EARLINESS OF SEXUAL REPRODUCTION IN WHEAT AS INFLUENCED BY TEMPERATURE AND LIGHT IN RELATION TO GROWTH PHASES[1]

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INTRODUCTION

This paper deals with temperature and the photoperiod in relation to growth phases, earliness of sexual reproduction, and seasonal growth habit of the common wheat plant. In addition data are presented on the effects of two types of electric light used to lengthen the natural day in relation to the time of sexual reproduction and the number of seeds produced.

Part of the data here presented support portions of a note (*25*) [2] and of a previous paper (*27*) by the writers.

REVIEW OF LITERATURE

So far as the writers are aware, Adams (*2*) was the first to point out the importance of temperature in relation to the daily photoperiod in regulating the time of sexual reproduction in wheat. He claimed that these two factors are interchangeable. While the results of his tests suggest a compensatory relationship, they do not prove the point, since temperature was not varied concurrently with the length of the daily photoperiod. He obtained his different temperatures by conducting the tests during different periods of the year. The following year Adams (*3*) continued his study of temperature and the photoperiod, but he carried out no experiments with wheat that gave evidence on the interchangeable relationship between temperature and the photoperiod.

Enomoto (*9*) conducted experiments that showed the importance of both temperature and the photoperiod in relation to earliness in wheat and barley. The writers (*25*) presented brief data on temperature and the photoperiod and indicated their compensating relationship with respect to earliness in wheat. Maximov (*31*) indicated the same relationship with respect to wheat in a statement, but he presented no data. Hurd-Karrer (*19*) has shown the influence of temperature and the photoperiod on a spring wheat and of the photoperiod on a winter wheat. Several workers have studied temperature (*17, 21, 22*) and the photoperiod (*8, 10, 13, 30, 43*) independently in relation to the development of the wheat plant.

The majority of the environmental studies that have been conducted under controlled conditions have been managed so as to maintain as nearly constant conditions as possible throughout all the growth

[1] Received for publication June 1, 1935; issued December 1935.

[2] Reference is made by number (italic) to Literature Cited, p. 639.

phases of the plant, little or no attention being given to special requirements of the plant at different stages of development. This is the orthodox method, and while it is reasonably satisfactory for the study of certain types of plants such as the spring cereals, it is not satisfactory for many important studies on such plants as the winter cereals.

The literature shows that the temperature relations of the growth phases in winter cereals, especially the stimulating influence of low temperature during early germination on subsequent earliness in winter wheat, were recognized many years ago. However, this knowledge was not widely accepted, and it appears that these relationships have been lost sight of and rediscovered several times since the first record.

The writers (*27*) pointed out that Klippart (*23, p. 757*) knew before 1857 that low temperatures applied to germinated seed induced winter wheat when sown in the spring to mature and produce a good crop. Recently Martin [3] pointed out that this phenomenon was noted in winter wheat as early as 1837 by a grower in New York (*1*), but as irregular heading was reported by this grower it is apparent that the time of exposure to low temperatures was too short or that germination was incomplete during the period of low temperatures. In 1850 Allen (*4, p. 128*) made a similar report in his book, but he thought germination unnecessary before chilling. He was not aware that germination had started in the soaked seeds held near freezing. Klippart's report indicates that he had a better understanding of the importance of germination and of the exposure time than did those before him, but he and those before him did not seem to understand that freezing temperatures are less effective (*27*) than temperatures slightly above the freezing point. Recently this and other methods of accelerating sexual reproduction have been designated in Russia by the term "iarovization", meaning vernalization, the English equivalent. Literature and experiments on this subject are dealt with in other papers [4] (*6, 26, 28, 44*).

Hellriegal (*16*), working with barley advanced beyond the early germination stage, concluded that this plant has a lower optimum temperature during the tiller-formation phase than during the stem-elongation phase. Gassner (*15*), Maximov and Pojarkova (*33*), Pojarkova (*37*), and Papadakis (*35*) concluded from experimental data that earliness in winter wheat is favored when low temperatures obtain during the seedling stage and when higher temperatures obtain during the later stages of growth.

In studies on the photoperiod Wanser (*43*) concluded that the several growth phases of the plant have different length-of-day requirements. Rasumov (*39*) studied the influence of short days followed by long days, long days followed by short days, continued short days, and continued long days on earliness in millet, spring oats, and spring barley, and he conducted field plantings with spring wheats. No tests with winter wheat were reported. With millet Rasumov found earliness of sexual reproduction favored equally by the continued short day and by 10 short days followed by 6 long days. His data on oats and barley show that the constant long days

[3] Martin, J. H. IAROVIZATION IN FIELD PRACTICE. U. S. Dept. Agr., Bur. Plant Indus. 13 pp. 1934. [Mimeographed.]
[4] ——— Martin, J. H. See footnote 3.

favored earliness. A test carried out by Hurd-Karrer (*18*) indicated that a short day followed by a long day favored early jointing in Turkey winter wheat. The writers (*25*) presented preliminary data showing that early sexual reproduction in winter wheat is favored by an initial exposure to short days followed by long days. Maximov (*31*) drew the same conclusion but presented no data. In a later paper summarizing work on temperature and the photoperiod, Maximov (*32*) erroneously stated that the writers (*27*) found that shortening the day at the higher temperatures during the first week of growth made it possible for winter cereals to fruit the first year. The writers' studies indicate that an exposure of but 1 week is too short to induce more than an exceedingly slight acceleration of earliness in the winter wheats studied. Forster et al. (*10*) conclude that an initial short day hastens maturity in winter wheats.

In addition to the environmental studies made under controlled or semicontrolled conditions, there have been a number of studies based on date-of-seeding tests in the field, a few of which are cited (*5, 11, 14, 24, 36*).

METHODS AND TERMINOLOGY

The experiments were conducted during the winter and spring seasons in culture chambers or in greenhouses, and some tests were conducted outdoors during the summer. The plants were grown in good soil in earthen pots 8 inches in diameter. Each pot supported two plants. Care was exercised in maintaining uniform soil moisture throughout a given test by frequent applications of water.

