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COMPARATIVE RESPONSES OF A SPRING AND A WINTER WHEAT TO DAY LENGTH AND TEMPERATURE[1]

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INTRODUCTION

Garner and Allard (*15*)[3] have emphasized the fact that in certain cereals a fundamental physiological distinction between spring and winter varieties is shown by the difference in their response to the length of the daily period of illumination. Many other investigators (*5, 8, 10, 11, 12, 19, 26, 37, 39*) have observed such varietal differences, and their reports have called attention to the importance of the day-length response in the geographic distribution of the different varieties of cereals, as especially emphasized in the case of wheat by Wanser (*39*), Doroshenko (*10, 11*), and Tincker (*37*).

The present paper contains observations and measurements illustrating the differences in growth habit, rate of development, height, tillering, and yield of individual wheat plants of two varieties, Hard Federation, an extreme spring type, and Turkey, an extreme winter type, grown in the greenhouse under controlled day-length and temperature conditions.

REVIEW OF LITERATURE

Reviews of the literature on photoperiodism in plants by Maximov (*25*), Kellerman (*21*), Redington (*34*), and Berkley (*7*) will serve to give the background of the present investigation.

As with most of the plants studied, the major emphasis in the case of wheat has been on the acceleration of reproductive processes by long light periods, and their retardation by short ones (*2, 3, 4, 5, 9, 10, 11, 12, 15, 22, 23, 26, 36, 37*). The extent to which the vegetative period can be shortened by increasing the day length differs for different varieties, the spring wheats having been found especially responsive to the hastening influence of a long light period. These investigations leave no doubt that the day-length responses of spring and winter types of cereals are as distinctive as their temperature adaptations (*12, 16, 26, 29*).

The length of the daily period of illumination has been found to determine not only height, tillering, and date of heading, but also root development (*15, 26, 40*), leaf and head development (*10, 11*), and

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[2] The writer is indebted to John W. Taylor, of the Division of Cereal Crops and Diseases, and to H. A. Allard, of the Division of Tobacco and Plant Nutrition, for their helpful suggestions in the course of this investigation; to A. G. Johnson and R. W. Leukel, of the Division of Cereal Crops and Diseases, for planning and supervising the installation of the temperature-control equipment; and to Fred Young for designing equipment used in controlling day length.

[3] Reference is made by number (italic) to Literature Cited, p. 886.

growth habit (*19*). In general it can be concluded from the literature that as the day length is made shorter the plants are more vegetative, with more tillers and larger leaves. As it is made longer, opposite effects are obtained. Some of Adams' results (*1, 3*) apparently constitute exceptions to these generalizations, but the explanation probably lies in his experimental procedure.

The interrelationship of temperature, light intensity, soil moisture, and other environmental factors in these various day-length effects has been discussed by many investigators (*2, 4, 6, 12, 14, 15, 17, 18, 19, 26*). Their reports confirm those of Garner and Allard in giving evidence that other factors may modify, to a certain extent, responses to the length of the daily light period.

METHODS

On December 2, 1930, seeds of a spring-wheat variety, Hard Federation (C. I.[4] No. 4733), and of a winter variety, Turkey (C. I. No. 1558), were sown in greenhouse benches at the Arlington Experiment Farm, Rosslyn, Va., in soil that was 10 inches deep. The plants were 4 inches apart in rows 6 inches apart. Different day-length conditions were provided for the different benches by means of artificial light and light-tight covers. The sowings were duplicated in the south-end sections of two adjacent greenhouses, one of which was kept at a favorable low temperature (12° ± 1° C.), the other at a temperature too high for the best growth of wheat (21° ± 1°). The temperature was regulated by means of thermostatic control of the steam valves and of the dampers admitting cold air from the outside. An air distributor, 6 feet above the floor, circulated the incoming cold air fairly uniformly, so that the total variation in temperature in those parts of the houses used for the experiment was not over 1 degree.

Combination soil and air thermographs and standardized maximum and minimum thermometers were kept on stands 1 foot above the soil in each bench. During the period of temperature control—from December 2, 1930, the date of sowing, until April 3, 1931, when outdoor temperatures became too high—the cold house was held at 12° ± 1° C. except for a few hours on sunny afternoons, when it often rose to 15° in midafternoon, rarely to 20°. In the warm house the temperature was similarly well controlled at 21° ± 1° until April 8. On sunny afternoons it rose to 25°, but rarely above. Soil temperatures were approximately 2 degrees lower than the air temperatures in each house. Unless otherwise specified, the temperatures referred to in this paper are air temperatures.

Although the desired temperatures could not be maintained in either house after the first week of April, the low-temperature house was kept approximately 5 degrees colder than the other by means of a sprinkler system which kept a thin sheet of water running over practically the entire area of the glass of the roof and sides.[5]

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[4] C. I. refers to accession number of the Division of Cereal Crops and Diseases (formerly Office of Cereal Investigations).

[5] This method of lowering the temperature in the greenhouse, suggested by S. Karrer, was inexpensive and easily installed. Water pipes with spray nozzles at 1-foot intervals were laid on the roof just below the ventilators, and across the south end of the house. The nozzles were directed downward at such an angle as to cause the water to strike the glass a short distance from the pipe, where it spread to the width of the pane.

[6] Throughout the following discussions the terms "long-day," "short-day," "low-temperature," and "high-temperature" are used to denote the relative conditions under which the plants were grown, and not, in the sense of Garner and Allard (*14*), to denote the optimum condition for flowering. In the latter sense wheat is a long-day plant because flowering is induced by long days, and is delayed, as in Hard Federation, or prevented, as may occur in Turkey, by short days.

For the long-day [6] plants in each house the natural day was supplemented with light from six 100-watt Mazda C lamps in standard deep-bowl reflectors, distributed at 32-inch intervals, 4 feet above the bench. These lights were turned on and off automatically by a time switch which was adjusted periodically so as to maintain a constant 17-hour light period. The intensity of the artificial light at the level of the bench varied but slightly from 40 foot-candles. As the plants increased in height, the distance of the lights from the bench was increased to 5 feet. The thermograph records showed no discernible heating effects of these lights at the level of the plants.

The short-day condition was produced for the plants in another bench in each house by means of a light-tight black cloth cover supported on a slender framework 4 feet above the level of the bench. The cover was hung several inches out from the bench in order to insure ventilation. At the corners the side and end pieces overlapped and were attached to the framework with snap fasteners when the cover was in place. A piece of 1-inch pipe constituted the back edge of the framework, and to it was attached a crank handle by means of which the curtain could be rolled upon the pipe and lifted to one side when not in place over the bench. The plants were darkened every day from 4 p. m. until 8 a. m., leaving them a light period of eight hours in the middle of the day. The cover was thick enough to protect the plants from the lights of the neighboring long-day bench, and was always in place before these lights were turned on.

