Flowering of Sugarcane:
Mechanics and Control

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INTRODUCTION

Flowering of sugarcane is a mixed blessing for the grower: on the one hand, flowering is essential for the improvement by commercial cane breeding; on the other hand, it can cause very substantial losses of yield in commercial fields.

Yield losses caused by flowering were demonstrated at Ewa, on the Island of Oahu (22) in an experiment comparing blossoming and nonblossoming plots of the cane variety H37-1933. The crop was started in March 1949 and harvested January 30, 1951. Certain plots were given interrupted night treatments, using square reflectors that precisely limited the exposure to the treated plots without lighting the intervening check plots. At induction time the crop was about 6 months old. The experiment showed that interrupting the night during this induction period prevented tasseling and increased the yield by 2 tons sugar; plots that were not treated blossomed heavily— 26.0 and 36.2 percent—and the yield was reduced by 2 and 3 tons sugar per acre. Blossoming during the second season only was shown to be not serious when harvest followed within 8 to 10 months. Preventing blossoming during both seasons resulted in a gain of 2.3 tons sugar over allowing blossoming during both seasons (Table 1).

Table 1. Effect of blossoming on the yield of sugarcane, H37-1933, Ewa, Oahu, 1949-1951 (average of six replications)

Light treatment	Yield		Percent tasseling	
	Tons cane/acre	Tons sugar/acre	1st season	2nd season
First season only	147.8	16.9	0.0	10.3
Second season only	138.8	14.9	26.0	0.8
Both seasons	141.1	16.2	0.3	0.8
Neither season	123.4	13.9	36.2	16.7

A second experiment of the same kind was installed in an adjoining field, but it was started in June. Because the crop was too young in September, there was no blossoming in the first year regardless of treatment, nor, for some reason, was there any substantial blossoming in the second season. However, a comparison of the actual field yields is very revealing. Field 23.2 (56 acres), started as a first ratoon in March, blossomed heavily both seasons, and, when harvested at 22.6 months of age, yielded 119 tons cane, 12.58 tons sugar, and 0.557 ton sugar per acre per month. The adjoining field 25 (86 acres), also a first ratoon that was started in June but which blossomed very lightly, was harvested at 24.0 months of age and yielded 119 tons cane, 17.44 tons sugar, and 0.727 ton sugar per acre per month. Quality in field 23.2 was poor (9.47 tons cane per 1 ton sugar), while in field 25 it was excellent (6.82 tons cane per 1 ton sugar). Both fields were given ripening control, and, although June is a "better juice month" than January, excellent results could also have been obtained if there had been no tasseling.

Since the tassels promote the production of lalas (branches, or side shoots) on the cane top, vertical growth of that stalk essentially ceases. Then in the spring following a heavy blossom, the crop produces a heavy stand of suckers, which grow very rapidly and begin to lodge by the middle of the following August. As they do, they weight down and smother the top-heavy stalks that had blossomed the previous year. These stalks then become buried, start to sour, and cause poor quality. Thus, if there is no first-season blossoming, but there is a second-season blossoming (for example, as in the first treatment in Table 1), the quality can be excellent if the harvest is done early the next year but very poor if the harvest occurs after the top-heavy stalks are buried by the lodging of the second-season suckers.

Because of such effects, varieties that are not heavy tasselers have been selected in Hawaii; some, in fact, have never been known to tassel. The nontasseling varieties, however, are unfortunately not completely acceptable for commercial canes because they fail to yield as much as required to be profitable. The problem posed, therefore, is how to select canes that do not blossom under ordinary field conditions but which can be made to blossom under artificial conditions to permit their improvement through breeding.

This bulletin presents relevant data from many years' research on the mechanics of flowering and the methods available to prevent or induce blossoming.

HISTORICAL BACKGROUND

According to Mangelsdorf (47), the first evidence that sugarcane produced seed was provided in 1858 by Parris of Barbados, who grew to maturity some cane seedlings found in his field. It was not until the *sereh* disease threatened the industry in Java, however, that serious work was undertaken. Soltevedeh, a Dutch botanist, undertook a study of the reproductive organs of *Saccharum* and, in 1887, succeeded in germinating the very small seeds and growing the seedlings to

maturity. As observed by Martin-Leake (48), this accomplishment revolutionized the sugar industry.

Vijayasaradhy et al. (57, 58, 59) reported that Dutt (33, 34) and Yusuf (63) were conducting as early as 1932 the first experiments to compel cane to flower. Sartoris (53), in 1938, reported that S. spontaneum flowered during day lengths of 12:00 to 13:30.[1] At the same time, Yamasaki and Oda (60) reported the tendency of sugarcane to blossom more profusely along the edges of the fields. Brandes and Matz (4), in 1939, were able to flower Co 281 in a day length of 12:30. Dutt (34) and Yusuf (61, 62, 63), singly and together, did considerable work from 1943 on. Their methods included irrigating daily and fertilizing with manure, exposing an Assam S. spontaneum to a 9-hour day from 1 month of age onward, and inducing a Burma S. spontaneum to blossom by taking marcotted tops and exposing them to 22 hours of darkness for 2 months from September 10 on. Another normally nontasseling S. spontaneum flowered after treatment for 2 months with 22 hours of darkness and 2 hours of sunlight in the middle of the day, after which it was exposed to normal daylight. It began to bolt 1½ months later, while the checks did not.

De Almeida, Valsecchi, and Gomes (32), in Brazil in 1945, observed that varietal differences in flowering exist, but that abundant rainfall and high temperatures favor flowering, especially of the largest canes of a clone. Engard and Larsen (36) began their studies of organogenesis of Saccharum, which were, however, brought to a halt by Engard's untimely death. They had, however, published some illustrations of the various floral reversions, some of which are included in this bulletin (see pages 13 and 25).

Allard (1), in 1938, and Allard and Evans (2), in 1941, regarded S. spontaneum as belonging to the intermediate group of plants so far as day length and blossoming were concerned.

Brett (5, 6, 7, 8, 9), in South Africa, began a long series of reports dealing with the manner in which he was able to overcome the lack of adequate tassels for his breeding program. In 1947 (5) he reported that drought reduces the intensity of blossoming by causing the reversion to vegetative growth and that often a bunch-top condition resulted. He had to contend not only with drought but also with low temperatures. To overcome these he began marcotting both male and female stalks that were already initiating and then transplanting them into greenhouses, where a more favorable minimum temperature could be maintained. In 1949 (6) he reported that increasing the day length had no effect on pollen viability and that humidity was not important. In 1950 (7) he observed that, in addition to favorable minimum temperature, the length of day, age of the stalk, and

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[1] Throughout this bulletin, a time period is designated as 12:30, meaning 12 hours and 30 minutes, or 12:30:22, meaning 12 hours, 30 minutes, and 22 seconds. If the time of day is being referred to, the designation is followed by a.m. or p.m.; thus, 12:30 a.m. and so forth.

rainfall are all important factors in blossoming. To emphasize the importance of proper temperatures, he reported getting 158 seedlings from two tassels of NCo 310 produced under cool natural conditions, but 1574 seedlings from two tassels produced under artificially warmer conditions. Paliatseas et al. (49, 50), in 1953 and 1956, also used marcotting as a successful technique.

At Rudrur in central India, in 1954, Sastry (54) considered low minimum temperatures as well as low humidity responsible for failure of seed setting.

In 1950 at Pingtung, Taiwan, Lee and Lin (46) succeeded in blossoming a native S. spontaneum upon exposure to days of 9 hours, 12 hours, 15 hours, and the natural day as a check. The 12-hour day performed about the same as the check, but the 9- and 15-hour days delayed blossoming, thus making possible a longer breeding season and bringing a wider array of forms into blossom several times. Then in 1968 Lee, Hu, and Tu (45) reported using 8 hours of direct sunlight with 4 hours of weak incandescent light (3–55 lux) applied from 6 to 8 a.m. and from 4 to 6 p.m. Still later they went to a 12:30 day, which they found best of all.

In the meantime, at Coimbatore, Vijayasaradhy et al. (57, 58, 59) continued to flower various members of the large S. spontaneum collection merely by extending the night 4 hours. (When this treatment was undertaken in Honolulu, none of the Hawaii clones used responded.)

In Louisiana, Chilton (11, 12, 13, 14, 15, 16) and Paliatseas (49, 50) and their associates developed a sound basis for their breeding program by exposing cane plants to a day of 12:44 plus the period from sunset to dark. Each 24 hours, the night was lengthened by 1 minute. In 1953, seven varieties were induced to tassel; in 1954, 34; and in 1955, 41. In 1965 (16) they reported having blossomed 109 clones in all—most of them Canal Point (CP) clones but others as well.

In Hawaii, the idea developed that all varieties that initiate blossoms do so more or less on the same date. Thus, if a variety exserted a blossom in November and another the following April, the assumption was made that both flowers were initiated on the same date in August or September. In general, if growth is more or less normal, such an occurrence is a morphological impossibility. As has been pointed out (21, 24, 25), once the meristem changes to a blossom, leaves are no longer produced and only those already formed will emerge. At the maximum, within the spindle leaf +1 (24) there are only eight leaves in various stages of development, and with normal emergence rates no more than 3 months could elapse from initiation in August or September before the blossom would appear.

Panje and Srinivasan (51, 52), working with the Coimbatore collection of 450 different clones of S. spontaneum, showed that, over a 6-year period, of the 200 or so that normally blossom there, 124 varied from 0 to 9 days in their blossom dates; 65 from 10 to 19 days; 8 from 20 to 29 days; 4 from 30 to 39 days; and 3 from 40 to 49 days. Early or late blossoming is not constant for given clones, although they tend in the same direction. Differences in time of blossom appearance are due to differences in initiation, although there can be delays if a drought occurs after

initiation. Panje and Srinivasan also moved 340 of these clones north from Coimbatore ($11°N$) to Karnal ($30°N$). Of the 178 clones that blossomed at both places, those at Karnal blossomed some 40 days later than those at Coimbatore. They estimated that the shift in time of blossoming can be calculated at $2.40 ± 0.09$ days per degree of displacement. Yet, when they compared species native to the Coimbatore area with those native to Karnal, those at Karnal actually blossomed earlier in the year than did those at Coimbatore. But these species, when moved to Coimbatore, blossomed 40 days earlier than at Karnal, and the Coimbatore species blossomed some 40 days later at Karnal. This behavior probably is related to the evolution of these more northern species, which had to contend for survival with frosts and freezing temperatures. Over a long period, only the early blossoming ones would survive. The fact that the more southerly species blossom later probably is related to the monsoon periods, particularly since it has been pointed out repeatedly that very low soil moisture tension is a prime requirement for blossoming.

Daniels (*31*), in Fiji, produced blossoms for his breeding work by imitating the day lengths in Hawaii until a night of 11:30 was reached, and then he maintained this nyctiperiod indefinitely.

Van-Breemen and Ellis and their associates (*35, 56*), at Central Romana, report much more profuse blossoming at 1500 feet elevation than at 200 feet. They explain by observing that the maximum temperatures are $81°F$ at the higher elevation versus $89°F$ at the lower, and the minimum temperatures are $69.1°F$ at the higher elevation versus $70.4°F$ at the lower—thus making for narrower daily temperature ranges.

Several papers by Clements (*18, 19*) and Clements and Awada (*20, 21, 22, 23*) defined the conditions required for inducing blossoming of reluctant tasselers, which, of course, result in profuse blossoming of the willing tasselers.

James (*40, 41*), in Florida, prolonged his cane breeding season by imposing a graduated delay in the 11:30 nyctiperiod from September 13 onward.

Chu and Serapión (*17*), in Puerto Rico, showed that early and late flowering varieties do not initiate at the same time and that the photoperiod is a dominant factor but is influenced by low temperatures and moisture stress.

Burr et al. (*10*), Coleman (*26, 27, 28, 29, 30*), and, more recently, Julien (*42, 43, 44*), report studies on the fundamental problem of the physiology of flowering. The approaches include defoliation, various wavelengths of light, use of various chemicals, and night interruptions. As with other plants, the revelation of the process has been elusive.

MECHANICS OF FLOWERING

In an effort to describe with relative accuracy the morphological changes that occur after the meristem stops producing vegetative leaves up until the inflores-

cence is mature, a program was set up for collecting field-grown plants twice a week beginning August 22, 1966. The day before, 300 very vigorous plant cane stalks of NCo 310, growing at Waimanalo, on the Island of Oahu, in an irrigated, well-fertilized field, were selected, and a label was placed under leaf +5 (24) of each stalk. This became the anchor point from which later counts were begun. The plan called for a random selection of 10 from among these 300 cane stalks twice each week. Unfortunately, because of illness of one staff member, the first collection was not made until September 2, and it was soon evident that the meristem had already changed from vegetative to flowering activities. Because no outwardly apparent morphological changes were evident on September 2, collections continued until November 21.

To trace the earlier meristematic changes, a similar series of counts was undertaken in 1967, beginning July 23. Meristematic tips from 10 stalks were collected twice each week, killed in FAA fixative, embedded in paraffin, sectioned, mounted, and stained.

The 1967 series will be described first, and the 1966 series second.

Over 25 years ago, Engard and Larsen (36), working with a Hawaii clone, made similar studies and took many photographs of the inflorescences at various stages of normal development (Figures 36–45) and also various types of reversions (Figures 60–69). Some of these observations are included in the following descriptions, even though the photographs by Engard and Larsen were from a different clone and occurred on different dates than homologous stages for NCo 310 described here.

Sequence of Floral Development (1967 Series)

