both days to heading and maturity significantly in all genotypes, some more than others. San Pastore, Sturdy and Bezostaia 1 were the least affected and behaved as insensitive types, while Parker and Scout 66 were greatly affected by day length and behaved as strongly sensitive. Triumph 64 was intermediate in this respect. Based on the day length control of heading response, the six parents could be ranked in order of increasing sensitivity as follows: San Pastore, Sturdy, Bezostaia 1, Triumph 64, Parker and Scout 66. The response to heading of hybrids between sensitive and insensitive parents indicated that insensitivity was at least partially dominant in the F_1.

Yield per plant was also significantly affected by day length. All of the genotypes produced a higher yield under long days than under short days. Whether this was the result of the control by day length on metabolic systems within the plant leading to spikelet and seed formation is not known. It is possible that the short day treatment imposed restrictions on photosynthetic activity and altered respiration rates which subsequently resulted in a decrease in yield.

On the average, no significant difference was observed in plant height, tiller number, spike length, spikelet and seed number due to day length.

Experiment II

The same 6 winter wheat parents and their 15 F_1 hybrids that were used in Experiment I were also involved in Experiment II. The purpose of the experiment was to study the effects of long and short photoperiods on the parents and their F_1 hybrids in controlled environmental growth chambers.

The light source was a combination of inflorescent and incandescent bulbs with light intensity of about 3500 foot candles. Conditions of the short day test were 10 hours of light and 14 hours of darkness. The temperature inside the chamber was maintained at 75^{o}F during the light period and 65^{o}F during the dark period. The long day test had exactly the same conditions except that it provided 16 hours of light and 8 hours of darkness.

Two identical sets of vernalized seedlings of each of the 21 wheat genotypes (6 parents and their 15 F_1 hybrids) were transplanted to 4-inch pots, in 5 replications of 1 plant each. One set was grown in the short day growth chamber while the other set was grown in the long day chamber. In each chamber, the pots were arranged in a randomized complete block design.

Observations were made on various plant characters. The effects of long and short day treatments were determined using the means of the traits measured. The results indicated that all the traits studied, excpet for seed number per spike, were affected significantly by day length. Short days prolonged days to heading and days to maturity in all wheat genotypes. San Pastore, Sturdy and Bezostaia 1 were the least affected and behaved as insensitive types, while Parker and Scout 66 were sensitive to day length and required a longer time to head and/or mature. Triumph 64 was intermediate in this respect. On the other hand, the hybrids were intermediate to the parents but generally inclined toward the earlier parent. The heading response of the genotypes to the day length treatments imposed in the growth chamber was similar to that observed in the field study. Most of the wheat genotypes were also taller under short days.

With regards to tiller number, most genotypes tended to produce more tillers under long days. However, the two sensitive parents, Parker and Scout 66, had slightly more tillers under short days than under long days.

Total leaf number per plant increased under long day for most of the wheat genotypes, while short days favored more leaf production for Parker and Scout 66. On the other hand, the primary tiller leaf number, for most genotypes including Parker and Scout 66 increased under long days. Exceptions were San Pastore, Sturdy, Triumph 64 and the Triumph 64 X San Pastore hybrid whose leaf number of the primary tiller was not affected by day length.

The two insensitive parents, San Pastore and Bezostaia 1 had longer spikes under long days while Parker, Scout 66, Triumph 64 as well as the hybrids between them produced longer spikes under short days. The number of spikelets per spike in most wheat genotypes, including Parker and Scout 66 were greater under long days. A similar trend was also shown for seed number. Low seed production under short day by some genotypes appeared to be associated with sterile florets. This was quite evident in Parker X Scout hybrid which produced no seed under short days.

The effects of photoperiod on winter wheat observed in this experiment were parallel to those found by other workers (4, 5, 15, 19, 24, 27, 31, 32, 33, 37), utilizing spring wheats. However, in addition this study showed that spike length in winter wheat was affected by day length.

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APPENDIX

TABLE XXXIX

ANALYSIS OF VARIANCE OF $(W_r - V_r)$ VALUES OF VARIOUS TRAITS OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN THE LONG DAY FIELD STUDY, 1971-72

		Traits							
Source	df	Days to Head	Days to Head	Plant Height	Tiller Number	Spike Length	Spikelets/ Spike	Seeds Spike	Yield Plant
Arrays[1]	5	3.0536**	122.0155	325.0557	35.0103	0.0118	0.1650	133.6308	15.7401
Replications	5	1.4207*	156.2544	245.4410	56.4076**	0.0206*	0.3698**	298.4099*	7.4906
Error	25	0.4509	61.4181	183.9048	6.8365	0.0078	0.0915	103.9431	8.6968

*,**Significantly different at the .05 and .01 levels of probability, respectively

[1]Nonsignificant differences of arrays indicate that all the assumptions of diallel analysis for the trait are fulfilled, while significant differences of arrays indicate that one or more of the hypothesis are not valid for that particular trait.

