PHOTOTHERMAL INDUCTION OF FLOWERING IN SUGAR BEETS

By F. V. Owen, geneticist, Eubanks Carsner, senior pathologist, and Myron Stout, assistant physiologist, Division of Sugar Plant Investigations, Bureau of Plant Industry, United States Department of Agriculture

INTRODUCTION

Induction of flowering in sugar beets (Beta vulgaris L.) has two important practical aspects. Development of seedstalks, called bolting, is objectionable when the crop is grown for sugar production, but when the crop is grown for seed production initiation and complete development of seedstalks in all the plants is desirable. The first curly top-resistant varieties were easy-bolting types (4). Their bolting tendency was sometimes objectionable in plantings for sugar, but it was beneficial in plantings for seed. Therefore seed of these varieties could be produced abundantly in relatively mild climates by planting in early fall and allowing the plants to grow in the field through the winter (21). Breeding to combine nonbolting with curly top resistance was started as soon as it became evident that there were objections to the easy-bolting tendency of the first curly top-resistant varieties. Nonbolting varieties with curly top resistance were promptly developed; but, when the effort was made to produce seed by the method of overwintering in the field in the relatively mild climates where beet-seed growing had become established, these varieties failed to reproduce satisfactorily (22). Nonbolting varieties bred in northern Europe gave similar results.

These experiences emphasized the need for fuller knowledge of the principles concerned in bolting and sexual reproduction. This paper presents results of studies of some of the physiological and genetic aspects of the problem.

REVIEW OF LITERATURE AND DEFINITION OF TERMS USED

In much that has been written about causes of flowering, the combined effect of temperature and day length, or photoperiod, which is required by some plants, has not been considered. This is especially true in much of the literature on photoperiodism that has appeared since the classic discovery of Garner and Allard (9). The specific effect of temperature has been given prominent attention, however, in extensive Russian work that began with the treatment of seed to induce flowering. The action of temperature has been referred to (12) as thermal induction and the influence of day length as photoperiodic induction. Chroboczek (5) and Steinberg and Garner (24) showed that both low-temperature treatment and long photoperiods are

1 Received for publication November 16, 1939.
2 The Curly Top Resistance Breeding Committee cooperated in the work in northern Utah and southern Idaho and in the bolting test at Riverside, Calif. This committee represents all the beet-sugar companies in the Western States. Land was furnished for the bolting test at Riverside by the California Agricultural Experiment Station.
3 Italic numbers in parentheses refer to Literature Cited, p. 123.
favorable to flowering in beets. Roberts and Struckmeyer (23) reported important associations between temperature and photoperiod in relation to flowering in a number of species, including beets. The effect of temperature and photoperiod on beets will be considered further in this paper.

Induction of flowering under the influence of prolonged low temperature and long photoperiods may be tentatively regarded as a single process and may therefore be designated by a single term. The term “vernalization” has sometimes been used for this purpose, including induction of flowering as it occurs in nature and under artificial conditions, but this term has been applied mostly to thermal induction (16) and generally to hastening of flowering by prolonged low-temperature treatment of germinating seed. Furthermore, “vernalization” has also been used (7, 25, 27) to include beet-seed treatments involving germination at higher temperatures, even though such treatments do not induce flowering. The term “vernalization” will be used in this paper to mean prolonged low-temperature treatment of seed during germination to hasten flowering. For the broader meaning, including thermal induction and photoperiodic induction, the new term “photothermal induction” 4 will be used. Photothermal induction occurs in beets (5, 24), celery (26), some wheats (17), and many other species.

Photothermal induction of flowering in beets is influenced by genetic factors. Munerati (20) investigated an annual beet and showed that a single genetic factor was associated with a clear-cut annual habit. Working with this annual strain obtained from Munerati, Abegg (1) demonstrated linkage between the bolting factor B and the factor R for red hypocotyl color described by Keller (13). These findings were helpful in the present study.

“Bolting” as used in this paper is the appearance of the seedstalk or the appearance and development of the seedstalk whether or not flowering is involved.

SCOPE OF STUDIES AND EXPERIMENTAL METHODS

Extensive field observations have been made on commercial and experimental sugar-beet-seed fields in the relatively mild climates of southern Utah, southern California, southern New Mexico, and southern Arizona, and also in the colder climates of northern Utah and southern Idaho, where there is usually some winter snow cover. These observations were started in 1930. More recently, similar observations have been made in Oregon and northern California. All these studies were on plantings made in late summer or early fall and were conducted by the method of overwintering the plants in the field (21).

Field observations regarding the factors involved in induction of flowering have also been made on commercial fields of beets grown for sugar production in California and other Western States.

Intensive bolting studies were conducted in field plots at Riverside, Calif., in the years 1935–36, 1936–37, and 1937–38. Shading experiments to modify the natural environment were included in these studies.

Greenhouse studies were made with variations in both temperature and photoperiod. An idea of the temperatures used is given by

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4 This term was suggested to the writers by Dr. E. J. Kraus, chairman, Department of Botany, University of Chicago.
showing means obtained by averaging the daily minimum and maximum temperatures. (See table 6.) In interpreting these averages it should be borne in mind that daily maximum temperatures were frequently reached as peaks caused by brief periods of sunshine before ventilators could be opened. Minimum temperatures were reached much more gradually. In general, comparisons were made between rather widely separated temperature levels where precise control was not essential.

Photoperiods were controlled by using artificial light to supplement the natural day length. Mazda globes with 150- to 500-watt capacity were placed over the plants at distances to give intensities of 10 to 100 foot-candles. The photoperiod most commonly used was between 17 and 18 hours. An 8-hour day and a 24-hour day were also used in a few experiments.

Storage experiments were conducted in darkness with plants of intermediate size, usually with a root diameter of 1 to 3 inches. Usually the storage temperature was maintained between 33° and 36° F., with a few tests at approximately 40°.

Seed was given vernalization treatment in cold storage. In most cases the seed lots were first disinfected with a 10-percent solution of commercial formalin for 10 minutes, then washed and soaked overnight and incubated at room temperature under high humidity until the radicles began to emerge. Then in moist condition the seed was stored in closed containers at 33° to 36° F. The germinating seed was allowed to remain at this temperature for various lengths of time, but in most experiments this treatment was continued about 100 days. The sprouted seed was then planted in the field or in the greenhouse.

Material of known genetic constitution with regard to bolting tendency was utilized in some tests. An annual beet obtained from Munerati and previously investigated (1, 20) was used extensively. A few observations were also made with the annual from Milpitas, Calif. (3), and also the more extreme annual type from the Imperial Valley of California (3). Greenhouse observations were made with several wild species. Vegetative clones were used for the most critical work, and these were propagated and studied over a period of years.