Figures 1 to 31 show the stages in floral development from July 23, 1967, to complete maturation on November 21, 1967. Since Figures 1 to 8 and 32 show very small leaf primordia, it is clear that the meristems shown up to August 18 were vegetative. From August 22 onward, however, no more vegetative leaf primordia developed; instead, the shape of the meristem changed to a somewhat elongated dome-type structure (Figures 9, 33). Later (Figures 10–15), the meristem enlarged and spaces began to appear about it, as though providing room in which the flower could expand unimpeded. By September 1 (Figure 12), the enlargement was considerable, and the lower part of the structure began to show the primordia of the branches of the inflorescence (Figures 10–13, 34, 35). When viewed in three dimensions, it is clear that, while in the vegetative phase prior to August 18 (Figure 32) the meristem produced leaves alternately in two rows, but during the 10 days from August 22 to September 1 the orientation changed. Small glistening domelike structures, spirally arranged (Figures 36–38), made their appearance at the base and continued to develop acropetally. In the meantime (Figures 12, 38), floral branch primodia development proceeded acropetally and rather rapidly (Figures 13–19,
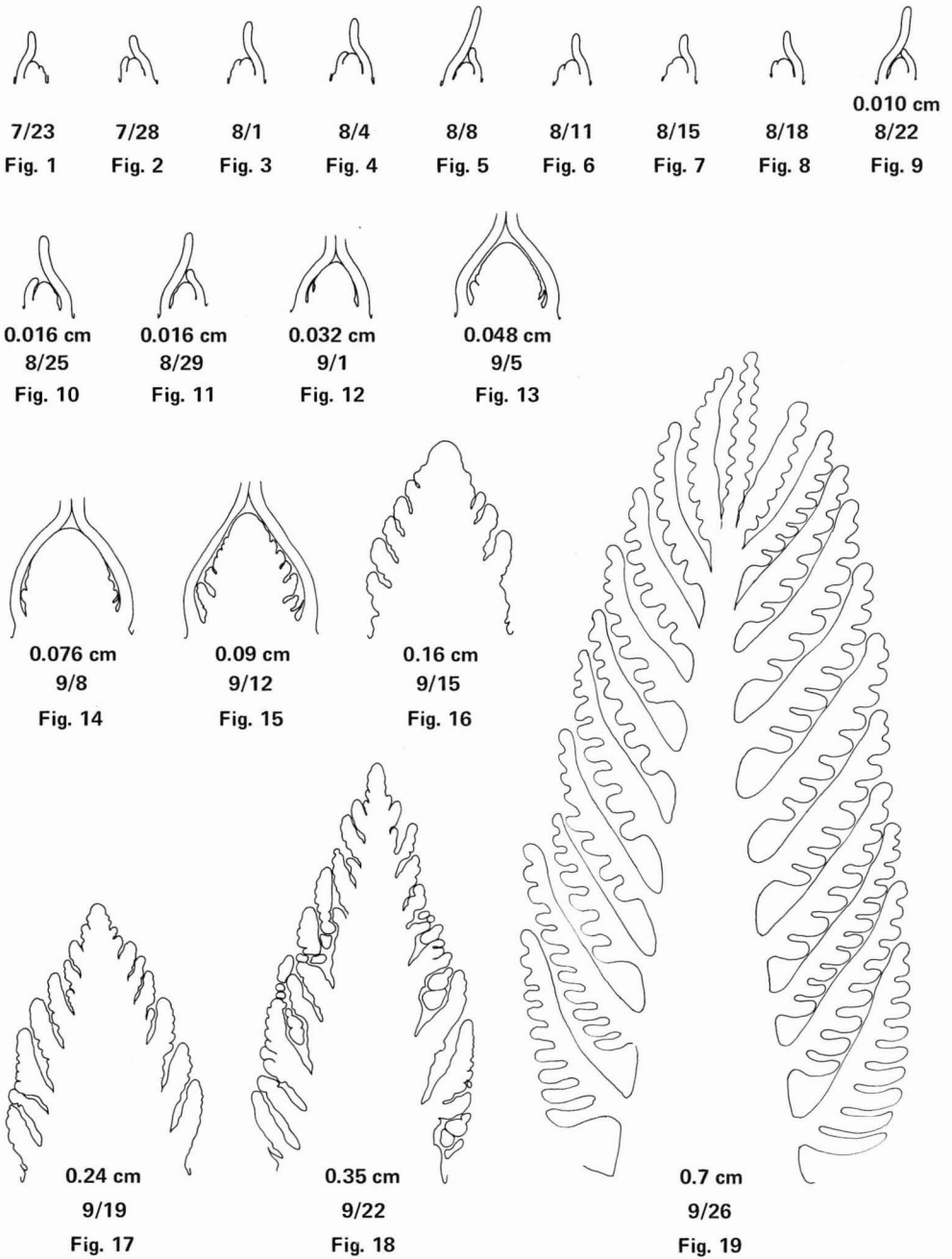
Figures 1–19. Early stages: development of the meristem from vegetative to flowering activity, July 23–September 26. Figure 9 shows the first stage in the development of the blossom. Figures 1 to 18 are drawn in the same scale.

1 cm
9/30
Fig. 20

2.5 cm
10/3
Fig. 21

4 cm
10/7
Fig. 22

7 cm
10/10
Fig. 23

20 cm
10/14
Fig. 24

240 cm (bottom of stem to emergence tassel)   11/4
Fig. 26

40 cm
10/17
Fig. 25
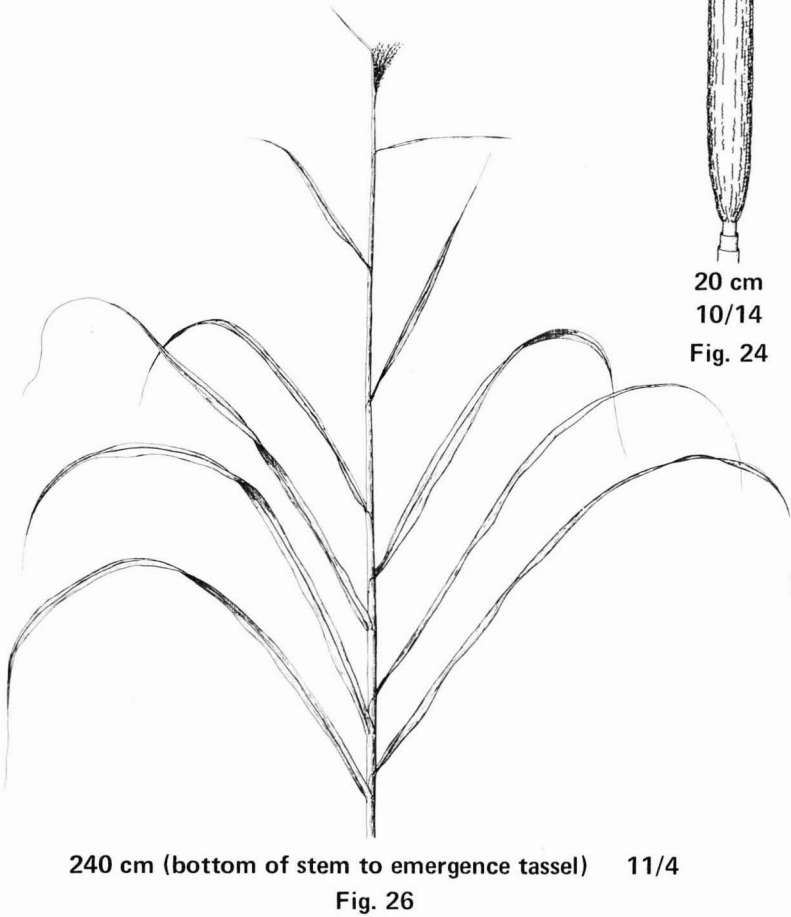
Figures 20–26. Later stages: development of the inflorescence, September 30–November 4. The tassel makes its appearance at the tip of the boot. Figures 20 to 25 are drawn in the same scale, which is different from Figures 1 to 18.
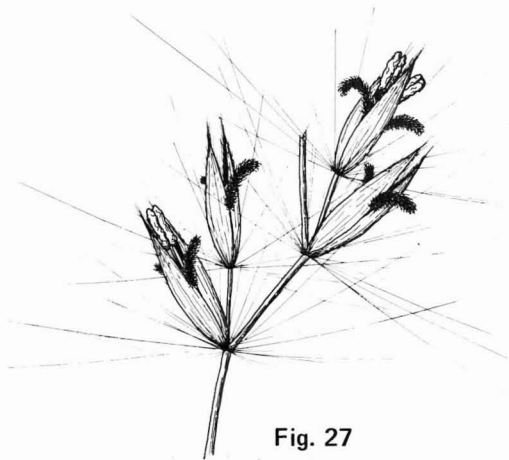
Fig. 30

Fig. 27
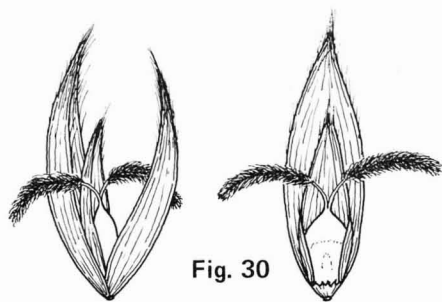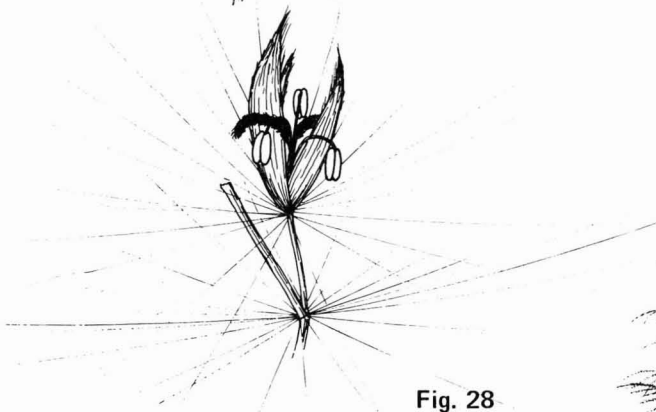
Fig. 28
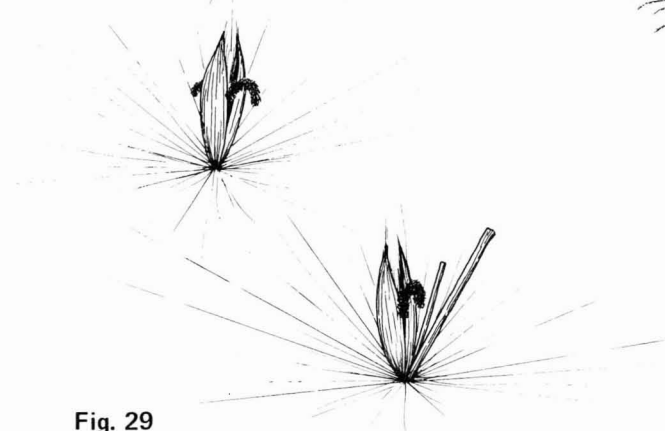
Fig. 29
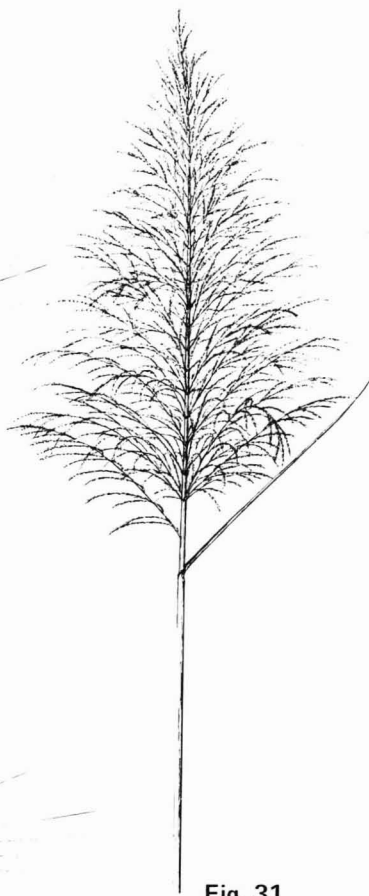
Fig. 31

Figures 27–31. Final stage: the tassel, spikelets, and mature fruits, November 21. Figure 30 shows the mature spikelet: *left*, side view; *right*, front view with lemma removed. Figure 31 shows the mature inflorescence about 150 cm long.
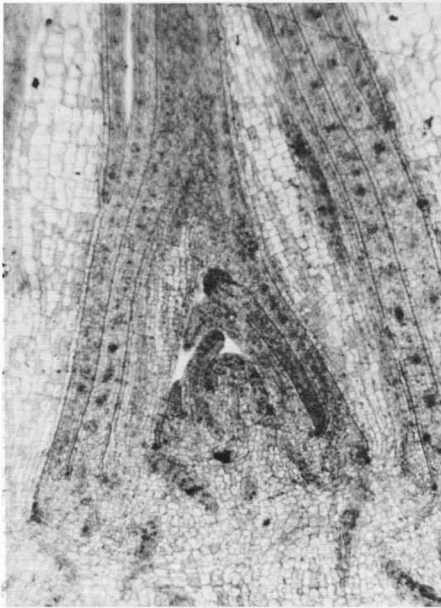
Fig. 32

Fig. 33
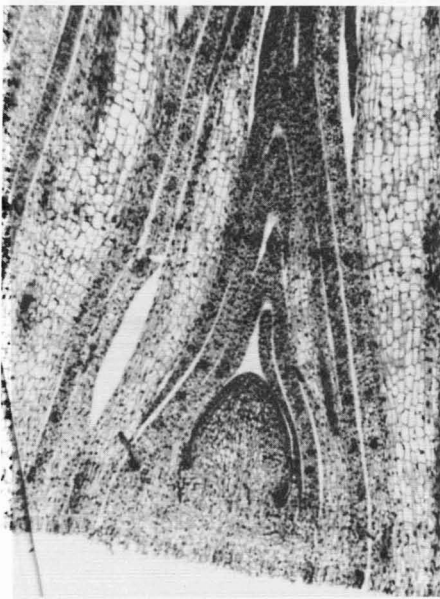
Fig. 34
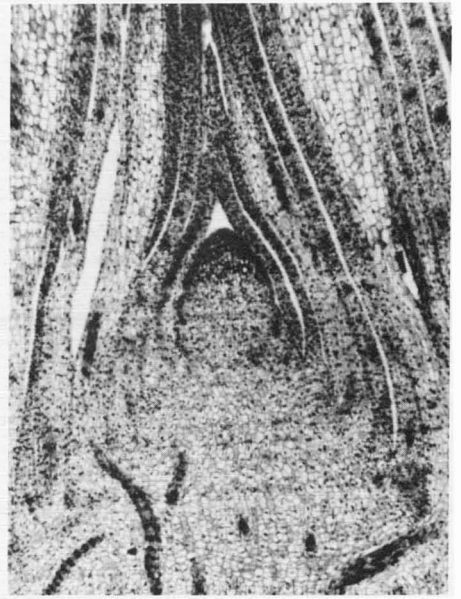
Fig. 35

Figures 32–35. Photomicrographs of longitudinal sections, showing the vegetative meristem (Figure 32); the change to an elongated dome, which indicates the shift to the flowering cycle (Figure 33); and the start of development of branch primordia at the base (Figures 34 and 35).
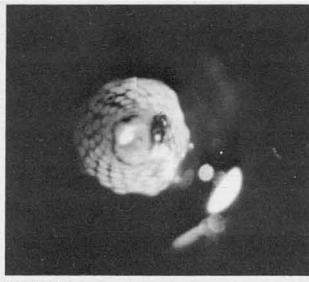
10/24   Fig. 36   10/25   Fig. 37   10/27   Fig. 38
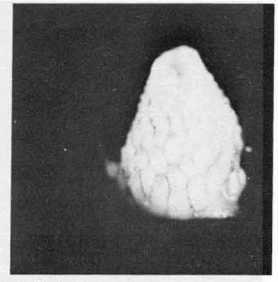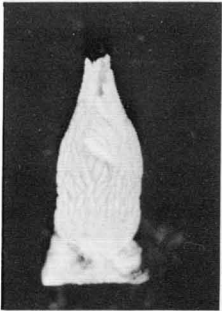
11/20 Fig. 39   11/20   Fig. 41
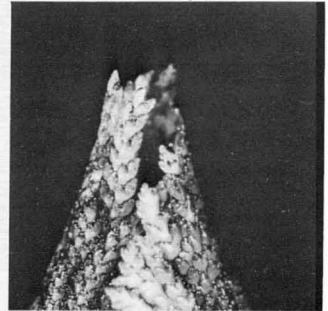
11/20   Fig. 40
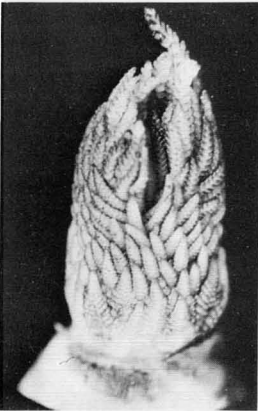
11/26   Fig. 42   11/26 Fig. 43   12/4   Fig. 44   12/4 Fig. 45
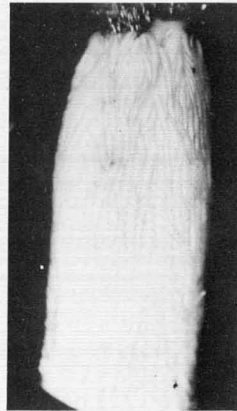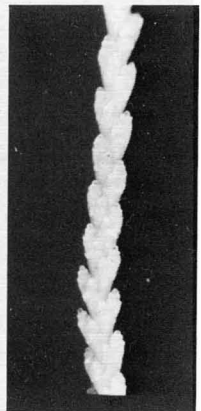
Figures 36–45. Photographs of the apex, from the collection of C. J. Engard and N. Larsen Hanson, showing the development of the inflorescence from October 24, the early stage, through December 4, at which time the blossom is ready for exsertion. Figure 40 is a close-up of Figure 39.