Control plants with the natural light period were grown on an adjacent bench and protected from the lights over the long-day bench by a heavy black curtain 6 feet high, hung in the aisle and extending well past the ends of the benches. This curtain was in place whenever the lights were on, and was pulled to one end, where it did not shade the plants, when the lights were turned off. The natural length of day, from sunrise to sunset, increased over the period of the experiments from 9.5 hours in December to 15 hours in June.

The following observations and measurements are based on approximately 60 plants of each variety, exclusive of border plants, grown under each of these six different conditions of day length and temperature.

RESULTS

EFFECTS OF DAY LENGTH AND TEMPERATURE ON RATE AND TYPE OF DEVELOPMENT

The seedlings of the low-temperature house (12° ± 1° C.) emerged in 10 days, and those of the high-temperature house (21° ± 1°) in 6 days. The long (17-hour) light period so accelerated the development of the young plants of the spring variety, Hard Federation, that at first they greatly exceeded the others in height. At the natural and at the short (8-hour) days, Turkey, the winter variety, assumed, for about three months, the recumbent growth habit, typical of young plants of this and similar varieties in winter; but at the 17-hour day the plants were erect or semierect from the first, as in experiments previously reported by the writer (*19*).[7] In the low-temperature house these erect plants matured normally and produced good yields of grain. In the high-temperature house they remained largely vegetative, as did the Turkey plants of the other light periods at this temperature.

The contrast between the erect growth of the young plants of Turkey at the long day and their recumbent growth at the shorter ones, especially marked at the low temperature, is illustrated in Figure 1, which also shows the relative development of Hard Federation plants of the same age. The plants of Turkey with the 8-hour day, A, were still prostrate at the time the photographs were taken, while the control plants, B, with the natural day, which was nearly 11 hours long at this time, had become semierect, indicating the resumption of active growth. The 17-hour-day plants, C, were never prostrate.

The comparative rates of development of Hard Federation and Turkey under the different conditions are shown in Table 1, where the dates of first flowering, together with the averaged growth measurements and their probable errors, are recorded. Heading occurred during the week or 10 days preceding the date of first flowering, except in the case of the short-day plants, which headed irregularly over a longer period.

Representative plants from the different environments, selected for photographing when maximum growth had been attained but while most of the foliage was still green, are shown on the same scale in Figures 2 and 3. Later, after the plants had matured and their measurements were obtained and averaged, the photographs of plants conforming most closely to the averages for the groups were chosen for the illustrations. Occasionally none of the plants photographed from a given group happened to conform to the size shown by the averages in Table 1 to be typical. Such was the case in Figure 3, where all the plants have more than the average number of tillers for their group.

[7] Since the present paper was prepared, Forster, Tincker, Vasey, and Wadham (*13*) have reported that in their wheats growth did not completely cease at temperatures as high as 10° C., and that therefore they do not agree with the writer's statement (*19, p. 119*) that a resting stage is produced by 8 and 9.5-hour light periods at this temperature. The term "resting stage" was used in this earlier publication to designate the prostrate stage of development of Turkey in winter, preceding the erect leafy growth of the later period of the tillering stage. In Turkey and similar varieties the plants are recumbent during this early tillering stage, as described and illustrated by Percival (*31, p. 69–71*), and growth is almost imperceptible over a considerable period. A rest period is referred to by Maximov (*28, p. 290*) and others as typical of some cereals in winter, "* * * when growth completely ceases and the plant enters into a state of rest." Maximov states further: "This condition may be of various intensity and duration. It may involve the whole plant or only parts of it." Undoubtedly, as Forster and his associates have stated, all growth during the recumbent stage is not completely stopped in winter cereals at a temperature as high as 10° to 12°, the low temperature of this and the previous investigation (*19*). However, whether or not there is a true dormant or rest period is immaterial to the purpose of these investigations, the term being used with the sole purpose of designating the period during which the plant is in the prostrate or recumbent condition characteristic of the early tillering stage of Turkey and similar winter wheats grown with short light periods.