TABLE XL

ANALYSIS OF VARIANCE OF (W_r-V_r) VALUES OF VARIOUS TRAITS OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN THE SHORT DAY FIELD STUDY, 1971-72

Source	df	Tiller Number	Spike Length	Spikelets/ Spike	Seeds/ Spike	Yield Plant
Arrays[1]	5	255.3616	0.4393	4.3262**	1919.2065*	21.0930
Plant Number	7	2331.4235*	0.5283	5.6065**	2030.4999*	50.2892
Error	35	353.9838	0.2411	1.7231	887.6863	22.5335

*,**Significantly different at the .05 and .01 levels of probability, respectively.

[1]Nonsignificant differences of arrays indicate that all the assumptions of diallel analysis for the trait are fulfilled while significant differences of arrays indicate that one or more of the hypothesis are not valid for that particular trait.

TABLE XLI

$(W_r\ W'_r)$ REGRESSION COEFFICIENTS OF THE VARIOUS TRAITS OF THE PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN THE LONG DAY FIELD STUDY, 1971-72

Trait	Coefficient[1]	95% Confidence Limits
Days to Head	2.062	1.895 - 2.229
Days to Mature	1.813	1.260 - 2.366
Plant Height	2.475	1.891 - 3.059
Tiller Number/Plant	1.863	1.567 - 2.159
Spike Length	1.538	1.285 - 1.791
Spikelets/Spike	1.828	1.544 - 2.112
Seeds/Spike	1.038	0.534 - 1.538
Yield/Plant	0.851	0.257 - 1.445

[1]The regression coefficient of a particular trait is expected to be significantly different from zero but not significantly different from 0.5 if the assumptions of diallel analysis for the trait are valid.

TABLE XLII

(W_r, W'_r) REGRESSION COEFFICIENTS OF THE VARIOUS TRAITS OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN THE SHORT DAY FIELD STUDY, 1971-72

Trait	Coefficient[1]	95% Confidence Limits
Tiller Number/Plant	1.621[1]	1.040 - 2.202
Spike Length	2.419	1.888 - 2.944
Spikelets/Spike	1.188	0.812 - 1.564
Seeds/Spike	1.352	0.354 - 2.351
Yield/Plant	1.911	1.401 - 2.421

[1]The regression coefficient of a particular trait is expected to be significantly different from zero but not significantly different from 0.5 if the assumptions of diallel analysis for the trait are valid.

TABLE XLIII

(V_r, W_r) REGRESSION COEFFICIENTS OF THE VARIOUS TRAITS OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN THE LONG DAY FIELD STUDY, 1971-72

Trait	Coefficient[1]	95% Confidence Limits
Days to Head	1.073	1.006 - 1.140
Days to Mature	0.472	0.194 - 0.750
Plant Height	0.558	0.258 - 0.858
Tiller Number/Plant	0.763	0.469 - 1.057
Spike Length	0.790	0.723 - 1.217
Seeds/Spike	0.363	(-0.025)--0.751
Yield/Plant	0.333	0.039 - 0.627

[1]The regression coefficient of a particular trait is expected to be significantly different from zero but not from one if all the assumptions of diallel analysis for the trait are valid.

TABLE XLIV

(V_r, W_r) REGRESSION COEFFICIENTS OF THE VARIOUS TRAITS OF PARENTS AND F_1 HYBRIDS OF A DIALLEL CROSS OF WINTER WHEAT GROWN IN THE SHORT DAY FIELD STUDY, 1971-72

Trait	Coefficient[1]	95% Confidence Limits
Tiller Number/Plant	0.475	0.166 - 0.783
Spike Length	0.715	0.492 - 0.937
Spikelets/Spike	0.697	0.298 - 1.099
Seeds/Spike	0.440	0.147 - 0.733
Yield/Plant	0.298	(-0.052)- 0.648

[1]The regression coefficient of a particular trait is expected to be significantly different from zero but not from one if all the assumptions of diallel analysis for the trait are valid.

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