39–43), for by September 19 the whole apex had been transformed into branch primordia arising from the central axis. By this time the basal branches were developing secondary branch primordia (Figures 15–19, 40). All of the stages (Figures 1–25, 32–45) were actually enclosed—at first within the primordium of flag blade ⁻8 and then within the sheath of the flag. The cluster shown for September 26 (Figure 19) was 0.7 cm in total length; by September 30 (Figures 20–25), the overall length was 1 cm; by October 7, 4 cm; by October 10, 7 cm; by October 14, 20 cm; and by October 17, 40 cm. These data illustrate the increasing speed of development, hence the aptness of the word "bolting" to describe the outward appearance of the activity.

During this period the primary and secondary branches developed very rapidly (Figures 39–44), and soon the spikelet primordia began to appear (Figure 45). The tassel was first seen in this series emerging October 31 to November 4 (Figures 26, 47), by which time the inflorescence itself had already reached its full length.

Just as all previous developments were acropetal, so were those which followed, up until exsertion began on November 4, by which time all the spikelets were formed. The uppermost ones, being exserted first, were the first to mature, and, hence, the final process proceeded basipetally. At each rachis joint, two spikelets appeared (Figures 27–29)—one sessile, the other pedicilate. Figure 31 shows a mature paniculate inflorescence with its small flag-leaf blade and a part of the flag-leaf sheath. [The flag is the final vegetative leaf to appear.] Of physiological significance is the size of the flag: when bolting has been vigorous, indicating a strong stimulus and response, the flag is very small; when the conditions prior to flowering result in a weak stimulus or when a normal response is interrupted, the flag leaf is relatively much larger, sometimes as large as a normal leaf. Most commonly, the inflorescence in such cases fails to emerge, and dissection reveals its deterioration or a reversion. Sometimes, too, the dewlap so firmly clasps the inflorescence that it is unable to exsert. Then, when the flag leaf is small, cutting off the top of the dewlap and splitting the sheath (13) will allow the blossom to emerge; but when the flag leaf is quite large, indicating a weak inductive stimulus, a cutting and splitting operation usually fails to help. Figure 28 (see also Plate I, Appendix) shows a pedicilate spikelet opening its glumes and allowing the three anthers to emerge, as well as the two beautifully colored plumose stigmas attached to the top of the ovary. At the base of the ovary are the two lodicules (Plate I, Appendix). Similarly, Figure 27 shows four spikelets, two of which show anthers. These spikelets (Figures 28, 29) represent the "fuzz" that later begins to break loose to be carried about by air currents. Frequently, certain small birds pick this fuzz and use it for nesting material. Finally, Figure 30 shows two spikelets, each of which contains the mature one-seeded fruit (caryopsis). On the left is a side view; on the right is a front view with the lemma removed, showing in outline the mature embryo with its cotyledon, radicle, and endosperm. A complete description of the ovule and its megagametophyte development and the anther with the microgameto-

phyte development, as developed by Artschwager et al. (3), is given in the Appendix (Plates I–IV). Grassl (39) gives an excellent account of the development of the spikelets found in *Saccharum*.

Sequence of Leaf and Stem Development (1966 Series)

The 1966 procedure was the same as that in 1967, except the objective was the careful measurement of all the parts of the cane top. Twice each week, 10 randomly selected cane tops were taken from among the 300 stalks originally labeled in the field. The position of the label under the original leaf +5 was the starting point for the count of leaves for each top. Starting with the third or fourth leaf below the tag, each leaf up to the spindle was removed in turn, and the lengths of the sheath, blade, and internode were determined. Finally, 1.5 cm of the base of the spindle cluster containing the actual meristem was cut off just below node +1 and preserved for later dissection. The unrolling and measuring of leaves +1, 0 – 1, and so on, was continued until the last leaf blade, sometimes only 1 mm long, was reached. The preserved meristems were later sectioned to complete the count. As many as 17 or 18 leaves from each of the 10 plants collected twice a week were so measured, and the measurements for sheaths, blades, internodes, and later inflorescences and floral stems, were then averaged. These data are plotted in Figures 46 and 47, beginning with September 2 and continuing until November 21 when no further growth occurred. The biweekly measurements are drawn as actual lengths in cm, read off the left-hand legend.

In Figures 46 and 47, the internodes are shown at the bottom and are numbered 5, 4, 3, and up to – 8 on November 21. As each internode reaches its full length, only the node is shown as a horizontal line with the number below it. Thus, on September 2, internode +5 had already reached its full length, but 4, 3, 2, 1, and so on were still lengthening; +4 reached its full length by September 12. Leaves and sheaths are shown as lines attached to a horizontal line, which is used to represent the stem tip. Each leaf is represented by the upper line, the blade, which, when very young, is simply attached to the horizontal line because there is as yet no sheath. When the sheath appears, the leaf blade line is shown attached to it as the joint of the two lines. The same scale is used throughout, and the gradual rise in the successive figures represents the actual growth made by the stalks in the field. Each measured part is shown until it reaches its mature length, after which it is no longer shown, even though it remains on the plant long after blossoming is complete. Thus, by September 2, internode 5 had already reached its maximum length; by September 12, internode 4 had reached its maximum length, and so forth. As the various internodes reached their maturity, the whole cane top was carried up, as shown by the rising levels of the horizontal line carrying the sheaths and blades. By September 2, leaf blade 2, attached to its sheath, reached its full length, and so had its sheath, so neither is shown for September 5. Leaf blade – 1 reached its full length on September 12, and so is not shown thereafter, but its sheath continued to grow

Figure 46. Measurements, in cm, averages of 10 cane tops, of the various sheaths, blades, and internodes associated with the development of the flower from September 2 to October 10. The organ measurements in each case are taken from 10 specimens on each date, beginning with leaf +5 in August. As an organ reaches its maximum length, it is no longer shown, even though it remains a part of the cane top until well after the full development is completed.
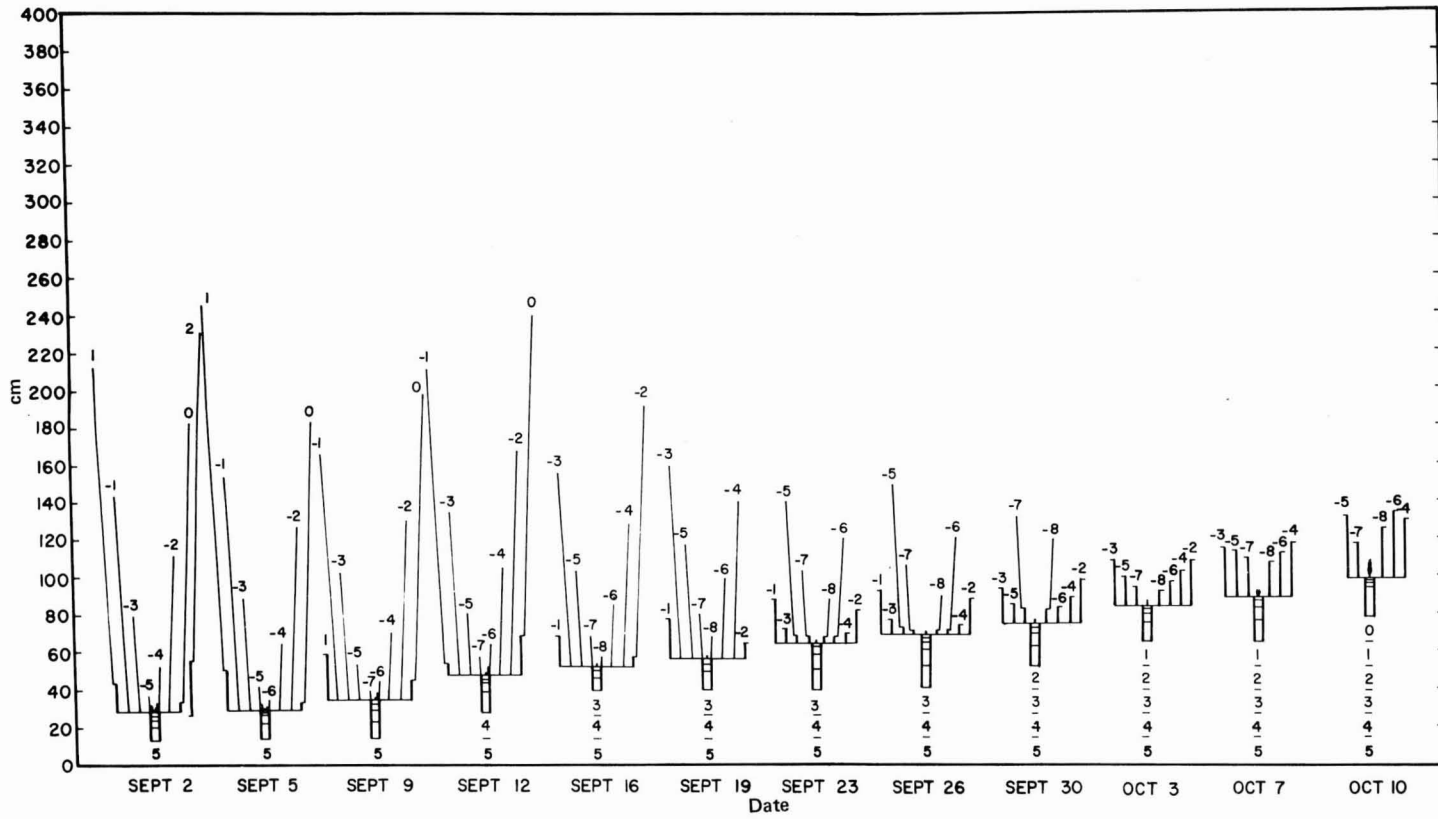
Figure 47.   Continuation of measurements, in cm, averages of 10 cane tops, of the various sheaths, blades, and internodes associated with the development of the flower from October 14 to November 21.

until September 26, after which it is not shown. By September 30, all the blades had reached their full lengths and are not shown again, even though, of course, they remained on the plant. The marked shortening of the successive blades is very evident.

When blade -8 completed its growth on September 30, the sheaths began to lengthen, and this was the start of the bolting. The blossom which first appeared on August 22 (Figure 9) was at that time enclosed within the meristematic leaf blade -8. Not until about September 19 to 23 did sheath -8 make its appearance, and, from this time, the blossom continued its development within it. At first there was considerable room provided for the blossom, made possible by the circumferential enlargement of the sheath (the boot). The dewlaps of these sheaths, however, were very tightly clasped around a central cavity, making for an hourglass appearance. The obvious advantage of this clasp is the sealing of the inner structure against leakage of water and possible infection, entry of insects, and so on. Sheath -8 grew faster at first than did the blossom, but the sheaths together continued to provide a cylindrical space in which the blossom could grow. As late as October 7, the central cavity extended some 18 cm to within about 7 cm of the clasping dewlaps, but after this the blossom began to grow rapidly (October 10–21), not only in length but in circumference, rather quickly occupied the entire central cavity, and very soon pressed very tightly against the inner wall of sheath -8. Its continued lengthening, undoubtedly, was aided by the lengthening of the older sheaths, which were now in their rapid bolt. Beginning about October 14, however, the blossom was lengthening rapidly along with the sheaths and creeping upward within the boot. The structure of the inner epidermis of the sheath is such that it grasps the blossom and helps carry it along but also permits the upward movement of the blossom within it. For example, after removing all the sheaths up to -8, by exerting pressure on the floral stem it was easy to push the inflorescence upward in the boot, but it was impossible to pull it back downward. Also, at this stage, the blossom is very resistant to wetting, water simply balling up and rolling off. By about October 21 to 24, the hollow central portion was found only at the top of the boot, and not only was the tip of the inflorescence being pushed upward into the space but also the terminal floral branches were growing up into it.

Beginning October 28 to 31, the blossom tip began to appear above the flag leaf, and by November 4, it was well out (see also Figure 26). Associated with this was the appearance of branches (lalas) coming from nodes -2, -1, 0, and $+1$. During this period, lateral buds failed to develop in -3, -4, -5, -6, and -7 leaf axils. By November 21, the process was complete. During this exsertion phase, as the spikelets reached the atmosphere, the glumes opened to permit pollination, fertilization, and fruit formation.

The final expression following these morphological changes is shown in Figure 48, which was compiled from the actual measurements of all the various plant parts of the final collection made November 21. The boldfaced number on each of the

horizontal dashed lines is the organ number applying to blade, sheath, or internode. The number beside each organ is the measured final length of each mature part, expressed in cm as an average of that part from the 10 plant tops. The leaf blades from +2 downward grew to normal lengths—180, 186, 185, and so on. Blades +1 upward show progressive shortening—168, 156, 146, 119, 95, 80, 67, 52, 36, and, finally, the flag, 26. The sheaths were next to respond, but not until the blade
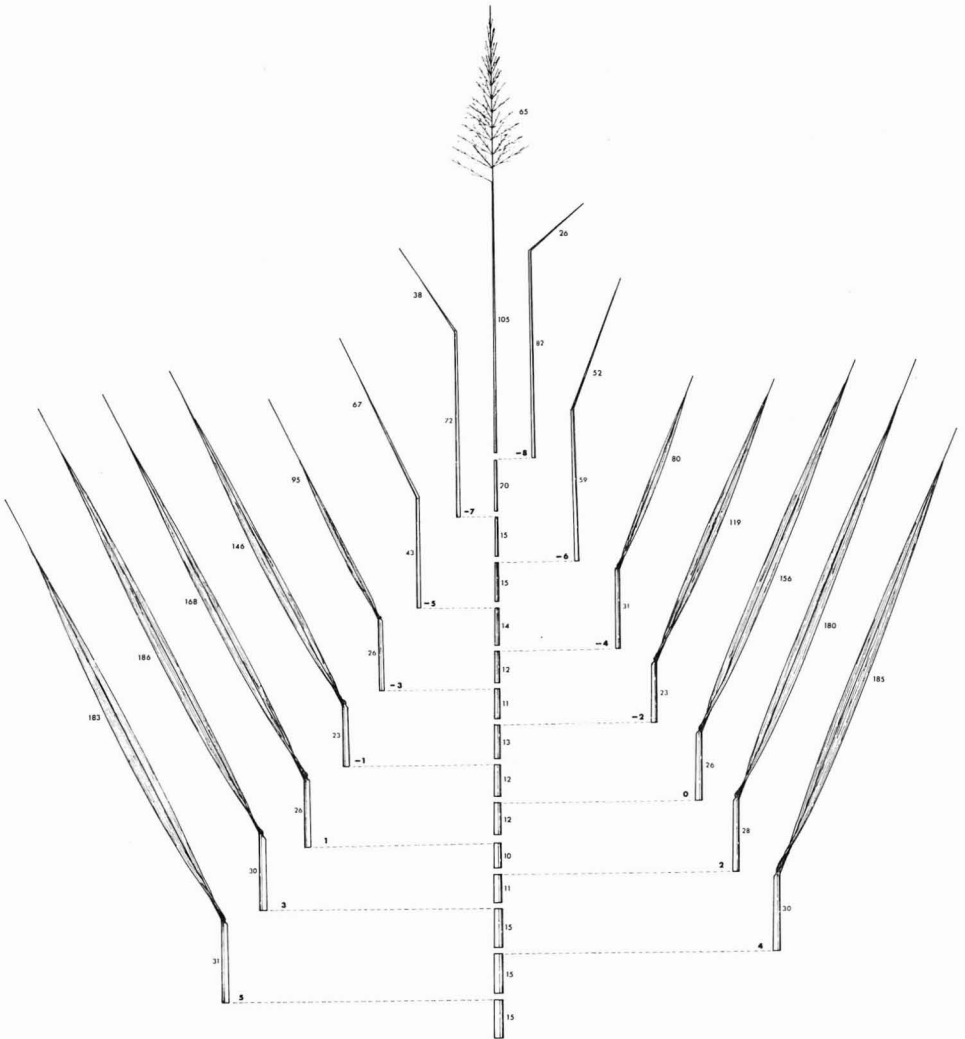
Figure 48.   Final set of measurements, in cm, averages of 10 cane tops, November 21. The numbers on the dashed horizontal lines represent the leaf-blade, sheath, and internode numbers, based on the starting point in August. The numbers beside each part represent the length of each in cm.

shortening was completed. Thus, sheath -2 was 23 cm long; -3, 26 cm; -4, 31 cm; -5, 43 cm; -6, 59 cm; -7, 72 cm; and -8, 82 cm. After the sheaths had completed their part, the stem became active. Internodes -7, and perhaps also -6, showed a slight response, and internode -8 showed more. Then the floral stem became extremely active and pushed the blossom on up and out of the boot which had already reached its full length in the period October 24–28.