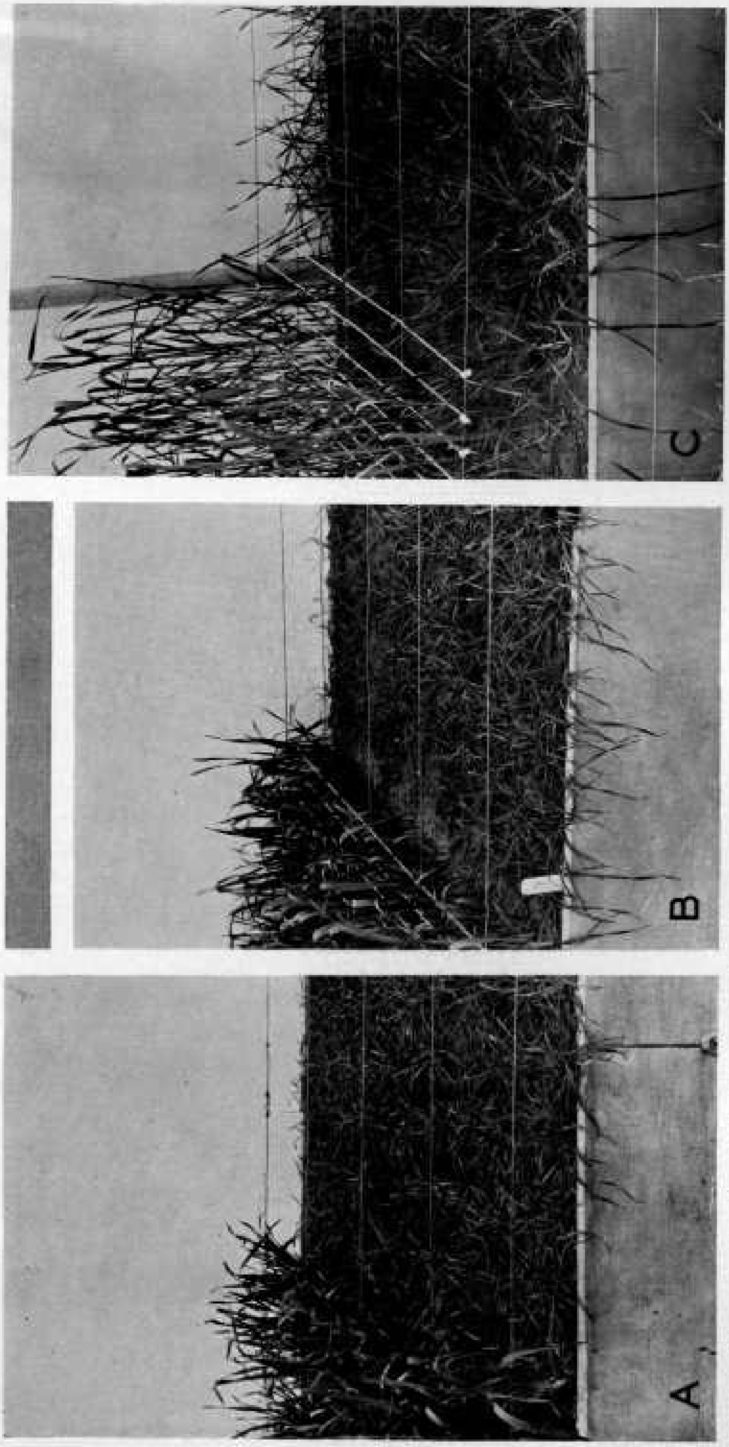

FIGURE 1.—Comparative development of winter-sown Turkey wheat (at right in each photograph) and Hard Federation (at left) 10 weeks after sowing, grown with constant low temperature (12°±1° C.) and different light periods: A, Short day (8 hours); B, natural day (9.5 to 10.5 hours); C, long day (17 hours)

TABLE 1.—*Effects of day length and temperature on the average height, tillering, head development, and yield of a spring wheat (Hard Federation) and a winter wheat (Turkey) sown December 2, 1930*

Item	Short day (8 hours)	Natural day (9.5–15 hours)	Long day (17 hours)
	Hard Federation at 12°±1° C.		
Date of first flowering	May 9	Apr. 13	Feb. 19
Dry weight of straw ... grams	9.5	7.7	1.2
Height of plants ... centimeters	90±0.75	98±0.93	66±0.86
Total tillers per plant ... number	5.8±.27	3.7±.16	[a] 3.8±.16
Fertile heads per plant ... do	3.9±.19	3.5±.17	1.3±.10
Length of heads ... centimeters	9.5±.07	8.6±.06	5.4±.05
Kernel weight ... gram	.035±.0007	.054±.0005	.055±.0009
Weight of grain per fertile head ... do	.51±.02	.85±.06	.37±.02
Yield of grain per plant ... do	1.91±.11	2.81±.21	.45±.05
	Hard Federation at 21°±1° C.		
Date of first flowering	Apr. 25	Mar. 18	Jan. 13
Dry weight of straw ... grams	10.3	8.1	([b])
Height of plants ... centimeters	82±1.20	84±1.07	48±.77
Total tillers per plant ... number	8.1±.32	6.2±.28	2.7±.11
Fertile heads per plant ... do	2.9±.14	4.1±.25	1.6±.06
Length of heads ... centimeters	8.5±.08	7.8±.05	5.4±.06
Kernel weight ... gram	.028±.0004	.039±.0007	.036±.0007
Weight of grain per fertile head ... do	.24±.04	.61±.03	.38±.02
Yield of grain per plant ... do	.77±.06	2.40±.18	.67±.03
	Turkey at 12°±1° C.		
Date of first flowering	June 8	May 16	Apr. 13
Dry weight of straw ... grams	12.9	8.7	3.8
Height of plants ... centimeters	110±0.76	115±0.88	101±0.71
Total tillers per plant ... number	6.6±.28	5.3±.24	3.4±.09
Fertile heads per plant ... do	2.0±.13	4.3±.17	2.9±.09
Length of heads ... centimeters	13.7±.11	10.0±.05	8.4±.04
Kernel weight ... gram	.022±.0008	.035±.0002	.043±.0005
Weight of grain per fertile head ... do	.23±.02	.98±.04	1.15±.03
Yield of grain per plant ... do	[c] .53±.04	4.06±.19	3.57±.09

[a] Very short secondary tillers without grain and but a few inches long, characteristic of these plants, were not included in this average. If included, the average would be 6.9.
[b] Straw inadvertently discarded.
[c] In the year preceding and the year following, in both of which the seed was sown 2 weeks later than in this experiment, the heads of Turkey at the short day produced no grain. (Table 2.)

Hard Federation was extremely sensitive to the forcing action of the lengthened light period. At both temperatures the plants with the 17-hour day were forced into the reproductive stage so rapidly that there was insufficient leaf development before maturation processes began. The plants were extremely stunted, with short, narrow leaves and small, poorly developed heads. (Fig. 2, C, F.) In the low-temperature house they began to flower the third week of February, 10 weeks after emergence. They were eight weeks ahead of the control plants (fig. 2, B), which flowered the second week of April. In the high-temperature house, development was still more rapid, the long-day plants flowering the second week of January, only five weeks from emergence and nine weeks ahead of the control plants (fig. 2, E), which bloomed the third week of March.

Maturation of the short-day plants of Hard Federation was as markedly retarded as that of the long-day plants was hastened. Whereas the rapid development at the 17-hour day had resulted in stunted plants with reduced foliage, the 8-hour day caused a highly vegetative type of growth, with increased tillering and large leaves. (Fig. 2, A, D.) In the cold house the plants began to flower the second week of May, a month later than the control plants with the natural light period. At the higher temperature they flowered the last week of April, more than five weeks later than the natural-day plants in that house.

