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A SCIENTIFIC JOURNAL ISSUED BY

THE ESCUELA AGRICOLA PANAMERICANA

THOMAS E. FURMAN, EDITOR

TEGUCIGALPA, HONDURAS JANUARY, 1959 VOL. 8 No. 1

THE EFFECT OF PHOTOPERIOD ON THE GROWTH AND DEVELOPMENT OF TEOSINTE (*Euchlaena mexicana* Schrad).

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The photoperiodic response of some tropical plants limits their distribution and utilization in temperate climates. In the same way some temperate climate plants are excluded from the tropics. Plants moved from regions of one day length to another may show varying responses. For example, plants moved from regions of short-day to long-day may continue to vegetate, and flower and fruit only when the days become short. In other instances the vegetative and reproductive generations may follow in normal sequence, but the flowers may be infertile. In still other plants corm and tuber formation fail when the days are long and occur only under short-day conditions.

Changing the day length for plants may have effects that enhance their utilization as shown by Allard and Garner (1940), Whyte (1949), Naylor (1953) and others. Fortunately, through experience and careful experimentation, ways of modifying to some degree the effects of length of day reaction have been discovered. Examples are the influence of temperature, the development of suitable genetic strains, modifying factors of cultural practices, such as changing the time of planting, increasing or decreasing the light by artificial means, or applying hormones (Leopold and Thimann, 1949) to induce flowers and fruit.

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Tropical plants are mainly short-day and temperate zone plants long-day in their flowering responses. Some of the short-day plants are millet, poinsettias, strawberries, coffee, beans, and teosinte. A few of the long-day plants are wheat, oats, and red clover. There are, of course, within some short-day species certain strains or varieties that behave as day-neutral or long-day plants. A similar variation occurs in long-day species. This variation in short-day plants accounts for the wide distribution of some species throughout the temperate zone. Notable examples are the wide distribution and utilization of corn and beans. In these two crops, primitive man played an important role in isolating day-neutral and relatively long-day strains. Through modern breeding the number of these strains has been increased and they have been improved in quality and productivity.

However, in some short-day plants no day-neutral or long-day strains have been found and as a result the distribution of the plant is limited to a narrow range of latitude. Teosinte may be such a plant. It grows wild from north central Mexico southeastward into Honduras (Lat. N. 14° to 26°) in semi-arid climates at altitudes from 2000 to 8000 feet. There are several strains of teosinte which differ in their photoperiod response, but they all fail to mature seed when grown during the long days of spring and summer in the United States. However, all the strains may be grown in the tropics where the temperate climate cereals such as wheat, rye, oats and barley fail.

Teosinte has long been known to the aboriginal people of Central America and Mexico. There are fragmentary records reporting that the plant played a role in the diet of the Mayan and earlier races of man. Had the historical records of this civilization been preserved, rather than destroyed by the Spanish conquistadors, our knowledge of teosinte and its early uses as food might be greater than it is today.

There is indirect evidence based on custom that teosinte was used as food, at least in times of famine. Recent analysis showing its high nutritive value adds validity to the fragmentary records and customs pertaining to the early use of teosinte as food. Melhus and Chamberlain (1953) have recently established that the grain is richer in protein than wheat, rice, oats, corn or rye. Melhus, Aguirre and Schrimshaw (1953) found that the protein value of teosinte is 20 to 22 per cent of the dry weight, while commercial corn is only 8.5, wheat 12, and rice 7. Of significance too is the high methionine content of teosinte. Methionine is an essential amino acid, often deficient in the predominantly vegetable diets of most under-developed areas in the world.

The grain of teosinte when made into food products, cooked and baked, has a desirable, individual flavor. The grain has been made into breakfast foods and baked products such as muffins, tortillas, and tamales.

These desirable qualities of teosinte as a potential new cereal crop for some parts of the tropical and the temperate zones have motivated a study of its growth and development. In this paper it is proposed to discuss work relating to the photoperiodic responses of teosinte.

Earlier Studies of Photoperiodic Response in Teosinte

The first demonstration of a photoperiodic response in teosinte was made by Emerson (1924) under greenhouse conditions in 1924 at Ithaca, N. Y. The purpose of his studies was to facilitate hybridizing teosinte with maize for genetic studies. The plants were grown in the greenhouse and exposed to 14 hours darkness in a room adjoining the greenhouse and then moved into the open for 10 hours daily, beginning 13 June.