These events are plotted in Figure 49 as they occurred: flag-leaf growth started before August 22 and finished by September 30. Sheath -8 showed slight growth by September 26 and essentially completed its elongation by October 24. During this time the blossom held within sheath -8 was also lengthening and also completed its cycle by October 24. Finally, the floral stem became active about the time the sheath and blossom had finished and completed its cycle by November 21. Internode -8 seemingly had no part to play but it, too, was influenced by the stimulus that affected the floral stem, and its elongation paralleled the early phase of the latter, but internode -8 completed its extra growth well before the floral
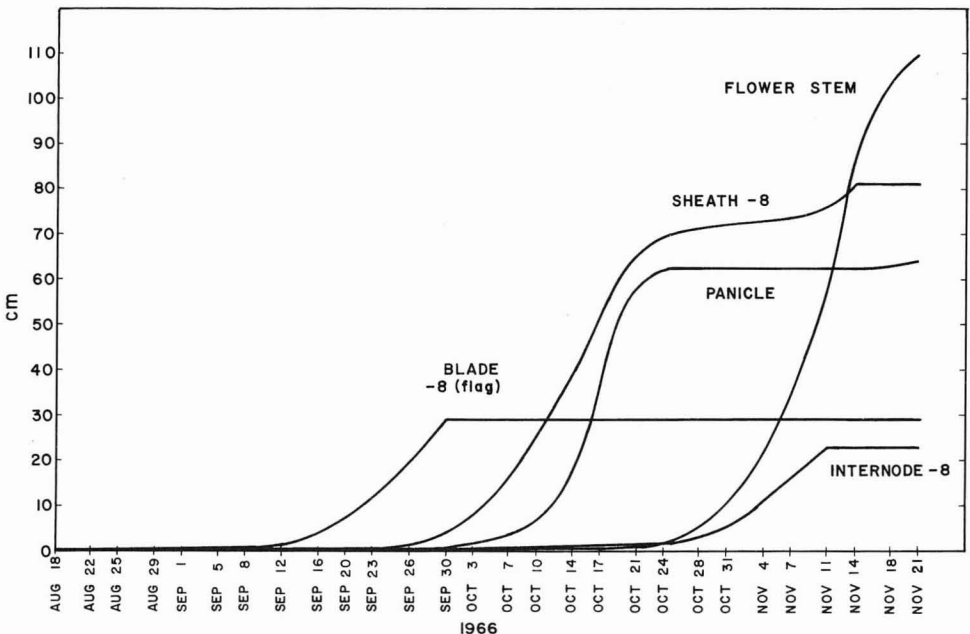
Figure 49.   Succession of growth activities that may be regarded as stages of blossoming: first, the growth of flag leaf blade occurs, within which the meristem changes to a flowering apex; then, the bolting of the sheaths takes place. Within blade -8 is the inflorescence, which elongates at the same time as bolting occurs, after which the floral stem becomes active and exserts the inflorescence. Internode -8 also shows a small amount of activity at the same time as exsertion. It is striking that each part essentially completes its activity before the next one takes over.

stem did. Internodes -7 and -6 also were somewhat affected by the stimulus that affected the top internode and floral stem and which probably was responsible for the failure of the lateral buds to develop in the axes of the corresponding leaves.

In the preceding descriptions, reference is made to plant part -8. Yet, in earlier reports (24, 25), it was clearly shown that, within a vegetative cane tip, the youngest leaf at the meristem is -7, starting the count from the spindle as 1. This apparent discrepancy is due to the fact that the leaf counts were made beginning with +5, and that one leaf was formed after August 22, 1966, and before actual counts were begun on September 2.

Flowering Stages

Several investigators have suggested that the flowering process occurs in stages. Paliatseas and Chilton (49) suggest four: (1) floral initiation without an actual morphological change in the meristem, (2) floral development and maturation within the elongating sheaths, an actual morphological change, (3) floral emergence, and (4) flower maturation, fertilization, and seed formation.

George and Lalouette (38) suggested five stages somewhat in the manner of Paliatseas and Chilton: (1) the induction of the flowering stimulus, (2) the differentiation of the apex and the initiation of the inflorescence, (3) the growth and development of the rachis and the flower parts, (4) the emergence of the arrow, and (5) the opening of the flower parts.

Clements and Awada, in 1965 (23), attempted to estimate the time required at each stage. The time needed in stage 1, for the accumulation of the stimulus to have the meristem stop producing leaf primordia, was estimated at 18 to 21 days in plants being treated artificially during February. It seems to be only about half as long in summer. This estimate was based on the leaf-counting method (23). Stage 2, representing the entire time from floral organization to incipient bolting, required 7 to 8 weeks. Stage 3 represents the development of the inflorescence in the bolting process up until incipient exsertion, and required 4 to 5 weeks at warm temperatures but as many as 8 weeks at colder temperatures. Stage 4 includes the full upward exsertion (4 to 5 weeks), and stage 5 represents the opening of the flowers, pollination, fruit formation, and final ripening, all of which may not take more than 2 to 3 weeks.

Coleman, in 1968 (30), in emphasizing the role of growth substances, suggested the following five stages, ending (1) when the plant has reached the ripeness-to-flower stage, (2) when the plant is exposed to an inductive photoperiod (at inductive temperatures), (3) when the translocation of a stabilized stimulus to the apical meristem occurs, (4) when, within the apex, the storage of a substance over a number of days, or the synthesis of another substance, is completed, and (5) when the differentiation of floral primordia occurs. No actual data are offered in support of this hypothesis, but the observations are based on the consensus of knowledge-able people working with other plants.

On the basis of the measurements made in this study and shown in the many figures, another set of stages, based on observable morphological developments, can be suggested. The ripeness-to-flower stage of Coleman really is not a stage preceding induction, because this stage is simply a matter of age and occurs at any time of the year, based on the time of start, and is commonly passed with no subsequent change in the meristem. The following stages require a plant of a certain size or age before flower induction can take place—usually plants which have three to five well-exposed stem internodes on entering into the proper range of nyctiperiods. Stage 1 represents the period, varying in length according to the clone, which ends upon the cessation of leaf primordia production.

Stage 2 may well be called the period of leaf-blade shortening, which begins when the meristem stops producing leaf primordia and changes from bilateral activity to spiral and ends when the innermost meristematic leaf blade, destined to be the flag, appears. When applied to this study, this stage lasts from about August 22 to September 30, during which time the meristematic blossom grows from about 0.015 to 0.7 cm. At the end of stage 2, the secondary branch primordia are beginning to take shape at the bottom of the flower bud.

Stage 3 may well be called the period of sheath lengthening, which begins at the end of stage 2 and, in this study, continued from October 3 to about October 24. Except for the final measurement of sheath −8, all those from October 24 through November 11 are essentially the same. The average length of sheath −8 on November 11 was 73.9 cm, however, and on November 14, 81.40. The "t" value of the difference is 3.12. It may be that, even though the difference is significant, the final sample was not reliable. Had the basal meristem of sheath −8 remained active from October 3 until November 14 without producing growth, which is impossible for someone to imagine, the top might well have broken off since, by this time, much of the support of the inflorescence depended on sheath −8. During stage 3, the inflorescence developed from 0.7 cm to 64.5 cm, its full length on October 24. During this stage the inflorescence seemed carried along by the lengthening sheath −8, which now held it very tightly except for the blossom tip which was loosely held. Also during stage 3, the spikelets developed from initials to complete structures.

Stage 4 may be called the period of stem lengthening, which began when sheath lengthening stopped on October 24 and continued until November 18 when the full length and floral maturation was achieved. Although internodal growth of internodes −7 and −8 contributed a little to this lengthening, the greatest part by far was the result of the floral-stem growth from its attachment at the topmost node to the base of the inflorescence. This growth is carried on by the meristem at the base of the floral stem and the subsequent elongation of these cells. This is remarkable because the base of the floral stem is very soft and very easily crushed—yet, because of the firm support from the encircling sheaths and the structure of the inner epidermis of the sheaths, the inflorescence is pushed upward.

During this exsertion stage, the flowers mature very quickly upon reaching the open atmosphere and, well before the inflorescence is fully exserted, the anthers of the top flowers are already shedding their pollen.

Such, then, is the remarkable coordinated performance of the cane top during the reproduction cycle. Very likely, the stimulus for stages 1 through 3, the sheath-lengthening period, comes from the associated leaf blades and may include an inhibitor responsible for the blade shortening as well as a substance responsible for the lengthening of the sheaths and blossom. The origin of the substance responsible for the tremendous lengthening of the floral stem may well be from within the inflorescence itself.

Floral Reversions

Under field conditions, many cane stalks may be found with lalas emerging from the upper joints, much as occurs when a normal blossom is produced, but which do not exsert inflorescences. Sometimes the stalk may revert to normal vegetative growth with only the lalas to show that the meristem was on the verge of entering a flowering cycle. At other times, cane tops may be found that had gone into the blade-shortening stage but then reversed and returned gradually to normal blade lengths (20). These will show normal nodes and internodes. Some cane tops will show a bilateral as well as a spiral malformation, which has come to be called a witch's broom (Figures 50, 51, 52). Often the bilateral brooms will reveal zigzag nodes (Figures 53, 54), indicating that, at that moment, the meristem was changing to a spiral orientation, but then reverted to bilateral. Such nodes will carry normal vegetative buds which are capable of germination (Figure 55). A mild form of this type results in two or three blades appearing only as half blades without central midribs. True witch's brooms may appear as terminals (Figures 52, 56), ending the growth of the stem, or they may seem to be lateral appendages of the stem. In this latter case, early in the development of the witch's broom within the boot, one of the stems making up the broom becomes dominant (Figures 57, 58, 59) and reverts to normal vegetative growth. This pushes the witch's broom to the side, giving it the appearance of a lateral appendage, even though it originated at the tip of the stem. Many stalks, with lalas which develop neither normal inflorescences nor the various kinds of witch's brooms, may show a complete deterioration of the blossom. In some, the blossom is quite small; in fact, it may be in the meristematic phase (Figures 60, 61).

There are as many variations to be found in the early meristems as there are reversion types. Figure 60 shows a tip completely changed to the spiral arrangement but with several of the primordia beginning to grow faster than the others. Such a tip may ultimately appear as a dead top with a witch's broom at the top and dead blossoms at the bottom. Figures 61 and 62 show others of the same type. Figures 63 and 64 show tips that have a few shoots of a witch's broom at the bottom and
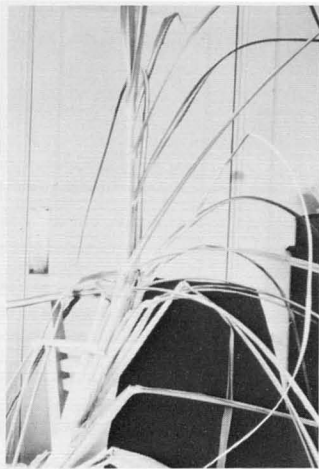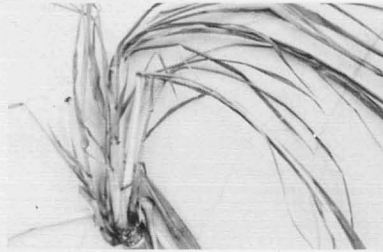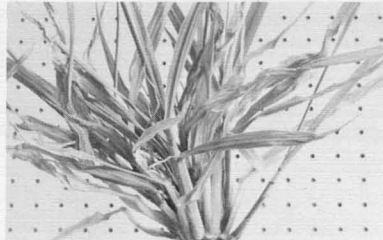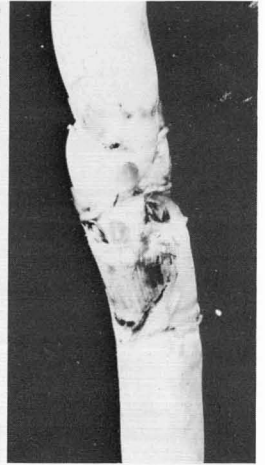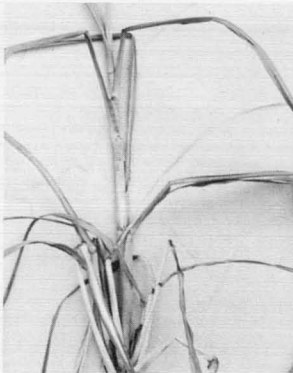
Figures 50–59. Various malformations and floral reversions that resulted from transferring H37-1933 (except Figure 53, which is Co 312), which had already begun to shift from vegetative to flowering, from Waimanalo to Honolulu.
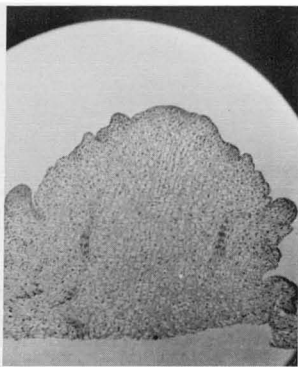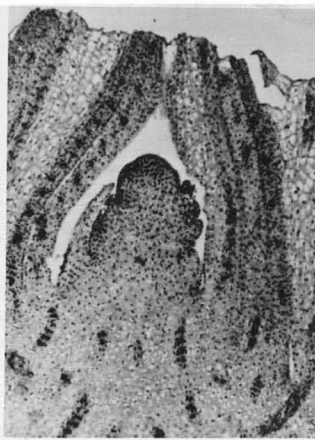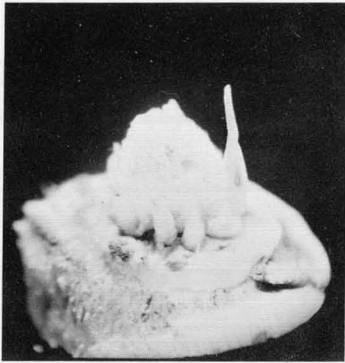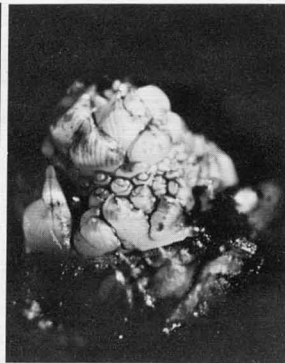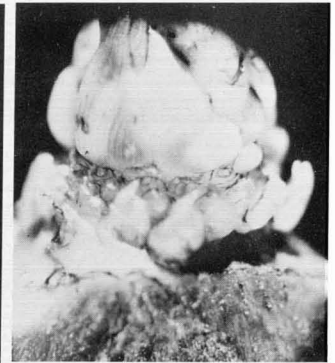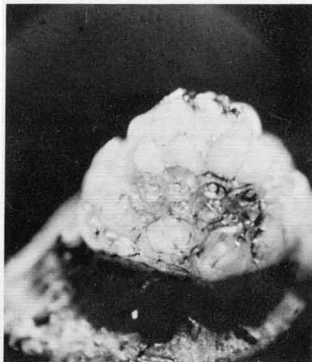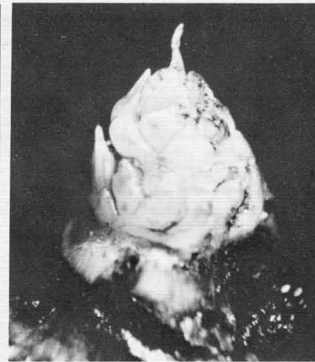
Figures 60–69. Photographs and photomicrographs of various malformations of the apex of seedlings of H32-8560, from the collection of C. J. Engard and N. Larsen Hanson.

inflorescence racemes at the top, but they would likely be dead at normal blossoming time. Those tips in Figures 65 to 67 would also probably die, but dissection would reveal vegetative shoots at top and bottom and a few racemes in between. Tips in Figures 68 and 69 might actually exsert living witch's brooms with remnants of racemes intermingled with the vegetative shoots. In others, the development may have proceeded to form a blossom that would develop with the bolting sheaths but begin to deteriorate before emergence. Such blossoms may be a few cm in length or they may be of full length but the floral stem fails to become active. Thus, failure to exsert a complete inflorescence may occur anytime— sometimes even after exsertion has begun.