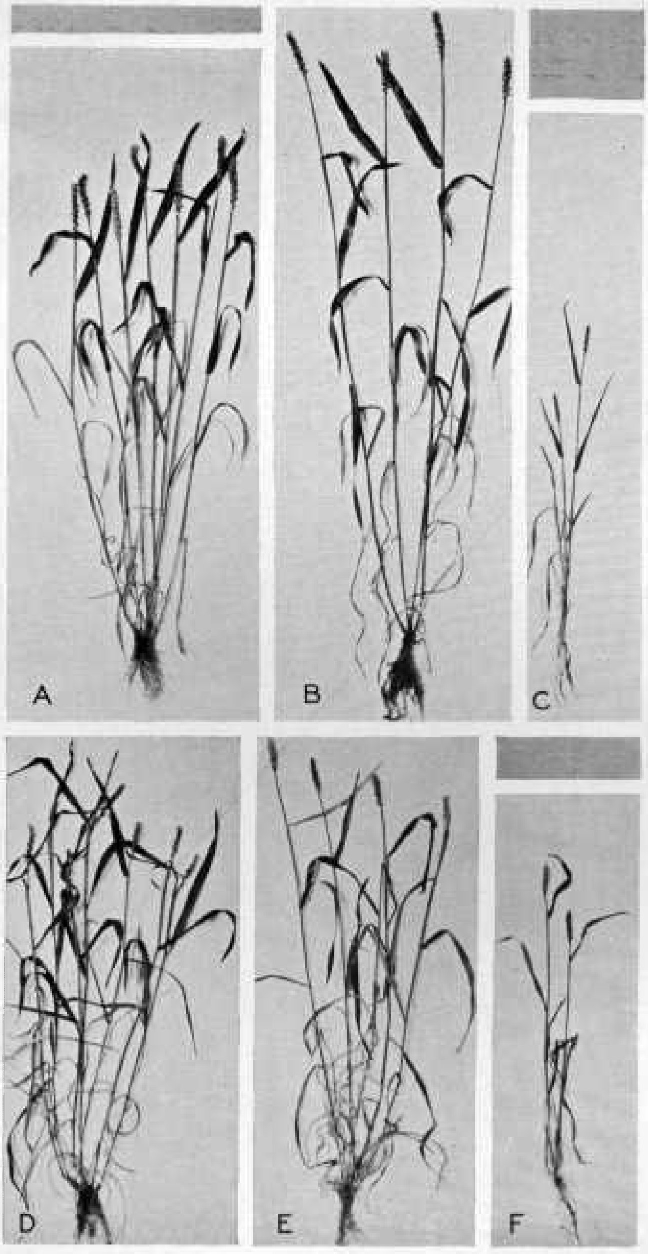

FIGURE 2.—Mature plants of winter-sown Hard Federation wheat grown with different light periods and temperatures (12±1° and 21±1° C. for the first four months): A, B, C, Short-day, natural-day, and long-day plants, respectively, grown at the lower temperature; D, E, F, short-day, natural-day, and long-day plants, respectively, grown at the higher temperature

At the low temperature, Turkey, the winter variety, while less susceptible to the forcing action of the lengthened light period than Hard Federation, also developed more rapidly with the 17-hour day than with the natural day. The plants were not stunted as were the

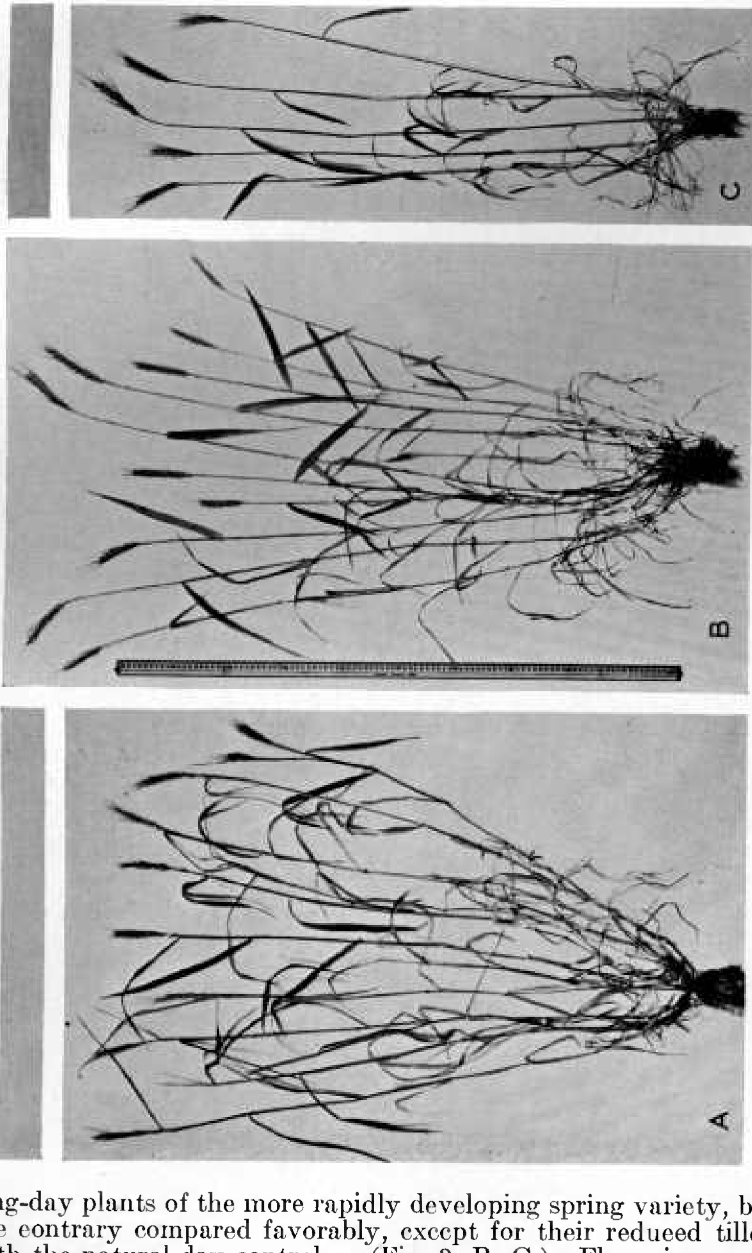

FIGURE 3.—Mature plants of winter-sown Turkey wheat grown with different light periods and, for the first four months, at a constant temperature of 12±1° C.: A, Short day (8 hours); B, natural day (9.5 to 15 hours); C, long day (17 hours).

long-day plants of the more rapidly developing spring variety, but on the contrary compared favorably, except for their reduced tillering, with the natural-day controls. (Fig. 3, B, C.) Flowering occurred during the second week of April, five weeks ahead of the natural-day plants, while those of Hard Federation growing beside them had flowered the third week of February, eight weeks ahead of their controls. The short day resulted in a vegetative type of growth, as in Hard Federation, with maturation considerably delayed. (Fig. 3, A.) Thus, at the 8-hour day Turkey did not head until June 8, three weeks later than the natural-day plants.

In the high-temperature house but few heads were produced by Turkey at any day length, most of the plants being completely sterile. They remained green and mostly vegetative until the following October, when they were discarded. Excessive tillering, together with the common failure of the culms to elongate, gave the plants of all the light periods the bushy appearance characteristic of spring-sown winter wheats that fail to head (*6*). The photographs in Figure 4 were taken in August, when the plants were still green, long after all the other lots had ripened. The vegetative condition of the long-day plants in this house gave evidence of the fact that the ordinarily dominant action of the light period becomes imperceptible at temperatures unfavorable for reproduction.