PHOTOTHERMAL INDUCTION IN ANNUAL AND BIENNIAL BEETS

All varieties of Beta vulgaris investigated are long-day plants. The chief difference between biennial and annual beets in regard to photothermal induction is the longer period of low-temperature exposure required for flowering in biennials. There is also much variability among biennial types with regard to this requirement, and commercial varieties are made up of a mixture of such types. In biennial beets, photothermal induction is frequently reversed by increasing the temperatures (fig. 1) or by decreasing the length of the photoperiods. This reversal causes the plants to turn vegetative after they have started to develop in the direction of flowering. In annual beets, also, photothermal induction is reversible, but with annuals the influence of photoperiod is stronger than the influence of temperature.

To induce bolting in biennials when grown in the greenhouse with 17- to 18-hour photoperiods it was necessary to hold the average

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*These wild species were obtained from Dr. G. H. Coons, principal pathologist, Division of Sugar Plant Investigations, Bureau of Plant Industry.
temperature under about 58° F., although temperatures somewhat higher were effective with continuous light (a 24-hour day), as previously reported by Steinberg and Garner (24). All varieties, including annuals, remained vegetative in an 8-hour day under relatively warm temperatures.

Other Beta species are also long-day plants. Beta maritima L., B. atriplicifolia Rouy, the wild or escaped beets of Milpitas, Calif., and the wild beet from the Imperial Valley of California (3) are all more or less annual types, but they all remained vegetative in the green-

![Figure 1](image)

**Figure 1.**—Photothermal induction reversed by changes in temperature. Plants of clone 90 and hence of identical genetic constitution. Seedstalks about 1 inch in height were initiated in both plants under a cool temperature and 17- to 18-hour photoperiod: A, Taken to a warm temperature after the initiation of seedstalk, but length of day not changed; B, received same treatment as A but was returned to the cool temperature after it became somewhat vegetative in the warm temperature.

house under 8-hour days and relatively warm temperatures. The wild species B. procumbens Chr. Sm., B. patellaris Soland, and B. webbiana Moq. developed decumbent branches under both short and long photoperiods, but they failed to produce flowers under the 8-hour day.

The Munerati annual has been investigated (1, 20) more carefully than any other annual variety, and its behavior has been relatively uniform. It is very sensitive to photoperiod, and at Salt Lake City, Utah, in a warm greenhouse (60° to 85° F.) it will not start a seedstalk under natural day length until nearly June 1. It is easily held vegetative in an 8-hour day at any time of the year under a relatively warm temperature. Plants of this variety, even after 30 days’ storage at 33° to 36° F., remained completely vegetative under 8-hour days.
For 3 years it has been noted that in October plantings at Riverside, Calif., the Munerati annual remains vegetative all winter and the roots sometimes reach 3 or 4 inches in diameter. Under these conditions its bolting tendency cannot be easily distinguished from that of some commercial sugar-beet varieties. In fact, a portion of the plants in the U. S. 12 variety (22) initiated seedstalks somewhat faster during the month of March at Riverside than the Munerati annual.

The influence of temperature on the flowering of annual beets is less obvious than that of photoperiod but under certain conditions can be clearly demonstrated. This opinion is based upon detailed studies with the Munerati annual. Two plants of clone 62, a selection from the Munerati annual, initiated seedstalks in 22 days in a warm room with a 17- to 18-hour photoperiod (average maximum temperature 78.0° and average minimum 54.6° F.). Under the same conditions two other plants from the same clone, previously held at approximately 40° for 39 days, started seedstalks in 15 days, or 7 days sooner than those without the low-temperature treatment. In another experiment with the Munerati annual, two groups of plants were compared that had been grown from seed for 69 days at different temperatures. One group had been grown at a relatively cool temperature (average maximum 74.4° and average minimum 43.5°) and the second group had been grown at a relatively warm temperature (average maximum 80.2° and average minimum 52.9°). On December 2, 1937, after the 69-day treatments at these contrasting temperatures, both groups of plants were placed in the same greenhouse compartment under a 17- to 18-hour photoperiod and relatively cool temperature (average maximum 60.0° and average minimum 43.4°). The plants from the cool temperature, although much smaller than those from the warm temperature, all bolted in 79 days, whereas the plants from the warm room required 92 days for all individuals to bolt. Both experiments show that while seedstalk development in this annual is influenced chiefly by photoperiod, nevertheless low temperature also exerts an influence in the same direction.

A dominant factor B is responsible for the annual habit in the Munerati annual (1), but the F₁ hybrids with biennial types, heterozygous for B and possibly other complementary genes, are slower to bolt than the annual parent. Some of the annual segregates (having the B factor) from backcrosses to biennials are very slow to bolt and may easily be confused with biennials under many combinations of temperature and photoperiod. One annual segregate (5357–1), from a backcross to a biennial from a hybrid with the Munerati annual, was propagated vegetatively for 4 years and studied in some detail. It bolted in midsummer temperatures at Salt Lake City, Utah, under the naturally long days occurring at that time. In this way it could be distinguished from biennials, but under relatively cool or intermediate temperatures (40° to 65° F.) several varieties that are considered biennial bolted just as readily. It is evident, then, that the presence of the B factor is most easily distinguished by maintaining relatively high temperatures and a long photoperiod.

Some of the wild annuals from Milpitas, Calif., differ from the Munerati annual in that they will bolt in shorter photoperiods. The population of plants from Milpitas is a mixture of genetic types varying in bolting tendency, but most of the plants are annuals. In
spring plantings at Salt Lake City, Utah, they were quite similar to the Munerati annual, but in an October planting at Riverside, Calif., some of the Milpitas plants bolted much faster than the Munerati annual.

On March 12, 1938, at Riverside, Calif., an interesting comparison was available between the Munerati and Milpitas annuals. The planting was made October 6, 1937. In the Munerati annual, seedstalks were just starting to develop on March 12, 1938, and were not over 2 inches in height, whereas the seedstalks of some of the Milpitas plants were over 3 feet in height on the same date and had well-developed flower buds. It is clear that the short photoperiod during the winter at Riverside was responsible for the delayed bolting in the Munerati annual, and the comparison indicates that some of the Milpitas annual plants do not require as long a photoperiod for bolting as does the Munerati annual. Other experiments have shown that the Imperial Valley annual will flower in still shorter photoperiods than the Milpitas annual. At Salt Lake City, Utah, September 9, 1938, seeds of the Munerati annual and Milpitas and Imperial Valley annuals were planted in flats in a warm greenhouse under the natural photoperiod. By November 11 all of the Imperial Valley annual plants had bolted whereas none of the others showed any bolting.