Such, then, are the examples of meristem tips in which the normal sequence of physiological controls goes awry. Most of these reversions occur very early in the flowering cycle, some even during the time of change from vegetative to flowering meristems.

It is entirely possible that the very young floral meristems (Figures 9–14) may revert to vegetative activity without leaving a remnant. Were this to be established by further study, it could be the criterion to follow in applying chemicals or droughts to prevent flowering. But even after the bolt has begun, the inflorescence may not be exserted because of the failure of the floral stem to enter into its bolt and, of course, the enclosed inflorescence will die. Always associated with the reversions described (Figures 50–68) is a very large flag leaf, sometimes even as large as a normal vegetative leaf blade. Only the very small flags are associated with normal induction, blossom formation, and exsertion. It would seem that several biochemical systems are involved, perhaps at several loci.

In the course of these studies, one experiment that was planned for other objectives resulted in a complete display of these abnormalities. Single bud setts of H37-1933 were planted in pots on May 9, 1963, and were grown in a lath house at Waimanalo on the northeast side of Oahu. As in all such plantings planned for induction studies, the pots were filled with a fertile garden soil, watered well, and fertilized. After 4 months, these pots were transferred to the University campus on the southeastern side of the Island and were exposed to natural days plus several hours of artificial light until November 8, when all except three outdoor check pots were put into darkrooms with a fixed 11:39 nyctiperiod beginning at 4:00 p.m. each day and continuing until interrupted by mechanically controlled fluorescent lights that came on at 3:39 a.m. At exactly 8 a.m., all the plants were taken out into strong daylight, watered well, but fertilized very lightly. The objective was to determine the length of exposure to the 11:39 night necessary to induce flowering. To this end, beginning 3 weeks later, on November 29, and continuing each week until January 31, four pots were taken from the controlled night and placed outdoors under natural conditions, by which time the nyctiperiods were beyond the inductive length. Finally, four pots were continued in the nyctiperiod control as end checks until the end of April.

On November 8, a tag was placed under leaf +5. On that date, a normal vegetative cane top should have had five exposed leaves, including the spindle, and eight more within the cluster for a total of 13 leaves above the tag. Very soon after treatment began, however, it was apparent that internal changes had already occurred prior to November 8. Nevertheless, the experiment was continued on schedule until late April, at which time all the cane tops were dissected and the status of each stalk determined and recorded.

At the start, most of the pots contained two stalks. Of the 91 stalks dissected, 23 were vegetative, with the spindle leaf being numbers 17 to 19 (counting from the original tagged leaf +5 as 1). Thus, in these canes, 12 to 14 new leaves emerged between November 8 and late April. Of the 23 normal vegetative tops, four showed zigzag nodes at 9, 10, 11, and 12 (Figures 53, 54), thus indicating that these leaves were formed between September 12 and November 8 when the meristem returned to normal leaf production.

Thirty-two stalks showed normal inflorescences with the very small flags. These stalks had been in the darkroom for at least 7 weeks. For the most part, the flags were at nodes 16 and 17, showing that leaf formation ceased about 2 weeks after being placed in the nyctiperiod control, although actual blossom formation was not firmly established until some time later. The period between the 2 weeks after leaf formation stopped and the minimum of 7 weeks exposure to the proper night length apparently represents the blade-shortening stage, during which the meristem, even though becoming changed, could revert rather easily and with little or no distortion to show for it.

Ten stalks had bolted and had very large abnormal flag leaves. Inside each of these was a fully developed inflorescence that had reached the point of exsertion but had not exserted, and each was dying or dead. Somehow, the size of the flag seems related to the failure of the base of the floral stem to become activated. The possibility exists that the growth substance responsible for the rapid growth of the floral stem is produced by the inflorescence itself and that an inhibitor is produced by the leaf associated with the node. If the leaf is very small, as is normal for a flag, the amount of the inhibitor produced is too small to affect the stem growth. All of the large flags were at nodes 7 or 8, showing that the meristems had reverted shortly after they were moved from Waimanalo.

Three stalks had abnormally large flags, but within each was a live, nearly fully-developed inflorescence. Probably, in view of the experience thus far, they would not have been exserted.

Seventeen stalks, all with abnormally large flags, had developed witch's brooms (Figures 50–59, probably 69). Four of these were at nodes 15 and 17, showing that they had developed long after the darkroom treatments began. The other 13 had witch's brooms mostly at nodes 7; two stalks had witch's brooms at node 8, one at 9, and one at 10. A large shoot of one of the largest witch's brooms was bolting and contained a perfectly normal appearing inflorescence. All of these 13 obviously

began to form very shortly after the plants were moved from Waimanalo. Eleven of the cane tops as well as the witch's brooms within were dead. Only the four brooms at nodes 15, 17, 9, and 10 were alive and growing.

One stalk, which had started to produce a witch's broom at node 5, returned to a normal vegetative shoot. Leaf blades associated with this change had begun to shorten and then gradually to lengthen again until normal, but this stalk was bolting with a large flag leaf within which was an inflorescence 40 cm long. This inflorescence, because of its large flag, would have continued its growth until it filled the boot, but it probably would not have been exserted.

One stalk had bolted but its top was dead. Inside sheath 7 was a dead tip, the lower part of which had started to form an inflorescence and the upper part a witch's broom, but both were dead (Figures 63, 66, 67).

Three other stalks showed just the opposite. At nodes 6 and 7, fairly long but now dead inflorescences had formed at the apex while underneath each were several shoots of dead witch's brooms (probably Figures 62, 64, 65, 68).

One stalk, which seemed to be growing normally, had at nodes 15 and 16 several double leaf blades, none of which had midribs. Considering these various occurrences, it is clear that moving the plants from Waimanalo to Honolulu caused a major turmoil among the delicate flowering processes already begun. The final expression in each case reflects the precise point in the process at which the upset occurred. In fields, similar situations may result from a storm or from the development of a moisture stress after the earliest stages of induction have occurred. Such reversions, if they cause the complete inactivation of the meristem, are just as serious to the grower as are normal inflorescences.

EFFECTIVE NYCTIPERIOD

With the observations recorded in Figures 1 to 47, it should be possible to estimate the actual time when induction by NCo 310, at the particular site and time, occurred and from this to estimate the nyctiperiod.

The change from the vegetative to the flowering cycles in the meristem occurred sometime between August 18 and August 22. It can be postulated that, under ideal conditions for flowering, the time needed to accumulate the necessary stimulus might well be related to the time needed to form a leaf. Although actual leaf counts were not made in 1967, the ones made early in September 1966 should be reasonably similar. On September 2, taking an average of 10 stalks, the label was under leaf 6.1. Since the labels were placed under leaf 5 on August 21, it is clear that 1.1 leaves were formed during the 10-day period. It is reasonable to assume that, about 10 to 11 days prior to August 22, 1967, the stimulus began to accumulate in quantities sufficient to prevent the formation of the next leaf. This period would begin about August 12. According to Ephemeris (37), on August 12

sunrise was at 5:39 a.m. (Pacific time) and sunset at 6:31 p.m., allowing for a day of 12:52 but not allowing for any part of the twilights.

To obtain some estimate of the amount of twilight that is an effective part of a photoperiod, the intensity of sunlight was measured on September 17, 1966, a clear day, at a spot near the experimental area (Figure 70). Morning twilight began at 5:05 a.m. (Hawaiian local time). Sunrise was at 6:19 a.m., but light became measurable at 5:59 a.m. With the instrument at right angles to the brightest part of the horizon, the reading was 2 footcandles (ft-c) at 6:02 a.m.; 5 minutes later (6:07 a.m.), it was 10 ft-c. Intensity increased very rapidly from then on. By 6:15 a.m., the reading was 48 ft-c; by 6:20 a.m., 94 ft-c; by 6:30 a.m., 230 ft-c; by 6:40 a.m., 395 ft-c; by 6:50 a.m., 500 ft-c; and by 6:59 a.m., 768 ft-c. At 6:59 a.m. the direct sun peeked over the horizon, and ½ minute later (6:595 a.m.) the meter read 2000 ft-c. During the day some high cloudiness developed, which probably tended by reflection to intensify the light, for, on several occasions, the meter, with a film interposed, indicated intensities as high as 15,000 ft-c. In the evening, the direct sun disappeared behind campus buildings at 6:09 p.m., and the intensity dropped to about 400 ft-c. Sunset was at 6:33 p.m., by which time intensity had dropped to 64 ft-c. By 6:41 p.m. it was 10 ft-c; by 6:46 p.m., 4 ft-c; by 6:49 p.m., 1 ft-c; and by 6:50 p.m. the intensity was too low to be measured with the meter used. Official end of twilight was 7:48 p.m.

If the assumption is made that 5 ft-c is the start of effective intensity, the plant begins to receive the stimulus about 15 minutes before sunrise and continues to receive it some 12 minutes after sunset. If the assumption is made that 10 ft-c is the threshold value, then the nyctiperiod ends 12 minutes before sunrise and begins 10 minutes after sunset. Thus, using the 10 ft-c value, the total night length on August 12 was 10:46, and by August 22, when the meristem had already started the flowering cycle, it was 10:54. Using the 5 ft-c light intensity, the nyctiperiods would by 10:41 on August 12 and 10:49 ten days later. These times are shorter than those usually used for artificial induction. The common artificial night is 11:30, first used by Sartoris (53) but used later by many others. However, even ignoring the twilight periods altogether, that is, calling the night the period from official sunrise to sunset, a night of 11:30 was not reached until September 2, by which time the meristem was well on its way to forming a blossom (Figures 12, 13).

It must be recognized that NCo 310 is a very ready tasseler, that its growth at Waimanalo was under very excellent culture, and that the area itself is considered an ideal area for sugarcane flowering. Other varieties referred to as late tasselers would either require longer exposures or perhaps longer nights. In a controlled nyctiperiod study reported earlier (18), which included no twilight periods, NCo 310, Co 312, and H37-1933 were subjected to lengthening nights, shortening nights, and natural nights beginning June 21. It was found that the effective nyctiperiod for the lengthening nights were 11:08 to 11:26 for H37-1933; 10:56 to 11:16 for NCo 310; and 10:57 to 11:04 for Co 312. For a series started in

SUNLIGHT INTENSITY - UNIVERSITY OF HAWAII CAMPUS

September 17, 1966

MAXIMUM INTENSITY
9 AM TO 3 PM

VERY CLEAR MIDDAY

VERY LIGHT, WISPY CLOUDS

CLOUDS ON HORIZON

SUNRISE
6:19 AM

SUNSET
6:33 PM

9 AM TO 3 PM
OMITTED

6:59 AM
DIRECT SUN APPEARS
OVER THE HILL

6:09 PM
DIRECT SUN DISAPPEARS
BEHIND CAMPUS BUILDINGS

A CURVE— LIGHT RECEIVED PERPENDICULAR TO SUN'S POSITION

B CURVE— LIGHT RECEIVED HORIZONTAL TO GROUND LEVEL

A

B

A

B

START OF TWILIGHT
5:05 AM

END OF TWILIGHT
7:48 PM

LIGHT INTENSITY (FOOT CANDLES)

TIME (HAWAIIAN LOCAL)

Figure 70.   Light intensity from morning until night on the University of Hawaii at Manoa campus. The A curve represents the intensity measured perpendicular to the sun's rays; the B curve represents the intensity received horizontal to the ground level.

December, with the same lengthening nights, 11:33 to 11:51 was required for H37-1933; 11:36 to 12:15 for NCo 310; and 10:58 to 11:12 for Co 312. Under a condition of shortening nights but including the same total range of night lengths as above, H37-1933 failed to blossom, as did NCo 310 in two of the three series, but Co 312 blossomed even though there were many reversions. The effective shortening night lengths ranged from 12:50 to 12:29 in one December series, 11:36 to 10:53 in the summer series, and 11:22 to 11:12 in another December series.

In the present study, the relatively short nyctiperiod for NCo 310 (10:46–10:54) is somewhat surprising since, with fixed night lengths, such short nights were not effective. Thus, an experiment was undertaken to determine the desired night length as well as prior day lengths, using two very willing tasselers. Beginning December 2, treatment A plants (in pots) outdoors were given artificial light throughout the night; B plants received the natural daylight, and C plants were given extra light to have a day of 13:20. Beginning April 2, plants were transferred to darkrooms with controlled nyctiperiods of 10:58, 11:32, 11:58, and 12:36. The bolting responses are shown in Table 2. Here, H37-1933 flowered only under an 11:32 night. Co 312 also preferred 11:32, but three blossoms were produced under 10:58, and three under 11:58.

After it became apparent that there would be no further bolting, new plants were added to the four treatments, and the nights were changed to 11:24, 11:35, 11:48, and 11:52. The bolting record is in Table 3. In this set, H37-1933 again showed a relatively narrow range. Exposed to a night of 11:25, 12 plants bolted; to 11:25, 13; to 11:48, 17; and to 11:52 only one. Co 312 was less sensitive, however: under 11:25, 38 plants bolted; under 11:35, 19; under 11:48, 25; and under 11:52, 33.

There appears to be some effect of additional light prior to actual induction treatments. When lights were left on all night for several months (Treatment A) prior to putting the plants into inductive treatment, 77 stalks flowered; when the

Table 2. Number of bolting plants in relation to night lengths after preinduction light treatment, H37-1933 and Co 312

| | Treatment | | | | | |
| | A | | B | | C | |
Night length	H37-1933	Co 312	H37-1933	Co 312	H37-1933	Co 312
10:58	0	2	0	0	0	1
11:32	8	7	9	8	5	8
11:58	0	3	0	0	0	0
12:36	0	0	0	0	0	0
Total		20		17		14

Table 3.   Number of bolting plants in relation to other night lengths after preinduction light
           treatment, H37-1933 and Co 312

	Treatment					
	A		B		C	
Night length	H37-1933	Co 312	.H37-1933	Co 312	H37-1933	Co 312
11:25	3	17	3	7	6	14
11:35	3	3	4	2	6	14
11:48	6	9	6	6	5	10
11:52	1	15	0	12	0	6
Total	57		40		61	

plants had only the natural days prior to inductive treatments, 57 stalks flowered;
and when a uniform 13:20 day was maintained, 75 stalks flowered. This extra light
may merely have provided more photosynthate and vigor, or it may suggest that
cane tends toward being a long-short day plant, even though it will blossom without
such a combination treatment.

In the study on which Figures 46 and 47 are based, the effective nyctiperiod for
NCo 310 was 10:46 to 10:54. The difference between this result and the ones
reported in Tables 2 and 3, is that, in the former, the night lengths were increasing
each night, while, in the latter, they were fixed. It can be concluded that, although
proper fixed night lengths will result in blossoming, approaching the proper night
length through small increases in dark periods, especially under natural field
conditions where rooting is much more extensive than in pots, results in a faster
response by the plants and under shorter nyctiperiods. Even so, the range of
nyctiperiod lengths is very narrow and shows that sugarcane is neither a long-day
nor a short-day plant, but intermediate.

BLOSSOMING BEHAVIOR IN THE FIELD—HAWAII

The blossoming of a given clone varies considerably in different parts of the
State and even in different parts of a plantation.