The Chalco, Mexico strain began flowering after a 31 day induction period. Checks held constantly in the greenhouse or in the open required about 82 days to flower. Day length in Ithaca on 13 June is about 15 hours. A 20 day induction period was nearly as effective as 30, 40, or 50 day treatments. Plants only a month old failed to respond to short day treatments as well as older ones did. Emerson found a difference in the time required to flowering in the three annual teosintes he studied. The Chalco, Mexico strain was earliest, Durango, Mexico next, and Florida, U. S. A. last. The perennial species of teosinte had approximately the same maturity as the annual Mexico strains. Emerson believed that with the information he gained it was possible to induce flowering in summer at any chosen date, plus or minus five days.

Langham (1940) forced teosinte into flower in the greenhouse to facilitate hybridization with corn. His induction periods began when the plants were in the seedling stage and continued to anthesis. The three Mexican strains, Durango, Nobogame and Navacayan required 35, 31 and 34 days respectively. The Guatemalan strain, Huixta, required 47 days to anthesis under the conditions of Langham's experiments. His studies of intergeneric differences between teosinte and maize showed that the weak response of corn was dominant to the strong response in teosinte and segregated as a Mendelian character. He also reported that mutation to the teosinte form occurred in corn.

Rogers (1950) also studied the inheritance of photoperiod in teosinte but grew his corn and teosinte for hybridization in the field, at College Station, Texas (about 31° N. Lat.) He used three strains from Mexico, two from Guatemala and one from Florida.

appeared until 20 July, 30 days after the beginning of the short-day treatment. The first ripe seed was harvested 100 days after moving the plants to the field. Seed development in the checks was interrupted by frost in October.

The five hills in block III received the same treatment as those in block II and the response was comparable except that the short-day treatment continued only 15 days instead of 20. The data on time to anthesis and ripe seed are shown in Table I.

These trials, using two strains of teosinte, which were started in the greenhouse and transplanted to the fiield, showed that a short day treatment of 10 hours per day for 15 to 20 days at Ames, Iowa, 42° N. Lat. induced flowering and the maturing of seed. Anthesis nd maturity of seed seemed to be influenced by the age of the plant at the time the induction periods were begun. The check plants continued to grow vegetatively until

TABLE I

Two strains of teosinte transplanted to the field were submitted to 10 hour induction periods for 15 or 20 days.

Ames, Iowa, 1956.

Strains	No. hills	Days of induction	Dates of induction	Days to tassel emergence	Days to anthesis	Days to ripe seed
406-51	2	20	6-4 to 6-24	34	44-47	85-90
65-51	2	20	6-4 " 6-24	33	44-47	80-85
406-51	2	20	6-20 " 7-10	60	70-75	100-110
65-51	2	20	6-20 " 7-10	60	70-75	100-110
406-51	2	15	6-20 " 7-5	72	80-85	110-120
65-51	2	15	6-20 " 7-5	72	80-85	110-120
406-51 (check)	3				1.)	2.)
65-51 (check)	3				1.)	2.)

1.) Late September.
2.) Seed killed by frost in October.

September when short days (13 hours and less) began. Although the check plants tasseled in late September, no mature seed developed before frost. The response of these greenhouse transplants was much like that described by Emerson (1924).

Trial With Plants in the Field

In the above experiment teosinte was started in the greenhouse and taken to the field in the four to six leaf stage on 20 May. It would simplify the problem of studying the growth and development of teosinte if the seed could be planted in the field much as corn is planted. To learn whether this could be done, 15 hills of each of three different strains, 406-51, 65-51, and 35-51 of teosinte where planted on 19 May.

The 15 hills were divided into five hill blocks (See Table II.) On 18 June three hills of each strain in block I were subjected to 10 hour induction periods for 20 days. Two of the five hills in each block were held as checks. The plants of 406-51 and 65-51 were in the four to six leaf stage and 8 to 12 inches tall when the induction periods began. Although the growing conditions were unfavorable, incident to lack of rain, the plants were 3 feet tall at the end of the 20 day induction period. The 35-51 was only 18 inches tall, and had stooled extensively. The two strains 406-51 and 65-51 developed tassels and silks at the end of the induction period. Mature seed was collected 96 days after the seed was planted. (See figure 2). The strain 35-51 was later. It flowered 36 days after the beginning of the induction period and made ripe seed 120 days after planting. The plants in the two check hills of each strain flowered in late September and failed to make ripe seed. The plants treated in this experiment were more vigorous than the transplants in the previous experiment.

TABLE II

Three strains of teosinte were planted in the field and exposed to 10 hour induction periods for 10, 15 and 20 days.

