EFFECT OF ABNORMALLY LONG AND SHORT ALTERNATIONS OF LIGHT AND DARKNESS ON GROWTH AND DEVELOPMENT OF PLANTS[1]

By W. W. GARNER, *Principal Physiologist, in Charge,* and H. A. ALLARD, *Senior Physiologist, Division of Tobacco and Plant Nutrition, Bureau of Plant Industry, United States Department of Agriculture*

INTRODUCTION

One of the striking facts developed in the study of plant response to relative length of day and night is that, so far as concerns initiation of flowering and fruiting, darkening the plant for a period in the middle of the day fails to produce the same effects as those resulting from excluding the early morning or late afternoon light. Early in the investigations of the present writers on this subject[2] it was shown that in such typical short-day plants as Biloxi soybeans (*Soja max* (L.) Piper) and *Aster linariifolius* L., darkening from 10 a. m. to 2 p. m. each day has but little effect in hastening flowering as compared with that produced by exposure to an unbroken short day. Further studies have shown that other short-day plants, as well as typical long-day plants, also show a curious indifference to darkening in the middle of the day with respect to flowering and fruiting, even when the amount of light thus excluded is vastly greater than that excluded with decisive effects in the early morning and late afternoon. These results indicate that, with a given total number of hours of daily illumination, two short periods do not produce the same result as a single unbroken period of illumination. Indeed, the effect of midday darkening is much the same as if the plants remained in the light for the whole day.

Another prominent feature of photoperiodic response in plants is that species and varieties differ widely in their sensitivity to change in length of day. Comparatively small changes in day length may exert marked formative action on some plants, while in other plants wide variation in the daily light period may produce only slight quantitative effects. The question naturally arises as to the character and extent of the effects that would be produced on the two classes of plants by alternations of light and darkness falling outside the range commonly experienced in nature. To obtain further information on this problem, with the results previously obtained by darkening soybeans and Aster in the middle of the day as a basis, the experiments discussed in this paper were undertaken. These experiments have been carried out on a number of plants of long-day, short-day, and indifferent types, with sunlight and with the tungsten-filament lamp as sources of illumination. A preliminary account of some of the earlier, less comprehensive tests appeared in 1927.[3]

[1] Received for publication Jan. 2, 1931; issued May, 1931.

[2] GARNER, W. W., and ALLARD, H. A. EFFECT OF THE RELATIVE LENGTH OF DAY AND NIGHT AND OTHER FACTORS OF THE ENVIRONMENT ON GROWTH AND REPRODUCTION IN PLANTS. Jour. Agr. Research 18: 553-606, illus. 1920.

[3] GARNER, W. W., and ALLARD, H. A. EFFECT OF SHORT ALTERNATING PERIODS OF LIGHT AND DARKNESS ON PLANT GROWTH. Science (n. s.) 66: 40-42. 1927.

METHODS OF PROCEDURE

Efforts were first directed toward amplifying the original results obtained with soybeans and Aster by testing other plants and by employing several modifications of the light treatment. It was desired to obtain as many data as possible with sunlight, bearing on the effects of alternations of light and darkness not commonly experienced by plants in nature, in order to furnish a check on the results obtained with artificial light. However, the opportunities for the use of sunlight in securing these alternations are rather limited because of the inevitable sequence of day and night in a cycle of 24 hours. In one series of tests the plants were subjected alternately to a 10-hour day and to the full day length of summer. For this and the two following series of tests with sunlight, the usual arrangement of light-proof houses and trucks on steel tracks for transferring the plants was employed. The midsummer day length at Washington, D. C., from sunrise to sunset, is slightly less than 15 hours.

In another series of tests conducted in midsummer the plants were darkened throughout the daylight period and exposed to full-day illumination on alternate days. In this way the alternations of light and darkness involved a cycle of 48 hours instead of the usual 24 hours. The plants were illuminated for about 15 hours in each 48-hour period, which would correspond to an average of 7½ hours of light daily. Along with these tests, another treatment involved daily darkening from 10 a. m. to 3 p. m. In this case the plants were illuminated for an average of about 9½ hours in each 24-hour period. In two instances the darkening was from 10 a. m. to 2 p. m. daily.

In the final series of tests with sunlight the plants were placed in the light-proof houses from 10 a. m. to noon and from 2 to 4 p. m. Thus they were exposed to three short periods of illumination each day, and the total daily illumination ranged from 11 hours to about 9 hours or slightly less, depending on the duration of the test.

To obtain systematic alternations of light and darkness of fixed duration it is necessary, of course, to employ artificial light. For the tests with artificial light a series of small light-proof compartments was used, each compartment being provided with a 1,000-watt Mazda lamp, with reflector, as a light source. The plants were protected from excess of radiant heat from the lamps by interposing a 2-inch screen of distilled water which was constantly recirculated from a tank by means of an electrically driven pump. A current of air was driven through the plant chambers at a uniform rate by means of a fan. The lights were turned on and off automatically at definite intervals by passing the electric current through a series of revolving drums having a segment cut away and fitted with copper brushes so as to provide for making and breaking the electric circuit. The time relationship between complete revolutions of the different drums was rigidly maintained by means of a series of gears, the whole being driven by a synchronous electric motor.

Except in the final tests, means were not at hand for maintaining constant temperature and humidity. Each series of tests, however, was essentially complete in itself, and thermographic records indicate that in each series the difference in the temperature of the different compartments was not at any time more than 1 or 2 degrees Fahrenheit. A fairly large number of experiments were carried out at various temperatures and on various plant species. As an additional check, in some instances the alternations of light and darkness allotted to the different compartments were interchanged, in order to eliminate the effects of abnormal conditions that might exist in any compartment. In each series the mean temperatures were computed from the thermographic records. In the shorter alternations of light and darkness no changes in temperature due to the light coming on or going off could be detected. In the alternations of one hour or longer a rise of 1 or 2 degrees in temperature usually resulted when the lights came on. In the final tests a system of automatic control of temperature and humidity was in operation and, except on abnormally warm days, the temperature was held constant within $\pm 2°$ F., while the relative humidity was held constant within about ± 3 per cent.

By means of the water screen the proportion of infrared in the radiation from the lamp was reduced to a level considerably below that in sunlight. The visible portion of the spectrum of the tungsten filament lamp is deficient in the shorter wave lengths, as compared with sunlight. As regards intensity, values of 2,000 to 4,000 foot-candles were obtained immediately below the water screen, except at the outer edges near the walls of the compartment. The intensity decreased, of course, with increasing distance below the screen. The plants were grown in ordinary potting soil in wooden boxes. The containers were so adjusted as to bring the tops of the plants reasonably near the bottom of the water screen. Observations on the test plants were planned to show the effect of the different light treatments (1) on time of flowering and (2) on the nutrition and growth of the plants, as measured by appearance, height attained, and fresh and dry weights at the end of the test.

EXPERIMENTAL DATA

EXPERIMENTS WITH SUNLIGHT

In the first series of experiments, early, medium, and late varieties of soybeans and *Cosmos sulphureus* L., *Perilla frutescens* (L.) Britton, and *Impatiens balsamina* L. (garden balsam) were exposed alternately to a 10-hour day and to the full length of day during the latter part of June, July, and August. The control plants were exposed daily to the full length of day. Mandarin, the early variety of soybeans used, is relatively indifferent to seasonal changes in day length in the latitude of Washington. The three other varieties of soybeans and Cosmos and Perilla are to be classed as short-day plants, while garden balsam is a long-day type. Table 1 shows the results of the experiment with respect to date of first flowering and height attained by the plants at flowering.

In the next experiment, representative short-day and long-day plants were darkened throughout the daylight period and exposed to full-day illumination on alternate days. The controls were exposed to the full illumination period each day. Additional treatments included daily darkening of the plants from 10 a. m. to 3 p. m. or 10 a. m. to 2 p. m. and exposure to day lengths of 5, 8, 10, and 12 hours. The short-day plants used were Biloxi soybeans, *Tithonia tubaeformis* (Mill.) Blake, *Helianthus angustifolius* L., *Cosmos bipinnatus* Cav., and *Perilla frutescens* (L.) Britton. The long-day group was represented by *Monarda didyma* L. and *Steironema ciliatum* (L.) Raf. The effects of the several treatments on date of first flowering and on average height of the plants are shown in Table 2.