In certain tests the seeds of Harvest Queen winter wheat were germinated and chilled at 26° to 32° F. in a dark mechanical refrigerator for several weeks before planting, as indicated.

Days longer than the natural day were obtained by means of electric lamps turned on at sunset. Except when otherwise stated, the electric source consisted of Mazda C tungsten lamps which gave an intensity ranging from 20 to 40-foot candles at the soil line. The length of the natural day was taken as from middawn to midtwilight, an increase of 1½ to 1¾ hours over a natural day length taken as from sunrise to sunset. Days longer than the natural day were computed from middawn. The 8-hour day started at 8 a. m. and ended at 4 p. m.

The initial growth phase of winter wheat, which, under cultural conditions, takes place in the autumn and winter, has commonly been referred to as the rosette phase or as the resting or dormant stage. However, it has been pointed out that this is not always a true resting stage and that a resting or a dormant condition during early growth is not essential for sexual reproduction in winter wheat (*10, 22, 42*). These conclusions are borne out by the writers' studies. In regions of very cold winters the plants are dormant during the winter period, but at Rosslyn, Va. (near Washington, D. C.), growth continues slowly throughout the winter except in an occasional year when there may be a short dormant period. In this paper this stage is referred to as the "leaf-and-internode-formation phase", and the term is applied to winter and spring varieties. Hellriegal (*16*) used a similar terminology for barley. The so-called jointing stage is designated the "stem-elongation phase."

All data on earliness are based on the date when the tip of the head reached a point as high as the ligule of the flag leaf. Fertilization occurred 2 to 4 days after heading.

Further details on methods are taken up throughout the paper under the several experiments.

EXPERIMENTAL RESULTS

TEMPERATURE AND THE PHOTOPERIOD IN RELATION TO THE GROWTH PHASES AND SEXUAL REPRODUCTION

During the winter of 1928–29 a test was conducted with Harvest Queen, a typical winter wheat. Plantings were made in a greenhouse with germinated seeds that had been held in a refrigerator for 67 days at 30° to 35° F. Unchilled germinated seeds were planted as controls. Some of the plants were exposed to the natural day, which ranged from 11 hours at the beginning of the test to 15 hours at the end, and others to a long day, ranging from 16 to 17 hours. Mazda C tungsten lamps were used for supplementing the natural day. The temperature of the greenhouse was usually about 55° to 65° F., though on bright days the temperatures went higher.[5]

Table 1 and figure 1 show that of the plants from the chilled seedlings, those under the long day headed first; of the plants from the unchilled seedling, those under the short day headed first; under both the long and the short day, the plants from the chilled seedlings headed earlier than the plants from the unchilled seedlings. This test shows the stimulating influence of low temperatures during early germination, in the absence of light, on subsequent earliness of sexual reproduction in long days with high temperatures.

TABLE 1.—*Period from planting to first heading in Harvest Queen wheat as influenced by chilling in darkness during germination and by the length of the photoperiod after chilling in comparison with plants from seed not chilled before planting*

[Seed was planted Dec. 18, 1928]

Length of daily photoperiod after planting	Germination temperature 30° to 35° F. for 67 days in darkness, followed by 55° to 65°		Germination temperature 70° F. for 4 days in darkness, followed by 55° to 65°	
	Period from planting to heading	Tillers per plant when internodes started to elongate	Period from planting to heading	Tillers per plant when internodes started to elongate
Hours	*Days*	*Number*	*Days*	*Number*
11 to 15	118	5.1	125	12.2
16 to 17	66	2.9	128	12.9

Since the length of day in the short-day series was 4 hours shorter during early growth than during later development, it seemed probable that this initial short day was a factor in the earlier heading noted in the plants from the unchilled seedlings. The following winter this relationship was studied further with Harvest Queen winter wheat and Purplestraw, a facultative wheat.[6] As stated in a note (*25*), a 7-

[5] This statement was inadvertently omitted in a previous publication (*27*).
[6] The writers have discussed the basis of distinction between spring, facultative, and winter varieties of wheat in another publication (*27*).

to 8-hour day during the early development of the plant favored earliness slightly in Harvest Queen, but this short day retarded heading slightly in Purplestraw.

During the same winter another test was carried out with Harvest Queen wheat and with Marquis, a spring wheat. The seeds were germinated but not chilled before planting. Some of the plants of

FIGURE 1.—Harvest Queen winter-wheat plants: *A* and *C*, From germinated seeds chilled at 30° to 35° F. in the dark for 67 days; *B* and *D*, from seeds that were not chilled; *A* and *B*, grown with a daily photoperiod of 11 to 15 hours; *C* and *D*, grown with a daily photoperiod of 16 to 17 hours.

each variety were grown at low temperatures in plant-culture chambers during the first 54 days, and later they were given high growing temperatures in a greenhouse. Other plants of each variety were grown at high temperatures in a greenhouse throughout the test. Short, medium, and long days were maintained during the first 54 days at the low and high temperatures (table 2).

Table 2 and figures 2 and 3 show that the longest days at the high temperatures from the beginning of growth induced the earliest heading in Marquis spring wheat (46 days) and the latest heading in Harvest Queen winter wheat (155 days). The shortest days at the low temperatures during the first 54 days induced the earliest heading in