Ames, Iowa. 1956.

Strains	No. hills	Days of induction	Dates of induction	Days to tassel emergence	Days to anthesis	Days to ripe seed
406-51	5	20	6-18 to 7-8	46	50	96
65-51	5	20	,, ,, ,,	46	50	96
35-51	5	20	,, ,, ,,	57	67	107
406-51	5	15	6-27 ,, 7-12	52	60	100
65-51	5	15	,, ,, ,,	50	61	100
35-51	5	15	,, ,, ,,	54	73	120
406-51	5	10	6-27 ,, 7-7	72	80	135
65-51	5	10	,, ,, ,,	72	76	120
35-51	5	10	,, ,, ,,	80	91	No seed
406-51 check	2	—		—	—	,,
65-51 ,,	2	—		—	—	,,
35-51 ,,	2	—		—	—	,,

Three hills of each strain in blocks II and III were treated for 10 and 15 days respectively. All the plants that were exposed for 15 days fruited. Of the plants exposed to 10 hours of light for 10 days only the strains 406-51 and 65-51 made seed. The strain 35-51 failed to mature seed under these conditions, also the checks in all three strains failed to make seed due to frost.

The data in Table II indicate that seed of teosinte may be planted in the field in the spring and the plants made to blossom and mature in 96 to 135 days when exposed to 10 hour photoperiods for 20 days. The 10 and 15 day induction periods required more days to flowering and ripe seed than the plants exposed to 20 day inductions. The strain 35-51 treated with a 10-day induction period failed to mature seed. This experiment shows that the induction period required varies in different strains of teosinte and that the duration of the induction period may be as short as 10 days in some strains.

Photoperiod Trials Under Greenhouse Conditions.

In the two experiments reported above, there was wide variation in the conditions supporting growth. The spring and summer of 1956 was unusually dry and the temperature was above the state long time mean for June, July and August. As a result it was feared the growing conditions might have exaggerated the effect of the photoperiod response. Since many factors influence length of day reaction: among them temperature, moisture, time of seeding, and cultural care of the plants, an experiment was undertaken in the greenhouse where the temperature, moisture and light conditions were more amenable to control.

The strain 406-51 was planted in composted greenhouse soil in 8-inch pots on 20 August. The pots were arranged in three randomized blocks on a central greenhouse bench. The temperature of the house fluctuated from 70° to 80° F. The plants emerged about 7 days after planting, and were thinned to two plants per pot. They were less vigorous than those grown in the field.

At varying times after emergence, induction periods in light-controlled chambers of 5, 10, 14, 15, 17, or 21 days were begun. During the induction periods either a 10 or 12 hour daylength was imposed. Before and after termination of the photoinductions the plants were exposed to long days of 14 hours.

The strain 406-51 flowered readily after some of the treatments, and the results are shown in Table III. Five and 10 days of 10 hour photoperiods applied when the plants were in the 2-3 leaf stage were not always sufficient to cause flowering, even though tassel emergence occurred in some plants. In such cases a reversion to vegetative proliferation commonly occurred. The same length of photoinductive treatment when the plants were in the 7-8 leaf stage resulted in normal flowering. It is possible that the plants in the 2 to 3 leaf stage failed to form normal staminate flowers because the reproductive stage had not differentiated sufficiently in these young plants.

TABLE III

The response of 406-51 to photoperiod under greenhouse light controlled conditions, Ames, Iowa. 1956

Plant Age, Days	No. leaves	No. Plants	Hours photo-period	Days induc-tion	Days tassel emer-gence	Days anthesis average	Ear shoots silking average
14	2-3	6	10	5	66[1]	—	—
,,	,,	,,	,,	10	90[2]	—	—
,,	,,	,,	,,	17	53	63	3.3
21	6-7	,,	,,	14	64	73	—
,,	,,	,,	12	14	65	79	0.7
,,	,,	,,	10	21	55	66	6.5
,,	,,	,,	12	21	64	73	0.7
35	7-8	,,	10	5	84	93	—
,,	,,	,,	,,	10	67	80	2.2
,,	,,	,,	,,	15	67	75	4.0
Check		,,	14	—	97[3]	—	—

[1]/Two of the six plants treated had tassels emerge. The other four failed.

[2]/Four of the six showed tassels.

[3]/Although two of the plants in the check showed tassels, staminate flowers had reverted.