TABLE 1.—*Time of flowering and growth of plants of the short-day, indifferent, and long-day types exposed on alternate days during the summer months to full-day and to 10-hour day illumination as compared with daily full-day illumination*

Type and species or variety	Treatment	First day of test	First flowering	Average height at flowering
Short-day type:				*Inches*
Peking soybeans	Full-day and 10-hour day alternations	June 29	July 24	6
Control	Full day daily	do	Aug. 10	12
Toyko soybeans	Full-day and 10-hour day alternations	do	Aug. 2	13
Control	Full day daily	do	Aug. 17	21
Biloxi soybeans	Full-day and 10-hour day alternations	do	Aug. 10	15
Control	Full day daily	do	Sept. 9	28
Cosmos sulphureus	Full-day and 10-hour day alternations	June 23	Aug. 30	38
Control	Full day daily	do	Oct. 15	
Perilla frutescens	Full-day and 10-hour day alternations	June 17	Aug. 11	24
Control	Full day daily	do	Sept. 9	30
Indifferent type:				
Mandarin soybeans	Full-day and 10-hour day alternations	June 29	July 23	7
Control	Full day daily	do	July 28	9
Long-day type:				
Impatiens balsamina	Full-day and 10-hour day alternations	June 17	July 12	9
Control	Full day daily	do	July 10	7

TABLE 2.—*Effects of complete darkening on alternate days and of daily midday darkening on time of flowering and growth of short-day and long-day plants, as compared with effects of exposure to the full day and to various short days*

Type and species or variety	Duration of daily illumination	First day of test	First flowering	Height of plants	
				Measured on—	Average
Short-day type:					*Inches*
Tithonia tubaeformis	5 hours	June 19		Aug. 2	32
Do	8 hours	do	July 25	do	53
Do	10 hours	do	do	do	58
Do	12 hours	do	Aug. 22	do	53
Do	Darkened on alternate days	do	Sept. 8	do	32
Do	Darkened 10 a. m.–3 p. m	do	Nov. 10	do	33
Control	Full day	do	do	do	45
Helianthus angustifolius	5 hours	June 12	Aug. 1	do	22
Do	8 hours	do	July 18	do	23
Do	10 hours	do	July 24	do	27
Do	Darkened on alternate days	do	Aug. 14	do	19
Do	Darkened 10 a. m.–3 p. m	do	Oct. 9	do	13
Control	Full day	do	Oct. 7	do	16.5
Perilla frutescens	10 hours	June 29	July 24	July 24	15
Do	Darkened on alternate days	June 9	July 17	July 17	14.5
Do	Darkened 10 a. m.–3 p. m	do	Sept. 1		
Control	Full day	do	Sept. 2		
Giant Crimson Cosmos	Darkened on alternate days	do	Aug. 4	Aug. 4	18
Do	Darkened 10 a. m.–3 p. m	do	Oct. 7	Oct. 7	72
Control	Full day	do	Sept. 28	Sept. 28	84
Biloxi soybeans	Darkened on alternate days	June 8	Aug. 3	Aug. 3	12
Do	Darkened 10 a. m.–3 p. m	do	Sept. 18	Sept. 18	8
Control	Full day	do	Sept. 11	Sept. 11	35
Long-day type:					
Monarda didyma	10 hours	Mar. 9		June 21	15
Do	Darkened 10 a. m.–2 p. m	do	June 21	do	26
Control	Full day	do	June 15	June 15	36
Steironema ciliatum	10 hours	Mar. 25			
Do	Darkened 10 a. m.–2 p. m	do	June 20	June 20	35
Control	Full day	do	June 29	June 29	28

In order to obtain an indication of the effects of further shortening the light-and-darkness alternations, the group of plants listed in Table

1 was darkened each day from 10 a. m. to noon and again from 2 to 4 p. m. during the summer and early fall. The controls were exposed to the full day length. The date of first flowering and average height of plants are shown in Table 3.

TABLE 3.—*Time of flowering and growth of plants of the short-day, indifferent, and long-day types darkened from 10 a. m. till noon and again from 2 to 4 p. m. each day during the summer months, as compared with full-day illumination*

Type and species or variety	Treatment	First day of test	First flowering	Average height at flowering
				Inches
Short-day type:				
Peking soybeans	Darkened twice a day	June 29	Aug. 10	9
Control	Full-day illumination	do	do	12
Tokyo soybeans	Darkened twice a day	do	Aug. 30	22
Control	Full-day illumination	do	Aug. 17	21
Biloxi soybeans	Darkened twice a day	do	Sept. 23	11
Control	Full-day illumination	do	Sept. 9	28
Cosmos sulphureus	Darkened twice a day	June 24	Oct. 11	24
Control	Full-day illumination	do	Oct. 20	51
Perilla frutescens	Darkened twice a day	June 30	do	17
Control	Full-day illumination	do	Oct. 16	25
Indifferent type:				
Mandarin soybeans	Darkened twice a day	June 29	July 29	8
Control	Full-day illumination	do	July 28	9
Long-day type:				
Impatiens balsamina	Darkened twice a day	June 17	July 10	4
Control	Full-day illumination	do	do	9

EXPERIMENTS WITH ARTIFICIAL LIGHT

In the experiments with artificial light, a number of separate tests were first conducted in which all light treatments involved the same number of hours of total illumination daily, namely, 12 hours of light in the 24-hour cycle. Thus the total number of hours of illumination was the same as would be received by plants exposed to a 12-hour day. The first experiment in this group involved alternations of light and darkness of 6 hours in some instances and 4 hours in others, as compared with a 12-hour alternation. The long-day plant, *Rudbeckia bicolor* Nutt., and the Peking, Biloxi, and Mandarin varieties of soybeans were employed. The results are summarized in Table 4.

TABLE 4.—*Time of flowering and growth of plants exposed to 6-hour and 4-hour alternations of artificial light and darkness, as compared with 12-hour alternations*

Type and species or variety	Length of alternation	Duration of test	Time required for flowering	Average height at flowering
	Hours	*Days*	*Days*	*Inches*
Long-day type:				
Rudbeckia bicolor	6	51	34	33
Control	12	51	29	33
Indifferent type:				
Mandarin soybeans	6	51	34	45
Control	12	51	29	25
Mandarin soybeans	4	37	35	30
Control	12	37	21	24
Short-day type:				
Peking soybeans	6	51	(a)	42
Control	12	51	29	29
Peking soybeans	4	37	(a)	30
Control	12	37	21	20.5
Biloxi soybeans	6	51	(a)	40
Control	12	51	43	51

[a] Had not flowered at termination of experiment.

The next step in the investigations was the use of much shorter alternations of light and darkness, retaining the 12-hour alternation as a control. The three light intervals employed in addition to the control interval were 1 hour, 1 minute, and 15 seconds, respectively. In some of the tests continuous illumination also was used for the sake of comparison. In these experiments soybeans, Rudbeckia, Perilla, and Coleus were used. In some instances the green and the dry weights of the plants were obtained at the end of the test. Young seedlings of soybeans, Rudbeckia, and Perilla were employed, while for the Coleus cuttings that had already made considerable growth were used. This Coleus is a short-day type, flowering in winter. The results of the test are shown in Table 5. Under the shorter light intervals the soybeans presented a pale, etiolated appearance, and the stems were of a spindling, stringy type of growth, particularly under the 1-minute intervals. In Perilla the leaves showed the deepest purple color under continuous illumination. Under the 12-hour illumination the leaves were almost pure green in color, as is usually the case when the plants are in the flowering condition. The 1-hour light period gave larger, finer leaves than the 1-minute or the 15-second intervals. In Coleus the 12-hour light period gave normally colored, large, healthy leaves, while continuous light and the shorter intervals resulted in decided etiolation and poor coloration. Rudbeckia suffered a reduction in growth under the shorter light alternations, including the 1-hour period; and under the 1-minute exposure the young seedlings were unable to survive.

For the purpose of obtaining a more detailed picture of the comparative effects on plants of alternations of various short periods of light and darkness a series of eight artificially lighted compartments was brought into use. The 12-hour light period was retained as a control, and the experimental periods of light and darkness used in the remaining seven compartments were 5 seconds, 15 seconds, 1 minute, 5 minutes, 15 minutes, 30 minutes, and 1 hour, respectively. In this group of experiments the short-day type of plant was represented by *Cosmos sulphureus*, the long-day type by *Rudbeckia bicolor, Delphinium ajacis* L., *Althaea rosea* Cav., and *Beta vulgaris* L., while of two additional species that were included, *Fagopyrum vulgare* Hill and *Ipomoea batatas* (L.) Poir., the former may be classed as belonging to the indifferent type, and little is known as yet concerning the proper classification of the latter. The results of the tests with respect to time of flowering, height attained, and the green and dry weights for the several species are summarized in Table 6.