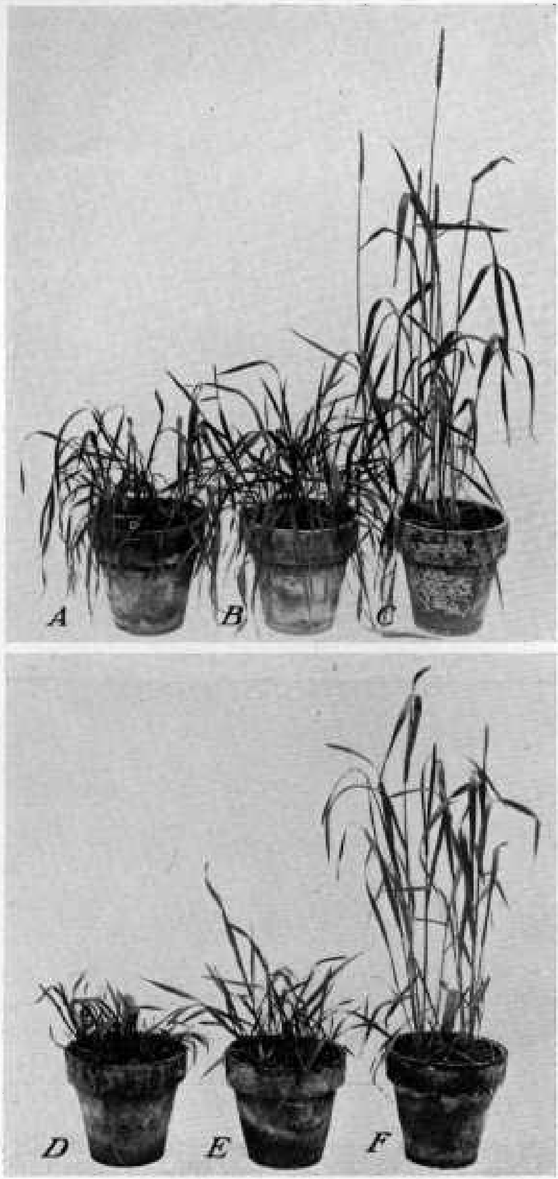

FIGURE 2.—Marquis spring-wheat plants (table 2): *A*, *B*, and *C*, Grown in a greenhouse at temperatures averaging near 70° to 75° F. and above; *D*, *E*, and *F*, grown in a culture chamber near 51° for 36 days, followed by temperatures near 59° for 18 days, followed by 70° to 75° and higher; *A* and *D*, with daily photoperiod 8 hours long for first 54 days; *B* and *E*, with daily photoperiods 12 to 14½ hours long for first 54 days; *C* and *F*, with daily photoperiods 16¼ to 17¾ hours long for first 54 days; subsequent daily photoperiods, 17¾ to 19 hours.

Harvest Queen (88 days) and the latest heading in Marquis (88 days). Fertilization started 2 to 4 days after heading in both varieties. These results, like those of Garner and Allard (*13*), indicate that Marquis spring wheat is a long-day plant with respect to earliness of sexual reproduction.

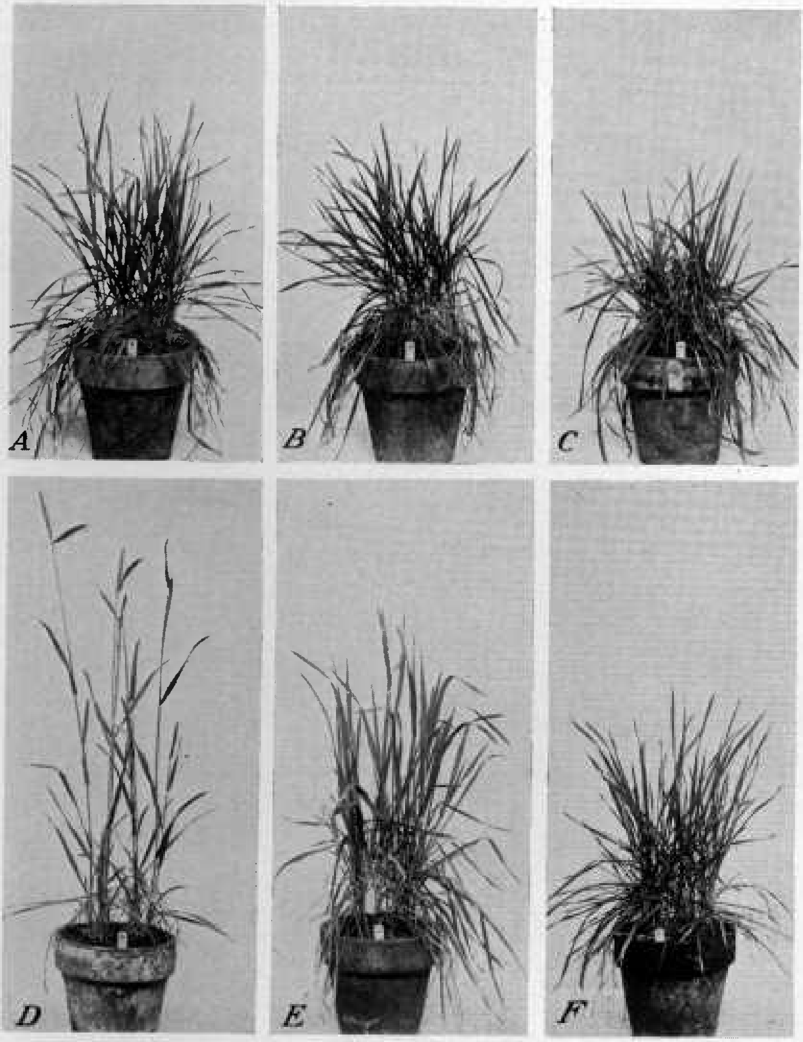

FIGURE 3.—Harvest Queen winter-wheat plants (table 2): *A*, *B*, and *C*, Grown in a greenhouse at temperatures averaging near 70° to 75° F. and above; *D*, *E*, and *F*, grown in a culture chamber near 51° for 36 days, followed by temperatures near 59° for 18 days, followed by 70° to 75° and higher; *A* and *D*, with daily photoperiod 8 hours long for first 54 days; *B* and *E*, with daily photoperiods 12 to 14½ hours long for first 54 days; *C* and *F*, with daily photoperiods 16¼ to 17¾ hours long for first 54 days; subsequent daily photoperiods, 17¾ to 19 hours.

It is evident from the data and the illustrations that the short days and the low temperatures during early growth (the leaf-and-internode-formation phase), followed by the longer days and higher temperatures, favored the earliest sexual reproduction in the winter variety, thus indicating that the early growth phase has different temperature and photoperiodic optima from those of the subsequent growth phases.