Elevation

In general, blossoming does not occur above certain elevations—usually 1000 to
1300 feet on north and east slopes and somewhat higher on south and west slopes.
Very likely this is related to night temperatures.

In one controlled series, plants of Co 312 and H37-1933 were exposed to a fixed
11:40 nyctiperiod, natural day temperatures, and four different night temperatures
(Table 4). Essentially all of the plants flowered. It took longer for blossom

Table 4. Number of days required for blossom emergence at various night temperatures

Variety	Average night temperature (F)			
	76.7	73.7	64.6	60.3
Co 312	96.8	98.0	121.8	152.0
H37-1933	108.8	99.0	144.8	176.5

emergence under the cool conditions, however, and more leaves were produced before the flags were finally produced. Thus, for Co 312 at 76.7 and 73.7°F, an average of three and one-half leaves was produced after dark treatment started before the flag was produced at the meristem; at 64.6°F, four and one-quarter; and at 60.3°F, five. Under field conditions with such low minimum temperatures, the critical nyctiperiods would have been passed before induction occurred.

In another controlled series, plants of NCo 310 and H37-1933 were exposed to an 11:39 night at an average night temperature starting at 58.3°F and continuing at about 54°F. After 9½ months of treatment, not a single stalk of H37-1933 blossomed, and 21 of 25 stalks of NCo 310 remained vegetative, showing that this temperature was too low for blossom induction even though leaf production continued throughout the period at a rate of slightly less than two per month. The four stalks that bolted were shown by leaf count to have started during the 58.3°F period. Thus, the critical temperature for blossoming appears to be between 58.3 and 54.0°F.

Ranges in Night and Day Temperatures

The temperature relationships account in large part for the blossoming behavior of a given variety at ordinary elevations. One area in which tasseling is very profuse is Kahuku, on Oahu. Six-year average temperatures for August 15 to September 15 were 83.5°F maximum and 72.1°F minimum, with a range of 11.4, quite different from the situation at Hawaiian Agricultural Co.

Hawaiian Agricultural Co., at Pahala, experiences very little tasseling and this only at the lower elevations. The temperatures in 1961 for three areas are shown in Table 5. Only in the general Pahala area will blossoms on occasion be found.

At Hawaiian Commercial and Sugar Co., a plantation of more than 25,000 acres in central Maui, blossoming ranges from very heavy to none. Eleven-year average temperatures for the second half of August and the first half of September for several distinct areas are shown in Table 6. It seems clear that, as long as the night temperatures are in a range favorable to blossoming, the narrower the day and night ranges, the more favorable the conditions for blossoming.

Table 5.   Temperatures (F) at Hawaiian Agricultural Co., generally a nontasseling area, 1961

Station	Elevation (ft)	August			September		
		Maximum temperature	Minimum temperature	Range	Maximum temperature	Minimum temperature	Range
Pahala	865	83.6	65.6	18.0	83.3	65.1	18.2
Keaiwa	1650	79.8	61.7	18.1	77.9	61.3	16.6
Moaula	1950	76.8	60.3	16.5	76.2	58.9	17.3

Table 6.   Blossoming in relation to maximum-minimum temperatures and ranges at various locations in central Maui, averages Aug. 15–Sept. 15, 1948–1958 inclusive

Station	Blossoming intensity	Average maximum temperature	Average minimum temperature	Range
Paia	very heavy	83.9	70.6	13.3
Field 102	very heavy	81.9	69.9	12.0
Field 306	heavy	81.9	68.3	13.6
Spreckelsville	heavy	83.7	68.7	15.0
Field 305	medium	82.4	68.0	14.4
Camp 10	medium	85.4	66.8	18.6
Puunene	light	85.7	69.1	16.6
Field 400	light	86.2	65.8	20.4
Kihei	none	91.1	65.2	25.9

Direction of Slope

Direction of slope *per se* seems to have no effect on blossoming. Wailuku Sugar Co. is a very heavy blossoming area, and its fields generally face east. Heavy blossoming areas at Paia and field 102 (Hawaiian Commercial and Sugar Co.) face north-northwest. At McBride Sugar Co. on Kauai, very heavy tasseling occurs on south-southeast slopes, and at Lahaina, on Maui, blossoming occurs on west-facing slopes.

Cloudiness

Cloudiness *per se* seems to have little effect on blossoming. In general, in cloudy areas, night temperatures are higher than in clear areas and are responsible for blossoming. At higher elevations where clouds are common, blossoming does not occur, undoubtedly due to low temperatures. On the other hand, brightness of sunlight during the day suggests lack of cloud cover at night and low minimum

temperatures, but it is also possible that this combination causes moisture stress within the plant, which also tends to prevent tasseling.

Drought During the Induction Period

Drought during the induction period is another environmental factor that has a decisive negative effect on blossoming. Conversely, abundant soil moisture during this period where temperatures are favorable is correlated with heavy blossoming.

In one experiment, in an effort to maximize yields, plots of cane of several acres, each in several parts of two plantations, were set aside to be given what was considered ideal treatment. These were called manager's plots. During the induction period, a shortage of water placed most of the fields on a longer than normal irrigation interval, but the manager's plots continued to receive water as considered ideal. The result was that these plots blossomed very profusely with counts up to 100 percent, whereas the surrounding cane which was under stress failed to blossom and outyielded the manager's plots.

Nearness to Mountains

It has often been claimed that when cane is planted next to a mountain whose shadows shorten the period of direct sunlight, blossoming will be affected. There seems to be no consistency in this, however, since in some cases blossoming seems heavier, in others lighter. It is likely that the shadows themselves are of no moment but that they influence night temperatures, either because of cold air drainage from the higher elevations or because of winds from the opposite side of the mountain, which shields the cane and causes warmer nights. Such shadows may also be associated with heavier than normal rainfall if rains come from the direction of the shadow, or they may be associated with drought if the rains come from the opposite direction.

Thus, in Hawaii, where the proper nyctiperiod occurs at the latitude of 19 to 21.5°N, blossoming may be very heavy or completely absent. Factors that are directly influential on blossoming include night temperatures, day and night temperature ranges, and moisture conditions. Direction of slope, presence of mountain shadows, and so on seem related to blossoming only insofar as they are related to temperatures and moisture conditions.

BLOSSOMING PERFORMANCE IN THE FIELD— AT VARIOUS LATITUDES

Blossoming is generally very heavy in southwest Thailand and adjacent Burma and Malaya (5–14°N), while farther north in Thailand it is generally lighter. In New Guinea (4–11°S), considered to be the home of *S. robustum* as well as some of the *S. officinarum*, these canes blossom heavily. In eastern Puerto Rico (17–18°N),

blossoming is extremely heavy when rainfall is normal to heavy, but it is absent if a drought occurs during the critical August–September period. In South Africa (30°S), blossoming can be very heavy or nonexistent, depending on minimum temperatures in March (Du Toit and Brett, *private communications*). On the other hand, at Haft Tappeh, Iran, at 32°N, blossoming of such ready tasselers as NCo 310, Co 421, CoL 29, and Cl 41-223 has never occurred. On one occasion, numerous tops of NCo 310 revealed a very strange type of adnation of sheaths and blades (Kobe Shoji, *private communication*). Quite unexpected was one demonstration at Ingenio San Carlos, in Ecuador (at about 1.5°S), where very willing tasselers, such as NCo 310, H37-1933, Co 421, PR 980, and POJ 2878, did not blossom, while Cl 41-223 and F36-819 blossomed profusely.

Explanations for these various observations undoubtedly lie in the lengths of nights in combination with temperatures. Table 7 gives the night lengths between official (Ephemeris, *37*) sunset and sunrise, without allowing for twilight time, and the average length of the two astronomical twilights. Astronomical twilights for these five latitudes, either N or S, are 2:17:00 at 0°; 2:22:00 at 10°; 2:30:00 at 20°; 2:48:00 at 30°; and 2:57:00 at 35°. At 20°N, with combined twilights of 2:30, 12 minutes before sunrise and until 10 minutes after sunset, the light intensity exceeded 10 ft-c. Thus the nights would be shortened by that length of time. At 0° and 10°N or S latitudes, the twilights are shorter by 13 and 8 minutes, respectively, and the effective twilight light would be 1 minute or so less. Thus, at 0° the effective night might be considered to be about 11:35, which would seem ideal for all the varieties listed. Local factors might well account for the blossom behavior, however. At San Carlos, in the August–September period, flowering occasionally occurs and seems related to the nature of the day (A. Scott, *private communication*). The plantation is irrigated, but during these months of the dry season there is a very heavy coastal haze. Darkness sets in before sunset, with the sun showing as a very dull red ball. Even though the sky clears during the night, by sunrise the sun again shows as a dull red ball. Thus, probably during this period the nights are too long for blossoming. From February to April is the wet season. The

Table 7. Night lengths at various latitudes and dates[a]

Date	Latitude (N or S)				
	0°	10°	20°	30°	35°
September 2	11:53	11:42	11:29	11:15	11:07
October 2	11:53	11:59	12:03	12:08	12:11
November 1	11:53	12:17	12:35	12:59	13:13

[a]*See* Ephemeris (*37*).

days are hot and clear, but late in the afternoon the rain clouds build up and hasten the disappearance of sunlight. Perhaps low minimum temperatures combined with the high daytime temperatures also help to prevent tasseling.

At a latitude of $10°$N or S, the nights, shortened by 20 minutes, are about 11:05 in August, 11:22 in September, and 11:59 in October, making induction possible even in July. At $20°$ latitude, as noted earlier, blossom induction for willing tasselers occurs as early as the middle of August.

The situation in Iran (at $32°$N) is similar to that in South Africa (at $30°$S). Longer twilights occur in Iran, resulting in shorter nights than needed, until early in October, by which time the minimum temperatures are too low for induction. Moreover, the rapid lengthening of the nights in Iran results in the night on September 2 being 11:08 but on November 1 13:06. At $10°$N or S, official nights are 11:42 on September 2 and only 35 minutes longer on November 1. In addition, in Iran, despite heavy irrigation, the humidity is very low, and with a heavy demand for water, the plants experience internal moisture stresses, perhaps adequate to prevent induction.

PREVENTION OF BLOSSOMING IN CANE

Nontasseling Varieties

The culture of light, or nontasseling, varieties is the best solution to the problem of tasseling, if such varieties are available, and considerable progress can be made in producing these varieties by artificial nyctiperiod control. It is, however, not practical to use a second-rate commercial variety just because it does not tassel since there are ways of preventing or reducing blossom intensity.

Time of Starting the Crop

A plantation that has nontasseling as well as tasseling areas has a good opportunity to prevent the more destructive first-season tassel as well as to reduce the losses incurred by second-season tasseling associated with late-started crops. In general, in the northern hemisphere, harvesting and ratooning or planting of 2-year crops in heavy-tasseling areas should be done from about May 15 to August 1. These dates may vary somewhat from area to area, but generally crops started between these dates will not tassel the first season, and, if the crops tassel the second season, the tasseled tops will not be buried by the strong-growing suckers of the current season. Fields in areas which normally do not blossom can be scheduled for starting before May 15 and after August 1. Irrespective of flowering, top elevation fields, which normally do not blossom because of low night temperatures, should be harvested from December through May because the growth made will result in the field closing in before the next winter. Such fields should not be started from June to November because the first year of growth made will be poor. Thus, flowering in such fields is not a serious consideration.

In earlier times, it was not uncommon for a plantation to cut back cane in May in fields started early in the year with a known heavy tasseler. The advantage was that the field would not tassel the following fall. The obvious disadvantages were the cost of cutting back and the loss of the growing time. Another practice, which minimizes the losses after a heavy first-season tassel, is harvesting the field during the following spring, even at the very young age of 12 to 14 months. Such practices, however, disrupt the orderly cycling of fields.

Withholding Water from August 4 to September 7

Irrigated plantations may very effectively control blossoming in a field likely to tassel by not irrigating between August 4 and September 7. It is essential that the sheath moisture level drop to at least 77 percent. If this drop does not occur or if rains interfere with the drought treatment, irrigation should not be resumed until the 77 percent moisture level is reached or, in any event, not later than September 26. At McBryde Sugar Co., on Kauai, two drought-treated areas within field 21C showed, from August 5 to September 10, 0.6 and 1.1 percent flowering as against 12.0 and 47.4 percent for the untreated. Similar results were experienced at Lihue Plantation Company in 1953 (55).

Wailuku Sugar Co. is a heavy-tasseling area, and use of the drought treatment has given some rather good results in 1959 and again in 1962 (Table 8).

If the drought was imposed a little late, there might be no blossoming produced, but partial reversions instead. So far as the particular stalk is concerned, this is no better than a blossom, since the meristem will not become vegetative again.

The drought treatment has one other advantage, which can be called midcrop ripening. If there is an inadequate water supply to maintain a full irrigation at the

Table 8. Effect of drought treatment on blossoming of H37-1933, Wailuku Sugar Co., 1959 and 1962 averages

Field	Drought date	Blossom intensity (%) on	
		Treated fields	Check fields
103	8/9–9/16	0.5	4.5
94	8/12–9/8	20	43
92	8/14–9/8	6	18
100	8/19–9/10	2	6
59	8/19–9/10	0	6
36	8/8–9/17	22	48
70	8/8–9/15	41	73
88	7/31–9/11	50	73
92	8/5–9/15	25	69
100	8/8–9/9	50	71
95	8/8–9/12	43	66

Table 9.   Yields from a blossom-control experiment, Wailuku Sugar Co., 1960

Variable	Treated	Check
Area (acres)	58.20	43.30
Tons cane/acre	106.30	95.70
Tons cane/ton sugar	8.77	9.13
Tons sugar/acre	12.12	10.48
Tassel (%)	0.50	4.50

plantation, rather than extend all intervals, it is better to select certain fields that are very luxuriant and apply droughts to them. Again, the moisture index can be lowered to 77 to 79 percent, during which time the crop goes off color and may seem seriously distressed. However, when irrigation is resumed and when fertilizer is applied at the next irrigation after a short interval, growth quickly recovers and actual gains in yield will result. As an example, field 103 had the drought treatment for tassel control, and yet the check area showed only 4.5 percent blossom while the treated showed 0.5 percent (Table 9).

A possible explanation for this probably lies in the stronger and deeper development of the root system, the thorough aeration and warming of the soil, as well as nitrification and probably also a buildup of the storage of carbohydrate reserves in the roots. When water and fertilizer are applied under these warm, well-aerated soil conditions, growth is excellent.

Use of Chemicals to Control Tasseling

Many chemicals, mostly of the herbicide type, have been used (*10, 26, 27, 28, 29, 30, 55*). There is no question that most of them prevent tasseling, but generally with a very marked setback of the crop. At Wailuku, field 14, in 1959, was treated with a CMU suspension (5 pounds 80 percent in 5 gallons of H_2O) sprayed by plane over the field. The treated portion showed a 1 percent tassel as compared with 17 percent for check. The treated portion, however, yielded 9.05 versus 9.58 tons of sugar per acre. A similar test in 1958 showed no blossoms for the treated areas versus 50 percent blossoming for the untreated. Even with very heavy blossom in the check, the treated portion yielded 10.91 tons of sugar per acre, and the check 12.59 tons. A third experiment showed essentially complete suppression of flowering. The treated had a 1 percent blossom, and the check 55 percent. In this case, the treated portion yielded 10.69 tons of sugar per acre, and the check 8.59 tons.

Diquat has given good control of blossoming, also, as have paraquat, DCMU, maleic hydrazide, and other herbicide-type compounds. One of several experiments in eastern Puerto Rico with diquat gave perfect blossom control but nearly a 50

percent loss of yield. In these experiments, the cane was very dry at the time of treatment, and the resulting setback was very severe. Since cane is grown in the area as a 1-year crop, there is little time for the crop to regain its growth. It is doubtful that any chemical should be applied over a crop which is under severe moisture stress, for two reasons: (1) such a crop would not tassel anyway, and (2) such a crop is much more susceptible to spray damage. A good combination of drought and chemical treatment has been worked out at Paauhau Sugar Co., on the Island of Hawaii. The fields susceptible to blossoming are put on drought control which, if successful, obviates the need for chemical control. But if the drought is broken before September 6, a chemical spray may be applied.