The facts presented show that while bolting in annual beets is induced mainly by long photoperiods, the process is also influenced by low temperature. The evidence also shows distinct differences in bolting tendency between different types of beets. Some are influenced more strongly by photoperiod and others more strongly by low-temperature exposure.

EFFECT OF PROLONGED LOW-TEMPERATURE EXPOSURE

The induction of flowering in beets by prolonged low-temperature exposure has been observed in experimental field plantings at Riverside, Calif., made in September, October, and November. Here the climate is such that the plants grow all winter, and temperatures during December, January, and February are in the main favorable for induction of flowering. The photoperiod during these months is, of course, short. All the varieties of beets, including some annuals, when grown from seed planted in the fall, remained vegetative in these tests until about March 15 or later, and some of the more vegetative varieties never developed more than a trace of bolters. The behavior was different when plants previously stored for a long period at low temperatures were planted. Plants selected June 2, 1937, for nonbolting, from a strain planted as seed on October 13, 1936, were stored at 36° to 38° F. from June 2 to November 4, 1937, and then transplanted in the field. On January 20, 1938, 7 out of 31 of these beets, or 23 percent, had started to bolt and in one case a stalk was 17 inches high. Later in the spring all the plants flowered normally. The same variety planted as seed in the field October 6, 1937, did not bolt until April 1938. Less than half of the plants in this lot bolted, and none flowered completely. Obviously, induction of flowering was strongly influenced in the plants given prolonged low-temperature exposure.

Evidence of a similar nature was observed with the nonbolting variety U. S. 15. The seed was planted in a 5-acre field near River-
side, October 15, 1935, and a part of the field was maintained 2 years. There was less than 1 percent bolting in the spring of 1936, and in 1937 also most of the plants remained vegetative or bolted too late to produce seed. Roots taken from this field were stored at 36° to 38° F. from June 16 to November 1, 1936, and then planted in an experimental plot at Riverside.

On the same date, November 1, stecklings were transplanted directly from the 5-acre field to the experimental plot. By February 5, 1937, seedstalks had started on two of the plants that had been stored at low temperatures. By March 2, several more showed short seedstalks, and on May 11 all 44 of the plants had bolted, and with fair uniformity in that all but one had buds formed or open flowers. Out of 49 plants transplanted in November directly from the field, only 28 produced seedstalks, and these were extremely irregular in development. Here again, prolonged low-temperature exposure resulted in earlier and more complete flowering.

Greenhouse studies showed that after prolonged low-temperature treatment stecklings or mother beets may be so strongly inclined toward flowering that they will develop seedstalks a few inches in length in an environment unfavorable to photothermal induction. Beetle 138, selected in 1932 and maintained as a clone since that time, was studied in detail in relation to the length of low-temperature treatment required for initiation of the seedstalk. No. 138 is a nonbolting type and remains vegetative under many conditions where most beets develop seedstalks. A 3-month treatment at 33° to 36° F. did not induce bolting in beet 138 except when followed by a favorable bolting environment, a long photoperiod, and cool temperature. In an experiment started June 6, 1935, a supply of thrifty plants grown from cuttings of No. 138 was taken to cold storage and held at 33° to 36°. On November 25, after a treatment for 172 days, these cuttings were removed from cold storage and planted in the greenhouse in two environments. One environment was favorable to bolting, with a relatively cool temperature (40° to 65°) and a photoperiod of 17 to 18 hours, while the other was unfavorable, with a relatively warm tem-

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**Figure 2.—Short seedstalks produced in an unfavorable environment after a long period of low temperature storage.**
perature (60° to 75°) and with only the natural light of the short winter days.

By January 15, 51 days after planting, seedstalks had appeared on all the plants in both environments. In the favorable environment the plants continued normal reproductive development, whereas in the warm room the seedstalks turned vegetative after making a short growth and before developing any visible signs of flowers. The two most vigorous plants of the seven in the warm room developed seedstalks 7 to 9 inches in height. A comparable experiment with another variety gave similar results, and the short vegetative seedstalks produced in the unfavorable environment are shown in figure 2. It is evident that the prolonged low-temperature treatment not only prepared the plants for bolting but actually induced a reserve of some sort, so that the reproductive tendency continued for a time in spite of an unfavorable environment.

In other experiments prolonged low-temperature treatment was followed by a controlled 8-hour day under warm temperature, making the environment still more unfavorable for bolting. Out of 20 stecklings of U. S. 33 (3407) (22) stored 246 days at 33° to 36° F., 3 plants developed 2-inch seedstalks.

EFFECT OF SHADE UNDER FIELD CONDITIONS

Early in the work of breeding sugar beets for curly top resistance, difficulty was encountered in producing seed at Riverside, Calif. Field observations in this mild climate from 1919 to 1928 revealed that better flowering resulted in the colder seasons and that in the warmer seasons, when dormancy in peaches and walnuts was seriously prolonged, flowering in sugar beets was unsatisfactory.

Two simple experiments in regard to the effect of temperature on flowering in sugar beets were conducted at Riverside in the winter of 1928-29. In one case a portion of two short rows planted late in the fall was shaded through the winter months by means of unbleached muslin. The cloth was on a frame that rested on the ground on the south side of the rows and leaned to the north, so that no direct sunlight could reach the beets or the soil in the protected part of the plot. Soil temperatures at a depth of approximately one-half inch in the shaded and in the unshaded soil were recorded by means of thermographs. The records were not taken during the entire period, but the difference between the temperatures in the two environments from January 8 to March 1, a period of 1,248 hours, is indicative of the contrast in conditions to which the shaded plants and those in full sunlight were exposed. During the period mentioned the soil temperature in the shade was continuously below 60° F. During this same period the temperature of the unshaded soil was above 60° for a total of 289 hours, or 23 percent of the total time. Bolting counts on June 4, 1929, revealed that in the unshaded plants 62 of the 347, or 18 percent, had bolted, while in the shaded plants 50 of the 130, or 38 percent, had bolted.

Another test in the same winter involved growing one lot of potted plants in full sunlight and another lot on the north side of a nursery lath house, where the plants were protected from direct sunlight throughout the winter months. Owing to the elevation of the site and consequent air drainage, the temperatures were relatively warm.
Some of the pots in each case were submerged in the soil and others were left on top of the ground. There was only a trace of seedstalk development in the plants exposed to sunlight, while nearly all the shaded plants developed vigorous seedstalks. Soil temperature records were not taken. The temperature differences probably corresponded to those in the previous experiment.