Tests of 5, 10 and 15 Day Photoinductions

An attempt was made again in 1957 to learn whether a 5 day induction period would induce a growth and development comparable to that induced by 10 and 15 day photoinductions. Three strains of teosinte were planted in the field and the seedlings emerged 1 June. Five hills were used in each of the three photoinduction treatments. The induction periods began 30 days after the plants emerged on 30 June and continued for 5, 10 and 15 days. The plants were about 1 foot tall and beginning to stool when the photoinduction began.

At the end of the induction periods those covered 10 to 15 days were taller than the checks as a result of the rapid elonpotatoes and corn. U. S. maize hybrids, when planted in Guatemala, are often dwarfed, their yield reduced and their time to maturity shortened. Kiesselback (1950) found that moving maize hybrids from Nebraska to Texas caused the plants to flower 13 days earlier than when grown in Nebraska. On the other hand, when southern varieties were moved north to Nebraska they required 18 days longer to flower. Certain wild grasses respond similary, e.g. side-oats gramma studied by Olmsted (1944). He found that northern strains moved to lower latitudes became dwarfed.

In 1952, a much larger experiment, four half acre plots, were planted, 2 August in Tiquisate to 35-51 on land adjoining the site used in 1951. The plants grew 10 to 15 feet tall and again flowered in 50 to 60 days. The seed crop was ready to harvest in 100 to 119 days. There was a marked range in maturity, probably due to the heterozygosity of the population. The difference in day-length between 1951 and 1952 experiments was nominal because there were only six days difference in the planting dates.

Definitely late July and early August were better times to plant teosinte than on 9 March, incident to the days becoming progressively shorter in the former case and longer in the latter.

The photoperiod of teosinte offers a more difficult problem in the United States than in the tropics. The tropical zone is not plagued by early autumn frosts as the short-day season of the year begins, like the higher latitudes of the United States. Again the tropical zone is not confronted with long-days of 14 to 15 hours. There is, however, in the southern United States a fringe along the gulf of Mexico below latitude 30° where the short-day season is long enough to mature teosinte. Dr. George Godfrey of Weslaco, Texas, in 1951, 1952 and 1953, in cooperation with the senior author, grew 35-51 on a field basis for seed increase purposes. The plantings were made from 20 August to 10 September. The plants grew 6 to 10 feet tall, branched profusely and flowered in 50 to 60 days. The seed matured before frost in 100 to 120 days. The latitude of Weslaco is 26° N. The day lengths varied from 10 to 12½ hours during the growth and development of teosinte.

In Table V an attempt has besn made to bring together the responses of teosinte to the photoperiods associated with different latitudes and time of planting. Teosinte was grown at eight different latitude sites from 1948 to 1953. Each site had a different day-length due to the latitude and time of planting. The climatic factors surrounding the growth of teosinte such as temperature, rainfall, light intensity, etc. were generally favorable except for a time at College Station where the late growing season was dry and warm

TABLE V

The Influence of Daylength on the Development of Teosinte at Different Latitudes.

Strain teosinte	Location and latitude		Daylength 1/	Planting date	Year	Days to anthesis	Days to mature seed	Grown by
35—51	Ames, Iowa	42°	14'—35"	5—15	1953	110	—	F. Smith
35—51	Milford, Illinois	41°	14'—47"	6—2	1953	105	—	W. Mumm
97—51	El Centro, California	35°	13'—58"	8—2	1953	80	2/	M. Woods
Nobogame 4/	College Station, Texas	31°	13'—20"	4—28	1948	110	—	J. Rogers 3/
Huixta 5/	College Station, Texas	31°	13'—20"	4—28	1948	207	—	,, ,,
406—51	Beaumont, Texas	29°	13'—35"	7—9	1953	52	112—120	R. Ford
35—51	,, ,,	,,	,, ,,	,, ,,	1953	101	155—170	,, ,,
97—51	Everglades, Florida	27°	13'—17"	7—30	1953	70	100—106	V. Green
35—51	Weslaco, Texas	26°	12'—30"	9—2	1952	60	100—115	G. Godfrey
97—51	,, ,,	,,	,, ,,	8—20	1953	71	,, ,,	,, ,,
406—51	,, ,,	,,	,, ,,	,, ,,	1953	61	105—110	,, ,,
35—51	Tiquisate, Guatemala	14°	12'—25"	8—26	1952	55	100—105	I. Melhus
35—51	,, ,,	,,	12'—23"	9—8	1953	50	94—100	W. Paddock
406—51	,, ,,	,,	,, ,,	,, ,,	1953	45	90—100	,, ,,

1/ Approximate day-length on the date of planting. In each case the day-lengths increased or decreased before or after summer solstice, which influenced the light period and the response of the plants as recorded.