TABLE 2.—*Heading time in Marquis spring wheat and Harvest Queen winter wheat as influenced by low and high growing temperatures and by short, medium, and long daily photoperiods during the first 54 days, after which all plants received high temperatures and long days as indicated*

[Seeds were soaked and germinated for 2 days before being planted Feb. 13, 1930]

Variety and photoperiod [1]	Temperature, 51° F. for 36 days; then 59° for 18 days; subsequently 70° to 75° and above			Temperature, 70° to 75° F. for 54 days; subsequently 70° to 75° and above		
	Period from soaking of seed to heading	Tillers per plant	Heads per plant	Period from soaking of seed to heading	Tillers per plant	Heads per plant
	Days	*Number*	*Number*	*Days*	*Number*	*Number*
Marquis:						
8 hours	88	14.5	8.0	78	8.5	4.0
12 to 14½ hours	83	8.5	6.2	76	12.5	4.0
16¼ to 17¾ hours	65	8.2	7.2	46	4.5	4.0
Harvest Queen:						
8 hours	88	17.7	4.2	[2] 107	19.2	4.7
12 to 14½ hours	95	22.5	5.2	[3] 134	21.2	2.0
16¼ to 17¾ hours	[3] 114	22.5	4.7	[3] 155	22.5	3.0

[1] After 54 days all daily photoperiods were maintained at 17¾ to 19 hours.
[2] Many of the tillers on these plants did not head, but this condition was less marked than in the plants designated in footnote 3.
[3] All plants were very vegetative and heading was slow, requiring 50 to 60 days for completion in the case of some plants. On Aug. 15 some plants still were producing tillers that were jointing and heading.

It was not possible to include simultaneously a series of temperatures and photoperiods held constant or nearly so during the life cycle to serve as additional controls in this experiment. However, other tests have been carried out with Harvest Queen and similar winter wheats grown constantly near 60° F. and also at temperatures between 60° and 75° in constant long days and in constant short days. In all instances, more than 100 days to more than 200 days elapsed from planting to heading and fertilization. Tests of Hutcheson and Quantz (*21*), Klages (*22*), and Hurd-Karrer (*17*, *19*) also show that heading in winter wheat is relatively slow when the temperature requirements of the growth phases are disregarded.

An experiment was conducted with Harvest Queen winter wheat during midsummer with daily photoperiods of 8, 15, 18, and 24 hours. Each photoperiod remained unchanged throughout the test. The 8- and 15-hour days comprised sunlight only, whereas the 18- and 24-hour days comprised sunlight for 15 hours and electric light from Mazda C tungsten lamps for the remainder of the photoperiod. The seeds were soaked in water and germinated before planting, but they received no low temperatures. The plants given 18 and 24 hours of light daily headed 129 and 110 days, respectively, from the time the seeds were placed in water. No heads were produced by plants given 8 and 15 hours of light daily up to the time the test was terminated on November 11—178 days from the beginning of the test.

These results by themselves would lead to the conclusion that winter wheat is a typical long-day plant with respect to early sexual reproduction, as was concluded by Forster et al. (*10*) from similar tests, and by Hurd-Karrer and Dickson (*20*) from tests (*19*) conducted in a cool greenhouse during the winter. However, in table 2 it will be noted that Harvest Queen headed in 88 days when the plants were grown with a daily photoperiod of 8 hours at low temperatures followed by long photoperiods at high temperatures. Thus heading was 22 days earlier with this treatment than it was when continuous light and high summer temperatures obtained from germination to heading.

Under the conditions of Hurd-Karrer's (*19*) test, flowering started in Turkey winter wheat 188, 165, and 132 days from planting when grown with daily photoperiods of 8, 9½ to 15, and 17 hours, respectively, and with the temperature held at $12° \pm 1°$ C. throughout the test. With the same strain of Turkey the writers (*27*) found that flowering started 113 days from planting when moderately low temperatures and short days preceded higher temperatures and the long day. In later tests, this strain of Turkey started to flower 105 days after planting, when the temperatures and exposure periods were nearer their optima. Other varieties of winter wheat have been tested and found to head and flower sooner when suitable low temperatures and short days were followed by suitable high temperatures and long days.

The results of more than 500 dissections of many varieties of winter and spring wheats indicate that the first signs of differentiation of the floral organs become evident soon after the last leaf primordium is differentiated, and that the internodes of the stem start their major elongation a little before or simultaneously with the differentiation of the floral organs.

The number of leaves and stem internodes formed by a shoot in winter wheat as well as in spring wheat (*27*) is influenced by temperature and the photoperiod. Harvest Queen wheat has produced as few as 7 internodes[7] per shoot when fully germinated seeds were first chilled for 67 days in darkness and subsequently grown with continuous light at summer temperatures. Heading started 33 days after the completion of the chilling process. As many as 22 internodes per shoot have been produced by this variety when the seed was not chilled and when the plants were grown in uninterrupted light at warm temperatures, and under these conditions heading started 110 days after planting. Similar results were obtained when a continuous 8-hour day and warm temperatures were maintained from the beginning of germination. In field culture Harvest Queen has been observed to form 12 or 13 leaves and internodes on the primary stalk. When small numbers of internodes are formed most of them elongate, but when large numbers are formed many fail to elongate appreciably. The early cessation of the formation of leaf primordia in Harvest Queen wheat does not take place during the exposure to the low growing temperatures and short days, but during the subsequent exposure to the high temperatures and long days.

To classify accurately varieties of wheat with respect to their earliest sexual reproduction in relation to temperature and photoperiod it is necessary to determine the optimum temperatures and

[7] Only the internodes above the subcrown internode were included, and these were determined by counting the leaves.

optimum photoperiods for the formation of a reduced number of stem-internode primordia, the early differentiation of the floral primordia, the rapid elongation of the internodes, and the rapid development of the floral organs and maturity. It seems reasonable to believe that ultimately a graphic representation of the optimum temperature and photoperiod characteristic of a given variety of winter wheat can be expressed in the form of more or less smooth gradient curves. However, until more perfect methods are available, approximations must suffice.