TABLE 5.—*Time of flowering and growth of plants exposed to equal alternations of artificial light and darkness of 15 seconds, 1 minute, and 1 hour, respectively, as compared with 12-hour alternations and continuous light*

Type and species or variety	Length of alternations	Duration of test	First day of test	Time required for flowering	Height of plants: Measured on—	Height of plants: Average	Average green weight per plant: Entire plant	Average green weight per plant: Tops	Average green weight per plant: Roots	Average dry weight of 10 plants: Entire plants	Average dry weight of 10 plants: Tops	Average dry weight of 10 plants: Roots	Average dry weight of 10 plants: Ratio of tops to roots
		Days		*Days*		*Inches*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	
Indifferent type:													
Mandarin soybeans	15 seconds	37	June 25		July 17	27							
Do	1 minute	37	do		do	27							
Do	1 hour	37	do		do	27							
Control	12 hours	37	do	21	do	27							
Short-day type:													
Biloxi soybeans	15 seconds	37	do		do	27							
Do	1 minute	37	do		do	27							
Do	1 hour	37	do		do	27							
Control	12 hours	37	do	34	do	27							
Biloxi soybeans	15 seconds	20	May 18		June 6	17.5	7.0	5.4	1.6	7.6	6.7	0.9	7.4
Do	1 minute	20	do		do	19	4.2	2.8	1.4	3.7	3.2	.5	6.4
Do	1 hour	20	do		do	16	12.4	7.8	4.6	12.5	10.0	2.5	4.0
Control	12 hours	20	do		do	13	11.2	7.0	4.2	11.8	8.9	2.9	3.1
Do	Continuous light	20	do		do	15	12.4	7.8	4.6	14.7	11.1	3.6	3.1
Perilla frutescens	15 seconds	43	June 7		July 20	26	31.2	23.5	7.7	41.0	33.2	7.8	4.3
Do	1 minute	43	do		do	21.5	21.9	17.8	4.1	26.3	22.0	4.3	5.1
Do	1 hour	43	do		do	18.5	40.2	30.9	9.3	53.0	42.8	10.2	4.2
Control	12 hours	43	do	32	do	37	58.7	49.8	8.9	69.3	58.8	10.5	5.6
Do	Continuous light	43	do		do	38	68.6	47.2	21.4	104.3	80.0	24.3	3.3
Coleus sp	15 seconds	43	do		do	9	41.5	36.4	5.1	27.8	23.3	4.5	5.2
Do	1 minute	43	do		do	9.5	48.0	43.8	4.2	28.5	25.0	3.5	7.1
Do	1 hour	43	do		do	10	46.4	42.3	4.1	31.8	27.5	4.3	6.4
Control	12 hours	43	do		do	24	75.0	60.0	15.0	50.8	45.5	5.3	8.6
Do	Continuous light	43	do		do	17	68.2	59.0	9.2	46.2	41.2	5.0	8.2
Long-day type:													
Rudbeckia bicolor	15 seconds	56	Mar. 23	37	May 18	20	14.0						
Do	1 minute	56	do	([a])									
Do	1 hour	56	do	33	May 18	20	16.8						
Control	12 hours	56	do	56	do	20	28.0						
Do	Continuous light	56	do	31	do	40	36.9						

[a] Died.

TABLE 6.—*Time of flowering and growth of plants exposed to equal alternations of artificial light and darkness of 5 seconds, 15 seconds, 1 minute, 15 minutes, 30 minutes, and 1 hour, respectively, as compared with 12-hour alternations*

Type and species or variety	Length of alternations	Duration of test	First day of test	Time required for flowering	Height of plants: Measured on—	Height of plants: Average	Average green weight per plant: Entire plant	Average green weight per plant: Tops	Average green weight per plant: Roots	Average dry weight of 10 plants: Entire plants	Average dry weight of 10 plants: Tops	Average dry weight of 10 plants: Roots	Average dry weight of 10 plants: Ratio of tops to roots
		Days		*Days*		*Inches*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	
Short-day type:													
Cosmos sulphureus	5 seconds	42	Nov. 1		Dec. 10	31	16.0	14.8	1.2	14.3	13.0	1.3	10.0
Do	15 seconds	42	do		do	13	1.9	1.8	.1	1.5	1.4	.1	14.0
Do	1 minute	42	do		do	7	.5	.4	.1	.6	.5	.1	5.0
Do	5 minutes	42	do		do	8.5	1.1	1.0	.1	.9	.8	.1	8.0
Do	15 minutes	42	do		do	18	4.0	3.7	.3	3.3	3.0	.3	10.0
Do	30 minutes	42	do		do	20	3.3	3.1	.2	2.7	2.4	.3	8.0
Do	1 hour	42	do		do	22	11.0	10.0	1.0	9.9	9.0	.9	10.0
Control	12 hours	42	do		do	45	70.1	65.3	4.8	47.8	43.8	4.0	11.0
Long-day type:													
Rudbeckia bicolor	5 seconds	42	do	40	do	30	53.5	49.6	3.9	56.7	53.0	3.7	14.3
Do	15 seconds	42	do	40	do	25	30.5	26.8	3.7	38.7	35.0	3.0	11.7
Do	1 minute	42	do	40	do	17	15.0	14.0	1.0	17.1	15.5	1.6	9.7
Do	5 minutes	42	do	36	do	24	19.2	18.1	1.1	23.3	21.4	1.9	11.3
Do	15 minutes	42	do	36	do	28.5	27.3	25.1	2.2	29.6	26.6	3.0	8.9
Do	30 minutes	42	do	40	do	25	17.9	16.7	1.2	19.7	18.1	1.6	11.3
Do	1 hour	42	do	40	do	22	29.4	27.5	1.9	30.2	27.5	2.7	10.2
Control	12 hours	42	do		do	12	43.1	40.1	3.0	29.1	26.4	2.7	9.8
Delphinium ajacis	5 seconds	50	Dec. 13	37	Feb. 1	46	23.8	21.3	2.5	52.5	48.5	4.0	12.1
Do	15 seconds	50	do	37	do	40	20.0	17.8	2.2	44.8	41.8	3.0	13.9
Do	1 minute	50	do	41	do	33	19.0	17.5	1.5	43.8	40.8	3.0	13.6
Do	5 minutes	50	do	45	do	23	10.0	9.0	1.0	24.0	21.0	3.0	7.0
Do	15 minutes	50	do	41	do	27	11.5	10.2	1.3	27.5	25.0	2.5	10.0
Do	30 minutes	50	do	42	do	33.5	18.3	16.5	1.8	38.0	35.5	2.5	14.2
Do	1 hour	50	do	48	do	39	25.8	22.5	3.3	52.5	47.0	5.5	8.5
Control	12 hours	50	do	41	do	42	28.9	25.6	3.3	52.3	47.3	5.0	9.4
Althaea rosea	5 seconds	50	do		do	31	103.0	88.0	15.0	130.0	97.0	33.0	2.9
Do	15 seconds	50	do		do	30	85.7	76.3	9.4	95.6	78.3	17.3	4.5
Do	1 minute	50	do		do	15	33.0	29.0	4.0	34.3	28.0	6.3	4.4
Do	5 minutes	50	do		do	11.5	34.0	31.0	3.0	38.0	31.0	7.0	4.4
Do	15 minutes	50	do		do	20	65.7	58.0	7.7	68.3	57.7	10.6	5.4
Do	30 minutes	50	do		do	27	97.3	84.3	13.0	112.0	90.0	22.0	4.1
Do	1 hour	50	do		do	23	72.0	63.0	9.0	86.0	68.3	17.7	3.5
Control	12 hours	50	do		do	28	146.0	123.0	23.0	190.0	131.0	59.0	2.2
Beta vulgaris	5 seconds	75	Mar. 22		June 5	[a] 18	77.5	38.4	39.1	88.8	37.0	51.8	.7
Do	15 seconds	75	do		do	[a] 15	29.8	16.6	13.2	35.3	19.1	16.2	1.2
Do	1 minute	75	do	51	do	[a] 16	49.8	32.6	17.2	48.9	29.0	19.9	1.4
Do	5 minutes	75	do		do	[a] 20	68.5	49.5	19.0	70.0	42.9	27.1	1.5
Do	15 minutes	75	do		do	[a] 8	6.4	5.6	.8	3.7	3.6	.1	36.0