2/ Trial plot destroyed.

3/ Unfavorable growing season.

4/ A strain of teosinte collected at Nobogame (26° N. Lat.), Mexico.

5/ A strain of teosinte collected at San Antonio Huista (16° N. Lat.), in Huehuetenango, Guatemala.

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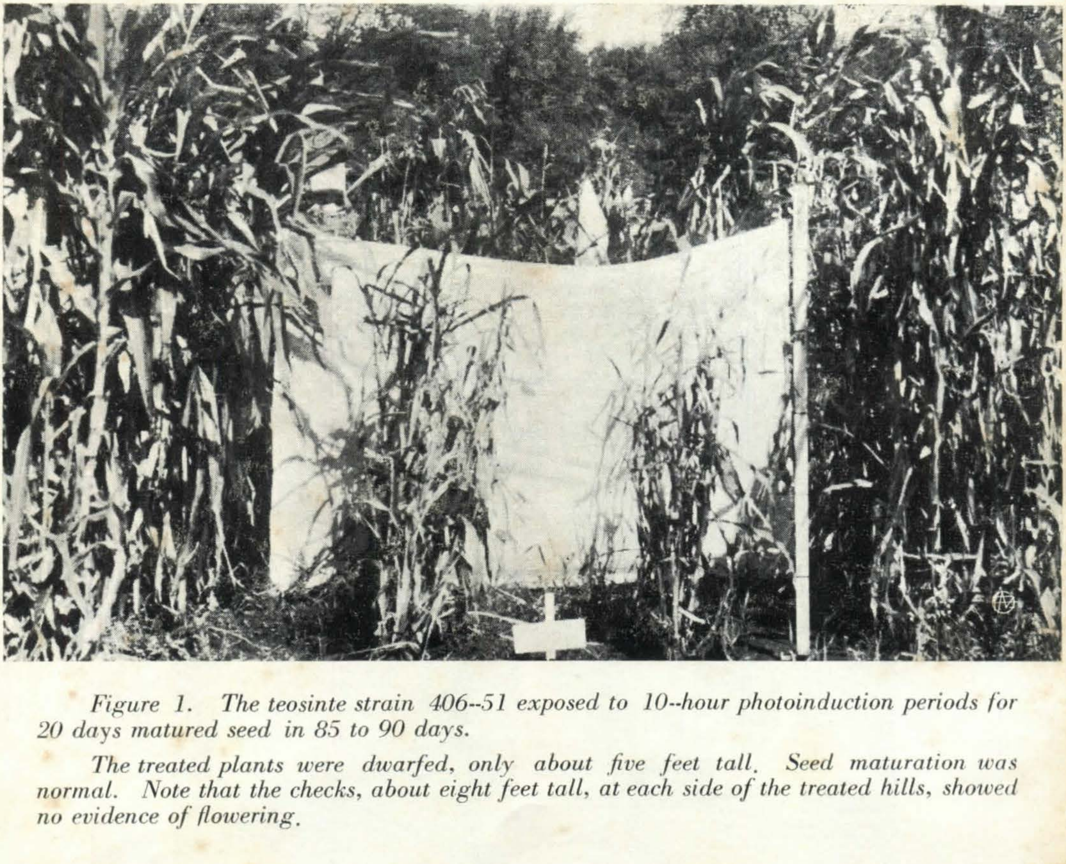

Figure 1. The teosinte strain 406--51 exposed to 10--hour photoinduction periods for 20 days matured seed in 85 to 90 days.

The treated plants were dwarfed, only about five feet tall. Seed maturation was normal. Note that the checks, about eight feet tall, at each side of the treated hills, showed no evidence of flowering.

Figure 2. A hill of 406--51 exposed to 10-hour photoperiods for 20 days and a hill of plants held as checks. This picture was made after tassel emergence. The treated plants grew 6 to 7 feet tall and matured much seed.

Figure 3. These are abnormal and normal tassels of teosinte strain 65--51 that developed on plants exposed to 10--hour photoperiods for five days. The flowers reverted to vegetative growth.

Figure 4. Three rows of Guatemalan teosinte 35--51 at the left and three rows of Florida teosinte 97--51 at the right. The strain 97--51 was shorter and sowewhat dwarfed. It matured about 10 days earlier than 35--51. The response of 97-51 is probably due to moving it 15° farther south.