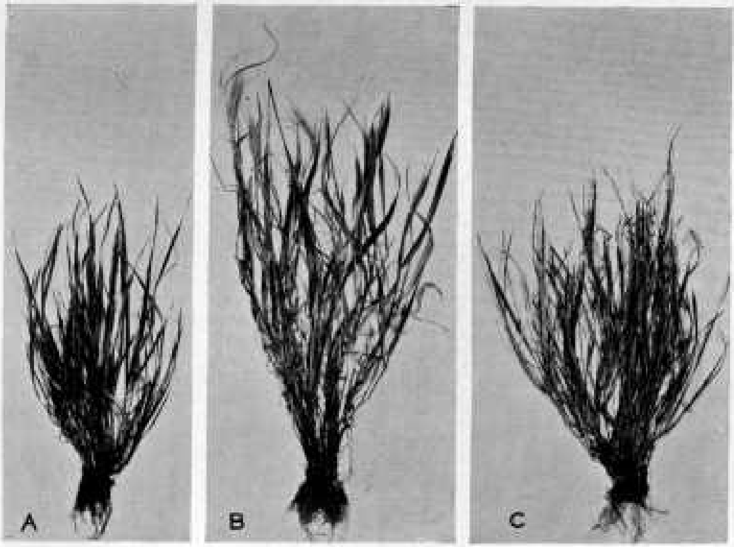

FIGURE 4.—Effect of the higher temperature (21°±1° C. for first four months) on the growth of Turkey at the different day lengths: A, Short day (8 hours); B, natural day (9.5 to 15 hours); C, long day (17 hours)

The tendency of the shortened day to favor continued vegetative growth and that of the long day to inhibit it are evident in both the winter and the spring variety on comparing the weights of the dried plants from the different environments. The average weights of straw per plant shown in Table 1 were obtained by weighing the fully ripened air-dry plants, exclusive of the heads and roots. In the low-temperature house the average weight of a short-day plant of Turkey was more than three times that of a long-day plant. In the case of corresponding plants of Hard Federation, the short-day plants averaged eight times the weight of those with the long day. The straw of the long-day plants of Hard Federation from the high-temperature house was inadvertently discarded, but approximately the same relation is evident from the appearance of the plants in

Figure 2, F. The weights of the natural-day plants of both varieties were intermediate between those of the short and long days, but re-

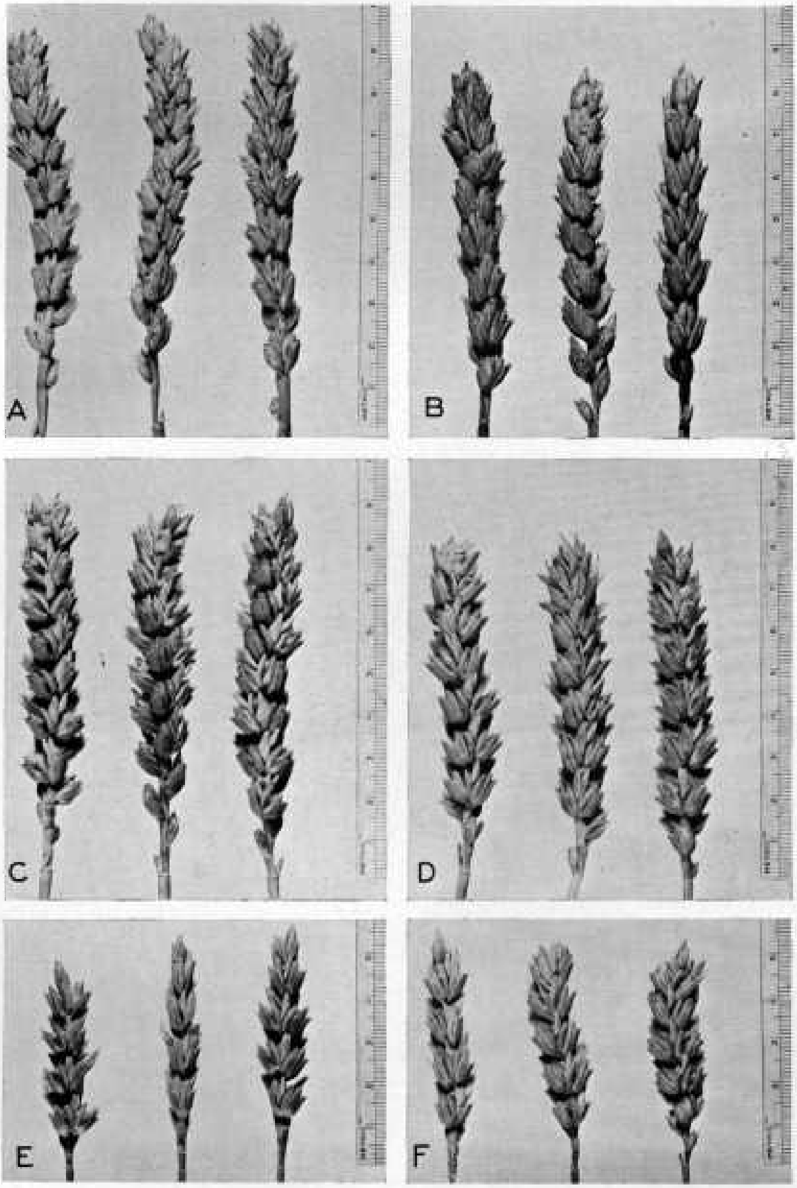

FIGURE 5.—Typical heads of Hard Federation wheat grown with different day lengths and temperatures (12° and 21° C. for the first four months): A and B, Short day (8 hours) at the low and high temperatures, respectively; C and D, natural day (9.5 to 15 hours), at the low and high temperatures, respectively; E and F, long day (17 hours) at the low and high temperatures, respectively

duction in size by the long day was always more pronounced than was the increase brought about by the short day.

The average heights recorded in Table 1 represent the final measurements on the mature plants, including the heads. The data show that the 17-hour light period shortened the plants in every case, the effect on Hard Federation being much more extreme than the effect on Turkey. The 8-hour day also reduced the average height of the plants of both varieties, but the effect was less pronounced than that of the lengthened light period. At every day length the plants of the cold house were taller than the corresponding plants of the warm house, the difference reflecting the injurious effects of temperatures above 20° C. on the growth of even the spring wheat.