The results of these two tests indicate that in mild climates, such as that of Riverside, Calif., induction of flowering was increased when the beets were kept cooler during the winter by means of shade.

As a result of renewed interest in the factors involved in induction of flowering in beets, a field experiment with artificial shade was started at Riverside, Calif., in the fall of 1936, to get further evidence on the influence of temperature. The beets were planted September 18 on single-row beds running east and west. Portions of these rows were then shaded by frames made of shingles coated on both sides with aluminum paint. The frames were placed in series, so that they would shade the beet rows to the north and reflect light on the rows to the south. This vertical type of frame, together with a flat or horizontal type used in a later experiment, is shown in figure 3. There were three different treatments with the vertical frames, as follows: (1) Portions of rows were shaded only during the warmer part of the fall, September 18 to November 12, 1936; (2) other portions of rows were shaded only during the colder part of the season, November 12, 1936, to April 1, 1937; and (3) other portions of rows were shaded from September 18, 1936, to April 1, 1937. Five varieties, all rather low in bolting tendency, were used. There were duplicate plots for each shading treatment. Soil temperatures close to the north side of the beets and at a depth of about one-half inch were
taken in the shaded and unshaded plots by means of soil thermographs. Temperatures of the beet crowns at about one-half inch below the soil surface were determined by means of chemical thermometers inserted snugly into holes made with a cork borer in the sides of the roots. The temperatures of the roots were almost the same as the soil temperature.

Bolting counts on May 10, 1937, gave the following averages: Unshaded, 66 percent; shaded (1) September 18 to November 12, 63 percent, (2) November 12 to April 1, 89 percent, and (3) September 18 to April 1, 79 percent. Temperature records are given in table 1. Shading during the warmer part of the fall did not increase bolting and may have been detrimental in some way. Shading during the colder weather increased bolting.

### Table 1.—Temperatures of shaded and unshaded soil at one-half-inch depth and percentage of bolters in varieties 550 and 617 with and without artificial shade

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Temperature</th>
<th>Plants bolting</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Daily average</td>
<td>Mean daily deviation</td>
</tr>
<tr>
<td></td>
<td>°F</td>
<td>Above average</td>
</tr>
<tr>
<td>Nov. 23, 1936, to Mar. 21, 1937:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No shade</td>
<td>49.16</td>
<td>5.13</td>
</tr>
<tr>
<td>Vertical shade</td>
<td>45.69</td>
<td>3.41</td>
</tr>
<tr>
<td>Nov. 22, 1937, to Mar. 20, 1938:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No shade</td>
<td>51.34</td>
<td>3.09</td>
</tr>
<tr>
<td>Vertical shade</td>
<td>50.51</td>
<td>2.40</td>
</tr>
<tr>
<td>Horizontal shade</td>
<td>52.17</td>
<td>1.90</td>
</tr>
</tbody>
</table>

1 Average temperature determined by planimeter measurements of thermograph charts.
2 Averages of the two varieties.
3 "Day degree" is defined as a measure of accumulated temperature and represents an average of 1 degree of deviation from the base temperature during a period of 24 hours. Day degrees were measured as areas above and below the base temperature on thermograph charts by means of a planimeter.

Another shading experiment in the field was started at Riverside in the fall of 1937. Vertical frames, of the type used in the previous experiment, and horizontal frames were used. The latter were made of heavy kraft paper coated on both sides with aluminum paint and supported on frames of wood and wire. These frames were 18 inches wide and 12 feet long. The beet rows were 20 inches apart, so that when the frames were laid between the rows nearly all the soil between the rows was shaded (fig. 3). The beets were planted October 6, and the shading was started November 19. Two of the varieties included in the previous year's test, 550 and 617 (U. S. 14), were used in the experiment. These two varieties have practically the same bolting tendency. The shading was discontinued March 21. The results in percentage of bolters and the soil-temperature records are summarized in table 1. The bolting percentages are averages for the two varieties used.

The percentage of bolting was higher in the shaded than in the unshaded plots each season (table 1), and higher in the colder season of 1936–37 than in 1937–38 (table 1).

The fact that in the second season more bolting occurred in the plots with horizontal shades than in the unshaded plots was probably due to the temperature having been lower in the fall and early winter in the shaded plots (fig. 4). The mean temperature for the 7 weeks November 22, 1937, to January 10, 1938, was 1.08°F. higher in the
unshaded plots than in the plots with horizontal shades. The accumulated deviation above 51.19° (the mean for the plots with horizontal shades) was 149.49 day degrees greater in the unshaded plots; the accumulated deviation below 51.19° was practically the same for the shaded and unshaded plots. It is thus evident that during the late fall and early winter the beets under the horizontal shades were in a colder soil environment than were the unshaded beets. Later, as the leaves grew larger and shaded the soil more effectively, the mean soil temperature in the unshaded plots dropped a little lower than in the plots with horizontal shades. However, the soil temperatures in both plots were favorable to thermal induction during most of the latter part of the winter. The fact that the horizontal shades kept the soil temperatures relatively low in late fall and early winter apparently allowed thermal induction to continue longer in the shaded beets, with the result that 81 percent of them bolted, as compared with 47 percent in the unshaded beets (fig. 5).

Many field observations in California and southern Arizona have revealed that with rows running east and west the north sides of two-row beds have more bolters than the south sides. For example, in a field of the low-bolting variety R. & G. Old Type, planted near Calexico, Calif., October 8, 1937, there was a striking difference between bolting on the north and south sides of the beds. On May 15, 1938, there were 37 percent bolters on the north side of the beds and 7 percent on the south side. The temperature of the soil and consequently that of the beet crowns at the same level was often 4° to 5° F. cooler on the north side of the beds. In the field at Calexico the leaf area on the south side of the beds was larger, which gave that side an advantage in regard to induction by light, if it is assumed that leaf area is a factor in this process in beets. It seems probable, therefore, that the greater amount of the bolting on the north side of the beds resulted from induction by temperature.
These observations and experiments gave evidence of the relation of the temperature of beets, as influenced by the temperature of the surrounding soil, to bolting. In mild climates where winter temperatures may be too high for flowering or even for bolting, more bolting and flowering result from a slight lowering of the temperature for a prolonged period. Shading the soil surrounding the beets during the winter keeps the beets enough colder to increase bolting.