In view of the evidence based on present methods for approximating these optima, it seems justifiable to conclude that Harvest Queen, Turkey, and similar winter wheats are not typical long-day plants with respect to their earliest sexual reproduction, but are what may be termed short-day→long-day plants, and they may be considered as low-temperature→high-temperature plants. This method of expression indicates that the temperature and the photoperiod must increase with the development of the plant in order to induce early sexual reproduction. A similar situation seems to apply to the facultative varieties and to certain late varieties commonly placed in the spring group (*27*), but in these the initial optimum temperatures are higher or the periods of exposure to low temperatures are shorter than is the case with the strictly winter varieties (*27*).

None of the above tests was planned for yield determinations. However, tiller counts are recorded in tables 1 and 2 and head counts in table 2. Conditions favoring earliness favored a reduction in the number of tillers. Observations indicated that Marquis produced larger and more completely filled heads when the initial temperatures were low. In Harvest Queen the plants receiving the initial low temperatures with the initial 8-hour day produced an average of 75 seeds per plant, and these plants were similar to the average Harvest Queen plant grown in the field. Although no seed counts were made on the remaining Harvest Queen plants, it appeared from observations that the greatest number of seeds was produced by the plants receiving the initial low temperatures with the medium length of day, and these plants were considered to exceed the normal. The continuous high temperature and the initial long day at the initial low temperatures favored a large number of tillers in Harvest Queen, but the few heads produced were relatively small and poorly filled and the plants were decidedly abnormal in all respects in comparison with the field type.

MISCELLANEOUS TESTS RELATING TO CHILLING OF SLIGHTLY GERMINATED SEED

DARKNESS V. LIGHT DURING CHILLING PERIOD

An experiment was carried out to determine if darkness during the chilling treatment has any stimulating influence on subsequent earliness. Germinated seeds of Turkey winter wheat were chilled for 61 days at 38° F. Some of the seeds were in total darkness and others received daylight. After chilling, growth continued outdoors at summer temperatures with a daily photoperiod of 17 to 18 hours. The plants from seed chilled in daylight headed 47 days after planting, and those from seed chilled in darkness headed in 49 days. From these results it seems evident that the low temperature is the stimulating agent for subsequent early heading.

Importance of Moisture and Germination During Chilling Period

An experiment was carried out with dry and with moist ungerminated seeds, with seeds that were germinated and then dried and with seeds that were germinated and kept moist during the process of chilling. All seeds were chilled for 65 days near 34° F. After being chilled the seeds were planted with an unchilled control at temperatures near 70° to 75° and photoperiods that ranged from 16 to 18 hours.

Plants from dry seeds, whether germinated or not, and from unchilled seeds had produced no heads when the test was discontinued 150 days after planting. Plants from seeds that were germinated and kept moist during the chilling process headed in 45 days. The plumules and radicles of seeds kept moist but not germinated before the beginning of the chilling process were showing slight activity at the end of the chilling treatment. Plants from these seeds started to head in 135 days, but heading was irregular.

Stage of Development of the Seed

A test was carried out with Harvest Queen seed in the soft-dough stage and in the hard-dough stage and with completely ripened seed 1 year old, to determine whether low temperatures during germination stimulate subsequent early heading in plants from seeds in the soft-dough and in the hard-dough stage. All seeds were first germinated at 60° F. and then chilled near freezing for 72 days. After chilling, growth continued at 68° to 90° with a daily photoperiod of 16 to 17½ hours. Plants from seed in the soft-dough stage headed in 43 days, those from seed in the hard-dough stage headed in 45 days, and those from the old seed headed 43 days from the date of planting, thus showing that seed in the soft-dough and hard-dough stages reacts efficiently to the chilling treatment. This permits a more rapid increase of winter-wheat populations in genetic work.

Earliness and Tiller Reduction

When germinated seeds have been chilled sufficiently, several tillers ultimately joint and produce heads relatively quickly at suitable temperatures and day lengths, thus indicating that the function altered by the low temperature is not confined entirely to the plumule (primary shoot).

It was thought that the effects of chilling on early stem elongation and heading at high temperatures might be due directly to the reduction in the number of tillers, which is correlated with the early heading of plants from chilled seedlings. If this were true, another method of reducing tillers might accelerate stem elongation and heading. To test this theory, several Harvest Queen plants from unchilled seedlings were grown outdoors during the summer of 1931. Some of these plants were allowed to grow in the usual manner, whereas others were not allowed to produce more than one shoot each, all extra shoots being cut from the plants as soon as observed. The single shoots developed very long, wide dark-green leaves and very large stems, in comparison with the unpruned plants. However, the fact that pruning did not stimulate early heading indicates that the reduced tillering in plants from chilled seedlings is not the direct cause of early heading.

Localization of the Region of the Functional Changes Induced by Low Temperatures

In an attempt to localize the region in which the functional changes occur at low temperatures, seeds of Kanred winter wheat were germinated until the roots were 2 mm long; the roots and plumules were then cut off before the initiation of the chilling process, care being taken to remove the tips and as much of these organs as possible without total destruction of the embryo. These and unmutilated seedlings were chilled near freezing in the dark for 65 days. At the completion of the process the seedlings were given continuous light at 70° to 80° F. All the mutilated seedlings headed at the same time as the unmutilated controls. It is evident, therefore, that the active region in question is not confined to the apical regions of the seminal roots, the coleoptile, or the first leaf. It is also apparent that this active region is not confined to the endosperm, because under field conditions at the Arlington Farm the endosperm frequently is completely absorbed in early autumn before the onset of cold weather, and under these conditions the winter wheat plants mature normally the following summer.