The number of tillers per plant was highest in both varieties at the short day, and generally lowest at the long day. If only normal tillers with heads were counted, the number was always lowest at the long day. At equivalent day lengths, more tillers were produced at the high than at the low temperature, except in Hard Federation at the long day.

FIGURE 6.—Typical heads of Turkey grown at 12°±1° C. for the first four months, with different light periods: A, Short day (8 hours); B, natural day (9.5 to 15 hours); C, long day (17 hours)

Among the conspicuous formative effects of the length of the light period were the effects on head length. (Table 1.) In both Hard Federation (fig. 5) and Turkey (fig. 6) the long day produced abnormally short heads. The short day produced very long heads, largely as the result of abnormal elongation of the basal internodes of the rachis. This elongation was especially pronounced in Turkey, some of the heads reaching 20 cm, measured from the lowest node of the rachis. Occasional abnormal heads like those in Figure 7, showing indeterminate growth of the spikelets, were produced by Turkey at this day length.

Other structural abnormalities were the shortened peduncles of the plants of the short day. (Figs. 2, A, D; 3, A.) Sometimes elongation of the peduncle ceased as soon as the head emerged from the boot.

The short day resulted also in a tendency toward abnormal branching. Sometimes the culm branched at one of the upper nodes (fig. 3, A) and sometimes nearer the base. This effect calls to mind Garner and Allard's finding (*15*) that a change in the light period from optimum to suboptimum for stem elongation promotes branching.

A striking abnormality, occurring frequently in the long-day plants of Turkey at the high temperature, is shown in Figure 8. In these plants, heading was almost completely inhibited, and masses of leaves and roots often grew from the nodes of the culm. Although most pronounced at the 17-hour day, occasional instances occurred at the natural day, which was 15 hours long in July when the tendency was first observed.

FIGURE 7.—Abnormal heads of Turkey grown at the low temperature with a short light period (8 hours)

EFFECTS OF DAY LENGTH AND TEMPERATURE ON PRODUCTION OF GRAIN

As a result of a tendency toward increased sterility in both varieties with light periods other than the natural one, the relationship of day length to yield was not that which might have been expected from its effects on tillering. In Hard Federation the abnormally long heads of the short-day plants, as well as the short stunted heads of the long-day plants, were poorly developed. Maximum yield per plant, therefore, occurred with the natural length of day and not in the many-tillered short-day plants. In Turkey also the poorly developed heads of the short-day plants and the reduced tillering of the long-day plants resulted in the greatest yield occurring at the natural day. (Table 1.)

In the case of the winter variety, Turkey, the shortened light period was more damaging to yield than the long one, as many heads were completely sterile or only partly filled with small and shriveled grains. But in the case of the spring variety, Hard Federation, the long light period was the more damaging, many heads being sterile or incompletely filled.

An interesting distinction between the two varieties appeared also in the relative effects of the lengthened light period on individual head yield. Table 1 shows that in the low-temperature house Turkey produced the highest yields of grain per head with the 17-hour day, but in Hard Federation the highest yield occurred at the natural day, the long day greatly reducing the number of grains per head. This same difference appeared also in the other experiments. (Table 2.)

The short-day plants of both varieties produced the smallest grains. (Table 1.) Those of Turkey were especially poor, being shriveled, dark in color, and much reduced in weight. Thus the short-day condition reduced yields not only by increasing sterility but by reducing the size of such grains as were formed. In other experiments (Table 2), for which the seed was sown two weeks later, the short day prevented flowering in Turkey and so resulted in complete sterility.

FIGURE 8.—Abnormal growth of long-day Turkey wheat plants grown at the high temperature. Bunches of leaves and roots grew from the nodes, the plants remaining erect

The 17-hour day did not affect the kernel weight of Hard Federation appreciably at either temperature, so the greatly reduced grain weights shown in Table 1 for the long-day plants were caused by a decrease in the number of fertile tillers per plant and grains per head, rather than by a decrease in the size of the kernels. In the winter variety, Turkey, there was an increase in the average kernel weight at the long day. A similar increase occurred in this variety in all the experiments. (Table 2.)

Relative kernel size for the different groups of plants is illustrated in Figure 9. This figure shows the reduced size of the grains of the short-day plants of both varieties, and the large plump grains of the long-day low-temperature plants. The high-temperature grains were always smaller than the corresponding ones from the low-temperature plants.

The following year (1932) grain from each of these seed lots was grown in the low-temperature house with the natural light period.

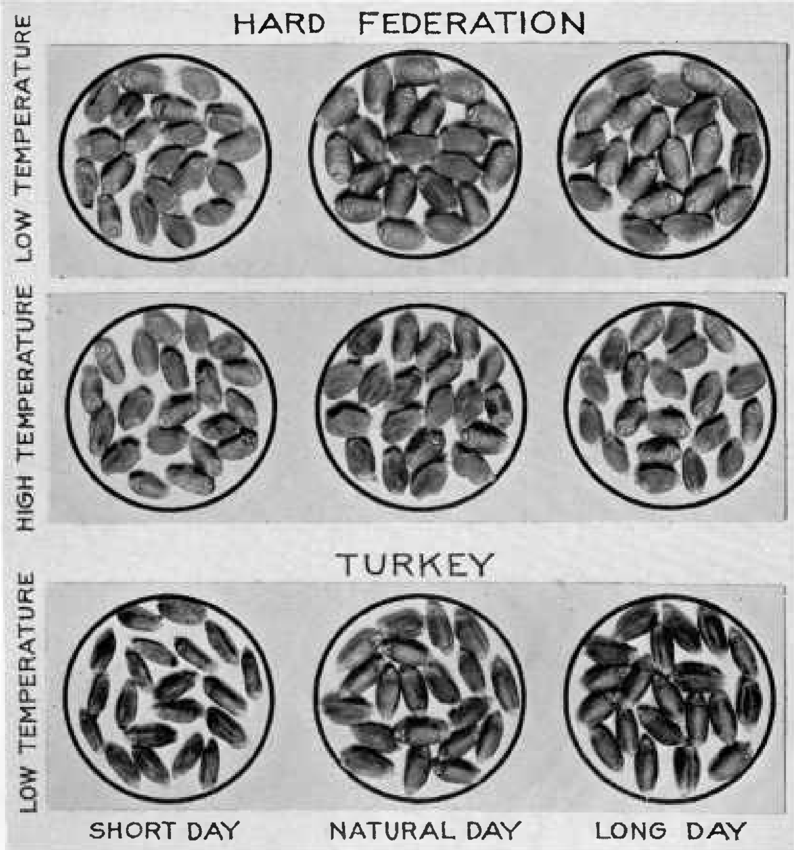

FIGURE 9.—Effects of day length and temperature on kernel development of wheat. (Twenty grains in each circle)

Except for somewhat reduced size in early growth stages, the plants grown from the small shriveled grains of the short day were very similar to those from the larger grains of the other day lengths. There were no significant differences in height, tillering, dry weight, or yield of any of the plants. It is concluded, therefore, that the conditions of day length and temperature under which the grain was produced had no appreciable effect on the development of the plants grown from the grain.