**VERNALIZATION OF SEED AND EFFECTS OF IRREGULAR GERMINATION**

Increased bolting in sugar beets as a result of subjecting germinating seed to low-temperature treatment has been previously described
Numerous tests by the writers showed increased bolting in plants grown from seed that had been subjected to vernalization treatment, but in some instances no effect was observed. Results of the following experiments explain this apparent inconsistency.

In May plantings at Salt Lake City, Utah, of seed subjected previously to vernalization treatment, little or no increase in bolting occurred. A considerable increase in bolting was observed, however, when a comparison of vernalized and untreated seed was made in an early March planting (table 2). This difference is to be explained by the fact that there was additional thermal induction in the field in the March plantings and this influence added to that accomplished by vernalizing the seed resulted in the effect noted. Seed that had been subjected to vernalization treatment was planted at Riverside, Calif., in October. There was no increase in bolting the following spring. Evidently the relatively warm weather in the fall resulted in enough reversal of the inductive process to overcome the effect of the seed treatment.

<table>
<thead>
<tr>
<th>Variety</th>
<th>Seed treatment</th>
<th>Plants observed</th>
<th>Plants bolting</th>
</tr>
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<tbody>
<tr>
<td>U. S. 12 (618)</td>
<td>No treatment</td>
<td>95</td>
<td>1.05</td>
</tr>
<tr>
<td>Do</td>
<td>Washed, incubated and dried, but not vernalized</td>
<td>96</td>
<td>5.20</td>
</tr>
<tr>
<td>Do</td>
<td>Washed and incubated and then vernalized at 33° to 36° F. for 61 days</td>
<td>162</td>
<td>12.85</td>
</tr>
<tr>
<td>U. S. 14 (617)</td>
<td>do</td>
<td>122</td>
<td>22.20</td>
</tr>
</tbody>
</table>

Striking results with seed vernalization were obtained in the greenhouse under relatively cool temperatures and with a 17- to 18-hour photoperiod when seed subjected to vernalization treatment was planted in comparison with untreated seed. Two strains low in bolting tendency, 2168 and 4919, and the easy-bolting biennials U. S. 12 and 3401 were used. In addition to these varieties, nonvernalized seed of U. S. 1 and the Munerati annual were included in the test. The results are given in detail in table 3. Eighty-two days after planting, untreated seed of U. S. 12 had given rise to 2.8 percent bolters and the vernalized seed had produced 14.3 percent bolters. With 3401, the untreated seed had given rise to no bolters, while the vernalized seed had produced 36.1 percent bolters. At this time there were no bolters in 2168 and 4919, even with the vernalized seed. Vernalization increased the rate of bolting in the easy-bolting biennials, but did not sufficiently affect the two varieties inherently low in bolting tendency to cause them to bolt in the 82-day period.

The relationship of sprouting to vernalization has been noted in several instances. In a series of experiments in 1933 and 1934, where dry seed was planted in moist soil in flats and held at approximately 40° to 45° F., the germination of most varieties was noticeably irregular. After all sprouted seed in some of the flats was killed by drying and freezing, these flats were watered and placed under temperatures favorable for germination and growth of the surviving seed. The seed that had not sprouted during the vernalization treat-
ment was then found to be unaffected. Similar seed that sprouted during the vernalization treatment was thermally induced to a considerable extent.

**Table 3.—Greenhouse test with vernalized seed**

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<thead>
<tr>
<th>Variety or strain</th>
<th>Plants bolting from—</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Nonvernalized seed</td>
<td>Vernalized seed</td>
</tr>
<tr>
<td></td>
<td>Percent</td>
<td>Percent</td>
</tr>
<tr>
<td>2168</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>4919</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>U. S. 12 (4900)</td>
<td>2.8</td>
<td>14.3</td>
</tr>
<tr>
<td>3401</td>
<td>0</td>
<td>36.1</td>
</tr>
<tr>
<td>U. S. 1 (9183)</td>
<td>7.5</td>
<td></td>
</tr>
<tr>
<td>Munerati annual (2240)</td>
<td>100.0</td>
<td></td>
</tr>
</tbody>
</table>

1 Vernalized seed was incubated a short time at 70° F and then held at 33° to 36° for 55 days previous to planting. There were 8 replications of each variety and treatment. Each replication consisted of a single row 30 inches long with 20 to 30 plants to the row. Planted Sept. 24, 1934; bolters counted Dec. 15, 1934.

In a field planting at Salt Lake City made March 16, 1937, vernalized seed of U. S. 12 was compared with two kinds of nonvernalized seed (table 2). Lot 1 of the nonvernalized seed was wholly untreated; lot 2 was washed, incubated at 70° F., and finally dried. This treatment of lot 2 hastened germination in the field during the relatively cold weather of early spring and thereby resulted in more thermal induction, and consequently the bolting was increased. However, the vernalized seed gave more than twice as many bolters as did lot 2 of the nonvernalized seed.

In this same field planting, a vernalized lot of seed of the nonbolting variety U. S. 14 gave even more bolters than the vernalized seed lot of U. S. 12 (table 2). It is well known from experience that U. S. 12 is much more likely to bolt in the field than U. S. 14 (22). Before planting it was observed that the vernalized seed of U. S. 14 had germinated to a greater extent than the vernalized seed of U. S. 12. This greater germination during the vernalization treatment probably accounts for the fact that plants grown from the vernalized seed of U. S. 14 bolted more than those grown from the vernalized seed of U. S. 12.

In preparing the seed for vernalization treatment, it was first thoroughly soaked and washed and then held at about 70° F. until the majority of the seed balls showed radicles about 1 mm. in length. It was difficult, however, to obtain a uniform degree of germination, and this lack of uniformity in germination was still more noticeable after a 60-day treatment at 33° to 36°. Some radicles were over an inch in length, while other seeds showed no evidence of germination.

The results of an experiment to discover the extent to which sprouting influences thermal induction in seed are given in table 4. Seed previously moistened and then held at 33° to 36° F. for 55 days was sorted into three classes. Class 1 included seed balls with no visible radicles; class 2 those with such radicles as were evidently less than 3 mm. in length; and class 3 those with all radicles developed and all over 3 mm. in length. Bolting counts 82 days after planting revealed approximately twice as many bolters in classes 2 and 3 as in class 1.
The increased bolting from the seed with visible radicles is highly significant (table 4).

Heritable differences complicate the problem of thermal induction in seed. Strain 2168, for example, was found to sprout more rapidly at low temperatures than strain 3401. It might be expected, therefore, that when treated similarly strain 2168 would be more effectively vernalized. Contrary to such expectation, vernalization may not cause any bolting in strain 2168, but it may cause abundant bolting in strain 3401 (table 3). Such results are explained by inherent differences in bolting tendency. Strain 2168 is inherently a non-bolter, while strain 3401 is an easy-bolting strain. If one of two strains of the same bolting tendency germinated more readily than the other at low temperatures, it would be expected to respond more strongly to vernalization.