Do	30 minutes	75	do		do	[a] 11	18.6	13.9	4.7	15.5	10.9	4.6	2.4
Do	1 hour	75	do		do	[a] 14	41.0	25.4	15.6	44.0	23.4	20.6	1.1
Control	12 hours	75	do		do	[a] 17	68.0	31.1	36.9	94.6	33.2	61.4	.5
Indifferent type:													
Fagopyrum vulgare	5 seconds	34	Feb. 7	24	Mar. 12	58	45.2	44.2	1.0	42.4	40.7	1.7	23.9
Do	15 seconds	34	do	34	do	43	18.5	18.2	.3	14.8	14.3	.5	28.6
Do	1 minute	34	do	23	do	36	12.0	11.6	.4	8.8	8.2	.6	13.7
Do	5 minutes	34	do	24	do	38	20.0	19.5	.5	16.0	15.2	.8	19.0
Do	15 minutes	34	do	29	do	28	10.6	10.3	.3	7.9	7.6	.3	25.3
Do	30 minutes	34	do	24	do	33	15.5	15.1	.4	11.1	10.6	.5	21.2
Do	1 hour	34	do	29	do	40	20.6	19.7	.9	15.5	14.4	1.1	13.1
Control	12 hours	34	do	21	do	54		32.3		31.1	29.4	1.7	17.3
Type undetermined:													
Ipomoea batatas	5 seconds	98	Feb. 3		May 11	49	248.0	146.0	102.0	[b] 644.0	122.0	26.0	.23
Do	15 seconds	98	do		do	49	201.0	140.0	61.0	[b] 434.0	124.0	16.0	.40
Do	1 minute	98	do		do	52	156.0	135.0	21.0	[b] 136.0	112.0	13.0	4.7
Do	5 minutes	98	do		do	60	105.0	92.5	12.5	76.5	69.5	7.0	9.9
Do	15 minutes	98	do		do	35	18.0	12.5	5.5	20.5	16.0	4.5	3.6
Do	30 minutes	98	do		do	32	32.0	27.0	5.0	37.0	32.0	5.0	6.4
Do	1 hour	98	do		do	60	43.0	35.0	8.0	48.5	44.0	4.5	9.8
Control	12 hours	98	do		do	62	352.0	221.0	131.0	[b] 931.0	179.0	32.0	.24

[a] Length of longest leaves.

[b] Includes weights of "tubers," which are not included in the column "roots."

The Rudbeckia seedlings used were somewhat older than those employed in the previous experiment, and the flowering stage was reached under all the short alternations. Under the light periods ranging from 1 minute to 30 minutes the plants were chlorotic, but under all other light treatments they showed the normal dark-green color. In Cosmos the same general relations existed, the etiolation being most marked under the 1-minute, 5-minute, and 15-minute light intervals, and the normal color showing under the 5-second, 1-hour, and 12-hour intervals. Delphinium seemed to be most adversely affected by the 5-minute light interval, and under this period only one plant survived. First-year seedlings of *Althaea rosea* were used in the test, and none flowered or developed flowering stems although the leaves developed abnormally long petioles. The 5-second and 12-hour plants showed the darkest green color, the 15-second and 1-hour individuals being next, and the others showing a decidedly lighter, yellowish green color. Only one seedling survived under the 5-minute light interval. For the experiment with the table beet (*Beta vulgaris*) young seedlings of the Early Eclipse variety were used. A single plant under the 1-minute light interval flowered, and one plant developed a stem under the 15-second light period. The heights recorded in Table 6 refer to the lengths of the longest leaves. The smallest plants, with leaves of poorest color, were those under the 15-minute light interval. The buckwheat (*Fagopyrum vulgare*) showed most etiolation under the 15-minute light interval, with progressive improvement in the green color under both longer and shorter intervals. In the sweetpotato (*Ipomoea batatas*) the foliage was yellow under the 15-minute, 30-minute, and 1-hour intervals, and no tubers or thickened roots were formed under these exposures or under the 5-minute interval. The best development of tubers occurred under the 12-hour and the 5-second intervals.

In all the foregoing experiments with artificial light the total number of hours of light and darkness received daily by the plants was the same. In the following series of tests the same plants and equipment were used, but the intervals of light and darkness were of unequal value, although the complete cycles remained the same as in the preceding experiments. In the first group of tests the interval of light was just half that of darkness in each case. For example, instead of the previous alternation of 5 seconds of light and 5 seconds of darkness, the new cycle consisted of 3⅓ seconds of light and 6⅔ seconds of darkness; and in place of 1 hour each of light and of darkness, the new cycle was composed of 40 minutes of light and 80 minutes of darkness. In all cases the total daily illumination was 8 hours. As a control, an 8-hour light period was employed. Biloxi soybeans, *Cosmos sulphureus*, and *Rudbeckia bicolor* were used for the tests. The soybeans did not long survive the unfavorable effects of the ⅔-minute, 3⅓-minute, and 10-minute light intervals, and the Cosmos soon perished under these intervals and also under the 10-second and 20-minute intervals, so that data on comparative weights of the plants could not be obtained. Under these intervals the heights of the soybeans and Cosmos recorded were those reached at the time of death, while in other cases the heights attained at the end of the experiment are reported. The results of the tests are summarized in Table 7. None of the soybeans presented a healthy appearance except those exposed to the 8-hour light period, and Cosmos also showed unfavorable effects from the shorter light intervals. Rudbeckia showed a more or less normal green color under the 3⅓-second, 10-second, and 8-hour light periods.

In the final series of experiments the durations of the intervals used in the preceding tests were reversed, so that in each complete cycle the light interval was double the darkness interval, and the total daily illumination was 16 hours in each case. In the first experiment Rudbeckia and Cosmos were used. In this experiment an installation for automatic control of temperature and relative humidity was employed. A current of conditioned air sufficiently rapid to insure substantially the same temperature and humidity in each compartment was forced through the light compartments. On four unusually warm days the midday temperatures reached 75° to 80° F. and on a single day 90°. At other times the temperature was held at 71°±2° and the relative humidity was maintained at 53±2 per cent. The weekly mean temperature ranged from 71° to 75° during the period of the test. In the early morning of the thirty-fifth day there was a breakdown in the control system that caused the temperature to rise above 100° for a few hours. It was therefore decided to discontinue the experiment. The Cosmos plants were so badly dried out by the excessive heat that satisfactory data on weights of the plants could not be obtained. The Rudbeckia, however, showed no sign of material injury.

The increased illumination produced obvious improvement in nutrition and growth under all treatments, as compared with the results in the preceding experiment; but the contrasts in condition of the plants under the different light treatments were more or less similar to those in the preceding experiment. The Rudbeckia plants had not flowered when the test was interrupted, but all had formed flower buds. None of the Cosmos plants showed flower buds. The results of the experiment are summarized in Table 8. A similar experiment with Mandarin and Peking soybeans is also shown in Table 8. In this case an effort was made to maintain the temperature at 77° F. and the relative humidity at 55 per cent so far as weather conditions would permit. As it happened, the weather was unseasonably warm for a considerable portion of the time so that the temperature was beyond control, and toward the end of the experiment it became necessary to cut off all artificial heat.