SUPPLEMENTARY EXPERIMENTS

The question arises in connection with the generalizations discussed in the preceding sections as to the reproducibility of these effects of day length and temperature. Data from several similar experiments but with different dates of sowing and different spacings are summarized in Table 2 in order to show that the relative effects of the different environments and the varietal differences in the responses to these environments were not fortuitous variations.

The experiment with spring-sown grain (A) included only Hard Federation, and differed from that just described in its closer spacing, the plants being 2 instead of 4 inches apart. The experiment with grain sown in the winter of 1931 (B) also differed with respect to spacing, in that the rows were 1 foot apart instead of 6 inches. The experiment with grain sown in the winter of 1929 (C) resembled that described in the preceding sections of this paper, the plants being spaced at 4-inch intervals in rows 6 inches apart. The experiment A differed from all the rest in that temperature control could be maintained for the first month of growth only, whereas the winter sowings had controlled temperatures for the first four months. The temperatures were similar in all the experiments, namely, between 10° and 14° C. in the low-temperature house and between 20° and 23° in the high-temperature house. All border plants were discarded.

The data in Table 2 are in accordance with the generalizations indicated by the data in Table 1. They show that the 17-hour day accelerated the development of both Hard Federation and Turkey and produced smaller plants, with lower dry weights and reduced tillering. Acceleration of heading was less marked in Turkey than in Hard Federation, as before. Yield per head at the long day was always higher than at the natural day in Turkey but lower in Hard Federation. The short day consistently produced large vegetative plants with the most tillers, whose development was retarded. Grain production was decreased or, in Turkey, entirely prevented by the short day.

A significant difference between the Turkey plants of the experiments of Table 2 and those of Table 1 was the failure of the former to flower at the short day. The difference may be attributed to the fact that the grain for the experiments of Table 2 was sown two weeks later than that of Table 1, the retardation by the short day resulting in the later-sown lots reaching the preflowering stage when greenhouse temperatures were higher.

TABLE 2.—*Effects of day length and temperature on average height, tillering, head development, and yield of Hard Federation and Turkey wheat in supplementary experiments, 1930–1932*

Item	Experiment [a]	Hard Federation: Low temperature: Short day (8 hours)	Hard Federation: Low temperature: Natural day (9.5–15 hours)	Hard Federation: Low temperature: Long day (17 hours)	Hard Federation: High temperature: Short day (8 hours)	Hard Federation: High temperature: Natural day (9.5–15 hours)	Hard Federation: High temperature: Long day (17 hours)	Turkey: Low temperature: Short day (8 hours)	Turkey: Low temperature: Natural day (9.5–15 hours)	Turkey: Low temperature: Long day (17 hours)
Date of first flowering	A	June 13	May 15	May 7	June 30	May 4	Apr. 18	-----	-----	-----
	B	May 4	Apr. 17	Feb. 29	-----	-----	-----	-----	May 15	May 4
Dry weight of straw ... grams	A	2.9	2.7	1.1	3.8	2.9	0.8	12.7	11.4	8.1
	B	6.3	8.2	1.6	-----	-----	-----	-----	-----	-----
Height of plants ... centimeters	A	72	81	55	72	62	37	-----	-----	-----
	B	76	99	64	-----	-----	-----	76	118	119
Total tillers per plant ... number	A	1.8	1.3	1.1	3.9	1.5	1.4	12.8	9.3	7.2
	B	5.9	5.0	3.9	-----	-----	-----	-----	-----	-----
Fertile heads per plant ... do	A	1.1	1.1	1.0	1.5	1.4	1.0	0	8.6	7.0
	B	4.4	4.4	1.1	-----	-----	-----	-----	-----	-----
Length of heads ... centimeters	A	9.0	7.2	4.6	7.8	7.2	4.3	-----	-----	-----
	C	8.9	8.1	4.6	8.0	7.6	3.9	-----	-----	-----
Kernel weight ... gram	A	.030	.045	.045	.03	.041	.033	-----	-----	-----
	B	.021	.049	.048	-----	-----	-----	0	.032	.037
	C	.034	.049	.045	.03	.041	.032	0	.038	.043
Weight of grain per fertile head ... do	A	.23	1.00	.51	.11	.95	.30	-----	-----	-----
	B	.26	1.44	.33	-----	-----	-----	0	.78	.88
	C	.79	1.17	.03	.40	.88	.21	0	1.04	1.18
Yield of grain per plant ... do	A	.25	1.10	.51	.16	1.33	31	-----	-----	-----
	B	1.08	6.23	.38	-----	-----	-----	0	6.89	6.07

[a] Experiment A, seed sown Mar. 2, 1931; B, seed sown Dec. 15, 1931; C, seed sown Dec. 13, 1929.

DISCUSSION

A shortened daily light period induces an abnormally vegetative type of growth in wheat, whereas, at temperatures low enough to permit heading, a lengthened one induces abnormally hastened reproduction. However, the results of the present investigation show that plants so rapidly forced into the reproductive stage by a long light period are not made more fruitful thereby, but, on the contrary, yield is reduced, especially in the case of a spring wheat like Hard Federation. Plants of this variety are stunted, the leaves small, and the heads often sterile. The winter variety, Turkey, is not forced so rapidly into reproduction by a long day, but, at favorably low temperatures, it grows tall and vigorously, its leaves are large, and it produces an even higher yield of grain per head than it does with the natural day. Nevertheless it does not produce the greatest yield per plant at the long day, for the number of heads is reduced.

It is interesting to note that although a shortened light period always increased the number of tillers per plant in both varieties, and, in Turkey, a lengthened one increased the kernel and head weights, still the highest total yield of both varieties was produced by the plants with the natural day, possibly because of the favorable effect of the changing light period (*19*, *27*, *33*), which increased from 9.5 to 15 hours during the experiments.