Vernalization increased the rate and percentage of bolting provided that (1) the seed sprouted during the cold treatment and (2) the vernalized seeds were planted in an environment favorable enough for induction of flowering to continue. Vernalization did not overcome inherent differences in bolting tendency.

A NEW GENETIC FACTOR FOR BOLTING

The action of certain genes in relation to the physiological process responsible for flowering should be known for a better understanding of photothermal induction. The factor $B'$ now to be described has an important role in the process in beets. It is responsible for an easy-bolting tendency but appears to differ from the factor $B$ described by Munerati (20) and Abegg (1), because plants carrying $B'$ remained vegetative under field conditions, whereas plants carrying $B$ were strictly annual. It will be seen that $B'$ and $B$ are regarded as allelic factors and dominant to the factor $b$ associated with a nonbolting tendency. Linkage discovered between $B'$ and the color factor $R$ (13) made the genetic analysis possible. In order to study the factor $B''$, it was necessary to give careful attention to environmental conditions affecting photothermal induction as well as to the genetic material to be investigated.
PARENTAL MATERIAL

The parental material consisted of three clones selected in 1932 and subsequently studied in detail. Their bolting tendencies were therefore well known. Clone 70, \textit{rr}B'\textit{b}, provided the factor \textit{B'} for bolting, while clone 79, \textit{RR}bb, and clone 90, \textit{rr}bb, were vegetative types. These clones were selected from rather closely bred lines that had been characterized by a fair degree of uniformity.

Clone 70 was selected from 2769, a strain obtained from William W. Tracy, Jr. This plant was a fast-bolting biennial. Experience with vegetative cuttings from it, and with seed from its parental strain and its selfed progeny, showed that it was not an annual under field conditions at Salt Lake City, but it was a fast bolter and was easily confused with annuals under relatively low temperatures in the greenhouse. Clone 70 also carried a genetic factor for self-fertility, which distinguished it from most sugar beets.

Clone 79, \textit{RR}bb, was a strongly vegetative or nonbolting type. It was first propagated vegetatively because of interest in its male-sterile character, which is a convenience in hybridization work. The plant was apparently normal in every other respect, but the pollen grains were completely aborted.

Clone 90, \textit{rr}bb, came from Salt Lake City strain 2167, a curly top-resistant strain with a strongly vegetative or nonbolting tendency. An advantage of clone 90 for crossing is its strong self-sterility, for when it is used as a female parent one can be sure of obtaining hybrids without taking the trouble to emasculate.

METHODS

The male-sterile clone 79, \textit{RR}bb, was pollinated from clone 70, \textit{rr}B'\textit{b}, and several \textit{F}_1 plants were grown. The \textit{F}_1 plants segregated for male sterility and self-fertility. \textit{F}_2 progenies were produced from some of the self-fertile \textit{F}_1 plants. Backcross progenies were also produced by hybridizing clone 90 (\textit{rr}bb) with pollen from a few of these \textit{F}_1 plants selected at random from those producing normal pollen.

Respective progenies were tested for bolting by subjecting some of the seed to a vernalization treatment and growing the plants in the greenhouse. The seed was vernalized for 101 days at 33° to 36° F. At planting time most of the seed had sprouted and the radicles were approximately 0.5 to 2 cm. in length. Some seed lots were more uniform in sprouting than others, and some were affected by the development of mold. Seed of the backcross progeny (4615), which gave the most interesting results (table 5), however, was nearly free from mold, and the radicles were more uniform in length than in most of the other progenies. This proved to be a fortunate circumstance, because the uniformity of the vernalized seed when planted is believed to have had an important bearing upon the clear-cut differentiation secured for the bolting types in this progeny (table 5).

The plantings were made in greenhouse beds 30 inches wide with rows 4 inches apart. Progeny 4615 was planted in 15 of these rows, and 250 plants, or about 17 plants per row, grew from uniformly spaced seed. Owing to limited space, plants of other progenies were more closely spaced, with about 34 plants per row. Nonvernalized seed of the respective progenies was planted at the same time for comparison. Artificial light was used to supplement the regular day
length to make approximately a 17-hour day. The temperature was controlled rather roughly, and a record was taken each day from a minimum and maximum thermometer.

Table 5.—Correlation between time of bolting and hypocotyl color from backcross progenies 4615 and 4612

<table>
<thead>
<tr>
<th>Days after planting</th>
<th>Bolters</th>
<th>Vegetative plants</th>
<th>Total plants</th>
<th>Cross-overs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Red hypocotyl</td>
<td>White hypocotyl</td>
<td>Red hypocotyl</td>
<td>White hypocotyl</td>
</tr>
<tr>
<td>47</td>
<td>29</td>
<td>104</td>
<td>98</td>
<td>19</td>
</tr>
<tr>
<td>105</td>
<td>29</td>
<td>108</td>
<td>98</td>
<td>15</td>
</tr>
<tr>
<td>136</td>
<td>71</td>
<td>108</td>
<td>50</td>
<td>14</td>
</tr>
</tbody>
</table>

Table 6.—Daily greenhouse temperatures, 1934–35

<table>
<thead>
<tr>
<th>Month</th>
<th>Temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Average maximum</td>
</tr>
<tr>
<td>September 24 to 30</td>
<td>75.1 °F.</td>
</tr>
<tr>
<td>October</td>
<td>81.3 °F.</td>
</tr>
<tr>
<td>November</td>
<td>73.9 °F.</td>
</tr>
<tr>
<td>December</td>
<td>71.5 °F.</td>
</tr>
<tr>
<td>January</td>
<td>75.3 °F.</td>
</tr>
<tr>
<td>February</td>
<td>71.0 °F.</td>
</tr>
<tr>
<td>March</td>
<td>62.4 °F.</td>
</tr>
<tr>
<td>April</td>
<td>72.1 °F.</td>
</tr>
<tr>
<td>May</td>
<td>80.5 °F.</td>
</tr>
</tbody>
</table>
Bolting records were taken at intervals as bolters appeared, and in most cases the bolters were pulled when counted in order to allow more space for the remaining plants.

EXPERIMENTAL RESULTS

The extreme differences in bolting due to heredity are shown in figure 6. The Munerati annual plants had all started seedstalks within 50 days after planting, whereas the vegetative strain 2167 showed only a small percentage of bolting 200 days after planting. The selfed progeny of clone 70 was between these two extremes but somewhat closer to the early-bolting side. This performance was in agreement with considerable additional evidence that clone 70 represented a rather fast-bolting type.