INFLUENCE OF INTENSITY OF LIGHT FROM TUNGSTEN LAMP

Since the Mazda tungsten lamp is commonly used for lengthening the natural day, a test was conducted to determine the influence of intensity of this artificial source of light during the winter and spring months. Marquis, Siberian No. 1, and Romanov spring wheats were used. Each variety was grown in earthen pots 8 inches in diameter, each pot containing two plants. The pots were placed in 3 parallel rows 12 feet long on a bench in a small glasshouse, pots containing plants of the same variety being placed in the same row.

Two 150-watt Mazda C tungsten lamps in a large reflector were placed at one end of the bench but not directly over the first pots. The plants farthest from the lamps, therefore, received less light at night than those nearest the lamps. The lamps were turned on at sundown and off at sunrise each day during the test, after which daylight only was provided, giving the plants a continuous exposure to light.

The intensity of the light from the lamps was determined during the night at three distances above each pot in the center row, as indicated in table 3. The test plate of a Macbeth illuminometer was held at right angles to the shortest distance between the light source and the center of the plate. Owing to the shape of the lamp reflector and to shadows from intervening plants, the intensities reduced more rapidly than is provided for in the inverse-square-distance law.

Care was exercised in maintaining a uniform temperature near 70° F. throughout the experiment by means of oscillating fans. As spring advanced there was a rise in temperature outdoors, but the uniformity of the temperature was maintained throughout the greenhouse.

TABLE 3.—*Influence of intensity of Mazda C tungsten lamps on 3 varieties of wheat when grown near 70° F. during the short days of winter, the tungsten source being used from sunset to sunrise, making continuous illumination*

[Test started Dec. 8, 1931]

Pot no.	Intensity of lamps at indicated heights above soil line over each pot in center row			Heading time			Culms per plant			Average final height of plants		
	4 inches[1]	18 inches[2]	28 inches[3]	Siberian No. 1	Marquis	Romanov	Siberian No. 1	Marquis	Romanov	Siberian No. 1	Marquis	Romanov
	Foot-candles	*Foot-candles*	*Foot-candles*	*Days*	*Days*	*Days*	*Number*	*Number*	*Number*	*Inches*	*Inches*	*Inches*
1	76.3	100.0	272.5	39	48	50	3	8	6	20	26	31
2	56.7	63.0	93.7	42	51	50	4	14	12	22	28	31
3	38.1	25.0	38.1	43	51	51	5	10	9	21	26	31
4	25.1	12.0	22.9	42	51	52	5	11	7	21	27	31
5	20.0	9.0	15.3	43	53	53	4	10	9	23	23	34
6	8.7	5.0	7.0	45	52	56	5	9	12	17	28	29
7	6.8	4.3	5.4	45	53	53	4	10	12	19	28	37
8	5.8	2.0	4.0	50	63	63	6	18	11	22	28	37
9	4.5	1.2	3.4	50	64	64	8	11	12	27	25	39
10	3.6	.7	2.8	52	69	69	9	8	8	21	31	42
11	3.1	.65	2.4	59	75	76	16	10	7	27	32	43
12	2.5	.5	2.0	69	91	91	14	11	10	34	33	45

[1] When this reading was made the plants did not cast a shadow on adjacent plants.
[2] When this reading was made the plants ranged from 20 to 28 inches tall, and the test plate was shaded by adjacent plants except in the case of the first plant in the row.
[3] When this reading was made the test plate was not shaded by adjacent plants.

The data in table 3 show that earliness was favored by the more intense light. In general, the differences in response of the plants became most evident when the light intensity at 28 inches above the soil line during the night period reached two foot-candles and less. Siberian No. 1 produced the least number of tillers near the lamps and the greatest number when at the greatest distance from the lamps. Tillering in the other varieties did not vary appreciably as the light intensity was varied. The final height of the plants was greatest in plants farthest from the lamps. Romanov, with slight exceptions, showed the most consistent gradual increase in height as the light intensity was reduced.

Leaf and straw sizes were greatest when the supplementing light intensity was reduced. The leaves averaged five-sixteenths of an inch wide by 11 inches long near the lamps and one-half of an inch wide by 18 inches long farthest from the lamps. The largest nodes on plants near the lamps averaged 0.107 inch in diameter, whereas those of plants growing farthest from the lamps averaged 0.175 inch in diameter.

Romanov and Marquis heads did not fill well, whereas Siberian No. 1 filled well in all intensities of light. Many heads on Marquis plants contained but two or three kernels.

The most rapid stem elongation occurred in the plants that were first to head (fig. 4), but the plants that headed last continued their growth for a longer period and at maturity were much taller than the ones that headed first (table 3).

FIGURE 4.—Romanov spring wheat grown near 70° F. with uninterrupted light during the winter and early spring months. Mazda C tungsten lamps were turned on at sunset and off at sunrise; during the day all plants received equal intensities of sunlight; during the night different plants received different intensities of light. Pots *A*, *B*, and *C* correspond to pots 1, 6, and 12 in table 3.

Although the intensity of the supplementing light influences earliness and other responses of the plant, the data presented indicate that changes did not become marked until the light intensity had changed to a relatively great extent. This is borne out also in Garner and Allard's (*12*) and Shirley's (*41*) studies with several species, and in Hurd-Karrer and Dickson's (*20*) studies with wheat.

The Mazda C tungsten lamp was compared with summer sunlight in a test with Marquis spring wheat. This variety was grown with a daily photoperiod of 15 hours outdoors during midsummer. One series received direct sunlight alone and another received 8 hours of direct sunlight supplemented by 7 hours of light from a Mazda C tungsten lamp delivering 8 to 10 foot-candles at the soil line.

Plants receiving full sunlight produced 14.2 tillers per plant and headed in 50 days, whereas those receiving both sunlight and electric light produced only 7.3 tillers per plant and headed in 46 days.

It seems likely that a reduction in the light intensity during part of the day, as well as the spectrum characteristic of the Mazda C tungsten lamp, caused the rapid completion of the vegetative period and sexual reproduction in this test. This lamp is especially strong in the yellow, orange, red, and infrared (*7*). Yellow, orange, and red have been reported to favor rapid development in certain plants (*34*, *38*).