TABLE 7.—*Time of flowering and growth of plants exposed to various short alternations of artificial light and darkness in a ratio of 1 to 2, as compared with alternations of 12 hours each of light and darkness or 8 hours of light and 16 hours of darkness*

Type and species or variety	Length of alternations		Duration of test	Time required for flowering	Average height of plants	Average green weight per plant			Average dry weight of 10 plants			Ratio of tops to roots
	Light	Darkness				Entire plant	Tops	Roots	Entire plants	Tops	Roots	
			Days	*Days*	*Inches*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*
Short-day type:												
Biloxi soybeans	3⅓ seconds	6⅔ seconds	41	--------	30	--------	--------	--------	--------	--------	--------	--------
Do	10 seconds	20 seconds	41	--------	25	--------	--------	--------	--------	--------	--------	--------
Do	⅔ minute	1⅓ minutes	41	--------	14	--------	--------	--------	--------	--------	--------	--------
Do	3⅓ minutes	6⅔ minutes	41	--------	19	--------	--------	--------	--------	--------	--------	--------
Do	10 minutes	20 minutes	41	--------	17.5	--------	--------	--------	--------	--------	--------	--------
Do	20 minutes	40 minutes	41	--------	25	--------	--------	--------	--------	--------	--------	--------
Do	⅔ hour	1⅓ hours	41	--------	30	--------	--------	--------	--------	--------	--------	--------
Control	12 hours	12 hours	41	36	32	--------	--------	--------	--------	--------	--------	--------
Cosmos sulphureus	3⅓ seconds	6⅔ seconds	39	--------	13	--------	--------	--------	--------	--------	--------	--------
Do	10 seconds	20 seconds	39	--------	5	--------	--------	--------	--------	--------	--------	--------
Do	⅔ minute	1⅓ minutes	39	--------	5	--------	--------	--------	--------	--------	--------	--------
Do	3⅓ minutes	6⅔ minutes	39	--------	6.5	--------	--------	--------	--------	--------	--------	--------
Do	10 minutes	20 minutes	39	--------	5	--------	--------	--------	--------	--------	--------	--------
Do	20 minutes	40 minutes	39	--------	7	--------	--------	--------	--------	--------	--------	--------
Do	⅔ hour	1⅓ hours	39	--------	13	--------	--------	--------	--------	--------	--------	--------
Control	8 hours	16 hours	39	--------	32	--------	--------	--------	--------	--------	--------	--------
Long-day type:												
Rudbeckia bicolor	3⅓ seconds	6⅔ seconds	50	35	32	9.7	9.2	0.5	9.3	8.8	0.5	17.6
Do	10 seconds	20 seconds	50	35	28.5	7.7	7.3	.4	8.0	7.6	.4	19.0
Do	⅔ minute	1⅓ minutes	50	38	18	4.3	4.1	.2	5.8	5.6	.2	28.0
Do	3⅓ minutes	6⅔ minutes	50	40	18.5	4.8	4.6	.2	5.6	5.3	.3	17.7
Do	10 minutes	20 minutes	50	42	21	5.0	4.8	.2	3.8	3.6	.2	18.0
Do	20 minutes	40 minutes	50	45	26	6.4	6.1	.3	5.0	4.6	.4	11.5
Do	⅔ hour	1⅓ hours	50	49	17	7.9	7.5	.4	6.3	5.9	.4	14.8
Control	8 hours	16 hours	50	--------	8	30.0	26.3	3.7	28.1	24.5	3.6	6.8

TABLE 8.—*Time of flowering and growth of plants exposed to various short alternations of artificial light and darkness in a ratio of 2 to 1, as compared with an alternation of 16 hours of light and 8 hours of darkness*

Type and species or variety	Length of alternations: Light	Length of alternations: Darkness	Duration of test	Time required for flowering	Average height of plants	Average green weight per plant: Entire plant	Average green weight per plant: Tops	Average green weight per plant: Roots	Average dry weight of 10 plants: Entire plants	Average dry weight of 10 plants: Tops	Average dry weight of 10 plants: Roots
			Days	*Days*	*Inches*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*
Short-day type:											
Cosmos sulphureus	6⅔ seconds	3⅓ seconds	36		25						
Do	20 seconds	10 seconds	36		21						
Do	1⅓ minutes	⅔ minute	36		14.5						
Do	6⅔ minutes	3⅓ minutes	36		9						
Do	20 minutes	10 minutes	36		14						
Do	40 minutes	20 minutes	36		18						
Do	1⅓ hours	⅔ hour	36		22						
Control	16 hours	8 hours	36		23						
Peking soybeans	6⅔ seconds	3⅓ seconds	42		50	8.1	7.5	0.6	13.5	12.8	0.7
Do	20 seconds	10 seconds	42		50	10.4	9.6	.8	12.7	11.9	.8
Do	1⅓ minutes	⅔ minute	42		50	15.3	14.3	1.0	20.9	19.9	1.0
Do	6⅔ minutes	3⅓ minutes	42		50	10.2	9.1	1.1	13.7	12.9	.8
Do	20 minutes	10 minutes	42		50	9.2	8.5	.7	12.7	11.8	.9
Do	40 minutes	20 minutes	42		50	8.2	7.6	.6	11.7	11.1	.6
Do	1⅓ hours	⅔ hour	42		42	11.6	10.7	.9	16.2	15.1	1.1
Control	16 hours	8 hours	42		44	12.4	11.6	.8	15.1	14.0	1.1
Long-day type:											
Rudbeckia bicolor	6⅔ seconds	3⅓ seconds	36	[a] 35	25	23.2	22.0	1.2	21.4	19.9	1.5
Do	20 seconds	10 seconds	36	[a] 35	21	16.1	15.0	1.1	17.1	15.7	1.4
Do	1⅓ minutes	⅔ minute	36	[a] 35	20	18.1	16.8	1.3	14.4	12.9	1.5
Do	6⅔ minutes	3⅓ minutes	36	[a] 35	14.5	14.0	12.3	1.7	15.0	13.0	2.0
Do	20 minutes	10 minutes	36	[a] 35	18	16.3	14.7	1.6	16.6	14.7	1.9
Do	40 minutes	20 minutes	36	[a] 35	22	15.9	14.8	1.1	16.9	14.9	2.0
Do	1⅓ hours	⅔ hour	36	[a] 35	22	29.9	27.6	2.3	30.4	27.1	3.3
Control	16 hours	8 hours	36	[a] 35	23	25.4	23.7	1.7	18.9	17.0	1.9
ndifferent type:											
Mandarin soybeans	6⅔ seconds	3⅓ seconds	42		50	12.7	11.7	1.0	15.7	14.9	.8
Do	20 seconds	10 seconds	42		50	17.1	16.1	1.0	23.8	22.6	1.2
Do	1⅓ minutes	⅔ minute	42		50	13.5	12.3	1.2	17.1	15.8	1.3
Do	6⅔ minutes	3⅓ minutes	42		50	13.9	13.0	.9	18.7	17.8	.9
Do	20 minutes	10 minutes	42		50	14.4	13.4	1.0	22.8	21.7	1.1
Do	40 minutes	20 minutes	42		50	12.6	11.9	.7	16.9	16.1	.8
Do	1⅓ hours	⅔ hour	42		46	15.4	14.4	1.0	20.5	19.6	.9
Control	16 hours	8 hours	42	32	50	22.9	21.6	1.3	35.2	33.0	2.2

[a] Flower buds were present but none had opened.

A summary of the thermographic records obtained in the light chambers during the experiments is given in Table 9. The data include the maximum and minimum temperatures recorded in each series; also the mean maximum, the mean minimum, and the approximate mean or average of the latter two values.

TABLE 9.—*Temperature in light-proof chambers used in experiments summarized in Tables 5 to 8*

Table No. and plant	Temperature of light chambers (° F.)				
	Maximum	Minimum	Mean maximum	Mean minimum	Mean of mean maximum and mean minimum
Table 5:					
Mandarin and Biloxi soybeans	88	64	82	71	76
Rudbeckia	99	69	88	72	80
Biloxi soybeans	84	65	80	67	74
Perilla and Coleus	86	66	84	70	77
Table 6:					
Rudbeckia and Cosmos	81	65	75	69	72
Delphinium and Althaea	77	64	72	68	70
Fagopyrum	79	65	74	69	72
Beta	80	60	73	67	70
Ipomoea	80	62	74	67	71
Table 7:					
Biloxi soybeans and Cosmos	85	70	83	76	80
Rudbeckia	87	61	78	71	75
Table 8:					
Rudbeckia and Cosmos	90	69	74	71	73
Mandarin and Peking soybeans	99	62	82	73	78

DISCUSSION OF RESULTS

In nature, plants are normally exposed to a 24-hour cycle of day and night, there being, of course, only one period of light and one of darkness in the cycle. Under these circumstances the variation in relative length of day and night dependent upon latitude and season may profoundly affect the development of the plant. By excluding the daylight of early morning or late afternoon so as to shorten the daily light period, on the one hand, and by using artificial light to prolong the daily illumination, on the other hand, the distinctive effects of short days and long days on flowering and fruiting and other features of growth may be reproduced, under suitable conditions, in any latitude and at any season. Results of the experiments presented in this paper, however, indicate that different variations from the 24-hour cycle of light and darkness may produce radically different effects, even though the total number of hours of illumination is the same.