Although the plants in the selfed progeny of clone 70 were fast bolters there was considerable variability, as shown in figure 6. Some

![Figure 6](image-url)  
**Figure 6.** The gradation of beet types from strong annual to strongly vegetative biennial habit is shown in this graph summarizing results obtained with nonvernalized seeds. Clone 70 indicates selfed progeny of clone 70. Clone 70 and strain 2167 represent parental types, and 4612 and 4615 are backcross progenies from hybrids between clone 70 and clones from strain 2167 described in text.

plants in the progeny bolted much faster than others, but it is uncertain how much of this was due to heredity and how much to environmental differences between different plants. The question of whether or not clone 70 was homozygous for bolting tendency is made clearer by studying its hybrid progenies. Clone 70 is represented by backcross progenies numbered 4612 and 4615 and F2 progenies numbered 4608 and 4609. The heterozygosity of clone 70 is believed to be shown in the performance of these backcross and F2 progenies. For the backcross progenies, figure 7 and table 5 illustrate the fact that 4615 segregated for fast-bolting types while 4612 was almost equal to the vegetative parental types. Likewise, the data in table 7 show that the F2 4608 was fast in bolting while the F2 4609 was much slower.

It seems probable that clone 70 was of heterozygous constitution, $B' b$, assuming $B'$ to be responsible for the bolting tendency. When crossed to clone 79 ($RRbb$) the F1 plants would be expected to be $RrB'b$ and $Rrbb$ in equal proportion. Backcrossing the F1 plants at random to clone 90 ($rrbb$) would then yield some backcross progenies
like 4615, consisting of both $B'b$ and $bb$ plants that show sharp segregation for bolting and vegetative types, and other backcross progenies like 4612, all $bb$, which lean rather strongly to the vegetative side. Likewise in F$_2$ progenies, data presented in table 7 indicate that progeny 4608 was derived from a plant of constitution $RrB'b$ and progeny 4609 from a plant of constitution $Rrbb$.

LINKAGE BETWEEN $B'$ AND $R$

The correlation between bolting tendency and hypocotyl color is a point of much interest. This correlation is shown for the backcross progeny 4615, clone 90, $rrbb$, × (clone 79 × clone 70), $RrB'b$, in figure 7 and table 5. Figure 7 shows, especially with the vernalized seed, than the plants with white hypocotyls ($rrB'b$) bolted much more rapidly that those with red hypocotyls. Evidently because of their genetic constitution, the white hypocotyl plants were in large part so strongly affected by the seed treatment that they bolted quickly after planting. Since the bolting tendency was associated with the recessive hypocotyl color in the clone 70 parent, it can be assumed that the respective genetic factors responsible for these characters were linked in their inheritance.

A cross-over value of 15.5 percent between the factor $R$ for hypocotyl color and the factor $B$ for annual habit has been reported by Abegg (1). In table 5, progeny 4615 shows a cross-over value of 17.6 percent between $R$ and $B'$ at 105 days after planting, which is very close to Abegg's value. Since the rate of bolting is perhaps not entirely clear-cut, even at 105 days after planting, it may be assumed that a more perfect separation between bolting and vegetative types would lead to a slightly lower figure than 17.6 percent crossing over. Calculations from figures obtained from a less desirable classification, made at 136 days after planting, give 35 percent crossing over, which is a poor estimate because of an excess of observed plants in the bolting class over the expected proportion. It is assumed from the similar association of $B'$ with $R$, and of $B$ with $R$, that $B$ and $B'$ may be alleles with identical positions on the chromosome. There is, however, no critical proof that $B$ of the Munerati annual and $B'$

![Figure 7.—Bolting reaction of color types in backcross progeny 4615.](image-url)
of clone 70 are not the same gene with the apparent difference between them caused by additional modifying factors.

The F2 progenies were not expected to yield data that would be as clear-cut as those from the backcross progenies. This was particularly true because in the F1 cross, clone 79 (RRbb) × clone 70 (rrBb'), the characters entered in the repulsion phase. However, table 7 shows that a significant negative correlation was obtained between bolting and hypocotyl color in F2 progeny 4608. The $\chi^2$ value has been used to measure this correlation in table 7. This value is highly significant, but it does not give an accurate idea of the percentage of recombinations.

### Table 7.—Correlation between time of bolting and hypocotyl color from F2 progenies 4608 and 4609

<table>
<thead>
<tr>
<th>Days after planting</th>
<th>Bolters</th>
<th>Vegetative plants</th>
<th>Total plants</th>
<th>$\chi^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Red hypocotyl</td>
<td>White hypocotyl</td>
<td>Red hypocotyl</td>
<td>White hypocotyl</td>
</tr>
<tr>
<td>40</td>
<td>77</td>
<td>26</td>
<td>387</td>
<td>89</td>
</tr>
<tr>
<td>85</td>
<td>171</td>
<td>75</td>
<td>282</td>
<td>40</td>
</tr>
<tr>
<td>172</td>
<td>235</td>
<td>85</td>
<td>162</td>
<td>26</td>
</tr>
</tbody>
</table>

PROGENY 4609

<table>
<thead>
<tr>
<th>Days after planting</th>
<th>Number</th>
<th>Number</th>
<th>Number</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>39</td>
<td>6</td>
<td>4</td>
<td>282</td>
<td>90</td>
</tr>
<tr>
<td>108</td>
<td>69</td>
<td>25</td>
<td>219</td>
<td>69</td>
</tr>
<tr>
<td>192</td>
<td>161</td>
<td>55</td>
<td>127</td>
<td>41</td>
</tr>
<tr>
<td>257</td>
<td>278</td>
<td>90</td>
<td>12</td>
<td>4</td>
</tr>
</tbody>
</table>

All data are from vernalized seed of progenies 4608 and 4609. According to Fisher's tables (9), with 1 degree of freedom $\chi^2$ should exceed 6.635 for the 1-percent point of significance.

### DISCUSSION AND CONCLUSIONS

Initiation of seedstalks and flowering of biennial beets is brought about mainly by the cumulative effect of low-temperature exposure followed or accompanied by the effect of long photoperiods. The effect of temperature may be as pronounced as the effect of photoperiod. With beets it is difficult in many cases to distinguish between these two principal environmental effects; hence "photothermal induction" is used in this paper to denote induction of flowering and includes both photoperiodic and thermal induction.