The retarding influence of bright sunlight on plant growth has been observed by others (*40*, *41*). In the writers' tests, reducing summer sunlight to 41.3 percent reduced the heading time in Marquis to 50 days as compared with 55 days in unobstructed sunlight. Reducing the light to 27.9 percent increased the heading time to 58 days, and no heading took place when the intensity was reduced to 11.5 percent. The stems elongated most slowly in unobstructed sunlight, but the heads were more numerous and better filled than in the shaded series. Temperatures were equalized by means of fans.

COMPARISONS BETWEEN TUNGSTEN LAMP AND COOPER-HEWITT WORK LAMP

Tests were carried out for the purpose of comparing clear Mazda C tungsten lamps with a Cooper-Hewitt mercury-arc lamp having a lead-glass tube 50 inches long, as sources of light for lengthening the autumn and winter days.

The Mazda C lamp, as stated above, is especially strong in the infrared, red, and yellow, whereas the Cooper-Hewitt lamp emits yellow, green, blue, and violet, the red and orange being absent. The foot-candle intensities of the lamps were determined by means of the Macbeth illuminometer. Special screens were used in the illuminometer to procure this information for the Cooper-Hewitt lamp. Of the two factors (0.2 and 0.5) recommended for computing the foot-candle intensity of the Cooper-Hewitt lamp, the former was used. Two tungsten bulbs were used in white reflectors in order to obtain a uniformity of light distribution approaching that of the Cooper-Hewitt lamp. The plants received 8 hours sunlight and 8 hours artificial light daily. Temperatures ranged from 68° to 77° F.

Marquis spring wheat and Harvest Queen winter wheat served as test plants. Both chilled and unchilled seeds of Harvest Queen were used.

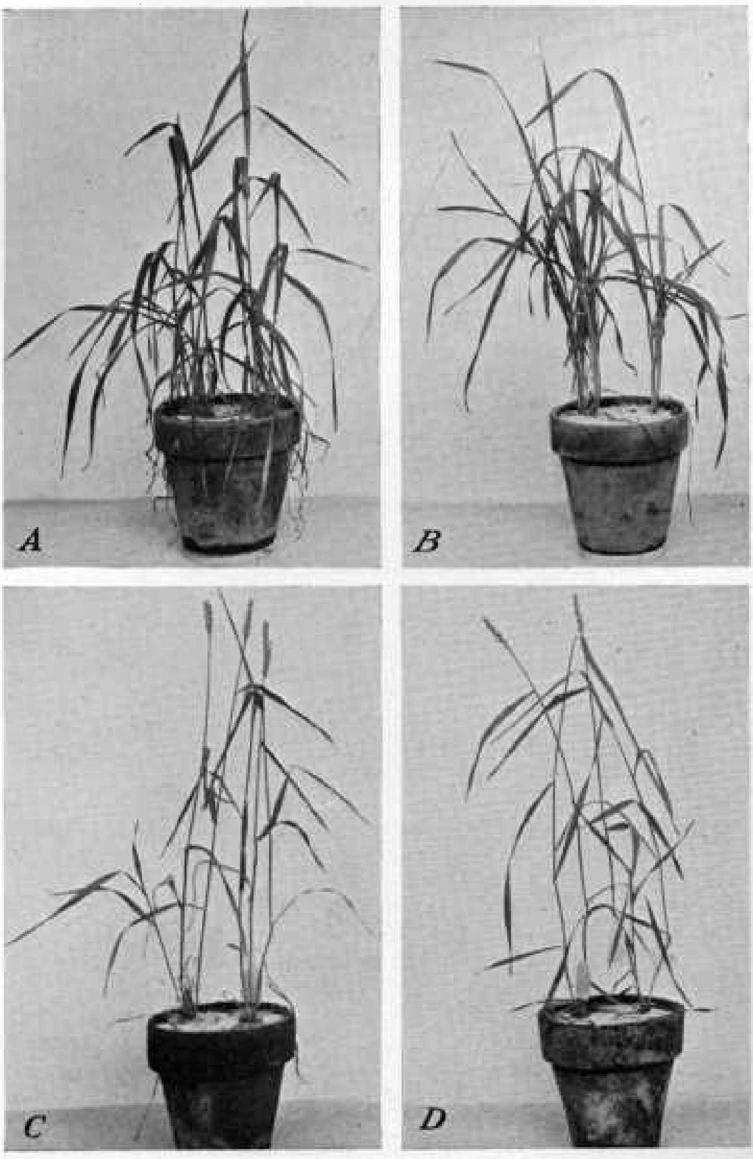

FIGURE 5.—*A* and *C*, Marquis spring wheat; *B* and *D*, Harvest Queen winter wheat from chilled seeds. *A* and *B*, grown with 8 hours of daylight and 8 hours of light from the Cooper-Hewitt mercury-arc lead-glass-tube lamp daily; *C* and *D*, grown with 8 hours of daylight and 8 hours of light from the Mazda C tungsten lamp daily.

It will be noted in table 4 and figure 5 that the tungsten source had a greater accelerating influence on the time of heading than did the Cooper-Hewitt lamp, but more tillers were produced under the Cooper-Hewitt lamp. Seed yields were not obtained, as mice destroyed some of the heads, but observations indicated that more heads and more seeds per head were produced in the plants grown under the Cooper-Hewitt lamp.

Mason (*29*), working with the date palm, observed that the Mazda lamp favored the pushing of the leaves from the growth center, whereas the Cooper-Hewitt lamp had an inhibiting influence.

TABLE 4.—*Period from planting to heading as influenced by the Mazda C tungsten lamp and the Cooper-Hewitt mercury-arc lamp with lead-glass tube, when used to supplement sunlight* [1]

[Planted Sept. 19, 1930]

Variety and treatment of germinated seed	Mazda C tungsten lamp (44.7 foot-candles)	Cooper-Hewitt lamp (69.7 foot-candles)
	Days	*Days*
Marquis:		
Seed not chilled	50	81
Harvest Queen:		
Seed chilled for 65 days	50	85
Seed not chilled	(2)	(2)

[1] Lamps operated 8 hours before sunrise, followed by sunlight alone for 8 hours. Temperatures ranged from 68° to 77° F.
[2] There was no sign of stem elongation at the end of 90 days.