A better practice would be to observe closely the start of blossom formation (Figures 9–16) and apply chemicals only after there is justification for it. Many times chemicals have been applied early in September when even the checks have not blossomed. Under such conditions, the losses are doubled—the cost of the chemical and its application and the setback to the cane. Obviously, the only acceptable solution is for the breeder to produce clones that blossom under artificial conditions but not under field conditions.

ARTIFICIAL INDUCTION OF FLOWERING IN SUGARCANE

The original objective of this work was to aid the breeder in eliminating tasseling from commercial canes. Studies at Hawaii Agricultural Experiment Station (HAES) were begun in 1959 and have continued since then, to work out the techniques of artificial induction. At first, even such very easy tasselers as NCo 310, Co 312, and H37-1933 did not respond. In time, the various factors affecting tasseling were recognized and, once these were worked into the control program, most of even the very reluctant varieties were made to flower. Four darkrooms, each 7½ x 12 x 15 ft, were equipped with a cooling system and with eight fluorescent (daylight) lights, each 8 ft long, connected to electric clocks for control. Each room could hold 44 pots on 11 carts.

The clones intended for treatment were grown in well-irrigated and fertilized fields—first in Manoa Valley and later at Waimanalo, both places regarded as very heavy-tasseling areas. Only the largest diameter canes of each clone were selected from plant or first ratoon canes and put under a mist spray for 24 hours before cutting into one-bud setts. The cuts were made so that the internode portion below the bud was twice as long as that above. The setts were treated with phenylmercuric acetate (1–4000) for 20 minutes at ambient temperatures. The setts were then taken from the solution and allowed to dry in a shaded and screened area for 4 to 5 hours. Usually, four setts were planted in each 12-inch concrete pot filled with a fertile, well-drained garden soil. After watering, the pots were fertilized with a 16-16-16 fertilizer and placed where sunlight would be full and where wind would be at a minimum. After germination was complete, each pot was thinned to three

or to two of the strongest plants. For the next 4 to 6 months, through fertilization and moderate watering, every attention was directed to the production of large diameter, vigorous plants. Once the plants showed three to four fully-exposed internodes (usually at a minimum of 4 to 6 months of age), they were considered ready for treatment. They were then placed onto iron carts provided with supporting sides and were ready for nyctiperiod control. From this point on, they were drenched with water before and after being put into the darkroom and again when taken out the next morning. Fertilization was stopped altogether, for it had been shown that excessive nitrogen (22) prevents tasseling. If the plants showed extreme deficiency after 6 months or so of treatment, they were given a very small amount of fertilizer. Each darkroom was equipped with a fan and a cooling system so that night darkroom temperatures would drop from 80 to $85°$ F when the plants were wheeled in to between 70 to $74°$ F by morning. The dark period began precisely at 4:00 p.m. and ended when the lights were turned on by the control clocks. The plants were rolled out of the nyctiperiod control rooms at 8:00 a.m. into the natural bright day. Experience had shown that lengthening nights are more effective than nights of a fixed length or shortening nights (18, 19). The amount of lengthening made each day depended on the latitude being imitated. This was done to correspond exactly to the natural nyctiperiod as determined from Ephemeris (37), and was accomplished by stopping the clocks for the exact number of seconds each day. Thus, at $20°$N, the nights were of the same length from June 21 to 29. From this time until July 11, the nights were lengthened each day by 20 seconds, then 40 seconds, 60 seconds, and finally the maximum of 70 seconds in September. In most experiments, when a night length of 11:30 to 11:40 was reached, no further changes of night lengths were made. In some special experiments, the natural night lengths were imitated throughout the treatment period.

The first clones worked with were provided in May 1959 by A. J. Mangelsdorf of the Hawaiian Sugar Planters' Association: Co 312, NCo 310, H37-1933, H44-3098, H39-7028, H45-2708, H50-6877, H48-4178, H51-4336, and H51-8319. These were all planted in lower Manoa Valley, considered to be a relatively heavy-tasseling area. In the field that fall, however, only the first three varieties (Co 312, NCo 310, and H37-1933) tasseled. They were ready tasselers and were included as pilot clones. The other clones were described as being either moderate or reluctant tasselers. Many experiments were conducted in greenhouses, but no success was achieved under controlled conditions, even with the willing pilots. In the early spring of 1960, the clones were all cut down and the field ratooned. Again in the fall, the only clones to flower were the first three, demonstrating that all the others were indeed reluctant, even including H44-3098, which was considered to be moderate.

Beginning in October 1961, two tall darkrooms, X and Y, became available so that plants on carts could be moved outdoors for exposure to direct sunlight during the day. Two treatments were set up, using Co 312, NCo 310, H37-1933, H48-4178, and H45-2708. These plants had all been in the greenhouse and were

exposed to a 16-hour night, but none had blossomed. Darkroom X was continued on a 16-hour night; Y was placed under 11:35 nights. Co 312, NCo 310, and H37-1933 blossomed; H45-2708, which had not blossomed in the Manoa Valley field, also blossomed.

Two more tall darkrooms, O and P, became available and, in succession, it was shown that keeping the pots and plants drenched with water was essential. It was also necessary to grow the plants in a rich soil before starting treatment and then reduce the nitrogen nutrition. Finally, night temperatures of 70 to 74°F were required for blossom formation. It was also verified, as Chilton et al. had demonstrated (11, 12, 13, 14, 15, 16), that starting with a natural night on June 21 and lengthening the night, as occurs naturally, until reaching a nyctiperiod of 11:30 to 11:40 results in success of blossoming even with most reluctant tasselers. By 1963, all of the plants listed above, except H51-4336, were forced into blossom many times, even though none of them except the first three ready tasselers blossomed in the Manoa Valley field during the previous 5 years.

On February 17, 1964, a new set of 15 reluctant and zero tasselers were obtained from Don Heinz, head of the genetics department of the Hawaiian Sugar Planters' Association, and, together with the first ten clones listed above, were planted at Waimanalo, which is a very heavy-blossoming area. The Hawaii clones added included H55-7054, considered to be a medium tasseler; H48-4178 and H53-3025, considered light tasselers; H52-3086, H57-4370, H53-1051, H51-5328, H51-4637, and H53-263, considered to be very light tasselers; and H50-5340, H52-4610, H52-4450, H58-5116, H54-7094, H58-5087, and H56-6724, considered to be zero tasselers. In 1967 S. spontaneum (Dacca), S. robustum, S. sinensis, and S. officinarum ('Yellow Caledonia,' 'Badilla,' 'Lahaina,' 'Rose Bamboo,' and 'Louisiana Purple') were also received, but not all of these were planted at Waimanalo.

In the fall of 1964, the following newly added clones produced in each field row some two to eight flowers out of a total of more than 600 stalks: H56-6724, H53-3025, H55-7054, H51-5328, H58-5116, and H53-1051. Of the original ten clones, NCo 310, Co 312, H37-1933, and H50-6877 blossomed heavily. H39-7028 also blossomed, as did a few stalks of H44-3098 and H48-4178.

During the 1967 season, only the following clones flowered in the Waimanalo field: NCo 310, Co 312, H37-1933, H44-3098, H45-2708, H53-263, and H55-7054, the last four very lightly. By the end of the 1970 season, none of the following clones had blossomed at all at Waimanalo: H51-4336, H51-8319, H52-3086, H50-5340, H52-4610, H57-4370, H54-7094, H58-5087, H51-4637, and H40-1010.

Another experiment involved subjecting the reluctant tasselers to darkroom treatments of 11:37 nights, beginning June 26, 1964, and continuing for 1 year. Varieties H51-5328, H53-3025, H55-7054, H40-1010, H56-6724, H58-5116, H53-1051, H52-4450, and H41-4637 blossomed heavily. H45-4178 and H39-7028 blossomed at least one stalk each. Varieties H57-4370, H52-3086, H54-7094,

H51-4336, H50-5340, H52-4610, and H50-5087 failed to blossom in this run.

Later, another experiment, carried out in 1969, used essentially all the Hawaii varieties as in the experiment above, but it included also the *Saccharum* species listed above. In the field, in 1969, only NCo 310, Co 312, H37-1933, H44-3098, H53-263, 'Uba,' *S. robustum*, and 'Yellow Caledonia' blossomed. Very late in the year, H52-4450 produced a few flowers. In this experiment, night lengths, shortened by 25 and 26 minutes of twilight, respectively, imitated latitudes $7\frac{1}{2}°$ and $20°$N and a fixed night of 11:35. The $7\frac{1}{2}°$ and $20°$N treatments became fixed at 11:35 and 11:38, respectively.

Under the $20°$N latitude, H37-1933, 'Uba,' Co 312, NCo 310, *S. spontaneum* (Dacca), 'Lahaina,' and H45-2708 blossomed. Exposed to the 11:35 fixed period, H50-5340, H44-3098, H37-1933, 'Uba,' Co 312, NCo 310, H45-2708, H48-4178, H51-4637, *S. spontaneum* (Dacca), and *S. robustum* blossomed. Under the $7\frac{1}{2}°$N latitude exposure, H57-4370, H44-3098, H39-7028, H53-1051, H54-7094, H52-4450, H52-4610, H50-5340, 'Uba,' 'Yellow Caledonia,' 'Badilla,' Co 312, NCo 310, H45-2708, H48-4178, H53-3025, H51-5328, *S. spontaneum* (Dacca), and *S. robustum* blossomed. Thus, seven clones blossomed under $20°$N conditions, 11 under fixed night, and 19 under the $7\frac{1}{2}°$N conditions. Of the 36 clones used in 1969, the following eight failed to blossom under one condition or another: H53-263, H51-4336, H51-8319, H53-7054, H50-5087, H40-1010, 'Rose Bamboo,' and 'Louisiana Purple.'

In 1970, the final trial of the experiment, 30 clones were subjected to night lengths found at $0°$, $5°$, $10°$, and $15°$N latitudes, and included parts of the twilights as part of the day. Of these 30, 27 were in the field and only eight blossomed there: H44-3098, H39-7028, H37-1933, NCo 310, Co 312, 'Yellow Caledonia,' *S. robustum*, and 'Uba.' Fifteen of the clones at $0°$ produced 36 blossoms, ten of the clones at $5°$N produced 32 blossoms, 19 of the clones at $10°$N produced 46 blossoms, and 11 of the clones at $15°$N produced 36 blossoms. Considering both the 1969 and 1970 results, night lengths at latitudes from $7\frac{1}{2}°$ to $15°$N seem best for flowering of cane. Considering the three latitudes and the fixed 11:35 night, all of the clones used produced blossoms except H51-4336, H53-263, and 'Louisiana Purple.' H51-4336 has never been known to flower and may have lost the genetic ability to do so. It is of interest, however, that, at Waimanalo, lalas on a large number of the varieties were produced one spring, suggesting a partial flowering response. In this situation, H51-4336 showed a very small but similar response, suggesting that it, too, has at least a part of the essential complex of systems. Why H53-263 and 'Louisiana Purple' failed to blossom under control, although they both blossom in the field, is baffling, especially since so many of the other clones which did not blossom in the field were blossomed repeatedly under control. One factor may be root restriction. Neither H53-263 nor 'Louisiana Purple' grew as well in the 12-inch pot as the other clones. In general, this also applies to the several *S. officinarum* clones used, even though all the others bolted and

blossomed—albeit less vigorously than in the field. Another factor may be that some clones require more or less of the natural light rays of sunrise and sunset than others.

One further bit of information, important to the breeder, regarding the artificial induction of the clones, is the degree of grouping possible. As an example, the week-by-week boltings are given in Table 10. Bolting is used rather than blossoming because blossoming always followed, unless the bolt became too tall for the darkrooms. Wherever there were large flags, indicating unsuccessful flowering, these clones were not counted as having blossomed.

By applying nyctiperiods characteristic of $5°$, $7½°$, $10°$, and $15°N$ latitudes, a considerable range is shown. NCo 310 was bolting from July 15 to September 17, Co 312 from July 15 to September 1, H37-1933 from July 15 to October 3, S. robustum from August 16 to December 14, and so forth. It should be realized that,

Table 10. Dates on which several clones have been forced into blossom, 1970–1971

Date	Clones bolting
7/15–7/22	NCo 310, Co 312, H37-1933
7/23–7/30	Co 312, NCo 310
7/31–8/7	NCo 310, Co 312
8/8–8/15	Co 312, H37-1933
8/16–8/23	NCo 310, 'Uba,' S. robustum
8/24–8/31	Co 312, NCo 310, 'Uba'
9/1–9/8	H44-3098, S. robustum, 'Uba,' H37-1933, Co 312, 'Rose Bamboo,' NCo 310
9/9–9/16	H37-1933, H44-3098, 'Uba,' H53-3025, H54-7094, H53-1051
9/17–9/24	'Uba,' NCo 310, S. spontaneum (Dacca), H53-3025, S. robustum, 'Rose Bamboo'
9/25–10/2	'Uba'
10/3–10/10	H53-1051, H37-1933
10/11–10/18	H45-2708, S. spontaneum (Dacca), H53-3025, H52-3086
10/19–10/26	H53-3025, S. robustum, S. spontaneum (Dacca)
10/27–11/4	H53-3025, 'Rose Bamboo,' S. robustum, H51-8319
11/5–11/12	H40-1010, H39-7028, 'Uba,' S. spontaneum (Dacca), H48-4178, S. robustum, H53-3025, H53-1051, 'Rose Bamboo'
11/13–11/20	H45-2708
11/21–11/28	H45-2708, H58-5087
11/29–12/5	H45-2708, H39-7028, H44-3098, 'Badilla'
12/6–12/13	'Badilla,' H50-5087, H53-1051
12/14–12/21	H53-1051, S. robustum, S. spontaneum (Dacca), H53-3025
12/22–12/29	H51-4637, H53-1051
12/30–2/15	None
2/16–2/23	'Yellow Caledonia,' H53-1051
2/23–3/2	H48-4178
3/3–3/10	H53-3025, H52-4450

in each night period, only one or, at most, two pots of each clone were used. Were it very desirable to cross two particular clones, the best strategy would be to use a larger number of pots at several night lengths.

SUMMARY

Losses resulting from blossoming of sugarcane can be very substantial. Actual yields of sugar from adjoining fields were 0.557 ton sugar per acre per month where blossoming occurred both in the first as well as the second season and 0.727 where blossoming did not occur in the first season and was very light in the second.

Field-grown plant cane of NCo 310 was collected twice a week from July until November 1967. Drawings are presented of the meristem stage observed at each collection. The meristem changed from vegetative to flowering between August 18 to 22, 1967, hence must have begun to accumulate the stimulus as early as August 8.

A similar set of collections was made in 1966. Measurements were made twice each week on all the blades, sheaths, and internodes of 10 randomly selected stalks. On the basis of these data, flowering was divided into four stages:

1. *Stage 1* ends with the cessation of leaf primordia production and with a change in the shape of the meristem. Under favorable conditions this stage may last for 10 days only.

2. *Stage 2* is the blade-shortening stage during which the flower primordium grows from 0.015 to 0.7 cm in length and changes from bilaterial to spiral arrangement. Under favorable conditions this stage ends with the formation of the flag, and may last about 6 weeks.

3. *Stage 3* begins with the cessation of blade growth and is the period of sheath elongation or bolting. The inflorescence within the sheath of the flag leaf elongates at the same time. Under very favorable conditions this stage lasts about 3 weeks and starts fairly precisely when stage 2 ends, and ends when the sheath of the flag leaf completes its elongation. During this stage the blossom grows from the primordium 0.7 cm in length to its full length and includes the central rachis as well as the primary and secondary branches and the spikelets completely developed.