In previous experiments it has been shown that diminishing the number of hours of the midsummer daylight to which plants are continuously exposed hastens the flowering of short-day plants and retards that of long-day plants, whereas an equal period of darkening in the middle of the day, by which the short day is divided into two parts, has little or no effect on the time of flowering.

Table 1 summarizes the results of an experiment in which short-day and long-day plants were subjected on alternate days to a full day and to a 10-hour day of sunlight. These data show that under the conditions that prevailed the interposition of the long day did not nullify the hastening effect of the short day on the flowering of the short-day plants, while it did very nearly prevent the retarding action on the long-day plants. Reduction in height attained was associated with early flowering under the long-day and short-day alternations.

When the 24-hour cycle of day and night was replaced by a 48-hour cycle (illumination on alternate days, see Table 2), consisting of about 15 hours of light and 33 hours of darkness, there was a pronounced hastening action on flowering in five typical short-day plants. The short-day effect, therefore, is still in evidence, although comparison with the results of 8, 10, and 12 hours of light daily shows that the hastening effect has been much reduced in Tithonia and Helianthus.

The present data, however, bear chiefly on the effects of cycles of light and darkness much shorter than the 24-hour cycle provided

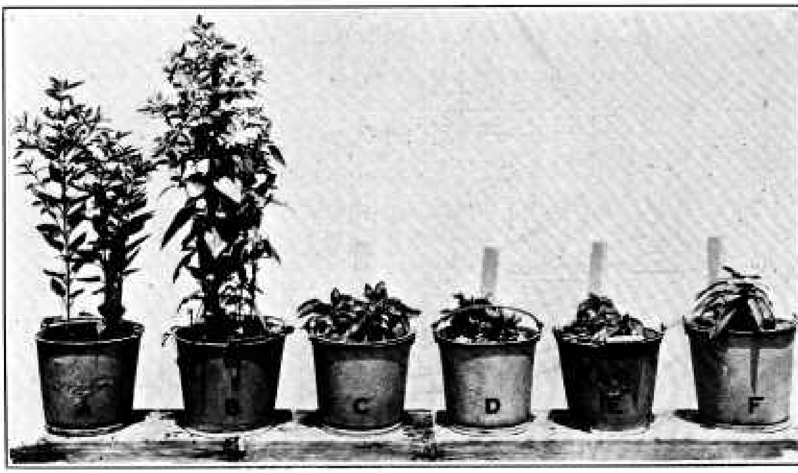

FIGURE 1.—Fringed loosestrife (*Steironema ciliatum* (L.) Raf.), a long-day plant, exposed to the full day length of late spring and early summer and to regulated daily light periods, beginning March 25. The illumination conditions were: A, Full day; B, darkened 10 a. m. to 2 p. m.; C, 12-hour day; D, 10-hour day; E, 8-hour day; F, 5-hour day. Midday darkening (B) failed to suppress flowering, the usual effect of the short day (C–F)

by nature. The results in Table 2 bring out the remarkable fact that darkening during the middle of the day for as long as 5 hours has either no effect at all or only a slight effect on the time of flowering as compared with the full day length of summer. This is in sharp contrast with 8, 10, or 12 hours of uninterrupted daily illumination. In earlier experiments much the same results were obtained by a 2-hour midday darkening. All short-day plants studied have failed to show response to midday darkening with respect to flowering; that is, they have behaved about the same as when exposed to the full day length. The majority though not all of the long-day plants tested also have failed to respond to the midday darkening.

The ineffectiveness of midday darkening in delaying elongation of flowering stems in Steironema is shown in Figure 1. It will be observed that the effect of this treatment was to break up the normal 24-hour cycle, for in each 24-hour period the plants were subjected to two intervals of light and two intervals of darkness. The Steironema plants exposed to the full day length, beginning March 25, began flowering June 29; those darkened in the middle of the day began flowering nine days earlier; all other treatments suppressed flowering. Midday darkening, even though prolonged, as a rule does not produce the usual effects of a short day on either the long-day or the short-day type of plant.

Further evidence that relatively short cycles of light and darkness tend to produce effects similar to those of a long day or of continuous light in that they favor flowering in long-day plants but not in short-day plants is furnished by the results shown in Table 3. Three daily light periods, aggregating about 10 hours in duration, failed to materially change the date of flowering in the long-day or indifferent types, and in the short-day plants either failed to change or actually delayed the date of flowering, as compared with the effect of the full summer-day length. With one exception, the darkening had the effect of reducing the heights of the plants.

EFFECTS ON FLOWERING

As regards the normal 24-hour cycle, an even division into 12 hours of daylight and 12 hours of darkness permits of eventual flowering and fruiting in the majority of plants of both the long-day and short-day types. As a rule, however, the 12-hour day is above the optimum for flowering in the short-day group and below the optimum for the long-day group. In studying with artificial illumination the effects of relatively short cycles involving an even distribution of light and darkness, the 12-hour day naturally was employed as the control. In the long-day plant Rudbeckia, a 6-hour alternation of light and darkness somewhat hastened the appearance of blossoms. (Table 4.) In the short-day varieties of soybeans, flowering was decidedly delayed by 6-hour and 4-hour alternations. The effects on height attained by the plants were somewhat variable.

Results obtained with alternations of light and darkness of 1 hour or less soon showed that a distinction must be drawn between effects on reproduction and those on growth and general nutrition of the plant. In the experiments with alternations of light and darkness of 1 hour, 1 minute, and 15 seconds (Table 5) and those including alternations of 1 hour, 30 minutes, 15 minutes, 5 minutes, 1 minute, 15 seconds, and 5 seconds (Table 6), it will be observed that flowering did not take place in the short-day plants—soybeans, Perilla, Coleus and Cosmos—under any of these exposures, the effect being that of a long day or continuous light. Under a 12-hour day all flowered except Coleus and Cosmos, and these had formed flower buds when the experiment was stopped. Of the long-day plants used, it is evident that Rudbeckia flowered much earlier under all the short alternations than under the 12-hour day, and about the same time as under continuous illumination. Delphinium, a less pronounced long-day plant, flowered about the same time under all of the light periods. The first-year plants of Althaea, another long-day type, did not flower under any of the alternations. The beet (Beta) is a long-day plant and when exposed to a long day and a cool temperature may behave as an annual. Under the warm temperature of the present experiment a single plant flowered with the

1-minute alternations, and a single seed stalk was formed with the 15-second alternations, although it did not flower. These results show a tendency of the plants under the short alternations to behave as when exposed to a long day. Buckwheat (Fagopyrum), which is relatively indifferent to changes in day length with respect to flowering, apparently was slightly delayed in flowering by the short alternations. The sweetpotato (Ipomoea) is ordinarily a nonflowering type of plant at the higher latitudes, and failed to blossom in the present experiment.

With the cycles remaining the same as in the preceding tests but with the light periods having one-half the value of the periods of darkness (Table 7), Rudbeckia still flowered under all the short alternations; but flowering was progressively delayed with increase in the length of the alternations. Biloxi soybeans again failed to flower under the short alternations. After 39 days Cosmos was showing flower buds only under the 8-hour day. Therefore, even with a total of only 8 hours of illumination daily, the effect on flowering of the short alternations is essentially that of a long day or continuous light. Finally, with the same cycles as before but with the light periods double the periods of darkness (Table 8), Rudbeckia readily developed flower buds. At the end of 36 days Cosmos had formed no flower buds, and neither the Peking nor Mandarin soybeans had flowered. The Peking variety of soybeans is a short-day type, while the Mandarin behaves as such only in regions having a summer day length of more than 17 hours. Here, again, with total daily illumination of 16 hours, the effects of the short alternations are those of a long day or continuous light on both the long-day and the short-day type of plant.