Seed yields were obtained in another test, however. Marquis spring wheat and five varieties of winter wheat from chilled seedlings were grown in a greenhouse near 70° to 75° F. during late autumn and winter. For the first 36 days the natural photoperiod of about 11 hours was maintained. After this period uninterrupted light was provided. In one-half of the series, daylight was supplemented with artificial light from the Cooper-Hewitt work lamp; in the other half, Mazda C tungsten lamps were the supplementary source. The lamps were turned on at sunset and off at sunrise. The light intensities in both tests were maintained as nearly as possible at 60 foot-candles at a point midway between the soil and the top of the plant.

In table 5 it will be observed that when the Cooper-Hewitt lamp was used the seed yield was increased in all varieties except White Winter. The White Winter plants were less uniform in their growth than the other varieties, and this may account for their response. There were not many plants in the winter varieties, but there was a reasonably large number in Marquis.

TABLE 5.—*Seed production as influenced by the Mazda C tungsten lamp and by the Cooper-Hewitt mercury-vapor lamp with lead-glass tube* [1]

[Seeds were planted Oct. 13, 1931]

Variety	Plants under—		Heads produced under—		Seeds per head produced under—	
	Mazda C tungsten lamp	Cooper-Hewitt lamp	Mazda C tungsten lamp	Cooper-Hewitt lamp	Mazda C tungsten lamp	Cooper-Hewitt lamp
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
Harvest Queen	2	2	10	7	10.9	18.8
Crimean	2	2	10	8	9.6	16.5
Minhardi	2	2	8	7	15.7	19.4
White Winter	2	2	11	10	13.7	10.9
Sol	2	2	7	10	5.29	13.5
Marquis	20	20	28	29	1.35	2.93

[1] During the first 36 days the natural photoperiod obtained, after which uninterrupted illumination was provided, the augmenting sources operating from sunset to sunrise.

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The following winter another test was carried out with F_1 plants from winter-wheat crosses. The germinated chilled seeds were planted in the greenhouse. The temperatures were about 70° to 75° F. and the daily photoperiod was about 16 hours. Mazda C tungsten lamps were used after sunset. This photoperiod was maintained until the flag leaves appeared, when the series was divided into two groups of 16 plants each. Each group contained exactly the same progenies, and the plants were selected for uniformity of development. One group was placed under tungsten lamps and the other under the Cooper-Hewitt lamp combined with tungsten lamps. The light intensities in this test were maintained as nearly as possible at 120 foot-candles at a point midway between the soil and the top of the plant. The plants received full daylight. The lamps were turned on at sunset and off at sunrise.

Seed counts were made on the primary head of each plant. The 16 primary heads under the Cooper-Hewitt and Mazda C lamp combination produced 314 seeds, and the 16 primary heads under the Mazda C lamps produced only 216 seeds. The number of seeds per head ranged from 16 to 22 under the combined lamps and from 10 to 17 under the Mazda C lamps.

Very poor seed sets have been obtained when wheat plants begin to head in December and early January. Even when the day was lengthened artificially, the heads were frequently poorly developed and fertilization usually was not normal. Tests carried out in reduced sunlight in midsummer give similar results, thus indicating that the low intensity of daylight may be the chief cause of the poor heads in midwinter. All evidence seems to indicate that the success of a long day in which artificial light is used depends to a large extent on the amount of sunlight available.

CONCLUSIONS AND SUMMARY

Sexual reproduction in the spring wheats and in the winter wheats is not dependent on a critical temperature or a critical photoperiod, as this process occurs over very wide ranges of these factors. However, the time when sexual reproduction occurs is greatly influenced by the temperature and the photoperiod.

The proper classification of wheat varieties with respect to their temperature and photoperiodic characteristics for the earliest sexual reproduction is dependent on methods that make it possible to determine the optimum conditions of temperature and the photoperiod for the rapid completion of each growth phase, from the beginning of growth through sexual reproduction.

Spring wheats such as Marquis and earlier varieties complete their life cycle quickly when given a long day and temperatures at 70° F. or above throughout the life cycle, and therefore are considered to be typical long-day high-temperature plants. On the other hand, Harvest Queen, Turkey, and other varieties of winter wheat complete their life cycle most rapidly when given a short day and low temperatures during the early stages of growth and a long day and high temperatures during the later stages of development.

In the light of these relationships the writers conclude that winter wheats are not typical long-day plants but are what may be termed short-day→long-day plants and low-temperature→high-temperature plants. This method of expression indicates that the temperature and the length of the photoperiod must increase with the development of the plant in order to induce early sexual reproduction.

Temperatures and photoperiods favoring earliness in the winter and spring wheats favor the formation of a reduced number of internodes and leaves by each tiller. The formation of the stem internodes and leaves stops and the major elongation of the stem begins at about the time that floral differentiation becomes evident.

When the Mazda C tungsten lamp was used to lengthen the day, Marquis headed sooner than when the same photoperiod consisted of sunlight alone. Heading was earlier under the Mazda lamp than under the Cooper-Hewitt lamp when these light sources were used to lengthen the winter day.

In 5 of the 6 varieties tested the number of seeds was greater when the winter day was lengthened by means of the Cooper-Hewitt lamp alone, or when in combination with the Mazda lamp, than when the Mazda lamps were used alone for supplementing daylight. It appears that a combination of these lamps may be better for certain studies than the Mazda lamp alone for lengthening the natural day. The Mazda lamp stimulated earliness at the sacrifice of vegetation and seed yield, and the Cooper-Hewitt lamp apparently offset this by increasing vegetation and the yield of seed.

Earliness and other characteristics of the wheat plant are influenced by the intensity of the light, and while this influence is less than that of the daily photoperiod so far as concerns earliness of sexual reproduction, it is sufficient to warrant attention in experimental work.

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