4. *Stage 4* begins when the sheaths complete their elongation and the floral stem begins its elongation resulting in the exsertion of the inflorescence. Under very favorable conditions this stage lasts about 3½ weeks. During this stage, as the inflorescence is exserted, the spikelets, on exposure to the atmosphere, open to extrude the stamens and stigmas; pollination takes place followed by fruiting and maturation.

At any point in the several stages, the flowering process can be interrupted by some even relatively minor change in the environment. If this occurs in stage 1, the

tip reverts to normal activity and no abnormality remains. If it occurs during the first half or so of stage 2, again the tip could return to normal activity, leaving as evidence a progressive shortening of successive blades, followed by a progressive lengthening back to a normal bilateral arrangement, but sometimes zigzag nodes may be found. If it occurs late in stage 2, the meristem may deteriorate completely, or it may develop into a living witch's broom which will emerge as a terminal formation. Sometimes one of the many shoots of the broom may become dominant and continue the growth of the stem, and may even form a normal blossom the next season. The remnants of such a living witch's broom would appear as a lateral growth, even though it was terminal at the beginning. Between the deterioration of the meristem and the living witch's broom, several intergrades may be found—all of them associated with very large flag leaves. If the process is interrupted during stage 3, a blossom will be found in the boot, varying in length from perhaps 1 cm to full length, but exsertion will not occur and the structure will die. If it occurs after stage 4 has been entered, the inflorescence will be only partly exserted.

The inductive nyctiperiod for NCo 310 was found to be 10:54, and this occurred on August 22 when the meristem had changed to a blossom primordium. About this same length applied also to both Co 312 and H37-1933 growing under very ideal conditions for blossoming. Under less than ideal conditions or under fixed nyctiperiods, the proper night length would be longer.

In Hawaii, field blossoming varies from none to very heavy, depending on variety, time of starting the crop, minimum temperatures as well as temperature ranges of the area, and soil moisture tensions during the induction period.

Blossoming at low elevations at various latitudes may range from very light to none at latitudes of $1.5°$S, as found in Ecuador, at $30°$S in South Africa, and $32°$N in Iran. Heaviest blossoming normally occurs between $5°$ and $18°$N or S in warm areas with abundant rainfall and high humidities.

Blossoming in the field may be avoided by using very light or nontasseling varieties, by starting the crop in heavy tasseling areas at carefully chosen times, by imposing a drought during the inception period, or by the use of certain herbicide-like compounds.

To produce blossoms under artificial conditions, 23 clones of Hawaii varieties were used, including the very willing tasseler H37-1933 as well as NCo 310, Co 312, and four *Saccharum* species, including five *S. officinarum.* Twenty-two of the Hawaii clones were classed as moderate, reluctant, or nontasselers. Efforts to force blossoming included the imposition of a fixed night period, as well as starting with the night lengths noted on June 21 at latitudes $0°$, $5°$, $7½°$, $10°$, $15°$, and $20°$N. The nights were lengthened each 24 hours as occurs naturally at each latitude. Those portions of dawn and dusk which exceeded 10 ft-c were excluded from the night length. As a result, all but three of the clones used were forced into blossom. Included among the three were H51-4336, which never has been known to blossom anywhere, 'Louisiana Purple,' and H53-263, both of which do blossom in Hawaii. A

substantial number of the Hawaii clones that were blossomed never did so either in lower Manoa Valley or at Waimanalo—both areas considered to be very favorable for blossoming. It is obvious that, by using this technique, breeding programs can be greatly extended and many normally nontasseling or very reluctant tasselers can be used regularly. The best latitudes were found to be 5 to $18°$N or S.

Best results at artificial induction were obtained by planting the largest stalks of a clone some 3 or 4 months prior to June 21. On this date the plants were wheeled into darkrooms equipped with a cooling system and fluorescent lights operated by time clocks. The nyctiperiods used were those found on June 21 at each of the latitudes, imitated with deductions made for the twilight portions exceeding 10 ft-c. The nights were lengthened as occurs naturally at each latitude, imitated until a night of 11:30 to 11:40 was reached, after which the nyctiperiod remained fixed. After June 21, the plants were not fertilized unless there was danger of the spindle dying, and then very lightly. During this period the pots were kept drenched with water. Also, during this period, all dead and dying leaves were left attached to aid in maintaining moistness of the atmosphere and reduce the likelihood of internal moisture stress. The plants during the day outdoors were exposed to maximum sunlight, little or no wind, and a temperature range near 80 to $82°$F. Night temperatures remained in the 70 to $74°$F range. Exposing the plants to a 22-hour day, including the natural sunlight plus artificial light, for a month or more prior to nyctiperiod control seemed helpful.

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APPENDIX
Additional Stages in Flowering

To present a more nearly complete series on floral development, permission was obtained from the Director of the Agricultural Research Service in Beltsville, Maryland, to reproduce some of the very excellent illustrations done by the late Artschwager and published by the now defunct Journal of Agricultural Research.[2]

Plate I. The sugarcane flower of U.S. 779: inner glume (i gl), outer glume (o gl), sterile lemma (sl), fertile lemma (fl), palea (p), lodicules (l), ovary (o), two feathery stigmas (s), anther (a), and filament (f).
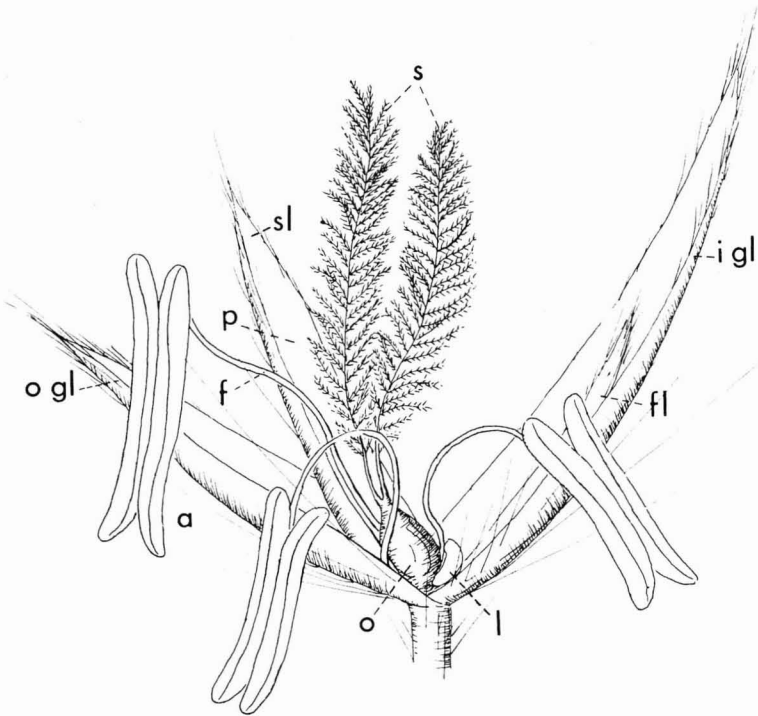
[2]Ernst Artschwager, E. W. Brandes, and Ruth Colvin Starrett. 1929. Development of flower and seed of some varieties of sugar cane. J. Agr. Res. 39:1–30.

Plate II. Development of the anther; cross and longitudinal sections. **A.** Longitudinal section through the stamen (stam) showing the rows of the microspore mother cells. **B.** Lateral branch of the feathery stigma with a germinating pollen grain (pt). **C.** Cross section through one anther lobe showing completed reduction division. **D.** Cross section of a young flower showing the relative positions of all parts: inner glume (ig), outer glume (og), sterile lemma (st l), and three- to four-lobed anthers; in the center are the two styles. If the section had been lower down, it might have shown the ovary in cross section as well as the two lodicules. **E.** Mature pollen grain, or microgametophyte, with a vegetative nucleus (vn), generative nuclei (gn), and germ pore (gp).
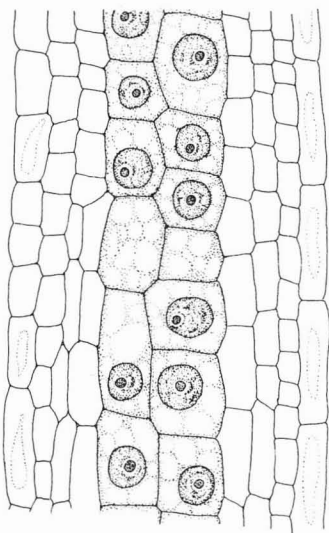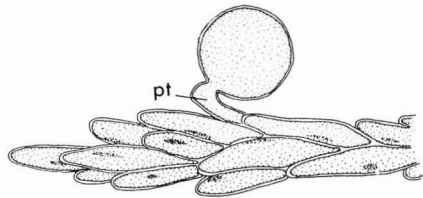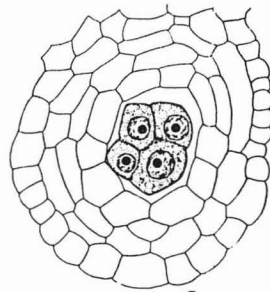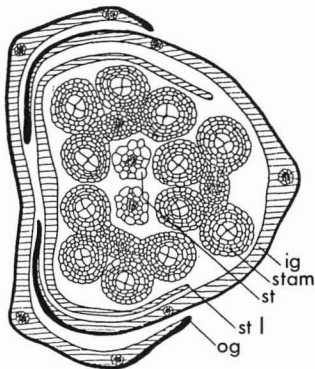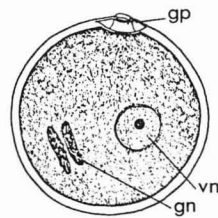
Plate III. Development of the ovary. **A.** Cross section through a very early flower stage. Outer glume (og), inner glume (ig), sterile lemma (sl), lodicules (l), stamens (st), and palea (p). The ovule shows the megaspore mother cell (mmc) and the ovary wall (ow). **B.** Enlarged view of the young ovule showing the prominent megaspore mother cell and the start of the integuments. **C.** The megaspore mother cell is entering the reduction division process. The integuments are already well developed. They would normally fit more closely to the nucellar tissue. **D.** The outer three megaspores of the linear tetrad are degenerating and the innermost one will germinate to produce the megagametophyte.
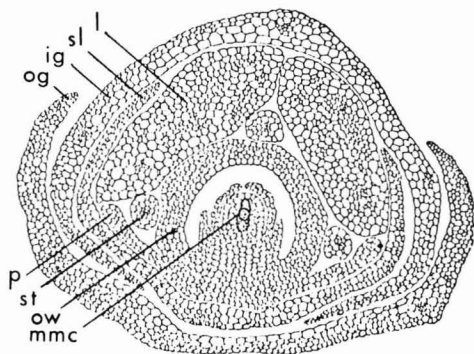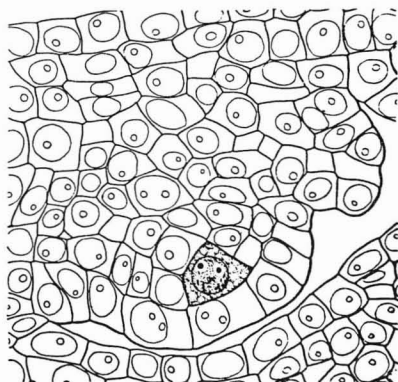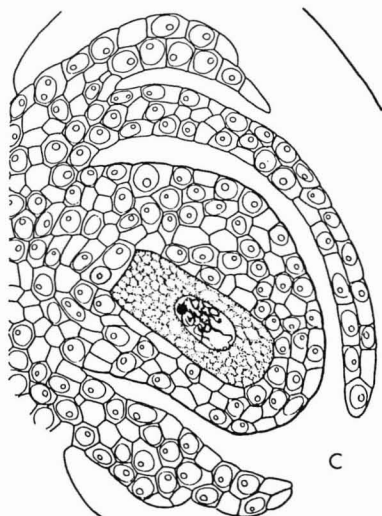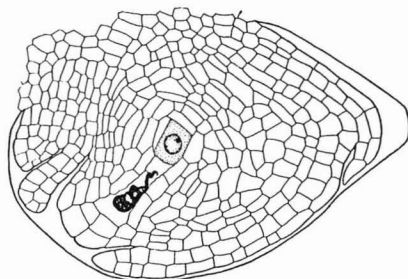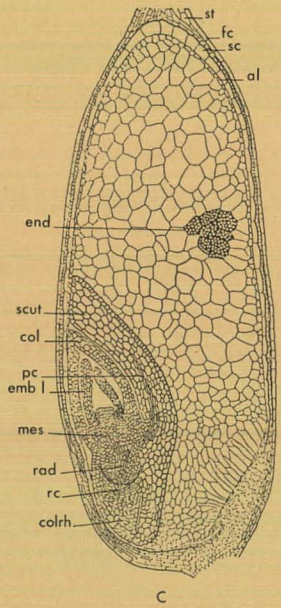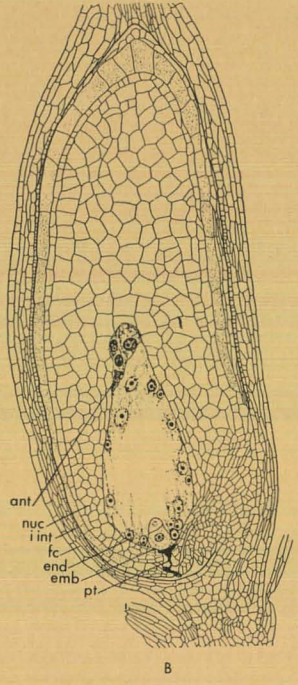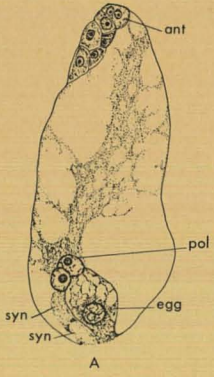
Plate IV. Development of the new sporophyte before and after germination. **A.** The mature megagametophyte showing the egg, with the two synergids (syn) beneath it, the two polar nuclei (pol) and the antipodals (ant). **B.** Fertilization has been accomplished, and the very young embryo (emb) has started to grow. The two polar nuclei (pol) have fused with the second sperm nucleus, and this fusion has already produced several nuclei, which soon will fill the entire space and then, along with the developing embryo, continue to destroy the entire nucellus (nuc) as they enlarge. The remains of the pollen tube (pt) may be seen in the micropyle, and the antipodals (ant) are at the opposite end. **C.** The mature, resting seed within the fruit coat (fc) making up the fruit (a caryopsis). The endosperm (end), which replaced the nucellus, is now made up of cells gorged with starch. The integuments have given rise to the seed coat (sc). The aleurone layer (al) is the outermost layer of the endosperm. The embryo is made up of the first node (mes), from which arises the scutellum (scut), or actually the single cotyledon, which secretes enzymes into the endosperm, absorbs the simple carbohydrates, nitrogen, fatty compounds, and minerals, and passes them back to the growing points. The plumule and the radicle (rad) are capped by the root cap (rc), which, in turn, is capped by the coleorhiza (colrh). Coming from the plumule are the young embryonic leaves (emb l) within the coleoptile (col). At the top of the fruit are the stylar remains and at the bottom the fruit scar. **D.** The young seedling, or the new sporophyte, on germination produces the young shoot, which grows through the coleoptile and then produces the new foliage, leaves, and stem. The primary root (the only true primary root of sugarcane) has broken through the coleorhiza but continues to be capped by its own root cap. Numerous root hairs develop, and soon the secondary roots will begin to break through the cortex. Unlike the dicotyledons, the single cotyledon of the monocotyledons never escapes from the seed. Soon the young sugarcane plant emerges.

Figure labels:

A — ant, pol, syn, egg, syn

B — st, fc, sc, al; ant, nuc, i int, fc, end, emb, pt

C — st, fc, sc, al, end, scut, col, pc, emb l, mes, rad, rc, colrh

D