EFFECTS ON GROWTH AND GENERAL NUTRITION

In the experiments with short alternations of light and darkness of equal duration it was quickly observed that pathological symptoms are apt to develop and that the severity of the symptoms depends on the particular alternations employed. In soybeans it was found that the leaves are most severely affected by the 1-minute intervals of light and darkness. The leaves may be much reduced in size, assume a pale yellowish green color, and soon develop numerous areas of dead tissue. (Fig. 2.) Similar though less pronounced effects were produced by other alternations, ranging from 30 minutes to 15 seconds, but the leaves developed normally when the alternations of light and darkness were reduced to 5 seconds. Other plants also showed more or less severe pathological symptoms in the leaves when exposed to the light intervals of 1 minute or to those ranging from 15 seconds to 15 minutes, although the symptoms were not always so clearly defined as in soybeans. In some instances young seedlings of Rudbeckia and other plants were unable to survive under the 1-minute light intervals. Destruction of chlorophyll seems to be an important feature in the unfavorable effects of these particular alternations of light and darkness. With change in the length of the light interval in either direction there was definite improvement in the appearance of the foliage leaves. With a decrease to 5 seconds or an increase to 30 minutes or an hour in the duration of the intervals, the plants usually became normal in color and general appearance, except sweetpotatoes, which were still chlorotic under the 1-hour intervals.

Attenuation was another outstanding feature in the unfavorable effects of the intermediate intervals of light and darkness. In soybeans the stems were not necessarily shortened, but they were weak and much reduced in size, thus tending to become viny. In most other species, also, the stems seemed to be abnormally small in comparison with the height, as if there were a stimulus toward stem elongation out of proportion to the basal nutrition of the plant.

The results shown in Tables 5 and 6 make it clear that, except in soybeans, the heights attained by the plants usually were reduced by the alternations ranging from 15 seconds to 30 minutes or an hour.

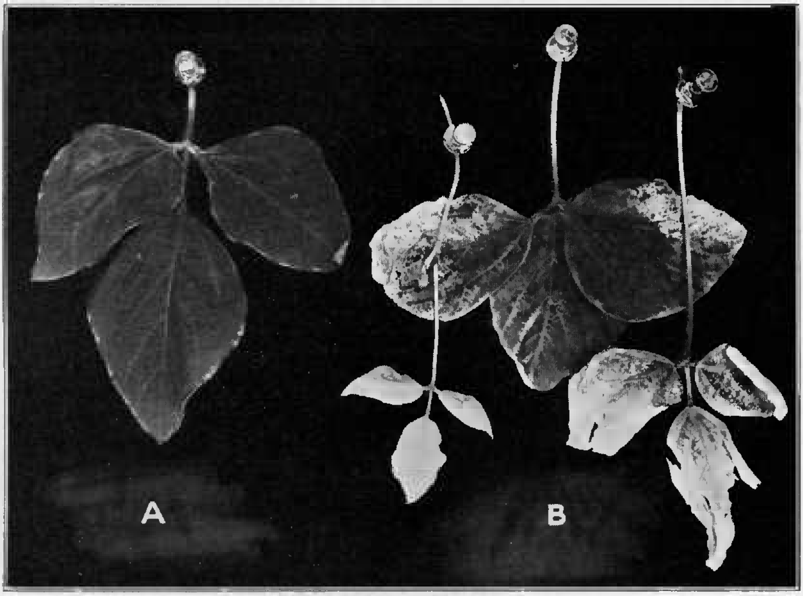

FIGURE 2.—Leaves of soybeans (*Soja max* (L.) Piper) grown with artificial illumination: A, Leaves of plants exposed to 12-hour alternations of light and darkness, normal in color and general development; B, leaves of plants exposed to 1-minute intervals of light and darkness, markedly chlorotic and much reduced in size, containing numerous spots of dead tissue, and showing a tendency to die prematurely

It is quite clear, also, that the 5-second alternation generally gave increases in height almost or quite equal to those produced by the relatively long alternations used as controls. In the long-day plant Rudbeckia, the 12-hour day retarded elongation of the flowering stem, as would be expected, and some indication of this effect persisted in the 1-hour alternation. The comparative effects of the different alternations on the height attained, as well as on flowering and degree of attenuation, in Cosmos and Delphinium are well shown in Figures 3 and 4. It is seen that in the former there is a progressive decrease in stem elongation and in size or mass of the plants from the 12-hour alternations down to the 1-minute periods of light and darkness, and a corresponding increase in elongation and stockiness as the periods are further shortened to five seconds. In Delphinium the same relations hold, except that the maximum depressing effects are produced with the 5-minute intervals and there is even greater improvement in growth with the 5-second alternations. In the short-day plant Cosmos, flower buds formed only under the 12-hour intervals of light and darkness; whereas in the long-day type Delphinium, flowering occurred with equal readiness under all alternations employed.

Total growth, as measured by green weights and oven-dried weights of the entire plants, shows much the same effects from the different alternations of light and darkness as does the height attained by the plants. In nearly all cases maximum depressing effects on green and dry weights of the plants are associated with maximum depression in height. In practically every instance the minimum green weight

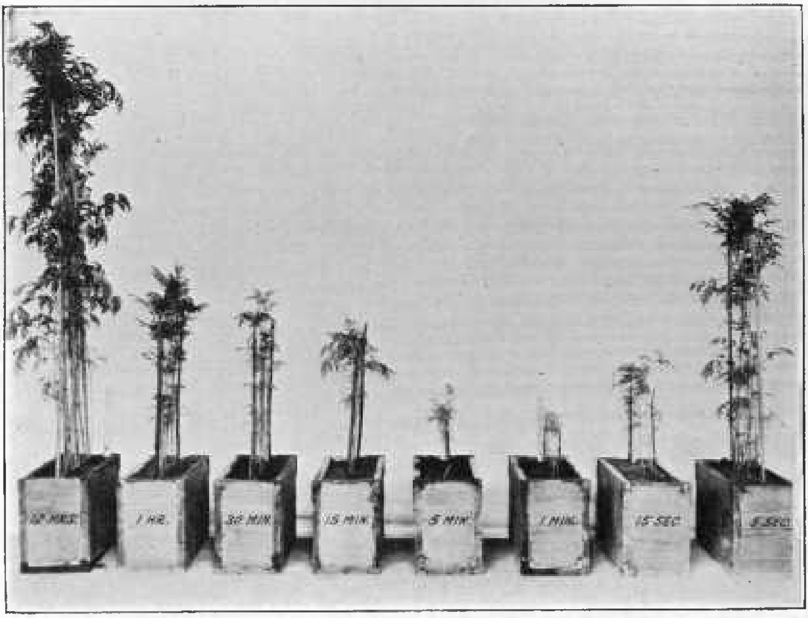

FIGURE 3.—Yellow cosmos (*Cosmos sulphureus* Cav.), a short-day plant, grown with equal alternations of light and darkness ranging from 12 hours to 5 seconds. With decrease in the intervals of light and darkness there is progressive decrease in height, size, and weight of the plants (see Table 6) and increase in etiolation and attenuation till the 1-minute intervals are reached. Further shortening of alternations causes marked improvement in growth and appearance of the plants. All intervals from 1 hour downward are almost equally unfavorable for flowering

is associated with minimum dry weight. The indicated values for water content of the green plants can be regarded as only approximations and do not show any very definite contrasts under the different alternations, except that in several instances the water content seems to be relatively high under the 12-hour alternations. Data were collected on the relative weights of tops and roots under the different treatments, and values for the ratio of tops to roots are included in the tables. The values for weights of roots are not accurate, however, because of difficulties in recovering all roots from the soil, and no great importance can be attached to the results. In the case of Ipomoea no tubers were formed under the alternations ranging from five minutes to one hour. To obtain some indication as to whether failure in absorption of soil nutrients could be responsible for the unfavorable results with the intermediate short alternations, determinations of total ash in the tops of Delphinium and Fagopyrum (Table 6) were made by C. W. Bacon, of the Division of Tobacco and Plant Nutrition, Bureau of Plant Industry. With alternating periods of light and darkness of 12 hours, 5 minutes, and 5 seconds, the corresponding percentages of total ash in Delphinium were 12.15, 13.64, and 10.49, respectively; in Fagopyrum, alternations of 12 hours, 15 minutes, and 5 seconds gave percentages of 14.97, 18.80, and 13.77, respectively. These data give no indication of deficiency in ash constituents under the harmful alternations of light and darkness.