Differences between the reactions of the spring and the winter variety to the different environments were conspicuous at every stage of development. In the early tillering stage, the prostrate growth habit of the short-day and natural-day plants of Turkey distinguished them from the erect plants of Hard Federation in the same benches. Within the first 5 to 10 weeks after emergence, depending on the temperature, heads were appearing in the long-day plants of Hard Federation, while Turkey in the same bench was still in the tillering stage. Turkey continued in this vegetative stage for some time after the spring plants had fully matured; so, although the long-day plants of Hard Federation were much taller at first than the adjacent plants of the winter variety, their growth was soon ended by the early maturation of the heads, leaving the plants abnormally short and with reduced leaf and head development. At the low temperature the more slowly developing long-day plants of Turkey grew to twice the height of the Hard Federation plants beside them and produced fully developed leaves and heads. The extreme reduction in yield in Hard Federation at the long day, with less injury at the short day, and, conversely, in Turkey, the occurrence of extreme injury at the short day with increased head and kernel weights at the long day, gave interesting evidence of a fundamental distinction between spring and winter wheats. Other evidence of the physiological difference between the two varieties was, of course, the greater tolerance of Hard Federation for the higher temperatures.

The appearance and measurements of the plants in the present investigation show that excellent growth can be obtained in the greenhouse with no source of ultraviolet light. In 1931 the control plants of the winter variety, Turkey, with the natural length of day averaged 115 cm in height at maturity, with an average of 5.3 tillers and 4 g of grain per plant, testing 62 pounds to the bushel. In 1932, when the rows were 1 foot apart instead of 6 inches, still larger plants

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were obtained which averaged 8.6 fertile heads, giving 6.9 g of grain per plant. (Table 2.) The plants, therefore, compared favorably with field-grown plants (*6*) of this variety.

The excellent growth and yield of the plants of Turkey at the 17-hour day were of special interest because the recumbent growth habit typical of this variety in a natural winter environment at this latitude was inhibited by the long light period. The subsequent normal development of the plants showed, in agreement with the conclusions of other investigators (*29*, *30*, *38*), that a resting or recumbent stage was not essential for good yield. Since 17-hour-day plants of this variety yielded so well in all the experiments, the suggestion that the failure of spring plantings of winter wheat to head may be attributed to too long light periods (*29*)—or to the resulting absence of a prostrate growth phase in the tillering stage (*19*)—now seems untenable, for the longest summer day is only 15 hours at this latitude. In view of the fact that temperatures above 20° C. in the greenhouse are so deleterious to winter wheat (*20*) and, in the present experiments, always prevented normal development at all the day lengths used, it seems probable that the onset of warm weather before the end of the long vegetative period is responsible for the abnormal growth of Turkey in spring sowings.

Gassner (*16*), McKinney and Sando (*24*), Maximov (*26*), and others have shown that stimulation of the transition from vegetative to reproductive growth in winter wheat can be brought about by germinating the plants at temperatures near freezing. However, Murinov (*30*) and Wacar (*38*) have reported that, in the winter varieties they studied, very low germination temperatures were not essential for heading. It now seems from other investigations (*29*, *32*) that very low temperatures in early stages stimulate heading in the case of late sowings only, for when germination takes place in the winter such low temperatures have no noticeable effect, presumably because the short winter day supplies a similar stimulus (*27*). In accordance with these reports, the low-temperature plants of the present investigation (for all of which the seed was sown in December) progressed normally from the vegetative condition to reproduction with normal yields of grain without experiencing either soil or air temperatures below 9.5° C. It would seem, therefore, that statements (*35*, *p. 53*) to the effect that winter cereals "grown from seed germinated above 5° C. and not allowed during growth to fall below this temperature do not form ears but grow vegetatively only" are not applicable to the winter wheat used in these investigations.

It is of interest to note that three groups of the Hard Federation plants, including one in the low-temperature house (Table 1) flowered within the period of temperature control, which continued through the first week of April. With the exception of the natural-day plants, for which the light period was increasing, these plants flowered with no apparent change in the external environment other than the change in light intensity as the season advanced. This fact would appear to controvert the opinion (*27*) that a rise in temperature as well as an increase in day length is necessary for further development after the plant has reached the preflowering stage.

Wanser (*39*) thought that specific critical day lengths are necessary to bring about the transition from the vegetative to the reproductive phase of growth in winter wheats, and to initiate jointing and heading. The fact that in the present investigation Turkey plants have progressed from the seedling stage to culm elongation, flowering, and maturation at both the constant short and constant long days shows that the stimulus of a changing length of day is not essential for development in all winter wheats.

Turkey and some other varieties of winter wheats have been shown (*19, 27, 33*) to be stimulated to more rapid development by transferring them from short to long light periods in early stages of growth. In the writer's experiments, transplanting young Turkey plants from the short-day to the long-day bench at the age of 2 months, when they were still in the recumbent stage, resulted in rapid emergence from this stage. Culm elongation proceeded so rapidly that the plants soon surpassed all the others. Flowering and maturation of such transplanted plants in experiments of three different years occurred without exception from one to two weeks earlier than in the adjacent plants with the constant long day, which were themselves two months earlier in heading than were the natural-day plants.

The various reports (*16, 19, 24, 26, 27, 29, 32, 33, 38*) of favorable effects of a change from low temperatures or short days in early growth stages to higher temperatures or to longer days in later ones have proved that under some conditions such changes hasten the subsequent transition from vegetative to reproductive growth. There still remains the question as to what brings about the transitions in growth phases that occur in the absence of any apparent change in the external environment.

SUMMARY

Hard Federation, a typical spring wheat, and Turkey, an extreme winter type, were grown in the greenhouse with short (8 hours), natural (9.5 to 15 hours), and long (17 hours) light periods at each of two temperatures, a low one (12° ± 1° C.), favorable for the growth of wheat, and one too high for the best development of even the spring variety (21° ± 1°). Temperature control was maintained from the first of December until early April.

The long day hastened the development of both varieties, but the acceleration was much more pronounced in the case of the spring variety. The short day retarded the development of both varieties.

At the low temperature, the short day increased leaf size, head length, and generally the number of tillers, and decreased kernel weight and yield of the plants of both varieties, causing complete sterility in Turkey in two out of three experiments. The long day decreased dry weight, tillering, head length, and total yield of grain in both varieties, although Turkey's yield per head and average kernel weight were always highest at this day length. Yield per plant of this variety at the long day was reduced because of the reduction in tillering.

The short day was more damaging than the long day to the yield of grain in Turkey, whereas the long day was the more damaging to Hard Federation.

The high temperature was more damaging to the winter variety than it was to the spring variety, heading of the former being sparse and the growth of the plants abnormal above 20° C.

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