Thermal induction and photoperiodic induction probably result in the production of one or more flower-inducing substances, or hormones, as indicated by work with other plants by Cajalchjan (2), Moškov (19), Melchers (18), Loehwing (15), and by one of the writers with beets.5 Prolonged thermal induction in some cases influences the reproductive tendency so strongly that this tendency continues for some time after the environment has become distinctly unfavorable for reproduction. It appears, therefore, that if induction of flowering is caused by some substance, enough of this substance accumulates while temperatures are favorable to last for some time after conditions become unfavorable.

5 Stout, M. Unpublished work.
In the reproductive process the role of low-temperature exposure comes in mainly in the initial stages. In biennial beets somewhat higher temperatures are more favorable for growth of the seedstalks and flowering, as has been reported in the case of tulips (10) and spinach (14). However, continuation of relatively cool temperature is necessary for completion of flowering in beets. Steinberg and Garner (24) reported that in a biennial variety of beets seedstalks were initiated and some flowers produced at 73° F. with continuous light, but the photographs published by these writers show that the seedstalks were somewhat vegetative under this relatively warm temperature. Obviously, the induction was inadequate for complete reproductive development. The writers have observed that vegetative seedstalks similar to those pictured by Steinberg and Garner commonly result from inadequate low-temperature exposure during seedstalk initiation or from excessively high temperatures during seedstalk development.

The relative importance of thermal induction and photoperiodic induction varies with different types of beets according to their genetic constitution. A comparison of the biennial U. S. 12 and the Munerati annual in fall plantings at Riverside, Calif., illustrates this point. In early spring, when the days were relatively short, some individual plants of the biennial U. S. 12 showed seedstalks before any stalks appeared in the Munerati annual. Evidently the U. S. 12 plants were so strongly influenced by thermal induction that they started to develop seedstalks during relatively short days that were unfavorable. The Munerati annual, on the other hand, needs little or no thermal induction, but it requires a relatively long photoperiod. Evidently the Munerati annual requires more photoperiodic induction for initiation of flowering than does U. S. 12 or else does not respond to low-temperature exposure so readily.

The bolting factor $B$ (1, 20) is responsible for much of the annual tendency in the Munerati annual. All plants with this factor that have been studied critically at Salt Lake City, Utah, have initiated seedstalks and flowered under long days during midsummer temperatures. A factor $B'$ with an effect comparable to that of $B$ is described in this paper. Plants with this factor, when grown under long days and at warm temperatures, will flower as readily as the Munerati annual if they have had a short treatment with low temperature.

The influence of the genetic factors $B, B', \text{and } b$, which determine the tendency for bolting in beets, is comparable in importance to the influence of temperature and photoperiod. Furthermore, the discovery of these genetic factors affords a new approach to the study of induction of flowering. It is now clear that this physiological process would be better understood if more knowledge were available regarding the physiological action of the genes. In the case of *Hyoscyamus niger* L., Melchers (18) gives evidence for a gene for biennial tendency with physiological significance somewhat similar to that of $B$ or $B'$ in beets. Genes in soybeans that influence time of flowering also have been reported (28), and this fact should be useful in studying the effect of photoperiod peculiar to this plant.

Reversal or prevention of the induction of flowering is an important factor in vegetative development in beets. This reversal or prevention permits continuation of growth and the accumulation of food reserves.
These food reserves are necessary for beets to survive as biennials, and it is because of the abundant supply of stored food in the form of sucrose that sugar beets are of commercial importance as a source of sugar. Reversal of induction of flowering makes possible the perennial tendency in biennial beets that is evidenced in seed fields where many plants survive and resume vegetative development after the seed is harvested. In contrast to the behavior of biennial beets in this respect, the Munerati annual, after seed has been harvested from it in July at Salt Lake City, either dies or produces more flowering branches. Evidently induction of flowering in this annual is stronger than the reverse process, even in midsummer. The reverse process becomes evident in beet-seed fields of the Southwestern States when, owing to the fact that the temperatures have been too warm for adequate induction, some plants with seedstalks several feet in height turn vegetative. The same type of reaction is often evident with bolters in fields grown for sugar. It is on this account that the bolters classed as late are much less objectionable than those described as early (6). The flowering process in such plants is reversed, and nearly normal vegetative development of the roots takes place.

A knowledge of the principles of photothermal induction is useful to the plant breeder in breeding for a desired bolting tendency. Irregular germination under temperatures conducive to vernalization causes variability in degree of induction obtained. This may constitute a stumbling block to the breeder who selects for nonbolting without knowing that some of his nonbolting phenotypes failed to bolt merely because they were delayed slightly during the early period of germination. Nonbolting selections from early spring plantings may, on this account, be untrustworthy. Breeding for nonbolting is also handicapped by difficulties in obtaining photothermal induction adequate for propagation of the most extreme nonbolting selections. The strongest nonbolters are usually the poorest seed producers and tend to be neglected or dropped in the breeding process. Optimum and uniform conditions for induction of flowering are therefore required for the best results in developing nonbolting types.

A knowledge of the factors that influence photothermal induction is also of practical importance in the selection and maintenance of beet-seed-growing areas, particularly where the method (21) of overwintering the plants in the field is to be used. Success or failure in producing seed of some particular variety may depend on the choice of a suitable area. In some of the areas now growing seed, where temperatures are too high for the best thermal induction, it is important to develop promptly in the fall and hold an extensive growth of leaves to shade the soil and thereby reduce soil temperatures. The relation of the leaf area to induction by light may also be important, but this phase of the problem has not yet been adequately investigated.

SUMMARY

“Photothermal induction” of flowering is a new term used to signify induction of flowering by both light and temperature. In beets the effect of photoperiod was found to be intimately associated with and dependent upon temperature exposure. The effect of low-temperature exposure favorable to subsequent flowering was demonstrated
with germinating seed, with beets kept for a time in cold storage, and with growing plants.

Some of the factors that influenced bolting in the field acted indirectly by altering the range or duration of effective temperatures. Thus, shade increased bolting by lowering the temperature of the soil and consequently the temperature of the beet crown under conditions where the unshaded soil was too warm. Irregularity in germination of seeds under temperatures conducive to induction of flowering resulted in variation in bolting because of the fact that seeds retarded in sprouting escaped some of the low-temperature influence.

Genetic variability in beets with regard to response to temperature and photoperiod was shown in both annuals and biennials. A factor for bolting was identified, which is designated $B'$ and is regarded as allelic to the factor $B$ discovered by Munerati (20) and further described by Abegg (1). Identification of the factor $B'$ was accomplished by hybridizing selected parental material and testing the backcross progenies under controlled environmental conditions.

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