When the light periods were reduced to one-half the periods of darkness, without change in duration of the total cycles, the unfavor-

FIGURE 4.—Rocket larkspur (*Delphinium ajacis* L.), a long-day plant, grown with equal alternations of light and darkness ranging from 12 hours to 5 seconds. The comparative effects of the different alternations on nutrition and growth are about the same for long-day as for short-day plants. (Fig. 3.) As regards flowering, however, it is apparent that none of the shorter alternations show a retarding action, whereas all have this effect on short-day plants

able effects on growth of the cycles ranging from 30 seconds to 1 hour were accentuated. (Table 7.) Cosmos soon died when exposed to these alternations, and soybeans were able to survive only under the 30-second and 1-hour cycles, so that satisfactory data on green and dry weights could not be obtained. Rudbeckia survived under all treatments, and the effects on growth of reducing the light periods to one-half the periods of darkness, as compared with equal alternations of light and darkness in the corresponding cycles, are indicated in Figures 5 and 6. The relative effects of the different cycles on growth are approximately the same in the two cases, but it is obvious that reduction in the ratio of light to darkness in each cycle has greatly reduced the vigor and the amount of growth. This is clearly shown also in the green and dry weights recorded in Tables 6 and 7. The retarding action on stem elongation of the 12-hour alternation decreases progressively in the next three shorter alternations (fig. 5), and the retarding action of the 8-hour light period decreases in the next two shorter alternations (fig. 6).

FIGURE 5.—Pinewoods coneflower (*Rudbeckia bicolor* Nutt.), a more pronounced long-day plant than Delphinium (fig. 4), grown with equal alternations of light and darkness ranging from 12 hours to 5 seconds. The relative effects of the different alternations on growth and on flowering resemble those in Delphinium, except that the 12-hour light period retards stem elongation and flowering, and these effects still persist in decreasing degree with the 1-hour and the 30-minute periods. In this case maximum growth was obtained with the 5-second alternations. (Table 6)

When the light period was increased to twice the period of darkness in each of the cycles, there was decided improvement in the vigor and general nutrition of the plants. (Table 8.) In Rudbeckia and

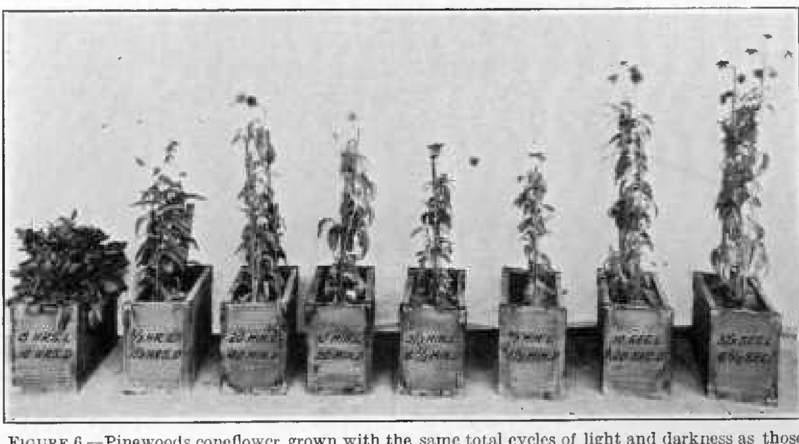

FIGURE 6.—Pinewoods coneflower grown with the same total cycles of light and darkness as those applied to the plants shown in Figure 5, but with the light periods in each cycle only one-half as long as the periods of darkness. Thus the plants in all cases received a total of 8 hours of light daily instead of 12 hours. There was no fundamental change in relative effects of the different cycles on growth and flowering, but comparison with Figure 5 shows there was a decided reduction in growth of the plants in all cases

Cosmos the same differential effects of the shorter alternations previously noted were still in evidence with respect to both height and weight in the former and height in the latter plants. With soybeans,

37552—31——3

however, the increased ratio of light to darkness seemed largely to overcome the adverse effects of the alternations ranging from 15 seconds to 30 minutes. The heights attained by Rudbeckia and Cosmos are comparable to those produced with an even ratio of light and darkness, except under the 16-hour as compared with the 12-hour light period. In Rudbeckia the increase in the ratio of light to darkness failed to increase the weights of the plants.

The results presented in this paper relate primarily to effects of relatively short alternations of light and darkness ranging from 6 hours to 5 seconds, with a 12-hour alternation of light and darkness as the principal basis for comparison. As already pointed out, the 12-hour alternation, which supplies the only equal distribution of light and darkness occurring in the normal 24-hour cycle, is not optimum for flowering in most plants of either the long-day or the short-day type. A light-and-darkness ratio of 5:7, as supplied in a 10-hour day, or a ratio of 2:1, as in an 8-hour day, is more likely to be optimum for most short-day plants; and the reverse ratios of 7:5 and 2:1, as in day lengths of 14 and 16 hours, respectively, are more nearly optimum for typical long-day plants. It will be of considerable interest in this connection to study the effects of 10-hour and 8-hour alternations having equal periods of light and darkness, and other alternations between those of 12 hours and 6 hours with both equal and unequal periods of light and darkness, which do not occur in the natural 24-hour cycle. It is hoped that these studies can be carried out with rather rigid control of temperature and other environmental factors.

SUMMARY

Breaking the continuity of the daily illumination period of plants by darkening them in the middle of the day for periods of 1 or 2 hours to as long as 5 hours may materially affect the general nutrition and amount of growth, but as a rule it fails to influence reproductive activities to a degree at all comparable with that produced by excluding the early morning or late afternoon light of the long summer days. This applies to all short-day plants that have been studied and to a majority of long-day plants, and means that reducing the hours of daily illumination by thus breaking the continuity of the illumination is not generally effective in inducing reproductive activity in short-day plants or in interfering with initiation of the process in long-day plants. The effects are essentially those of the long day.

Further breaking up of the daylight period by darkening the plants from 10 a. m. to noon and from 2 to 4 p. m. seemed to accentuate the lack of effectiveness of this method of reducing the hours of illumination in bringing about the characteristic effects of a short-day length. In some short-day plants flowering was actually delayed as compared with results under the full day of summer.

When the test plants were completely darkened on alternate days during the summer months, thus substituting a 48-hour cycle of light and darkness for the normal 24-hour cycle and furnishing about 15 hours of light and 33 hours of darkness in the cycle (corresponding to 7½ hours of light daily), the effects were those of a short day, although these effects were much weaker than those of a normal 8-hour or 10-hour day.

Exposing a group of short-day plants alternately to a 10-hour day and to the full day length of summer produced an effect intermediate between the effects of a long day and a short day as regards initiation of flowering. *Impatiens balsamina* (garden balsam), the only long-day plant tested, behaved as when exposed daily to a long day.

Following the experiments in which sunlight was the source of illumination, a number of species were grown under a series of different, relatively short alternations of light and darkness ranging from six hours to five seconds, the plants being illuminated with electric light of high intensity. The plants were grown at approximately outdoor summer temperatures in small light-proof chambers fitted with 1,000-watt Mazda lamps and provided with forced ventilation. In the major series of tests the duration of the light intervals was the same as that of the intervals of darkness in all the alternations. The differential effects of the several alternations on general nutrition and growth were in striking contrast with the comparatively uniform action on initiation of flowering.

As the equal intervals of light and darkness, beginning with 6 hours, were progressively shortened, there was increasing evidence of malnutrition and retardation in growth, which in several instances culminated in the 1-minute intervals. With further shortening of the alternations below the point at which maximum injurious action occurred, there was pronounced improvement in the nutrition and growth of the plants, so that the 5-second alternations often gave about as good results as the 12-hour controls. The injurious effects of the intermediate alternations included apparent destruction of chlorophyll, general etiolation, localized dying of the leaf tissue, reduction in leaf development, attenuation, and decrease in stem elongation and in production of dry matter. The effects on short-day plants and long-day plants seemed to be much the same.

When, with the same total cycles of light and darkness, the light intervals were reduced to one-half the intervals of darkness, the unfavorable effects of the intermediate alternations were intensified to such an extent that most of the plants soon died. On the other hand, increase of the light interval to twice the interval of darkness in each of the cycles had the effect of improving the general appearance of the plants exposed to the intermediate alternations, and in some cases seemed largely to overcome the retarding action of these alternations on growth.

As regards action on flowering, the effects in any particular case seemed to depend mainly on whether the plant belonged to the long-day or short-day type rather than on the duration of the alternations. In general, all the alternations, from 6 hours downward, were found to favor flowering in long-day plants but were unfavorable for flowering in short-day plants. The effects on flowering, therefore, are much the same as those resulting from midday darkening with natural illumination. The plants behave essentially as if exposed to a long day or continuous illumination.